Reports

Fossil Grass Anthoecia Within Miocene Rhinoceros Skeletons: Diet in an Extinct Species

Abstract. *Silicified anthoecia (fertile lemmas and paleas) of grasses (*Berriochloa communis, Berriochloa primaeva, *and* Berriochloa *cf.* nova*) were found in the oral cavity and rib cage in articulated skeletons of* Teleoceras major *buried in late Clarendonian volcanic ash in Nebraska. The plant fossils, thought to be food residues, help clarify the enigmatic paleobiological role of* Teleoceras, *which had hippotamus-like proportions but very high-crowned teeth.* Teleoceras *was probably amphibious, but siliceous grasses formed a significant portion of its diet.*

New light has been shed on the paleoecology of the savanna ecosystem of North America in the late Miocene by the discovery of the remains of many large mammals that were rapidly killed and buried in a volcanic ash bed in Nebraska at a time when the ungulate fauna had reached its apogee with "an array of taxa fully comparable to that in African savannas today" (*1*). Our finding of well-preserved grass anthoecia (*2*) within several of the skeletons of an extinct rhinoceros, *Teleoceras major*, affords a rare glimpse of detailed trophic relationships in an ancient ecosystem. Most conclusions about diet in ancient vertebrates must be based on extrapolation from living relatives or on functional analysis of the feeding mechanism. Occasionally, fossilized skeletons of carnivores are found that contain the undigested remains of prey (*3*), but equally conclusive evidence of diet in extinct herbivores is much less frequently preserved—famous exceptions are frozen mammoths (*4*) and dinosaur "mummies" (*5, 6*).

Bones and teeth of *Teleoceras* are among the most common mammalian fossils in strata of late Miocene age in the Great Plains. Indeed, these rhinos were probably the dominant herbivores on the northern Great Plains from approximately 10 through 7 million years before present (*7*). In general, though, the mode of life of *Teleoceras* has been difficult to assess because several of the animal's most characteristic anatomical features appear to be mutually incompatible. Thus the abbreviated limbs and barrel-like body have led some authors (*8*) to attribute amphibious habits to *Teleoceras*, whereas others [such as Gregory (*9*)] have noted that the marked hypsodonty of its molar teeth violates the general correlation of high-crowned teeth with cursorial limb structure in ungulates.

The fossils discussed in this report were part of a remarkable death assemblage of Miocene vertebrates discovered by M.R.V. in a 2-m-thick bed of pure volcanic ash in the Cap Rock Member (*10*) of the Ash Hollow Formation in the drainage basin of Verdigre Creek, Antelope County, northeastern Nebraska (*11*). The mammalian species in the assemblage indicate a late Clarendonian (*12*), approximately early late Miocene, burial. Numerous complete skeletons, mostly of *T. major* (*13*) but including those of horses, camels, and other animals (*14*), lie near the base of the ash, which appears to have accumulated very rapidly in a shallow body of standing water and to have buried the animals in the pond. Most of the *Teleoceras* skeletons are preserved three-dimensionally in what almost certainly are undisturbed death poses (Fig. 1). The former presence of standing water is shown by the symmetrically ripple-marked bedding planes of the ash bed as well as by the remains of aquatic turtles and diatoms in the ash.

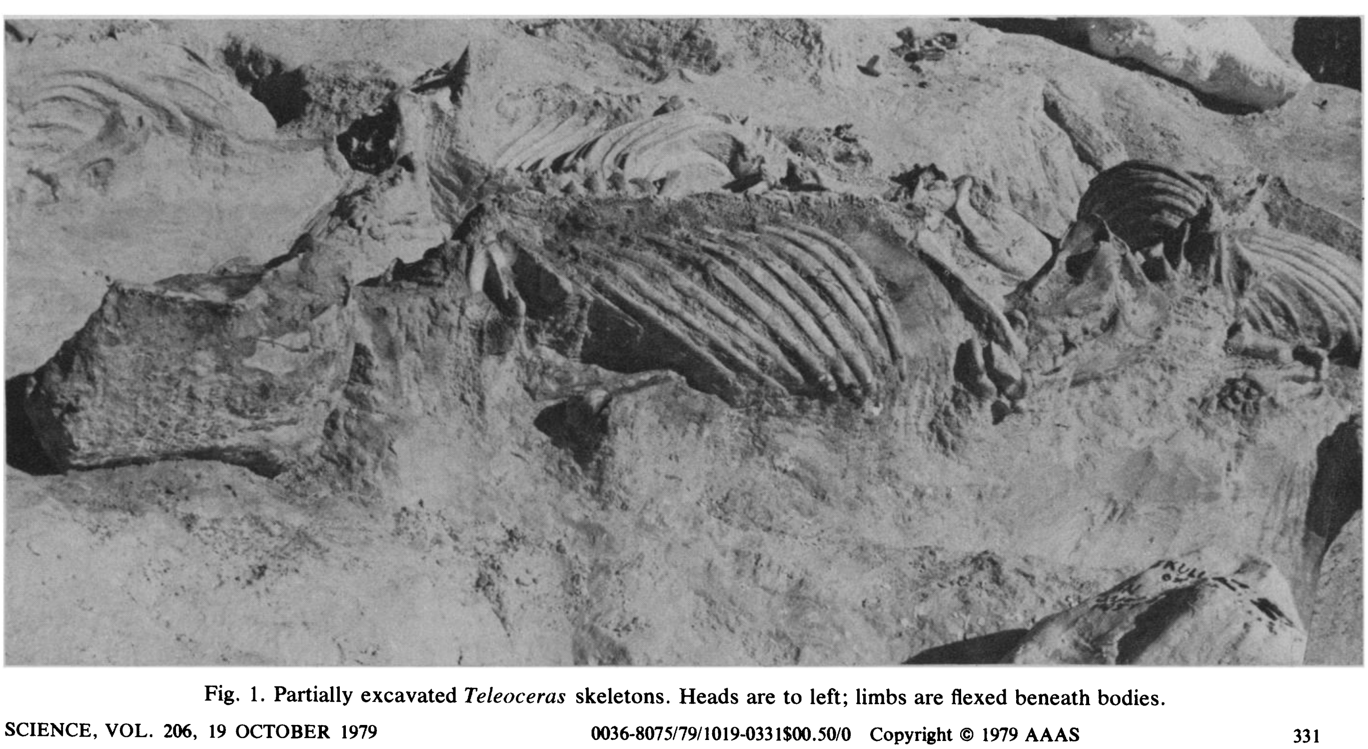

Fig. 1. Partially excavated *Teleoceras* skeletons. Heads are to left; limbs are flexed beneath bodies.

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The fossil reproductive structures of several taxa of angiosperms (for example, grass anthoecia, sedge achenes, pondweed seeds, borage nutlets, and hackberry endocarps) from the late Tertiary strata of central North America have been widely described (*15, 16*). They are three-dimensional silicifications that frequently exhibit detailed preservation of micromorphological features (Fig. 3) (*17*). Although the stratigraphic association of fossil plants and vertebrates has been noted (*18*) in late Tertiary High Plains strata, ours is probably the first documented report of plants collected in situ in skeletal remains.

To date, four skeletons at the site have been found to contain silicified anthoecia. The plant remains were first noticed during cleaning of the hyoid apparatus (tongue bones) of an adult female *Teleoceras* [University of Nebraska State Museum (UNSM) specimen 52286; see Fig. 2]. Since then, anthoecia have been recovered from the oral cavity of a juvenile with worn deciduous teeth (UNSM 52294), the oral cavity of an adult female (UNSM 52218), and the rib cage of an adult female bearing fetal bones in its pelvic cavity (UNSM 52373). There is little doubt that the plant fossils represent the remains of food ingested by the rhinos. Careful screening and flotation of several cubic meters of ash surrounding the skeletons failed to yield any trace of plant fossils. This strongly indicates that the plants arrived at the site already inside the animals and were not fortuitously carried in by wind or water currents.

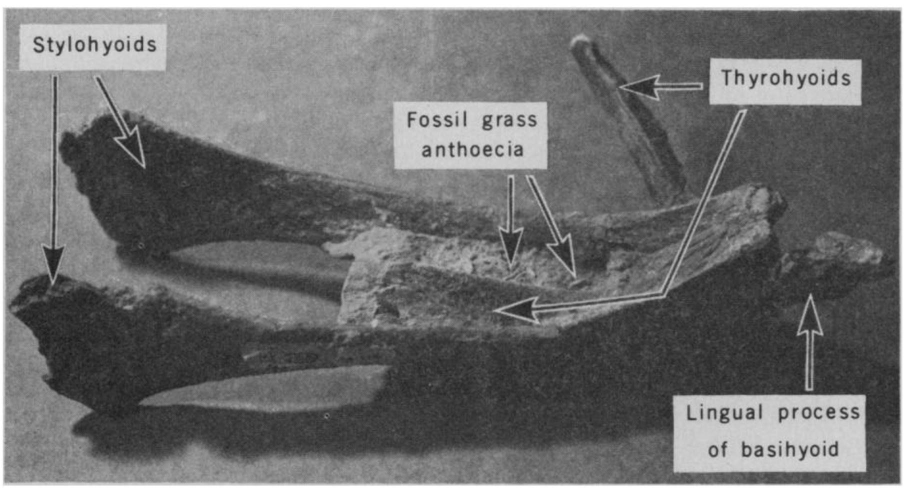

Fig. 2. Articulated hyoid bones from the skull of an adult female *Teleoceras* (UNSM 52286) with silicified grass anthoecia of *B. communis* in situ. Specimen is about 21 cm in length.

Specimens of *Berriochloa* collected from *Teleoceras* skeletons were cemented to brass disks with silver cement of high purity, coated with carbon and 12 cm of 0.008-inch-diameter 99.9 percent gold wire in a Varian vacuum evaporator, and examined at 15 kV in a scanning electron microscope (JEOL-35) (*19*).

The anthoecia from the rhinoceros skeletons include *Berriochloa communis*, *B.* cf. *nova*, and *B. primaeva* (Fig. 2) (*20*). *Berriochloa communis*, one of the most widely collected fossil grasses from late Tertiary strata in Nebraska, was considered by Elias (*15*) to be indicative of a floral zone equivalent to the Valentine Formation and lowermost Ash Hollow Formation. This is only the second report of *B.* cf. *nova* and *B. primaeva* from the fossil record and may be the first reported occurrence from the Ash Hollow Formation (*21*).

Specimens of *B. communis* recovered from the hyoid apparatus of specimen UNSM 52286 have well-preserved hairs at the bases of the anthoecia. The location of the fossil anthoecia in the oral cavity and the presence of the hairs appear to rule out any long-distance transport of the fossil plants or lengthy digestive action and would seem to indicate that the anthoecia were ingested by the rhinoceros shortly before its death at or very near the site of the skeletal remains.

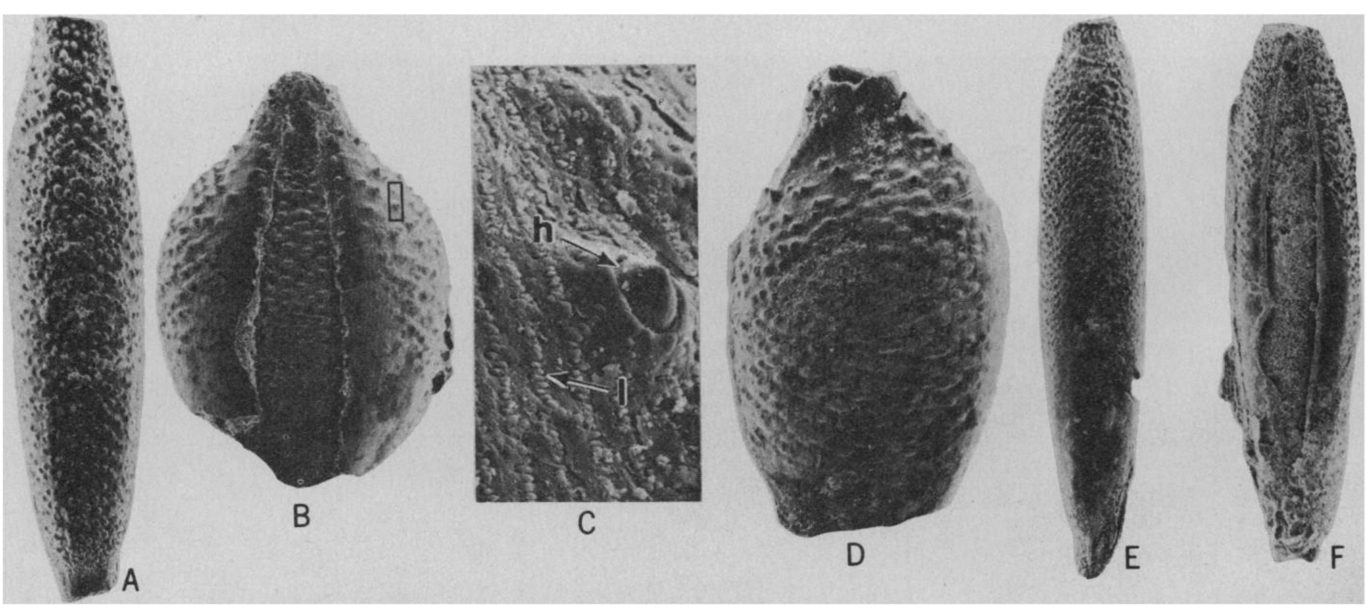

Fig. 3. Fossil anthoecia from *Teleoceras* remains. (A) *Berriochloa* cf. *nova* from the rib cage of an adult female (UNSM 52373), dorsal view, brass plate (BP) 545 (×25). (B) *Berriochloa primaeva* from the oral cavity of a juvenile (UNSM 52294), front view, BP 548 (×34). (C) Enlargement of outlined area in (B) showing hook (*h*) and long cells (*l*) with well-developed sinuous walls (×450). (D) *Berriochloa primaeva* from the oral cavity of UNSM 52294, lateral view, BP 547 (×38). (E) *Berriochloa communis* from the hyoid apparatus of an adult female (UNSM 52286), lateral view, BP 541 (×18). (F) *Berriochloa communis* from the rib cage of an adult female (UNSM 52373), front view, BP 544 (×23).

Our findings indicate that *Teleoceras*, although possibly amphibious, was a grazer that ate siliceous grasses as a significant portion of its diet (*22*). The presence of fossil grass anthoecia has been considered (*20, 23*) to be indicative of arid or semiarid paleoenvironmental conditions, but evidence from late Cenozoic strata in Nebraska shows that this interpretation is an overgeneralization (*24*). None of our evidence precludes the possibility that *Teleoceras* obtained its forage in a mesic, lacustrine paleoenvironment.

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References and Notes

1. S. D. Webb, *Annu. Rev. Ecol. Syst.* **8**, 355 (1977).
2. The anthoecium consists of the fertile bracts (lemma and palea) that surround the caryopsis in grasses. In paleontological literature, the anthoecium is frequently referred to as a seed.
3. G. A. Bishop, in *The Study of Trace Fossils*, R. W. Frey, Ed. (Springer-Verlag, New York, 1975), p. 261.
4. J. P. Tolmachoff, *Trans. Am. Philos. Soc.* **23**, 11 (1929).
5. R. Kräusel, *Paleontol. Z.* **4**, 80 (1922).
6. J. H. Ostrom, *Am. J. Sci.* **262**, 975 (1964).
7. *Teleoceras* has been found in nearly all well-sampled Great Plains fossil vertebrate localities of the late Clarendonian and early Hemphillian ages. Although outnumbered by horses, *Teleoceras*, with an estimated adult weight between 1000 and 2000 kg (depending on species), outweighed contemporary equids by a factor of 10 or more. On the basis of the ungulate biomass in fossil samples, we estimate, for example, that one *Teleoceras* weighed as much as 15 *Cormohipparion* or 40 *Pseudhipparion*. Thus, *Teleoceras* comprised more than two-thirds of the herbivore biomass in the Minnechaduza Fauna (late Clarendonian of Nebraska), even though it is represented in only 20.5 percent of the identifiable mammalian fossils from the type locality, Little Beaver B Quarry [S. D. Webb, *Univ. Calif. Publ. Geol. Sci. 78* (1969)].
8. H. F. Osborn, *Bull. Am. Mus. Nat. Hist.* **10**, 81 (1898); B. Kurtén, *The Age of Mammals* (Columbia Univ. Press, New York, 1972).
9. J. T. Gregory, *Univ. Calif. Publ. Geol. Sci.* **26**, 307 (1942).
10. M. F. Skinner, S. M. Skinner, R. J. Gooris, *Bull. Am. Mus. Nat. Hist.* **138**, 379 (19→ M. R. Voorhies, *J. Paleontol.* **45**, 119, (1971).
11. University of Nebraska State Museum Locality Antelope County (Ap.) 116. Detailed locality information is available to qualified investigators in our museum files.
12. H. E. Wood, II *et al.*, *Bull. Geol. Sci. Am.* **52**, 1 (1941).
13. On the basis of taxonomic studies (M. R. Voorhies, in preparation), the *Teleoceras* population from the ash bed is referred to as the genotypic species *T. major* Hatcher, the common Clarendonian species [Skinner *et al.* (*10*); L. G. Tanner, *Bull. Nebr. State Mus.* **10**, 23 (1975)], rather than as *T. fossiger*, the characteristic Hemphillian form, which is larger and has more complex molars.
14. Nonrhinocerotic taxa recognized among the prepared fossils include five species of three-toed horses (*Pseudhipparion gratum*, *Cormohipparion occidentale*, *Pliohippus supremus*, *Calippus* sp., and *Astrophippus* sp.), several camels (*Procamelus grandis* and *Aepycamelus* sp.), a cervoid (*Longirostromeryx* sp.), an oreodont (*Ustatochoerus skinneri*), and several kinds of turtles and birds. In contrast with the rhinoceros fossils, many of the fossils of these smaller animals are partially disarticulated and badly crushed, apparently by trampling.
15. M. K. Elias, *Geol. Soc. Am. Spec. Pap. 41* (1942).
16. J. C. Frye, A. B. Leonard, A. Swineford, *Bull Kans. Geol. Sur. 118* (1956); A. B. Leonard and J. C. Frye, *N.M. Bur. Mines Miner. Resour. Circ. 161* (1978). J. R. Thomasson, *Bull. Kans. Geol. Surv.*, **218**, 1 (1979).
17. J. R. Thomasson, *Science* **199**, 975 (1978); *Am. J. Bot.* **65**, 34 (1978).
18. _____, *Univ. Wyo. Contrib. Geol.* **16**, 39 (1977); *ibid.*, **17**, 59 (1979).
19. Scanning electron microscopy was done by J. R. Thomasson in the Bessey scanning electron microscope (SEM) facilities at Iowa State University. Specimens examined by SEM are numbered in a brass plate series.
20. J.R.T. (*16*) recently transferred all fossils previously known as *Stipidium* (such as *S. commune* and *S. novum*) to *Berriochloa*.
21. Elias (*15*) reported both *B. novum* and *B. primaeva* from the Spottedtail Member at the Sheep Creek Formation (middle Miocene) *Pliohippus* draw in Sioux County, Nebraska. The collection of anthoecia from UNSM locality Ap. 116 represents a considerable extension of the known stratigraphic range of *B.* cf. *nova* and *B. primaeva*. See T. Galusha [*Bull. Am. Mus. Nat. Hist.* **156**, 1 (1975)] for a modern interpretation of the stratigraphic relationship of the Ash Hollow and Sheep Creek Formations.
22. *Teleoceras* may have eaten other siliceous plants, such as sedges. Discoveries by J. R. Thomasson in Ash Hollow strata of grasses and sedges associated with rhinoceros (possibly *Teleoceras*) and *Gomphotheridae* remains supports such an assumption.
23. K. O. Stanley, *Geol. Soc. Am. Bull.* **87**, 297 (1976).
24. J.R.T. has collected fossil *Berriochloa*, *Leersia*, *Nassella*, *Oryzopsis*, and *Panicum* (Gramineae); *Carex* (Cyperaceae); *Potamageton* (Zosteraceae); *Equisetum* (Equisetaceae); and *Chara* (Characeae), as well as freshwater ostracods from Ash Hollow strata in west-central Nebraska. These fossils were found in association with disarticulated bones of *Gomphotheridae* and rhinoceroses.
25. Supported by grants from the National Geographic Society and by grant DEB-7809150 from the National Science Foundation. For assistance in the field we thank G. Brown, E. Ewbank, S. Fuerniss, K. Imig, M. A. Jones, K. Kolster, K. Maley, D. McBride, E. McBride, J. McBride, C. Messenger, K. Messenger, R. Otto, C. Palmer, S. Stover, K. Terrell, and J. Voorhies.

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Nitrogen-15 Dioxide Uptake and Incorporation by *Phaseolus vulgaris* (L.)

Abstract. *The sorption rate and metabolic fate of nitrogen dioxide, a major air pollutant, have been determined for* Phaseolus vulgaris *(L.). Sorption was determined kinetically by chemiluminescent monitoring of* $^{15}NO_2$ *removal from the test atmosphere and directly by mass spectrometric analysis of nitrogen derived from the plant tissue. Sorptive processes were first order with respect to* $^{15}NO_2$ *concentration. Virtually all of the* $^{15}NO_2$ *taken up was metabolized.*

Vegetation is recognized as a sink for atmospheric pollutants, and efforts have been made to characterize the interactions between plants and pollutants. Studies of pollutant sorption by plants furnish information that can help in assessing the efficacy of atmospheric scrubbing and in understanding the fate of pollutant molecules within plants. Some of these molecules can be phytotoxic and some can serve as plant nutrients (for example, S and N pollutants). Nitrogen dioxide (NO_2), a major air pollutant, might conceivably serve in either role, depending on dosage. A detailed review of its biological activity has been published (*1*).

Only two investigations of $^{15}NO_2$ uptake by plants have been reported (*2, 3*), and both were conducted with concentrations of NO_2 that were higher than concentrations in the normal atmosphere, which range from about 0.0002 to 0.5 parts per million (ppm). Durmishidze and Nutsubidge (*2*) used $^{15}NO_2$ at 5400 ppm to demonstrate the incorporation of ^{15}N into amino acids for a variety of plant species. They also observed ^{15}N translocation between shoots and roots. Yoneyama *et al.* (*3*), using $^{15}NO_2$ concentrations of 0.5 to 4.0 ppm, demonstrated that ^{15}N accumulation by three plant species was accompanied by increases in both nitrite and nitrite reductase levels. The interpretation of these results, however, is limited by the static exposure conditions used, which would have limited CO_2 fixation and produced maximum stomatal opening.

The purpose of the present study was to estimate foliar sorption of $^{15}NO_2$ at normal atmospheric concentrations and to measure the extent of ^{15}N incorporation into the major nitrogenous fractions. For comparison, NO_2 uptake was also measured with a sensitive kinetic method that depended on chemiluminescent monitoring of NO_2 removal from the test atmosphere.

Phaseolus vulgaris (L.) 'Bush Blue Lake 290' (snap bean) was seeded three to a 177-ml Styrofoam cup containing a substrate of one part of peat moss–vermiculite mixture (Redi-Earth) and two parts of gravel. Plants were grown in a controlled environment room of the North Carolina State University Phytotron (*4*) with a day length of 9 hours and day and night temperatures of 26° and 22°C, respectively. The quantum flux density was 660 microeinsteins per square meter per second (400 to 700 nm), and relative humidity ranged from 55 to 65 percent during the day and 75 to 85 percent at night. Cups were watered lightly with deionized water until seedling emergence, after which they received a nutrient solution (*4*) twice daily. Plants were

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