3

Army Ants

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I. INTRODUCTION

"I was glad to go to sleep early, but was scarce soundly asleep when I was turned out of the house by a furious attack of the bashikouay ants. They were

already all over me when I jumped up, and I was terribly bitten." Thus, DuChaillu (1861), an intrepid explorer of equatorial Africa, described an unpleasant encounter with army ants. He apparently was no less impressed with these diminutive but fearsome creatures than he was with the gorilla, which, with great bravado, he described as a "monstrous and ferocious ape." Few nineteenth century explorers and naturalists in the Old and New World tropics could ignore the cohesive, regimented behavior, let alone the often painful attacks, of these ants; ants that Wheeler (1910) referred to as the "Huns and Tartars of the insect world." Their journals and adventurous accounts are replete with references to the predatory exploits of these ants. Bates (1863), a naturalist who roamed Amazonas collecting biological specimens, noted that when a "pedestrian falls in with a train of these ants," they "swarm up his legs with incredible rapidity, each one driving his pincerlike jaws into his skin, and with the purchase thus obtained, doubling in its tail, and stinging with all its might." Another naturalist, Thomas Belt (1874), recorded how one small species of army ant in Nicaragua would "visit our house, swarm over the floors and walls, searching every cranny, and driving out the cockroaches and spiders, many of which were caught, pulled or bitten to pieces, and carried off." The Rev. Thomas S. Savage (1847), a medical missionary to west Africa, noted in his observations on army ants of the subgenus *Anomma,* that this kind of ant "drives every thing before it capable of muscular motion, so formidable is it from its numbers and bite." Even Charles Darwin (1859) was fascinated with army ants, although his interest was not so much in their spectacular foraging behavior as it was with the striking allometry and polymorphism exhibited by the worker caste. He examined a series of *Anomma* workers and described their morphology with the following analogy:

> . . . the difference [between worker ant sizes] was the same as if we were to see a set of workmen building a house, of whom many were five feet four inches high, and many sixteen feet high; but we must in addition suppose that the larger workmen had heads four instead of three times as big as those of the smaller men, and jaws nearly five times as big.

Although ant taxonomists, particularly Emery (1895), were actively considering the army ants during the latter half of the nineteenth century, especially at the alpha level, little was recorded in any systematic fashion about the biology of army ants. Sumichrast (1868) and Müller (1886) described their observations of New World species as did Savage (1847, 1849), F. Smith (1863), Perkins (1869), and Wroughton (1892) for a few Old World forms, but much of the literature remained in the realm of natural history.

Similarly in the twentieth century, naturalists have alternately cursed and marveled at these ants. Carpenter (1920) and Loveridge (1949, 1953) both recorded observations of army ants, in particular of *Anomma* driver ants, in popular accounts of their field research in Africa. In one narrative, Loveridge (1949) described a remarkable invasion of these ants in his house in which the

"the whitewashed walls were a moving mass of Siafu." The nonscientific literature, particularly of colonial Africa, also includes references to the activities of army ants. For instance, Isak Dinesen (a pseudonym taken by the Danish baroness Karen Blixen-Finecke) (1937, p. 35) in her memorable book, "Out of Africa," noted with annoyance how her dogs had been attacked by these "murderous big ants" and how the ants had to be picked from the dogs "one by one." However, the scientific study of army ant behavior had also begun. Beebe (1919), for example, made some organized observations of the New World genus *Eciton* and was one of the first biologists to examine carefully activities other than foraging. Other biological observations of army ants were recorded in the first 4 decades of the twentieth century by Wheeler (1900), von Ihering (1912), Gallardo (1915, 1929), Luederwaldt (1926), M. R. Smith (1927), and Reichensperger (1934) in the New World and by Brauns (1901, 1903), Vosseler (1905), Arnold (1915), Swynnerton (1915), Burgeon (1924a,b), and Cros (1939) in the Old World. However, it was not until T.C. Schneirla, a psychologist by training, began his research on *Eciton* that an understanding of army ant behavior was significantly extended beyond the fragmentary and often anthropomorphized observations of the naturalists.

Army ants have also captured the imaginations of the indigenous peoples of the Old and New World tropics, and tales of these ants have been incorporated into the oral traditions and folklore of numerous cultures. Whether these ants are referred to as Tauoca in Amazonas, Tepeguas in Mexico, or Ensanafu, Siafu, or Kelelalu in Africa, they are generally regarded with fear engendered respect. For instance, the Ashanti of Ghana allegorically communicate this respect in a tale about the hungry python. They say that before a python takes a large meal, one that might immobilize it and thus make it more vulnerable to army ant attack, it circles the immediate area in search of driver ants or Nkran. If it sees no such ants, it will take its meal, but if the ants are present, then the python will forego, in its own prudent self-interest, the much desired meal. Curiously, even the name of the capital city of Ghana, Accra, may have been derived from Nkran, the Akan word for driver ants, through a former spelling Akra. Reputedly common to the "medical" practices of numerous tribes, such as the Kikuyu (Murray-Brown, 1972, p. 40), is the use of the soldier subcaste of some army ant species in suturing wounds. Alex Haley (1976, p. 12) in his much celebrated book, "Roots," gives a fictional account of the process:

> . . . Grandma Yaisa tightly pressed together the skin's split edges, then pressed one struggling driver ant after another against the wound. As each ant angrily clamped its strong pincers into the flesh on each side of the cut, she deftly snapped off its body, leaving the head in place, until the wound was stitched together."

While it is true that army ants, particularly of the soldier subcaste, can inflict a painful bite on human skin (and draw blood as this author can attest) and while some species are excellent general predators, they do not deserve

their reputation as the scourge of tropical forests that not only devour all animal life they contact but defoliate, in the process, all vegetation that stands in their way. Although it is easy to unknowingly step in the midst of a raiding swarm of workers or in an emigration or foraging column, it is just as easy, and decidedly judicious, to step out of their midst. Certainly the only vertebrates caught and killed by army ants are those individuals that for some reason or other are incapacitated and immobilized. Caged vertebrates, such as snakes, commonly fall prey to army ant attack, and there has been one unsubstantiated report, of a human infant that, left shaded beneath a tree while its mother cultivated her crops, died of a driver ant attack. Contrary to some prevailing mythologies, army ants do not defoliate plants, though they may take some vegetation as food. Yet to witness an army ant colony foraging or emigrating can be an awe-inspiring experience not soon forgotten. Army ant colonies display an extraordinary cohesiveness unmatched by other ant species, and for this reason alone, they are worthy of special attention.

II. ARMY ANTS DEFINED

A. Behavioral Characteristics

Generally the term "army ant" refers to any species in the ant subfamily Dorylinae [many other common names, such as legionary ants, driver ants (usually *Anomma*), soldier ants, raiding ants, and others, have been applied to members of this subfamily]. While this is a convenient taxonomic definition, it does not include species that qualify behaviorly, but not morphologically, as army ants. There are two features that characterize army ant behavior: (1) group predation, and (2) nomadism (Wilson, 1958a). All species within the Dorylinae exhibit these patterns that are, for all intents and purposes, inextricably joined together in the army ant adaptive syndrome. However, other ant species, notably of the subfamily Ponerinae, have also achieved army ant lifeways and combine, in varying degrees of complexity, group predation and nomadism.

Group predation, as defined by Wilson (1958a), includes both group raiding and group retrieval of living prey. He pointed out that these two processes involve different innate behavior patterns and are "not invariably linked." Although, for instance, many nondoryline ants may group retrieve prey, few also group raid. Those that combine both behavior patterns and thus qualify as group predators are found in such ponerine genera as *Cerapachys, Phyracaces (= Cerapachys), Leptogenys* (e.g., in the *L. processionalis* group), *Termitopone, Megaponera, Paltothyreus,* and *Simopelta* (Wheeler, 1936; Wilson, 1958a,b; Gotwald and Brown, 1966; Brown, 1975). The convergent development of group predation among nondorylines may be

associated with concomitant morphological adaptations among the different castes. For example, the two queens thus far described for the genus *Simopelta* are both dicthadiiform, a peculiar habitus found chiefly among doryline queens in which wings are absent and the petiole and gaster are hypertrophied (Borgmeier, 1950; Gotwald and Brown, 1966). The extent to which nomadism is associated with group predation in these ponerine genera is not well known.

Nomadism or emigration of ant colonies is not in itself unusual. Colonies of numerous species commonly shift their nesting sites in response to unfavorable environmental conditions. Some species, such as *Iridomyrmex humilis,* may normally emigrate one or more times in a single season (Wilson, 1958a), but no species move with the regimented precision and frequency of the doryline army ants. For example, in the New World genus *Eciton,* colonies pass through a functional cycle that includes a nomadic phase during which emigrations to new temporary nesting sites occur on a daily basis (Schneirla, 1971). Among nondoryline group predators, nest-changing emigrations have been observed for such species as *Megaponera foetens* (Arnold, 1914) and *Leptogenys purpurea* (Wilson, 1958a); the emigration of the latter closely resembles that of some dorylines. Noteworthy is the fact that the larvae of the Cerapachyini are slender and cylindrical, as in the dorylines that carry their larvae on emigrations slung longitudinally beneath their bodies, and may circumstantially indicate that these ants are also nomadic (Brown, 1975).

B. Classification of Army Ants

1. Subfamily Dorylinae

Because the males of doryline ants are unusually large, wasplike and infrequently found with the worker caste, the early taxonomic history of the subfamily is complex and sometimes enigmatic. Indeed, the first species of doryline described was based on a male of *Dorylus* that Linnaeus (Linné, 1764) initially placed in the wasp genus *Vespa.* The type specimen of this species, now *D. helvolus,* was collected at the Cape of Good Hope. Later in the twelfth edition of "Systema Naturae," Linnaeus (Linné, 1767) transferred the species from *Vespa* to the genus *Mutilla* and in doing so precipitated a taxonomic controversy that was not to be settled for another 8 decades. In 1793, Fabricius removed the Linnaean species from the genus *Mutilla* and created the genus *Dorylus,* which he placed between the ants and mutillids. It was not until 1858 that the worker of *helvolus* was described by F. Smith and then as *Typhlopone punctata.* However, the relationship of the doryline males to the ants, in the absence of an associated worker caste, remained unrecognized. Shuckard (1840), in what constituted the first monographic review of the dorylines, noted "many points of analogy between *Ponera* and

the Dorylidae" but still considered the dorylines as being distinct from the ants. In fact, he speculated that "these extraordinary genera [*Dorylus* and *Labidus*] may possibly be parasites upon the Social Ants," and grouped them as the "Parasiticae" within the "Heterogyna." Even so, he described three species of *Labidus* based on workers in the absence of any direct evidence of their association but considered the workers to be "females." Although Lepeletier de Saint-Fargeau (1836) perceptively placed the males of *Dorylus* and *Labidus* close to the ants, it was not until Savage (1849) collected males and workers together, of an *Anomma* species that he described as *A. rubella*, that the true relationship of *Dorylus* and *Labidus* to the ants became clear. When Savage first observed the males moving in a column of workers he initially supposed them to be "capitives" but later concluded that "they seemed to be no unimportant members of the community." After finding a total of ten dealate males he noted that,

> I was soon convinced that they belonged to the drivers, and proceeded to test the truth of the conclusion. I took one or two [males] from the lines to a distance of six and ten feet. They seemed at once to miss their companions, and manifested great trepidation, and made continuous efforts to find a way of return. At last they reached the lines and instantly resumed their places, displaying at the same time decided gratification.

Taking note of Savage's observations, F. Smith (1858) suggested that *Labidus* might prove to be the male of the ant genus *Eciton*, a conjecture that seemed to Sumichrast (1868) "to be sustained by the fact that in Mexico it is in the season when the sorties of the *Eciton* are the more frequent that the *Labidus* also show themselves." This supposition was finally shown to be true by Mayr (1886) and Müller (1886).

The first doryline female described and recognized as such was that of *D. helvolus* (Trimen, 1880), although Emery (1887) later noted that some doryline queens had been described as workers. Still by the year 1900 few doryline queens had been described so that such descriptions were in themselves of special interest. For instance, Wheeler (1900) described in detail the newly discovered queen of *Eciton sumichrast* (= *Neivamyrmex sumichrasti* Norton) and noted that, "One of the most interesting problems confronting the student of ant life in subtropical and tropical America is the determination of the sexual forms of the foraging, or driver, ants . . ." Even today a great majority of doryline species, from both the New and Old Worlds, are known only from the workers and males.

A comprehensive revision of doryline ant taxonomy will only be possible after the association of all three phena (i.e., workers, females, and males) is established for a majority of species. Even so, numerous systematic studies of the dorylines have been attempted. Emery (1895) taxonomically revised the genus *Dorylus*, and later (1910) reviewed the entire subfamily. A rather unusual interpretation of the subfamily was advanced by Ashmead (1906).

Smith (1942) considered the taxonomy of *Neivamyrmex* army ants in the United States, and Borgmeier (1953, 1955), in a monumental effort, revised the New World dorylines. His conclusions will endure for years to come, although Watkins (1976, 1977) recently supplemented Borgmeier's work. In 1964 Wilson revised the Indo–Australian species of *Aenictus* and *Dorylus*. Only the African forms of *Aenictus* and *Dorylus* remain in taxonomic disarray, and these await completion of a revision in which I am currently engaged. Phenetic studies of *Dorylus* major workers and males have yielded only four integral species clusters, and these correspond to the subgenera *Alaopone*, *Dorylus, Rhogmus,* and *Typhlopone*. Members of the subgenera *Dorylus* and *Anomma* form a single, diverse, but continuous taxon, while the status of the subgenus *Dichthadia* remains unclear (Gotwald and Barr, 1980; Barr and Gotwald, 1982).

The true army ants traditionally placed in the subfamily Dorylinae are now regarded as belonging to two subfamilies, the Dorylinae and the Ecitoninae. However, as a matter of convenience, throughout this chapter these species are referred to in both subfamilies as dorylines. The army ants are classified as follows, although the status of the subgenera of *Dorylus* will change in the impending revision of that genus:

Subfamily Dorylinae (Old World)
    Tribe Aenictini
      Genus *Aenictus*
    Tribe Dorylini
      Genus *Dorylus*
        Subgenus *Alaopone*
          Anomma
          Dichthadia
          Dorylus
          Rhogmus
          Typhlopone
Subfamily Ecitoninae (New World)
    Tribe Cheliomyrmecini
      Genus *Cheliomyrmex*
    Tribe Ecitonini
      Genus *Eciton*
        Labidus
        Neivamyrmex
        Nomamyrmex

2. Nondoryline Army Ants

Ant species not belonging to the Dorylinae or Ecitoninae that qualify behaviorly as army ants (i.e., supposedly manifest both nomadism and group

predation) are confined to the subfamily Ponerinae. Most are ter-
mitophagous and myrmecophagous species in the genera *Leptogenys,
Megaponera, Onychomyrmex, Simopelta,* and *Termitopone* (Wheeler, 1936;
Wilson, 1958a; Gotwald and Brown, 1966; Hermann, 1968a). Army ant life-
ways in early stages of development in the cerapachyines, a group now
relegated to tribal status within the Ponerinae, and the genus *Acanthostichus*
are apparently evident (Brown, 1975). Also of interest are the genus *Aenic-
togiton* and the small biologically cryptic ants of the subfamily Leptanillinae;
both groups were once considered a part of the Dorylinae (Emery, 1910).
Aenictogiton, a genus containing only seven species, is known only from the
male caste collected in central Africa. Although Brown (1975) placed this
genus within the Ponerinae in the tribe Aenictogitini, he admitted that such
placement was provisional until the workers and queens for the genus could be
identified with certainty. The habitus of the males is generally like that of
some army ants, and they lack metapleural gland openings as do the males of
all army ants.

Although the Leptanillinae have undergone extreme morphological reduc-
tion that obscures their affinities, they are nevertheless regarded as close to the
Dorylinae (Brown, 1954). Queens, workers, and males are known, and while
the queens are dicthadiiform, nothing is known of their biology. The best that
can be surmised is that they are probably subterranean (Wheeler, 1910;
Brown, 1954). Emery (1904), Kutter (1948), and Petersen (1968) have con-
tributed to the knowledge of the leptanillines and Baroni Urbani (1977) has
recently revised the entire subfamily.

All of the doryline and nondoryline ants discussed thus far are tropical or
subtropical in distribution and constitute such a diverse taxonomic
assemblage that it suggests that the adaptive value attached to adopting army
ant lifeways in tropical environments is significant.

III. IDENTIFICATION OF DORYLINE ARMY ANTS

A. Subfamily Characteristics

1. Workers

In doryline workers (Fig. 1C,D), the frontal carinae are raised and lack the
lateral expansions typical of most other ants outside the Pseudomyrmecinae.
Thus, when viewed dorsally, the antennal insertions are exposed. This condi-
tion in combination with the fact that the workers either lack eyes or have eyes
that are reduced to an ocelluslike structure, makes it relatively simple to
separate these forms from the workers of other subfamilies (Wheeler, 1910,
1922; Bolton, 1973). Additionally, the clypeus is so reduced that the antennal

insertions are located close to the anterior margin of the head (Wheeler, 1910; Bolton, 1973). In other respects, worker morphology is more ambiguous. For example, the waist has either one or two segments, and although all workers possess an apparently complete sting apparatus (Hermann, 1969), some species do not sting (Gotwald, 1978).

2. Females (Queens)

All female dorylines are dichthadiiform (Fig. 1A,B), that is, they are either blind or possess reduced or vestigial eyes, and they are apterous and have a hypertrophied petiole and gaster (Wilson, 1971). The dichthadiiform condition is found only in the dorylines and in some of the ponerines that exhibit army ant behavior patterns, such as *Simopelta oculata* (Gotwald and Brown, 1966). The females are always much larger than the workers. Other characters include antennae that have 10–12 segments, a waist that always has one segment, and an alitrunk in which suturing is reduced (Emery, 1910).

3. Males

The males (Fig. 1E,F) are alate and much larger than the workers. Their antennae have 13 segments; they possess large compound eyes and three conspicuous ocelli; their thoracic suturing is not reduced; their waist always has one segment; and their genitalia are completely retractile (Emery, 1910; Wheeler, 1910). Curiously, the metapleural glands, structures found only in ants, are not present in doryline males (Brown, 1968).
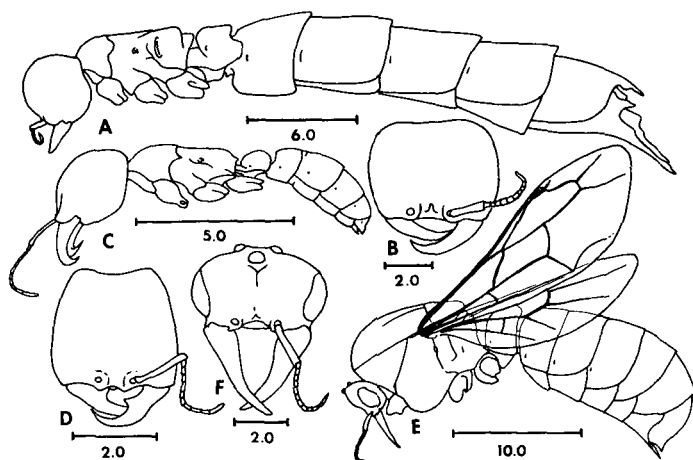

Fig. 1. *Dorylus (Anomma) molesta.* (A) Queen, habitus, lateral aspect, legs omitted; (B) head of queen dorsal aspect; (C) soldier, habitus, lateral aspect, legs omitted; (D) head of soldier dorsal aspect, (E) male, habitus, lateral aspect, legs omitted; (F) head of male dorsal aspect. All scales are in millimeters.

B. Keys to the Tribes, Genera, and Subgenera of Doryline and Ecitonine Army Ants

1. General Considerations

The following keys are adapted from Emery (1910), Wheeler (1910, 1922), Borgmeier (1955, 1958), Raignier and van Boven (1955), Schneirla (1971), Bolton (1973), van Boven (1975), and Watkins (1976); some of the characters used in the keys to the subgenera of *Dorylus* are employed here for the first time. For determinations to the species level, one should refer to Borgmeier (1955) and Watkins (1976) for the New World species and Wilson (1964) for the Indo–Australian species. Complete keys to the African species of *Dorylus* and *Aenictus* are not yet available.

Although keys are provided for the identification of workers, females (or queens), and males, those for the workers of polymorphic species (e.g., *Eciton* and *Dorylus*) refer most often to characteristics that are either exclusive to or best developed in the major workers and/or soldiers.

2. Tribes of Dorylinae and Ecitoninae

Workers

1. Waist, 2 segments (Fig. 2A) 2
   Waist, 1 segment (Fig. 2B) 3
2. Antenna, 10 segments; Old World species................. Aenictini (genus *Aenictus*)
   Antenna, 12 segments; New World species ....Ecitonini
3. Pygidium impressed, armed with 2 lateral spines, 1 on each side; Old World species (Fig. 2C,D)..Dorylini (genus *Dorylus*)
   Pygidium simple; New World species (Fig. 2E).................................
   ....Cheliomyrmecini (genus *Cheliomyrmex*)
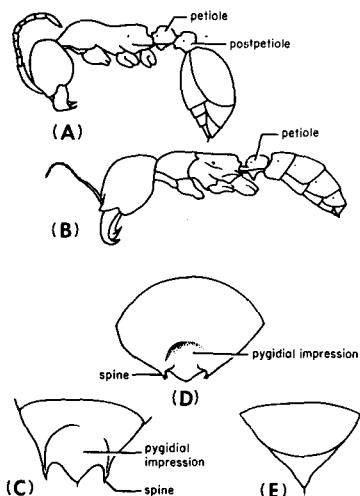

Fig. 2. (A) *Aenictus* worker, habitus, lateral aspect, legs omitted; (B) *Dorylus (Anomma)* worker, habitus, lateral aspect, legs omitted; (C) pygidium of *Anomma* worker, dorsal aspect; (D) pygidium of *Typhlopone* worker, dorsal aspect; (E) pygidium of *Cheliomyrmex* worker, dorsal aspect.

Queens

1. Antenna, 10 segments; Old World Species .... Aenictini (genus *Aenictus*)
    Antenna, 11 or 12 segments; Old or New World species 2
2. Copulatory bursa covered by the pygidium; hypopygium not prominent; New World
    species (Fig. 3A,B) .... Ecitonini
    Copulatory bursa open, not covered by pygidium; hypopygium forked, conspicuously
    extended beyond the pygidium; Old World species (Fig. 3C,D,E) ....
    .... Dorylini (genus *Dorylus*)
(Note: the female of the Cheliomyrmecini is unknown)

Males

1. Wing vein Mfl originating adjacent or distal to crossvein cu-a; Old World species
    (Fig. 3F) 2
    Wing vein Mfl originating considerably proximal to cu-a; New World species (Fig.3G)
    3
2. Stigma of forewing narrow (Fig.4A); total body length (exclusive of mandibles) usually
    greater than 18 mm .... Dorylini
    Stigma of forewing wide (Fig.4B); total body length (exclusive of mandibles) usually less
    than 8.5 mm .... Aenictini
3. Flagellum of antenna only slightly longer than width of the head ...... Cheliomyrmecini
    Flagellum of antenna much longer than width of the head .... Ecitonini

3. *Genera of the Ecitonini*

Workers

1. Tarsal claws simple, without teeth (Fig.4C) .... *Neivamyrmex*
    Tarsal claws with teeth (Fig.4D) 2
2. Scape and flagellum of antenna wide (apical width of scape greater than one-third its
    length) .... *Nomamyrmex*
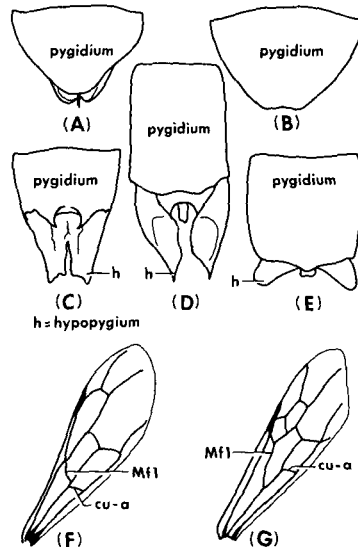
Fig. 3. Pygidia of army ant queens, dorsal aspect: (A) *Eciton,* (B) *Labidus,* (C) *Anomma,* (D) *Rhogmus,* and (E) *Alaopone.* Forewing of army ant males, dorsal aspect: (F) *Typhlopone,* and (G) *Eciton.*
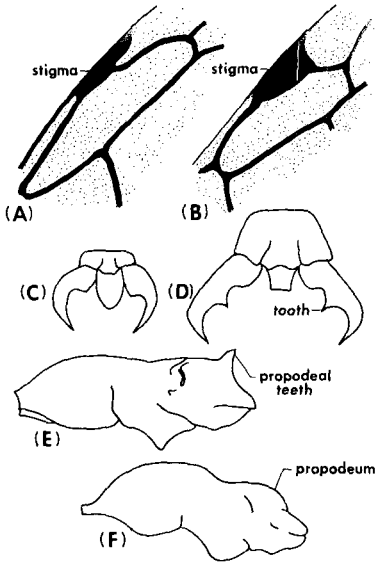
Fig. 4. (A) Wing stigma of *Dorylus* male, dorsal aspect; (B) wing stigma of *Aenictus* male, dorsal aspect; (C) tarsal claws of *Neivamyrmex* worker; (D) tarsal claws of *Eciton* worker; (E) alitrunk of *Eciton* worker, lateral aspect; (F) alitrunk of *Labidus* worker, lateral aspect.

Scape and flagellum of antenna slender (apical width of scape less than one-third its length) 3
3. Propodeum armed posteriorly with teeth or lamellae (Fig.4E); soldiers usually with falcate mandibles . . . . *Eciton*
Propodeum unarmed (Fig.4F); mandibles of soldiers not falcate . . . . *Labidus*

Queens

1. Tarsal claws simple, without teeth (Fig.4C) . . . . *Neivamyrmex*
Tarsal claws with teeth (Fig.4D) 2
2. Propodeum armed posteriorly with two horns or blunt teeth (Fig.5A) . . . . *Eciton*
Propodeum unarmed (Fig.5B) 3
3. Promesonotum strongly convex in lateral view; propodeum sloped obliquely (Fig.5B) . . . . *Labidus*
Alitrunk in lateral view more or less straight . . . . *Nomamyrmex*

Males

1. Legs long, metafemur reaching or surpassing the posterior margin of the second gastral segment 2
Legs short, metafemur not reaching the posterior margin of the second gastral segment . . . . *Neivamyrmex*
2. Apices of lateral aedeagal sclerites (penis valves) without setae (Fig.5C) . . . . *Eciton*
Apices of lateral aedeagal sclerites with setae (Fig.5D) 3
3. Gastral tergites with clusters of long setae . . . . *Nomamyrmex*
Gastral tergites without conspicuous clusters of long setae . . . . *Labidus*

4. Subgenera of Dorylus

Workers

1. Antenna, 12 segments . . . . *Dichthadia*
Antenna, 9–11 segments 2
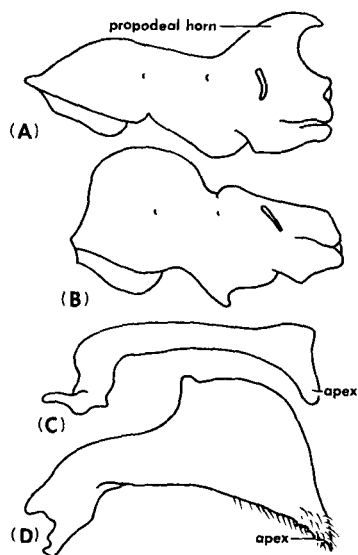
Fig. 5. (A) Alitrunk of *Eciton* queen, lateral aspect; (B) alitrunk of *Labidus* queen, lateral aspect; (C) lateral aedeagal sclerite of *Eciton* male, lateral aspect; (D) lateral aedeagal sclerite of *Labidus* male, lateral aspect.

2. Antenna, 9 segments ....*Alaopone*
   Antenna, 10–11 segments 3
3. Pygidial impression with sharp, well-defined margins (Fig.2C) 4
   Pygidial impression without distinct margins (Fig.2D) 5
4. Antenna short and thick, all segments of the flagellum except the last as wide or wider than they are long; each frontal carina *usually* armed with a caudally projecting spine (Fig.6A) ....*Dorylus*
   Antenna long and slender, at least some segments of flagellum longer than wide; frontal carinae never armed with spines (Fig.6B) ....*Anomma*
5. Subapical tooth of mandible simple (Fig.6C); frontal carina in lateral view drawn to a ventrally directed point (Fig.6F); promesonotal suture only slightly impressed ....
   ....*Typhlopone*
   Subapical tooth either truncate or notched at the middle (Fig. 6D); frontal carina in lateral view rounded, not pointed (Fig.6E); promesonotal suture deeply impressed ...*Rhogmus*

Queens

1. Antenna, 12 segments ....*Dichthadia*
   Antenna, 11 segments 2
2. Posterior margin of pygidium with a deep, median, semicircular notch (Fig. 3C) 3
   Posterior margin of pygidium straight or only slightly concave, without a semicircular notch (Fig. 3D,E)..4
3. Propodeum in dorsal view wider than the pronotum (Fig.7A); posterior angles of petiole considerably divergent (Fig.7A) ....*Anomma*
   Propodeum not as wide as pronotum (Fig.7B); posterior angles of petiole only slightly divergent (Fig.7B) ....*Dorylus*
4. Posterior margin of pygidium straight; in dorsal view, hypopygium extending only a short distance beyond posterior margin of pygidium and terminating in two rounded, diverging lobes (Fig.3E)..*Alaopone*
   Posterior margin of pygidium slightly concave; hypopygium extending far beyond posterior margin of pygidium and divided by a median cleft so that it terminates in two apically pointed processes (Fig.3D) 5
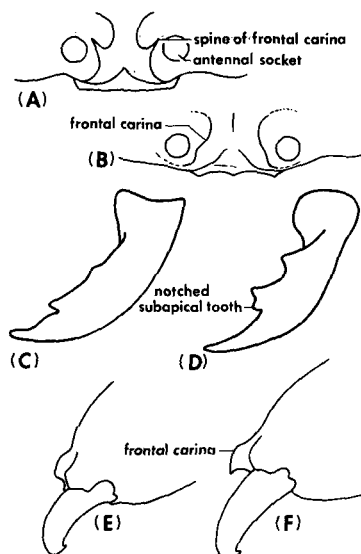
Fig. 6. (A) Frontal carinae of major worker of *Dorylus*, dorsal aspect; (B) frontal carinae of major worker of *Anomma*, dorsal aspect; (C) mandible of major worker of *Typhlopone;* (D) mandible of major worker of *Rhogmus;* (E) anterior half of head, major worker, *Rhogmus*, lateral aspect; (F) anterior half of head, major worker, *Typhlopone*, lateral aspect.

5. Hypopygium forming a dorsoventrally flattened plate, in dorsal view its median cleft ending considerably caudal of the posterior margin of the pygidium . . . . *Typhlopone*
    Hypopygium not forming a flattened plate, in dorsal view its median cleft appears to totally subdivide the hypopygium into two lateral parts (Fig. 3D) . . . . *Rhogmus*

Males

1. Forewing with "second recurrent" vein (Fig.7C); aedeagus enlarged distally, in dorsal view apex is knoblike; mandible as in Fig.7D. . . . . *Rhogmus*
    Forewing without second recurrent vein; aedeagus smoothly tapered distally, not terminating in a knoblike enlargement; mandible shaped otherwise 2
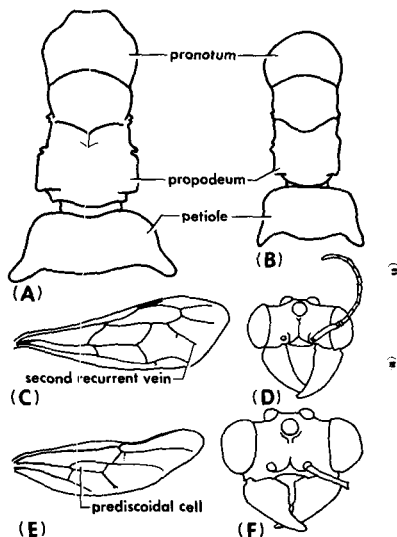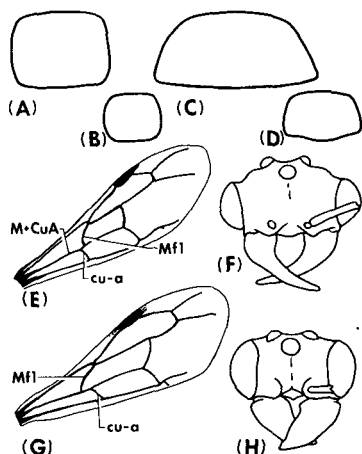

Fig. 7. (A) Alitrunk and petiole of *Anomma* queen, dorsal aspect; (B) alitrunk and petiole of *Dorylus* queen, dorsal aspect; (C) forewing of *Rhogmus* male, dorsal aspect; (D) head of *Rhogmus* male, dorsal aspect; (E) hindwing of *Dichthadia* male, dorsal aspect; (F) head of *Dichthadia* male, dorsal aspect.

Fig. 8. Petioles of the males of the genus *Dorylus:*
(A) *Typhlopone,* (B) *Alaopone,* (C) *Anomma,* and
(D) *Dorylus.* (E) Forewing of *Typhlopone* male, dor-
sal aspect; (F) head of *Typhlopone* male, dorsal
aspect; (G) forewing of *Alaopone* male, dorsal
aspect; (H) head of *Alaopone* male, dorsal aspect.

2. Hindwing with a prediscoidal cell (Fig.7E); mandible as in Fig. 7F . . . . *Dichthadia*
   Hindwing without prediscoidal cell; mandible shaped otherwise 3
3. Petiole in dorsal view nearly square or round (Fig.8A,B). 4
   Petiole in dorsal view wider than long, its posterior surface concave or at least flattened
   (Fig.8C,D) 5
4. Crossvein cu-a of forewing intersects with M + CuA, i.e., proximal to the intersection of
   Mfl (occasionally the cu-a and Mfl intersections are opposite one another) (Fig.8E);
   anterior margin of labrum medially cleft; mandible as in Fig.8F . . . . *Typhlopone*
   Crossvein cu-a intersects with CuA, i.e., distal to the intersection of Mfl (Fig.8G);
   anterior margin of labrum entire; mandible as in Fig.8H . . . . *Alaopone*
5. Antennal fossa projects beyond the anterior margin of the head forming a prominent
   tooth (Fig.9A); prongs of the subgenital plate are parallel or only slightly divergent at
   their apices (Fig.9C) . . . . *Anomma*
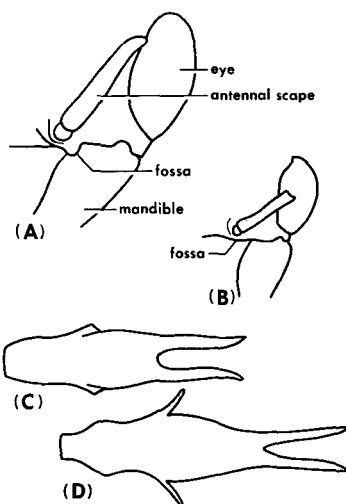
Fig. 9. (A) Head of *Anomma* male, left anterior
quadrant, including base of mandible, dorsal aspect;
(B) head of *Dorylus* male, left anterior quadrant, in-
cluding base of mandible, dorsal aspect; (C) subgeni-
tal plate of *Anomma* male, dorsal aspect; (D) sub-
genital plate of *Dorylus* male, dorsal aspect.

Antennal fossa forming a wide but inconspicuous protrusion (Fig.9B); prongs of
subgenital plate are divergent, not parallel (Fig.9D) . . . . *Dorylus*

IV. COLONY COMPOSITION AND CASTE POLYETHISM

A. Army Ant Polymorphism

Even a cursory examination of the genetic females (i.e., workers and
queens) of army ants dramatically demonstrates why the earlier classifica-
tions of dorylines were often incomplete and contradictory. Many of the
species are highly polymorphic and when collected as single, unassociated
specimens they are difficult, more often impossible, to relate to previously
collected conspecific individuals of different castes or subcastes.

For the social insects, polymorphism is defined as the coexistence of two or
more functionally distinct castes within the same sex (Wilson, 1971). Thus in
the dorylines two full castes are present: neuter females or workers and
reproductive females or queens. Soldiers are present in some species and
represent subcastes since they constitute the largest individuals in a con-
tinuous polymorphic series of workers (Wilson, 1971). Other worker sub-
castes among highly polymorphic forms such as *Anomma* and *Eciton* are ar-
bitrarily designated, on the basis of size as either major, or media, or minor
workers. Such distinctions are not made where the size differential between
the smallest and largest workers is slight, such as in *Aenictus*. Although it is
sometimes convenient to refer to the males as yet another caste, such a
designation is not faithful to the definition of caste.

The caste distinctions made between some individuals of a polymorphic
species result not only from obvious size differences but also from the mor-
phological manifestations of allometric growth; allometry being a growth
phenomenon that produces differences in the relative proportions of body
parts that are a function of total body size (Wilson, 1971). Although Darwin
(1859) certainly noted the allometric nature of *Anomma* worker morphology,
it was not until much later, when Huxley (1927) examined what he called
"heterogonic growth" in *Anomma,* that this growth phenomenon was quan-
titatively analyzed in army ants. While Cohic (1948) claimed that the workers
of *Anomma* could be divided into distinct morphological and functional
types, Hollingsworth (1960) demonstrated that such discontinuities did not
exist. Indeed, he showed that the *Anomma* workers of a single colony could be
placed in a continuous series from the smallest to the largest. On the other
hand, although morphological discontinuities in *Anomma* [in particular in *D.
(A.) wilverthi*] are not evident and only one worker caste exists, van Boven
(1961) determined that four subcaste phases were morphologically dis-
tinguishable. These he referred to as minima, minor, media, and major

workers. Hollingsworth (1960) found that allometry in *Anomma* is not simple since "various parts of the body have different allometric constants in different individuals." Because the relative growth curve of the workers changes slope, the *Anomma* species analyzed is said to exhibit diphasic allometry (Hollingsworth, 1960; Wilson, 1971).

All true army ants, with the exception of *Aenictus* and some species of the genus *Neivamyrmex,* are strongly polymorphic (Gotwald and Kupiec, 1975). In terms of total body length, the size differential between the smallest and largest workers for *Eciton burchelli* is 8.1 mm; *D. (A.) wilverthi,* 8.0 mm; *Cheliomyrmex morosus,* 4.12 mm; *Neivamyrmex nigrescens,* 2.8 mm; and for *Aenictus gracilis,* 0.5 mm (Gotwald and Kupiec, 1975). In polymorphic species, the size frequency distribution of workers is asymmetric. For instance, in *E. hamatum,* "small intermediate" workers are most numerous, large intermediates and minors next and major workers least numerous (Schneirla, 1971). In *E. burchelli,* the minor workers predominate, and in both species, the majors constitute less than 2% of the entire colony (Schneirla, 1971). Topoff (1971), who calculated the frequency distributions of total body length for army ant worker pupae, noted that the smaller workers predominate, even in essentially monomorphic species such as *Aenictus laeviceps.*

Among the army ants *Anomma* species have been most thoroughly examined in terms of their polymorphism and allometry. To the previously cited studies of Huxley (1927), Cohic (1948), Hollingsworth (1960), and van Boven (1961) must be added those of Raignier and van Boven (1955), van Boven (1958) and Raignier *et al.* (1974). Polymorphism and allometry have also been studied in the brood of New World species by Schneirla and Brown (1952), Tafuri (1955), Lappano (1958), and Schneirla *et al.* (1968).

B. Army Ant Castes and Subcastes

1. Workers

a. Morphology. Details of doryline worker ant morphology are included in comparative studies of the mouthparts (Bugnion, 1930; Gotwald, 1969), thorax (Tulloch, 1935; Reid, 1941), proventriculus (Eisner, 1957), and poison apparatus (Hermann and Blum, 1967; Hermann, 1969). The morphology of Old World species has been studied by Mukerjee (1933), Cohic (1948), and Hollingsworth (1960) and of New World species by Whelden (1963), Gotwald (1971), and Gotwald and Kupiec (1975). A review of structures and morphological features that are important in either interpreting doryline phylogeny or understanding army ant behavior follows.

The workers of *Dorylus, Aenictus,* and *Cheliomyrmex* are eyeless, while, with few exceptions, those of *Eciton, Labidus, Neivamyrmex,* and

Nomamyrmex possess reduced compound eyes. Although the Old World species and some New World forms are blind, Werringloer (1932) attributed to them a subdermal or integumental light sense. While Schneirla (1971) suggested that eyes are better developed in surface-adapted species (i.e., in species that commonly forage and even nest on or above the soil or substrate surface), Gotwald (1978) pointed out that several species of *Dorylus* (particularly *Anomma*) and *Aenictus* frequently and even habitually forage on the soil surface and climb vegetation. Furthermore, Gotwald (1978) constructed a scenario to account for eyelessness in surface foraging species. In this scenario, eyeless species arose from predatory ancestors that were surface-active and possessed well developed eyes; eyelessness was a consequence of subterranean living that became selectively advantageous for these predorylines. Because numerous extant Old World species of surface foragers are blind, their readaptation to surface lifeways may be a recent event. Gotwald (1978) noted that the reduced palpal segmentation common to doryline army ants also supports the hypothesized subterranean existence of the ancestral forms.

Although the mandibles of doryline workers exhibit a diverse morphology, those of the soldiers of *Eciton* and *Anomma* are morphologically similar and are celebrated for their ability to pierce human skin. In soldiers of both, the mandible is falcate and sharply pointed, and is clearly a piercing type considered best adapted to a defensive function (Wilson, 1971) (Fig.1D). In polymorphic species such as *D. (A.) nigricans* and *C. morosus,* the mandibles undergo a gradual but continuous transition in shape from the smallest to the largest workers (Hollingsworth, 1960; Gotwald and Kupiec, 1975). According to Gotwald (1978), this produces mandible morphologies that are variously adapted to different tasks. The mouthparts are morphologically distinctive at the tribal level and the Ecitonini, Aenictini and Dorylini can be separated on the basis of mouthparts alone (Gotwald, 1969). On the other hand, mouthpart morphology shows the Ecitonini and Cheliomyrmecini to be closely related (Gotwald, 1969). The number of palpal segments is significantly reduced from the primitive number in ants of six in the maxillary palpus and four in the labial palpus. In the dorylines, the maxillary palpus ranges from one to two segments and the labial palpus from two to three segments (Gotwald, 1978).

Reid (1941) found that there were two distinct types of worker alitrunk in the army ants, one typical of the Dorylini and the other of the Ecitonini. In the former, the alitrunk consists of two parts of approximately equal size, an anterior part consisting of the pronotum and a posterior part composed of the mesonotum, metanotum, and propodeum. In the latter, the alitrunk is a single, undivided structure in which the sutures are usually greatly reduced. Reid (1941) noted that the alitrunk of *Aenictus* most closely resembles that of the genus *Eciton*.

The worker waist has two segments or is binodal in the Ecitonini and Aenictini. In the Dorylini and Cheliomyrmecini the worker waist has one segment or is uninodal (Fig.2A,B). If the Dorylinae (*sensu lato*) are monophyletic, the segmental nature of the waist in this subfamily is certainly less conservative than it is in other subfamilies where the number of segments may be constant for an entire subfamily (e.g., the Formicinae) (Gotwald, 1978). Pullen (1963) suggested that the binodal waist facilitates stinging by making the gaster more maneuverable, and Schneirla (1971) added that this condition is important to surface-adapted species in subduing strong, fast moving prey. Schneirla also concluded that this flexibility is of some advantage in laying chemical trails and in carrying brood and prey (generally beneath the worker's body). These assumptions remain to be demonstrated empirically.

The doryline poison apparatus, including the sting sclerites, has been described by Whelden (1963), Hermann and Blum (1967), Hermann (1969), and Gotwald (1971). The soft parts of the poison apparatus include an elongate, pear-shaped or spherical, poison sac or venom reservoir with a conspicuous duct that terminates in the sting bulb (Hermann, 1969; Gotwald, 1971). Free poison filaments arise from the base of the poison sac or its duct. These filaments are sometimes branched and are distributed in the vicinity of the poison sac. An elongate Dufour's gland composed of cuboidal and/or columnar cells is present, but its function remains to be discovered (Hermann, 1969). Among the skeletal components, two are of special interest. The furcula, a sclerite located anterior to the sting bulb, is common to all ants thus far examined except the dorylines, cerapachyines, and one species of ponerine (Hermann, 1969). Its absence in the dorylines and *Simopelta oculata*, a ponerine with army ant lifeways, suggests that this sclerite is convergently lost in species adopting army ant behavior patterns (Hermann, 1968b). The sting, the other sclerite of interest, is broad and spatulate in the Dorylini, a morphological development that may be correlated with this group's inability to sting. The sting is slender in those doryline species that do sting (Hermann, 1969; Gotwald, 1978).

All New World army ants possess a functional sting. When attacking prey, these forms may bite and sting simultaneously. However, the Old World species of *Dorylus* are not known to sting, although they are ferocious, effective biters (Gotwald, 1978). Schneirla (1971) noted that the *Aenictus* workers that he observed in the Philippines had "potent stings," but Gotwald (1978) observed that African *Aenictus* may not sting. The absence of stinging in *Dorylus* may be a behavioral manifestation of the spatulate condition in the sting. Although Hermann (1969) found the sting of *Aenictus gracilis*, a species in which stinging is documented, to be slender as in New World stinging species, Gotwald (1978) noted that at least one apparently nonstinging species of African *Aenictus* possessed a spatulate sting.

Few studies have focused on the internal morphology of army ant workers. Mukerjee (1933) examined internal structues of *D. (Alaopone) orientalis,* Whelden (1963) published an extensive study of *E. burchelli* and *E. hamatum* and Gotwald (1971) and Gotwald and Kupiec (1975) produced anatomical descriptions of *C. morosus.* Other such observations are fragmentary at best. Bugnion (1930) described the pharynx of *Anomma* as reduced and hypothesized that the reduction is correlated with the absence of trophallaxis in the dorylines. Eisner (1957) found the army ant proventriculus to be degenerative and concluded that since the damming of this membranous valve is probably dependent on muscle contraction, crop storage in these ants may be of relatively short duration. The Malpighian tubules are probably histologically uniform throughout the army ants, although the numbers of tubules vary considerably. Even so, overlap in the ranges of tubule numbers between species is common, and the number of tubules per individual is so closely correlated with body size as to preclude their use taxonomically in polymorphic species (Gotwald, 1971). The rectal papillae, on the other hand, may be more constant in number, although Whelden (1963) reported a range of 3–6 in *E. burchelli* and *E. hamatum.*

Glands thus far identified in the workers include the mandibular glands, maxillary glands, pharyngeal glands, labial glands, metapleural glands, Dufour's gland, and the convoluted gland of the poison sac (Gotwald and Kupiec, 1975). Of these, only the convoluted gland has been studied in detail (Hermann and Blum, 1967).

The army ant nervous system has received some attention. In the brain, the corpora pedunculata or "mushroom-bodies," the size of which is often used as an indicator of mental capacity, are smallest in *Eciton hamatum* when compared to all other ants examined (Vowles, 1955; Bernstein and Bernstein, 1969). They are largest, for instance, in the formicine ant, *Formica rufa.* However, the relative size of the doryline brain is predictably smaller than in other similarly sized ants because, without eyes, the optic centers are greatly reduced (Werringloer, 1932; Vowles, 1955).

Ovaries composed of polytrophic ovarioles are found in the workers of *D. (A.) orientalis* (Mukerjee, 1933), *E. burchelli* and *E. hamatum* (Whelden, 1963), and *C. morosus* (Gotwald, 1971). In some species, each ovary consists of a single ovariole, while in others the number of ovarioles per ovary may range from one to three (Gotwald and Kupiec, 1975). Although ovaries are probably present in a majority of workers, Holliday (1904) failed to find them in *Neivamyrmex nigrescens.* Whether or not army ant workers actually lay these eggs is unknown, although the production of "trophic eggs" (i.e., eggs consumed by other colony members) among other ant species is not uncommon (Wilson, 1971).

b. Worker Functions. Wilson (1953) considered worker polymorphism, which is developed to some degree in all army ant genera except *Aenictus,* a

special adaptive characteristic that results "in various types and degrees of worker labor." Schneirla (1971) noted that colony tasks in the monomorphic *Aenictus* are probably carried out by all workers at various times. Indeed, Topoff (1971) indicated that although "differences in sensory thresholds to chemical stimuli may exist among workers of different size groups" in *Eciton, Labidus,* and *Neivamyrmex,* workers of *Aenictus* all react similarly, for instance, to arousal stimuli.

Caste polyethism for worker subcastes has been documented in some cases and hypothesized in others. Rettenmeyer (1963b) found that major workers of *Eciton* participate in the formation of hanging clusters essential to assembling the bivouac (or temporary nest), in capturing prey, and in defense. However, both he and Schneirla (1971) pointed out that *Eciton* major workers are "automatically excluded from nearly all transport work since with their great double-fishhook jaws they cannot pick up, hold, or release objects." Topoff and Mirenda (1978) have shown that the callow workers of *Neivamyrmex nigrescens* do not participate in colony foraging excursions until 3–7 days after eclosion. Gotwald (1978) noticed that although some functions (e.g., the construction of soil particle walls) in *Anomma* correlate with body size, they are an adaptive consequence of mandible morphology, which in turn is allometrically determined.

A defensive function of major workers in *Eciton* is evident when a bivouac is torn apart. At the time of disturbance a large number of excited majors gather about the queen; in the undisturbed bivouac, the queen is surrounded by a "tight ball" of the smallest workers (Rettenmeyer, 1963b). Schneirla (1971) generalized about polymorphic species suggesting that media workers are less involved in "rough operations." Schneirla further noted that during emigration in *Eciton* there is a positive correlation between size of worker and load (i.e., brood) carried and that, in the nest, the smallest workers generally handle and feed the small larvae of a young brood. Among Old World species, a division of labor in prey retrieval in *Anomma* is apparent. Gotwald (1974a) observed that nearly all "preyless" foragers returning to the nest, i.e., workers not carrying visible pieces of prey, have liquid-filled crops. Statistical analysis revealed that larger workers tend to carry pieces of prey while smaller workers specialize in carrying prey liquids. Also in *Anomma,* the workers that construct the soil particle walls that often border their chemical trails are among the smallest in the colony (Kistner and Gotwald, 1982).

Although worker subcaste polyethism in polymorphic species of army ants is documented in some cases, a paucity of quantitative studies is clearly evident.

2. Queens

a. Morphology. Most observations of doryline queen morphology are limited to external features, specifically to those of taxonomic interest. For Old World species such observations have been reported by Emery (1887),

André (1900), Brauns (1903), Menozzi (1927), Arnold (1953), Raignier and van Boven (1955), van Boven (1967, 1968, 1972, 1975), Raignier *et al.* (1974), Gotwald and Cunningham-van Someren (1976), and Gotwald and Leroux (1980) to cite only a few. New World queens have been similarly described by Wheeler (1900, 1921, 1925), Bruch (1934), Weber (1941), and Rettenmeyer (1974). Studies that are entirely morphological in focus and include internal features are limited to those of Whelden (1963) and Hagan (1954a,b,c).

Army ant queens are dichthadiigynes, i.e., they possess a greatly enlarged gaster and petiole, are blind or nearly so, are permanently wingless, and have strong legs (Fig. 1A). Wilson (1971) pointed out that this unusual morphology adapts the queen to nomadic life in two ways: (1) the enlarged gaster contains ovaries composed of many ovarioles that enable the queen to "deliver large quantities of eggs during a short span of time," and (2) the queen is able to move under her own power from one temporary nesting site to the next. This specialized reproductive design is correlated with the acquisition of an expanded tracheal system and the ability to store large amounts of fat as a reserve energy source (Wheeler, 1928).

Since *Eciton* colonies alternate between statary and nomadic phases, an endogenously controlled rhythm, on a regular schedule, it is possible to observe certain external changes in the queen that are synchronized with these cyclic phases (Schneirla, 1971). As the colony enters the nomadic phase, the queen's ovaries undergo remarkable development, causing the gaster to become physogastric. The intersegmental membranes of the gaster stretch as they accommodate the hypertrophying ovaries, and the gastral sclerites are separated from one another (Schneirla, 1971). Although other doryline queens become physogastric, the regular alternation of statary and nomadic phases may be atypical of army ants in general. Rettenmeyer (1963b) noted, for instance, that Schneirla studied perhaps the most highly specialized species of *Eciton* (i.e., *E. burchelli* and *E. hamatum*) and that many of the generalizations offered by Schneirla about the army ant functional cycle are based on his knowledge of these species.

The mandibles of doryline queens differ in one conspicuous respect from those of the workers: they are devoid of subapical teeth (Gotwald, 1969) (Fig. 1B). They also depart from the triangular-shaped mandible typical of a majority of ants and are, instead, linear and slightly curved apically. The queen mandibles of the ponerine army ant, *Simopelta oculata,* are of a similar design (Gotwald and Brown, 1966). The maxillary palpus has two segments in the Aenictini, Dorylini and Ecitonini; the labial palpus has one segment in the Old World dorylines and two segments in the ecitonines (Gotwald, 1969). While compound eyes in the form of ocelluslike structures are common to the New World forms, they are entirely absent in Old World queens.

The alitrunk of the army ant queen is characterized by a general reduction

in suturing, although the extent of reduction is far from universal. Even within a single genus the variation in suturing may vary considerably. For instance, queens of African *Aenictus* have a simplified (derived) thorax, whereas Asian species possess a more complex (primitive) suturing (Gotwald and Cunningham-van Someren, 1976). In fact, the differences between the Asian and African queens prompted Wheeler (1930) to suggest that the Asian species "would seem to belong to a distinct genus." However, a comprehensive, comparative survey of thoracic suturing in queens is wanting.

The petiole of doryline queens, at least in the Ecitonini and Dorylini, is enlarged and armed with caudally directed dorsal or lateral horns. These are most conspicuously developed in the ecitonines. In two *Eciton* matings reported by Schneirla (1949), each of the males involved grasped a petiolar horn in its mandibles during copulation. According to Rettenmeyer (1963b), this grasping behavior "suggests that contact between the mandibles and the queen's petiole may be important for mating and perhaps for preventing interspecies mating," since the petioles of the queen and the mandibles of the males differ so strikingly among the species. Schneirla (1971) assumed that these petiolar horns also serve a protective function.

The expansive gaster of the army ant queen is uniquely developed in the Dorylini where the bifurcated hypopygium extends conspicuously beyond the posterior of the pygidium, and the copulatory bursa is open, i.e., not covered by the pygidium (Raignier and van Boven, 1955; van Boven, 1967). In the Aenictini and Ecitonini, the hypopygium is not so extended and the bursa is closed by the pygidium. Hagen (1954a) noted that in *Eciton* during the nomadic phase, when the queen is contracted, the five visible gastral segments are strongly telescoped with the gastral sclerites greatly overlapping one another. During physogastry, of course, these sclerites are widely separated.

Internal features of interest include a proventriculus that is smaller than in the *Eciton* worker, although the structure is identical in both castes. The ventriculus of the *Eciton* queen is different from that of the worker both in shape and in the morphology of its component cells. For instance, the ventriculus of the queen is more or less cylindrical while that of the worker is pear-shaped. Whelden (1963) found approximately 30 Malpighian tubules in the *Eciton* queen, a number that is almost twice as many as in the workers. The number of rectal papillae, elliptical to nearly circular structures, in *Eciton* queens is "frequently six, infrequently three" (Whelden 1963).

Whelden (1963) described for the *Eciton* queen numerous glands. In the head there are mandibular glands, maxillary glands, pharyngeal glands, and three small glands (unnamed) that open through a membrane that extends from the mandibles to the bases of the mouthparts. The alitrunk contains the labial glands, metapleural glands, six small glands (one at the base of each leg), and a "moderately large" gland that is not present in the workers.

Although Whelden found the cells of this latter gland to be easily confused with those of the metapleural glands, their ducts open through the membrane that connects the alitrunk with the petiole. A gland is also present in the petiole. In the gaster, each segment contains a pair of large glands the cells of which each possess a duct that opens separately through the intersegmental membranes. Also present are the poison sac and the "alkaline" gland (Dufour's gland).

The brain or supraesophageal ganglion is larger in the *Eciton* queen than in the worker, but while the most conspicuous cranial nerves in the workers are those that innervate the antennae and mandibles, the optic nerves are most fully developed in the queen. The queen nervous system departs most noticeably from that of the worker in its possession of five large gastral ganglia instead of the single fused ganglionic mass of the worker.

The reproductive systems of the queens of *Eciton* and *Neivamyrmex* include a vagina and a median oviduct which bifurcates to form the paired lateral oviducts. These in turn lead to the ovaries which are composed of large numbers of polytrophic ovarioles (Holliday, 1904; Hagan, 1954a; Whelden, 1963). The lateral oviduct in *Neivamyrmex* extends for the entire length of the ovary; the ovarioles open into the duct (Holliday, 1904). In *Eciton* the lateral oviduct expands within the ovary to form a calyx and is capable of accommodating the vast numbers of oocytes that are discharged simultaneously into it by the ovarioles (Hagan, 1954a). There are approximately 1200 ovarioles in the ovary of the *Eciton* queen (Hagan, 1954a) and about 500 in the ovary of *Neivamyrmex* (Holliday, 1904).

Other reproductive structures in *Eciton* include an exceptionally long (probably longer than the gaster itself) spermathecal duct that originates on the dorsal wall of the vagina (Hagan, 1954a). This duct forms several tight coils that are peculiar in shape and position in the individual queens. This duct leads to a spherical or irregularly ovoid spermatheca (Whelden, 1963). Also present are a pair of irregularly twisted, tubular spermathecal glands that attach to the spermatheca directly above its junction with the spermathecal duct and a pair of accessory glands that arise anterior to the basal bulb of the ovipositor.

b. Queen Functions.   Above all else, the army ant queen is the reproductive core of the colony. So vital is she to the colony that it cannot survive as an integrated social unit without her. As Schneirla (1953) pointed out, "although the *Eciton* queen does not directly lead the activities of her colony, her role is critical in the functional pattern." In fact, Schneirla (1944) regarded the queen as a "pacemaker" in the colony behavior pattern of each species. There is but a single, functional queen per colony in the Ecitoninae and Dorylinae. The only known exception to this rule are colonies of *Neivamyrmex*

carolinensis which regularly have 3 to 13 queens (Rettenmeyer and Watkins, 1978).

While the queen influences colony function by the types of eggs she produces (i.e., worker eggs versus sexual brood eggs), Schneirla (1971) concluded that the schedule of egg laying is determined by intracolony processes external to the queen. Central to this "colony-situation-feedback" hypothesis is the effect of brood-stimulative phenomena that regulate colony activities through the mediation of the queen's corpora allata. This in turn accounts for the egg-laying cycles in the queen. This is true, at least, for those army ants that exhibit a well marked functional cycle of regularly alternating nomadic and statary phases. Hagan (1954c) found that the oocyte cycle in *Eciton* "harmonizes" perfectly with colony behavior.

During the nomadic phase of those species of *Eciton, Neivamyrmex,* and *Aenictus* studied by Schneirla (1971), the queen remains contracted but as this phase ends and the statary begins, the queen's gaster swells, exposing the intersegmental membranes. The distension continues for about 1 week into the statary phase at which time the queen achieves full physogastry and egg laying commences. The adaptive advantage of cyclic physogastry that coincides with the statary phase is that is reduces the dangers that confront the queen during the emigrations of the nomadic phase. For instance, she must move under her own power along emigration routes that are often strewn with obstacles that could abrade or puncture her intersegmental membranes if exposed.

However, many army ant species, perhaps even a majority, do not have a well defined functional cycle, and emigrations occur as single events often separated by lengthy intervals. The queens of these species, e.g., of *Dorylus,* do not function on a precise reproductive schedule (Raignier and van Boven, 1955). The interval between emigrations of *D. (Anomma) molesta,* for instance, may vary from 3 to 67 days, and evidence suggests that during adverse conditions such as drought, a colony may remain at a single nest site for many months (W. H. Gotwald and G. R. Cunningham-van Someren, unpublished data). Long intervals may result from the inability of this species to maintain an elevated, optimal nest temperature (Raignier and van Boven, 1955). In some species of *Anomma,* Raignier and van Boven (1955) found that the queen is in a permanent but moderate state of physogastry, although egg laying may be discontinuous. In *D. (A.) wilverthi,* they observed that egg laying peaks occur at 20 to 25-day intervals and that it usually intensifies just after emigration. A period of physogastry longer than that in *Eciton* queens may also exist in *Labidus,* and certainly *Labidus* produces asynchronous broods or at least much less synchronous than *Eciton* (Rettenmeyer, 1963b).

The egg-laying capacity of the army ant queens is truly extraordinary. Schneirla (1971) estimated that a single queen of *Aenictus gracilis* produces as many as 240,000 eggs per year and that the annual yield of an *E. burchelli*

queen may be as high as 2,400,000 eggs. But the queen of *D. (A.) wilverthi* may be unsurpassed. Raignier and van Boven (1955) estimated her egg production to be from 3 to 4 million per month.

If a colony of army ants loses its queen, it cannot ordinarily replace her unless a sexual brood is already present in the colony. Not only will the colony not flourish without its queen, but if it cannot join another conspecific colony, it faces certain extinction. Schneirla (1971) noted that a queenless colony of *Eciton* will within 1 or 2 hr of meeting a queen-normal colony begin merging with it. Workers of the queenless colony, with their brood, abandon their nest in favor of joining the columns of workers of the adoptive colony. The brood of the adopted colony is consumed within 1 or 2 days.

3. Males

a. Morphology.   Because the army ant male represents a unique morphology (i.e., it is unusually large, has a long cylindrical gaster, highly modified mandibles, and uncommonly developed genitalia), Wheeler (1910), in his classification of caste variants, assigned to it the term "dorylaner" (Fig. 1E). Although this term is no longer used, it does point to the fact that these males are undoubtedly exceptional. However, in spite of their conspicuous appearance and the fact that they are commonly represented in museum collections, there is a dearth of information on army ant male morphology.

The males have well developed compound eyes and ocelli (Fig. 1F). The mandibles are distinctive enough to be of practical value in identifying some forms, e.g., in separating the subgenera of *Dorylus*. The maxillary palpus has two segments in all four tribes, while the labial palpus has one segment in the Aenictini and Dorylini, two segments in the Ecitonini, and three segments in the Cheliomyrmecini (Gotwald, 1969).

Tulloch (1935) noted that the alitrunk of *Dorylus helvolus* displayed the "greatest departure from the fundamental type of any of the [ant] subfamilies." He regarded the male doryline thorax as highly specialized. The male is the only doryline phenon with wings, and their wing venation is regarded as relatively primitive (i.e., unreduced) (Brown and Nutting, 1950). Within the army ants, *Cheliomyrmex* is the most primitively veined. Brown and Nutting (1950), in their analysis of formicid wing venation, placed great emphasis on the position of wing vein Mf1. Because this vein arises proximal to crossvein cu-a in the doryline specimens included in their study, they concluded that the dorylines arose from the main formicid line at an early date. However, within the genus *Dorylus*, the position of Mf1 varies considerably (Fig. 8E,G). Indeed, in the subgenus *Alaopone* it is distal to cu-a and in *Rhogmus*, the subgenus figured by Brown and Nutting, it may be found on either side of cu-a. Certainly wing venation patterns in the subfamily await careful analysis of large numbers of congeneric and conspecific specimens.

As in the queen, the waist of the male always has one segment, but unlike the queen, the male petiole is unarmed. The external genitalia of the male have been studied in greater detail than most other external features because of their potential taxonomic value. Even so, published comparative genitalic studies are nonexistent. The genitalic capsule of these males is retracted into a large cavity ventral to the rectum and anus in the last few gastral segments (Borgmeier, 1955; Forbes, 1958; Forbes and Do-Van-Quy, 1965). Of the genitalic sclerites, only the ninth sternum, or subgenital plate, projects beyond the tip of the gaster. As in other ants, the external genitalia consist of three pairs of valves that are surrounded anteriorly by a basal ring (lamina annularis) (Forbes and Do-Van-Quy, 1965). The outer valves are generally referred to as the parameres, the middle valves as the volsellae and the inner valves as the aedeagus. In *Dorylus* the basal ring is narrow and the parameres and volsellae are simple (Raignier and van Boven, 1955). Although the parameres and volsellae are also simple in the ecitonines, the basal ring is conspicuously wider (Forbes, 1958; Forbes and Do-Van-Quy, 1965).

The internal anatomy and histology of the army ant male remains virtually unexplored. Only the alimentary canal and the reproductive system have received attention.

Mukerjee (1926) noted that the alimentary canal of *D. labiatus* is straight and simple and lacks a crop and a well developed proventriculus. Shyamalanath and Forbes (1980) detailed the anatomy of the digestive system of the male of *Aenictus gracilis* and concluded that the unique features of this system lent support to the proposition that *Aenictus* arose independently of other army ants. It was pointed out by Brown (1968) that the metapleural gland is absent in army ant males and that these males must mate with apterous queens in alien conspecific colonies. Brown speculated that the metapleural glands might produce a substance that labels the individuals of one colony as aliens or enemies should they enter another colony of the same species. Without this labeling substance, the army ant male can enter an alien colony unmolested. As attractive as this hypothesis is, and Brown included in his observations a number of other instances in nondoryline ants where these glands are also absent, it does not explain the obvious exception when the workers of a queenless colony merge with a queen-normal colony.

The testes of *N. harrisi* and *E. hamatum* are composed of long, slender tubules that number 20–25 per testis (Forbes, 1958; Forbes and Do-Van-Quy, 1965). In *D. labiatus* the testicular tubules are quite small (Mukerjee, 1926). While a single capsule covers both testes in *N. harrisi,* each testis is invested with its own capsule in *E. hamatum* and in *D. labiatus* there is no capsule at all. Other structures in the system include the vasa deferentia, accessory glands, the bound accessory gland ducts, the ejaculatory duct, and the aedeagal bladder (Forbes, 1958). The accessory glands of *D. labiatus* are large

and thick walled (Mukerjee, 1926), whereas those of *Eciton* and *Neivamyrmex* are formed of tightly coiled tubes (Forbes, 1958; Forbes and Do-Van-Quy, 1965). Curiously, in many studies of male ants, the accessory glands were not identified as such until Hung and Vinson (1975) examined males from five subfamilies including the army ants. They found the coiled accessory glands of the ecitonines to be unique among the ants, while the glands of *D. labiatus* are similar to those of the Myrmicinae and Ponerinae. They concluded that these differences gave credence to the polyphyletic hypothesis of doryline origins. Ford and Forbes (1980) described male reproductive anatomy of the Old World species *D. (A.) wilverthi* and *D. (A.) nigricans,* and Gotwald and Burdette (1981) compared the morphology of the male internal reproductive system in representative species of both New and Old World species. In this latter study, it was concluded that spermatogenesis and storage of newly formed sperm cells in the seminal vesicles occur during pupal development before emergence. In most species the testes greatly atrophy prior to the time of eclosion and little evidence of their existence can be found in the adult. Gotwald and Burdette (1981) further noted that the extraordinary differences in male internal genitalic morphology between New and Old World forms constitute further evidence of the polyphyletic origin of army ants.

b. Male Functions. Male ants do not contribute to the daily maintenance of a colony; they are, for all intents and purposes, little more than "flying sperm dispensers" (Wilson, 1971). In *Eciton* and other genera where colonies pass through alternating statary and nomadic phases, males appear periodically in large sexual broods (which include queens as well) that are coordinated with all-worker broods that precede and follow them (Schneirla, 1971). This precision in the appearance of males is probably absent in army ant species without the regular statary-nomadic functional cycle. For instance, in *Anomma,* sexual broods can appear during any season of the year (Raignier, 1959, 1972). Thus the male exodus from the nest following eclosion from the pupal stage is "relatively precise and genus typical" in species with a regular functional cycle and variable in other groups such as *Dorylus* (Schneirla, 1971).

The presence of sexual brood is prerequisite to colony division, and although males may fly from the nest site directly following eclosion, alate males may emigrate with their colonies (in *Eciton* this would be during the first nomadic phase of a new daughter colony following colony division) and may break away from the columns of workers and fly off. In this way they "literally seed the area through which they pass" (Schneirla, 1971). In *Anomma* the male brood, fully grown larvae and pupae, are left in the old nest with the new queen following colony division. The pupae then eclose and the adult males fly away (Raignier, 1972). *Anomma* males may also emigrate with

the workers, but more often than not, these males are dealate and probably move with their adoptive colonies following their initial exodus flight (Savage, 1847; Donisthorpe, 1939; Raignier and van Boven, 1955).

When the exodus flight is ended, the males lose their wings, possibly as a physiological consequence of the flight itself, although in some cases they are torn off by workers. However, in order for fertilization to occur, these males must in some way find and gain entrance to another conspecific colony. By running on the substrate surface, the males may intersect with foraging or emigration trails of other colonies which they may then follow to the nest site; males that enter columns or nests of other species are killed (Schneirla, 1971). *Anomma* males, for example, can locate and follow the abandoned chemical trails of other colonies and follow these trails to the nest site (Raignier and van Boven, 1955). Schneirla (1971) conjectured that postflight *Eciton* males may attract conspecific workers to themselves by releasing a pheromonal attractant that is spread on the substrate surface by a brushlike collection of setae at the tip of the gaster.

Schneirla (1971) suggested that males of surface-active species leave their colonies around dusk and those of subterranean species leave in the evening or at night. However, males of *D.* (*A.*) *nigricans* and *D.* (*A.*) *wilverthi,* which are certainly surface-active species, fly in complete darkness only after 2000 hr, at least in Rwanda (J.K.A. van Boven, personal communication). Schneirla also noted that males of different species may respond differently to environmental stimuli once they have landed following their exodus flight. For example, surface-active species of *Neivamyrmex* have relatively small, flat eyes, react positively to doryline chemical trails and may on landing after their dusk flight, reach other conspecific colonies primarily through chemical stimuli. On the other hand, subterranean species have large eyes, react weakly to chemical trails and may rely on visual stimuli by moving toward moonlight silhouetted objects, such as rocks and logs, places where the trails of subterranean species are most likely to be located (Schneirla, 1971). Rettenmeyer (1963b) concluded that following eclosion New World males are initially negatively phototaxic and unable to fly for 1 to 3 days. He proposed that only after flight do they become positively phototaxic. Haddow *et al.* (1966) found that *Dorylus* males (of all five African subgenera) fly at all times of the year. Leston (1979) noted that there is a regular cycle in the timing of *Dorylus* male flight in which males are produced about every 30–32 days from March through September and around every 28–29 days from December through February. He also observed that this cycle is synchronous in the four most commonly trapped species and that males are produced "more or less" throughout the year, although with distinct seasonal peaks. Leston concluded that the syncronicity evident in these cycles was not related to climatic factors, as Schneirla suggested for ecitonine males, but was instead a mechanism for oversaturating an area with their numbers. In this way, the survival of at least

some males from an onslaught of predators is enhanced. In a survey of New World army ant flights, Kannowski (1969) collected males of two species only during the dry season, of three other species during the dry season and well into the wet season, and of one species during the entire four months of the study. The males of nine remaining species were collected almost exclusively after the wet season began. Kannowski concluded that the rains may serve as triggering mechanism for these nine species. Seasonal flight periodicities in Nearctic army ant males have been reviewed in detail by Baldridge *et al.* (1980).

Haddow *et al.* (1966) also noted that the males of each species consistently peak, in total numbers of individuals trapped using light, at different times of night, starting at about 1800 hours and ending about 0600 hours. Because "dusk" is a phenomenon of higher latitudes, it is impossible to use the data of Haddow *et al.* to support or refute the Schneirla hypothesis that surface-active species fly at dusk. Kannowski (1969) examined the frequency distribution of ecitonine males during the hours of night and discovered that the species form two distinct groups: one which conducts "post sunset" flights and another that launches predawn flights. One species, *Neivamyrmex pilosus,* was found to be essentially "circum-nocturnal." Temporally spaced flights may in some way contribute to a species isolating mechanism. Apparently the males of several Nearctic species of *Neivamyrmex* have diurnal flights and this explains their absence in light traps used to determine seasonal periodicities (Baldridge *et al.,* 1980).

The frequency with which males may inseminate queens of their own mother colony,whether the queens be old or newly emerged, is not known. However, the genetic advantages of promoting gene flow between colonies may keep the frequency low. Once in an adoptive colony, a dealate male may remain there for days or even weeks before it mates and dies (Schneirla, 1971). Rettenmeyer (1963b) noted that such males probably live a few days but seldom more than 3 weeks.

One thing more is intuitively obvious: between the time that a male leaves its own colony and finds a foster colony, it is subject to many life-threatening risks. Predators and vagaries in the environment may, as risks, be so great that relatively few males ever achieve fertilization of a conspecific queen, which seems to be, after all, their only function.

C. Army Ant Brood

1. Morphology

Of the army ant brood, the larvae have been studied most thoroughly. The larvae were examined taxonomically by G. C. Wheeler (1943) and Wheeler and Wheeler (1964, 1974, 1976). Doryline larvae are "elongate, slender, sub-

cylindrical'' with the anterior end slightly curved; 12 or 13 distinct somites are evident. Spiracles are minute. Vestigial legs (imaginal discs) are large and conspicuous (Wheeler, 1938). Setae are short, sparse to moderately abundant and mostly simple, except in *Neivamyrmex* where they are branched or plumose. The head is large, with short, simple setae and antennae composed of two sensillae each. The mandibles are weakly developed and of two types: "elongate, slender, slightly curved and denticulate" or "short, small, acuminate and feebly sclerotized". The maxillary palpi are either absent or represented by a slightly elevated group of sensillae. The trophorhinium ("the aggregate of roughened surfaces of the mouthparts which might be used in triturating food") is poorly developed or absent (Wheeler, 1943; Wheeler and Wheeler, 1964). Petralia and Vinson (1979) pointed out that the larvae of *Neivamyrmex nigrescens* do not show specializations for holding food on the ventral body region as do other ant species. This lack of specialized development they noted probably relates to the fact that prey food items are placed next to the larvae but never on them. Thus army ant larvae are not required to hold or manipulate their food items. Wheeler (1943) noted that the male larva in *Anomma* is "enormous" when compared to the worker larva and that the anterior portion is bent ventrally at an angle of 90°. Raignier (1972) observed that young male larvae of *Anomma* one week or older can be distinguished from worker larvae, because they are slender and they make curling movements. Those movements may provoke increased foraging activity in adult workers.

Lappano (1958) provided a detailed description of the external morphology of *E. burchelli* larvae. Schneirla *et al.* (1968) analyzed allometric growth in the larvae of *Eciton*, *Neivamyrmex*, and *Aenictus*. Their results confirmed the "empirical expectation" that the larval brood of *Eciton* and *Neivamyrmex* are polymorphic and that those of *Aenictus* are "quasi-monomorphic." Tafuri (1955) studied the larvae of *E. hamatum* and noted that several external features (such as the leg discs, shape of the head segment, and pilosity) are correlated with specific days in the nomadic phase. As a result, he was able to formulate a key for separating larvae according to the nomadic day represented in their stage of development.

Internal features of *E. burchelli* (Lappano, 1958) and *N. nigrescens* larvae (Wang and Happ, 1974) have been described. In the latter species, the labial gland was specifically targeted as a possible source of worker stimulating substances produced during the nomadic phase. The alimentary canal of *E. burchelli* is essentially a straight tube consisting of a foregut, midgut, and hindgut. The midgut is a blind sac, and the lumina of the midgut and hindgut are not continuous until late in the prepupal phase or in the pupa (Lappano, 1958). Wheeler and Bailey (1925) found the "stomach" of *E. burchelli* larvae to be unlike that in other known ant larvae because it is "very long and

slender'' and has ''unusually thick, muscular walls.'' They assumed that the larva is fed at considerable intervals with large pellets of the ''rolled up soft-parts of insects.'' Because these pellets are so compact, they retain their shape even in the lumen of the midgut. Four Malpighian tubules are present throughout larval development. The nervous system is composed of a central division, consisting of a brain and a ventral nerve cord with twelve paired ganglia, and a stomatogastric division. The *E. burchelli* larvae have a ''secretory system'' that includes the corpora allata and labial glands. The latter undergo striking morphological and histological changes during the course of larval development. Other *Eciton* features include the dorsal vessel and the ovaries (Lappano, 1958).

Larval cocoon spinning in the army ants varies remarkably from genus to genus, but the functional and phylogenetic significance of this variation remains a mystery. Cocoons are not spun in *Dorylus* and *Aenictus* but are present in *Eciton* and *Labidus*. In *Neivamyrmex* cocoons are spun only by sexual brood. It is not known whether cocoons are present in *Cheliomyrmex* and *Nomamyrmex* (Schneirla, 1971). Since it is assumed that the ant cocoon is inherited from a wasplike ancestor (Wheeler, 1915), the absence of a cocoon is a derived characteristic. While watching *Eciton* larvae spin cocoons, Beebe (1919) noted that, ''I watched the very first thread of silk drawn between the larva and the outside world, and in an incredibly short time the cocoon was outlined in a tissue-thin, transparent aura within which the tenant could be seen skillfully weaving its own shroud.''

2. Biology

Army ant colonies that are functionally normal always contain developing brood. In species with regularly alternating nomadic and statary phases, it is evident that the brood are produced on a periodic schedule. Larvae are present in the nomadic phase, a period characterized by elevated colony activity, and pupae are present in the statary phase when colony activity is low (Schneirla, 1971). In studies regarded by many as ethological classics, Schneirla (1933, 1938) determined that it was the larvae that somehow energized the colony to the activity level of the nomadic phase and that it was the inertness of the pupae that produced the depressed activity levels of the statary phase (Fig. 10).

All-worker broods that normally appear in a cyclic sequence are occasionally interrupted by a sexual brood that also has a profound influence on the colony via the process of colony division. In the family Formicidae, the dorylines certainly produce the largest all-worker broods per colony. These range from 30,000 individuals in *A. laeviceps* (Schneirla and Reyes, 1966) to 1,500,000 in *D. (A.) wilverthi* (Raignier and van Boven, 1955). The polymorphism evident in the brood of all genera except *Aenictus* is a function of

Fig. 10. Functional cycle of group A dorylines. Eggs are deposited by the queen during the statary phase. These hatch and develop as larvae during the latter one-half of this phase and the entire nomadic phase. Pupation of these larvae triggers the beginning of the statary phase. During the statary phase these pupae continue to develop. Their emergence as callow workers stimulates the start of the next nomadic phase. Note that two sets of brood are present during the statary phase, one consisting of eggs and young larvae and the other of pupae.
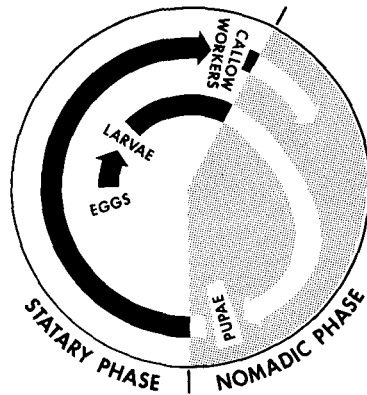
nongenetic factors that include trophogenic effects, stimulative effects of the workers on the larvae, "incubative" factors, and the physiological condition of the queen at the time of egg laying (Schneirla, 1971).

From his observations, Schneirla (1938) developed the concept of a brood-stimulative theory of army ant cyclic activity. Initially working with *Eciton,* he demonstrated that the nomadic phase begins with the emergence of callow workers from their cocoons which has a stimulatory effect on the colony. Colony activities in this phase are characterized by a nightly emigration from one nesting site to another preceded by almost frenzied foraging. During the nomadic phase, the queen is contracted and the larvae stimulate, on a sustained basis, the level of activity typical of the phase. This phase ends and the statary begins with maturation of the larvae. At this time of low brood stimulation, daily emigrations cease and the queen achieves full physogastry. At the middle of the phase, she deposits a single series of eggs that constitute a unitary population. Larvae hatch from these eggs prior to the emergence of the callow workers that will stimulate the next nomadic phase. Thus two brood populations overlap one another in time and space. These well-marked functional cycles have been identified in at least some species of *Eciton, Neivamyrmex,* and *Aenictus.*

However, in *Dorylus,* and perhaps in numerous species in the other genera, the functional cycles are irregular at best and probably not even homologous to those investigated by Schneirla. Although Raignier and van Boven (1955) found that emigrations in *D. (A.) wilverthi* can be initiated by the eclosion of callow workers, 6–40 day intervals separate emigrations. *Anomma* driver ants do not follow a functional cycle of alternating nomadic and statary phases. In fact, they appear to exist in successive "statary" phases separated by emigrations that may last for 2 or 3 days or even longer. Indeed, Raignier and van Boven (1955) recorded one intermigratory interval for *D. (A.)*

nigricans of 125 days. Thus the influence of brood on the nesting and emigration behavior of *Dorylus* may be far less significant than it is in *Eciton*.

The periodically produced sexual broods of army ants are evidenced by an occasional mass exodus of alate males from the nest. Male emergences of this kind have been recorded for *Dorylus* (Mayr, 1886; Brauns, 1901), *Eciton* (Rettenmeyer, 1963b; Schneirla, 1971), and *Neivamyrmex* (Gallardo, 1915; Bruch, 1923) among others. In two species of *Eciton*, Schneirla and Brown (1952) found that "fertile individuals" are produced in distinctive annual broods. In *E. hamatum* a mature sexual brood may contain, for example, only six new queens but as many as 1500–2000 males. Schneirla and Brown (1952) believed that the trophallactic relationship between the workers and the sexual brood is more intensive than it is between workers and an all-worker brood.

In *Eciton, Neivamyrmex,* and *Aenictus,* the onset of dry weather in areas with distinct seasonal changes may stimulate the production of sexual broods (Schneirla, 1971). Although Schneirla (1971) convincingly argued his "dry-impact" hypothesis for the initiation of sexual broods, Rettenmeyer (1963b) pointed out that all colonies of *E. hamatum* in the same locality do not produce sexual broods at the same time nor in the same dry season. In fact, he noted that some species of *Eciton* actually produce sexual broods in the rainy season. Schneirla (1971) surmised that the abrupt environmental change represented by the onset of the dry season radically affects the reproductive physiology of the queen. The physiological changes thus wrought can inhibit the process of fertilization and establish the pattern for sexual broods. However, the first group of eggs in a sexual brood series are deposited before the mechanism inhibiting fertilization is fully operative. These eggs are fertilized and are destined to become new queens. A second set of eggs in the series goes unfertilized and will produce the males which are haploid. Schneirla (1971) postulated that a third series of eggs, also unfertilized, might be laid and later used to feed the newly hatched queen larvae. The number of eggs laid in a sexual brood series may initially approximate the number produced in an all-worker series, but perhaps for a variety of reasons the number of sexual brood eggs is substantially reduced (Schneirla, 1971). Therefore sexual broods are small and individuals are assured greater attention and heavier feeding from the workers than is the case in all-worker broods where the sheer numbers of individuals guarantee intense competition for food. Flanders (1976) hypothesized that the physiological change induced by the dry season and responsible for the inhibition of fertilization is "simply the lack of sperm gland stimulation," i.e., the failure of sperm-activating secretions to be produced by the spermatheca. To explain the presence of sperm that fertilizes the first set of eggs, he suggested that some sperm remains in the coils of the spermathecal duct between broods. This residual sperm is reproductively impor-

tant only when egg deposition occurs during the dry season and spermathecal activity is inhibited (Flanders, 1976).

In *Anomma,* sexual broods can appear during any season of the year, although they appear with greater frequency during the last third of the dry season (Raignier and van Boven, 1955; Raignier, 1959, 1972). Male brood can number from 200 to 3400 individuals per nest, while the maximum number of queens ever observed in one nest was 56 (Raignier, 1959). As in *Eciton,* the *Anomma* male and queen larvae enjoy greater attention from the workers which includes over-feeding. Developmentally, however, the queens are approximately 10 days ahead of the males and are already adults when the males are reaching the pupal stage (Raignier, 1959). Males may appear in worker broods.

V. BEHAVIOR OF ARMY ANTS

A. Pheromonal Communication

1. Trail Pheromones

Given the fact that a majority of army ant species are blind and that the remainder are nearly so, pheromonal communication along with tactile stimuli assume added importance in the biology of these ants (Topoff and Lawson, 1979). In no instance is this more pertinent than in trail following where visual orientation, except perhaps to light intensity, is at best of little significance. As Blum (1974) noted, odor trails are an effective method of coordinating the movements of groups and individuals. Furthermore, in few colonies of ants are there more reasons than in the dorylines, with their extraordinarily large colonies, to effectively organize the workers into a cohesive, moving force. After all, other ant species do not combine group predation and nomadism to the extent that the army ants do, and both activities require an exceedingly sophisticated system for group organization and orientation.

Watkins (1964) concluded that trail substances in *Neivamyrmex* may be contained in the feces, perhaps even added to the feces by some hitherto undescribed glands. In *Eciton,* the hindgut was similarly implicated as the source of trail pheromone (Blum and Portocarrero, 1964). However, the specific source is unknown. Although the pheromone in *Eciton* may be produced by specialized gland cells in the digestive tract, circumstantial evidence indicates that this substance may in fact be a digestive product. There may be more than a single source for trail substances, at least in *Eciton.* For example, *E. burchelli* workers whose gasters have been removed and whose petioles are sealed with wax are still capable of laying a trail that elicits trail-following behavior. However, the substance responsible for this trail, perhaps a "foot-

print'' secretion, is probably not a true pheromone since it is of short duration (Torgerson and Akre, 1970a,b). After examining trail following in *Neivamyrmex nigrescens,* Topoff and Mirenda (1975) concluded that "it is not surprising that the ants can utilize not only the non-volatile and volatile components of the chemical trail deposited from the hindgut, but other chemicals secreted from the surface of the ants' bodies." The sources of trail substances in *Aenictus* and *Dorylus* have not been determined.

The functional duration or stability of army ant trails, at least in the genus *Eciton,* depends on four factors: (1) the nature of the substrate, (2) the kind of trail laid (foraging versus emigration), (3) the amount of precipitation that falls on the trail, and (4) the lifeway of the ant producing the trail (i.e., whether the ant is surface-adapted or subterranean). Trails are more stable when established on "porous substrates with many adsorptive sites such as roots, logs and lianas" and less persistent on soil and leaf-litter surfaces. Emigration trails are more stable than are foraging trails but this stability may result from the fact that a greater number of workers are involved in establishing emigration trails and that emigration trails are used for a longer period of time. Trails are less persistent when subjected to rain, and once a trail is wet, the workers encounter considerable difficulty in sensing the trail. Surface-adapted species apparently establish trails that are significantly more durable than those created by subterranean species (Torgerson and Akre, 1970a). Increased trail stability certainly seems advantageous to surface-adapted species, since their trails are more vulnerable to the effects of air currents, humidity, rain, and solar light and heat.

The chemistry of doryline trail substances is unknown, except that, for the social Hymenoptera in general, trails are "usually generated with a mixture of compounds" (Blum, 1974). Laboratory experiments on the *Eciton* trail substance have demonstrated its stability, low vapor pressure, and water insolubility.

A lack of trail odor specificity is apparently common among the ecitonines. Watkins (1964) demonstrated that three species of *Neivamyrmex* followed each other's trails. In fact, two of the species followed trails prepared from 70% alcohol extracts of whole workers of *Eciton dulcius.* However, this promiscuity in trail following did not extend to extracts prepared from nondoryline ants. Males of *N. opacithorax* followed the trails of all three *Neivamyrmex* species, and *Neivamyrmex* queens of two species also followed the trails of other congeneric species (Watkins, 1964). Although Watkins *et al.* (1967a) showed experimentally that the trails produced by four species of *Neivamyrmex* and *Labidus coecus* elicited trail following by all five species, they did note that some species preferred trails laid by conspecific workers. This indicates that trail substances vary from species to species and that workers can detect these differences. However, the lack of specificity

among army ant trail substances is not universal. In the laboratory studies of Watkins *et al.* (1967a), *Neivamyrmex pilosus* did not readily follow the trails of other species. Torgerson and Akre (1970b) also noted that although army ants can detect interspecific trails, the trail-following behavior elicited is variable. They hypothesized that trail following involves two chemical components, one which serves as a general releaser and to which all ecitonines respond, and another which is genus- or species-specific and results in sustained trail following.

Intraspecific subcaste and age differences in trail following behavior were investigated by Topoff *et al.* (1972a,b, 1973). Although callow workers of *Eciton* have the same relative ability to detect and follow conspecific trails as do the mature adult workers, their running speed along the trails is significantly slower (Topoff *et al.*, 1972b). Topoff *et al.* (1973) proposed that major workers of *Eciton* are less responsive than small workers to trail substance and that in the field major workers are more prone to leave trails than are smaller workers, particularly when disturbed. Experimental data revealed that differences between major and intermediate-sized workers in trail following performance are not significant. Topoff *et al.* (1972b) hypothesized that the readiness with which the major workers left a trail and approached sources of disturbance is attributable to the differences in sensitivity of major workers to other compounds, in this case, alarm substance.

A veritable menagerie of arthropods are known to follow army ant trails (Rettenmeyer, 1962a), and in fact, interordinal trail following includes vertebrates as well, since certain species of blind snakes have also found an adaptive advantage in detecting and following the pheromonal trails of doryline ants (Watkins *et al.*, 1967b, 1969, 1972; Gehlbach *et al.*, 1968, 1971; Brown *et al.*, 1979). Myrmecophilous species of millipeds (Rettenmeyer, 1962b), mites (Akre and Rettenmeyer, 1968), thysanurans (Rettenmeyer, 1963a; Torgerson and Akre, 1969), phorid flies (Rettenmeyer and Akre, 1968), sphaerocerid flies (Richards, 1968), beetles of the families Histeridae (Akre and Rettenmeyer, 1968), Staphylinidae (Wasmann, 1904, 1917; Patrizi, 1948; Paulian, 1948; Seevers, 1965; Akre and Rettenmeyer, 1966, 1968; Akre and Torgerson, 1968, 1969; Kistner, 1976) and Carabidae (Plsek *et al.*, 1969; Topoff, 1969), and diapriid wasps (Masner, 1976, 1977) are all capable of following the chemical trails of army ants.

Blum (1974) pointed out that although ants use "subtle blends of exocrine products" to insulate their trails from a majority of other ant species, they have not been able to deter unrelated animals from using their trails. Furthermore, many myrmecophiles are proficient in detecting species-specific differences in doryline trails and apparently respond more frequently to these differences than do the army ants themselves (Akre and Rettenmeyer, 1968).

The ability of myrmecophiles to follow chemical trails is, for the most part,

of some detriment to the army ants. Although dorylophilous millipeds and phorids function primarily as scavengers on organic debris in and around the ant nest (Rettenmeyer, 1962b; Rettenmeyer and Akre, 1968) and the thysanurans appear to feed mainly on surface secretions and particles scraped from the bodies of the adult ants and their brood (Rettenmeyer, 1963a), the coleopterous dorylophiles feed on army ant prey and brood. For example, in laboratory colonies staphylinid beetles feed on both prey and brood (Akre and Rettenmeyer, 1966; Akre and Torgerson, 1969). However, although the staphylinid genus *Diploeciton* is recorded in the field to feed on army ant brood, Akre and Torgerson (1969) surmised that "in nature," staphylinids may feed almost exclusively on prey returned to the nest. Carabids of the genus *Helluomorphoides* also prey on army ant brood and occasionally on the adults (Plsek *et al.,* 1969). Watkins *et al.* (1967b) theorized that the blind snake *Leptotyphlops dulcis* enters raiding columns of *N. nigrescens* and is subsequently able to locate the nest and feed on the brood and possibly prey. Curiously, the indigenous peoples of the Usambara Mountains of Tanzania report that blind snakes of the genus *Typhlops,* which they call mkonko, are often seen slithering along in the columns of *Anomma* driver ants (Loveridge, 1949). They refer to the snake as the "cow" of the ants that the ants keep until there is a food shortage, whereupon they kill and devour it. It would seem that once the snake reaches the *Anomma* nest the reverse is true.

In all of these instances, trail following is essential for the myrmecophiles either to gain entry to the ant nest or to maintain a more or less permanent association with a particular colony. It would not be imprudent to conjecture that army ants that can insulate their trails from myrmecophiles are being selected for.

2. Recruitment Pheromones

Recruitment of sister workers to a food source by foragers that discover the source is common among ants. However, until recently this phenomenon was not sufficiently documented in army ants. Chadab and Rettenmeyer (1975) discovered that *E. hamatum* and *E. burchelli* workers lay down recruitment trails that are qualitatively different from foraging trails. After being exposed to a food source, a recruiting worker returns to the foraging column, intermittently dragging her gaster on the substrate as she goes. When the recruiter reaches the foraging column, she runs 5–10 cm in each direction in the column, contacting workers with her antennae and body. She returns to and runs along the recruitment path periodically, and in doing so contacts new workers and reinforces the trail. Within 30 sec, workers from the column are diverted to the recruitment trail, and in the first 5 min, 50–100 workers are recruited. Some of the recruited workers in turn recruit new workers to the scene in a

process Chadab and Rettenmeyer called "secondary recruitment." Although there is a recruitment message in the recruitment trail substance, the effectiveness of the message is enhanced by recruiter behavior. Field experiments led Chadab and Rettenmeyer to conclude that (1) recruitment pheromone is either an entirely different substance from foraging trail substance or it is a combination of hindgut material and a substance from some other source; (2) the army ant recruitment system, "in terms of gathering large numbers of workers quickly," is among the most efficient in the ants; and (3) the "combination of continuous foraging columns, a recruitment trail that attracts and orients workers, secondary recruitment, and persistent recruiters results in the efficient gathering of the large attack force essential for army-ant raiding."

Laboratory experiments with *Neivamyrmex nigrescens* (Topoff *et al.,* 1980b) have confirmed the existence of a recruiting trail pheromone that is qualitatively different from the ants' exploratory trail pheromone. This recruitment pheromone alone is apparently sufficient enough to initiate mass recruitment equal to that brought about by recruiting workers that interact tactually with nestmates.

3. Alarm Pheromones

Releasers of alarm behavior in the doryline ants have not been chemically isolated or identified, although the existence of such substances is not in doubt. In the Formicidae, alarm pheromones are generally produced by the mandibular glands (Blum, 1974). Brown (1960) first demonstrated that alarm pheromone in *Eciton, Nomamyrmex,* and *Labidus* is produced in the head. The crushed head of a worker dropped into a column of workers elicits attack behavior during which the workers bite and attack the head, while crushed, headless bodies of workers attract only momentary attention. In *Eciton* and *Nomamyrmex,* the crushed worker heads emit a "meaty" odor that Brown (1960) assumed to be associated with the alarm substance. Inanimate objects, such as twigs, rubbed against the crushed heads also elicit attack behavior when placed among the workers. Brown speculated that workers emitting alarm pheromone are not themselves attacked by sister workers, either because the workers normally give off lesser amounts of alarm substance than is released by the crushed heads or because the worker also secretes, from its alitrunk or gaster, a substance that neutralizes the attack behavior of its nestmates. In the latter case, the substance might be an "identification pheromone" or a "nest odor" (Brown, 1960).

Torgerson and Akre (1970b) repeated some of Brown's field experiments and found that ecitonine alarm pheromones are more specific than is the case, for instance, in the Formicinae. While the crushed heads of *E. burchelli*

elicited alarm behavior from *E. hamatum,* and those of *E. hamatum* stimulated such behavior in *Nomamyrmex esenbecki,* reciprocal tests did not; *E. mexicanum* and *E. vagans* did not react at all interspecifically.

4. Queen Odor

Army ant workers are no doubt attracted to their queen and recognize her odor. Although the source of the odor remains to be identified, evidence of this attraction can be seen in *Eciton* where the queen is surrounded by a cluster of small workers in the undisturbed nest or bivouac and by larger workers when the nest is disturbed. In an emigration column, she is always accompanied by a retinue of workers (Rettenmeyer, 1963b; Schneirla, 1971). In the laboratory, if an *Eciton* worker is taken from a dish with a queen and added to a dish containing workers without a queen, the latter workers become greatly excited, apparently because the added worker carries with it some queen odor (Rettenmeyer, 1963b). Specifically, the workers are attracted to the anterior portion of the queen's gaster and rarely to her mouthparts or anal region (Schneirla, 1949; Rettenmeyer, 1963b). Laboratory experiments with five species of *Neivamyrmex* and one species of *Labidus* demonstrated that workers prefer secretions of their own queen over those of queens from other conspecific colonies and that although workers are attracted to the secretions of queens of other species, they are most attracted to conspecific queens (Watkins and Cole, 1966).

B. Mating Behavior

Mating in army ants has seldom been observed or recorded. Smith (1942) reported that a mating pair of *Neivamyrmex carolinensis* was found in a nest in 1932 and constituted the first such observation for army ants in the United States. Mating in *E. hamatum* has been observed twice (Schneirla, 1949) and in *E. burchelli* once (Rettenmeyer, 1963b). Matings in Old World dorylines have not been described. Schneirla (1971) suspected that in *E. hamatum* "the leading callow queens" (i.e., those that eclose first from the pupa and around which a new colony, as a result of fission, forms) are inseminated in or near the nest of the parent colony within a few days after they eclose or in the early part of the first nomadic phase of their new colony. Raignier and van Boven (1955) noted that queens of *Anomma* are fertilized many times during their lives and that they may even be inseminated by males of different subgenera. Intersubgeneric copulation and the subsequent "loss" of male gametes is reproductively inefficient and difficult to explain. Schneirla (1971), for instance, hypothesized that the male must be dealate before mating is possible and that once dealate, it must live for a period of time in its adoptive colony and acquire the colony's odor before being accepted by the queen and that,

after becoming habituated to the host-colony odor, it will mate only with a queen bearing that odor.

Because both matings in *E. hamatum* observed by Schneirla (1971) occurred after the ants were captured and consequently excited, he speculated that matings in nature may occur not in the nest but rather during emigration since it "presents intervals of excitement with opportunities for union when a dealate male nears the queen as she pauses at an obstacle or enters a new nest." In the first coupling he observed, the male was oriented over the queen's dorsum with its mandibles securely locked about one of her petiolar horns. Insertion of the male genitalia in the queen occurred with such penetration that the queen's gaster was considerably deformed as a result. While the male appeared "lethargic," the queen moved about the enclosure carrying the male with her. They remained in copula for 2 hr. The second coupling, between a different pair, lasted 10 hr and ended with the male apparently entering the first stages of death. An examination of the queen's spermatheca revealed the presence of several "ball-like" masses of sperm, but the ovarioles contained only immature eggs.

The *E. burchelli* mating occurred between a previously fertilized queen that was more than 1 year old and a dealate male, both of which were taken from the same emigration column and placed together in a petri dish. They remained in copula for 1 hr. The male held the queen with its middle and hind legs and grasped the queen's petiole with its mandibles posterior to the horns. It did not grasp the horns as was observed in *E. hamatum*. The *E. burchelli* mating lends support to Raignier and van Boven's claim that army ant queens mate more than once during their lives.

C. Foraging Behavior

1. Group Predation

Group predation enables species to exploit as food sources other social insects and large arthropods (Wilson, 1958a). In each case it is the collective efforts of cooperating foragers that permits these species to enter and ravage the vigorously defended nests of termites, wasps, and ants or to physically overwhelm prey larger than themselves. These are prey not ordinarily available to solitary foragers. Group predation also increases the efficiency with which a colony can flush and capture prey. This is particularly important for army ant species that function as general predators. Group predation combined with nomadism, which permits colonies to periodically shift trophophoric fields, makes possible exceptionally large colonies like those achieved in some species of *Anomma* (Raignier and van Boven, 1955). As defined by Wilson (1958a), group predation must include two components: group raiding and group retrieving of living prey.

2. Group Raiding

a. Column Raids.   Schneirla (1934) discerned two types of raiding (or foraging) patterns in army ants: column raids and swarm raids. These patterns are species specific, although gradations between the two patterns are evidenced in some species such as *Labidus coecus* (Rettenmeyer, 1963b). A column raid consists of a system of branching columns of foraging workers that diverge from a single base or trunk column that connects the nest with the foraging sector. Each of the branching columns usually terminates in an advancing group of workers that push forward into new territory with their antennae actively playing over the substrate and objects before them. At the same time, the trails over which the advancing columns move are chemically laid and augmented by the workers as they touch their gasters to the substrate. Membership in the advance guard of the terminal groups constantly changes as workers push forward and then retreat, only to be replaced by other workers that behave in the same way (Schneirla, 1934). In other words, there are no trailblazer specialists. The direction that each of these terminal groups takes is determined by the momentum of newly arrived workers and by topographical features.

As raiding continues, trails to prey-depleted areas are abandoned. However, one advancing trail is usually maintained, and this gives rise to new branches farther along as other previously established trails are vacated. Thus the one continuing base column grows progressively longer. "In this manner the typical fan-shaped complex of moving ant columns is moved forward" (Schneirla, 1934). Terminal raiding groups can advance rapidly, as much as 20 m/hr in *E. hamatum,* and to considerable distances, as far as 350 m in the same species (Schneirla, 1971).

The organization brought to column raiding ranges widely from the simplest of doryline systems, as exemplified by *Aenictus,* to the complex, specialized raids of *E. hamatum,* with species like *Neivamyrmex nigrescens* and *Nomamyrmex esenbecki* organizationally somewhere in between (Schneirla, 1971). In the Asian species *A. laeviceps,* the base column is 1–5 workers wide and often extends as far as 20 m from the nest. The terminal groups may range in width from a few centimeters to a few meters (Schneirla and Reyes, 1966). Foraging columns in some African species of *Aenictus* are weakly developed, consisting of small groups of 3 or 4 workers, running together in single file. These groups are often widely separated but all follow precisely the same trail, revealing its chemical basis (Gotwald, 1976). Rettenmeyer (1963b) noted that the column raider *Neivamyrmex pilosus* travels over its foraging trails in a similar manner, i.e., its workers move along in "spurts" with gaps between individuals and groups of individuals. The complexity of *E. hamatum* raids is evinced by the fact that this species usually develops three systems of trails on any one foraging expedition (Schneirla,

1971). The complexity and "strength" of a raid vary with the functional cycle of a colony. That is, in species with alternating nomadic and statary phases, such as *E. hamatum,* the workers conduct their heaviest, most complex raids during the nomadic phase when workers are most excitable (Schneirla, 1971).

b. Swarm Raids. In a swarm raid, the base column divides in the raiding area into a series of anastomosing columns that coalesce to form a single, advancing swarm of workers. These swarms in *E. burchelli* are commonly over 5 m in width and occasionally surpass 15 m (Schneirla, 1971), while in some species of *Anomma* they are likely to be 20 m or more in width (Kistner and Gotwald, 1982). In *E. burchelli,* the advancing swarm proceeds by alternate flanking movements, i.e., the swarm swings in its movement first to one side and then to the other. This is responsible for the meandering course that the base column takes as it lengthens behind the advancing foragers (Schneirla, 1934). Schneirla (1971) considered these flanking movements to be superior in organization to the advances of other swarm raiders and that they permit *E. burchelli* to better hold a single direction of advance than can *Anomma* and *Labidus praedator* (for a description of foraging behavior in *L. praedator,* see Fowler, 1979). Swarm behavior was considered by Schneirla (1940) to be a "highly complicated and variable phenomenon," although the organization of swarm activity rests on certain stereotypical responses of individual workers during raiding. He listed three individual behavior patterns that occur during swarm activity: (1) a "track phase" during which a worker runs rapidly over a chemically-saturated trail, (2) a "pioneering phase," in which the worker encounters chemically unsaturated terrain and reverses direction after a short advance, and (3) a "retreat phase" when the worker returns to the swarm and is directionally reoriented.

In *Anomma,* the raiding column swarm advances as rapidly as 20 m or more per hour. The raiding columns become so crowded with workers that they may achieve a density of 13 individuals per cm^2 (Raignier and van Boven, 1955) (Fig. 11A). The average length of the raiding column in *D. (A.) wilverthi* and *D. (A.) nigricans* is 125 m (Raignier and van Boven, 1955), although Leroux (1975) found that 63% of the raids of *D. (A.) nigricans* that he observed measured between 26 and 75 m. Raiding expeditions in *Anomma* commonly range from 9 to 27 hr in length (Raignier and van Boven, 1955; Leroux, 1975, 1977b).

A comparison of the two types of raiding systems reveals two strategies, one in which a series of terminal raiding groups forage over narrow strips of substrate (column raiders) and the other in which a single mass of workers sweeps across a wide area of substrate (swarm raiders). Intuitively it would appear that the latter strategy is most adaptively significant for the general predator, since it provides a mechanism for flushing simultaneously a taxonomically diverse group of prey.

c. Search Activities. While the discovery of prey by foragers is, in part, fortuitous, workers do respond positively to the movements of potential prey, perhaps through the detection of substrate vibrations. Prey odors are no doubt also important cues, but so are the odors of the excited foraging workers themselves, possibly via recruitment and/or alarm pheromones. Schneirla (1971) noted that column raiders are not as responsive to prey movements as are swarm raiders, and that they respond first to prey odors. Indeed, Rettenmeyer (1963b) noted that the swarm-raider *E. burchelli* was so responsive to movement that the raiding workers would attack even a blade of grass, if it moved. He found as well that some arthropods escaped being killed by these workers when they remained motionless.

In *E. hamatum,* the advancing workers "probe the surface and low vegetation, prying beneath surface cover and into insect burrows and other niches" (Schneirla, 1971). Rettenmeyer (1963b) found that *E. hamatum* workers run primarily on the ground and leaf surfaces, and although they climb vegetation and buildings, they rarely go beyond 2 m above the ground. This contrasts markedly with some *Anomma* species that are known to forage in trees to heights of more than 3 m (Raignier and van Boven, 1955; Gotwald, 1972a) and with *E. burchelli* which may raid into the tops of trees (Rettenmeyer, 1963b). In *Anomma,* at least, workers foraging on low vegetation to 1 m or more in height habitually drop to the substrate at the conclusion of their search activities instead of climbing back down. This creates a sound that resembles a light rain shower, as the workers strike the substrate surface. Their behavior probably functions to reduce the energy expended on search activities (Kistner and Gotwald, 1982). General search activities of some African *Aenictus* workers involves an apparent random meandering and an exploration of the soil surface as well as crevices and holes in the soil (Gotwald, 1976).

d. Swarm "Followers." Swarm raiders are not alone as they advance across the forest floor in their quest for prey. Indeed, they are frequently accompanied by animals that benefit from the ability of the raiders to flush from cover large numbers of arthropods. Most commonly, these swarm followers are insectivorous birds and parasitic flies.

Almost 150 years ago Lund (1831) noted, when observing army ants in Brazil, that "ces troupes des fourmis voyageuses sont constamment suivies par une bande d'oiseaux. . . " He further noted that one bird species "announce au loin par son crimonotone et lugubre la presence de ces troupes."

Fig. 11. (A) Raiding column of *D. (Anomma) nigricans;* (B) a major and media worker of *D. (A). nigricans* returning to the nest with prey (note that the workers straddle the prey); (C) an *Anomma* worker returning to the nest with prey. (Photographs by W. H. Gotwald, Jr.)

Thus detecting the presence of army ant swarms through the calls of attendant "antbirds" has long been a part of tropical forest lore. As Johnson (1954) noted,

> On a walk through the forest in tropical America, long periods may pass without the glimpse of a bird. Then, suddenly, all about one hears the chirring, twittering and piping of birds, and sometimes a dim murmur, as if a light [rain] shower were striking the leaves of the forest floor. This gentle pattering—it soon becomes clear—is caused by the frantic fluttering and hopping of countless insects trying to escape a swarm of raiding army ants...

The behavior of birds that follow or attend the swarm raids of the New World species *E. burchelli* and *L. praedator* was studied by Johnson (1954) and Willis (1960, 1966, 1967). These birds, e.g., the red-throated ant-tanager (*Habia gutturalis*) and the bicolored antbird (*Gymnopithys bicolor*), forage on the arthropods that so predictably flee the advancing swarm. Seldom do the birds take the army ants themselves. The presence of "professional ant-followers," such as bicolored antibirds, may also attract other birds to the swarming site, consequently a number of bird species are clearly opportunistic in taking ant-flushed prey (Willis, 1967). In fact, Willis (1966) found that even migrant bird species from North America (e.g., Acadian Flycatchers and Wood Thrushes) attend army ant swarms in the tropics. Noting the presence of "professional followers" and opportunists on Barro Colorado Island, Johnson (1954) defined the bird associations in the following way: (1) birds of the "feeding aggregations, whose association seemed wholly dependent on the feeding opportunities afforded by the army ant raids and which remained with the ants for long periods of time" (e.g., *Gymnopithys leucaspis, Hylophylax naevoides,* and *Formicarius analis*), and (2) birds of the "social aggregations, whose association was independent of army ant raids, but which would attend raids for varying periods of time" (e.g., *Dendrocincla fuliginosa, Dendrocolaptes certhis,* and *Microrhopias quixensis*). Willis and Oniki (1978) have reviewed what is known about the New World birds that follow army ant swarms.

Anomma driver ants attract a similar group of avian attendants (Bequaert, 1922). DuChaillu (1861) wrote of the behavior of one species:

> ... they fly in a small flock, and follow industriously the bashikouay [*Anomma*] ant in their marches about the country. The bird is insectivorous; and when the bashikouay army routes before it the frightened grasshoppers and beetles, the bird, like a regular camp-follower, pounces on the prey and carries it off. I think it does eat the bashikouay.

Some of these birds are from the genera *Alethe, Neocossyphus,* and *Bleda* (Bequaert, 1922).

Conopid flies of the genus *Stylogaster* and tachinid flies of the genera *Calodexia* and *Androeuryops* are commonly associated with the raiding

swarms of *E. burchelli* and *L. praedator* (Rettenmeyer, 1961). *Stylogaster* flies are parasitic on cockroaches driven from cover by the foraging workers. Darting at the arthropods fleeing the advancing swarm, these flies deposit eggs on the exposed cockroaches. *Calodexia,* on the other hand is larviparous and deposits larvae on its hosts. The *Androeuryops* flies are also parasitic, probably on arthropods flushed out by the ants (Rettenmeyer, 1961). In Africa, calliphorid flies of the genus *Bengalia* accompany the swarm raids of *Anomma* and steal prey directly from the workers. Lamborn (1913–1914) described the behavior of *B. depressa* as follows:

> Suddenly the fly rushed forward, and it must have driven its proboscis, which seems to me armed with strong bristles, into the pupa, for the ant was brought to a standstill with a sharp jerk. Then ensued a tug-of-war between ant and fly fastened on at opposite ends of the pupa, but neither had the advantage till, as it seemed to me, the ant must have got annoyed and loosening its hold rushed towards the fly, which of course instantly flew off with the pupa, and this it proceeded to suck on the ground about a foot away from the ants.

Stylogaster is also present around *Anomma* swarms and is parasitic on fleeing cockroaches, although it also parasitizes calypterate Diptera (Smith, 1967, 1969).

Certainly among the most surprising of swarm followers are several species of ithomiine butterflies. Drummond (1976) was the first to observe this puzzling association. He witnessed in the field six butterflies "flying low over the leading edge" of a swarm of *Eciton burchelli* but did not discover any functional reason for this association. He further noted the presence of antbirds foraging at the head of the swarm, and this observation was later to be seen as relevant to understanding this unusual association. Ray and Andrews (1980) have since shown that these butterflies feed on the bird droppings deposited by the antbirds. That is, the antbirds "provide a predictable source of droppings, an otherwise sparsely distributed resource."

Swarm raiders, their myrmecophiles and their "followers" constitute a complex and intricate balance of relationships that represents one of the most elegant coevolved systems in the tropics.

3. Hypogaeic and Epigaeic Foraging

A majority of army ants are subterranean foragers, although many will also forage beneath forest litter. Few chance to forage on the substrate surface exposed to solar light and heat and the evaporative effects of the air. Schneirla (1971) applied the term hypogaeic to species he regarded as subterranean and epigaeic to those that are surface adapted. However, he usually utilized the nesting behavior of species as a measure of their adaptation to a particular lifeway, essentially ignoring extranidal activities. In doing so, Schneirla failed to characterize accurately the composite nature of any one species' behavior.

In order to portray the biology of army ants precisely, the terms hypogaeic and epigaeic must be applied independently to the three basic components of army ant behavior: nesting, foraging, and emigration (Gotwald, 1978).

Although a majority of Old World dorylines are hypogaeic foragers, a significant number of species are not. Chapman (1964) considered five species of *Aenictus* in the Philippines to be epigaeic foragers. Raiding in two of these species, *A. gracilis* and *A. laeviceps,* was studied in detail by Schneirla and Reyes (1966). Most of the remaining Asian species and a clear majority, if not all, of the African species forage either hypogaeically or beneath forest litter, although raiding workers must sometimes surface to cross hardpacked footpaths and roads (Gotwald, 1976). Only one African species observed thus far may commonly forage exposed on the substrate surface (Gotwald, 1976).

Dorylus, in its numerous forms is also primarily a hypogaeic forager, although several species of *Anomma* are conspicuous exceptions and owe their sometimes exaggerated reputations to the fact that they commonly forage on the substrate surface. Epigaeic foraging in New World species appears to be less extraordinary than it is among Old World forms, but the literature is often vague in defining the nature of foraging in some of the New World species. Certainly the best known epigaeic foragers are *E. burchelli, E. hamatum,* and *N. nigrescens.*

In an analysis of nesting and foraging behavior in Old World dorylines, Gotwald (1978) placed species into one of three categories: (1) species in which nests and foraging are both hypogaeic, (2) those in which nests are hypogaeic and foraging is essentially epigaeic, and (3) species in which the nests are surface phenomena and foraging is epigaeic. He concluded that surface foraging from a hypogaeic nest is a relatively recent derivation from a totally hypogaeic lifeway and that surface foraging from a surface nest is the most recently derived army ant adaptation. This totally epigaeic life mode has been attained by only a few species and is especially evident in *A. gracilis, A. laeviceps, E. burchelli,* and *E. hamatum.* Because these species are so accessible, they are also the most thoroughly studied and understood, and yet, as Rettenmeyer (1963b) pointed out, these represent "the most highly specialized or atypical" army ant species. Therefore to extrapolate from our knowledge of these species conclusions about the biology of the more cryptic forms is unsound. Epigaeic foraging from a hypogaeic nest is strongly developed in *Anomma,* moderately so in *Labidus,* and weakly developed in numerous species of *Aenictus.* The primitive hypogaeic mode is maintained in some species of *Aenictus,* many species of *Dorylus,* in some species of Ecitonini, and most certainly in *Cheliomyrmex.* Gotwald (1978) speculated that selective pressures are operating on hypogaeic army ants to become surface foragers.

Raiding schedules are unrelated to whether or not a species is an epigaeic or hypogaeic forager. Surface-adapted species of *Eciton,* for example, have a

distinct diurnal routine, raiding from dawn until dusk, while *N. nigrescens,* also an epigaeic forager, raids from dusk to dawn. However, diurnal surface foragers are sensitive to daily rhythms in temperature change and exhibit a midday lull in foraging that Schneirla (1949) termed the "siesta effect." Common in *Eciton,* this effect has also been documented by Rettenmeyer (1963b). Raiding schedules may be quite flexible. Surface-foraging *Aenictus* may initiate raids at any time of day or night (Schneirla and Reyes, 1966). Raignier and van Boven (1955) reported that *D. (A.) nigricans* and *D. (A.) wilverthi* mount foraging expeditions at any time of day or night but show a preference for beginning in early evening and ending toward the middle of the following day. Leroux (1975) found that 68% of the raids of *D. (A.) nigricans* that he observed began during the cooler hours, between 1800 and 0800 hours. The hypogaeic foragers *L. praedator* and *Nomamyrmex* forage by day or night (Schneirla, 1971).

4. Group Retrieval of Prey

a. Prey Immobilization and Sectioning. After prey are captured by the foraging workers, they are immobilized, dismembered and sectioned (if they are large prey), transported back to the nest, and finally distributed to the nestmates.

Foraging workers bite their prey and in many instances also sting them. When large prey, such as scorpions, offer strong resistance to attack, they are "first pinned down by raiders anchored firmly by their tarsal hooks," and then are "spread-eagled by oppositely pulling groups" and torn apart (Schneirla, 1971). Earthworms are attacked in this manner by *Anomma* driver ants. While some workers anchor the earthworm in place (which is not an easy task), others tear small pieces of tissue from the captive (Gotwald, 1974b). New World species both bite and sting their prey, although the swarm raiders, *E. burchelli* and *L. praedator,* are considered more potent than column raiders in both respects (Schneirla, 1971). Even though *Dorylus* army ants possess a morphologically complete sting apparatus, they do not sting and instead rely exclusively on their ability to bite when capturing prey (Gotwald, 1978). Their sharp, cutting mandibles plus their great numbers permit them to kill and dissect even vertebrate prey that are not often attacked by New World species (Schneirla, 1971). The ability to sting is variable in *Aenictus.* While Schneirla (1971) found that Asian *Aenictus* possess potent stings and strong bites, Gotwald (1978) observed that African species do not readily sting.

Large prey organisms are usually sectioned before being transported to the nest, but even the smallest of prey may have its appendages torn from it, especially by *Anomma* (Gotwald, 1974a). A survey of prey unit size in *D. (A.) nigricans* conducted by Gotwald (1974a) revealed that the measured prey

units fell into two nonoverlapping size categories. All prey units from an-
nelids, arachnids, diplopods, insects, and snails measured between 0.1 and
1.5 cm along their longest axes, while chilopod prey units measured between
2.0 and 3.0 cm. He observed in the field that the long centipede prey units are
usually carried by two or more cooperating workers running in tandem. Other
less linearly shaped prey units are most often carried by individual workers
(Fig. 11B,C). Cooperating *Anomma* foragers straddle their centipede prey
just as do the workers of *Eciton* (Rettenmeyer, 1963b).

   b. Prey Transport to the Nest.   As a raid begins and progresses during its
early stages, worker traffic on the base trail and its branches is unidirectional
away from the nest. When the foragers encounter increasing numbers of prey,
traffic on the trails becomes bidirectional as prey-laden workers return to the
nest. Finally, as the raid diminishes in momentum and comes to a close, traffic
on the trails again becomes unidirectional, only this time toward the nest. This
temporal shift in the directional flow of workers has been documented for
Eciton (Schneirla, 1971), *Anomma* (Raignier and van Boven, 1955), and
Aenictus (Gotwald, 1976). In highly productive raids, particularly in *Eciton*
and *Aenictus,* large caches of prey are sometimes deposited at points where
columns branch from one another near the raiding area. This prey is later
returned to the nest (Rettenmeyer, 1963b; Schneirla and Reyes, 1966;
Schneirla, 1971).
   Labidus and *Anomma* commonly form walls and arcades that border and
cover their foraging columns. These are composed either of clustered workers
or of soil particles and pellets (Cohic, 1948; Raignier and van Boven, 1955;
Rettenmeyer, 1963b). Although this phenomenon may occur to an even
greater extent along emigration trails (Schneirla, 1971), these walls and ar-
cades, whether constructed of the workers themselves or of soil, probably
serve the same functions (Fig. 12A,B). Shade and perhaps increased humidity
are created by these structures, especially for the columns that cross open, ex-
posed surfaces. Further, the walls formed of clustered workers may serve to
keep itinerant arthropods and small vertebrates from accidentally straying
into the midst of the column and interrupting the flow of traffic. This author
has witnessed *Anomma* workers repel insects this way. Major workers often
assume a "defensive" posture when positioned at trail margins (Fig. 12C).
   The number of foraging workers returning to the nest with visible pieces of
prey is small in proportion to the total number of individuals that participate
in a raid. Raignier and van Boven (1955) calculated that 6–22% of the return-
ing workers of *D.* (*A.*) *wilverthi* carry prey and only 0.8–10% of the *nigricans*
workers do so. Gotwald (1974a) examined the crops of returning "preyless"
workers of *D.* (*A.*) *molesta* and found that most had liquid-filled crops. A
statistical analysis of prey-carrying and preyless workers disclosed a division
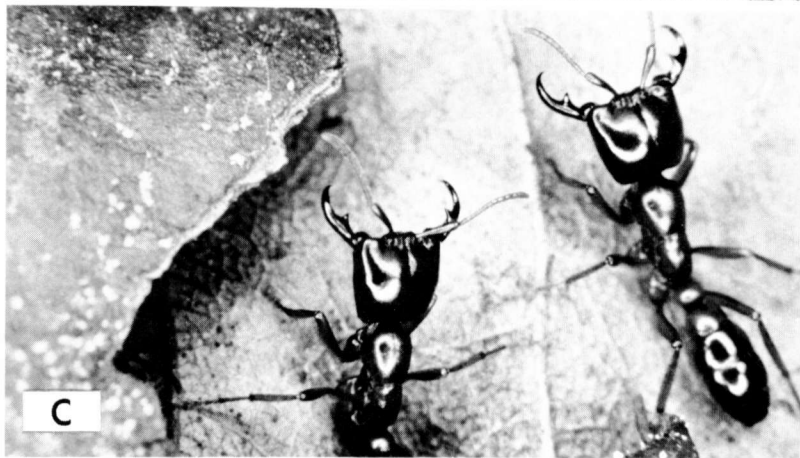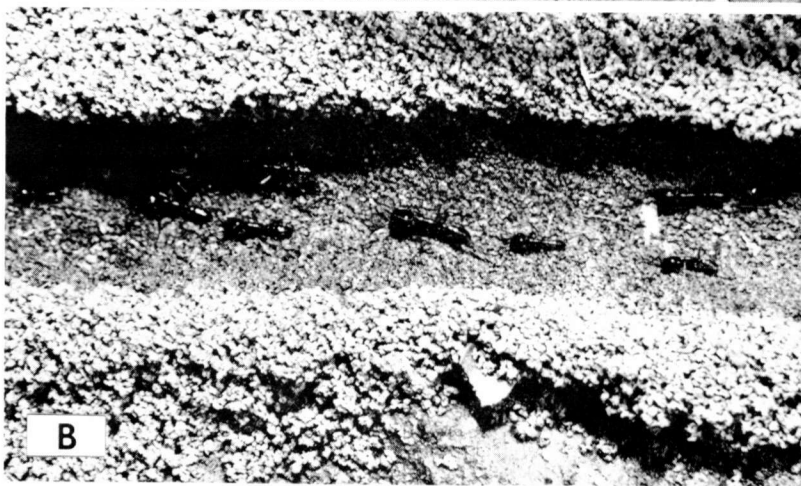
Fig. 12. (A) *Dorylus (Anomma) nigricans* foraging trail with conspicuous soil particle walls; note the workers on the trail; (B) as in A but at closer range; (C) *D. (Anomma) gerstaeckeri* soldiers in "defensive" posture. (Photographs by W. H. Gotwald, Jr.)

of labor corrlated with size: large workers most often carry prey units while smaller workers transport prey liquids.

c. Trophic Relationships within the Nest.   In terms of trophic relationship, the larvae are no doubt the focus of attention when foraging workers arrive at the nest with prey. However, it is not clear when, how, and what the adult workers themselves eat. Wheeler and Bailey (1925) suspected that *E. burchelli* larvae are fed at considerable intervals with large pellets composed of "the rolled up soft-parts of insects." They found these pellets so compact that they retained their shape even in the larval gut where they formed an "irregular longitudinal series." Because only occasional, minute, hard fragments occur in these pellets, Wheeler and Bailey (1925) concluded that the workers, when preparing these pellets, must trim away the hard, chitinous materials. They further surmised that the workers consumed the liquids expressed from the prey tissue when it was formed in the pellets. However, as the larvae grow larger, they also feed with their mouthparts applied directly to whole pieces of prey (Schneirla, 1971). Although army ant workers possess ovaries with maturing ova, it is not known whether the larvae consume worker produced eggs as happens in other ant species (Gotwald, 1971; Gotwald and Schaefer, 1982).

Schneirla (1971) noted that the larvae, through their movements and odors, attract the workers that both feed the larvae and "stimulate" them. In *Eciton*, as the larvae mature the workers become increasingly attentive and more frequently drop food on the larvae. At the same time, the larvae are more frequently carried and dropped by the workers on caches of prey in the nest (Schneirla, 1971).

5. Diet

a. Types of Prey Taken.   Dietary observations for army ants are often anecdotal, incomplete, and rarely quantified. Although some species may utilize plant nutrients, army ants are decidedly carnivorous. For the New World dorylines, ants rank as the most important and commonly taken food items. However, ecitonines do not take other ecitonines as prey (Rettenmeyer, 1963b). Only a few species appear to be generalists. One of these, *Labidus coecus*, "perhaps feeds on a greater variety of substances than any other species of Ecitonini" and takes ants, orthopterans, adult moths, homopterans, beetles, amphipods and spiders (Rettenmeyer, 1963b). Lenko (1969) observed *L. coecus* even attacking a Brazilian fresh water crab, *Trichodactylus argentinianus,* as it rested in its nonaquatic burrow. This species also takes a variety of plant products and is known to be attracted to walnut and pecan kernels (Wheeler, 1910), seeds, and cooked rice (Borgmeier, 1955). Another generalist, *E. burchelli,* takes, in decreasing

order of importance, ants, wasps (vespids of the subfamily Polistinae), Orthoptera, spiders, and scorpions (Rettenmeyer, 1963b). Most New World dorylines are specialized predators; *E. hamatum* capture ant and wasp brood and a few adult insects, and some species, such as *E. vagans, Nomamyrmex esenbecki,* and *Neivamyrmex pilosus* take almost exclusively ant brood (Borgmeier, 1955; Rettenmeyer, 1963b). *Neivamyrmex nigrescens* takes both termites and ants, with a decided preference for ants of the genus *Pheidole* (Mirenda *et al.,* 1980). Only one species, *Nomamyrmex hartigi,* consistently takes large numbers of termites as prey. *Neivamyrmex opacithorax* is unusual in that it feeds solely on ants and carabid beetles (both larvae and adults) (Rettenmeyer, 1963b). Wheeler and Long (1901) found a colony of this species in which the "workers had stored their nest with a considerable number of small carabid beetles that had evidently been captured on one of their marauding expeditions." Although Schneirla (1956b) noted that *E. burchelli* occasionally kills snakes, lizards, and nestling birds, Rettenmeyer (1963b) supposed that none of the New World dorylines kills vertebrates on a frequent basis. Rettenmeyer also noted that all of the New World army ants studied thus far kill many more arthropods than they can eat. The feeding habits of many of the more cryptic, hypogaeic species, particularly those belonging to the genus *Cheliomyrmex,* are unknown.

Dietary information on the Old World dorylines is so scattered and fragmentary that only a few of the more interesting observations can be cited here. Savage (1847) provided the first systematic description of *Anomma* behavior and listed as food sources for the driver ants, domestic fowl, lizards, snakes, fresh meat, and fresh oil, particularly of the oil palm, in addition to the usual bill of fare of assorted arthropods. Swynnerton (1915) investigated the food preferences of *D. (A.) molesta* experimentally but offered the foraging workers prey not normally available to driver ants. Some of the experimental prey he selected repelled the workers with defensive secretions. As for the "natural" diet of this species, Swynnerton (1915) listed such prey items as millipeds, ticks, and insects of the orders Orthoptera, Hemiptera, Coleoptera, Lepidoptera, and Diptera. The same east African species was recorded by Loveridge (1922) to capture grasshoppers, crickets, and pentatomoid bugs and to feed on a chamelion, geckos, a caged crocodile, and "eagle flesh" distributed as bait. Raignier and van Boven (1955) collected the prey of such general predator species as *D. (Anomma) burmeisteri, D. (A.) sjoestedti, D. (A.) terrificus,* and *D. (A.) wilverthi.* An analysis of their data (Gotwald, 1974a) revealed that 64% of the prey units collected were of insect origin, 16% from arachnids, 9.7% unidentifiable, 4.5% plant seeds, 3.6% from isopods, 0.7% from diplopods, and 0.5% from mollusks. Cohic (1948) noted that *D. (A.) nigricans* takes spiders, cockroaches (including oothecae), grasshoppers, crickets, and dipterous and ant pupae. In a quantitative study

of *Anomma* diet, Gotwald (1974a) determined that although these ants take a wide variety of invertebrates, insects comprise the largest portion of their diet. However, he concluded that this bias is more a reflection of insect abundance than it is an indication of food preference on the part of the ants. Earthworms and arachnids were the next most common sources of prey items. Much less is known about the hypogaeic species of *Dorylus*. While most of these species forage almost exclusively through subterranean galleries and beneath litter, they are attracted to vertebrate carcasses and meat baits on the soil surface (W.H. Gotwald, unpublished data). Certain of these species forage in compost heaps (Wheeler, 1910) and village trash deposits (W.H. Gotwald, unpublished data) for insect larvae. Some species of *Dorylus* are reportedly termitophagous. The subgenera *Typhlopone* and *Rhogmus* attack termites of the genera *Acanthotermes* and *Basidentitermes* respectively (Wheeler, 1936). Bodot (1961) observed *D. (Typhlopone) dentifrons* raiding the termitaria of *Bellicositermes natalensis* with devastating effectiveness. Some epigaeic foragers, such as *D. (A.) nigricans* also attack termites, though probably not often (Bequaert, 1913) and *D. (A.) wilverthi* destroys large numbers of swarming, alate males (Burgeon, 1942a).

Some *Dorylus* species also feed on plant materials, and Schneirla (1971) suggested that army ants that do so are usually hypogaeic species. Green (1903) reported that *D. (Alaopone) orientalis* in India feeds on potatoes, the tubers of dahlias, and the roots of the common sunflower and insisted that these ants are "confirmed vegetarians." Supporting Green's conclusion, Roonwal (1975) argued that *D. (A.) orientalis* is sometimes a serious pest of "vegetables, tubers, bulbs, shrubs, trees and . . . cash crops such as sugarcane, coconut palm, citrus and groundnut." *Anomma* driver ants commonly forage on fallen palm nuts (*Elaeis guineensis*) from which they remove the pithy outer covering, leaving the seed and numerous fibers behind (Gotwald, 1974a). *Dorylus (A.) nigricans* was observed to gather pieces of corn cob in a village refuse heap (Gotwald, 1974a) and *D. (A.) molesta* to take banana (Swynnerton, 1915).

African species of *Aenictus* studied thus far feed exclusively on ant brood. Prey collected by Gotwald (1976) from seven foraging columns of *Aenictus* yielded only ant larvae (36%) and pupae (64%). In fact, two *Aenictus* colonies that he observed displayed little or no hostility toward the adults of brood that the foragers carried away unchallenged. The prey adults abandoned their nest to the *Aenictus* foragers, although they remained close to the nest opening, slowly milling about the external features of the nests. Crawley and Jacobson (1924) made a similar observation of the Asian species, *Aenictus aratus,* when it attacked a nest of *Pheidole.* The *Pheidole* adults offered no resistance, but instead fled "with as many of their brood as they were able to save." Weber (1943) noted the prey of one colony of the African species *A. rotundatus* to be

ant brood of the subfamily Myrmicinae. Twenty-nine percent of the *Aenictus* prey collected by Gotwald (1976) belonged to the genus *Pheidole,* also a myr-micine ant. Chapman (1964) recorded that the Asian species *A. gracilis* and *A. laeviceps* feed primarily on ants (they take adults as well as brood) but also take a wide variety of other prey. Schneirla and Reyes (1966) confirmed Chapman's findings for these species, stating that the prey "may be described as almost any invertebrate that the ants can find and overcome, hunted down in crannies from the depths of the soil to the tops of tall trees." *Aenictus* species that are trophic specialists generally take prey that are approximately the same size as or smaller than the foraging workers themselves, whereas the general predators take prey of any size, subdividing larger prey into transportable pieces (Gotwald, 1976).

Army ants at times consume their own brood, but the extent to which cannibalism occurs and how important the brood are as a protein source are not known. Cannibalism of brood is common in ants, and the brood may in fact serve as an emergency food supply in times of food shortages (Wilson, 1971). After comparing the size of egg and young larval broods with the size of mature larval and pupal broods in *E. hamatum,* Rettenmeyer (1963b) noted a significant decrease in numbers of individuals over the time period during which maturation occurs and theorized that cannibalism of worker brood may be extensive. The cannibalism of sexual brood, particularly of potential queens, appears to be an important factor in the development and production of males and queens, particularly since it helps reduce the total number of immatures that must share the worker-supplied food (Schneirla, 1971).

The use of plant liquids as nutrient sources by doryline ants is problematic. Schneirla and Reyes (1966) observed instances when workers of *A. gracilis* and *A. laeviceps* gathered on plants, "clustering" near nectaries. Although nectar attraction has not been noted for other dorylines, Arnold (1915) recorded a report that the African species *D. (Typhlopone) fulvus* tended immature membracids feeding on the roots of maize. Similarly, Santschi (1933) noted that *Aenictus eugeniae,* an East African species, was once collected while tending a species of *Pseudococcus.*

b. Prey Determinants. A variety of factors combine to determine what the potential prey of army ants will be and whether or not these prey will actually be captured. Certainly army ant foragers, even the swarm raiders, are not as efficient in gathering prey as their reputations would have them be, i.e., that they capture and consume all living things in their path. Rettenmeyer (1963b) estimated that 30–50% of the arthropods attacked by *E. burchelli* escaped being killed and Schneirla (1945) noted that even when an *E. burchelli* colony stayed at a nest site for 23 days, the colony could not deplete the surrounding area of prey. He observed that (1) the colony incompletely covered

some sectors during foraging, (2) it entirely missed some sectors when forag-
ing, and (3) areas cleared of prey were quickly repopulated. Schneirla (1971)
reasoned that the dietary range of army ants was influenced primarily by (1)
the habitat, (2) worker structures, such as potency of the sting, (3) the
workers' chemotactic thresholds, (4) the species' raiding pattern and level of
excitability, and (5) the colony population itself, including colony conditions
and the degree of polymorphism present.

In a study of food preferences in three species of *Anomma,* Gotwald
(1974a) proposed that the habitat was the single most important factor in
determining the composition of *Anomma* diet. For example, earthworms
constitute a larger portion of *Anomma* diet in forest habitats than they do in
savanna, and this is directly related to the relative availability of earthworms
in these two ecosystems, not to the preferences of the *Anomma* foragers. The
influence of the habitat extends as well to the kind of insect prey taken. Got-
wald (1974a) further noted that prey vulnerability to *Anomma* attack must
strongly affect diet composition. A minimum of 61.8% of the insect prey
units collected from the foraging columns of 11 *Anomma* colonies were from
immature stages; 63.9% of the insect prey collected from 12 foraging
Anomma colonies were from holometabolous forms. The larvae of Diptera,
Coleoptera, Lepidoptera, and Hymenoptera (particularly the Formicidae)
are especially vulnerable to *Anomma* attack. Probably most arthropods that
escape army ant attack avoid capture by running, flying, or hopping away
from the foragers or by climbing vegetation (Rettenmeyer, 1963b; Schneirla,
1971). Adult polistine wasps detect foraging army ants by sight and odor and
flee their nest. Although the wasp brood cannot be rescued from the ensuing
attack, the adults can at least recolonize (Chadab, 1979). Some species of the
ant genus *Camponotus* evacuate their nests, carrying their brood with them,
when attacked by *Neivamyrmex nigrescens,* while other species defend their
nests through the recruitment of the major caste (LaMon and Topoff, 1981).
Some potential prey may employ specialized escape mechanisms. Ants of the
genus *Cryptocerus* (*Cephalotes*), for example, are so heavily armored that
they seem to be immune to attack (Schneirla, 1971). Another method of
escape effectively separates the prey from the predator by means of a slender
cord, a ''bridge'' that the foraging workers are unable to negotiate.
Lepidopterous larvae escape *Anomma* attack in this way, by dropping down
from the leaves of low vegetation, suspended on threads of silk (Swynnerton,
1915; Gotwald, 1972a). Gotwald (1972a) discovered that slugs (mollusks of
the order Pulmonata) employ an analogous method of escape from *Anomma*
foragers by suspending themselves from vegetation on a cord of integumental
slime. Spiders also drop down from vegetation on silken escape threads
(Swynnerton, 1915; Rettenmeyer, 1963b). Although poorly documented,
there can be little doubt that defensive secretions confer protection on a wide

variety of potential prey. Carpenter (1914–1915) observed a snail escape a driver ant attack when it withdrew into its shell and "produced a mass of bubbles of mucus which so completely surrounded it, shell and all, by a barrier about half an inch thick, that the ants could not get at any part of its body." Carpenter (1920) also witnessed an hemipterous bug repel driver ants, that tugged at its antennae and legs, with a "powerful odour" that "may have been disagreeable to the ants."

c. Trophic Specialists and Generalists. With the exception of the totally epigaeic forms, especially *A. gracilis* and *A. laeviceps, Aenictus* species are monophagous or oligophagous, specializing as predators of the immature stages of other ants (Brauns, 1901; Crawley and Jacobson, 1924; Sudd, 1959; Chapman, 1964; Gotwald, 1976). Most of these specialist species are, in turn, hypogaeic column raiders. Hypogaeic foragers of *Dorylus* are also specialists, primarily termitophagous and myrmecophagous, although some dietary departures have been recorded (Green, 1903; Lamborn, 1913–1914; Forel, 1928). All of these specialists are also column raiders and maintain hypogaeic nests. Although the nests of the social insects on which these *Aenictus* and *Dorylus* species prey are scattered about the trophophoric field, requiring a greater search investment on the part of the predator, they are an "exceptionally concentrated food source" and are well worth the energy expended in search activities (Carroll and Janzen, 1973). On the other hand, *A. gracilis* and *A. laeviceps* and other surface-adapted *Aenictus* are column raiders, frequently form surface-exposed nests, and are general predators, although they display a predilection for other ants (Schneirla and Reyes, 1966). Even though *Anomma* driver ants maintain hypogaeic nests, a number of species are epigaeic swarm raiders and general predators (Raignier and van Boven, 1955). Gotwald (1978) noted that these data suggest that epigaeic foragers become trophic generalists while hypogaeic foragers remain specialists. He also pointed out that it may be advantageous in tropical habitats for army ants to become epigaeic foragers since a concomitant development may include the qualitative and quantitative expansion of the diet. Since a taxonomically diverse prey is more uniformly distributed in the trophophoric field, less energy may be required of the predator in search activities. The polyphagous predator not only capitalizes on a diverse prey on a daily basis but can also exploit prey sources that are periodically abundant, such as emerging male termites (Gotwald, 1978).

In the New World army ants, the positive correlation between epigaeic foraging and dietary expansion is not as clear. *Eciton burchelli, L. coecus,* and *L. praedator* are evidently the most polyphagous of the New World species. *Eciton burchelli* forms a surface-exposed nest and is an epigaeic column raider. In contrast, *Labidus coecus* and *L. praedator* are both hypogaeic

nesters and both are swarm raiders, although Rettenmeyer (1963b) noted that
L. coecus is somewhat intermediate between column and swarm raiding.
Labidus praedator will raid on the substrate surface while *L. coecus* is more
negatively phototaxic. These two species behaviorly resemble some species of
Anomma. The epigaeic nester *E. hamatum* is an epigaeic column raider and a
specialist predator of ants and wasps. However, it does take other insects
(Rettenmeyer, 1963b). Other specialists such as *Nomamyrmex esenbecki* and
Neivamyrmex pilosus are column raiders and negatively phototaxic, although
they will forage on the soil surface.

From these facts and other data assembled by Rettenmeyer (1963b) and
Schneirla (1971), an evolutionary scenario can be constructed. Primitive
dorylines (i.e., those that have retained the ancestral life mode) are hypogaeic
nesters, hypogaeic column raiders, and specialist predators of social insects,
especially ants, wasps, and termites. There is a tendency for army ants to
become surface foragers and in doing so to expand their diet. However, if the
epigaeic forager retains column raiding, its dietary expansion is limited,
whereas, if the epigaeic forager becomes a swarm raider, its diet expands to in-
clude a wide variety of arthropods and even vertebrates. In some instances,
swarm raiding, at least to some extent, may evolve in species that often forage
hypogaeically. The most derived army ant lifeway is that in which the species,
in addition to being an epigaeic forager, also becomes an epigaeic nester. A
species that becomes totally epigaeic also develops a functional cycle of alter-
nating statary and nomadic phases. This has been achieved in so few species as
to be truly atypical for the army ants in general. With the acquisition of swarm
raiding and polyphagous feeding, plus occasional emigrations to new nesting
sites, extraordinarily large colonies, like those of *Anomma,* are possible.

6. Army Ants and Pest Control

The manipulation of ant populations in tropical agriculture is receiving at-
tention as a possible approach to integrated pest control, particularly in
tropical tree crops (see Leston, 1973). Army ants, especially those species that
are polyphagous, are obvious candidates for study in this respect.

Wellman (1908) considered *D. (A.) nigricans* of economic importance in
Angola, but primarily because as he explained, "careful housewives . . . wel-
come the approach of the ants and joyfully vacate for them the bungalow,"
for "after a column of 'army ants' has minutely explored a dwelling not a bug,
beetle, cockroach, mouse, rat, snake, or other pest remains behind." Dutt
(1912) remarked that *D. (Alaopone) orientalis* was a beneficial ant in India,
since it attacked and killed in large numbers *Pheidole indica* which he de-
scribed as an occasional nuisance. Burgeon (1924a) published some biological
observations on *D. (A.) wilverthi* and submitted that, "il est certain que ces
Fourmis rousses sont des utiles pour l'agriculture, detruisant foule d'insectes

nuisibles.'' Both Alibert (1951) and Strickland (1951) implied that driver ants might be beneficial in cocoa farming but offered no corroborative evidence. Gotwald (1974b) studied the foraging behavior of two species of *Anomma* in Ghana cocoa farms and discovered that these ants do not forage in the cocoa canopy, although they readily climb trees in other habitats. They are apparently repulsed in any attempt they might make to climb cocoa trees by dominant ant species in the canopy, such as *Oecophylla longinoda*. Although the effect of driver ants on the ground stratum fauna was not investigated, Gotwald concluded that driver ants were of little potential value in ant manipulation schemes to control cocoa pests, since they fail to have any visible effect on the composition of the canopy fauna.

In the New World, *Labidus coecus* is an important predator of the screwworm, *Cochliomyia hominivorax,* and other carcass-infesting, dipterous larvae. In fact, Lindquist (1942) concluded that the animals dying from screwworm infestations ''are the source of only a small emergence of flies during the warmer seasons of the year, chiefly because of the predatory actions of several species of ants.'' Ants effectively reduced the number of adult flies emerging from carcasses from about 93% to 4%, and *L. coecus* figured most importantly in this predatory control. Larvae dropping from the wounds of relatively healthy, ambulatory animals were also subject to intense ant predation but in this case, the role of *L. coecus* was not clearly delineated.

D. Emigration Behavior: Nomadism

1. Army Ant Nests

Theoretically, all army ant nests are temporary, since all army ants are presumably nomadic, but the frequency with which nest sites are abandoned by many species is unknown. Surely a majority of species occupy subterranean quarters, while a few maintain surface or above surface nests. Schneirla (1971) applied the term ''bivouac'' to all army ant nests and suggested that a bivouac was more ''the state of a colony'' than it was a physical place. However, many nondorylines also occasionally move from one nesting site to another (Wilson, 1971). What distinguishes army ants in this respect is that many of the better known species undertake emigrations with great frequency and regularity. However, recurrent and regular movement is by no means universal in the army ants, because even some surface-active species (e.g., *Anomma*) tend to move at irregular intervals (Gotwald and Cunningham-van Someren, 1982). Only in those species that have a distinct functional cycle of alternating statary and nomadic phases (e.g., *A. gracilis* and *E. hamatum*) are surface nests formed, and because these are hardly nests in the conventional sense, the name bivouac is appropriate. However, it is more descriptively accurate to restrict the term bivouac to these atypical surface formations and to

continue to apply the term nests to all situations where the nest indeed is a place, i.e., housed within the soil. This dichotomy in doryline nest formation was evident in Forel's (1896) classification of ant nests. He noted that some army ants have "earth nests" and others "migratory nests" and was unsure how to reconcile the two in what he considered to be a homogeneous and monophyletic group.

Raignier and van Boven (1955) found the subterranean nests of *Anomma* to be of two general types, one exemplified by *D. (A.) wilverthi* and other by *D. (A.) nigricans*. In the *D. (A.) wilverthi* type the entire colony population is clustered together in a central cavity, forming a compact mass in which a higher, presumably optimal, temperature can be maintained. The nest is 1-2 m deep. In the second or *D. (A.) nigricans* type, there is no central chamber; the colony members are dispersed in deep (2-4 m down) galleries and chambers, apparently without much control over nest temperature. The majority of both types of nests were located at the bases of trees, both living and dead, associated with the root systems, although the nests of *D. (A.) wilverthi* were also found in treeless, loose earth. No one species of tree was preferred for nest site locations, although nests were most often associated with living trees. In both types there may be surface manifestations of the nest in the form of craters composed of excavated soil particles. Leroux (1977a) noted, in a study of *D. (A.) nigricans* in savanna and gallery forest in Ivory Coast, that although a majority of nests are constructed at the bases of trees, 27 percent of the nests he examined were located in soil without a supporting network of roots. He observed that during the first week that a nest is constructed, as much as 20 kilograms of soil a day may be excavated. The location of the *D. (A.) wilverthi* queen in the nest is variable (e.g., she may be situated in the central group or in a lateral gallery), whereas the *D. (A.) nigricans* queen is typically lodged at great depth in the nest. The nests themselves do not appear to be highly organized structures, in fact driver ants use existing cavities in the soil where possible. Over a century ago, Savage (1849) wrote that the interior of the *Anomma* nest "exhibits no mechanical contrivance for the depositing of food, or hatching of eggs; for these purposes, spaces between the stone, sticks, etc., found within, are adopted." A nest of *D. (A.) nigricans sjoestedti* described by van Boven and Levieux (1968) departed from the *D. (A.) nigricans* type in three respects: it was shallow, only 60–80 cm deep; it had a large central cavity which was occupied by an enormous mass of workers; and it was not situated at the base of a tree or associated with a root system. The queen was found in the central cavity, to one side. Kistner and Gotwald (1982) also found that the *D. (A.) nigricans* nest had a central chamber. A nest of *D. (Typhlopone) fulvus,* described briefly by Normand (1931), consisted of a vaulted chamber, about 50 cm below the soil's surface, with numerous galleries leading from it in all directions, some extending deeply in the soil.

Normand communicated to Santschi (1931) that the chamber was filled with larvae, pupae, and workers, and that the queen was situated in the midst of the workers.

Most *Aenictus* species in both Africa and Asia are hypogaeic nesters, although their nests have yet to be described in detail (Gotwald, 1976). Menozzi (1936), for instance, located a colony of a new species, which he named *A. rhodiensis,* on the Island of Rhodes at a depth of 60–70 cm beneath a stone.

Some New World dorylines live in subterranean nests at some times and form bivouacs at other times. For example, *E. vagans* may form more or less exposed bivouacs, but more often than not lodges itself in underground or well sheltered nests (Rettenmeyer, 1963b). Rettenmeyer (1963b) found one colony of *E. vagans* clustered on small roots that traversed a subterranean cavity measuring 30 cm in diameter. This cavity, most likely not constructed by the ants themselves, was positioned 30 cm below the soil surface and gave rise to four principal galleries that descended into the soil to an unknown depth. Another colony formed a surface bivouac that was suspended from several support objects including a log, branch, and large rock (Rettenmeyer, 1963b). The nests of *L. coecus* may be located at great depths in the soil or they may be close to or on the soil surface but well sheltered. One nest found by Rettenmeyer (1963b) was fashioned in a decaying log. The eggs were concentrated in three long chambers, the cocoons situated primarily in a single, separate chamber, and the larvae were scattered throughout the nest in numerous chambers. The nests of *Neivamyrmex opacithorax* are hypogaeic as are those of *N. nigrescens.* In the *N. nigrescens* nest, a daily vertical migration takes place in which a portion of the colony's brood is brought to near the surface to a position beneath sun-exposed stones (Rettenmeyer, 1963b).

The nature of the bivouac or surface-exposed formation depends on the physiological state of the colony, i.e., on whether it is in the statary or nomadic phase. In the former phase, the nesting cluster is assembled in an enclosed or sheltered space where it remains for many days. In the latter, a new, exposed cluster is formed each night in a new location (Schneirla, 1971). Bivouacs in *E. hamatum* are seldom more than 1 m above the ground, whereas those of *E. burchelli* may be formed as high as 30 m above the ground in trees (Schneirla, 1971). A bivouac is formed essentially of the bodies of the ants themselves, suspended from a support object and from each other (for a discussion of the nesting behavior of *E. burchelli,* see Teles da Silva, 1977b). Fundamental to bivouac formation is a clustering group response. In *E. hamatum* during the nomadic phase, bivouac formation begins at dusk with the creation of clusters of workers that hang from the support object (e.g., a log) near a booty cache [note that *Anomma* workers can also produce hanging clusters (Raignier, 1959b)]. Other workers are attracted to the clusters and attach themselves, usually by means of interlocking tarsal claws.

As Wheeler (1900) picturesquely explained, in "forming these chains, which remind one of the pictures of prehensile-tailed monkeys crossing a stream, the insects make good use of their long legs and hooked claws." First strands, then "ropes" of workers are formed that ultimately fuse into a "heavy fabric" (Schneirla, 1971). Workers fastened into the bivouac wall usually hang head downward, a phenomenon that Wheeler (1900) attributed to the "positively geotropic" nature of the workers, but which Schneirla (1971) explained in terms of the physical stresses exerted by the placement of the tarsal claws and the weight of the ants. The bivouacs of surface-adapted species of *Eciton* are certainly the most specialized of all nesting formations in the army ants. In *E. hamatum* they may take the form of cylinders suspended between the support object and the substrate or of a curtain between the buttressed roots of a tree (Schneirla, 1971). In *Aenictus gracilis* and *A. laeviceps,* the bivouac during the nomadic phase is little more than a disc-shaped cluster of workers on the soil surface, usually beneath litter. The cluster in *A. laeviceps* is between 15 and 18 cm in diameter and 6 and 9 cm in height (Schneirla and Reyes, 1966).

The bivouac of such species as *E. hamatum* permits colony mobility and yet at the same time provides protection for the brood from the vagaries of the external environment. Temperature variations within the bivouac, for instance, are significantly less than ambient conditions and provide a constancy that optimizes conditions for the developing brood (Schneirla *et al.,* 1954; Jackson, 1957). In *E. hamatum* the general intrabivouac temperature is 1°–2°C above that of the environment and even higher in the compact brood mass (Jackson, 1957). Bivouac temperatures fall in early morning, rise in late morning, fall again in the afternoon and rise in the evening despite fluctuations in ambient temperature (Jackson, 1957).

Refuse deposits, some diffuse and others rather circumscribed are probably formed by most army ants and are located a short distance from the nest or bivouac. While the fate of refuse, such as the remains of prey and carcasses of dead workers, is difficult to determine in hypogaeic nests, it is fairly easy to study in surface-exposed formations. There is little refuse around the bivouac of *E. hamatum,* reflecting that the diet consists primarily of soft-bodied prey (Rettenmeyer, 1963b). However, the refuse deposits of *E. burchelli* are extensive and include the sclerotized parts of dead prey, dead workers, and empty cocoons. This refuse is placed in more or less distinct areas by workers that move along short trails in what Rettenmeyer (1963b) called "refuse columns." Workers defecate in the refuse deposits and along the trails with such frequency that the feces may form a distinct white trail during the statary phase. These refuse deposits usually contain thousands of living arthropods, most of whom are scavengers on the discarded refuse. Reference to refuse deposits associated with colonies in subterranean nests are rare. Bruch (1923), in

one such reference, found refuse deposits in three peripheral chambers of a leaf cutter ant nest that had been occupied by a colony of *E. dulcius.* He noted that the refuse was "repletas de incontables fragmentos, cabezas y alas de otras hormigas, formas sexuales que correspondian principalmente a *A. (M.) Heyeri* y *Trachymyrmex,* mezclados, a trozos quitinosis, élitros, miembros, etc. de coleópteros y otros artrópodos."

2. Origin of Nomadism: Evolutionary and Ontogenetic Considerations

Wilson (1958a, 1971) reasoned that group predation permits the exploitation of other social insects and large arthropods as food sources. Since these sources are more widely dispersed than other types of prey, nomadic behavior was a natural consequence of this new dietary adaptation. That is, nomadism either developed concurrently with group predation or it was added soon afterward as a means for colonies to shift trophophoric fields in order to find new food supplies. Some nondoryline ants, especially of the genus *Cerapachys,* have embarked on group raiding without a concomitant disposition toward nomadism (Wilson, 1971). In fact, there may be some army ants that emigrate infrequently; the biology of a majority of hypogaeic species is unknown. Species that maintain a pattern of precisely spaced emigrations are exceptional. Gotwald (1978) suggested that the selective pressures for the establishment and maintenance of regularly spaced emigrations may be significantly reduced for species that become epigaeic foragers and general predators via swarm raiding. This conclusion is a reasonable extension of Wilson's observation that large arthropods and social insects are widely spaced. Certainly the prey of the most general predator is more numerous and more uniformly distributed in the trophophoric field and less likely to be totally exhausted by intense foraging. Thus the adaptive value of emigrating to new trophophoric fields may consequently be reduced. While the ultimate evolutionary grounds for nomadism may seem obvious, the proximate reasons are still a matter of debate for some species. Schneirla (1938, 1957, 1971) determined that the initiation of the nomadic phase, during which time an *Eciton* colony emigrates daily, is the result of brood stimulative factors. In particular, the statary phase ends when the colony is aroused by the emergence of callow workers from their cocoons. Although the callow effect soon diminishes, the nomadic phase continues to be maintained, stimulated by the developing larval brood. When this brood matures and enters the prepupal and pupal stages, the colony settles into the statary phase at a single nest site (Fig. 10). With his discovery that brood stimulative cues are operating to provoke emigration, Schneirla (1971) concluded that while food shortage may have been the ancestral basis for nomadism, it is no longer so. In this author's

opinion he obscured the distinctions between the ultimate and proximate reasons for nomadism. Brood originated cues for colony movement constitute only the proximate, ontogenetic stimuli that effectively achieve the ultimate end of increasing food supply for the maturing brood. The foregoing conclusion would no doubt be refuted by Topoff (1972) who pointed out that Schneirla emphasized ontogenetic rather than evolutionary processes in his studies of army ant behavior, and that this author is therefore guilty of confusing these approaches and the answers they supply.

Brood stimulative factors appear to be operating in *E. burchelli* and *E. hamatum* (Schneirla, 1971), *Neivamyrmex nigrescens* (Schneirla, 1958, 1963), and *Aenictus gracilis* and *A. laeviceps* (Schneirla and Reyes, 1969), all of which evidence a functional cycle of alternating nomadic and statary phases. However, in *Aenictus* the nomadic phase appears to be initiated by the larvae rather than by the callow workers (Schneirla and Reyes, 1969). Even in army ants that do not pass through such cycles but instead emigrate irregularly, brood stimulative factors operate. In *Anomma,* for example, the emigration of a colony from one nesting site to another is not the direct result of food shortage or other environmental factors. Instead, Raignier and van Boven (1955) concluded that, "Le rythme des exodes est determine par le rythme du couvain." Specifically, emigrations are correlated with the emergence of callow workers. However, if this is the case, the irregularity of movement suggests that eggs are laid in unsynchronized bursts, and indeed, Raignier and van Boven came to such a conclusion. Additionally they found that when male larvae are present in *Anomma* nests, the colonies will remain at a single nest site for an average of 56 days. Colony emigrations in some *Anomma* are so irregular as to suggest that other factors may supersede the stimulative effects of the brood (Gotwald, 1978b). Gotwald and Cunningham-van Someren (1982) recorded the number of days between 38 emigrations observed for a colony of *D. (A.) molesta* in Kenya. In chronological order the intervals were: 9, 9, 19, 4, 14, 35, 11, 33, 7, 44, 5, 23, 4, 45, 14, 24, 10, 10, 7, 9, 5, 19, 23, 11, 12, 13, 18, 7, 8, 5, 14, 11, 12, 16, 3, 5, and 6 days. Rettenmeyer (1963b) believed that Schneirla went too far in discounting the influence of the amount of prey taken on the emigration activities of army ants. Since Rettenmeyer (1963b) demonstrated that the amount of prey in an area affects the "direction, distance, and duration of raids and emigrations," he presumed that the amount of food in the nest or bivouac must influence the larvae that in turn stimulate the adults. He speculated that as the larvae get larger and require more food, they stimulate the workers to raid and emigrate at greater distances.

Nevertheless, in some species brood stimulative factors in the role of proximate initiators of nomadism and other behavior patterns are of paramount importance. Observations of *Eciton* led Schneirla (1971) to expand Wheeler's

concept that trophallaxis, or oral food exchange, constituted the social cement of the colony, and included under the term all communicative relationships between workers and brood. Because these relationships, whether they be tactile or pheromonal, "entail a bilateral arousal basic to colony function," Schneirla (1971) termed them "reciprocal stimulation." This phenomenon is no more evident anywhere than in the army ant functional cycle, particularly as manifested in the callow arousal factor.

3. Army Ant Population Dynamics

Little is known about the number of army ant colonies that can be supported by any given unit of area and space. Unfortunately, colony censuses locate primarily those colonies whose behavior brings them to the soil surface, while the hypogaeic species, for the most part, go undetected. In African environments, one can intuitively conclude that species diversity and the number of colonies are greater in forest habitats than they are in drier, savanna localities (Kistner and Gotwald, 1982).

Leroux (1975, 1977a) calculated the density of *D. (A.) nigricans* colonies at the Laboratoire d'Ecologie Tropical, Lamto, Ivory Coast. The reserve at Lamto encompasses approximately 580 hectares of forest and 2120 hectares of savanna. Leroux reckoned that there were 3.16 colonies per 10 hectares of forest and 0.79 colonies for the same area of savanna, or for every 13 hectares there were 4 colonies in forest and 1 in savanna. Since his calculations did not consider numerous other dorylines that are also present, mostly hypogaeic species of *Aenictus* and non-*Anomma Dorylus,* the carrying capacity of these habitats for such predators remains undetermined.

Although similar calculations for New World species have not been made, Barro Colorado Island, because it is a water-bound unit of land, would seem to be a logical place to begin such an investigation.

4. Emigration

a. Process of Colony Movement

The purpose of these expeditions of *Eciton* is, without doubt, multiple, for the circumstances that these *sorties* . . . coincide more often with a change of season, hardly permits one to consider them exclusively as simple razzias undertaken at the expense of other insects. One can believe them to be sometimes expeditions of pillage, sometimes changes of domicile, veritable migrations.

With this declaration about New World ecitonines, Sumichrast (1868) recognized the dualism of army ant behavior. Especially did he note that army ants emigrate from one nesting site to another, a behavior pattern which was to be the focus of attention for much of Schneirla's exhaustive research (e.g., 1938, 1944, 1945). But long before this research, other observers noted that

army ants emigrate periodically. In Africa, Savage (1847), Brauns (1901) and Vosseler (1905) did so, Vosseler offering the explanation that colony emigrations were stimulated by food shortage. In the New World in addition to Sumichrast's (1868) observations, Müller (1886) and Wheeler (1900) noted that the army ant colony was prevented from moving at times by reproductive processes.

In *Eciton,* colonies always conduct day-long foraging expeditions before emigrating (Schneirla, 1938, 1945, 1971). As raiding progresses in the afternoon, at least in *E. burchelli* and *E. hamatum,* three conditions that preclude emigration are evident: (1) a high level of excitement in the colony is maintained which guarantees a continued exodus of foraging workers from the bivouac, (2) traffic complications among workers on the raiding trails prevent a general return of foragers to the bivouac, and (3) environmental changes at dusk trigger a behavioral shift in the raiding workers from foraging activities to actions essential to emigration (Schneirla, 1971). In *E. hamatum,* one of the three main raiding trails serves as the emigration route and teems with workers leaving the bivouac and with prey-laden foragers returning from the raiding system. These returning workers are intercepted and "sucked" into the outward moving stream (Schneirla, 1938). This exodus becomes an emigration when workers begin carrying brood from the bivouac. While some workers are still leaving the old bivouac, others form the new bivouac, a process that often begins between 1800 and 2000 hours in *E. hamatum* and 1930 and 2130 hours in *E. burchelli* (Schneirla, 1971). When the transport of brood is more than half completed, the queen passes with her retinue of workers. In the early nomadic phase this occurs between 1900 and 2000 hours in *E. hamatum* and 2000 and 2200 hours in *E. burchelli* (Schneirla, 1971). Rettenmeyer (1963b) found that in *E. hamatum* the size of the queen's retinue depends primarily on the speed with which the queen travels. If her progress is unimpeded, the retinue is small. The largest retinue seen by Rettenmeyer (1963b) included between 25 and 50 major workers and a larger number of smaller workers that stayed within 15 to 30 cm of the queen. The queen's retinue, at least in *Eciton,* is not a fixed group of individuals that remains with the queen throughout an emigration. Instead, membership in the retinue constantly changes. Even so, major workers comprise a greater percentage of the retinue than they do of the colony in general. Probably the retinue functions to protect the queen against predators and various environmental hazards and consequently is largest in army ant species that nest and forage epigaeically (Rettenmeyer *et al.,* 1978).

In *Neivamyrmex nigrescens* the general pattern of emigration is similar to that of *E. hamatum,* except that it may forego emigrating on some nights during the nomadic phase. Schneirla (1958) observed 60 emigrations in this species. All of the colony movements occurred at night and all grew out of raiding activities. Usually the emigrations began before midnight about 6 hr

following the beginning of raiding, which is also crepuscular and nocturnal. An emigration required about 6–8 hr to complete, thus most were over at dawn. Schneirla (1958) found that the "emigration always occurs over a principal trail developed from the bivouac in raiding." In some instances, when interrupted by such things as heavy rain, an emigration may require a second night to complete. The distances covered varied considerably and ranged from 2.5 to 76 m. The queen of *N. nigrescens* seems to leave the nest earlier than does the queen of *E. hamatum* and appears in the column of march at about the time when one-third of the emigration is completed (Schneirla, 1958).

Less is known about the emigrations of the more cryptic, subterranean species of New World army ants. For instance, *Labidus praedator* was observed emigrating by Schneirla (1971) on only four occasions. The emigration columns were commonly 4–10 ants wide and included thousands of callows. Large numbers of worker cocoons were carried. This species also constructs walls of earthern pellets that flank the columns and sometimes form arcades completely shielding the emigrating workers (Rettenmeyer, 1963b; Schneirla, 1957). Rettenmeyer (1963b) observed an emigration of this species that required more than 1 day to complete, but only a short portion of the column (about 4 m) moved on the soil surface and it was shielded by soil particle walls and arcades and by "guard" workers. Wheeler (1921) observed an emigration of *Cheliomyrmex megalonyx*. He described the workers as

> running along in dense, orderly columns under leaves, sticks or boards, wherever such cover was available, but where they had to cross open spaces, they had built covered galleries about four-fifths of an inch wide, of small particles of earth.

He noted that of the workers moving in the procession, the smallest were carrying larvae "tucked under their bodies."

In *A. gracilis* and *A. laeviceps* emigrations are usually initiated along a major raiding column that has been in progress for a considerable length of time. However, emigrations in these two species can begin within 20 min of the first signs of excitement in the bivouac and may occur without the raiding precondition evident in *Eciton*. Furthermore, emigrations may begin at any time of day or night and may start "early or late in raiding, as actions overlapping previous emigrations, or as actions ending a quiescent interval without extrabivouac group operations" (Schneirla and Reyes, 1969). The fact that emigration in these two species could arise from raiding or other colony activities prompted Schneirla and Reyes (1969) to propose that this may represent a "generalized, primitive condition of colony organization."

During the first emigrations of the nomadic phase in these two species of *Aenictus,* the brood, which are quite small, are carried in packets by the workers and consequently the entire brood may be transported out of the old

bivouac in less than 20 min. Later in the nomadic phase when the larvae are larger, each is carried by an individual worker, increasing the time required to remove the larvae from the bivouac. Generally the queen leaves the old bivouac in the second half of the emigration and is accompanied by a retinue of workers (Chapman, 1964; Schneirla and Reyes, 1969). In *A. laeviceps,* the queen's entourage is usually 5–8 cm at its widest point and as long as 1 m. Curiously, both of these species may average more than one emigration per day. Early in the nomadic phase the emigrations last from 2 to 3 hr, later they may take 4–7 hr.

Emigrations of African *Aenictus* were described by Brauns (1901) and Gotwald (1976). Brauns noted that the workers carry the larvae slung beneath their bodies. The emigration recorded by Gotwald was discovered, in progress, at 0950 hours crossing a path between plots planted with cassava. Except for an occasional worker, the column was unidirectional and approximately six individuals wide. All workers moving toward the new bivouac carried larvae; pupae were not seen. Workers did not assume "guard" positions along the column; nor did they construct earthen borders. At 1010 hours the queen, whose gaster was contracted, passed with a small entourage of workers.

Of the extensively studied army ants, the *Anomma* driver ants are most irregular in their emigrations. Savage (1847) noted, when observing *D. (A.) arcens,* that from "its locomotive habits the impression . . . has obtained, that it has no fixed habitation." Raignier and van Boven (1955) observed that *Anomma* emigrations often follow previously used foraging trails and that emigration columns are more often subterranean than are foraging columns. An emigration in *Anomma* is a single episode that may take 2 or 3 days (or more) to complete (mean duration: 56 hr) and may not be followed by another emigration for as long as 125 days, although this was an extreme case seen in *D. (A.) nigricans* (Raignier and van Boven, 1955). The mean distance covered by *Anomma* is 223 m. Raignier and van Boven noted that emigration columns can move along more rapidly than foraging columns and calculated some to move as fast as 155 m in 5 hr. Gotwald and Cunningham-van Someren (1982) discovered that some *Anomma* colonies emigrate only short distances and reuse emigration trails and nest sites. In fact, different conspecific colonies may utilize the same trails and nests at different times. For example, they found that one nest was occupied on 15 separate occasions by four different colonies.

b. Army Ant Functional Cycle.   Schneirla (1933, 1938, 1945, 1949, 1971) categorized army ants as either group A dorylines or group B dorylines, by virtue of the type of cyclic phenomena evident in their behavior. In the former group he placed species that exhibit a well defined cycle of alternating no-

madic and statary phases that are conditioned by brood stimulative factors (Fig. 10, p. 189). Surface-active species of *Eciton, Neivamyrmex,* and *Aenictus* belong to this group. In group B he placed species in which there is an absence of these alternating phasic events. This group is characterized by variable nomadism: emigrations occurring as single events separated by intervals of nonnomadic behavior.

The nomadic period in Group A dorylines is one of elevated activity. For *E. hamatum* this means a large daily raid that begins at dawn and which, at dusk, is converted into an emigration to a new nesting site. Daily raiding and nightly emigrations typify this phase. At the very beginning of the phase there are two broods present in the colony, one which emerges from cocoons as callow workers and energizes the phase to begin, and another that consists of young worker larvae that hatched from eggs laid in the immediately preceding statary phase (Fig. 12). During the nomadic phase, which lasts 16–18 days, the queen does not lay eggs and her gaster remains contracted. Initially the young larvae are maintained en masse at the center of the bivouac, which is generally exposed, but as they mature, the larger individuals are kept at the bivouac periphery. The nomadic phase ends when the larvae reach maturity and spin their cocoons; as they do this their stimulative effect on the workers wanes and the colony enters the statary phase.

Lasting for a period of 18–21 days in *E. hamatum,* the statary phase is best characterized by subdued colony activity. Emigrations cease and raids, although still executed on a daily basis, are small and often feeble. The bivouac is established in a sheltered location, such as a hollow tree or log, and the workers are less excitable and active. During the second week of the phase, the queen, who has by then become fully physogastric, delivers a new cluster of eggs. These hatch and larval development ensues. The phase ends when the pupating brood from the previous statary phase eclose. These phases alternate regularly throughout a colony's existence, except when sexual brood is present. At that time the nomadic phase is shortened.

Eciton burchelli has a similar cycle, although its nomadic phase of 11–16 days is considerably shorter and more variable than that of *E. hamatum* (Schneirla, 1945). The statary phase is 19–22 days long. An equivalent nomadic–statary cycle exists in *Neivamyrmex nigrescens,* although under Nearctic conditions, the functional cycle is completely interrupted during the winter months (Schneirla, 1958, 1961). Interestingly the first emigration of the nomadic phase, which is triggered as in *Eciton* by the emergence of callow workers, is not followed by a succeeding emigration until about the fourth night of the phase. Furthermore, the colony remains in the nomadic phase until the larvae enter the early pupal stage. Schneirla (1958) postulated that nomadism continues past the point of larval activity as a result of some "stage-specific" secretory or metabolic products or functions. It could be that

because the pupae are not enclosed in cocoons (i.e., there are no silken barriers between pupae and workers) their stimulative cues wane less abruptly. The nomadic phase for this species in Arizona lasts for 20–31 days, the statary phase for about 18 days. During the statary phase, *N. nigrescens* workers become more photonegative and exhibit a stronger tendency to cluster together, changes which correspond to the decrease in the excitability of workers during this phase (Topoff, 1975).

Schneirla (1971) concluded that of the Old World army ants, *Aenictus,* at least *A. gracilis* and *A. laeviceps,* most closely resemble *Eciton* and *Neivamyrmex* in their *functional* cycle. When nomadic, *A. gracilis* and *A. laeviceps* are capable of raiding and emigrating at any time of day or night. During the nomadic phase, the bivouac is a disc-shaped cluster of workers, either exposed or beneath litter, although near the end of the phase and throughout the statary phase the bivouacs are well sheltered or hypogaeic. The duration of the nomadic phase is about 14 days and thus similar to that of the New World group A army ants. However, the statary phase lasts about 28 days which is strikingly longer than in the New World forms. The statary phase begins when the advanced brood enters the prepupal stage, but the emergence of this brood as callows does not elevate the colony's activity level into a new nomadic phase. Instead, this phase begins some days later.

Schneirla's exhaustive studies of group A dorylines have been supplemented by numerous field and laboratory investigations. Studies of *Eciton burchelli* by Teles da Silva (1977a) have confirmed the endogenous nature of the nomadic-statary cycles in this species. Extensive observations of *Neivamyrmex nigrescens* support Schneirla's theory that brood stimulation is a proximate cause of the nomadic phase in group A dorylines. However, his theory does not account for characteristics such as frequency, direction, and distance of emigrations within the nomadic phase (Mirenda and Topoff, 1980; Topoff *et al.,* 1980a). Topoff and Mirenda (1980a, b) have explored the relationship between food supply and emigration frequency in *N. nigrescens* and have concluded that the "amount and location of food strongly influence the frequency and direction of emigrations." They found in laboratory studies that overfed colonies emigrate far less frequently during the nomadic phase than do underfed colonies.

Of the group B dorylines, *Anomma* is best known. Although the driver ants exhibit some regularity in raiding and emigration, they do not pass through alternating nomadic and statary phases (Raignier and van Boven, 1955), nor for that matter do a majority of dorylines. However, Schneirla (1957) attempted to homologize the functional cycle of *Eciton* with components of *Anomma* behavior, starting with the questionable premise that they are "similarly adapted on a nomadic, predatory basis probably by virtue of common ancestry." He concluded that the first part of the *Eciton* nomadic phase

and the single emigrations of *Anomma* involve "homologous reproductive processes as essential causes," i.e., the excitatory effects of eclosing callow workers. According to Schneirla, it then followed that each emigration in *Anomma* should be regarded as a nomadic phase and the interval between emigrations as a statary phase. "Consequently," Schneirla stated, "*Anomma* may be said to have an identifiable nomadic-statary functional cycle equivalent to that of *Eciton.*" However, it is just as valid, and perhaps even more empirically demonstrable to invoke the process of convergent evolution as an explanation for the presence of brood stimulative cues for nomadic behavior.

E. Colony Division

1. Colony Founding in Nondoryline and Nonecitonine Ants

Typically, the founding of new colonies in a majority of ants, in which the males and females are initially alate, is preceded by a nuptual flight (Wheeler, 1933). The emergence of conspecific males and females in a specific locality is often synchronized for a majority of colonies, a phenomenon that no doubt favors cross fertilization. Following the nuptual flight, the newly fecundated queen descends to the substrate and either removes her wings with her legs and mandibles or rubs them off against a readily available object. She then excavates a small burrow, lays eggs, and cares for the larvae once the eggs hatch. She feeds the growing larvae salivary secretions that are metabolically derived from her fat bodies and flight muscles. Once these larvae pupate and eclose as adult workers, the queen does little more than ingest food gathered by her offspring and lay eggs. The rearing of new brood becomes the preoccupation of overlapping generations of sister workers (Wheeler, 1933; Wilson, 1971).

2. Colony Founding in Doryline and Ecitonine Ants

Army ant colonies are founded by the subdivision of existing colonies into daughter colonies. Since the queens are apterous, there are no nuptual flights and queens are not left to found new colonies by themselves. New colonies come "ready made."

In *E. burchelli* and *E. hamatum,* worker broods are produced throughout most of the year, to the exclusion of sexual broods, on a 33–36 day cycle of development, and colony division does not take place. Sexual broods are prerequisite to division. In Central America, sexuals are produced in the first one-third of the dry season (Schneirla, 1956a). With a sexual brood present in the *Eciton* colony, a "bipolar organization arises" in which some workers become greatly attracted to the brood, while others remain fixed in their attachment to the functional queen. This organization is basic to the actual process of division itself, which does not begin until the sexual brood emerges

from their cocoons. The young queens eclose before the males, the first about 3 days earlier. The order in which the queens emerge is critical to queen selection, for usually only one callow queen will survive. In the hierarchy of attractiveness of callow queens to workers, the first one or two young queens to emerge normally have the advantage and are the leading candidates for survival in a new daughter colony. The first queens to eclose each attract an entourage of hundreds of workers. Queen number one leaves the bivouac, accompanied by her entourage and situates herself at a location usually within 1 m of the bivouac. The workers cluster about her. The next one or two virgin queens to emerge behave similarly, although they usually remain closer to the nest and have smaller clusters of affiliated workers. Generally these clusters and their queens gradually move farther away from the bivouac. Later eclosing queens are not greatly attractive to the workers and are confined by the workers to the bivouac wall. Thus the "period of a few days preceding appearance of the males . . . is one in which the young queens normally become consolidated in very different relations of acceptance or rejection with the worker population" (Schneirla, 1956a).

The eventual eclosion of the males galvanizes the statary colony to conduct a major foraging expedition that ends in an emigration. So vigorous is the raid that two or more base or trunk columns are established. This development is imperative for the division to take place. Once the raid is well established, about midmorning, the functional queen and her entourage leave the bivouac on one of the base trails. The leading virgin queen and her retinue then set out on another trail. Sometimes the functional queen is superseded by one of the virgin queens, but Schneirla (1956a) considered this a secondary form of the main pattern. Superfluous virgin queens are "sealed-off" by the workers and are eventually abandoned. In the final stage of division in *Eciton,* the newly eclosed males, the brood, and the workers are divided nearly equally, one group following the functional queen and the other the new queen. In most cases, fission is completed by nightfall.

Little is known about colony division in other New World species except *N. nigrescens.* Colony division in this species is not unlike that of *Eciton,* although the males, instead of being divided into two equal groups, all emigrate with the callow queen (Schneirla, 1971).

In *Aenictus,* the flight of newly eclosed males from the parent colony occurs prior to colony division, not following the process as occurs in *Eciton* and *Neivamyrmex* (Schneirla, 1971). While Schneirla (1971) found similarities between the patterns in *Aenictus* and the ecitonines, he concluded that the process of colony division in *Aenictus* is the most generalized of the known species.

Although the presence of male brood is necessary for colony division in *Anomma,* male larvae and pupae may be found in colonies that lack queen

brood (Raignier, 1959, 1972). This means that the appearance of male brood cannot always be interpreted to signify that colony fission is imminent. However, Raignier (1959) observed colony fission when only male brood was present. In fact, this kind of division occurs more frequently than does division with a mixed brood present. However, in this case, most of the colony emigrates with the functional queen, leaving behind the male brood and some workers. After the males eclose and fly from the old nest, the queenless workers die.

While *Anomma* males may be present and colony division can take place at any time of the year, division occurs with greatest frequency during the last third of the dry season. The new queen or queens eclose approximately 10–14 days before the males and actually achieve adulthood at about the time the males enter the pupal phase. Division begins with the exodus from the nest of the functional queen and about half the workers and worker brood, an exodus which is identical to a normal emigration (Raignier, 1959). A bipolar organization in the colony prior to division, as can be seen in *Eciton*, is evident. Even though the exodus appears to take place after a large scale emergence of callow workers, the sexual brood may be in various stages of development. The males may be larvae, pupae, or adults and the new queens may be callow or fully pigmented. The virgin queens and male brood are always left behind in the original nest, and once exodus of the functional queen takes place, the workers kill all but one of the remaining queens. Raignier (1959) found as many as 56 virgin queens in a single nest and pointed out that the first queen to eclose is not necessarily the one to be spared. Once the males eclose, they fly from the nest.

VI. ARMY ANT LONGEVITY

A. Caste-Related Determinants of Army Ant Life Spans

1. Workers

Army ant workers suffer enormous losses when attacking prey, therefore much of the developmental energy expended in the production of brood is devoted to the replacement of workers lost in foraging. That raiding is hazardous for workers is easily observed in *Anomma* when numbers of injured stragglers return to the nest from raiding forays long after most other foragers have reached the nest. Even these stragglers stand little chance of continued survival, since on their laborious return they often fall prey to other ants, especially those belonging to the genus *Crematogaster* (W. H. Gotwald, unpublished data). Schneirla (1971) speculated that swarm raiders must lose many workers to the defensive secretions of some potential prey and that hypogaeic foragers must suffer high mortality from the secretions of nasute

termites. He further presumed that large numbers of foragers are crushed in the mandibles of such ants as *Atta* and *Odontomachus* and that others succumb to the bites, stings and repellents of even less formidable ants. The actual turnover rate of workers in a colony has not been determined, nor would it seem reasonable that the rate could be easily calculated.

Environmental factors also play a role in determining the lifespans of workers. Increasing atmospheric dryness, for instance, may take its toll, particularly among the smallest workers since they appear to be the most susceptible to the fatal consequences of decreases in relative humidity (Schneirla *et al.*, 1954) (as one might predict given their surface area to volume ratio). Certainly workers are lost through excessive exposure to solar heat and many must drown when caught in torrential rains that characterize many of the tropical localities where army ants abound.

Watkins and Rettenmeyer (1967) determined that worker army ants live longer when in the presence of their queen, most likely because of certain secretions that are "licked" from the body of the queen.

2. Queens

Captured, marked, and recaptured queens of *Eciton* indicate that army ant queens may function in their colonies in excess of 4 years (Rettenmeyer, 1963b; Schneirla, 1971). While Schneirla (1971) assumed that some *Eciton* queens succumb to disease, parasites, and fatal accidents, he concluded that most queens probably die after being superseded by virgin queens during colony division.

3. Males

The male lifespan is relatively short and probably does not extend much beyond the time of copulation, if indeed copulation is achieved. It is not known whether such males expire at that time of "natural" causes or if they are exiled or killed by perhaps increasingly intolerant workers.

B. Predators of Army Ants

1. Invertebrate Predators

Army ants are themselves not without a myriad of predators. As noted previously (Sections V, A, 1 and V, C, 2, d), dorylines play host to a large number of inquilines and followers, many of which prey on army ant brood. In addition to the pressures brought about by these associates of army ants, the army ant lifespan is often shortened by the intervention of predators of a more general nature. For instance, it must be assumed that newly emerged males are subject to intense predation by invertebrates and vertebrates alike. I have witnessed evidence in both the New and Old World that doryline males are commonly attacked by spiders (Fig. 13). That males are attracted, often in

Fig. 13. Unidentified spider with captured army ant male of the subgenus *Dorylus*. The male was attracted to light between 2030 and 2200 hours which led to his capture (taken at Lamto, Ivory Coast). (Photograph by W. H. Gotwald, Jr.)

substantial numbers, to light at night no doubt increases their vulnerability to the attack of opportunistic predators. In Ivory Coast at Lampto, for example, I observed light-attracted males being captured by the ponerine ant *Megaponera foetens*.

Invertebrate predators of army ants, outside of those that could be classified as guests or followers, are, however, not numerous. Other ants appear to be the most common of these predators. Lamborn (1913–1914) observed workers of *Camponotus sericeus* on the earthenworks of a *D. (A.) nigricans* column, reaching down occasionally to grasp in their mandibles minor workers. However, he did not see any of the *Anomma* workers carried off for all were eventually released. *Crematogaster* workers will attack and drag away injured *Anomma* foragers and *Paltothyreus tarsatus* may attack *Anomma* brood under unusual circumstances (Gotwald, 1972b). Where *Anomma* columns cross the territories of the red tree ant, *Oecophylla longinoda,* this formicine ant may be a formidable predator of the driver ants (Gotwald, 1972b). In fact, in areas where these species are sympatric, *O. longinoda* may be the single most important insect predator of *Anomma*. An *O. longinoda* attack consists of individual workers reaching into an *Anomma* column, each seizing a driver ant worker in its mandibles and pulling it quickly from the column. The *Anomma* workers thus removed are then immobilized through prolonged stretching by numerous cooperating *O. longinoda* workers and transferred to the *O. longinoda* nest.

2. Vertebrate Predators

Vertebrates probably constitute the greatest predatory threat to army ants. Bequaert (1922) reported that of 1815 ants found in 194 stomachs of five species of Congo toads, 8% were dorylines. Three species of African frogs were also found to take dorylines of the subgenus *Anomma*. Certain forest species of African skinks of the genus *Mabuya* actually follow the columns of driver ants and feast on the workers (Bequaert, 1922). In India, *Dorylus* is among the ants taken by some species of birds (Bequaert, 1922). Chapin (1932) reported that driver ants are eaten by several species of African birds, including the Guinea fowl, *Phasidus niger.* Gotwald (1972b) noted that even the domesticated chicken can be counted among the predators of army ants that forage in village refuse heaps. Of the mammals, pangolins or scaly anteaters of the genus *Manis* probably take large numbers of dorylines. Lang

Fig. 14. (A) Chimpanzee inserting ant dipping tool into a nest of *D. (Anomma) molesta.* (B) As the disturbed driver ant workers climb the dipping tool, the chimpanzee monitors their progress. (C) The "pull-through"; the left hand, in this case, slides up the tool, catching the ants in a mass which accumulates as the hand advances. The mouth is open ready to receive the ants. (D) The ants are ingested at the end of the "pull-through." (Photographs by Caroline Tutin.)

(in Bequaert, 1922) observed the pangolin "lashing its sticky tongue through the confused crowds," and noted that it lost "no time in moving back and forth along the . . . [*Dorylus*] column as quickly as the dense clusters vanished into its mouth." Patrizi (1946) estimated that among the stomach contents of a female aardvark there were in excess of 100,000 individuals of *D. (D.) helvolus*. That these individuals were taken in all stages of development indicated that the aardvark probably plundered the *Dorylus* nest. *Dorylus* workers (of a non-*Anomma* species) have even been found in fecal samples of the aardwolf, *Proteles cristatus,* who normally is a termite feeder (Kruuk and Sands, 1972). No doubt an even greater list of army ant predators could be assembled for the New World species.

Perhaps the most interesting of all army ant predators, at least from the standpoint of the predator's behavior, is the chimpanzee. Goodall (1963) first described the use by east African chimpanzees of modified sticks in harvesting driver ants, a tool-using behavior referred to by McGrew (1974) as "ant dipping." Van Lawick-Goodall (1968) noted that chimpanzees at Gombe Stream Reserve in Tanzania frequently eat *Anomma* driver ants in January and occasionally do during September through November and February through May. Chimpanzees apparently find the driver ants visually, either by seeing the moving columns of workers or by recognizing the earthen works of the nest. In ant dipping the chimpanzee fashions a tool from living, woody vegetation, inserts the slender end of this stick into the *Anomma* nest, and waits until the workers swarm about three-quarters of the way up the stick (Fig. 14). At this point, it withdraws the stick and holds it in a vertical position with the distal end just below the mouth. The chimpanzee then slides its free hand up the stick, catching the ants in a mass the size of a "hen's egg" and shoves this mass into its mouth. "The chimpanzee's mouth closes and the jaws gnash frantically and exaggeratedly, audibly crushing the ants between the teeth" (McGrew, 1974). Driver ants seem to constitute an important protein source for chimpanzees, probably second only to termites for the females (McGrew, 1974).

VII. PHYLOGENY OF ARMY ANTS

A. Zoogeography

There are approximately 127 species of New World army ants arrayed among five genera. Five of the species belong to the monogeneric tribe Cheliomyrmecini, the remainder to the Ecitonini (Watkins, 1976). Because many of the species are based on descriptions of unassociated phena, the actual number of species may be considerably lower. *Cheliomyrmex* has a much more restricted distribution than the ecitonine genera and is decidedly more tropi-

cal. *Cheliomyrmex morosus* occurs as far north as San Luis Potosi, Mexico and *C. audas* as far south as La Paz, Bolivia (Watkins, 1976). Even though the workers of *Cheliomyrmex* are hypogaeic and behaviorly cryptic, the males are taken commonly enough at light to suggest that the range of the genus is truly restricted and not just a collecting artifact.

Some ecitonine species are wide ranging while others are severely restricted in distribution. *Labidus coecus,* for example, is found from Argentina to Oklahoma, whereas *Neivamyrmex baylori* is known only from Texas. *Labidus coecus* and some species of *Neivamyrmex,* including *N. nigrescens,* quite clearly are adapted in parts of their ranges to temperate climates. *Neivamyrmex* species extend to 40° latitude on either side of the equator, and *N. nigrescens,* for instance, has been collected in Iowa, Illinois, and West Virginia, all areas that are subjected to harsh winters. Curiously, *N. nigrescens* is the only group A doryline that maintains a subterranean nest throughout its functional cycle, and this may, in fact, be a secondary adaptation to temperate conditions.

The Old World tribe Aenictini is represented by 34 species in the Indo–Australian region and by approximately 15 species in Africa (Wilson, 1964). Continental Asian species are known from India, Thailand, Burma, Malaya, Sumatra, and southern China. *Aenictus* is also found in Australia (New South Wales and Queensland) and on such islands as the Philippines, Ceylon, New Guinea, Borneo, Java, Aru, and Taiwan (Wilson, 1964). A single specimen of *Aenictus* has been collected on Iriomote in the Ryukyu Islands (Onoyama, 1976). Although *Aenictus* ranges through the Middle East into Africa, the two populations do not appear to share any species. As noted by Wheeler (1930), Asian and African *Aenictus* queens differ from one another in a number of significant morphological details. Menozzi (1936) collected a previously undescribed species of *Aenictus* on the Mediterranean island of Rhodes and believed it to have certain affinities with the Indo–Australian species. In Africa, except for the most arid of areas, *Aenictus* is rather ubiquitous, although it is infrequently collected and does not exhibit the diversity apparent in Asia. It is not found on Madagascar, nor for that matter is *Dorylus.*

The Dorylini are well established in Africa with about 50 species, but poorly represented in Asia by only four species (Wilson, 1964; Gotwald, 1979). The Asian forms include two species of *Alaopone,* one of *Typhlopone,* and one of the endemic subgenus *Dichthadia.* Three subgenera, *Anomma, Dorylus,* and *Rhogmus,* are endemic to Africa and not present in Asia. Conversely, *Dichthadia* has not dispersed toward the African continent. The Asian species range, on the continent, from Nepal and India to southern China. As far as it can be ascertained *D. (Dichthadia) laevigatus* is the only species recorded from Java, Borneo, and the Celebes. Although all five of the *Dorylus* sub-

genera in Africa are widespread, *Anomma* is least successful in xeric and cool habitats. Driver ants, therefore, are not found in northern Africa or South Africa. As in *Aenictus, Dorylus* appears continuous in distribution across the Middle East, connecting African and Asian populations but without these populations sharing any species. Surely the Middle East should be carefully searched for evidence of sympatry between Asian and African forms. Donisthorpe (1950) reported the African species *D.* (*D.*) *affinis* from Turkey, and Wilson (1964) expressed misgivings about maintaining *D.* (*Typhlopone*) *labiatus,* a species from India, as separate from *D.* (*T.*) *fulvus* of North Africa.

B. Origin of Army Ants

1. Phylogenetic Scenarios and Hypotheses

Wilson (1958a) formulated an hypothesis for the origin of army ant behavior in terms of major adaptive steps. First, he proposed that group predation arose because it permitted feeding on large arthropods and on other social insects; second, that nomadism developed concurrently with or shortly after group predation to permit shifting of the trophophoric field; third, that prey preference was secondarily expanded to include smaller nonsocial insects and arthropods, making general predators of at least some species; and, fourth, that further refinements in nomadic and group predatory behavior permitted large colony size.

However, even if this scenario is accurate, the question must still be posed: From what group or groups of ants did the army ants arise? Throughout the literature, the cerapachyines are most often regarded to be somehow ancestrally related to the army ants. Emery (1895, 1901, 1904) presumed that the cerapachyines linked the army ants to the Ponerinae. Initially, Emery (1895) even placed the cerapachyines as a tribe within the Dorylinae and was most impressed with the fact that the males of both groups have retractile genitalia. Later he relented, most likely falling sway to the arguments of Forel (e.g., 1901) and placed the cerapachyines in the section Prodorylinae of the Ponerinae. Wheeler (1902, 1920) discussed the affinities of the cerapachyines and was inclined to regard them as ponerines, while admitting to their army ant characteristics, especially in the larvae. Although Brown (1954) refused to accept a cerapachyine origin for the army ants in his review of ant phylogeny, he most recently (1975) admitted that "Emery's notion that the Cerapachyini gave rise to the Dorylinae may have something to it still." However, he speculated that, because the army ants might be polyphyletic, "*Eciton* and relatives in the New World and/or *Aenictus* in the Old World arose separately from cerapachyines through the genus *Acanthostichus,*" a genus that Brown (1954) considered aberrant and on which he felt too much emphasis had been

placed because of this group's dichthadiiform queens. Pullen (1963) proposed that the army ants "passed through an intermediate termitophagous condition characteristic of some modern Ponerinae" and was convinced that the army ants were "amongst the first ants to exploit termites for food on a large scale." If the army ants are triphyletic, as is suggested in further discussion, then should one look to the cerapachyines as ancestral candidates for all three groups? If indeed diet provides clues to these phylogenetic relationships as Pullen would have one believe, then it should be noted that the tribe Cerapachyini, which is strongly developed in the Old World, raid the nests of other ants, while the Cylindromyrmecini and Acanthostichini [now regarded as distinct ponerine tribes and not cerapachyines by Brown (1975)], which are endemic to the New World, are termite predators. The myth persists, in the absence of quantitative, corroborative evidence, that termitophagy is prevalent among the army ants. To be sure, termites do constitute an important prey item for some hypogaeic species, but it may be misleading to make too much of this in phylogenetic interpretations.

The study of dorylophilous faunas, especially the Staphylinidae, may provide at least circumstantial evidence bearing on the phylogenetic relationship of the army ants. Seevers (1965), for instance, maintained that the pantropical staphylinid tribe Dorylomimini is monophyletic. If his conclusion were true, a strong case for monophyly in the army ants could also be argued. However, Seevers revealed his uncertainty by admitting that if it could be demonstrated conclusively that the army ants are polyphyletic, then retention of the Dorylomimini as a monophyletic group would be "indefensible." Kistner (1972) proposed, based on the relationship of Old and New World myrmecophilous staphylinids, that *Neivamyrmex* and *Aenictus* may share a common ancestry.

Wheeler (1928) supposed that the army ants were monophyletic, believing that *Cheliomyrmex,* with its uninodal waist, linked the New and Old World faunas. Schneirla (1971) felt strongly that the "concept of a monophyletic origin best fits available functional and behavioral evidence." Above all, he was convinced that the phasic behavior of the group A dorylines could be homologized with the cyclic activities of the group B species. Because Old World doryline workers and queens lack eyes, Schneirla (1971) hypothesized that the ancestors of *Aenictus* and *Dorylus* were subjected to harsh surface conditions and were "forced" to adopt a hypogaeic lifestyle. Retention of reduced eyes in the workers and queens of most New World forms indicated, according to Schneirla, that the ancestors of the New World forms separated early from *Aenictus*-like stock in Asia and dispersed to the New World over the northern route, which he assumed to be tropical at the end of the Cretaceous. His evolutionary scenario implies a common origin for the army ants in Laurasia.

However, even Borgmeier (1955) doubted that the Old and New World

forms were closely related, and in a personal communication to Seevers (1965), he admitted to believing that the two groups arose independently. Brown (1954) too professed that the army ants possibly were diphyletic, and Gotwald (1969) noted that mouthpart morphology could be used to support a triphyletic hypothesis. Gotwald and Kupiec (1975) stated that geographic, morphological, and behavioral evidence indicates a triphyletic origin and that the three lineages composing the Dorylinae are the (1) Ecitonini–Cheliomyrmecini, (2) Dorylini, and (3) Aenictini. They proposed, contrary to Schneirla's hypothesis, that the two New World tribes arose from a common ancestor that possessed a one-segmented waist; that the Ecitonini and Cheliomyrmecini diverged from one another quite early, and that the genus *Cheliomyrmex* retained the primitive, uninodal waist, while the ecitonines independently evolved a two-segmented waist.

2. The Fossil Record

Doryline army ants are completely absent from the fossil record. Although some ant genera in the Florissant Shales show Neotropical affinities and suggest that the Nearctic fauna was once rich in genera now restricted to the neotropics, army ants are not among them (Carpenter, 1930). The Baltic Amber contains a diverse ant fauna of which 56% of the genera represented are extant. Wheeler (1914) noted the absence of dorylines from the amber and hypothesized that they were either restricted to the tropics during the Oligocene or were so hypogaeic as to preclude their entrapment in resin. One can only speculate about the time of origin for the army ants.

Until the discovery of the Mesozoic ant *Sphecomyrma freyi,* the earliest known ant fossils were of Eocene age (Carpenter, 1929). Found in the amber of the Magothy Formation, *S. freyi* can be dated with reasonable certainty to the lower part of the Upper Cretaceous. Thus sociality probably developed in the ants prior to the mid-Cretaceous, although Wilson *et al.* (1967a,b) concluded that social life in the Hymenoptera in general might not be much older than *S. freyi* itself. Gotwald (1977, 1979) concluded that the primitive nature of *Sphecomyrma* and the diversity of the Oligocene ant fauna suggest a late Cretaceous or early Tertiary (and perhaps even later) origin for the doryline ants. Schneirla (1971) was of a similar opinion. Because the two Old World tribes have distinct endemic elements in Asia and Africa, Wilson (1964) proposed that this faunal differentiation occurred since Miocene times.

3. Plate Tectonics

The biogeography of some organisms can be explained, in part, as a consequence of continental drift. In turn, phylogenetic information can sometimes be gleaned from the geological data. For instance, plate tectonics can often ac-

count for the distribution of tropical disjuncts, i.e., tropicopolitan organisms that are related but are now separated by oceanic barriers (Keast, 1972).

According to continental drift theory, today's continents once formed a single land mass, Pangaea. By the late Triassic to mid-Jurassic, Pangaea began to split into a northern cluster of continents called Laurasia and a southern cluster called Gondwana (Dietz and Holden, 1970). The clusters, in turn, fragmented to form the northern and southern continents. By the end of the Cretaceous, Africa and South America were well separated and the South Atlantic Ocean had widened to 3000 km. In fact, at the conclusion of the Cretaceous, the three tropical areas in which true army ants are currently distributed were all separated by substantial ocean barriers.

Although true army ants superficially resemble tropical disjuncts, faunal exchange between Asia and Africa has occurred in relatively recent times so that there are some shared species groups. Since army ants are notoriously poor dispersers, mainly because the queen is apterous and new colonies are produced by colony fission, and since they most likely arose following the breakup of Gondwana and Laurasia, Gotwald (1977, 1979) postulated that the army ants are indeed triphyletic. In other words, the probability is low that the army ants dispersed from a single place of origin across significant oceanic barriers. As Brown (1973) noted in his zoogeographical analysis of Hylean and West African ant faunas, the Atlantic Ocean has been a "formidable barrier" to even those genera that most likely could have rafted across it. Less formidable is the barrier between the Ethiopian and Oriental regions. Although separated during much of the Mesozoic and Tertiary by the pre-Mediterranean Tethys Sea (Cooke, 1972), and now extensive xeric habitats, there is a great deal of sharing of species groups between the regions (Brown, 1973). These are patterns to which the army ants also conform.

Gotwald (1979) pointed out that land bridges connecting the continents periodically since the end of the Cretaceous cannot explain the current distribution of army ants. Even the North Pacific bridge, which sometimes permitted intense faunal exchange of a variety of taxa and which Schnerila (1971) favored as a dispersal route overwhich the progenitors of the New World army ants dispersed from Asia, can probably be ruled out as playing a role in army ant dispersal. Indeed, Darlington (1957) noted that the groups exchanged across this bridge probably belonged to cool environments; it was not a tropical route as Schneirla (1971) supposed.

Thus Gotwald (1979) concluded the geological data indicated that (1) the army ants arose convergently on three separate occasions in three separate tropical loci, (2) the genus *Aenictus* arose in tropical Laurasia, possibly in the early Tertiary, and dispersed into Africa between the late Oligocene and late Pliocene, (3) *Dorylus* evolved in Africa during the early Tertiary but did not

disperse into Asia until late in the Tertiary or even in Quaternary time, and (4) the ecitonines and *Cheliomyrmex* arose from a common ancestor in tropical South America, they underwent extensive diversification during a long period of geographic isolation, and they did not disperse into North America until the end of the Tertiary.

4. Polyphylogeny and the Ascendancy of the Army Ant Adaptive Syndrome

The true army ants may yet become a classic example of what convergent evolution can accomplish. Morphological, behavioral, and zoogeographical evidence point to a triphyletic origin for the army ants, but perhaps even more importantly a number of ponerine species can be judged as being or becoming army ants. *Leptogenys* and *Simopelta* are but two such genera containing some species that not only behave as army ants but show as well a concomitant morphological convergence toward the army ant habitus. In *Simopelta oculata,* for instance, the queen is dichthadiiform and the workers do not possess a furcula, the sting sclerite characteristically absent in the army ants. All of this means that army ant behavior must have arisen independently a minimum of seven times (Wilson, 1958a). Although it remains convenient to refer to the army ants as a single group, particularly when comparing them to other ants, it is not phylogenetically accurate. In fact, some investigators (e.g., Brown, 1973; Chadab and Rettenmeyer, 1975) have begun referring to the ecitonines as a separate subfamily, Ecitoninae, and Snelling (1981) has formally proposed this change in taxonomic status.

Clearly, army ant behavior in tropical environments confers considerable selective advantage on species that "earn" their living in this way. Army ants are exceedingly successful organisms and selective pressures for at least some ant species to evolve toward the army ant adaptive syndrome must be significant. In particular, ground stratum ants of the subfamily Ponerinae, ants that are committed predators and have not yet developed an obligatory "thirst" for plant liquids (especially via Homoptera), appear ready to become army ants where circumstances dictate. No doubt, the advantage in being an army ant lies in a qualitative and quantitative expansion of the diet. Army ants have access to a wide range of prey not available to the solitary forager.

C. Army Ant Role in Tropical Ecosystems: Some Reflections

Army ants cannot be dismissed merely as bizarre, albeit interesting, tropical creatures whose greatest claim is to have inspired breathtaking, fictionalized accounts of fearsome, ravaging hexapods on the loose. Instead, they must be accorded their very special place in tropical ecosystems. They constitute a

dominate form of tropical life. Their predatory effect on the total biomass cannot be overestimated for their numbers are prodigeous. A host of other organisms have coevolved with the army ants, inquilines and followers alike, all bound up in the delicate fabric of tropical life. Army ants are the evolutionary center of a coevolved system that, when fully understood, may be dazzling because of its complexity and its omnipresence in tropical habitats. There are few tropical animals that are not affected, either directly or indirectly, by army ants.

Army ants also assume an aesthetic place in tropical life and should be valued, along with all other tropical organisms, for their diversity and for the lessons in biology they have to teach. This aestheticism of living things (and the shared concern of scientists for the practical problems produced by a reduction in species diversity) must be translated into tangible efforts to halt the accelerating destruction of tropical habitats, before army ants and myriads of other tropical organisms become but a wistful memory in our collective conscience.

ACKNOWLEDGMENTS

REFERENCES

Akre, R. D., and Rettenmeyer, C. W. (1966). Behavior of Staphylinidae associated with army ants (Formicidae:Ecitonini). *J. Kans. Entomol. Soc.* **39**, 745–782.

Akre, R. D., and Rettenmeyer, C. W. (1968). Trail-following by guests of army ants (Hymenoptera:Formicidae:Ecitonini). *J. Kans. Entomol. Soc.* **41**, 165–174.

Akre, R. D., and Torgerson, R. L. (1968). The behavior of *Diploeciton nevermanni,* a staphylinid beetle associated with army ants. *Psyche* **75**, 211–215.

Akre, R. D., and Torgerson, R. L. (1969). Behavior of *Vatesus* beetles associated with army ants (Coleoptera:Staphylinidae). *Pan-Pac. Entomol.* **45**, 269–281.

Alibert, H. (1951). Les insectes vivant sur les cacaoyers en Afrique occidentale. *Mem. Inst. Fr. Afr. Noire* **15**, 1–174.

André, E. (1900). Sur la femelle probable de *l'Anomma nigricans* Ill. (Hyménoptère). *Bull. Mus. Natl. Hist. Nat.* **6**, 364–368.

Arnold, G. (1914). Nest-changing migrations of two species of ants. *Proc. Rhod. Sci. Assoc.* **13**, 25–32.

Arnold, G. (1915). A monograph of the Formicidae of South Africa. *Ann. S. Afr. Mus.* **14**, 1–756.

Arnold, G. (1953). Notes on a female *Dorylus (Anomma) nigricans* Ill. taken with workers. *J. Entomol. Soc. South. Afr.* **16**, 141–142.

Ashmead, W. H. (1906). Classification of the foraging and driver ants, or family Dorylidae, with a description of the genus *Ctenopyga* Ashm. *Proc. Entomol. Soc. Wash.* **8**, 21–31.

Baldridge, R. S., Rettenmeyer, C. W., and Watkins, J. F., II. (1980). Seasonal, nocturnal and diurnal flight periodicities of Nearctic army ant males (Hymenoptera:Formicidae). *J. Kans. Entomol. Soc.* **53**, 189–204.

Baroni Urbani, C. (1977). Materiali per una revisione della sottofamiglia Leptanillinae Emery (Hymenoptera:Formicidae). *Entomol. Bras.* **2**, 427–488.

Barr, D., and Gotwald, W. H., Jr. (1982). Phenetic affinities of males of the army ant genus *Dorylus* (Hymenoptera:Formicidae:Dorylinae). *Can. J. Zool.* (in press).

Bates, H. W. (1863). "The Naturalist on the River Amazons." Everyman's Library, Dutton, New York (reprinted in 1910).

Beebe, W. (1919). The home town of the army ants. *Atl. Mon.* **124**, 454–464.

Belt, T. (1874). "The Naturalist in Nicaragua." Murray, London.

Bequaert, J. (1913). Notes biologiques sur quelques fourmis et termites du Congo Belge. *Rev. Zool. Afr.* **2**, 396–431.

Bequaert, J. (1922). The predaceous enemies of ants. *Bull. Am. Mus. Nat. Hist.* **45**, 271–331.

Bernstein, S., and Bernstein, R. A. (1969). Relationships between foraging efficiency and the size of the head and component brain and sensory structures in the red wood ant. *Brain Res.* **16**, 85–104.

Blum, M. S. (1974). Pheromonal sociality in the Hymenoptera. *In* "Pheromones" (M. C. Birch, ed.), pp. 222–249. Am. Elsevier, New York.

Blum, M. S., and Portocarrero, C. A. (1964). Chemical releasers of social behavior. IV. The hindgut as the source of the odor trail pheromone in the Neotropical army ant genus *Eciton*. *Ann. Entomol. Soc. Am.* **57**, 793–794.

Bodot, P. (1961). La destruction des termitieres de *Bellicositermes natalensis* Hav., par une fourmi, *Dorylus (Typhlopone) dentifrons* Wasmann. *C. R. Hebd. Seances Acad. Sci.* **253**, 3053–3054.

Bolton, B. (1973). The ant genera of West Africa: A synopsis with keys (Hymenoptera:Formicidae). *Bull. Br. Mus. (Nat. Hist.), Zool.* **27**, 317–368.

Borgmeier, T. (1950). A fêmea dichthadiiforme e os estadios evolutivos de *Simopelta pergandei* Forel), e a descrição de *S. bicolor*, n. sp. (Hym. Formicidae). *Rev. Entomol.* **21**, 369–380.

Borgmeier, T. (1953). Vorarbeiten zu einer Revision der neotropischen Wanderameisen. *Stud. Entomol.* **2**, 1–51.

Borgmeier, T. (1955). Die Wanderameisen der Neotropischen Region (Hym. Formicidae). *Stud. Entomol.* **3**, 1–717.

Borgmeier, T. (1958). Nachtraege zu meiner Monographie der Neotropischen Wanderameisen (Hym. Formicidae). *Stud. Entomol.* **1**, 197–208.

Brauns, J. (1901). Uber die Lebensweise von *Dorylus* and *Aenictus*. *Z. Syst. Hymenopterol. Dipterol.* **1**, 14–17.

Brauns, J. (1903). Ueber das Weibchen von *Dorylus (Rhogmus) fimbriatus* Shuck. (Hym.). *Z. Syst. Hymenopterol. Dipterol.* **3**, 294–298.

Brown, C. A., Watkins, J. F., II, and Eldridge, D. W. (1979). Repression of bacteria and fungi by the army ant secretion:skatole. *J. Kans. Entomol. Soc.* **52**, 119–122.

Brown, W. L., Jr. (1954). Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Insectes Soc.* **1**, 21-31.

Brown, W. L. Jr. (1960). The release of alarm and attack behavior in some New World army ants. *Psyche* **66**, 25-27.

Brown, W. L., Jr. (1968). An hypothesis concerning the function of the metapleural glands in ants. *Am. Nat.* **102**, 188-191.

Brown, W. L., Jr. (1973). A comparison of the Hylean and Congo-West African rain forest ant faunas. *In* "Tropical Forest Ecosystems in Africa and South America: A Comparative Review" (B. J. Meggers, E. S. Ayensu, and W. D. Duckworth, eds.), pp. 161-185. Smithson. Inst. Press, Washington, D.C.

Brown W. L., Jr. (1975). Contributions toward a reclassification of the Formicidae. V. Ponerinae, Tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. *Search: Agric.* **5**, 1-116.

Brown, W. L., Jr., and Nutting, W. L. (1950). Wing venation and the phylogeny of the Formicidae (Hymenoptera). *Trans. Am. Entomol. Soc.* **75**, 113-132.

Bruch, C. (1923). Estudios mirmecológicos con la descripción de nuevas especies de dipteros ("Phoridae") por los RR. PP. H. Schmitz y Th. Borgmeier y de una araña ("Gonyleptidae") por el Doctor Mello-Leitao. *Rev. Mus. La Plata* **27**, 172-220.

Bruch, C. (1934). Las formas femeninas de *Eciton*. Descripción y redescripción de algunas especies de la Argentina. *An. Soc. Cient. Argent.* **108**, 113-135.

Bugnion, E. (1930). Les pièces buccales, le sac infrabuccal et le pharynx des fourmis. *Bull. Soc. Entomol. Egypte* **14**, 85-210.

Burgeon, L. (1924a). Les fourmis "siafu" du Congo. *Rev. Zool. Afr.* **12**, 63-65.

Burgeon, L. (1924b). Quelques observations sur les *Dorylus*. *Rev. Zool. Afr.* **12**, 429-436.

Carpenter, F. M. (1929). A fossil ant from the Lower Eocene (Wilcox) of Tennessee. *J. Wash. Acad. Sci.* **19**, 300-301.

Carpenter, F. M. (1930). The fossil ants of North America. *Bull. Mus. Comp. Zool.* **70**, 1-66.

Carpenter, G. D. H. (1914-1915). Observations on *Dorylus nigricans*, Illig., in Damba and Bugalla Islands. *Trans. R. Entomol. Soc. London* pp. 107-111.

Carpenter, G. D. H. (1920). "A Naturalist on Lake Victoria with an Account of Sleeping Sickness and the Tse-tse Fly." Unwin, London.

Carroll, C. R., and Janzen, D. H. (1973). Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* **4**, 231-257.

Chadab, R. (1979). Early warning cues for social wasps attacked by army ants. *Psyche* **86**, 115-123.

Chadab, R., and Rettenmeyer, C. W. (1975). Mass recruitment by army ants. *Science* **188**, 1124-1125.

Chapin, J. P. (1932). The birds of the Belgian Congo. I. *Bull. Am. Mus. Nat. Hist.* **65**, 1-756.

Chapman, J. W. (1964). Studies on the ecology of the army ants of the Philippines genus *Aenictus* Shuckard (Hymenoptera: Formicidae). *Philipp. J. Sci.* **93**, 551-595.

Cohic, F. (1948). Observations morphologiques et écologiques sur *Dorylus (Anomma) nigricans* Illiger (Hymenoptera Dorylidae). *Rev. Fr. Entomol.* **14**, 229-275.

Cooke, H. B. S. (1972). The fossil mammal fauna of Africa. *In* "Evolution, Mammals, and Southern Continents" (A. Keast, F. C. Erk, and B. Glass, eds.), pp. 89-139. State University of New York Press, Albany.

Crawley, B. A., and Jacobson, E. (1924). Ants from Sumatra. With biological notes. *Ann. Mag. Nat. Hist.* [9] **13**, 380-409.

Cros, A. (1939). *Dorylus (Typhlopone) fulvus* Westw. St. *juvenculus* Shuck.: Etude biologique. *Bull. Soc. Hist. Nat. Afr. Nord.* **30**, 205-220.

Darlington, P. J. (1957). "Zoogeography: The Geographical Distribution of Animals." Wiley, New York.

Darwin, C. (1859). "The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life" (6th ed., 1872) (reprinted in 1958 by Mentor Books, The New American Library of World Literature, Inc., New York).

Dietz, R. S., and Holden, J. C. (1970). Reconstruction of Pangaea: Breakup and dispersion of continents, Permian to Present. *J. Geophys. Res.* **75**, 4939–4956.

Dinesen, I. (1937). "Out of Africa." Random House, New York.

Donisthorpe, H. St. J. K. (1939). On the occurrence of dealated males in the genus *Dorylus* Fab. (Hym. Formicidae). *Proc. R. Entomol. Soc. London* **14**, 79–81.

Donisthorpe, H. (1950). Two new species of ants, and a few others from Turkey. *Ann. Mag. Nat. Hist.* [12] **3**, 638–640.

Drummond, B. A., III (1976). Butterflies associated with an army ant swarm raid in Honduras. *J. Lepid. Soc.* **30**, 237–238.

DuChaillu, P. B. (1861). "Explorations and Adventures in Equatorial Africa; with Accounts of the Manners and Customs of the People, and of the Chase of the Gorilla, the Crocodile, Leopard, Elephant, Hippopotamus, and Other Animals." Harper, New York.

Dutt, G. R. (1912). Life histories of Indian insects: (Hymenoptera). Memoirs Department Agriculture in India. *Entomol. Ser.* **4**, 183–267.

Eisner, T. (1957). A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). *Bull. Mus. Comp. Zool.* **116**, 437–490.

Emery, C. (1887). Le tre forme sessuali del *Dorylus helvolus* L. e degli altri Dorilidi. *Boll. Soc. Entomol. Ital.* **19**, 344–351.

Emery, C. (1895). Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. *Zool. Jahrb., Abt. Syst.* **8**, 685–778.

Emery, C. (1901). Notes sur les sous-familles des Dorylines et Ponérines (Famille des Formicides). *Ann. Soc. Entomol. Belg.* **45**, 32–54.

Emery, C. (1904). Le affinità del genere *Leptanilla* e i limiti delle Dorylinae. *Arch. Zool.* **2**, 107–116.

Emery C. (1910). Subfam. Dorylinae. *In* "Genera Insectorum" (P. Wytsman, ed.), Fasc. 102, pp. 1–34. V. Verteneuil & L. Desmet, Brussels.

Fabricius, J. C. (1793), "Entomologia systematica." Hafniae, Proft.

Flanders, S. E. (1976). Revision of a hypothetical explanation for the occasional replacement of a unisexual with a bisexual brood in the colonies of the army ant *Eciton*. *Bull. Entomol. Soc. Am.* **22**, 133–134.

Forbes, J. (1958). The male reproductive system of the army ant, *Eciton hamatum* Fabricius. *Proc. Int. Cong. Entomol. 10th, 1956* **1**, pp. 593–596.

Forbes, J., and Do-Van-Quy, D. (1965). The anatomy and histology of the male reproductive system of the legionary ant, *Neivamyrmex harrisi* (Haldeman) (Hymenoptera: Formicidae). *J. N. Y. Entomol. Soc.* **73**, 95–111.

Ford, F. C., and Forbes, J. (1980). Anatomy of the male reproductive systems of the adults and pupae of two doryline ants, *Dorylus (Anomma) wilverthi* Emery and *D. (A) nigricans* Illiger. *J. N. Y. Entomol. Soc.* **88**, 133–142.

Forel, A. (1896). "Ants' Nests," Smithson. Rep. 1894, pp. 479–505. Smithson. Inst. Press, Washington, D.C.

Forel, A. (1901). A propos de la classification des fourmis. *Bull. Ann. Soc. R. Entomol. Belg.* **45**, 136–141.

Forel, A. (1928). "The Social World of the Ants Compared with that of Man," Vol. II, Putnam, London.

Fowler, H. G. (1979). Notes on *Labidus praedator* (Fr. Smith) in Paraquay (Hymenoptera: Formicidae:Dorylinae:Ecitonini). *J. Nat. Hist.* **13**, 3–10.

Gallardo, A. (1915). Algunas hormigas de la República Argentina. *An. Mus. Nac. Hist. Nat.* **27**, 1–35.

Gallardo, A. (1929). Notas sobre las dorilinas Argentinas. *An. Mus. Nac. Hist. Nat.* **36**, 43-48.

Gehlbach, F. R., Watkins, J. F., II, and Reno, H. W. (1968). Blind snake defensive behavior elicited by ant attacks. *BioScience* **18**, 784-785.

Gehlbach, F. R., Watkins, J. F., II, and Kroll, J. C. (1971). Pheromone trail-following studies of typhlopid, leptotyphlopid, and colubrid snakes. *Behaviour* **40**, 282-294.

Goodall, J. (1963). Feeding behaviour of wild chimpanzees. A preliminary report. *Symp. Zool. Soc. London* **10**, 39-48.

Gotwald, W. H., Jr. (1969). Comparative morphological studies of the ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). *Mem.—N.Y., Agric. Exp. Stn. (Ithaca)* **408**, 1-150.

Gotwald, W. H., Jr. (1971). Phylogenetic affinities of the ant genus *Cheliomyrmex* (Hymenoptera: Formicidae). *J. N.Y. Entomol. Soc.* **79**, 161-173.

Gotwald, W. H., Jr. (1972a). Analogous prey escape mechanisms in a pulmonate mollusk and lepidopterous larvae. *J. N.Y. Entomol. Soc.* **80**, 111-113.

Gotwald, W. H., Jr. (1972b). *Oecophylla longinoda,* an ant predator of *Anomma* driver ants (Hymenoptera:Formicidae). *Psyche* **79**, 348-356.

Gotwald, W. H., Jr. (1974a). Predatory behavior and food preferences of driver ants in selected African habitats. *Ann. Entomol. Soc. Am.* **67**, 877-886.

Gotwald, W. H., Jr. (1974b). Foraging behavior of *Anomma* driver ants in Ghana cocoa farms (Hymenoptera:Formicidae). *Bull. Inst. Fondam. Afr. Noire, Ser. A* **36**, 705-713.

Gotwald, W. H., Jr. (1976). Behavioral observations on African army ants of the genus *Aenictus* (Hymenoptera:Formicidae). *Biotropica* **8**, 59-65.

Gotwald, W. H., Jr. (1977). The origins and dispersal of army ants of the subfamily Dorylinae. *Proc. Int. Congr. Int. Union Study Soc. Insects, 8th, 1977* pp. 126-127.

Gotwald, W. H., Jr. (1978). Trophic ecology and adaptation in tropical Old World ants of the subfamily Dorylinae (Hymenoptera:Formicidae). *Biotropica* **10**, 161-169.

Gotwald, W. H., Jr. (1979). Phylogenetic implications of army ant zoogeography (Hymenoptera:Formicidae). *Ann. Entomol. Soc. Am.* **72**, 462-467.

Gotwald, W. H., Jr., and Barr, D. (1980). Quantitative studies on major workers of the ant genus *Dorylus* (Hymenoptera:Formicidae:Dorylinae). *Ann. Entomol. Soc. Am.* **73**, 231-238.

Gotwald, W. H., Jr., and Brown, W. L., Jr. (1966). The ant genus *Simopelta* (Hymenoptera: Formicidae). *Psyche* **73**, 261-277.

Gotwald, W. H., Jr., and Burdette, A. W. (1981). Morphology of the male internal reproductive system in army ants: phylogenetic implications (Hymenoptera:Formicidae). *Proc. Entomol. Soc. Wash.* **83**, 72-92.

Gotwald, W. H., Jr., and Cunningham-van Someren, G. R. (1976). Taxonomic and behavioral notes on the African ant, *Aenictus eugenii,* with a description of the queen (Hymenoptera: Formicidae). *J. N.Y. Entomol. Soc.* **84**, 182-188.

Gotwald, W. H., Jr., and Cunningham-van Someren, G. R. (1982). Emigration behavior of the East African driver ant, *Dorylus (Anomma) molesta* Gerstaecker (Hymenoptera: Formicidae: Dorylinae). (In preparation).

Gotwald, W. H., Jr., and Kupiec, B. M. (1975). Taxonomic implications of doryline worker ant morphology: *Cheliomyrmex morosus* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* **68**, 961-971.

Gotwald, W. H., Jr., and Leroux, J. M. (1980). Taxonomy of the African army ant, *Aenictus decolor* (Mayr), with a description of the queen (Hymenoptera:Formicidae). *Proc. Entomol. Soc. Wash.* **82**, 599-608.

Gotwald, W. H., Jr., and Schaefer, R. F., Jr. (1982). Taxonomic implications of doryline worker ant morphology: *Dorylus* subgenus *Anomma* (Hymenoptera: Formicidae). *Sociobiology* (in press).

Green, E. E. (1903). Note on *Dorylus orientalis* West. *Indian Mus. Notes* 5, 39.

Haddow, A. J., Yarrow, I. H. H., Lancaster, G. A., and Corbet, P. S. (1966). Nocturnal flight cycle in the males of African doryline ants (Hymenoptera: Formicidae). *Proc. R. Entomol. Soc. London* 41, 103–106.

Hagan, H. R. (1954a). The reproductive system of the army-ant queen, *Eciton (Eciton)*. Part 1. General anatomy. *Am. Mus. Novit.* 1663, 1–12.

Hagan, H. R. (1954b). The reproductive system of the army-ant queen, *Eciton (Eciton)*. Part 2. Histology. *Am. Mus. Novit.* 1664, 1–17.

Hagan, H. R. (1954c). The reproductive system of the army-ant queen, *Eciton (Eciton)*. Part 3. The oöcyte cycle. *Am. Mus. Novit.* 1665, 1–20.

Haley, A. (1976). "Roots." Doubleday, Garden City, New York.

Hermann, H. R., Jr. (1968a). Group raiding in *Termitopone commutata* (Roger) (Hymenoptera: Formicidae). *J. Ga. Entomol. Soc.* 3, 23–24.

Hermann, H. R., Jr. (1968b). The hymenopterous poison apparatus. VII. *Simopelta oculata* (Hymenoptera:Formicidae:Ponerinae). *J. Ga. Entomol. Soc.* 3, 163–166.

Hermann, H. R., Jr. (1969). The hymenopterous poison apparatus: Evolutionary trends in three closely related sub-families of ants (Hymenoptera: Formicidae). *J. Ga. Entomol. Soc.* 4, 123–141.

Hermann, H. R., Jr., and Blum, M. S. (1967). The morphology and histology of the hymenopterous poison apparatus. III. *Eciton hamatum* (Formicidae). *Ann. Entomol. Soc. Am.* 60, 1282–1291.

Holliday, M. (1904). A study of some ergatogynic ants. *Zool. Jahrb., Abt. Syst.* 19, 293–328.

Hollingsworth, M. J. (1960). Studies on the polymorphic workers of the army ant *Dorylus (Anomma) nigricans* Illiger. *Insectes Soc.* 7, 17–37.

Hung, A. C. F., and Vinson, S. B. (1975). Notes on the male reproductive system in ants (Hymenoptera:Formicidae). *J. N. Y. Entomol. Soc.* 83, 192–197.

Huxley, J. S. (1927). Further work on heterogonic growth. *Biol. Zentralbl.* 47, 151–163.

Jackson, W. B. (1957). Microclimatic patterns in the army ant bivouac. *Ecology* 38, 276–285.

Johnson, R. A. (1954). The behavior of birds attending army ant raids on Barro Colorado Island, Panama Canal Zone. *Proc. Linn. Soc. N.Y.* 63–65, 41–70.

Kannowski, P. B. (1969). Daily and seasonal periodicities in the nuptial flights of Neotropical ants. I. Dorylinae. *Proc. Int. Congr. Int. Union Study Soc. Insects, 6th, 1969* pp. 77–83.

Keast, A. (1972). Continental drift and the evolution of the biota on southern continents. *In* "Evolution, Mammals, and Southern Continents" (A. Keast, F. C. Erk, and B. Glass, eds.), pp. 23–87. State University of New York Press, Albany.

Kistner, D. H. (1972). A new genus of the staphylinid tribe Dorylomimini from Africa and its possible significance to ant phylogeny. *Entomol. News* 83, 85–91.

Kistner, D. H. (1976). The natural history of the myrmecophilous tribe Pygostenini (Coleoptera: Staphylinidae). Section 3. Behavior and food habits of the Pygostenini. *Sociobiology* 2, 171–188.

Kistner, D. H., and Gotwald, W. H., Jr. (1982). Biological observations on African army ants of the genus *Dorylus* (Hymenoptera:Formicidae). (In preparation.)

Kruuk, H., and Sands, W. A. (1972). The aardwolf (*Proteles cristatus* Sparrman) 1783 as predator of termites. *East Afr. Wildl. J.* 10, 211–227.

Kutter, H. (1948). Beitrag zur Kennthis der Leptanillinae. Eine neue Ameisengattung aus Süd-Indien. *Mitt. Schweiz. Entomol. Ges.* 21, 286–295.

Lamborn, W. A. (1913–1914). Observations on the driver ants *(Dorylus)* of southern Nigeria. *Proc. R. Entomol. Soc. London* 5, 123–129.

LaMon, B., and Topoff, H. (1981). Avoiding predation by army ants: defensive behaviours of three ant species of the genus *Camponotus. Anim. Behav.* 29, 1070–1081.

Lappano, E. R. (1958). A morphological study of larval development in polymorphic all-worker broods of the army ant *Eciton burchelli*. *Insectes Soc.* 5, 31-66.

Lenko, K. (1969). An army ant attacking the "guaiá" crab in Brazil. *Entomol. News* 80, 6.

Lepeletier deSaint-Fargeau, A. L. M. (1836). "Histoire naturelle des insectes. Suites à Buffon. Hyménopteres. 1." Roret, Paris.

Leroux J. M. (1975). Recherches sur les nids et l'activité prédatrice des dorylines *Anomma nigricans* Illiger (Hym. Formicidae). Memoire présenté a L'Université Pierre et Marie Curie, Paris VI, pour l'obtention du Diplome d'Etudes Supérieures de Sciences Naturelles.

Leroux, J. M. (1977a). Densité des colonies et observations sur les nids de dorylines *Anomma nigricans* Illiger (Hym. Formicidae) dans la region de Lamto (Cote d'Ivoire). *Bull. Soc. Zool. Fr.* 102, 51-62.

Leroux, J. M. (1977b). Formation et déroulement des raids de chasse *d'Anomma nigricans* Illiger (Hym. Formicidae) dans une savane de Cote d'Ivoire. *Bull. Soc. Zool. Fr.* 102, 445-458.

Leston, D. (1973). The ant mosaic—tropical tree crops and the limiting of pests and disease. *PANS* 19, 311-341.

Leston, D. (1979). Dispersal by male doryline ants in West Africa. *Psyche* 86, 63-77.

Lindquist, A. W. (1942). Ants as predators of *Cochliomyia americana* C. & P. *J. Econ. Entomol.* 35, 850-852.

Linñe, Caroli (1764). "Insecta & Conchilla." Museum Ludoviciae Ulricae Reginae. Literis & Impensis Direct. Laur. Salvii. 111 pp.

Linné, Caroli (1767). "Systema Naturae," 12th ed., Vol. I, Pars II, Classis V. Insecta.

Loveridge, A. (1922). Account of an invasion of "Siafu" or red driver-ants—*Dorylus (Anomma) nigricans* Illig. *Proc. R. Entomol. Soc. London* 5, 33-46.

Loveridge, A. (1949). "Many Happy Days I've Squandered." The Scientific Book Club, London.

Loveridge, A. (1953). "I Drank the Zambesi." Harper, New York.

Luederwaldt, H. (1926). Observações biologicas sobre formigas Brasileiras, especialment do Estado de São Paulo. *Rev. Mus. Paul.* 14, 184-304.

Lund, M. (1831). Lettre sur les Habitudes de quelques Fourmis du Brésil, adressée à M. Audouin. *Ann. Sci. Nat.* [1] 23, 113-138.

McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *J. Hum. Evol.* 3, 501-508.

Masner, L. (1976). Notes on the ecitophilous diapriid genus *Mimopria* Holmgren (Hymenoptera:Proctotrupoidea, Diapriidae). *Can. Entomol.* 108, 123-126.

Masner, L. (1977). A new genus of ecitophilous diapriid wasps from Arizona (Hymenoptera: Proctotrupoidea:Diapriidae). *Can. Entomol.* 109, 33-36.

Mayr, G. (1886). Ueber *Eciton-Labidus*. *Wien. Entomol. Z.* 5, 33-36, 115-122.

Menozzi, C. (1927). Zur Kenntnis des Weibchens von *Dorylus (Anomma) nigricans* var. *molesta* Gerst. (Hymenoptera-Formicidae). *Zool. Anz.* 70, 263-266.

Menozzi, C. (1936). Nuovi contributi alla conoscenza della fauna delle isole Italiane dell-ego. *Boll. Lab. Zool. Gen. Agran. Portici* 29, 262-311.

Mirenda, J. T., and Topoff, H. (1980). Nomadic behavior of army ants in a desert-grassland habitat. *Behav. Ecol. Sociobiol.* 7, 129-135.

Mirenda, J. T., Eakins, D. G., Gravelle, K., and Topoff, H. (1980). Predatory behavior and prey selection by army ants in a desert-grassland habitat. *Behav. Ecol. Sociobiol.* 7, 119-127.

Mukerjee, D. (1926). Digestive and reproductive systems of the male ant *Dorylus labiatus* Shuck. *J. Asiat. Soc. Bengal* 22, 87-91.

Mukerjee, D. (1933). On the anatomy of the worker of the ant *Dorylus (Alaopone) orientalis* Westw. *Zool. Anz.* 105, 97-105.

Müller, W. (1886). Beobachtungen an Wanderameisen (*Eciton hamatum* Fabr.). *Kosmos* **1**, 81–93.

Murray-Brown, J. (1972). "Kenyatta." Dutton, New York.

Normand, H. (1931). Nouveaux Coléoptères du nord de l'Afrique. *Bull. Soc. Entomol. Fr.* **36**, 124–126.

Onoyama, K. (1976). A preliminary study of the ant fauna of Okinawa-Ken, with taxonomic notes (Japan;Hymenoptera:Formicidae). *Ecol. Stud. Nat. Cons. Ryukyu Isl.* **2**, 121–141.

Patrizi, S. (1946). Stomach contents of a female ant-eater from Nairobi. *J. East Afr. Nat. Hist. Soc.* **19**, 67–68.

Patrizi, S. (1948). Contribuzioni alla conoscenza delle Formiche e dei mirmecofili dell'Africa Orientale. IV. Descrizione di un nuovo genere e di una nuova specie di stapfilinide dorilofilo dello scioa e relative note etologiche (Coleoptera Staphilinidae). *Boll. Ist. Entomol. Bologna* **17**, 158–167.

Paulian, R. (1948). Observations sur les coléoptères commensaux d'*Anomma nigricans* en Cote d'Ivoire. *Ann. Sci. Nat., Zool. Biol. Anim.* [11] **10**, 79–102.

Perkins, G. A. (1869). The drivers. *Am. Nat.* **3**, 360–364.

Petersen, B. (1968). Some novelties in presumed males of Leptanillinae (Hym., Formicidae). *Entomol. Medd.* **36**, 577–598.

Petralia, R. S., and Vinson, S. B. (1979). Comparative anatomy of the ventral region of ant larvae, and its relation to feeding behavior. *Psyche* **86**, 375–394.

Plsek, R. W., Kroll, J. C., and Watkins, J. F., II (1969). Observations of carabid beetles, *Helluomorphoides texanus,* in columns of army ants and laboratory experiments on their behavior. *J. Kans. Entomol. Soc.* **42**, 452–456.

Pullen, B. E. (1963). Termitophagy, myrmecophagy, and the evolution of the Dorylinae (Hymenoptera, Formicidae). *Stud. Entomol.* **6**, 405–414.

Raignier, A. (1959). Het ontstaan van kolonies en koninginner bij de Afrikaanse trekmieren. (Formicidae, Dorylinae, Dorylini). *Meded. K. Acad. Wet., Lett. Schone Kunsten Belg., Kl. Wet.* **21**, 3–24.

Raignier, A. (1972). Sur l'origine des nouvelles sociétés des fourmis voyageuses africaines. *Insectes Soc.* **19**, 153–170.

Raignier, A., and van Boven, J. K. A. (1952). Quelques aspects nouveaux de la taxonomie et de la biologie des doryles africains (Hymenoptères, Formicidae). *Ann. Sci. Nat., Zool. Biol. Anim.* [11] **14**, 397–403.

Raignier, A., and van Boven, J. (1955). Etude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). *Ann. Mus. R. Congo Belg.* **2**, 1–359.

Raigner, A., van Boven, J., and Ceusters, R. (1974). Der Polymorphismus der afrikanischen Wanderameisen unter biometrischen und biologischen Gesichtspunkten. *In* "Socialpolymorphismus bei Insekten" (G. H. Schmidt, ed.), pp. 668–693. Wiss. Verlagsges., Stuttgart.

Ray, T. S., and Andrews, C. C. (1980). Antbutterflies: butterflies that follow army ants to feed on antbird droppings. *Science* **210**, 1147–1148.

Reichensperger, A. (1934). Beitrag zur Kenntnis von *Eciton lucanoides* Em. *Zool. Anz.* **106**, 240–245.

Reid, J. A. (1941). The thorax of the wingless and short-winged Hymenoptera. *Trans. Entomol. Soc. London* **91**, 367–446.

Rettenmeyer, C. W. (1961). Observations on the biology and taxonomy of flies found over swarm raids of army ants (Diptera: Tachinidae, Conopidae). *Univ. Kans. Sci. Bull.* **42**, 993–1066.

Rettenmeyer, C. W. (1962a). The diversity of arthropods found with Neotropical army ants and

observations on the behavior of representative species. *Proc. North Cent. Branch Entomol. Soc. Am.* pp. 14-15.

Rettenmeyer, C. W. (1962b). The behavior of millipeds found with Neotropical army ants. *J. Kans. Entomol. Soc.* **35**, 377-384.

Rettenmeyer, C. W. (1963b). The behavior of Thysanura found with army ants. *Ann. Entomol. Soc. Am.* **56**, 170-174.

Rettenmeyer, C. W. (1963b). Behavioral studies of army ants. *Univ. Kans. Sci. Bull.* **44**, 281-465.

Rettenmeyer, C. W. (1974). Description of the queen and male with some biological notes on the army ant, *Eciton rapax. Mem. Conn. Entomol. Soc.* pp. 291-302.

Rettenmeyer, C. W., and Akre, R. D. (1968). Ectosymbiosis between phorid flies and army ants. *Ann. Entomol. Soc. Am.* **61**, 1317-1326.

Rettenmeyer, C. W., and Watkins, J. F., II. (1978). Polygyny and monogyny in army ants (Hymenoptera:Formicidae). *J. Kans. Entomol. Soc.* **51**, 581-591.

Rettenmeyer, C. W., Topoff, H., and Mirenda, J. (1978). Queen retinues of army ants. *Ann. Entomol. Soc. Am.* **71**, 519-528.

Richards, O. W. (1968). Sphaerocerid flies associating with doryline ants, collected by Dr. D. H. Kistner. *Trans. R. Entomol. Soc. London* **120**, 183-198.

Roonwal, M. L. (1975). Plant pest status of root-eating ant, *Dorylus orientalis,* with notes on taxonomy, distribution and habits (Insecta:Hymenoptera). *J. Bombay Nat. Hist. Soc.* **72**, 305-313.

Santschi, F. (1931). La reine du *Dorylus fulvus* Westw. *Société d'Histoire Naturelle de l'Afrique du Nord. Bull. Algiers* **22**, 401-408.

Santschi, F. (1933). Contribution à l'étude des fourmis de l'Afrique tropicale. *Bull. Ann. Soc. R. Entomol. Belg.* **73**, 95-108.

Savage, T. S. (1847). On the habits of the "drivers" or visiting ants of West Africa. *Trans. Entomol. Soc. London* **5**, 1-15.

Savage, T. S. (1849). The driver ants of West Africa. *Proc. Acad. Nat. Sci. Philadelphia* **4**, 195-200.

Schneirla, T. C. (1933). Studies on army ants in Panama. *J. Comp. Psychol.* **15**, 267-299.

Schneirla, T. C. (1934). Raiding and other outstanding phenomena in the behavior of army ants. *Proc. Natl. Acad. Sci. U.S.A.* **20**, 316-321.

Schneirla, T. C. (1938). A theory of army-ant behavior based upon the analysis of activities in a representative species. *J. Comp. Psychol.* **25**, 51-90.

Schneirla, T. C. (1940). Further studies on the army ant behavior pattern. Mass organization in the swarm-raiders. *J. Comp. Psychol.* **29**, 401-460.

Schneirla, T. C. (1944). The reproductive functions of the army-ant queen as pace-makers of the group behavior pattern. *J. N.Y. Entomol. Soc.* **52**, 153-192.

Schneirla, T. C. (1945). The army-ant behavior pattern: nomad-statary relations in the swarmers and the problem of migration. *Biol. Bull. (Woods Hole, Mass.)* **88**, 166-193.

Schneirla, T. C. (1949). Army-ant life and behavior under dry-season conditions. 3. The course of reproduction and colony behavior. *Bull. Am. Mus. Nat. Hist.* **94**, 1-81.

Schneirla, T. C. (1953). The army-ant queen: Keystone in a social system. *Bull. Union Int. Etude Insectes Soc.* **1**, 29-41.

Schneirla, T. C. (1956a). A preliminary survey of colony division and related processes in two species of terrestrial army ants. *Insectes Soc.* **3**, 49-69.

Schneirla, T. C. (1956b). "Annual Report of the Board of Regents of the Smithsonian Institution," Publ. No. 4232, pp. 379-406. Smithson. Inst. Press, Washington, D.C.

Schneirla, T. C. (1957). A comparison of species and genera in the ant subfamily Dorylinae with respect to functional pattern. *Insectes Soc.* **4**, 259-298.

Schneirla, T. C. (1958). The behavior and biology of certain Nearctic army ants. Last part of the functional season, southeastern Arizona. *Insectes Soc.* **5**, 215-255.

Schneirla, T. C. (1961). The behavior and biology of certain Nearctic doryline ants. Sexual broods and colony division in *Neivamyrmex nigrescens*. *Z. Tierpsychol.* **18**, 1-32.

Schneirla, T. C. (1963). The behaviour and biology of certain Nearctic army ants: Springtime resurgence of cyclic function—southeastern Arizona. *Anim. Behav.* **11**, 583-595.

Schneirla, T. C. (1971). "Army Ants: A Study in Social Organization." Freeman, San Francisco, California.

Schneirla, T. C., and Brown, R. Z. (1952). Sexual broods and the production of young queens in two species of army ants. *Zoologica (N. Y.)* **37**, 5-32.

Schneirla, T. C., and Reyes, A. Y. (1966). Raiding and related behaviour in two surface-adapted species of the Old World doryline ant, *Aenictus*. *Anim. Behav.* **14**, 132-148.

Schneirla, T. C., and Reyes, A. Y. (1969). Emigrations and related behaviour in two surface-adapted species of the Old-World doryline ant, *Aenictus*. *Anim. Behav.* **17**, 87-103.

Schneirla, T. C., Brown, R. Z., and Brown, F. C. (1954). The bivouac or temporary nest as an adaptive factor in certain terrestrial species of army ants. *Ecol. Monogr.* **24**, 269-296.

Schneirla, T. C., Gianutsos, R. R., and Pasternack, B. S. (1968). Comparative allometry in the larval brood of three army-ant genera, and differential growth as related to colony behavior. *Am. Nat.* **102**, 533-554.

Seevers, C. H. (1965). The systematics, evolution and zoogeography of staphylinid beetles associated with army ants (Coleoptera, Staphylinidae). *Fieldiana, Zool.* **47**, 137-351.

Shuckard, W. E. (1840). Monograph of the Dorylidae, a family of the Hymenoptera Heterogyna. *Ann. Nat. Hist.* **30**, 188-201, 258-271, 315-328.

Shyamalanath, S., and Forbes, J. (1980). Digestive system and associated organs in the adult and pupal male doryline ant *Aenictus gracilis* Emery (Hymenoptera: Formicidae). *J. N. Y. Entomol. Soc.* **88**, 15-28.

Smith, F. (1858). Catalogue of hymenopterous insects in the collection of the British Museum. *Formicidae* **6**, 1-216.

Smith, F. (1863). Observations on ants of Equatorial Africa. *Trans. R. Entomol. Soc. London* **1**, 470-473.

Smith, K. G. V. (1967). The biology and taxonomy of the genus *Stylogaster* Macquart, 1835 (Diptera: Conopidae, Stylogasterinae) in the Ethiopian and Malagasy regions. *Trans. R. Entomol. Soc. London* **119**, 47-69.

Smith, K. G. V. (1969). Further data on the oviposition by the genus *Stylogaster* Macquart (Diptera: Conopidae, Stylogasterinae) upon adult calyptrate Diptera associated with ants and animal dung. *Proc. R. Entomol. Soc. London* **44**, 35-37.

Smith, M. R. (1927). A contribution to the biology and distribution of one of the legionary ants, *Eciton schmitti* Emery. *Ann. Entomol. Soc. Am.* **20**, 401-404.

Smith, M. R. (1942). The legionary ants of the United States belonging to *Eciton* subgenus *Neivamyrmex* Borgmeier. *Am. Midl. Nat.* **27**, 537-590.

Snelling, R. R. (1981). Systematics of social Hymenoptera. *In* "Social Insects" (H. R. Hermann, ed.), Vol. II, pp. 369-453. Academic Press, New York.

Strickland, A. H. (1951). The entomology of swollen shoot of cacao. I. The insect species involved, with notes on their biology. *Bull. Entomol. Res.* **41**, 725-748.

Sudd, J. H. (1959). A note on the behaviour of *Aenictus* (Hym., Formicidae). *Entomol. Mon. Mag.* **95**, 262.

Sumichrast, F. (1868). Notes on the habits of certain species of Mexican Hymenoptera presented to the American Entomological Society. *Trans. Am. Entomol. Soc.* **2**, 39-44.

Swynnerton, C. F. M. (1915). Experiments on some carnivorous insects, especially the driver ant *Dorylus;* and with butterflies' eggs as prey. *Trans. R. Entomol. Soc. London* Parts III, IV, pp. 317-350.

Tafuri, J. F. (1955). Growth and polymorphism in the larva of the army ant (*Eciton* (E.) *hamatum* Fabricius). *J. N. Y. Entomol. Soc.* **63**, 21–41.

Teles da Silva, M. (1977a). Behaviour of the army ant *Eciton burchelli* Westwood (Hymenoptera: Formicidae) in the Belém Region. 1. Nomadic-Statary Cycles. *Anim. Behav.* **25**, 910–923.

Teles da Silva, M. (1977b). Behavior of the army ant *Eciton burchelli* Westwood (Hymenoptera: Formicidae) in the Belém Region. 2. Bivouacs. *Bol. Zool.* **2**, 107–128.

Topoff, H. R. (1969). A unique predatory association between carabid beetles of the genus *Helluomorphoides* and colonies of the army ant *Neivamyrmex nigrescens. Psyche* **76**, 375–381.

Topoff, H. (1971). Polymorphism in army ants related to division of labor and colony cyclic behavior. *Am. Nat.* **105**, 529–548.

Topoff, H. (1972). Theoretical issues concerning the evolution and development of behavior in social insects. *Am. Zool.* **12**, 385–394.

Topoff, H. (1975). Behavioral changes in the army ant *Neivamyrmex nigrescens* during the nomadic and statary phases. *J. N. Y. Entomol. Soc.* **33**, 38–48.

Topoff, H., and Lawson, K. (1979). Orientation of the army ant *Neivamyrmex nigrescens:* integration of chemical and tactile information. *Anim. Behav.* **27**, 429–433.

Topoff, H., and Mirenda, J. (1975). Trail-following by the army ant, *Neivamyrmex nigrescens:* Responses by workers to volatile odors. *Ann. Entomol. Soc. Am.* **68**, 1044–1046.

Topoff, H., and Mirenda, J. (1978). Precocial behaviour of callow workers of the army ant *Neivamyrmex nigrescens:* Importance of stimulation by adults during mass recruitment. *Anim. Behav.* **26**, 698–706.

Topoff, H., and Mirenda, J. (1980a). Army ants on the move: relation between food supply and emigration frequency. *Science* **207**, 1099–1100.

Topoff, H., and Mirenda, J. (1980b). Army ants do not eat and run; influence of food supply on emigration behaviour in *Neivamyrmex nigrescens. Anim. Behav.* **28**, 1040–1045.

Topoff, H., Boshes, M., and Trakimas, W. (1972a). A comparison of trail following between callow and adult workers of the army ant *Neivamyrmex nigrescens* (Formicidae: Dorylinae). *Anim. Behav.* **20**, 361–366.

Topoff, H., Lawson, K., and Richards, P. (1972b). Trail following and its development in the Neotropical army ant genus *Eciton* (Hymenoptera:Formicidae:Dorylinae). *Psyche* **79**, 357–364.

Topoff, H., Lawson, K., and Richards, P. (1973). Trail following in two species of the army ant genus *Eciton:* Comparison between major and intermediate-sized workers. *Ann. Entomol. Soc. Am.* **66**, 109–111.

Topoff, H., Mirenda, J., Droual, R., and Herrick, S. (1980a). Onset of the nomadic phase in the army ant *Neivamyrmex nigrescens* (Cresson) (Hym. Form.): distinguishing between callow and larval excitation by brood substitution. *Insectes Soc.* **27**, 175–179.

Topoff, H., Mirenda, J., Droual, R., and Herrick, S. (1980b). Behavioural ecology of mass recruitment in the army ant *Neivamyrmex nigrescens. Anim. Behav.* **28**, 779–789.

Torgerson, R. L., and Akre, R. D. (1969). Reproductive morphology and behavior of a thysanuran, *Trichatelura manni,* associated with army ants. *Ann. Entomol. Soc. Am.* **62**, 1367–1374.

Torgerson, R. L., and Akre, R. D. (1970a). The persistence of army ant chemical trails and their significance in the ecitonine-ecitophile association (Formicidae:Ecitonini). *Melanderia* **5**, 1–28.

Torgerson, R. L., and Akre, R. D. (1970b). Interspecific responses to trail and alarm pheromones by New World army ants. *J. Kans. Entomol. Soc.* **43**, 395–404.

Trimen, R. (1880). On a supposed female *Dorylus helvolus* (Linn). *Trans. Entomol. Soc. London* pp. 24–25.

Tulloch, G. S. (1935). Morphological studies of the thorax of the ant. *Entomol. Am.* **15**, 93-131.

van Boven, J. K. A. (1958). Allometrische en biometrische beschouwingen over het poly-morfisme bij enkele mierensoorten. *Verh. K. Vlaam. Acad. Wet., Lett. Schone Kunsten Belg., Kl. Wet.* **56**, 1-134.

van Boven, J. K. A. (1961). Le polymorphisme dans la caste d'ouvrieres de la fourmi voyageuse: *Dorylus (Anomma) wilverthi* Emery (Hymenoptera: Formicidae). *Publ. Natuurhist. Genoot Limburg* **12**, 36-45.

van Boven, J. K. A. (1967). La femelle de *Dorylus fimbriatus* et *termitarius* (Hymenoptera: Formicidae). *Overdruk Natuurhist. Maandblad* **56**, 55-60.

van Boven, J. K. A. (1968). La reine de *Dorylus (Anomma) kohli* Wasmann (Hymenoptera: Formicidae). *Nat. Can. (Que.)* **95**, 731-739.

van Boven, J. K. A. (1972). Description de deux reines d'*Anomma* (Hymenoptera: Formicidae). *Bull. Ann. Soc. R. Belge Entomol.* **108**, 133-146.

van Boven, J. (1975). Deux nouvelles reines du genre *Dorylus* Fabricius (Hymenoptera, Formi-cidae). *Ann. Zool. (Warsaw)* **33**, 189-199.

van Boven, J. K. A. and Levieux, J. (1968). Les Dorylinae de la savane de Lamto (Hymenoptera: Formicidae). *Ann. Univ. Abidjan, Ser. E* **1**, 351-358.

van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.* **1**, 161-311.

von Ihering, H. (1912). Biologie und Verbreitung der brasilianischen Arten von *Eciton*. *Entomol. Mitt.* **1**, 226-235.

Vosseler, J. (1905). Die Ostafrikanische Treiberameise (Siafu). *Pflanzer* **1**, 289-302.

Vowles, D. M. (1955). The structure and connexions of the corpora pedunculata in bees and ants. *Q. J. Microsc. Sci.* [N.S.] **96**, 239-255.

Wang, Y. J., and Happ, G. M. (1974). Larval development during the nomadic phase of a nearctic army ant, *Neivamyrmex nigrescens* (Cresson) (Hymenoptera: Formicidae). *Int. J. Insect Morphol. Embryol.* **3**, 73-86.

Wasmann, E. (1904). Zur Kenntniss der Gäste der Treiberameisen und ihrer Wirthe am obern Congo, nach den Sammlungen und Beobachtungen von P. Herm. Kohl C. ss. C. bearbeitet. *Zool. Jahrb., Suppl.* **7**, 611-682.

Wasmann, E. (1917). Neue Anpassungstypen bei Dorylinengästen Afrikas (Col., Staphyl-inidae). *Z. Wiss. Zool.* **117**, 257-360.

Watkins, J. F., II (1964). Laboratory experiments on the trail following of army ants of the genus *Neivamyrmex* (Formicidae:Dorylinae). *J. Kans. Entomol. Soc.* **37**, 22-28.

Watkins, J. F., II (1976). "The Identification and Distribution of New World Army Ants (Dory-linae:Formicidae)." The Markham Press Fund of Baylor Univ. Press, Waco, Texas.

Watkins, J. F., II (1977). The species and subspecies of *Nomamyrmex* (Dorylinae:Form-icidae). *J. Kans. Entomol. Soc.* **50**, 203-214.

Watkins, J. F., II, and Cole T. W. (1966). The attraction of army ant workers to secretions of their queens. *Tex. J. Sci.* **18**, 254-265.

Watkins, J. F., II, and Rettenmeyer, C. W. (1967). Effects of army ant queens on longevity of their workers (Formicidae:Dorylinae). *Psyche* **74**, 228-233.

Watkins, J. F., II, Cole, T. W., and Baldridge, R. S. (1967a). Laboratory studies on inter-species trail following and trail preference of army ants (Dorylinae). *J. Kans. Entomol. Soc.* **40**, 146-151.

Watkins, J. F., II, Gehlbach, F. R., and Baldridge, R. S. (1967b). Ability of the blind snake, *Leptotyphlops dulcis*, to follow pheromone trails of army ants, *Neivamyrmex nigrescens* and *N. opacithorax*. *Southwest. Nat.* **12**, 455-462.

Watkins, J. F., II, Gehlbach, F. R., and Kroll, J. C. (1969). Attractant-repellent secretions in blind snakes (*Leptotyphlops dulcis*) and army ants (*Neivamyrmex nigrescens*). *Ecology* **50**, 1098-1102.

Watkins, J. F., II, Gehlbach, F. R., and Pisek, R. W. (1972). Behavior of blind snakes (*Lep-

totyphlops dulcis) in response to army ant *(Neivamyrmex nigrescens)* raiding columns. *Tex. J. Sci.* **23**, 556-557.

Weber, N. A. (1941). The rediscovery of the queen of *Eciton (Labidus) coecum* Latr. (Hym.: Formicidae). *Am. Midl. Nat.* **26**, 325-329.

Weber, N. A. (1943). The ants of the Imatong Mountains, Anglo-Egyptian Sudan. *Bull. Mus. Comp. Zool.* **93**, 263-289.

Wellman, F. C. (1908). Notes on some Angolan insects of economic or pathologic importance. *Entomol. News* **19**, 224-230.

Werringloer, A. (1932). Die Sehorgane und Sehzentren der Dorylinen nebst Untersuchungen über die Facetenaugen der Formiciden. *Z. Wiss. Zool.* **141**, 432-524.

Wheeler, G. C. (1938). Are ant larvae apodous? *Psyche* **45**, 139-145.

Wheeler, G. C. (1943). The larvae of the army ants. *Ann. Entomol. Soc. Am.* **36**, 319-332.

Wheeler, G. C., and Wheeler, J. (1964). The ant larvae of the subfamily Dorylinae: supplement. *Proc. Entomol. Soc. Wash.* **66**, 129-137.

Wheeler, G. C., and Wheeler, J. (1974). Ant larvae of the subfamily Dorylinae: second supplement (Hymenoptera:Formicidae) *J. Kans. Entomol. Soc.* **47**, 166-172.

Wheeler, G. C., and Wheeler, J. (1976). Ant larvae: Review and synthesis. *Mem. Entomol. Soc. Wash.* **7**, 1-108.

Wheeler, W. M. (1900). The female of *Eciton sumichrasti* Norton, with some notes on the habits of Texan *Ecitons. Am. Nat.* **34**, 563-574.

Wheeler, W. M. (1902). An American *Cerapachys,* with remarks on the affinites of the Cerapachyinae. *Biol. Bull. (Woods Hole, Mass.)* **3**, 181-191.

Wheeler, W. M. (1910). "Ants: Their Structure, Development and Behavior." Columbia Univ. Press, New York.

Wheeler, W. M. (1914). The ants of the Baltic amber. *Schr. Phys. öekon. Ges. Konigsberg* **55**, 1-142.

Wheeler, W. M. (1915). On the presence and absence of cocoons among ants, the nest-spinning habits of the larvae and the significance of the black cocoons among certain Australian species. *Ann. Entomol. Soc. Am.* **8**, 323-342.

Wheeler, W. M. (1920). The subfamilies of Formicidae and other taxonomic notes. *Psyche* **27**, 46-55.

Wheeler, W. M. (1921). Observations on army ants in British Guiana. *Proc. Am. Acad. Arts. Sci.* **56**, 291-328.

Wheeler, W. M. (1922). Ants of the American Museum Congo Expedition. A contribution to the myrmecology of Africa. *Bull. Am. Mus. Nat. Hist.* **45**, 1-1139.

Wheeler, W. M. (1925). The finding of the queen of the army ant *Eciton hamatum* Fabricius. *Biol. Bull. (Woods Hole, Mass.)* **49**, 139-149.

Wheeler, W. M. (1928). "The Social Insects: Their Origin and Evolution." Harcourt, New York.

Wheeler, W. M. (1930). Philippine ants of the genus *Aenictus* with descriptions of the females of species. *J. N. Y. Entomol. Soc.* **38**, 193-212.

Wheeler, W. M. (1933). "Colony-Founding Among Ants." Harvard Univ. Press, Cambridge, Massachusetts.

Wheeler, W. M. (1936). Ecological relations of ponerine and other ants to termites. *Proc. Am. Acad. Arts Sci.* **71**, 159-243.

Wheeler, W. M., and Bailey, I. W. (1925). The feeding habits of pseudomyrmine and other ants. *Trans. Am. Philos. Soc.* **22**, 235-279.

Wheeler, W. M., and Long, W. H. (1901). The males of some Texas *Ecitons. Am. Nat.* **35**, 157-173.

Whelden, R. M. (1963). Anatomy of adult queen and workers of army ants *Eciton burchelli* Westw. and *E. hamatum* Fabr. (Hymenoptera:Formicidae). *J. N. Y. Entomol. Soc.* **71**, 14-30, 90-115,158-178, 246-261.

Willis, E. (1960). A study of the foraging behavior of two species of ant-tanagers. *Auk* **77**, 150–170.

Willis, E. O. (1966). The role of migrant birds at swarms of army ants. *Living Bird* **5**, 187–231.

Willis, E. O. (1967). The behavior of bicolored antbirds. *Univ. Calif., Berkeley, Publ. Zool.* **79**, 1–132.

Willis, E. O., and Oniki, Y. (1978). Birds and army ants. *Annu. Rev. Ecol. Syst.* **9**, 243–263.

Wilson, E. O. (1953). The origin and evolution of polymorphism in ants. *Q. Rev. Biol.* **28**, 136–156.

Wilson, E. O. (1958a). The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution* **12**, 24–31.

Wilson, E. O. (1958b). Observations on the behavior of the cerapachyine ants. *Insectes Soc.* **5**, 129–140.

Wilson, E. O. (1964). The true army ants of the Indo-Australian area. *Pac. Insects* **6**, 427–483.

Wilson, E. O. (1971). "The Insect Societies." Belknap Press, Cambridge, Massachusetts.

Wilson, E. O., Carpenter, F. M., and Brown, W. L., Jr. (1967a) The first Mesozoic ants, with the description of a new subfamily. *Psyche* **74**, 1–19.

Wilson, E. O., Carpenter, F. M., and Brown, W. L., Jr. (1967b). The first Mesozoic ants. *Science* **157**, 1038–1040.

Wroughton, R. C. (1892). Our ants. *J. Bombay Nat. Hist. Soc.* **7**, 13–60, 175–203.