though such specializations are common in nervous systems, synapses in which they are absent cannot be visualized through this technique.

In summary, we found that, in the regions studied here, short projections or tufts of the postsynaptic cell membrane could be clearly visualized, and their presence was always associated with synaptic transmission verified electrophysiologically. When such processes were absent, even in cells that invariably make close anatomical contact, electrical signs of transmission were also absent.

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16. Details of electrophysiological procedures can be found in (*9*). Briefly, the nerve cord was prepared as if for dye iontophoresis, except that the sheath of the cord was removed at the exit point of the third roots. The preparation was transilluminated and F1's and occasionally the lateral giant axons were impaled under visual control with 15- to 25-megohm 3*M* KCl micropipettes. The preparation was maintained in oxygenated saline, cooled to 13° to 15°C.
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Paleozoic Seeds with Embryos

Abstract. *Seeds in a conifer cone from the Lower Permian of west Texas contain embryo tissue. These are the oldest plant embryos on record. Their development prior to seed dispersal shows that the sequence of embryo growth typical of most modern seed plants had evolved before the end of the Paleozoic Era.*

All seeds of Paleozoic plants recorded to date have one thing in common: they lack visible embryos (*1*). Reported here are the oldest known plant embryos. They occur in seeds of a new type of conifer cone (*2*) of the Voltziales or so-called "transition conifers" that comes from the Permian of west Texas.

The apical 2.5 cm of the cone preserved in a sandstone concretion was found loose in a steep gully at the Clay Slide locality (*3, 4*) in the Glass Mountains, Brewster County, Texas. The Clay Slide is 4 km west of the summit of Iron Mountain (*5*) and is exposed on the south-southeast side of a cuesta constructed of Lower Permian rocks (*4*). The fossil was resting on rocks of the Cathedral Mountain Formation, having eroded from them or from the overlying Road Canyon Formation. Both formations are included in the Lower Permian Leonard Series (*4*).

Since the cone was preserved in a rounded concretion and was not found in place, it is remotely possible that it was not indigenous to the rocks now exposed at the Clay Slide. The Triassic Bissett Formation occurs 11 km northwest of the Clay Slide, and foliage of *Voltzia* was identified from an exposure of this formation 26 km from the Clay Slide (*6*). It could thus be argued that the Bissett Formation once covered the Clay Slide but eroded, leaving the fossil behind. However, there is no evidence that the Bissett Formation ever extended as far south as the Clay Slide and, considering the steepness of the collecting site, it is doubtful that a rounded concretion could remain on the slope for any great length of time. Furthermore, additional Permian rocks occur stratigraphically between the Road Canyon and Bissett Formations in the Glass Mountains and would have eroded after the latter rocks, obscuring traces left behind. The cone itself is more similar to those of the Voltziales from the Upper Carboniferous and Lower Permian of Europe than to the Upper Permian and Mesozoic forms. Finally, the rounded nature of the concretion could suggest as well that the cone was reworked into the Cathedral Mountain Formation or the Road Canyon Formation from still older rocks. Thus, it must be concluded that the cone is at least as old as Lower Permian.

There are three complete seeds in the fossil and apices of two others extend into the specimen from the missing cone base. Each seed occurs singly on the adaxial side of a flattened dwarf shoot that is axillary to a bract. The dwarf shoot also bears about 30 sterile scales. The seeds are dorsiventrally flattened and are 10 to 12 mm long, with a maximum width of 8 mm. The integument extends beyond the seed body, producing two broad flaps of tissue with a slit between them leading to the micropylar region (Fig. 1A). The internal structure of these seeds is basically similar to that of the Cordaitales and other Voltziales.

The best-preserved embryo appears

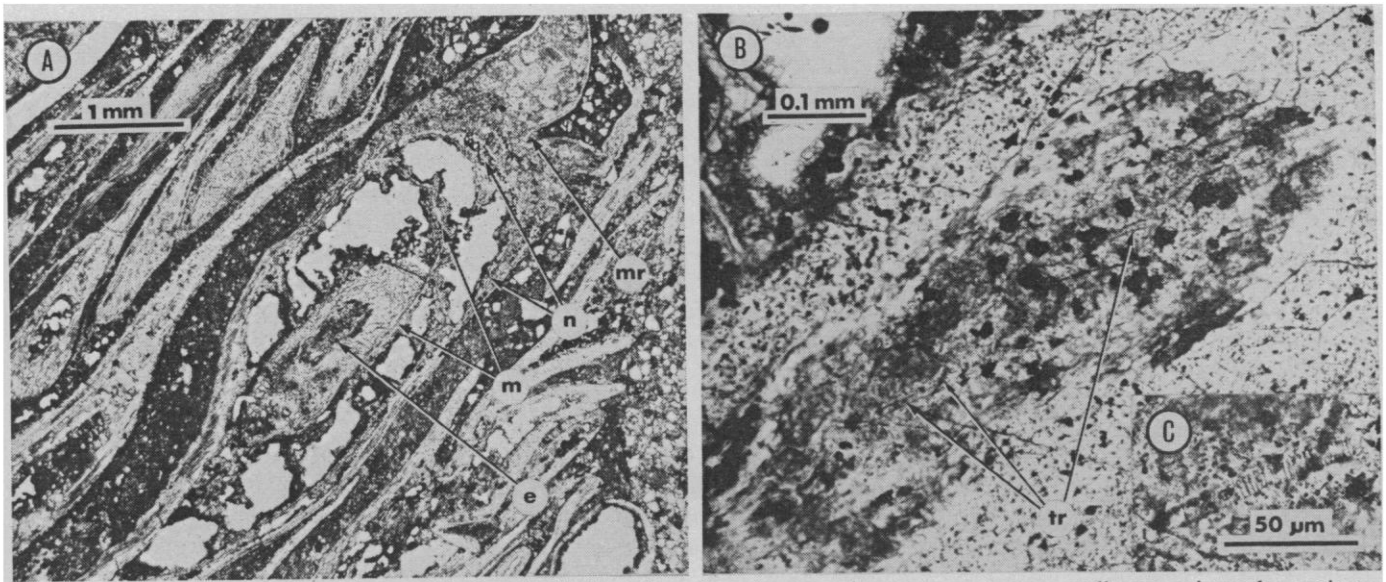

Fig. 1. Fossil seed with embryo tissue. (A) Longitudinal section of ovule; *e*, embryo; *m*, megaspore wall; *mr*, micropylar region (actual micropyle not in plane of section); *n*, nucellus. (B) Embryo tissue; *tr*, tracheids. (C) Tracheid with annular secondary wall thickenings.

in oblique longitudinal section as an elliptical area of parenchyma that includes three tracheids all within the megaspore membrane (Fig. 1, A, B, and C). The parenchymatous zone is 0.7 mm long and 0.3 mm wide, and is surrounded by an area of transparent mineral matter in which no cells are preserved. The parenchyma cells are elongate, measuring 30 μm long and 10 μm in diameter. Cell walls are better preserved at the periphery of the tissue than within. The tracheids (Fig. 1, B and C) are 8 to 12 μm in diameter; while annular thickenings dominate their secondary walls, one tracheid shows, in addition, some spiral thickenings. Two of the tracheids are sufficiently close that they might be connected, but the third is clearly not part of a single vascular strand (Fig. 1B). Both parenchyma cells and tracheids have their longitudinal axes generally parallel to that of the seed. A second seed contains four tracheids within the megaspore membrane but lacks preservation of any parenchyma.

While the tracheids, which are not normally produced in gametophytic tissue, constitute the main evidence for embryos in these seeds, additional support comes from the elongate shape of the embryo parenchyma. Megagametophyte cells are typically more isodiametric. The possibility that the tracheids and parenchyma result from the penetration of a foreign axis into the seeds must be ruled out. No foreign axes occur in the cone or surrounding matrix, and the integuments of the two seeds with embryos are intact in all sections in which they are visible. Furthermore, the tissue within the megaspore membrane in each case lacks a coherent vascular strand and extrastelar tissues indicative of a foreign axis. Thus, embryos had formed in these seeds prior to their dispersal from the cone.

Embryos large enough to produce tracheids in these Paleozoic seeds constitute the earliest known occurrence of the kind of development in most living seed plants in which embryo growth occurs before seed dispersal rather than after it. Embryos probably developed after seed dispersal in Paleozoic seed ferns and cordaites (*7*) because no embryos have been found in the hundreds of their dispersed ovules that have been observed, even though some of these show well-preserved megagametophytes with archegonia (*8*). In modern *Ginkgo biloba* fertilization and embryo growth is sometimes delayed until after ovules are shed (*9*), but in all other living seed plants embryo growth is essentially complete at the time of seed dispersal. Since *Ginkgo biloba* survived to the present in spite of its occasional delayed embryogeny, it is unlikely that production of the embryo after seed dispersal is any less efficient in the mechanics of embryo formation than embryo growth before dispersal. On the other hand, the inability of *Ginkgo biloba* seedlings to survive winters tolerated by older plants (*10*) suggests that production of embryos before seed dispersal may have evolved as an adaptation to climatic conditions to enhance seedling survival rather than as a better way of manufacturing an embryo. The earliest occurrence of the modern sequence near the close of the Paleozoic, when the climate became both cooler and drier, supports this interpretation. Regardless of the reason, evolution of the sequence of embryo growth typical of most living seed plants was accomplished by Lower Permian time as demonstrated by embryos in the seeds of this new conifer cone.

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