referred to as their intersection group or the symmetry of the Wulff plot (*1*).

Further examination of the symmetry elements common to the matrix lattice and that in each individual twin section of the precipitate reveals that four sections share only the $2/m$ monoclinic symmetry common to <110> Ge and <001> Al. However, the fifth is of higher symmetry. In addition to the $2/m$ symmetry along the needle axis, the germanium lattice in the lower segment also shares with the matrix $2/m$ symmetry along two further orthogonal axes, resulting in orthorhombic $2/m\ 2/m\ 2/m$ symmetry.

The observed symmetry points to two alternative mechanisms for the nucleation of this particle: (i) the nucleus is a single crystal, most likely in the orientation of the lower triangular segment, which then forms several twins during subsequent growth, or (ii) the nucleus is a pentagonal prism that changes to a pentagonally twinned crystal during growth by the insertion of two extra planes of atoms. The latter is the more interesting possibility of the two. Bagley (*7*) pointed out that whiskers of diamond and some metals are sometimes found to have pentagonal symmetry. This has usually been interpreted as arising from fivefold twinning of the crystal. However, another possibility is that growth occurs from a common axis of a close-packed arrangement of atoms with pentagonal point symmetry but translation symmetry only along its axis, in the manner shown in cross section in Fig. 2. The symmetry of this atomic arrangement is $5/mm2$ (alternatively referred to as $\overline{10}\ 2m$). The equilibrium shape of such a particle in a cubic matrix must conform to the intersection of the point symmetry groups of matrix and precipitate, that is, $m\bar{3}m \cap 5/mm2 = mm2$ (*1*). This is the point symmetry that is in fact observed, a symmetry that remains unchanged even by the addition of two extra half planes in the possible transition from the pentagonal structure with periodicity only along one axis to the face-centered cubic structure. This type of pentagonal twinning is different from that frequently found in small particles of gold and silver (*8–10*) with decahedral and icosahedral morphology. The multiple twinning in these particles is due to an anisotropy in surface energy: when twinned in a decahedral or icosahedral configuration, the particle surface consists of low-energy {111} facets only. The savings in surface energy more than offsets the energy of the additional twin boundaries necessary for this morphology above a critical particle size of about 5 to 10 nm (*10*).

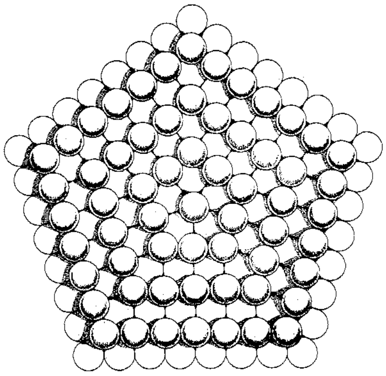

Fig. 2. Close-packing spheres with a fivefold axis of symmetry and translation symmetry only along the axis. [Adapted from (*7*)]

There is one substantial difference between the present and earlier examples of fivefold particle symmetry. The symmetry in the germanium particles develops during a solid-state treatment close to equilibrium. In contrast, the decahedral and icosahedral multiply twinned gold and silver particles, which have been produced by vapor deposition onto various substrates, are grown under conditions far from equilibrium. Similarly, the recently discovered quasi-crystals, which exhibit icosahedral point symmetry but no translational symmetry, observed in aluminum-manganese alloys (*11*) and in other materials (*12*), are formed only under conditions of extremely rapid cooling, for example, splat quenching. Tenfold twin domains similar to the fivefold configuration observed in the present work have been found in nickel-zirconium and iron-aluminum alloys with orthorhombic and monoclinic crystal structure, respectively, but only under conditions of rapid quenching (*13, 14*).

It is expected that further analysis of these particles at various stages in their growth will contribute to a fundamental understanding of underlying atomic mechanisms (*15*).

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A Fossil Grass (Gramineae: Chloridoideae) from the Miocene with Kranz Anatomy

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A fossil leaf fragment collected from the Ogallala Formation of northwestern Kansas exhibits features found in taxa of the modern grass subfamily Chloridoideae. These include bullet-shaped, bicellular microhairs, dumbbell-shaped silica bodies, cross-shaped suberin cells, papillae, stomata with low dome- to triangular-shaped subsidiary cells, and Kranz leaf anatomy. The leaf fragment extends the fossil record of plants that show both anatomical and external micromorphological features indicating C_4 photosynthesis back to the Miocene. On the basis of associated mammals, the leaf fragment is assigned a Hemphillian age (7 to 5 million years ago).

AN INTRIGUING PROBLEM IN BIOLOGY concerns the origin and evolution of C_4 photosynthesis, a physiological pathway that involves the formation of C_4-dicarboxylic acids as the initial products of CO_2 assimilation during the early stages of sugar formation in plants (*1*). Especially efficient at high temperatures and light intensities, this pathway is most often found in plants living in warm to hot tropical and subtropical areas. Although generally uncommon among plants, C_4 photosynthesis is

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found in at least 18 families of angiosperms, including both monocotyledons and dicotyledons (*1*). The majority of C_4 plants occur in the grasses, where half the species are C_4 (*2*). C_4 plants exhibit specialized leaf anatomy, referred to as "Kranz type" (*3*), whose features in grasses include, among others, vascular bundles that are never separated by more than four mesophyll cells (*4*) and low ratios of mesophyll area to bundle sheath area (*5*). Usually leaf veins are surrounded by a large bundle sheath and more or less radially arranged chlorenchyma (*4*).

Although the anatomical, physiological, and ultrastructural characteristics of C_4 photosynthesis have been studied widely in living plants (*1–6*), its phylogenetic history remains obscure, primarily because of the rarity of fossil evidence. Only a single record of an undoubted C_4 plant based on anatomical evidence has been reported, that of a grass from the late Miocene Ricardo Formation in California (*7*). Despite this meager fossil record, it has been suggested that C_4 photosynthesis may be as ancient as the Cretaceous (*8*), that it may be a late Tertiary or early Quaternary development (*1*), or that it may have evolved only recently (*6*). We describe a Miocene fossil that shows distinctive Kranz leaf anatomy and external micromorphological features similar to those found in a living, cosmopolitan subfamily of grasses that is composed probably exclusively of C_4 taxa.

The leaf fragment with Kranz anatomy was collected with a diverse biota at a site (Minium Quarry) in Graham County, Kansas, from deposits of Neogene age that are generally referred to as the Ogallala Group or Formation (*9*). Sediments at the site are presumably fluviatile in origin, and, although detailed sedimentological studies are incomplete, the fossils seem to have been deposited on a flood plain or point bar. Some sedimentary structures indicate trampling and mixing after deposition.

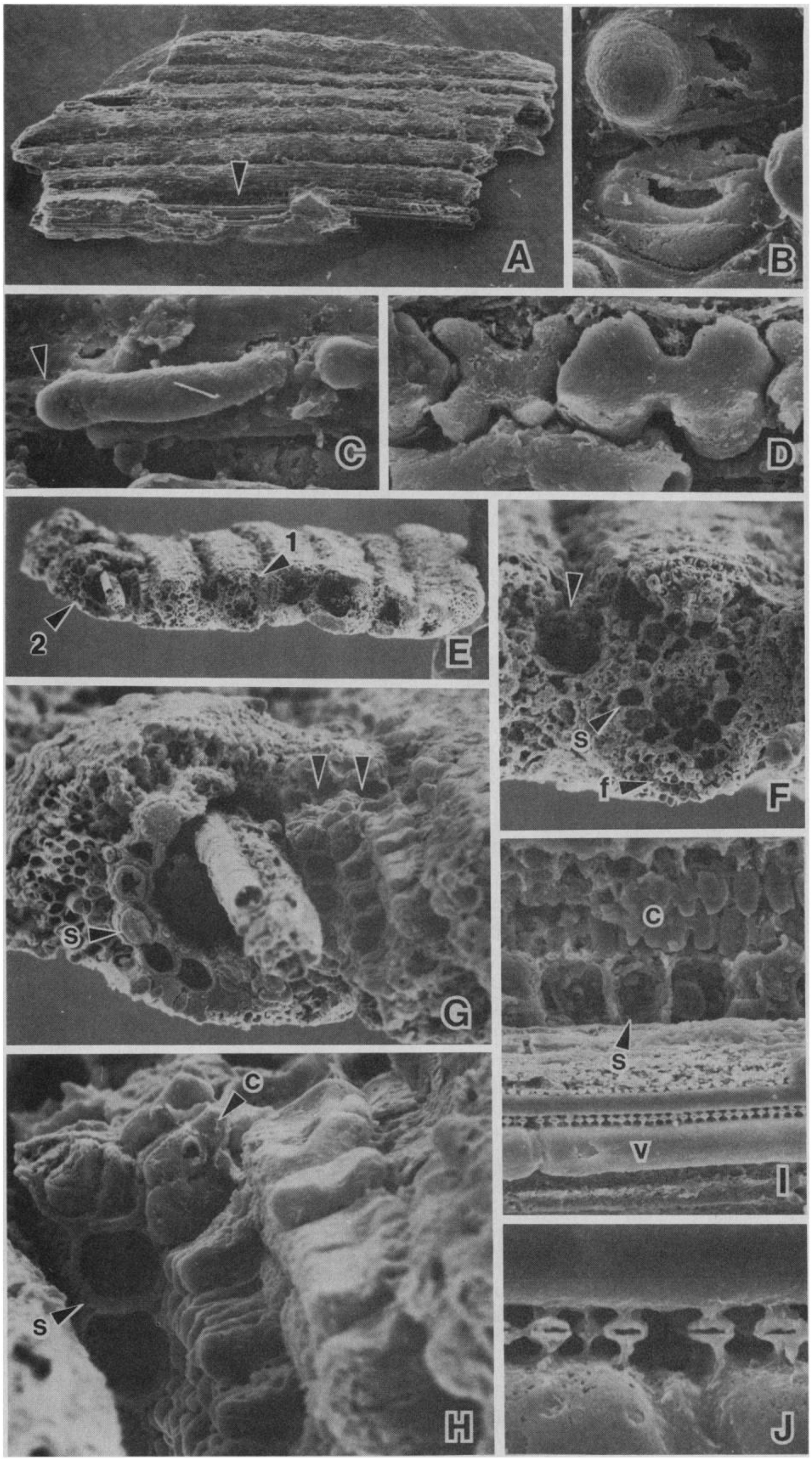

Fig. 1. Miocene chloridoid grass leaf fragment. (A) Upper surface of leaf fragment BP952h (*22*) with exposed longitudinal view of vascular bundle (arrowhead) (×46). (B) Papilla (top) and stomate (bottom) with low, dome-shaped subsidiary cells. Lower surface (×1400). (C) Bicellular microhair with short, dome-shaped apical cell (arrowhead). Upper surface (×800). (D) Cross-shaped suberin cell (left) and dumbbell-shaped silica body (right). Upper surface (×2000). (E) End view of leaf fragment (×81) [see legends of (F) and (G) for explanation of arrowheads]. (F) Enlargement of area at arrowhead 1 in (E) showing prominent vascular bundle sheath (s) and location of bulliform cells (unlabeled arrowhead) (×350). Sclerenchyma fibers (f) occur above and below the bundle. (G) Enlargement of area at arrowhead 2 in (E) showing well-developed bundle sheath (×390). (H) Enlargement of areas at arrowheads in (G) showing bundle sheath cells (s) and elongated, radially arranged chlorenchyma cells (c) (×930). (I) Enlargement of (A), showing exposed vascular bundle, adjacent bundle sheath (s), radially arranged chlorenchyma (c), and pitted vessel elements (v) (×600). (J) Enlargement of vessel elements in (I) showing pit pairs (×3300).

Fossil invertebrates collected from the site include ostracods and mollusks. Fossil vertebrates collected include fish, salamanders, turtles, birds, and mammals, with the latter being the most abundant. Preliminary identification of some of the mammals indicates that the following taxa are present: mole, *Scalopus*; ground squirrel, *Spermophilus*; two genera of canids, *Vulpes* (fox-size) and *Osteoborus* (bone crushing); bear, *Agriotherium* (*10*); large felid, gen. indet. (*10*); rhinoceros, *Teleoceras*; three-toed horse, *Neohipparion eurystyle* (*11*); peccary, *Prosthennops*; three genera of camels, *Megatylopus* (large), *Alforas* (medium), and *Hemiauchenia* (small); and a small cervid, gen. indet.

Preliminary correlation of the mammalian taxa at the generic level suggests that the Minium Quarry local fauna is about the same age as local faunas from Edson and Rhino Hill quarries in Kansas and the type Hemphillian fauna from the Coffee Ranch of Texas. These faunas are considered to be middle- to late-Hemphillian (late Miocene, 7 to 5 million years ago) in age (*11, 12*).

Fossil plants collected, in addition to the one described in this report, include more than 300 leaf fragments of at least five other undescribed taxa of grasses (*13*) and three taxa of sedges, stem and wood fragments, and reproductive structures of *Archaeoleersia, Berriochloa, Nassella*, and *Panicum* (Gramineae); *Carex, Cyperocarpus*, and *Eleofimbris* (Cyperaceae); *Limnocarpus* (Potamogetonaceae); *Biorbia* (Boraginaceae); *Chenopodium* (Chenopodiaceae); *Celtis* (Ulmaceae), and several unknown or undescribed taxa (*14*).

In cross section, the leaf fragment shows seven vascular bundles, all approximately equal in size. Low ribs are developed opposite each vascular bundle on both the upper and the lower surfaces of the leaf. Furrows between the bundles on both surfaces are shallow and apparently occupied, at least on the upper surface, by groups of bulliform or colorless cells (Fig. 1, A, E, and F) (*15, 16*).

Individual vascular bundles are surrounded by a single bundle sheath of large parenchyma cells that are approximately square (Fig. 1, F–I). There is no evidence of an inner sheath (*17*). The elongate chlorenchyma cells surround the parenchymatous bundle sheath in a radial arrangement (Fig. 1, F–I). Pitted xylem vessel elements are present in the vascular tissue (Fig. 1, I and J), and bands of sclerenchyma fibers are visible above and below each vascular bundle (Fig. 1F). On the basis of the size of the observable chlorenchyma cells and the physical relations of vascular bundles (Fig. 1, E–H), we estimated that the vascular bundles are separated by no more than four mesophyll cells, a feature particularly characteristic of C_4 grasses (*4*).

Features of the upper surface include dumbbell-shaped silica bodies, cross-shaped suberin cells, papillae, bicellular microhairs with rounded apical cells that are much shorter than the basal cells, and stomata with low, dome- to triangular-shaped subsidiary cells (Fig. 1, C and D). The stomata, papillae, and microhairs are located in the shallow furrows that alternate with the ribs. The silica bodies are generally found on the ribs, frequently occurring in rows of five or more and alternating with cork cells (Fig. 1D) (*18*). The lower surface is similar to the upper, although microhairs and bulliform cells were not observed and papillae seemed to be more common, especially in the furrows (Fig. 1B). Stomata (Fig. 1B) were located on the sides near the base of the furrows.

The leaf epidermis of living members of the grass subfamily Chloridoideae (*19*) is characterized by bullet-shaped bicellular microhairs; silica cells mostly cross- or saddle-shaped, but sometimes dumbbell-shaped; silica and cork cells over the veins, often in rows of five or more; and stomata with triangular or low, dome-shaped subsidiary cells (*17*). The leaf anatomy always includes an outer sheath of large, well-developed parenchyma cells and an inner sheath of small, thick-walled cells (at least in the primary veins), and elongate chlorenchyma cells that radiate outward from the bundle sheath (*17*). The occurrence of a combination of these features on the fossil suggests a close relation with this modern subfamily (*20*). To our knowledge, grasses from this subfamily have not been reported previously as fossils.

The existence of well-developed Kranz-type anatomy during the late Miocene indicates that the C_4 photosynthetic pathway is not a recent development, at least in the Gramineae. Its correlation with a large, widespread subfamily of living grasses that is, with the possible exception of one species (*21*), exclusively C_4 further suggests that the development of this photosynthetic pathway may be quite old (*8*).

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18. P. B. Kaufman, P. Dayanandan, C. I. Franklin, Y. Takeoka [*Ann. Bot.* **55**, 487 (1985)] have observed that combinations of silica and cork cells are often located over the vascular bundles in C_4 grasses but rarely so in C_3 grasses.
19. The subfamily Chloridoideae has a cosmopolitan distribution, although its principal development is in warm tropical and subtropical regions, with a surmised center of origin in east tropical Africa [W. Hartley and C. Slater, *Aust. J. Bot.* **8**, 274 (1960)]. Some of its common members include lovegrasses (*Eragrostis*), Bermuda grass (*Cynodon*), grama grasses (*Bouteloua*), buffalo grass (*Buchloë*), and *Zoysia*.
20. Within the Chloridoideae, the fossil seems to be allied near *Leptochloa* (sprangletops), a widespread genus with species in tropical, subtropical, and temperate regions. This relation is suggested by comparisons of micromorphological and anatomical features, made through the use of an automated data bank of grass generic descriptions (L. Watson, personal communication; compare with L. Watson, M. J. Dallwitz, C. R. Johnston, *Aust. J. Bot.*, in press).
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