most untouched regardless of the hare density at the feeding station. Adventitious shoots of each of the above four tree species normally contain at least twice this resin concentration (Fig. 1). Furthermore, balsam poplar and green alder resins were much more repellent than those of quaking aspen and paper birch ($P < .001$), indicating that resin repellence has a species-dependent qualitative component (Fig. 2). The ether-treated and untreated control twigs did not differ in their palatability ($P > .40$), indicating that treatment with ether had no effect on twig palatability.

Although slightly more treated twigs were eaten at the feeding stations that were visited by more hares ($P < .05$), presumably because the more dense hare subpopulations were more food-limited, most of the experimental variance was explained by the resin treatments (Fig. 2). Thus, it would appear that these resins effectively repel even food-limited snowshoe hares (*8*).

While the potency of these resins as hare repellents presumably explains why the adventitious shoots of the species tested are less palatable to snowshoe hares than their mature-growth-form twigs, neither the exact chemical composition nor the mode of biological activity of these resins is known. However, alder and poplar resins contain several methylated flavonols (*9*), which may lower protein digestibility (*4*). Alder, poplar, and birch resins contain antibiotics (*10*) that may upset vitamin production and digestion in the hare's cecum (*4*). Moreover, ingestion of mountain birch (*B. pubescens*) adventitious shoots by mountain hares (*L. timidus*) results in sodium loss (*11*). Sodium loss by hares under cold conditions may lead to a shock syndrome (*12*) similar to that described (*13*) for a declining snowshoe hare population.

Regardless of the biological basis for resin repellence, the fact that preferred browse species of the snowshoe hare—such as aspen, balsam poplar, and paper birch—produce unpalatable, resinous adventitious shoots after severe browsing by peak snowshoe hare populations (*3, 4*) suggests an extreme flexibility with respect to chemical defense in the snowshoe hare's preferred browse supply. Such defensive flexibility is advantageous to woody plants of the boreal forest because energy-rich substances such as resins (*14*) appear to be produced after severe hare browsing, and carbon is allocated to growth and other processes when there is little browsing. Moreover, because (i) hare browsing during the peak phase of the 10-year hare cycle results in the production of adventitious shoots by the snowshoe hare's preferred browse species (*3*), (ii) these adventitious shoots have been experimentally shown to be of extremely low palatability to snowshoe hares (*4*), (iii) the nutritive quality of browse to snowshoe hares has been experimentally demonstrated to be directly proportional to its palatability (*15*) and (iv) the low palatability of adventitious shoots is a consequence of a high secondary metabolite content, these results suggest that browsing-induced plant defenses may play a role in the regulation of the 10-year hare cycle.

JOHN P. BRYANT

Institute of Arctic Biology,
University of Alaska, Fairbanks 99701

References and Notes

1. L. Keith, *Wildlife's Ten Year Cycle* (Univ. of Wisconsin Press, Madison, 1963), pp. 1–201; M. Bulmer, *J. Anim. Ecol.* **43**, 701 (1974); *ibid.* **44**, 609 (1975).
2. D. Dodds, *J. Wildl. Manage.* **24**, 53 (1960); J. F. Fox, *Oecologia (Berl.)* **31**, 349 (1978); J. L. Pease, R. H. Vowles, L. B. Keith, *J. Wildl. Manage.* **43**, 43 (1979); J. O. Wolff, *Ecol. Monogr.* **50**, 111 (1980).
3. A. DeVos, *J. For.* **62**, 238 (1964).
4. D. Klein, *Proceedings of the 13th International Congress of Game Biologists*, Atlanta, 1977, p. 266; J. Bryant, *Proceedings of the 1st Lagomorph. Conference*, Guelph, 1979, in press; ——— and P. Kuropat, *Annu. Rev. Ecol. Syst.* **11**, 261 (1980).
5. Nomenclature follows E. Hulten, *Flora of Alaska and Neighboring Territories* (Stanford Univ. Press, Stanford, 1968), pp. 1–1008.
6. Chemical analysis of the diethyl ether–soluble fraction of these species (by Dr. P. Reichardt, University of Alaska, Department of Chemistry) has shown that this fraction is primarily composed of terpenes and diethyl ether–soluble phenolic substances. Nitrogen and phosphorus were analyzed on a Technicon autoanalyzer by a sulfuric/selenious acid digest and a colorimetric analysis with a ferricyanide blue reaction for nitrogen and a molybdate blue reaction for phosphorus.
7. G. West and A. Salo, *Oecologia (Berlin)* **41**, 207 (1979).
8. A browse survey and mark-recapture population estimate indicated that a hare population of four hares per hectare had destroyed more than 90 percent of the browse within the study area prior to the experiments. In this area a hare population of six hares per hectare was reached during the winter of 1972. This density of hares exceeded the carrying capacity of the study area and resulted in a population decline [J. O. Wolff, in (*2*)]. Differences among feeding stations in hare density were qualitatively assessed from the density of tracks, feces, and browsed shoots near the stations.
9. E. Wollenwebber, *Phytochemistry* **13**, 760 (1973); ———, M. Jay, J. Faure-Bovin, *ibid.*, p. 2618; D. Rhoades, personal communication.
10. J. Mokry, J. Kvidera, A. Banka, *Cesk. Biol.* **3**, 113 (1954); G. Dull, J. Fairley, R. Gottshall, E. Lucas, *Antibiot. Annu.* **51**, 114 (1957); H. Schildknecht and G. Rauch, *Z. Naturforsch.* **116**, 422 (1961).
11. A. Pehrson, *Proceedings of the 1st Lagomorph Conference*, Guelph, 1979, in press.
12. K. Meyers and H. Bults, in *ibid.*, in press.
13. R. Green and C. Larson, *Am. J. Physiol.* **119**, 319 (1937).
14. Terpene and phenolic resins have a high caloric content [R. Moss. *Condor* **75**, 2 (1973)] and a high carbon cost of synthesis [F. Penning de Vries, *Ann. Bot. (London)* **39**, 7 (1975)].
15. T. A. Bookhout, *Mich. Dep. Conserv. Res. Devel. Rep. No. 38* (1965).
16. I thank F. S. Chapin III, A. Bloom, P. Kuropat, D. Klein, A. Pehrson, S. Maclean, E. Haukioja, P. Niemala, M. Jokkinen, I. Hakkinen, R. White, and G. Shaver for criticisms. Supported by NSF grant DEB 7823919.

12 November 1980; revised 27 May 1981

Origin of Corn: Pollen Evidence

Abstract. *The origin of Indian corn remains controversial. Its closest wild relative is teosinte, with which it hybridizes freely to produce fertile progeny. Teosinte ears are smaller and simpler than those of corn. Searches for a more likely living ancestor have failed, but nine of its assumed pollen grains have been recovered in deep drill-core samples obtained from a stratum of soil under Mexico City, which is believed to antedate man in the Western Hemisphere. These nine largest grains are indistinguishable from pollen of modern corn. It has been assumed to be that of a postulated wild corn other than that of teosinte, but this does not account for the possibility that the pollen grains are those of a tetraploid teosinte-producing pollen with two sets of chromosomes. This likelihood has been examined by treating modern teosinte plants with colchicine, which induces tetraploidy. The result has been many teosinte pollen grains indistinguishable in size from modern corn. In interpreting this outcome it is important also to know that heat treatment of corn and other plants induces polyploidy, and that the deep drill-core pollen was recovered in a stratum of volcanic clay indicating the high temperature known to favor doubling of corn pollen volumes.*

The corn Columbus and his men found on the island of Cuba in 1492 was remarkable in more ways than they could possibly have imagined. The American Indians had made it the most important human food plant of the Western Hemisphere and had adapted it to suitable growing conditions from near the tip of South America to lower Canada. Their achievement is perhaps the most remarkable man-made plant transformation of all time, but in the process corn was so altered that it can no longer survive in the wild, for it has no means of disseminating its kernels (*1*).

When Linnaeus in 1753 assigned corn to the newly created genus *Zea* (from the Greek) and species *mays* (from the Taino language of the West Indies), he knew of no other plant that could reasonably have been placed in the genus of corn. Its closest relatives are a group of plants commonly known as teosintes. They grow wild in parts of Mexico and Guatemala. Plant taxonomists initially placed them in a newly created genus, *Euchleana mexicana*. Like corn, all annual teosintes normally have ten pairs of chromosomes; that is, they are diploids. Corn and teosintes hybridize freely, and the progeny are fully fertile in many combinations (*2*).

Some consider teosinte so unpromising a source of human food that there has been little or no incentive to harvest and cultivate it. However, it is not greatly different from wild wheat in the Near East—in yield, harvesting, and as a source of food. It is true that teosinte kernel cases are closed by hard lignified glumes that at first sight appear to be a formidable bar to use of teosinte as a human food source. However, prior to maturity both cases and kernels are readily edible. At the right maturity and proper moisture content, they can also be eaten directly, cases and all. At lesser moisture content, teosinte seeds will pop just as does domestic popcorn, in which edible kernels are easily freed from their cases. Whole dry teosinte can be ground, with the use of primitive pounding or grinding stones, and subsequently with a simple water flotation technique that permits cases and glumes to be skimmed largely free of their denser whole and cracked kernels. The resulting meal can be eaten in a number of ways (*3*).

The name teosinte is derived from the Nahuatl Indian language: *teotl*, God, and *centli*, ear of corn, thus God's corn, indicating that corn was derived from teosinte (*4*). Spanish-speaking native Indians in parts of Mexico refer to teosinte as *madre de maiz*, mother of corn.

This could be perhaps a kind of cultural memory? They also believe it is good for their corn to have teosinte growing with it or nearby. They are quite right, although they do not know why. The fact is that teosinte hybridizes freely with corn and in subsequent generations counteracts the deleterious effects of the close inbreeding characteristic of their small isolated plantings. Despite an impressive array of evidence that the most cornlike teosintes, *Zea mays* ssp. *mexicana* (*5*), were the direct ancestors of modern Indian corn, there continues to be a group of investigators who contend that an extinct corn other than teosinte was ancestral to modern corn (*6*).

Pollen evidence. Plant pollen grains, ancient and recent, are usually identifiable to genus, or in some instances to species, by their shape, size, and outer wall sculpturing. It is now agreed that pollen of corn and teosinte are indistinguishable except by size, and then only in some circumstances. Advocates of an extinct or yet-to-be discovered wild corn now base their case primarily on pollen size, modern corn pollen being up to twice the volume of teosinte pollens. The evidence consists of 5 of 14 pollen grains recovered in 1954 from a drill-core sample taken in connection with the construction of a high-rise building in Mexico City. These pollen grains, recovered at a depth of 70 m, are estimated to have been deposited some 25,000 to 80,000 years before the present, and are judged to predate man in the Western Hemisphere. These five pollen grains were in the size range of modern corn, thus leading Mangelsdorf, Barghoorn, and collaborators to conclude in 1954 that this was pollen of corn, not teosinte (*7*).

These conclusions can now be disputed for the following reasons: (i) Contamination of the drill-core samples may be a remote possibility but cannot be entirely excluded. The pollen could then be that of modern corn. (ii) The large drill-core pollen is too large for an ancient wild corn, for there is a known positive correlation of ear and silk length and pollen size. Archeological corncobs are short. Almost surely a wild corn progenitor would have been little or no longer (*8, 9*). (iii) With teosinte now so widely held to be the ancestor of corn, one would expect similar ratios to carry over to the teosintes. I have tested this theory and find it correct.

Finally, it is now well known that newly arisen tetraploids of corn have pollen approximately twice the volume of their diploid counterparts (*10, 11*). The five large drill-core pollen grains could have been from newly arisen tetraploids (or from tetraploid sectors of diploid plants) as a result of abnormally high temperatures in their environment. High temperature induces polyploidy in plants (*10*), and the Mexico City area has a long history of volcanic activity. That temperature-induced polyploidy was the source of the five large pollen grains appears likely since they were lodged in a stratum of volcanic clay rather than in the more abundant sand layers. On this hypothesis, the nine smaller pollen grains are those of normal diploid teosinte.

Mangelsdorf, Barghoorn, and Baner-

Table 1. Mean pollen diameters in micrometers of treated and untreated plants. S.D., standard deviation; Av, average.

Plants with large pollens (No.)	Number of large pollen grains per plant	Large pollen grains		Untreated controls	
		Mean diameter	S.D.	Mean diameter	S.D.
45	63	95.4	4	77.4	8
87	13	92.4	5	73.6	3
89	89	94.4	2	73.2	4
171	50	91.2	3	73.6	4
196	10	92.8	6	73.6	4
209	23	90.0	4	72.0	1
216	10	92.0	4	73.2	4
225	90	94.8	6	72.8	4
240	8	92.4	4	73.6	4
251	63	94.4	7	74.8	7
	419	Av 92.8		Av 73.6	

Table 2. Summary of corn-teosinte pollen sizes in mean diameter (micrometers), with number of pollen grains measured.

Source	Pollen	
	Size (μm)	Number
Illinois tetraploid dent*	106.8	60
Illinois diploid dent*	89.1	60
Chicago-adapted teosinte, colchicine-treated presumed to be tetraploid	92.8	419
Chicago-adapted diploid teosinte	72.8	80
Tetraploid *Zea perennis* Emerson clone	63.8	88
Miscellaneous wild annual diploid teosintes *Zea mays* ssp. *mays*	70.4	104
Composite diploid teosintes recovered from corn-teosinte hybrids	72.4	100
Composite of diploid recovered corn from corn-teosinte hybrids	80.4	8400
Composite of three hybrid diploid dent corns	88.3	120

*Data from Cavanah (*11*).

jee now agree with others "... that the pollen of corn cannot be distinguished from teosinte by their spinule patterns which are quite similar, the only criterion for making a distinction is one of size" (*9*). It is therefore entirely reasonable to assume that the five largest pollen grains of the 14 recovered in the Mexico City drill-core sample are diploid grains produced by tetraploid teosinte rather than diploid grains from wild corn. Thus there is no solid evidence that a wild corn other than teosinte ever existed.

I have tested this possibility experimentally by treating teosinte plants with the drug colchicine, which induces polyploidy. Plants of 244 annual diploid teosintes, adapted to Chicago summer latitudes but otherwise indistinguishable from wild teosintes, including pollen size, were treated with colchicine in the expectation of inducing pollen approximately double the volume of controls. These plants were grown during the summer of 1980 in greenhouse compartments isolated from all corn pollen. Ten plants each produced some large pollen with a volume approximately double that of pollen grains from untreated controls (Table 1). In sum, 419 large pollen grains were measured. The remaining 234 plants yielded only pollen of essentially normal size. These and the normal pollen grains among plants with large pollen also serve as controls. However, pollen grains from untreated controls were also measured with no large pollen detected.

It seems most improbable that the colchicine-induced large pollen grains did not carry two sets of chromosomes, but it would have been even more remarkable if all 419 pollen grains were then so closely double the volume of their ten-chromosome controls. It should be emphasized again that newly arisen tetraploid corn plants produce pollen whose volume is twice that of their diploid controls and that teosinte is now said to differ taxonomically only at the subspecies level.

GEORGE W. BEADLE
University of Chicago,
Chicago, Illinois 60637

References and Notes

1. To avoid possible confusion in use of common and taxonomic names of corn and teosinte, I shall use the following: corn, Indian corn or maize, taxonomically: *Zea mays* subspecies *mays*; postulated wild corn believed to be extinct or conceivably still undiscovered; and teosinte of four species, including *Zea mays* ssp. *mexicana*, presumed to be the direct ancestor of cultivated corn.
2. H. G. Wilkes, *Teosinte: The Closest Relative of Maize* (Bussy Institution of Harvard University, Cambridge, Mass., 1967).
3. G. W. Beadle, *Field Mus. of Nat. Hist. Bull.* **43**, 1010 (1972).
4. *Webster's Third International Dictionary of the English Language* (1961), p. 2357.
5. H. H. Iltis and J. F. Doebley, *Am. J. Bot.* **67**, 994 (1980).
6. P. C. Mangelsdorf, *Corn, Its Origin, Evolution and Improvement* (Harvard Univ. Press, Cambridge, Mass., 1974).
7. E. S. Barghoorn, M. F. Wolfe, K. H. Clisby, *Bot. Mus. Leafl. Harv. Univ.* **16**, 229 (1954); P. C. Mangelsdorf, R. S. MacNeish, W. C. Galinat, *ibid.* **17**, 125 (1954).
8. W. C. Galinat, *Econ. Bot.* **15**, 320 (1961).
9. C. Mangelsdorf, E. S. Barghoorn, U. C. Banerjee, *Bot. Mus. Leafl., Harv. Univ.* **26**, 237 (1978).
10. L. F. Randolph, *J. Agric. Res.* (1935), p. 591.
11. J. A. Cavanah, thesis, University of Illinois, Urbana (1962).
12. I thank my associates in the Biology Division of the University of Chicago for encouragement in this attempt to solve the long-standing problem of the origin of corn. David Toub, an undergraduate in the Department of Biology, assisted in inducing tetraploidy in teosinte by colchicine treatments. Professors James A. Teeri and Edward D. Garber have assisted and encouraged me. Professor D. E. Alexander of the University of Illinois, Urbana, referred me to the unpublished master's thesis of J. A. Cavanah, at the University of Illinois, Urbana, who then permitted me to refer to it. I am indebted to the individual referees who reviewed my account and significantly improved my presentation.

18 February 1981; revised 11 June 1981

Magnetic Material in the Head of the Common Pacific Dolphin

*Abstract. Magnetic material carrying natural remanent magnetization is present in the head of the common Pacific dolphin (*Delphinus delphis*). A sample of this material, isolated from the dura mater, has a moment of 2×10^{-5} gauss–cubic centimeter. The presence of such strongly magnetized material suggests that it may play a navigational role.*

Evidence has been accumulating that certain organisms use the geomagnetic field as a navigational aid. Probably the most convincing data are provided by studies on magnetotactic bacteria (*1–3*), bees (*4, 5*), and homing pigeons (*6, 7*). All these organisms contain magnetite (*8, 9*). In the homing pigeon, some of the magnetite occurs between the dura mater and the skull. We now report the discovery of magnetite in the head of the common Pacific dolphin (*Delphinus delphis*). This appears to be the first reported occurrence of magnetite in a mammal. The dolphins were obtained from the Los Angeles County Museum of Natural History through a program whereby dead stranded marine mammals are collected for research.

The head of the animal was cut into five 2.5-cm-thick coronal sections with a Stryker autopsy saw. These were cut parasagittally to give elongated sections that could conveniently be measured in a horizontal-access SQUID magnetometer (*10*). All the sections were detectably magnetized, with one section markedly more magnetic than the others. This section included the supraoccipital region, approximately 2 cm posterior to the ridge formed by the junction of the occipital, parietal, and frontal bones [the skull configuration of cetaceans differs from that of most mammals due to the so-called telescoping effect (*11*)].

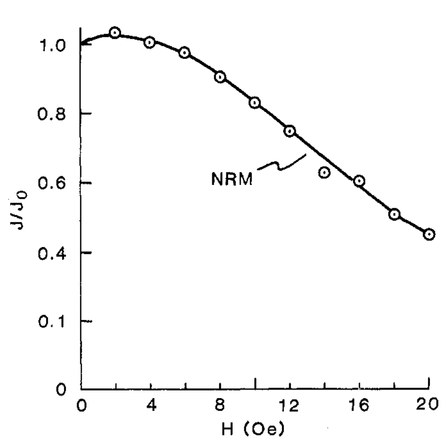

Fig. 1. Alternating field demagnetization of the tissue sample NRM. Abbreviations: J_0, initial magnetic moment; J, magnetic moment after demagnetization; H, magnetic field (alternating); and *Oe*, oersted.

The magnetic tissue is located in the falx cerebri, which in the dolphin is considerably ossified. The posterior part of the falx forms, with the tentorium cerebelli, a substantial septum separating the cerebrum from the cerebellum. The magnetic material was found on the left side of the falx cerebri between the roof of the skull and the juncture of the falx with the tentorium. We separated the dura from the bone with a stainless steel scalpel and isolated a few cubic millimeters of magnetic tissue. The moment of this sample was 2×10^{-5} gauss-cm^3 (2×10^{-8} A-m^2).

We sectioned a second dolphin head in the same manner and found, within the dura in the same region, another strongly magnetized piece of tissue. In all, five dolphins were studied and, with the exception of one that was so badly decomposed that the dissection was not satisfactory, each contained comparably magnetized tissue. However, it was not always found in precisely the same place. For example, in one animal the magnetized dura was on the right tentorium near the junction of the tentorium and the skull.

The natural remanent magnetization