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Army Ants: An Evolutionary Bestseller?

Dispatch

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Army ants are characterized by a complex combination of behavioral and morphological traits. Molecular data now indicate that army ant behavior has a unique evolutionary origin and has been conserved for over more than 100 million years.

One of the most striking forms of life to be found in tropical regions are the army ants (Figure 1). Originally renowned for their spectacular raids, army ants have attracted scientific attention for almost two centuries. Army ants are characterized by a unique combination of mass-raiding and recurrent migrations. Associated with their unusual life style, army ants form large colonies with specialized queens — known as dichthadiigynes — and reproduce by colony fission. This unusual combination of traits — mass-raiding, migrations, colony fission and dichthadiigyne queens — is commonly referred to as the 'army ant adaptive syndrome' [1].

Mass-raiding is probably the most outstanding feature of army ants. Originating from their temporary nest — the 'bivouac' — thousands of worker ants collectively scour about the surrounding area in search for food. Depending on the army ant species, they either prey on almost any animal they can overwhelm, or are specialized to feed on colonies of other social insects, such as termites, wasps or other ants. Their impact on prey populations is considerable, rendering them top predators of leaf-litter arthropods and even of small vertebrates in some areas [2,3]. In the tropics, army ants are an important factor contributing to the maintenance of biodiversity.

Related to their predatory efficiency, army ants move to new foraging areas at more or less regular time intervals [2]. Here, they resume their mass-raiding until they move again. As numerous workers are needed to conduct these mass-raids, army ants have large colonies which reproduce by fission: this is a rather unusual form of colony reproduction in which a mature colony splits, with parts of the colony and brood walking off and following either their old queen or a sister queen. Army ant queens thus never leave the ground for a nuptial flight and remain flightless throughout their lives. Furthermore, they are able to produce huge amounts of eggs in the relatively short time between successive migrations. The question of whether such a complex combination of behavioral and morphological traits could have arisen independently more than once in the evolutionary past has been the subject of much debate. A new genetic study by Brady [4] supports the view that army ant behavior has arisen just once in evolution, and then been conserved for more than 100 million years.

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To date, 298 army ant species from three subfamilies of the Formicidae have been described, all from tropical or subtropical regions [5]. This high diversity, and the fact that all investigated species show the entire set of army ant traits, are indicative of the ecological success of this lifestyle. For most of their taxonomic history, army ants have been assumed to form a single, monophyletic subfamily, the Dorylinae. From observations of the uneven zoogeographical distribution of army ant genera, however, Brown [6] suggested a diphyletic origin, with distinct neotropical (Ecitoninae) and palaeotropical (Dorylinae) subfamilies. Gotwald [7] later suggested, also on the basis of zoogeographical data, a triphyletic origin of army ants, with the convergent evolution of three groups: the Ecitoninae in South America; the Dorylinae in Africa; and the Aenictinae in Laurasia.

Gotwald [7] based his suggestion on an assumed origin of army ants in early Tertiary period. The fragmentation of Gondwana was completed at this time [8,9] and would have allowed the separate diversification of the postulated three subfamilies of army ants. The later connection of Africa and Asia could have led to today's species distributions. Although plausible, this view was called into question by detailed anatomical analyses, which again supported a monophyletic origin for the three extant army ant subfamilies, as well as the non-army ant subfamily Cerapachyinae [10]. Brady [4] has now shed molecular light on this issue: he has generated data from three nuclear genes and one mitochondrial gene which strongly support the view that all army ant species are indeed monophyletic, with Cerapachyinae forming the sister group of the three extant army ant subfamilies.

The phylogenic analysis carried out by Brady [4] implies not only that the army ant adaptive syndrome has a single evolutionary origin, but also that army ants have existed for much longer than was previously assumed. Fossil evidence recently extended the time over which ants are thought to have existed to approximately 125 million years [11]. Most basal lineages of ants are now believed to have diverged in mid-Cretaceous period, but given the lack of any fossil evidence to the contrary, army ants were assumed to have originated in the early-to-mid Tertiary period at the earliest [11]. The data reported by Brady [4] argue against this view, and suggest that the army ant adaptive syndrome originated about 105 million years ago. This would indicate that army ants arose at around the same time as most other basal ant lineages. Approximately 80 million years lie between this assumed origin and the first fossil army ant found in Dominican amber [12].

How could this long absence of army ants from the fossil record be explained? One obvious possibility is that army ant fossils from this period are relatively rare and simply have not been found yet. If early army ants were, like those living today, limited to tropical and

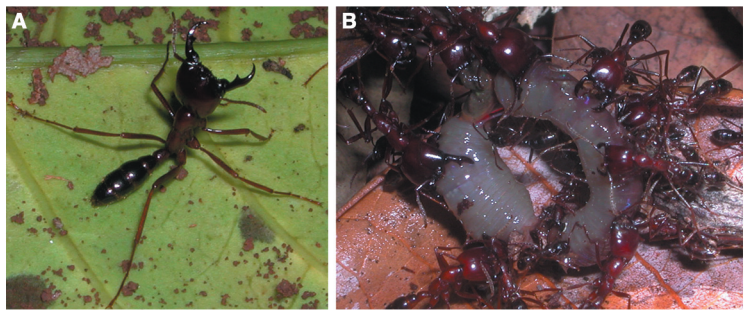

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Figure 1. Army ants of the subfamily Dorylinae.

(A) *Dorylus (Anomma) molestus* worker in defense position. (B) *D. molestus* workers preying on an earthworm. (Photographs by C. Schöning.)

subtropical habitats, this would explain their absence from amber found in more temperate regions. A subterranean lifestyle would also reduce their chances of being trapped in amber. Of today's army ants, only a small minority of the phylogenetically most-derived representatives of Ecitoninae and Dorylinae conduct the readily observed above-ground (epigaeic) mass-raids. The predominance of subterranean species, together with the fact that all extant army ants show characteristics common to species with strongly developed subterranean lifestyles, such as eyelessness and a reduction in palpal segments, indicate that they probably had a subterranean ancestor [13]. The fossil army ant found in Dominican amber could thus mark the adaptation of some species to epigaeic life.

The ancestral army ants were thus probably subterranean species which evolved to raid en mass on the increasing number of other ants, termites and larger arthropods in mid-to-late Cretaceous period. According to theory, mass raids evolved to allow specialized feeding on large prey or other social insects, leading either concurrently or shortly afterwards to the development of nomadism [14]. Although the biology of subterranean army ants is still largely unknown, and the first studies indicate several behavioral differences to epigaeically foraging species [15], remarkably, none of the extant species seem to have lost any of the traits of the army ant adaptive syndrome during their long existence.

Brady's [4] conclusions are also of consequence for dating major tectonic events. As army ant queens are flightless and need to be accompanied by numerous workers to found a new colony, their dispersal abilities are very limited. Even small rivers represent impassable barriers. If the army ant adaptive syndrome evolved only once it implies army ants originated on Gondwana prior to its fragmentation, and that this was followed by diversification of the various army ant subfamilies on the new-forming continents. Following Brady [4], the complete fragmentation of Gondwana should thus have occurred no earlier than about 100 million years ago. Modern textbooks stilvary in the dating of this event, which was long dated around 150–120 million years ago [8,9].

With their epigaeic raids, driving masses of fleeing insects and accompanied by numerous guest species hoping to obtain a share of the food, army ants are an outstanding sight of the tropics. Epigaeic as well as subterranean species are important ecological factors, shaping ground and soil arthropod diversity of most tropical and subtropical habitats. The new work of Brady [4] now indicates that, after its apparently unique evolutionary origin, the army ant adaptive syndrome has been retained by an increasing number of species on all continents. Army ants are thus not only highly efficient predators, but also an extraordinary example of the long-term conservation of a complex combination of behavioral and morphological traits and consequently an evolutionary model of success.

References

1. Gotwald, W.H., Jr. (1982). Army ants. In Social insects. Volume 4, H.R. Hermann, ed. (New York, Academic Press), pp. 157-254.
2. Gotwald, W.H., Jr. (1995). Army ants: the biology of social predation (Ithaca: Cornell University Press / Comstock Press).
3. Brosset, A. (1988). Le peuplement de mammifères insectivores des forets du nord-est du Gabon. Rev. Ecol. (Terre Vie) *43*, 23-46.
4. Brady, S.G. (2003). Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. Proc. Natl. Acad. Sci. U.S.A. *100*, 6575-6579.
5. Bolton, B. (1995). A New General Catalogue of the Ants of the World (Cambridge, London: Harvard University Press).
6. Brown, W.L., Jr. (1954). Remarks on the internal phylogeny and subfamily classification of the family Formicidae. Ins. Sociaux *1*, 21-31.
7. Gotwald, W.H., Jr. (1979). Phylogenetic implications of army ant zoogeography (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. *72*, 462-467.
8. Press, F., and Siever, R. (2000). Understanding Earth, 3rd Edition (New York: W. H. Freeman and Company).
9. Tarbuck, E.J., and Lutgens, F.K. (2000). Earth Science, 9th Edition (Upper Saddle River, New Jersey: Prentice Hall).
10. Bolton, B. (1990). Army ants reassessed: the phylogeny and classification of the doryline section (Hymenoptera, Formicidae). J. Nat. History *24*, 1339-1364.
11. Grimaldi, D., and Agosti, D. (2000). A formicine in New Jersey Cretaceous amber (Hymenoptera : Formicidae) and early evolution of the ants. Proc. Natl. Acad. Sci. U.S.A. 97, 13678-13683.
12. Wilson, E.O. (1985). Ants of the Dominican amber (Hymenoptera: Formicidae). 2. The first fossil army ants. Psyche *92*, 11-16.
13. Gotwald, W.H., Jr. (1978). Trophic ecology and adaptation in tropical Old World ants of the subfamily Dorylinae (Hymenoptera: Formicidae). Biotropica *10*, 161-169.
14. Wilson, E.O. (1958). The beginnings of nomadic and group-predatory behavior in ponerine ants. Evolution *12*, 24-36.
15. Berghoff, S.M., Weissflog, A., Linsenmair, K.E., Hashim, R., and Maschwitz, U. (2002). Foraging of a hypogaeic army ant: a long neglected majority. Ins. Sociaux *49*, 133-141.