(*8*). We added SOD to the ground water sample (13 mg liter^{-1}) and compared the H_2O_2 accumulation rate and the absolute concentration of H_2O_2 to that in a sample to which no SOD had been added. The accumulation rate with SOD was about double the rate in the control. After sunlight irradiation (1.0 watt-hour m^{-2}), the H_2O_2 concentrations were $2.8 \times 10^{-6}M$ and $5.4 \times 10^{-6}M$ in the sample without and with SOD, respectively. Thus, we conclude that $O_2{\cdot}^-$ is a precursor in the sunlight-induced production of H_2O_2 in natural waters.

It is also possible that organoperoxides might be formed. Catalase decomposes H_2O_2 and organic peroxides at different rates (*9*). Therefore, we could distinguish between these two peroxide species on the basis of a comparison of the rate of catalase decomposition of oxidants formed in situ relative to that of added H_2O_2.

Two samples of a ground water were exposed to sunlight for a total irradiation of 1.85 watt-hour m^{-2}, at which time they were brought in out of the sun and the H_2O_2 was measured. In both cases the final H_2O_2 concentration was $1.4 \times 10^{-5}M$ to $1.5 \times 10^{-5}M$. To a third flask of ground water that was not irradiated, stock H_2O_2 was added to give a $1.1 \times 10^{-5}M$ solution. These three solutions were then allowed to stand in the laboratory for 1 hour; no change in H_2O_2 concentration occurred. Catalase (1 mg liter^{-1}) was added to one of the flasks that had been exposed to sunlight and to the one to which H_2O_2 had been added, and the H_2O_2 concentrations were monitored in all flasks for 75 minutes. The H_2O_2 concentration was constant over the period in the control solution (that is, the one to which no catalase had been added). The solutions to which catalase had been added showed very similar decay curves with time. Had organoperoxides been present then, we would have expected an intermediate decay rate. These data suggest that the measured concentrations are indeed attributed to H_2O_2 and not to organic peroxides.

Both H_2O_2 and $O_2{\cdot}^-$ are known to affect biological systems (*10*) and geochemical cycles (*11*). At the concentration reported herein, it is very likely that H_2O_2 and $O_2{\cdot}^-$ are important factors in the maintenance of the *Eh* (redox potential) of natural waters high in organic matter. In addition, the occurrence of H_2O_2 and $O_2{\cdot}^-$ implicate other reactive transients (for example, OH^- and organic radicals and metastable intermediates of many transition metals and nonmetallic elements) in the overall chemistry of natural waters. Whether these transients exert significant effects on surface water quality remains to be shown.

WILLIAM J. COOPER
Drinking Water Research Center,
Florida International University,
Miami 33199

ROD G. ZIKA
Rosenstiel School of Marine and
Atmospheric Science,
University of Miami,
Miami, Florida 33149

References and Notes

1. G. L. Kok, *Atmos. Environ.* **14**, 653 (1980); R. G. Zika, E. Saltzman, W. L. Chameides, D. D. Davis, *J. Geophys. Res.* **87**, 5015 (1982).
2. C. Van Baalen and J. E. Marler, *Nature (London)* **211**, 951 (1966).
3. R. G. Zika, *Eos* **61**, 1010 (1980).
4. V. E. Sinel'nikov, *Gidrobiol. Zh.* **7**, 115 (1971); W. J. Cooper, R. G. Zika, R. G. Petasne, paper presented at the American Water Works Association Conference, Miami Beach, Fla., 16 to 21 May 1982.
5. W. L. Chameides and D. D. Davis, *J. Geophys. Res.* **87**, 4863 (1982).
6. R. G. Zika, P. Zelmer, R. Petasne, in preparation.
7. The ultraviolet absorbance showed differences between samples that resulted in the formation of H_2O_2 and those in which no (or little) H_2O_2 was formed. There is a linear relation between the absorbance at specific wavelengths and TOC (R. G. Zika, W. J. Cooper, R. Petasne, in preparation).
8. D. Klug, J. Rabani, I. Fridovich, *J. Biol. Chem.* **247**, 4839 (1972).
9. B. J. Chance, *ibid.* **179**, 1311 (1949).
10. J. P. McCormick, J. R. Fischer, J. P. Pachlatko, A. Eisenstark, *Science* **191**, 468 (1976); I. Fridovich, *ibid.* **201**, 875 (1978).
11. W. G. Breck, in *The Sea*, E. D. Goldberg, Ed. (Interscience, New York, 1974), vol. 5, pp. 153–179; R. Parsons, *The Nature of Seawater* (Department of Physical Chemistry, University of Bristol, Bristol, England, 1975).
12. We thank R. G. Petasne for technical assistance. Supported by the Drinking Water Research Center, Florida International University, and the National Science Foundation through grant OCE 78-25628.

22 November 1982; revised 21 January 1983

Adaptations for Climbing in North American Multituberculates (Mammalia)

Abstract. *A recently discovered skeleton of* Ptilodus *exhibits several specializations for climbing. A survey of postcranial bones of Cretaceous and early Cenozoic multituberculates from North America reveals similar locomotor specializations. Multituberculates possessed distinctive tarsal adaptations for a range of pedal mobility characteristic of arboreal mammals that descend trees headfirst. The divergent hallux could move independently of the other digits. The long robust tail of* Ptilodus *possessed musculoskeletal features that, among living mammals, are associated with prehensility.*

Multituberculates are an extinct, holarctic group of nontherian mammals that ranged in geologic history from the Late Jurassic to early Oligocene. They are particularly diverse in Late Cretaceous and Paleocene strata, where they are abundantly represented by teeth and jaws. The postcranial skeleton of multituberculates is, however, poorly known, and a variety of locomotor habits were postulated by early workers from limited evidence (*1*). The discovery of a nearly complete and well-preserved skeleton of *Ptilodus kummae* in the Paleocene Ravenscrag Formation of southeastern Saskatchewan (*2*) provides an opportunity to reassess hypotheses concerning the locomotor adaptations of North American multituberculates. Examination of all North American genera of Cretaceous and early Cenozoic multituberculates for which adequate postcranial material is available leads us to conclude that they possessed adaptations suited for arboreal life.

The articulated portion of the skeleton of *P. kummae* is virtually complete posterior to the anterior part of the rib cage. Portions of the dentition, pectoral girdle, and forelimbs were also recovered. Our analysis is based primarily on this skeleton as well as on a specimen of the hind limbs and pelvis of a multituberculate referred to the genus *Eucosmodon* by Granger and Simpson (*3*). We also examined all available postcranial remains of North American multituberculates of the suborders Ptilodontoidea and Taeniolabidoidea (*4*). These consist primarily of isolated limb bones, most of which have not been described.

The skeletal proportions of multituberculates are comparable to those of generalized, noncursorial mammals such as opossums and tree shrews (*5*). However, specializations in the structure of the ankle, in the joint between the entocuneiform and the hallucal metatarsal, and in the tail are similar to those in certain arboreally adapted Recent mammals.

A number of mammals that climb, many of which are arboreal, possess an unusual range of pedal mobility (particularly abduction and plantar flexion) that permits headfirst descent on vertical surfaces such as tree trunks (*6*). During such activity, the hind foot is reoriented so as to point the toes backward and position the claws to secure a grip. The tibioastragalar and astragalocalcaneal joints of the multituberculate ankle provide evidence of similar mobility. The distal end of the tibia bears two asymmetrical condyles (unlike the distal tibial facet in most mammals, which is a single concavity). The lateral condyle is longer than the medial and wraps spirally around the distal end of the tibia from its anteromedian to posteromedian margins (Fig. 1A). The short, linear medial condyle extends from the anterior margin to the center of the distal end; it is oriented anteromedially-posterolaterally. These condyles articulated with two sulci, one medial and the other lateral, on the proximal surface of the astragalus. Abduction and related movements suitable for securing grips over a wide range of foot postures appear to have been accommodated, in part, by the asymmetrical configuration of the tibial condyles. From the neutral position (Fig. 1B$_1$), translation of the astragalar sulci along the tibial condyles of different lengths results in abduction of the hind foot. In this movement, the lateral sulcus translates along the semilunar lateral condyle, whereas the medial sulcus rolls and pivots about the medial condyle (Fig. 1C$_1$). Among living mammals, the Virginia opossum (*Didelphis virginiana*) possesses a similar arrangement of tibial condyles and astragalar sulci that permits a large degree of abduction of the hind foot (*7*).

In addition to abduction, a hind foot must be plantar-flexed in order to secure a grip for headfirst descent. In multituberculates, this movement occurred at the astragalocalcaneal joint (Fig. 1, B$_2$ and C$_2$) and involved pivoting the calcaneum about an axis through the sustentaculum tali; the facet of the sustentaculum and its counterpart on the astragalus are nearly equal in size, and thus give no evidence of substantial translatory movement. Excursion at the proximal astragalocalcaneal joint, however, did involve translation. The bulbous proximal facet on the calcaneum provided a semilunar pathway for the much smaller, concave facet on the astragalus, thus permitting full plantar flexion as well as some conjoint inversion (Fig. 1C$_2$). Additional postural adjustments of the foot permitting inversion-eversion and dorsiflexion–plantar flexion were possible at the astragalonavicular and calcaneocuboid joints.

The structure of the femoral head and acetabulum indicates that, in the neutral position, the femur was abducted about 45° from a sagittal plane (*8*). The normal stance of the foot, therefore, probably also involved an abducted posture. We estimate that the longitudinal axis of the foot (passing along the third metatarsal) deviated 30° to 40° from a sagittal plane. With an additional 90° of abduction possible at the tibioastragalar joint, the foot could have readily assumed the postures depicted in Figs. 1C and 2. These postures required repositioning the tibia and fibula nearly parallel to the vertical substrate, in contrast to a more or less perpendicular orientation in a stance on a horizontal substrate.

A second specialization is in the divergent hallux, which could move independently of the other digits. The distal facet on the entocuneiform is saddle-shaped (concave dorsoventrally, convex medio-

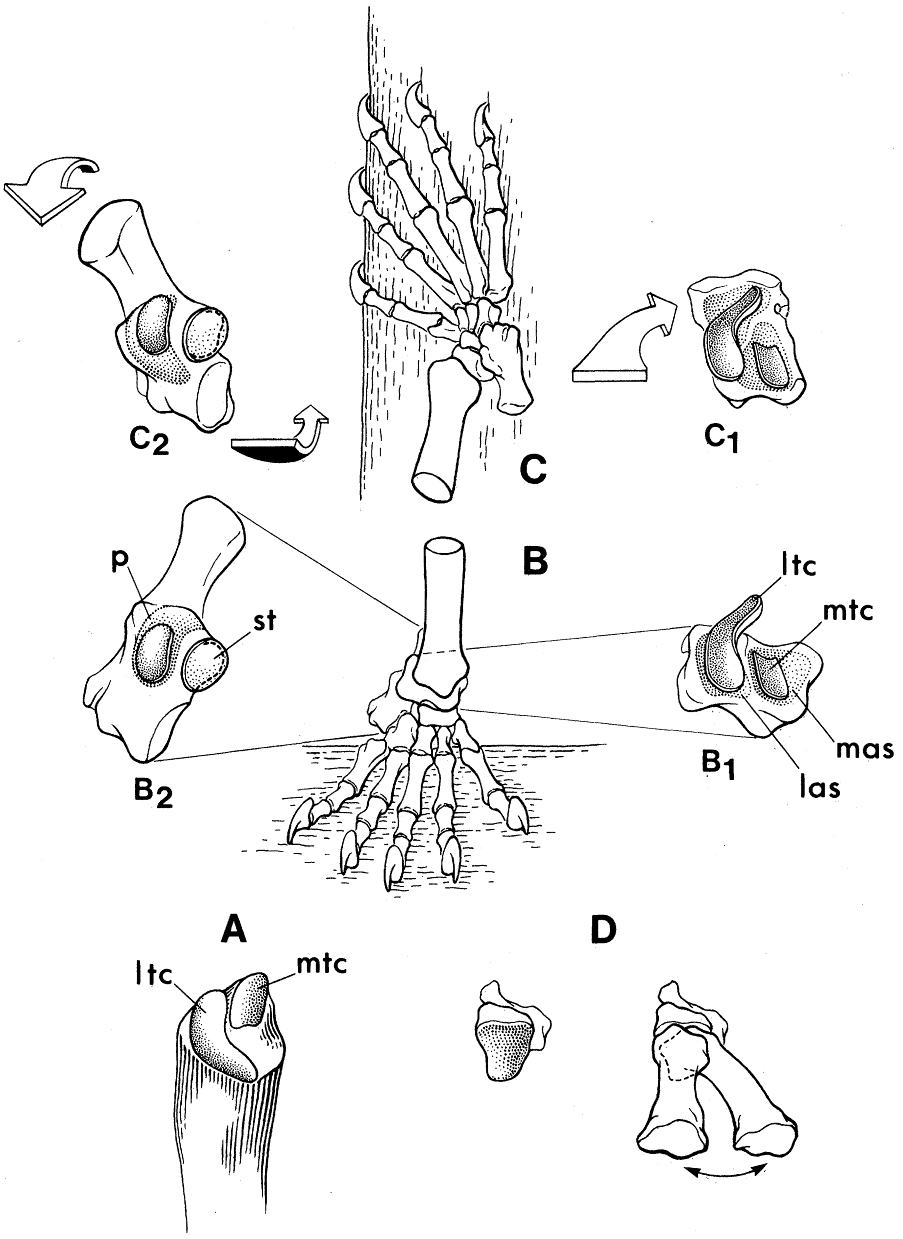

Fig. 1. Functional aspects of a multituberculate (right) hind foot interpreted from specimens of *Ptilodus kummae* (UA 9001) and ?*Eucosmodon* sp. (AMNH 16325). (A) The distal end of a tibia, viewed from posterior aspect, showing the configuration of the lateral (*ltc*) and medial (*mtc*) tibial condyles. (B) The hind foot, viewed from anterior aspect, in a neutral posture (such as would have been used in standing on flat ground). The relationships of the tibial condyles with the medial (*mas*) and laterial sulci (*las*) on the proximal surface of the astragalus are shown in B$_1$; the astragalocalcaneal joint, comprising the two ventral astragalar facets articulating with the sustentacular (*st*) and proximal (*p*) facets of the calcaneum, is shown in B$_2$. (C) The hind foot, viewed from dorsal aspect, in an abducted, plantar-flexed, and inverted posture, such as would have been used to secure a grip for headfirst descent (see Fig. 2). To achieve this posture, the foot was abducted at the tibioastragalar joint (C$_1$) and plantar-flexed and inverted at the astragalocalcaneal joint (C$_2$). The fibula has been intentionally omitted from this figure to provide a fuller view of the astragalus. (D) The saddle-shaped distal facet of the entocuneiform; the range of abduction-adduction of the hallucal metatarsal is indicated at the right.

laterally) and permitted both flexion-extension and abduction-adduction of the hallux (Fig. 1D). However, the convexity is asymmetrical; the facet extends farther medially than it does laterally, a feature that is directly indicative of an unusual degree of hallucal abduction (*9*). A divergent, abductable hallux is a typical grasping adaptation of mammals that move across uneven and discontinuous surfaces such as branches.

A third specialization occurs in caudal structure. The tail of *P. kummae* appears to have been prehensile. All living, prehensile-tailed mammals employ their tails in climbing; all may be considered to be arboreally adapted despite variations in allocation of time spent on the ground or in trees. A preliminary survey of these taxa reveals a number of shared features (*10*). The tail is long, commonly twice or more the length of the precaudal vertebral column; in a few taxa the tail is shorter (for example, in *Didelphis*, where the tail is 1.2 times the length of the precaudal vertebral column). Hemal arches are developed along nearly the entire length of the tail. Transverse processes are robust and are present even on the most distal caudals. Finally, the sacral spinous processes are relatively large, commonly nearly equaling in height the spinous processes of posterior lumbar vertebrae. The development of the various processes appears to be related to the hypertrophy of the caudal musculoskeletal system necessary for increased gripping strength.

The tail of *P. kummae* gives evidence of most of these bony features (Fig. 2). The estimated tail length is 1.2 to 1.4 times the length of the precaudal vertebral column. Transverse processes are well developed, even on the distal caudals. Hemal processes are large and present along the entire length of the tail. Sacral spinous processes, to the extent that their height can be estimated, appear to have been as prominent as those on the posterior lumbar vertebrae. From this evidence, *P. kummae* possessed structural adaptations that, in living mammals, are related to tail prehensility and climbing habits.

The interpretation of several features in *Ptilodus* and *Eucosmodon* as adaptations for climbing does not necessarily imply that the entire radiation was comprised of arboreal forms. However, tarsal bones and distal tibiae of taxa other than *Ptilodus* and *Eucosmodon* bear the same structural features that we have interpreted as adaptations for climbing. Furthermore, on the basis of all postcranial materials available for our review (*4*), we infer that North American multituberculates are strikingly homogeneous throughout the postcranial skeleton. The absence of any great variability is all the more striking in light of the diversity in size and in dental specializations known in the Multituberculata (*11*).

FARISH A. JENKINS, JR.
Department of Organismic and
Evolutionary Biology and
Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts 02138
DAVID W. KRAUSE*
Museum of Paleontology,
University of Michigan,
Ann Arbor 48109

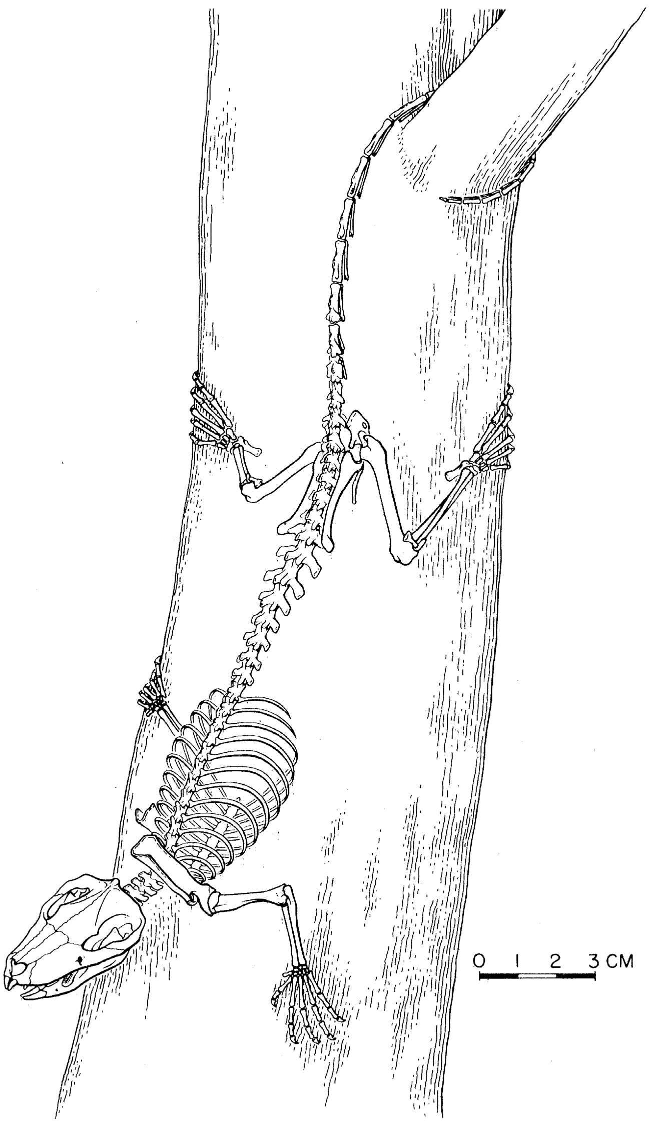

Fig. 2. Reconstruction of a multituberculate skeleton based principally on a specimen of *Ptilodus kummae* (UA 9001). The body is positioned for headfirst descent. In this resting posture the thoracolumbar region is extended, the hind foot is reoriented such that the toes point backward, and the tail is employed as a grasping and stabilizing organ. The reconstruction depicts the epipubic bones that were found in association with UA 9001.

References and Notes

1. J. W. Gidley, *Proc. U. S. Natl. Mus.* **36**, 611 (1909); R. Broom, *Proc. Zool. Soc. London* **1910**, 760 (1910); G. G. Simpson, *Am. J. Sci.* **11**, 228 (1926); ——— and H. O. Elftman, *Am. Mus. Novit. 333* (1928); L. Van Valen and R. E. Sloan, *Syst. Zool.* **15**, 261 (1966).
2. D. W. Krause, *Palaeontogr. Abt. A Palaeozool-Stratigr.* **159**, 1 (1977). University of Alberta specimen 9001.
3. W. Granger and G. G. Simpson, *Bull. Am. Mus. Nat. Hist.* **56**, 601 (1929). American Museum of Natural History specimen 16325.
4. Specimens representing or referable to the following genera were available for this study: *Catopsalis, Cimexomys, Cimolodon, Ectypodus, Eucosmodon, Meniscoessus, Mesodma, Ptilodus, Stygimys*, and *Taeniolabis*. For detailed descriptions of these specimens and comparative anatomical observations and analyses of function, see D. W. Krause and F. A. Jenkins, Jr. (*Bull. Mus. Comp. Zool. Harv. Univ.*, in press).
5. F. A. Jenkins, Jr., *J. Zool.* **165**, 303 (1971).
6. M. Cartmill, in *Primate Locomotion*, F. A. Jenkins, Jr., Ed. (Academic Press, New York, 1974), p. 45.
7. F. A. Jenkins, Jr., and D. K. McClearn, in preparation.
8. The position of the fovea on the femoral head in mammals is related to femoral posture and excursion [F. A. Jenkins, Jr., and S. M. Camazine, *J. Zool.*, **181**, 351 (1977)]. The location of the fovea on the proximoposterior side of the head in multituberculates is comparable to that in living mammals that have an abducted hind limb posture.
9. G. G. Simpson and H. O. Elftman (in *1*) interpreted the hallux in *Eucosmodon* as "partially opposable" (p. 3) or simply "opposable" (p. 15). Their analysis appears to have been based in part on an osteological study by W. Granger and Simpson (*3*) in which the authors illustrated the entocuneiform upside down. In this position, the asymmetry of the facet would permit an unusual degree of adduction. In the correct anatomical position, the entocuneiform allows the hallux to swing widely away from the foot, as well as adduct. Whereas we agree with Simpson and Elftman that the hallux served a grasping function, we avoid the term opposition which implies movements, typical of the human thumb, that cannot be demonstrated from available material.

10. This survey included arboreal, prehensile-tailed species of 20 genera distributed among the orders Marsupialia, Rodentia, Edentata, Pholidota, Carnivora, and Primates.
11. R. E. Sloan [in *The Encyclopedia of Paleontology*, R. W. Fairbridge and D. Jablonski, Eds. (Dowden, Hutchinson & Ross, Stroudsburg, Pa., 1979), p. 492] reviews the diversity of Multituberculata.

12. We thank D. Baird, W. A. Clemens, R. J. Emry, R. C Fox, P. D. Gingerich, M. C. McKenna, J. H. Ostrom, C. E. Ray, R. E. Sloan, and R. H. Tedford for access to collections in their care; M. Cartmill, Z. Kielan-Jaworowska, and P. D. Gingerich for their comments on a longer version of this report; and L. Meszoly for preparing the illustrations.

* Present address: Department of Anatomical Sciences, Health Sciences Center, State University of New York, Stony Brook 11794.

14 May 1982; revised 29 September 1982

The Effects of Direct-Current Magnetic Fields on Turtle Retinas in vitro

Abstract. *Direct-current magnetic fields of 10 to 100 gauss cause a significant short-term reduction of the in vitro electroretinographic b-wave response in turtle retina. This response compression is not accompanied by the usual reduction in retinal sensitivity that occurs with background illumination. Furthermore, this effect is obtained only briefly after the offset of ambient lighting in the diurnal light-dark cycle of nonhibernating animals.*

The magnetic susceptibility of the human visual system is manifested by magnetophosphenes induced in the retina by alternating-current (a-c) magnetic fields (*1, 2*). Direct-current (d-c) magnetic fields do not elicit magnetophosphenes, but do influence certain spatially ordered biological systems, including the visual photoreceptors (*3–7*), through a physical realignment of diamagnetically anisotropic molecules, cellular elements, or both. For instance, in an aqueous suspension, isolated rod photoreceptor outer segments will realign themselves with their long axes parallel to an external d-c magnetic field of several thousand gauss (1 G = 10^{-4} tesla). This diamagnetic anisotropy (*8, 9*) arises in the photopigment rhodopsin (*10–12*). We have used an in vitro retinal eyecup preparation to study the electrophysiological effects of acute exposures to d-c magnetic field intensities known to influence rhodopsin in solution.

Our studies assessed the functional capacity of the vertebrate retina to undergo visual adaptation (operationally defined here as the change in retinal sensitivity resulting from an altered level of background illumination) and contrasted this capacity with the effects of applied d-c magnetic fields. We examined whether or not d-c magnetic fields can produce changes in retinal sensitivity and function similar to those that follow normal photoisomerization.

On-line electroretinogram (ERG) recordings from an in vitro turtle eyecup preparation (*13*) before, during, and after brief d-c magnetic field exposures were used; all of the results presented here refer only to b-wave ERG data. Both cone-dominant (*Pseudemys scripta elegans*) and mixed, rod-cone (*Chelydra serpentina*) turtle retinas were used to determine whether differences in photoreceptor cell type exist in magnetic field susceptibility. The animals were maintained under a rigorous diurnal light-dark (LD) cycle (lights turned on at 6 a.m. and off at 6 p.m.) for a minimum of 2 weeks before the study. Although experiments were conducted at different times throughout the diurnal cycle, all results are grouped into one of four different LD cycle phases: (i) light (L), 8 a.m. to 6 p.m.; (ii) light-to-dark transition (L-D), 6 p.m. to 8 p.m.; (iii) dark (D), 8 p.m. to 6 a.m.; and (iv) dark-to-light transition (D-L), 6 a.m. to 8 a.m.

Extracellular microelectrodes (25- to 50-μm tip diameters, 350- to 500-kilohm resistance) were placed in the thin layer of vitreous humor remaining in the eyecup after dissection and drainage. The eyecup was placed in a continuously gassed (95 percent O_2 and 5 percent CO_2) chamber within the 10-inch pole piece separation of an SCR-controlled d-c electromagnet. Magnetic field profiles mapped at this point showed a maximum d-c field inhomogeneity of 0.2 percent over the dimensions of the eyecup (7 to 10 mm) and a maximum a-c magnetic field ripple component of 10 mG in the

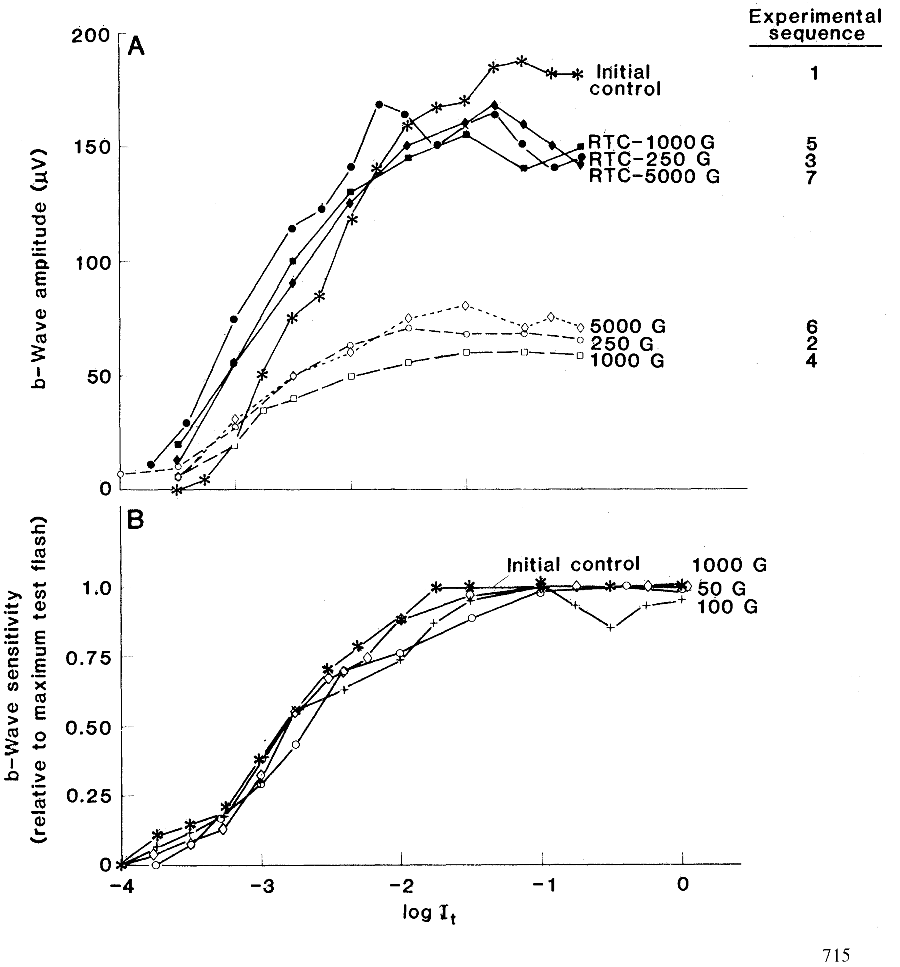

Fig. 1. (A) Retinal response of the turtle to photic stimuli during transition from light to dark. Intensity-response functions obtained with diffuse light flashes in an in vitro retinal eyecup (*Chelydra serpentina*) during d-c magnetic field exposures. Each curve is labeled with the d-c magnetic field intensity at which it was obtained. Note the extensive, but similar, amount of response amplitude decrement seen with each magnetic field intensity. (B) Normalized intensity-response functions that show no curve shifting as a result of retinal desensitization.