absorbing aerosol are known, and because local island sources are not evident, we suggest that most fine-particle absorption is, like Asian dust, transported from the continents and may be elemental carbon of submicrometer size that originated from combustion (soot). If the specific absorption of soot (~8.5 $m^2 g^{-1}$) is used to convert mean b_a values for the fine mode to soot concentrations, we obtain 12 ng m^{-3} for period A and 2.5 ng m^{-3} for period B; these values are not unlike minima reported for the remote Atlantic (20 ng m^{-3}) (*14*). Although soot concentrations are too low to be analyzed chemically on these filters, samples with more concentrated quantities or analyzed by spectral absorption (or both) may be useful in verifying our suggestion. If it is true, it implies that dispersal of combustion-derived aerosol may persist throughout the troposphere and over hemispheric spatial scales.

References and Notes

1. T. P. Ackerman and O. B. Toon, *Appl. Opt.* **20**, 3661 (1981).
2. J. M. Mitchell, *J. Appl. Meteorol.* **10**, 703 (1971).
3. O. B. Toon and J. B. Pollack, *ibid.* **15**, 225 (1976).
4. A. D. Clarke, R. J. Charlson, L. F. Radke, *Geophys. Res. Lett.* **11**, 5 (1981).
5. R. J. Ball and G. D. Robinson, *J. Appl. Meteorol.* **21**, 171 (1982).
6. T. N. Carlson and R. S. Caverly, *J. Geophys. Res.* **82**, 3141 (1977).
7. S. L. Thompson, *Ambio* **13**, 236 (1984).
8. A. D. Clarke, *Appl. Opt.* **21**, 3011 (1982).
9. B. G. Mendonca and W. T. Iwaoka, *J. Appl. Meteorol.* **8**, 213 (1969).
10. This time-based removal of upslope contamination was recently shown to be good (*11*), although a new multivariable monitor-controller is claimed to perform about 25 percent better in eliminating contamination.
11. J. R. Parrington, W. H. Zoller, N. K. Aras, *Science* **220**, 195 (1983).
12. B. A. Bodhaine, *J. Geophys. Res.* **88**, 10753 (1983).
13. A. D. Clarke and A. P. Waggoner, *Appl. Opt.* **21**, 398 (1982).
14. M. O. Andreae, *Science* **220**, 1148 (1983).
15. We thank K. Coulson, T. Defoor, and the staff of the Mauna Loa Observatory for daily sample collection, and B. Bodhaine for aerosol data from the observatory. This research was supported in part by NOAA under grant NA 79RAD00018.

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Invasion and Extinction in the West Indian Ant Fauna: Evidence from the Dominican Amber

Abstract. *Of 37 genera and well-defined subgenera identified in the amber of the Dominican Republic (late Oligocene or early Miocene), 34 have survived somewhere in the New World tropics to the present, although the species studied thus far are extinct. Of the surviving genera and subgenera, 22 persist on Hispaniola. Fifteen genera and subgenera have colonized the island since amber times, restoring the number of genera and well-defined subgenera now present on Hispaniola to 37. A higher extinction rate has occurred in genera and subgenera that are either highly specialized or possess less colonizing ability, as evidenced by their restriction to the New World.*

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The amber of the Dominican Republic, which contains large numbers of well-preserved insect remains, provides an unusual opportunity to study evolution and extinction in an insular fauna. The most abundant insects in the amber are the ants. Baroni Urbani and Saunders (*1, 2*) recorded the presence of the Neotropical genera *Anochetus, Gnamptogenys, Paracryptocerus, Pseudomyrmex,* and *Trachymyrmex*. Additional specimens placed by Baroni Urbani (*3*) in *Leptomyrmex*, which is today restricted to the Indo-Australian region, have recently been transferred to the Neotropical *Camponotus branneri* group (*4*). I have been able to study 602 pieces of amber containing an estimated 1254 ants; most of these pieces were accumulated during the past 10 years at the Museum of Comparative Zoology, Harvard University (*5*). The diversity at the generic and specific level parallels that found in the contemporary Hispaniolan fauna (*6*): 37 genera and well-marked subgenera are now known from the Dominican amber, and an identical number have been found on present-day Hispaniola. Twenty-two of the genera and subgenera in the two chronofaunas are the same (Table 1).

Although additional genera will undoubtedly be found in both the amber deposits and the living fauna, the lists in Table 1 can be regarded as including a large majority of the complete faunas for two reasons. First, the considerable collections of Baltic amber ants studied by Mayr (*7*) and Wheeler (*8*) (10,988 specimens) were found to represent 43 genera. Although this diverse Oligocene fauna is thus known from about ten times as many specimens, it contains only six more genera than the Dominican amber fauna, a difference of 16 percent. Second, collections of the modern faunas made in Haiti and the Dominican Republic have been reasonably thorough (*6*). Studies of other islands in the Greater Antilles, namely, Cuba (*9*), Jamaica (*10*), and Puerto Rico (*11*), have yielded lists consistent with a projection of the contemporary Hispaniolan fauna of not many more than 40 genera and well-marked subgenera.

The exact age of the Dominican amber has not yet been determined, but combined stratigraphic and foraminiferal analyses of its matrix suggest that most of the deposits originated no later than the early Miocene (*2*). I favor the minimal age (about 20 million years) or at most a late Oligocene origin. Only three of the 37 Dominican amber genera, or 8 percent, are unknown from the contemporary world fauna and hence can be provisionally considered extinct (Table 1). This condition contrasts with that of the Baltic amber, which is Eocene to early Oligocene in age (*12*) and of which 44 percent are extinct genera; that is, 19 of the 43 genera recorded to date are unknown among living ants (*8*). The Dominican amber ants also differ to a similar degree from the 20 genera of the shales from Florissant, Colorado, which are upper Oligocene in age and include eight, or 40 percent, that are now evidently extinct (*13*).

Most of the pieces of Dominican amber came from the western amber-bearing region, located in the mountainous La Cumbre region 10 to 20 km northeast of Santiago. A few came from the eastern amber-bearing region south of Sabana de la Mar. Still others originated from Cotui, more centrally located. The Cotui pieces, making up fewer than 5 percent of the specimens I have seen, are evidently much younger than those from other Dominican localities (*14*); for that reason I excluded them from the present analysis. The most common ant species, *Azteca alpha*, occurs in pieces from nearly all the localities, as well as in the same pieces as seven of the genera other than *Azteca*.

To provide a first analysis of the history of the Dominican fauna, I classified the amber and living genera into six biogeographic categories (Table 1). The traits considered were the presence or absence of the genera in the amber and the extent of their retreat since amber times. The lists from the modern fauna were based on regional monographs of all of the islands of the Greater Antilles (*6, 9–11, 15*), together with more recent collections made in Cuba, the Dominican Republic, and Puerto Rico by W. L. Brown and me. In addition to the generic identifications of the amber fauna, I have conducted species-level studies of portions of the subfamilies Ponerinae and Myrmicinae (*4, 16*) as well as the single representative of the Ecitoninae (*Neivamyrmex ectopus*) (*16*) and all of the Dolichoderinae (*16*). In every case the fossils are at least as different anatomically from modern species as the least different among the modern species are from each other. As a result, I have classified the amber populations as distinct species. The majority belong to recognizable species groups in the contemporary New World fauna.

Perhaps the biogeographically most notable of the amber forms is *Neivamyrmex ectopus*, the first fossil army ant discovered. No living ecitonine is known from the northern arc of the Lesser Antilles or any of the Greater Antilles (*17*). *Neivamyrmex ectopus* is closest to the species of the contemporary *N. agilis* species group, whose ranges lie predominantly in Mexico and the southern United States (*17*). The discovery of this ant in the Greater Antilles is therefore consistent with the view, based upon the results of geological and limited paleobotanical studies (*18*), that the Greater Antilles were larger and extended closer to the Mexican mainland during the middle and late Tertiary than is now the case.

The retreat of 15 ant genera and subgenera from Hispaniola since amber times permits a first evaluation of the factors influencing extinction in large island faunas. Table 2 lists the frequencies of the taxa exhibiting traits that can be expected to affect extinction rates, immigration rates, or both, and that can be ascertained from existing knowledge of the Neotropical ants (*19*). In testing for statistical differences among the frequencies (*G* test of independence, 2 by 2 tables), I have treated the living and fossil genera as samples drawn from imaginary and indefinitely larger pools of genera in a manner that is random with respect to the traits being examined. In addressing the question of whether the two percentages in each column of Table 2 are significantly different from one another, this procedure makes explicit the competing null hypothesis—that the differences observed are due to chance alone.

Each of the traits listed is conjectured to affect either dispersal ability or extinction rate, with the latter being enhanced by smaller populations of colonies. The data fail to support effects due to lower dispersal power of the queen, in spite of the clear-cut single example of army ants. Nor does evidence exist for an effect due to reduced populations of colonies that might be caused by large individual or colony size. On the other hand, a negative relation exists between survival on Hispaniola and extreme specialization in prey, social parasitism, and nest site ($P < 0.05$). As documented in the last column of Table 2, genera and subgenera that also occur in the Old World, and hence show evidence of greater colonizing ability, have reached the Greater Antilles more often and become extinct less frequently on Hispaniola since amber times ($P < 0.05$).

Several of the genera that retreated from the Greater Antilles, in particular, *Dolichoderus*, *Monacis*, and *Paraponera*, are today principal elements of moist tropical forests in South and Central America. Whether this reflects a corresponding change in the vegetation types of the Greater Antilles, at least to the extent of the loss of pockets of forests more like those now on the mainland, cannot be ascertained from existing paleobotanical evidence (*18*).

Table 1. The status of ant genera and well-marked subgenera on Hispaniola (Dominican Republic plus Haiti).

Present in Dominican amber

Now extinct worldwide: *Ilemomyrmex*, *Oxyidris*, new genus near *Rogeria*

Now extinct in the Greater Antilles but present elsewhere in the Neotropical region: *Azteca*, *Dolichoderus*, *Erebomyrma*, *Hypoclinea*, *Leptothorax (Nesomyrmex)*, *Monacis*, *Neivamyrmex*, *Paraponera*, *Prionopelta*

Now extinct on Hispaniola but present elsewhere in the Greater Antilles: *Cylindromyrmex*, *Octostruma*, *Prenolepis*

Still present on Hispaniola: *Anochetus*, *Aphaenogaster*, *Camponotus*, *Crematogaster (Acrocoelia)*, *Crematogaster (Orthocrema)*, *Cyphomyrmex*, *Gnamptogenys*, *Hypoponera*, *Iridomyrmex*, *Leptothorax (Macromischa)*, *Odontomachus*, *Pachycondyla (Trachymesopus)*, *Paracryptocerus*, *Paratrechina (Nylanderia)*, *Pheidole*, *Platythyrea*, *Pseudomyrmex*, *Smithistruma*, *Solenopsis (Diplorhoptrum)*, *Solenopsis (Solenopsis)*, *Tapinoma*, *Trachymyrmex*

New arrivals

New World genera and well-marked subgenera present in the modern Hispaniolan fauna but unknown in the Dominican amber: *Acropyga*, *Brachymyrmex*, *Ephebomyrmex*, *Eurhopalothrix*, *Hypocryptocerus*, *Leptogenys*, *Monomorium*, *Mycocepurus*, *Myrmelachista*, *Solenopsis (Euophthalma)*, *Strumigenys*, *Wasmannia* (possibly introduced by commerce)

Old World genera (or species groups within these genera) introduced within historical times by human commerce: *Cardiocondyla*, *Paratrechina (Paratrechina)*, *Tetramorium*

Table 2. Ant genera and well-marked subgenera found in the Dominican amber and the living fauna of Hispaniola (Dominican Republic plus Haiti), classified according to major traits that affect dispersal and extinction: Category A, amber genera that survived on Hispaniola; category B, amber genera that became extinct on Hispaniola but survived elsewhere. Some genera and subgenera possess more than one trait, and many possess none; hence the percentages do not sum to 100.

Genera in category (number)	Percentage of genera displaying trait			
	Flightless queen*	Large individuals or colonies†	Highly specialized as predators or social parasites or in nest site*†	Also found in living Old World fauna‡
		Category A		
22	0	4.5	4.5	68.2
		Category B		
12	8.3	25.0	33.3	33.3

*Less dispersal. †Smaller populations of colonies. ‡More dispersal.

References and Notes

1. C. Baroni Urbani, *Stuttgarter Beitr. Naturkd. B* **54**, 1 (1980); *ibid.* **55**, 1 (1980); *ibid.* **67**, 1 (1980).
2. ——— and J. B. Saunders, *Trans. 9th Caribbean Geol. Conf. Santo Domingo* **1**, 213 (1982).
3. C. Baroni Urbani, *Stuttgarter Beitr. Naturkd. B* **62**, 1 (1980).
4. E. O. Wilson, *Psyche* **92**, 17 (1985).
5. Of the amber pieces studied, 439 are in the Museum of Comparative Zoology, Harvard University; 157 are in the Florida State Collection of Arthropods, Gainesville; and six are in the Los Angeles County Natural History Museum.
6. W. M. Wheeler and W. M. Mann, *Bull. Am. Mus. Nat. Hist.* **33**, 1 (1914); W. M. Wheeler, *Bull. Mus. Comp. Zool. Harv. Univ.* **80**, 195 (1936). I have studied excellent collections made by W. L. Brown in the Dominican Republic during the past 10 years and placed in the Museum of Comparative Zoology.
7. G. Mayr, *Beitr. Naturkd. Phys.-Ökon. Ges. Königsberg* **1**, 1 (1868).
8. W. M. Wheeler, *Schrift. Phys.-Ökon. Ges. Königsberg* **55**, 1 (1914).
9. ———, *Bull. Mus. Comp. Zool. Harv. Univ.* **54**, 477 (1913); *ibid.* **72**, 3 (1931); *ibid.* **81**, 441 (1937); C. Baroni Urbani, *Entomol. Basil.* **3**, 395 (1978); P. Alayo, *Ser. Biol. Acad. Cienc. Cuba* **53**, 1 (1974); plus extensive, previously unreported collections in Cuba that I studied.
10. W. M. Wheeler, *Bull. Am. Mus. Nat. Hist.* **24**, 159 (1908); *ibid.* **30**, 21 (1911); *Univ. Iowa Stud. Nat. Hist.* **10**, 3 (1923).

11. M. R. Smith, *J. Agric. Univ. P.R.* **20**, 819 (1936); J. A. Torres, *Biotropica* **16**, 284 (1984).
12. S. G. Larsson, *Entomonograph (Klampenborg, Denmark)* **1**, 1 (1978).
13. F. M. Carpenter, *Bull. Mus. Comp. Zool. Harv. Univ.* **70**, 3 (1930).
14. D. Schlee, *Stuttgarter Beitr. Naturkd. C* **18**, 29 (1984).
15. W. W. Kempf, *Stud. Entomol.* **15**, 3 (1972).
16. E. O. Wilson, *Psyche* **92**, 1 (1985); *Isr. J. Entomol.*, in press.
17. J. F. Watkins II, *The Identification and Distribution of the New World Army Ants* (Baylor Univ. Press, Waco, Texas, 1976).
18. A. Graham and D. M. Jarzen, *Ann. Mo. Bot. Gard.* **56**, 308 (1969).
19. Data on the natural history of the Neotropical ants are drawn from a wide range of published reports. The references, together with a list of genera and subgenera in each of the eight cells of Table 2, are available from the author upon request.
20. This research was supported in part by grant BSR 8119350 from the National Science Foundation. I am grateful to the following persons for assistance and advice: G. Alpert, C. Baroni Urbani, J. Brodzinsky, W. L. Brown, Jr., F. M. Carpenter, J. Carpenter, R. M. Fagen, A. Graham, C. Kugler, D. S. Simberloff, R. Snelling, and R. E. Woodruff.

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Cyclic AMP Regulation of Eukaryotic Gene Transcription by Two Discrete Molecular Mechanisms

Abstract. *In experiments designed to study the mechanism by which peptide hormones binding to their plasma membrane receptors stimulate the expression of specific genes, the transcription of two neuroendocrine genes, prolactin and growth hormone, was analyzed in a rat pituitary cell line. The results showed that cyclic adenosine monophosphate (cyclic AMP) stimulates the transcription of discrete subsets of eukaryotic genes by at least two independent molecular mechanisms. Cyclic AMP stimulated growth hormone gene transcription and phosphorylation of a 19,000-dalton nuclear protein; this appears to reflect direct nuclear actions of the cyclic AMP–dependent protein kinase. In contrast, the stimulation by cyclic AMP of prolactin gene transcription appears to reflect activation of a discrete calcium-dependent event.*

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Evolutionary conservation of critical regulatory signal systems has been reported for organisms as distantly related as bacteria and mammals. An example of such a conserved system is 3′,5′-adenosine monophosphate (cyclic AMP). The discovery of the cyclic AMP receptor protein (CRP) and its identification as the regulatory subunit of cyclic AMP–dependent protein kinase in eukaryotes (*1*) has led to its characterization as an important regulator of prokaryotic gene expression. In the presence of cyclic AMP, bacterial cyclic AMP receptor protein binds to specific DNA sequences in the promoter region of catabolite-sensitive operons (about 10 percent of the bacterial genome), permitting the binding of RNA polymerase and subsequent transcription (*2*). In eukaryotic organisms, cyclic AMP or hormones that stimulate adenylate cyclase influence the synthesis of various proteins (*3*). A direct effect of cyclic AMP at the level of gene transcription has been shown for several genes, including prolactin (*4, 5*), phosphoenolpyruvate carboxykinase (*6, 7*), lactate dehydrogenase (*8*), and possibly the tyrosine hydroxylase (*9*) genes. The two mammalian forms of CRP appear to have lost the DNA-binding domain characteristic of bacterial CRP (*10*), which suggests the importance of the catalytic subunit in regulation of gene transcription. Analysis of mutations of cyclic AMP–dependent protein kinase in several cell lines has suggested that most, and perhaps all, of the intracellular effects of cyclic AMP are mediated by cyclic AMP–dependent protein kinase (*11*). The effects of cyclic AMP on tyrosine aminotransferase gene expression are mediated by an activation of cyclic AMP–dependent protein kinase (*12*).

We have previously used the clonal rat pituitary cell line GH$_4$ to characterize the regulation of prolactin gene transcription by peptide hormones—thyrotropin-releasing hormone (TRH) and epidermal growth factor (EGF)—and cyclic AMP and to describe the hormone-dependent phosphorylation in the nucleus of a 23-kilodalton (kD) basic protein, referred to as BRP (*5, 13*).

Although TRH produces only small stimulations of adenylate cyclase (*14*), various cyclic AMP analogs and forskolin rapidly stimulate prolactin gene transcription, inducing an increase in transcription by a factor of 3 to 5 in less than 10 minutes (*5*). In the present study, the maximum stimulation of prolactin gene transcription produced by cyclic AMP was no more than 50 to 60 percent of that produced by the peptide hormone TRH (Fig. 1) and was not augmented by simultaneous addition of the calcium ionophore A23187 to mimic the increase in intracellular free calcium produced by TRH (*15*). Simultaneous treatment of GH$_4$ cells with maximally stimulating concentrations of TRH and forskolin produced the same stimulation of prolactin gene transcription as treatment with TRH alone. This is consistent with the possibility that the effects of TRH and forskolin are mediated by the same mechanism.

One such mechanism may be the activation of cyclic AMP–dependent protein kinase by TRH. Cyclic AMP–dependent protein kinase phosphorylates two subtypes of histone H1 at a single site (Ser^{37}) both in vivo and in vitro (*16*). Tryptic peptide maps of the combined histone H1 fraction showed a marked phosphorylation of the peptide containing Ser^{37}

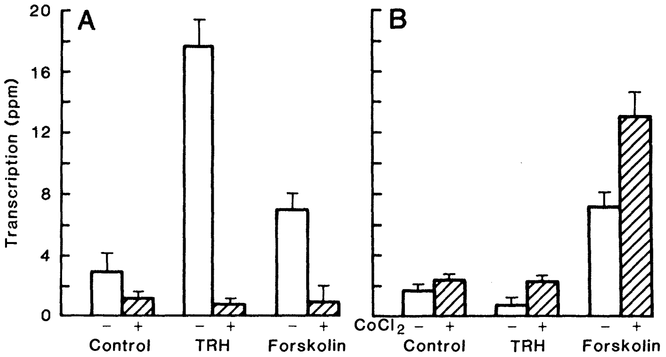

Fig. 1. Differential inhibition of forskolin-stimulated prolactin (A) and growth hormone (B) gene transcription. Rates of prolactin and growth hormone gene transcription were simultaneously measured in GH$_4$ cultures treated with TRH (3 × 10^{-7}*M* for 30 minutes) or forskolin (10^{-6}*M* for 30 minutes). Where indicated (shaded bars), cobalt chloride (CoCl$_2$, 1 m*M*) was added 5 minutes before addition of TRH or forskolin. Prolactin gene transcription was measured by DNA excess hybridization of nascent RNA transcripts isotopically labeled by chain elongation in isolated nuclei as described (*5, 13*). Results are the average of triplicate determinations ± standard error of the mean. TRH, forskolin, and cobalt had no effect on the transcription rate of three constitutively expressed genes.