epidermal growth factor (*24*). Other nonimmune functions proposed for molecules of the major histocompatibility complex (MHC) include binding of penicillin (*25*) and viruses (*26*) as well as participation in cellular adhesion and contact inhibition (*27*). If β_2m or the HLA complex are functionally related to the TXA_2 receptor, it is a new role for class I MHC molecules that will strengthen the concept that their function in cell biology is larger than that defined by their participation in immune responses.

RUSSELL A. CURRY
RONALD P. MESSNER
Department of Medicine, Section of Rheumatology, University of Minnesota Hospitals, Minneapolis 55455-0311
GERHARD J. JOHNSON
Department of Medicine, Section of Hematology/Oncology, Veterans Administration Medical Center, Minneapolis 55417

References and Notes

1. A. J. Marcus, *J. Lipid Res.* **19**, 793 (1978); R. R. Gorman, *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **38**, 83 (1979).
2. V. Bertelé *et al.*, *Science* **220**, 517 (1983); P. W. Majerus, *J. Clin. Invest.* **72**, 1521 (1983).
3. G. Vercelotti *et al.*, *Clin. Immunol. Immunopathol.* **23**, 691 (1982).
4. M. D. Poulik, S. Ferrone, M. A. Pellegrino, E. D. Sevier, S. K. Oh, R. A. Reisfeld, *Transplant Rev.* **21**, 106 (1974).
5. R. A. Curry, J. Thoen, R. P. Messner, *J. Immunol. Meth.* **47**, 365 (1981).
6. V. Quaranta, L. E. Walker, M. A. Pellegrino, S. Ferrone, *J. Immunol.* **125**, 1421 (1980).
7. A. G. Morell, G. Gregoriadis, I. H. Scheinberg, J. Hickman, G. Ashwell, *J. Biol. Chem.* **246**, 1461 (1971).
8. D. B. Rifkin, R. W. Compans, E. Reich, *ibid.* **247**, 6432 (1972).
9. M. D. Poulik, P. Gold, J. Shuster, *CRC Crit. Rev. Clin. Lab. Sci.* **10**, 225 (1979).
10. P. A. Peterson, B. A. Cunningham, B. Berggard, G. M. Edelman, *Proc. Natl. Acad. Sci. U.S.A.* **69**, 1697 (1972); P. A. Peterson *et al.*, *ibid.* **72**, 1612 (1975).
11. G. Csako, E. A. Suba, R. Wistar, Jr., *Clin. Exp. Immunol.* **39**, 461 (1980).
12. Measured by thin-layer chromatography by G. Rao by the method of G. H. Rao, G. J. Johnson, R. K. Reddy, and J. G. White [*Prostaglandins* **22**, 761 (1981)]. Thromboxane β_2, measured by radioimmunoassay and formed by gel-filtered platelets stirred with acid-soluble bovine collagen (0.5 to 1.25 μg/ml) was moderately decreased (mean = 42.6 ± 20.8 percent; $N = 7$) by prior incubation with UMR-304.
13. G. L. Bundy, *Tetrahedron Lett.* **24**, 1957 (1975).
14. I. F. Charo *et al.*, *Nature (London)* **269**, 66 (1977).
15. G. J. Johnson, G. H. R. Rao, L. A. Leis, J. G. White, *Blood* **55**, 722 (1980).
16. G. J. Johnson, L. A. Leis, G. H. R. Rao, J. G. White, *Thromb. Res.* **14**, 147 (1979); M. Chignard and B. B. Vargaftig, *Prostaglandins* **14**, 222 (1977).
17. G. C. LeBreton, D. L. Venton, S. E. Enke, P. V. Halushka, *Proc. Natl. Acad. Sci. U.S.A.* **76**, 4097 (1979).
18. B. L. Brown, R. P. Ekins, J. D. M. Albano, *Adv. Cyclic Nucleotide Res.* **2**, 25 (1972). We thank D. Confer for assistance in assay of cyclic AMP.
19. R. J. Haslam, M. M. Davidson, T. Davies, J. A. Lynham, M. D. McClenaghan, *Adv. Cyclic Nucleotide Res.* **9**, 533 (1978).
20. R. R. Gorman, *Adv. Prostaglandin Thromboxane. Res.* **6**, 417 (1980).
21. J. A. Lindgren, H. E. Claesson, H. Kindahl, S. Hammarstrom, *FEBS Lett.* **98**, 247 (1979); A. M. Siegl, J. W. Daly, J. B. Smith, *Mol. Pharmacol.* **21**, 680 (1982).
22. R. M. Lyons, N. Stanford, P. W. Majerus, *J. Clin. Invest.* **56**, 924 (1975); R. J. Haslam and J. A. Lynham, *Biochem. Biophys. Res. Commun.* **77**, 714 (1977); *Thromb. Res.* **12**, 619 (1978).
23. J. M. Gerrard and R. C. Carroll, *Prostaglandins* **22**, 81 (1981).
24. M. Edidin, *Immunol. Today* **4**, 269 (1983); M. Fehlmann, E. Van Obberghen, N. Kiger, *J. Cell Biol.* **97**, 402a (1983); P. DeMeyts *et al.*, *ibid.*, p. 402a.
25. F. H. J. Class, R. Runia-van Nieuwkoop, W. van den Berg, J. J. van Rood, *Hum. Immunol.* **5**, 83 (1982).
26. A. Helenius *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **75**, 3846 (1978); M. F. Clarke, E. P. Gelmann, M. S. Reitz, Jr., *Nature (London)* **305**, 60 (1983).
27. A. S. G. Curtis and P. Rooney, *Nature (London)* **281**, 222 (1979).
28. K. M. Fine, P. C. Ashbrook, L. P. Bridgen, J. E. Maldonado, P. Didisheim, *Am. J. Pathol.* **84**, 11 (1976).
29. R. D. Feinman, J. Lubowsky, I. Charo, M. P. Zabinski, *J. Lab. Clin. Med.* **90**, 125 (1977).
30. We thank L. Leis and S. Severson for technical assistance and G. C. LeBreton for a gift of 13-azaprostanoic acid. Supported by the Veterans Administration and by NIH grants HL 2807 and AM-26696, and grants from the Minnesota Arthritis Foundation and the 3M Foundation. R.P.M. is the research professor of the Minnesota Arthritis Foundation.

29 August 1983; accepted 13 February 1984

Ancient Bisexual Flowers

Abstract. Fossil flowers discovered in 94-million-year-old clays of the Dakota Formation in Nebraska are among the earliest known demonstrably bisexual flowers. The flowers are of medium size and have pentamerous whorls of clearly differentiated floral parts, petals alternate with the sepals, short stamens are borne opposite the petals, the carpels are fused, and a receptacular disk is present. The pollen is small and tricolporate. These flowers appear to be well adapted to insect pollination. The numerous floral features and pollen characters provide sufficient diagnostic data to assess its systematic position. No extant order accommodates the features of this flower and it shares some features of various extant orders. The classification of flowering plants and our understanding of their evolution must be influenced by the fossilized remains of ancient flowers.

Floral structure is the major basis on which living flowering plants of the world are classified (*1–3*). Orders, families, and lesser taxa can be characterized by certain common features of their reproductive organs. Pollen structure, wood anatomy, leaf morphology, and organic compounds have been used to supplement floral evidence in order to establish more "natural" groupings of major taxa (*3–5*) and to more clearly define relationships at the generic, specific, and subspecific levels.

The early fossil record of angiosperms (Barremian-Albian) consists mainly of pollen (*6–8*). Leaf remains are uncommon in deposits of this age but increase in abundance and complexity through the Aptian, Albian, and Cenomanian (*7–12*). A few early angiosperm reproductive remains have been reported (*8–17*).

We know from Tertiary sediments that fossil flowers do preserve and are of great importance in studying the evolution of flowering plants (*18*). However, there are very few detailed accounts of early angiosperm flowers from sediments of Cretaceous age (*14–17, 19*). Therefore, the discovery of one of the earliest known bisexual flowers with well-preserved floral parts is of particular interest. The collection of more than 50 whole or partial flowers preserved in different orientations and stages of development has allowed an accurate reconstruction of floral structure and reproductive biology (*20*). Remains of these flowers were discovered, collected, and studied as part of an ongoing project on the fossil plants of the Dakota Formation being conducted at Indiana University (*21*).

The flowers discussed in this report were collected at a locality in Nebraska from clays of the Dakota Formation (*22*). The Dakota Formation includes mainly nonmarine sandstones, shales, clays, and thin coals deposited along the shore and coastal plains of a mid-Cretaceous epicontinental sea which transgressed northward from the Gulf Coast area, eventually forming a connection with the Arctic Ocean. The beds from which the flowers were collected are dated at about 94 to 96 million years (*17, 23*) and are early Cenomanian (mid-Cretaceous) in age.

The flowers are pentamerous. Most frequently there remains only a thick receptacular disk with five sepals attached, forming a stellate pattern 2 to 3 cm in diameter (Fig. 1d). Ovate petals, 1 to 2 cm long, are preserved both isolated and occasionally attached to the receptacular disk. The five thin and delicate petals alternate with the robust sepals at the rim of the receptacular disk. Five stamens are attached to the receptacle, with one opposite each petal; the filament is flared at the base to form a broad connection to the receptacle (Fig. 1e). The stamens are 1 cm long, with filament and anther each being 0.5 cm long. The filaments are stout and the anthers are consistently four-locular and massive. The stamens preserved in place appear

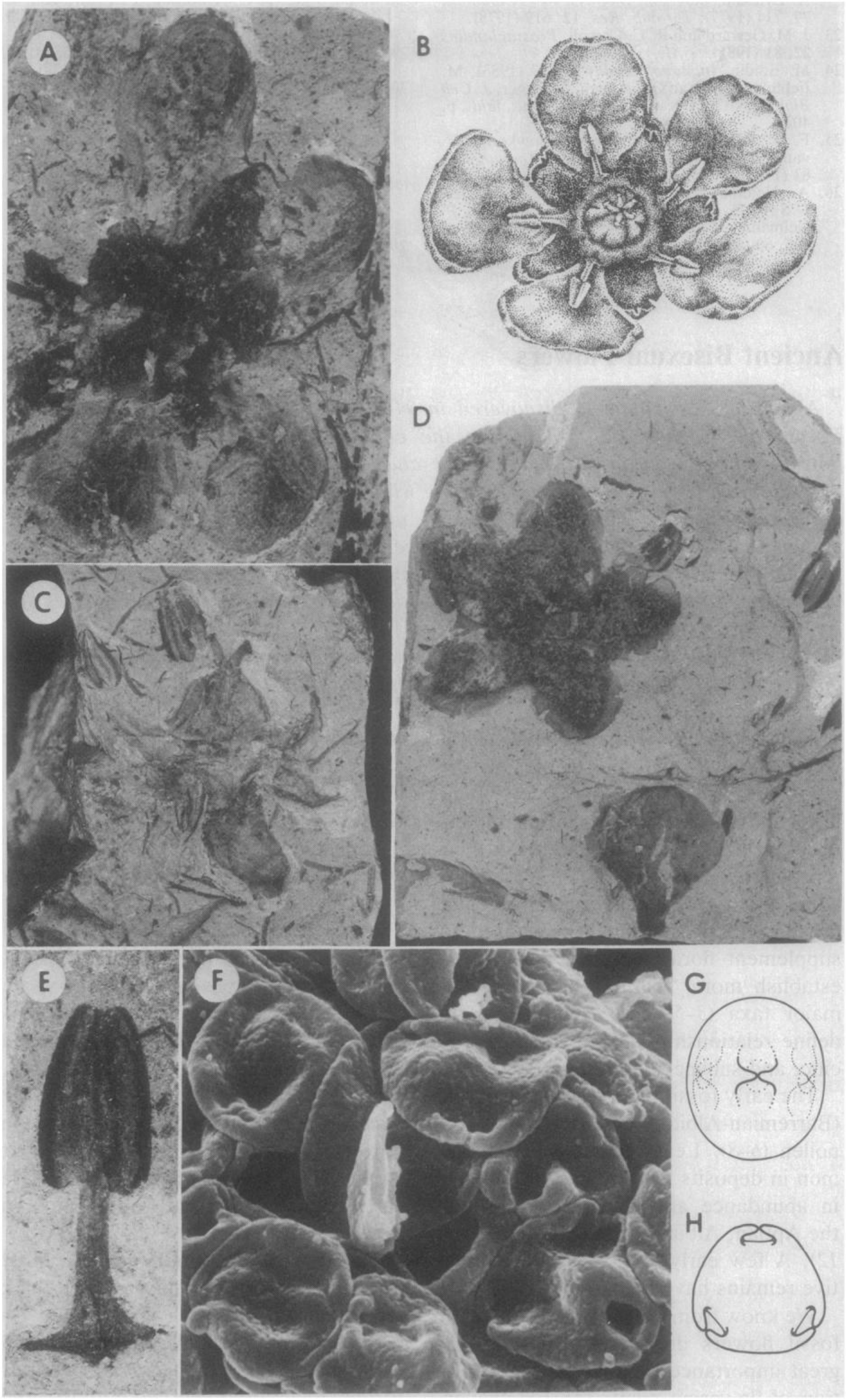

Fig. 1. (A) Flower with four of five petals still attached. Five sepals, which appear as lobes, are alternating with the petals. Specimen number 3427; all specimens are from locality number IU 15713 and are stored in the Indiana University Paleobotanical Collection (×2). (B) Reconstruction of flower, showing pentamerous whorls of sepals, petals, stamens, and carpels (×2). (C) Laterally compressed flower showing bisexuality. Three of five stamens are still attached (upper left and below center) and the gynoecium (center) has free styles at the top; No. 4026 (×2). (D) Calyx from which petals and most stamens have been lost prior to fossilization. Two of five stamens remain attached between sepals at the upper right and upper left. An isolated petal is located at the lower right. The sepals and receptacular disk are relatively thick and the petal is relatively thin; No. 3429 (×2). (E) Isolated stamen showing the large anther and the stout filament with a broadly flared base; No. 3426 (×5.5). (F) Scanning electron micrograph of tricolporate pollen from an anther. Equatorial projections are present over each colpus, as is the faintly scabrate exine; No. 3423 (×3000). (G and H) Reconstruction of pollen grains in equatorial and polar view, respectively (×2000).

to be erect and spreading (Fig. 1, c and d). The pollen is minute, 8 to 12 μm in diameter, psilate to scabrate, and tricolporate (Fig. 1, f to h). The gynoecium consists of five connate carpels, each of which has a short style and a stigmatic surface apparently restricted to the stylar tip. Mature capsules are about 1 cm wide and 0.7 cm high. Dehiscence is loculicidal, with capsules breaking into five triangular segments. Pentamerous calyces, similar to those of the flowers described in this report, occur elsewhere in the Dakota Formation and in the Amboy Clay of New Jersey (*10, 11, 15*). Poorly preserved Cretaceous fruits, vaguely resembling those presented here, have been found attached to a spike (*16*). Pedicels are not present on any of the Nebraskan fossil flowers, suggesting that they may have been borne on a spike also.

The flowers presented are the best evidence available for early insect pollination of angiosperms. The five spreading, showy petals, heavy receptacular disk, short styles, restricted stigmatic areas, large anthers, and abundance of minute pollen all indicate entomophilous pollination. The pollen is so small that it would lack sufficient impact velocity when carried toward a stigma by the wind (*24*). Pollen is also psilate to scabrate and is unlike the large, well-ornamented grains that have been thought of as typical for early entomophilous angiosperms (*8*). The receptacular disk is thick and may have produced nectar since swellings on the upper surface of the disk, between the androecium and gynoecium, resemble the nectariferous collars on disks of some extant flowers (for example, Malpighiaceae and Saxifragaceae). The large number of specimens found in a variety of orientations and stages of development, from young flowers to fruit-bearing forms, provide a broad data base upon which the detailed reconstruction of Fig. 1b has been based.

Because delicate petals are still attached in some specimens we suggest that they were preserved in the immediate vicinity of the plants that bore them. The fossil flowers are found associated with various angiosperm leaf remains and several specimens of *Brachidontes*, a brackish-water bivalve. Remains of this fossil flower on the same slab of clay as a *Brachidontes* buried in life position, suggest that this flowering plant and its associated community lived in a very low, coastal, or near marine environment. No organic connection nor anatomical evidence has yet been found to tie any particular one leaf, of the many types of associated leaves, to the fossil flowers.

Many characters of this early angiosperm flower illustrate the level of development of floral morphology for at least one taxon at an early time in angiosperm evolution. The pentamerous nature of all the flower parts, clear differentiation of the petals and sepals, medium size of the flowers, fused carpels and well-developed receptacular disk are generally believed to be derived floral characters (*1, 4, 25*). The free petals and stamens, bisexual nature of the flower, actinomorphy, probable entomophilous pollination, and hypogynous receptacle are generally considered "primitive" floral characters by most systematic botanists today. This mixture of characters indicates a level of floral evolution at a particular time in the history of the group. According to some hypotheses these flowers lived 15 to 20 million years after the probable latest origin (Barremian) of the angiosperms (*6–8*), thus providing time for considerable floral evolution. However, the actual evolutionary history of the group, which is evident from the considerable taxonomic diversity of mid-Cretaceous time (*14–17*), indicates great divergence early in the history of the flowering plants that cannot be easily dismissed as later evolutionary events.

The circumscription of modern plants is based primarily upon floral morphology, and the floral structure of the fossil flowers is very well known. However, assignment to a living family or order is complicated because no living flowering plant has the same floral features found in the fossil flower. This floral type is approached by members of the Saxifragales (Rosidae), Rosales (Rosidae), and Rhamnales (Rosidae). The fossil flower cannot actually be accommodated within any of these orders but it has a floral type similar to, and possibly basic in, three orders of flowering plants. This flower is of moderate size, with single, pentamerous whorls of organs borne on a very abbreviated receptacle. Its presence by mid-Cretaceous time is in agreement with the view that angiosperm evolution has not always been toward reduction and simplification, but has involved both reduction and elaboration from simple floral types (*15, 26*) as a result of coadaptive evolution with animal pollinators.

JAMES F. BASINGER*
DAVID L. DILCHER
Department of Biology, Indiana University, Bloomington 47405

References and Notes

1. A. Cronquist, *The Evolution and Classification of Flowering Plants* (Houghton-Mifflin, Boston, 1968); A. Takhtajan, *Flowering Plants—Origin and Dispersal* (Oliver and Boyd, Edinburgh, 1969); *Bot. Rev.* **46**, 225 (1980); A. Cronquist, *An Integrated System of Classification of Flowering Plants* (Columbia University Press, New York, 1981).
2. R. Thorne, *Evol. Biol.* **9**, 35 (1976).
3. R. Dahlgren, *Bot. J. Linn. Soc.* **80**, 91 (1980).
4. K. Sporne, in *The Origin and Early Evolution of the Angiosperms*, C. Beck, Ed. (Columbia Univ. Press, New York, 1976), p. 231.
5. G. L. Stebbins, *Flowering Plants, Evolution Above the Species Level* (Belknap, Cambridge, 1974); J. Walker, in *The Origin and Early Evolution of the Angiosperms*, C. Beck, Ed. (Columbia Univ. Press, New York, 1976), p. 241.
6. G. Brenner, in *The Origin and Early Evolution of the Angiosperms*, C. Beck, Ed. (Columbia Univ. Press, New York, 1976), p. 23; N. Hughes, *Palaeobiology of Angiosperm Origins* (Cambridge Univ. Press, Cambridge, 1976); N. Hughes, *Bot. Rev.* **43**, 105 (1977).
7. J. Doyle and L. Hickey, in *The Origin and Early Evolution of the Angiosperms*, C. Beck, Ed. (Columbia Univ. Press, New York, 1976), p. 139; J. Doyle, in *Patterns of Evolution in Early Angiosperms*, A. Hallam, Ed. (Elsevier, Amsterdam, 1977), p. 501.
8. L. Hickey and J. Doyle, *Bot. Rev.* **43**, (1977).
9. W. Fontaine, *U.S. Geol. Surv. Monogr. No. 15* (1889).
10. L. Lesquereux, *ibid., No. 17* (1891).
11. J. Newberry, *ibid., No. 26* (1895).
12. V. Samylina, *Bot. Zh. Leningrad* **53**, 1517 (1968).
13. J. Velenovsky, *Beitr. Palaeontol. Osterr. -Ung.* **5**, 1 (1885).
14. V. Krassilov, *Lethaia* **6**, 163 (1973).
15. D. Dilcher, *Rev. Palaeobot. Palynol.* **27**, 291 (1979).
16. V. Vakhrameev and V. Krassilov, *Paleobot. J. (Moscow)* **1**, 121 (1979).
17. G. Retallack and D. Dilcher, *Palaeontographica B* **179**, 103 (1981).
18. W. Crepet, D. Dilcher, F. Potter, *Am. J. Bot.* **62**, 813 (1975); J. Basinger, *Can. J. Bot.* **54**, 2293 (1976); W. Crepet and D. Dilcher, *Amer. J. Bot.* **64**, 714 (1977); W. Crepet, *Rev. Palaeobot. Palynol.* **25**, 241 (1978); **27**, 213 (1979); C. Daghlian, W. Crepet, T. Delevoryas, *Am. J. Bot.* **67**, 309 (1980).
19. B. Tiffney, *Nature (London)* **265**, 136 (1977); E. Friis and A. Skarby, *Ann. Bot.* **50**, 569 (1982).
20. In this report the nature and importance of this fossil flower are presented. The details concerning the relationships of the flowers are the subject of another report (D. L. Dilcher and J. F. Basinger, in preparation).
21. We thank Dr. Roger Pabian, Dr. Howard Reynolds, and Charles Beeker for help in locating and collecting the specimens.
22. R. Pabian, *Proc. Neb. Acad. Sci. (Lincoln)* **79**, 54 (1969).
23. E. Kaufman, personal communication.
24. D. Whitehead, *Evolution* **23**, 28 (1969).
25. C. Bessey, *Ann. Mo. Bot. Gard.* **2**, 109 (1915).
26. S. Carlquist, *Phytomorphology* **19**, 332 (1969); G. Gottsberger, *Plant Syst. Evol.* Suppl. **1**, 211 (1977); W. Burger, *Bot. Rev.* **43**, 345 (1977).
27. Supported by NSF grant DEB 79-10720 to D.L.D. and a Natural Sciences and Engineering Research Council of Canada Postdoctoral Fellowship to J.F.B.
* Present address: Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 0W0.

1 April 1983; accepted 6 March 1984

Magnetometry of Ingested Particles in Pulmonary Macrophages

Abstract. *Sensitive magnetometry has shown that, after inhalation of airborne magnetic dust by humans or animals, particles retained within the lungs rotate. A number of mechanisms for this rotation have been proposed, including motions of breathing, particle thermal energy, cardiac pulsations, surface fluid flows, and macrophage cytoplasmic movements. In this study the cellular mechanism was examined by magnetometry and videomicroscopy of pulmonary macrophages removed from hamster lungs 1 day after inhalation of a maghemite (γ-Fe_2O_3) aerosol. The field remaining after magnetization was measured in adherent cells and was found to decay rapidly to 30 percent of its initial magnitude within 12 minutes. The remanent-field decay rate was slowed by inhibitors of cytoplasmic motion. Videomicroscopy of pulmonary macrophages with phagocytized γ-Fe_2O_3 showed amoeboid motions that rotated the particles away from their original direction of magnetization. The results confirm that macrophage cytoplasmic movement is a primary cause of remanent-field decay in lungs and that magnetometry can be used to quantify intracellular contractile activity.*

Ferromagnetic particles can be present as contaminants in the lungs and other organs. As Cohen initially pointed out (*1*), retention in the lungs of inhaled magnetic dusts can be measured after a permanent magnetic moment in the retained particles is induced by brief application of a strong magnetic field. The combined effect of these aligned moments is to produce a remanent field that can be detected outside the body with a sensitive magnetometer. Sequential measurements have been used to determine long-term dust clearance from the lungs of smokers and nonsmokers (*2*). Cohen also noted that the magnitude of the remanent field dropped by as much as a factor of 6 during the first hour after magnetization, a phenomenon he called "relaxation." Since the particle magnetic moments are permanent and since the remanent field can be restored to its initial strength by remagnetization, Cohen attributed the relaxation to some viable process randomly rotating the magnetic particles retained in the lungs (*1*).

Cohen and others subsequently published lung clearance and relaxation curves for both humans and animals (*3, 4*). A number of speculations about the force driving relaxation have been put forward, including respiratory movements, surfactant and mucus flow, cardiac pulsations, particle diffusive motion, and cell motion. Conclusive evidence