

fact that the test reaction was highly exothermic made temperature control difficult. Control to within $\pm 3^\circ\text{C}$ was achieved with an automatic controller (Leeds & Northrup) by maintaining the catalyst in a fluidized state through vibration of the reactor. The reactor was suspended in a fluidized bed which served as the heat-transfer medium.

A series of polycrystalline perovskites was prepared by sintering mixtures of the constituent oxides. The products were shown by x-ray diffraction measurements to be single phase. Samples of LaMnO_3 , LaCrO_3 , and LaCoO_3 were of comparable activity in the CO oxidation, whereas LaVO_3 deteriorated rapidly and LaFeO_3 was considerably less active than the other oxides.

The oxide catalysts used most extensively were crushed single crystals. X-ray diffraction measurements confirmed the perovskite structure and showed that the oxides were single phase. Two Pt catalysts marketed by Engelhard Industries were used for comparison. The PTX catalyst, consisting of approximately 0.5 percent (by weight) Pt on $\text{SiO}_2\text{-Al}_2\text{O}_3$, was obtained in the form of a ceramic honeycomb structure. A catalyst of 0.5 percent Pt on Al_2O_3 in the form of pellets (0.32 cm) was also used. Both were crushed. For all catalysts a sieve fraction between 37 and 250 μm was used in the reactor.

The results in Table 1 show that

$\text{Nd}_{1-x}\text{Pb}_x\text{MnO}_3$ and PrCoO_3 were more active than the PTX catalyst, whereas the other manganites and cobaltites were approximately as active as the PTX catalyst. This is the more encouraging since the specific surface area S of these oxides was only 0.03 to 0.1 m^2 per gram of catalyst, whereas the specific surface area of Pt in the commercial catalysts is expected to be of the order of 0.3 m^2 per gram of catalyst. The activity of the 0.5 percent Pt on Al_2O_3 pellets was higher than that of any other catalyst, but it deteriorated rapidly even during the activity test.

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References and Notes

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2. W. F. Libby, *Science* **171**, 499 (1971); L. A. Pedersen and W. F. Libby (personal communication) have informed us that the use of an unseparated mixture of rare earths instead of La gave equally good results in catalyzing the hydrogenation of *cis*-2-butene.
3. Details are included in brochures EM-6366 Rev. 4/71 and EM-8778, available from Engelhard Industries, Newark, New Jersey.
4. We thank J. N. Carides, who cooperated in the construction of the test apparatus, and F. Schrey, who determined the specific surface areas of the catalysts. R. L. Hartless and A. M. Trozzolo conducted some preliminary tests on the reduction of the rare-earth oxides by CO.

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Spongy Mesophyll Remains in Fossil Leaf Compressions

Abstract. *Spongy mesophyll tissue has been discovered preserved in fossil leaf compressions. The fossils occur in an outcrop at Genesee, Alberta, Canada. The fossiliferous beds belong to the Edmonton formation of Upper Cretaceous-lower Tertiary age. The mesophyll characteristic, when taken in conjunction with other characteristics, was found useful in the identification of some fossil leaves. Numerous detailed observations as well as comparisons of both living and fossil leaves show that the remains represent neither the epidermal nor the palisade tissue.*

In the course of an intensive investigation of a large suite of carbonized compressions of fossil leaves collected from a single outcrop at Genesee, Alberta, Canada, the discovery was made that portions of the spongy mesophyll were preserved. The fossiliferous beds belong to the Edmonton formation (1) and are of Upper Cretaceous-lower Tertiary age. The full significance of the discovery of remains of mesophyll came to light subsequently when comparative morphological studies were

made between the compressions and cleared leaves of their presumed modern correlatives. Sixty percent of the fossils comprise deciduous angiosperm leaves of which 43 percent belong to the genus *Cercidiphyllum* and 2 percent belong to *Platanus*.

A pattern of lacunae (Fig. 1, A, B, and E) was observed in more than a hundred compressions of leaf variants of *Cercidiphyllum* and a few fragments of *Platanus*. The lacunae are more or less circular in configuration, and they are

Fig. 1. (A and B) Portions of fossil leaf variants of *Cercidiphyllum* showing remains of spongy mesophyll. (C and D) Portions of cleared long-shoot leaves of modern *Cercidiphyllum japonicum* Siebold and Zuccarini showing lacunose spongy mesophyll. (E) Portion of a fossil leaf compression of *Platanus* showing remains of spongy mesophyll. Fossil specimens A, B, and E bear numbers S 2825, S 1586 (A), and S 169 (L), respectively, of the paleobotanical collection in the Department of Botany, University of Alberta. Magnification: A, B, C, and E, $\times 25$; D, $\times 200$.

easily observed even under low magnification. The lacunae show a wide range of variation in size. On the basis of 50 random measurements in ten specimens, the lacunae show a mean diameter of 75 μm in *Cercidiphyllum* (Fig. 1, A and B) and 30 μm in *Platanus* (Fig. 1E). A remarkably similar pattern was observed in spongy mesophyll tissue in cleared leaves of the living species of *Cercidiphyllum* and *Platanus*. Figure 1, C and D, shows a portion of a cleared long-shoot leaf of *C. japonicum* Siebold and Zuccarini illustrating the highly lacunose spongy mesophyll. In Fig. 1D individual cells encircling the lacunae are seen. One hundred and fifty random measurements of the diameters of lacunae in 20 cleared leaves of both long- and short-shoot leaves of *C. japonicum* showed a wide range of variation with a mean of 80 μm in long-shoot leaves and 45 μm in short-shoot leaves. The presence of lacunose mesophyll in *Cercidiphyllum* was found to be universal, irrespective of the geographical location, the age of the plant, and the type of leaf. The mesophyll lacunae in the leaves of living *P. cuneata* Willdenow were observed to be small, with a mean diameter of 26 μm .

The size and configuration of the lacunae in fossil leaves are very similar to that of the intercellular spaces in the spongy mesophyll tissue seen in the living plant. These observations led me to conclude that the lacunae found in fossil leaves represent the remains of mesophyll tissue (see Fig. 1, A and C).

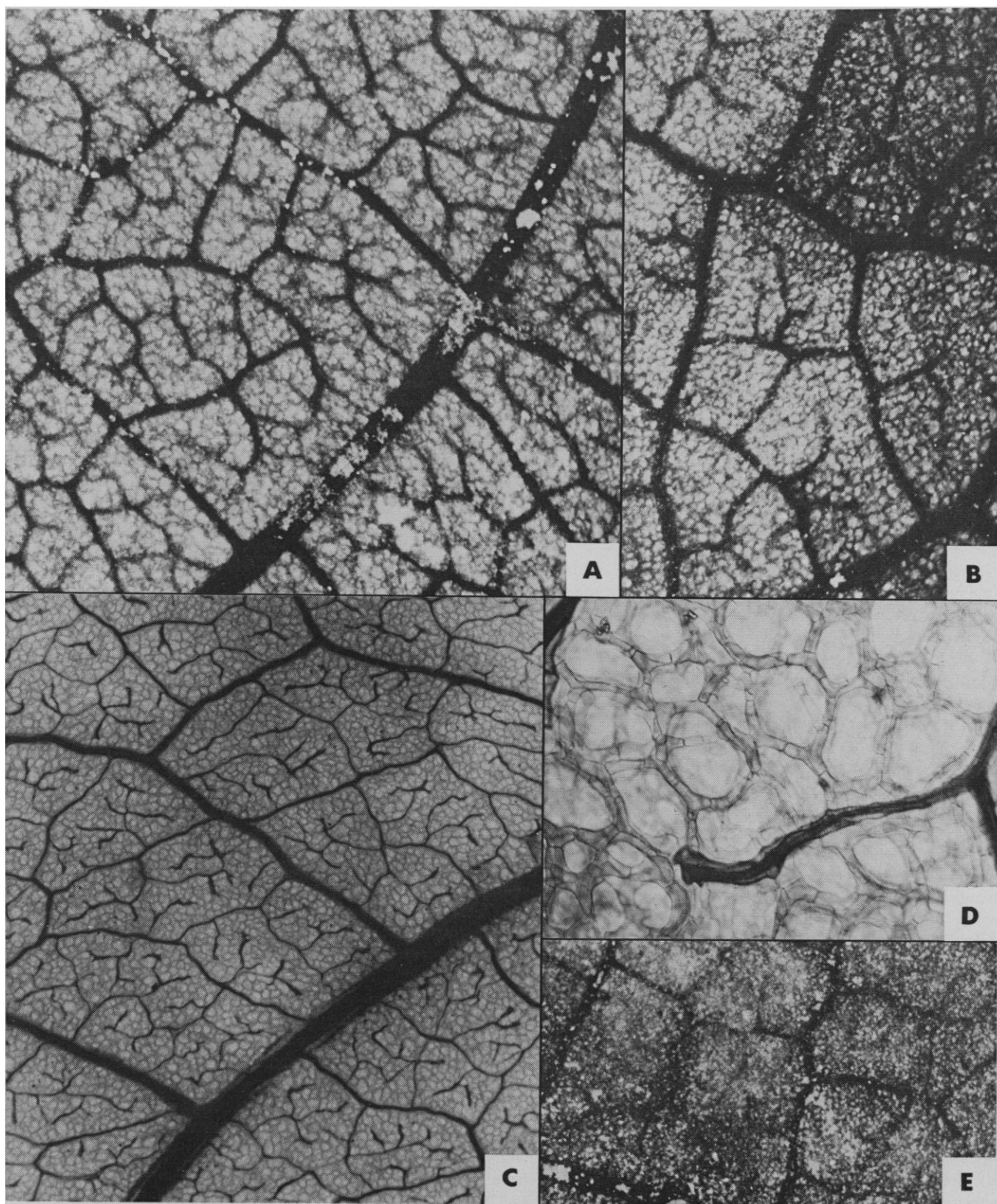
None of the compressions showed any recognizable cuticular remains. Epidermal cells in the extant species of *Cercidiphyllum* are roughly square to rectangular in shape, are small, and have wavy cell walls. These cells are in no way comparable to the lacunae found in the fossils (Fig. 1, A and B), thus eliminating the possibility that the lacunae might represent the intracellular spaces of epidermal cells. Furthermore,

it has been observed in transverse sections of a number of thin leaves of *C. japonicum* Siebold and Zuccarini that the palisade mesophyll tissue is poorly developed, consisting of short, thin-walled, small cells with a mean diameter of 10 μm and having small intercellular spaces. The intracellular

spaces of epidermal as well as palisade cells and the intercellular spaces in the palisade tissue are too small to be comparable with the lacunae observed in the fossils, thus eliminating the possibility that the lacunae might be remains of either epidermal or palisade tissue. These observations support the conclu-

sion that the lacunae observed in the fossil leaves are indeed intercellular spaces of spongy mesophyll and cannot be intra- or intercellular spaces in other tissues of the leaf.

Those familiar with the literature in paleontology are aware that instances of extremely fine preservation in fossils



are not uncommon. The preservation of remains of spongy mesophyll is remarkable, and no explanation or speculation with respect to the factors which were responsible is available at present. Experimental studies under laboratory conditions may throw light on the problem.

It is axiomatic to state that success in paleobotanical studies is determined by the quality of preservation of the material at hand. This is particularly true in investigations of fossil floras based upon leaf compressions. In general, the overall physiognomy of the leaf and the cuticular patterns, if preserved, provide the basic characteristics used in identifying fossil leaves. The patterns of mesophyll tissue, taken in

conjunction with these characteristics, were found to be valuable as an additional aid in identification.

It is premature to amplify the significance of this extraordinary finding as a diagnostic taxonomic feature. Nevertheless, the discovery is reported here as an unusual example of excellent preservation in fossil plant remains.

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Cochlear Inner and Outer Hair Cells: Functional Differences

Abstract. *The cochlear microphonic response was measured with differential electrodes from the first and third cochlear turns of normal guinea pigs and those treated with the ototoxic drug kanamycin. Histological controls showed that the outer hair cells in treated animals were missing over the basal half of the damaged cochleas, while the inner hair cells were intact. Measurements are consistent with the hypothesis that the potentials produced by inner hair cells are proportional to the velocity of the basilar membrane, whereas potentials generated by outer hair cells (which dominate the response of normal cochleas) are proportional to the displacement of the basilar membrane.*

In all auditory systems the immediate stimulation of the hair cells is mediated by a relative motion between the cells and their stereocilia. The adequate stimulus is probably the bending of the hairs and the concomitant deformation of the apical pole of the hair cells. The hairs can be bent by several mechanisms, and there are apparently four anatomical forms that have evolved to subserve this function (1). The most common such form is a tectorial membrane that is attached to the tips of at least some of the cilia. The relative motion between the tectorial membrane and the reticular surface of the organ of Corti provides the bending or shearing force to the hairs. Other anatomical arrangements include the presence of sallets, lateral connections among cilia, and free-standing cilia (2). It has been assumed that only the first type of anatomical arrangement, namely stimulation by means of a tectorial membrane, is important in the mammalian cochlea. This assumption implies that at least some stereocilia (probably the tallest ones only) of both inner and outer hair cells contact the bottom surface of the tectorial membrane. Electron micro-

scopic studies indicate, however, that whereas the cilia in the tallest row on the outer hair cells make intimate contact with the tectorial membrane, such contact is absent for any cilia of the inner hair cells (3). This observation then implies that the mammalian cochlea, like that of many lower vertebrates, is equipped with a dual stimulating system. According to Wever's classification (2), these are the tectorial system and free-standing cilia.

That the two types of hair cell would be stimulated by different mechanisms is not surprising, considering the profound morphological differences between them (4). What is important to consider, however, is that different mechanisms of stimulation imply different dynamic properties. Such differences in the dynamic behavior of inner and outer hair cells of the mammalian cochlea have been predicted by one of us (5). The mechanism of stimulation of the outer hair cells, because of their attached cilia, depends primarily on the relative displacement between tectorial membrane and reticular lamina (6), which in turn is directly proportional to basilar membrane dis-

placement (7). Thus the outer hair cells are primarily displacement detectors. In contrast, the bending of the free-standing cilia of the inner hair cells must depend on viscous forces exerted on them by the movement of endolymph around them. Such forces ultimately depend on the velocity of endolymph flow, which in turn is determined by the rate of displacement of the basilar membrane. Thus, the inner hair cells are primarily velocity detectors. Because the outer hair cells also possess free-standing cilia in addition to the attached ones, they too are stimulated with a velocity component. However, the displacement stimulus is much more prominent than the velocity stimulus over most of the audio frequency range; consequently, a good first approximation is that the output of outer hair cells is proportional to basilar membrane displacement, whereas the output of inner hair cells is proportional to basilar membrane velocity (5).

We report an experimental verification of the above-stated hypothesis. Cochlear microphonic (CM) potentials in response to well-defined test stimuli were recorded with differential electrodes from both normal cochleas and those with damaged outer hair cells. The first premise of this method is that in a normal cochlea the recorded CM primarily reflects the output of the outer hair cells (8). Because the CM magnitude produced by the inner hair cells is approximately 30 to 40 db less than that generated by the outer hair cells (9), the CM recorded from a normal cochlea can be assumed to reflect the dynamic properties of outer hair cells. Ototoxic drugs, particularly kanamycin, selectively damage outer hair cells (9, 10). With appropriately chosen doses of the drug one can generate patterns of hair cell destruction that yield virtually intact inner hair cells throughout the cochlea and virtually complete destruction of outer hair cells over the basal half of the cochlear spiral (11). In such cases a pair of differential electrodes placed in the basal turn of the cochlea would register the CM output of the inner hair cells in its vicinity. Thus by comparing the properties of the differentially recorded CM response from the basal turn of normal and kanamycin-treated animals, one can compare the microphonic output of outer and inner hair cells (12).

Guinea pigs in which hair cell damage was to be induced received subcutaneous injections of kanamycin (400 mg per kilogram of body weight)