To investigate the effectiveness of the new procedure in avoiding false minima, we arbitrarily selected three distinctly different false minima from the large number of solutions that were generated by a more conventional refinement procedure with the data at 23 K. Lattice constants differed from those cited above by as much as 2.1 Å and 6.9°. When these constants were introduced as starting parameters in the present procedure, all three smoothly refined to the solution tabulated above. Because the technique used to fit the data was based on adjustment of the entire pattern profile and was unconcerned with individual reflections as such, the overlapping of peaks introduced no difficulty. In fact, the approximately 40 peaks visible in Fig. 1 are composed of about 223 separate reflections. Each of the peaks shown is, on average, a superposition of six distinct reflections. It is therefore apparent why conventional indexing methods failed.

Subsequently, one of us (B.M.P.) investigated the pattern up to values of S of 2.5 $Å^{-1}$ at the highest resolution (λ = 4.1037 Å) for 23 K and, in a separate measurement, extended the range of data to S = 7.35 $Å^{-1}$ (λ = 1.48018 Å) for T = 23 and 85 K. These extensive intensity data were subjected to a full Rietveld refinement (*8*). Such an analysis is a means of extracting from powder data, once the proper identification of reflections has been established, the positions and motions of the atoms within the unit cell. In favorable cases, its precision is comparable to that attainable in refinements of intensity data from single crystals. In the present case the Rietveld analysis (*9*) fully confirmed the correctness of the cell constants reported here.

The structure of the low-temperature phase of SF_6 has been resolved and it corresponds to that predicted by the molecular dynamics simulations (*1*). Although some uncertainties remain about the full range of conditions required for the stabilization of the intermediate trigonal phase, the theoretical modeling of the thermal properties of a prototype molecular solid is now almost complete. The method that made it possible to interpret the low-temperature powder pattern should be equally effective with many other previously undecipherable diffraction patterns of materials that solidify only in a powdered form.

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Frequency Dependence of Electric Field Modulation of Fibroblast Protein Synthesis

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The effect of electric current on protein biosynthesis in mammalian fibroblasts was investigated with neonatal bovine fibroblast–populated collagen matrices. The field strength dependence of electric field modulation of proline incorporation into extracellular and intracellular protein was measured over a frequency range from 0.1 to 1000 hertz. A frequency- and amplitude-dependent reduction in the rate of incorporation was observed. In tissues containing cells aligned either parallel or perpendicular to the electric field, this response was dependent on the orientation of the cells relative to the direction of the applied electric field. This study demonstrates that currents of physiological strength can stimulate alterations in biosynthesis and thereby may influence tissue growth, remodeling, and repair.

CELLS WITHIN MAMMALIAN CONnective and skeletal tissues are regularly exposed to time-varying electric currents. These currents are produced endogenously, arising predominantly from the spatial and temporal integration of currents from excitable cells (*1*), and through currents generated by mechanical strain in glycosaminoglycan-rich connective tissues (*2*) and bone (*3*). These currents may well regulate the growth and remodeling of tissues (*4*) and alter cellular function.

Physiological electric currents (*5*) can modulate the behavior of nonexcitable cells. For example, the rate of DNA synthesis by pelleted chondrocytes was enhanced by applied current densities of less than 10 $\mu A/cm^2$ (*6*). Glycosaminoglycan synthesis by chondrocytes in monolayer culture was enhanced by current densities as low as 1 $\mu A/cm^2$ (*7*). In organ culture, current densities of 1 to 5 $\mu A/cm^2$ have been shown to alter calcium metabolism in chick tibiae (*8*).

We have measured the rate of incorporation of proline into protein by bovine fibroblasts cultured within collagen matrices and found that it is sensitive to sinusoidal electric currents in the frequency range from 0.1 to 1000 Hz. This response manifests an abrupt current density threshold that is frequency-dependent. In addition, we found this threshold of the current density to be dependent on the orientation of the cell with respect to the direction of the applied current.

The remodeling of connective tissue is regulated by physical stresses (*9*). Because fibroblasts are primarily responsible for this remodeling in soft connective tissue, they were selected for these experiments. Neonatal bovine fibroblasts were obtained by disaggregating superficial fascial tissue from the thigh of 2-week-old calves by serial trypsin and collagenase digestions. The cells obtained were plated in flasks, maintained in Dulbecco's modified Eagle's medium (DMEM) containing 10% calf serum, and transferred to new flasks to avoid overcrowding two to five times prior to incorporation into gels.

To control the extracellular matrix composition and cell density, we fabricated tissues of constant composition by incorporating fibroblasts in collagen matrices using the technique of Bell *et al.* (*10*). Native type I collagen (2 mg/ml) was obtained through extraction of the tail tendons of young (less than 2 months old) Sprague-Dawley rats

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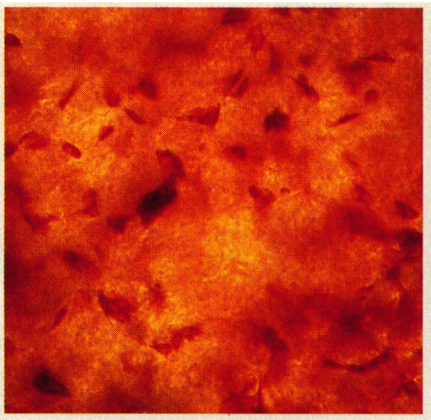

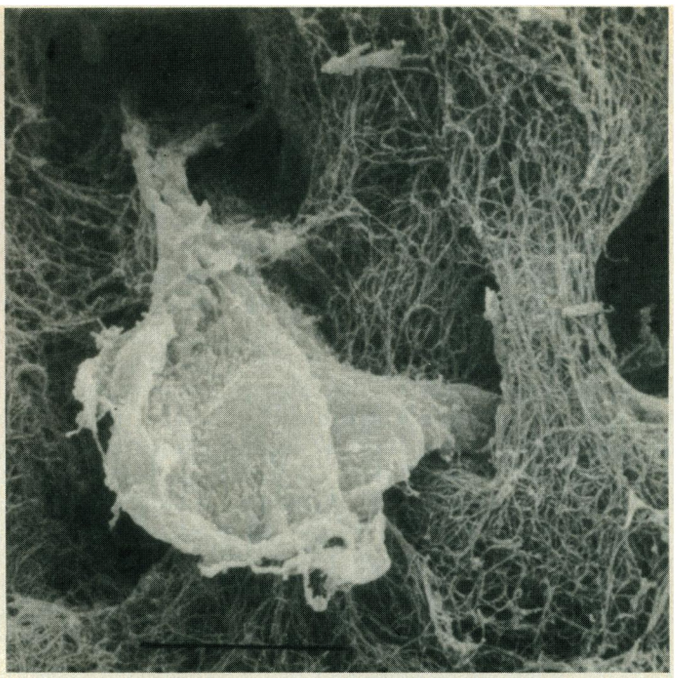

Fig. 1. (**Left**) Light micrograph (100×) of 500-μm, neutral red–stained 3-day-old FPCM demonstrating the relative distances between randomly oriented cells and the translucency of the matrix. Initial type I collagen concentration was 0.055 mg/ml, initial cell density was 80 × 10^3 per milliliter. (**Right**) Scanning electron micrograph, prepared by critical point drying, showing fibroblast in porous collagen matrix. Bar, 10 μm.

with 0.5*M* acetic acid. Neutralized collagen solution and cells suspended in media were mixed and warmed to 37°C. Gelation occurred within 10 minutes, and within several hours the gel was visibly contracting. After 3 days both matrix contraction and cell population plateaued, and the fibroblasts populated collagen matrix (FPCM) could be easily manipulated. Neutral red staining of an 800-μm-thick FPCM revealed randomly oriented cells and scanning electron microscopy revealed cells surrounded by a loose matrix (Fig. 1). More than 90% of the cells in these matrices were in the G_0 phase of mitosis, and the cell density approximated that of loose connective tissue (*10*). There was less than a 10% difference between the electrical conductivity of the FPCM and that of the surrounding media (65 ohm-cm). Samples (1 cm^2) were cut from the FPCM, and randomly assigned to control or exposure groups. Up to 16 samples could be obtained from a single FPCM.

Control and exposure samples were mounted in Teflon holders that had circular apertures and then mounted in a Teflon chamber (Fig. 2) containing fresh serum-free medium supplemented with 10 μCi/ml of [^{3}H]proline and 1 m*M* proline. The chambers were incubated in a mixture of 95% air and 5% CO_2 at 37°C and 99% humidity. A programmable current source provided stable low-frequency currents with dc flow limited to less than 0.1% of the ac amplitude. Current was passed through the exposure samples for 12 hours via platinum electrodes, which were separated from the bath by media bridges and convection barriers (membranes). We determined current density by dividing the total current by the aperture area of the holders, and we estimated field intensity in the FPCM samples by Ohm's law, using the determined value of the media resistivity.

We estimated accumulation of newly synthesized protein by measuring the incorporation of [^{3}H]proline into macromolecules. Immediately after a 12-hour exposure period, samples were washed at 4°C and then digested with bacterial collagenase, after which the cells were separated from the matrix components by centrifugation. After cell number was determined, the cells were disrupted (*11*), and intracellular protein was precipitated with cold trichloroacetic acid. The amount of ^{3}H in both the matrix and the cell fractions was determined by scintillation spectroscopy and normalized to cell number. Control studies demonstrated an incorporation rate of 450 pmol of proline per hour per million cells in serum-free medium; addition of 10% calf serum increased this synthesis rate by a factor of 1.7 to 2.0. Collagen, assayed by differential salt precipitation (*12*), accounted for approximately 4% of recovered synthesized protein (*13*), a result consistent with a previous report (*14*).

Experiments were performed over a range of current densities (0.1 μA/cm^2 to 1 mA/cm^2, root mean square) and frequencies (0.1 to 1000 Hz). Electric current caused an alteration in the rate of incorporation of [^{3}H]proline into secreted protein. Currents as low as 1 μA/cm^2 triggered a 30% reduction in normalized ^{3}H counts (Fig. 3A). This was interpreted as a reduction in the incorporation of newly synthesized protein into the extracellular matrix rather than a change in cell number, because there was no difference between field-exposed cell count and control cell count. Above this current density, increasing the current over two orders of magnitude did not significantly increase the response. However, halving the current density led to no statistically significant response. The threshold current density was frequency specific.

The frequency dependence of the re-

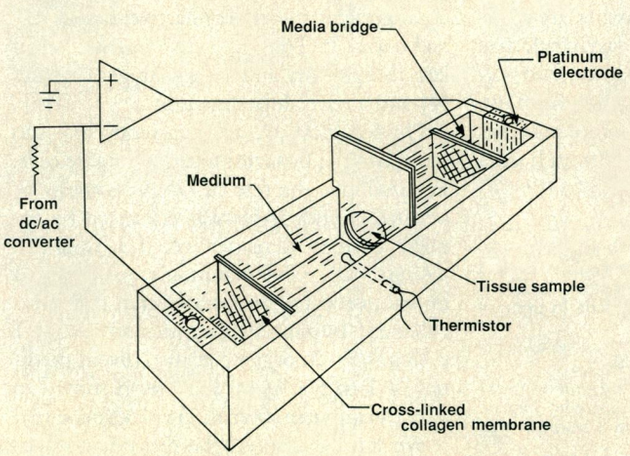

Fig. 2. Experimental apparatus for exposure of FPCM samples to electrical fields. Platinum electrodes were separated from the site of the tissue sample via media bridges. A programmable current source with series dc blocking capacitors maintained a constant current within the chamber media, independent of variations in electrode-electrolyte interfascial impedance. The lumen of the sample holder established a defined current density, and therefore field intensity, through the FPCM.

sponse suggests a frequency range that may be optimally effective for alteration of extracellular matrix protein synthesis (Fig. 3B). The effect of both frequency and electric field strength is shown in Fig. 3C over the range of 1 to 1000 Hz and 0.01 to 100 mV/cm, respectively. Peak sensitivity was recorded at 10 Hz, where a current density of only 0.5 $\mu A/cm^2$ produced a significant reduction in protein incorporation in the matrix component. Because the media resistivity was 65 ohm-cm (*15*), this corresponds to a peak field intensity in the medium of 45 $\mu V/cm$. The incorporation of radiolabel into intracellular protein reflected the pattern seen in the extracellular matrix.

To test whether chemical by-products of electrolysis were responsible for the response, we passed a current of 100 $\mu A/cm^2$ through the media for 12 hours and then discontinued the current immediately before transfer of the FPCMs to the chambers. The FPCMs were kept in the chambers for 12 hours while being bathed in the electrically conditioned media, then analyzed as usual. No significant difference in rates of proline incorporation was observed between the control samples and samples that had been in the electrically preconditioned media. This finding suggested that the responses required direct exposure to the electric field, and the electric field effects were not mediated by nonvolatile by-products of electrolysis. Similarly, to test whether the cellular responses were a consequence of thermal effects, we analyzed the magnitude of Joule heating. The temperature rise of the media adjacent to the sample position was measured as a function of both current density and time. A current density of 10 mA/cm^2 was required to produce a steady-state temperature increase of 0.5°C with an onset time constant of approximately 20 minutes (*15*). The steady-state temperature elevation was proportional to the square of the current density. For the range of current densities used in our experiments, the expected temperature rise was much less than 0.1°C, which is less than the temperature fluctuations in the incubators.

For the frequencies used in these experiments, plasma membrane impedance is many orders of magnitude higher than that of the cytoplasm. When a cell the size of a bovine fibroblast is placed in an applied field, the membrane essentially prevents current flow through the cell. Current exclusion results in the imposed potential difference occurring primarily across the cell membrane (*16*). The maximum imposed membrane potential is approximately proportional to $E_0L/2$, where E_0 is the applied field magnitude and L the maximum linear dimension of the cell in the direction of the

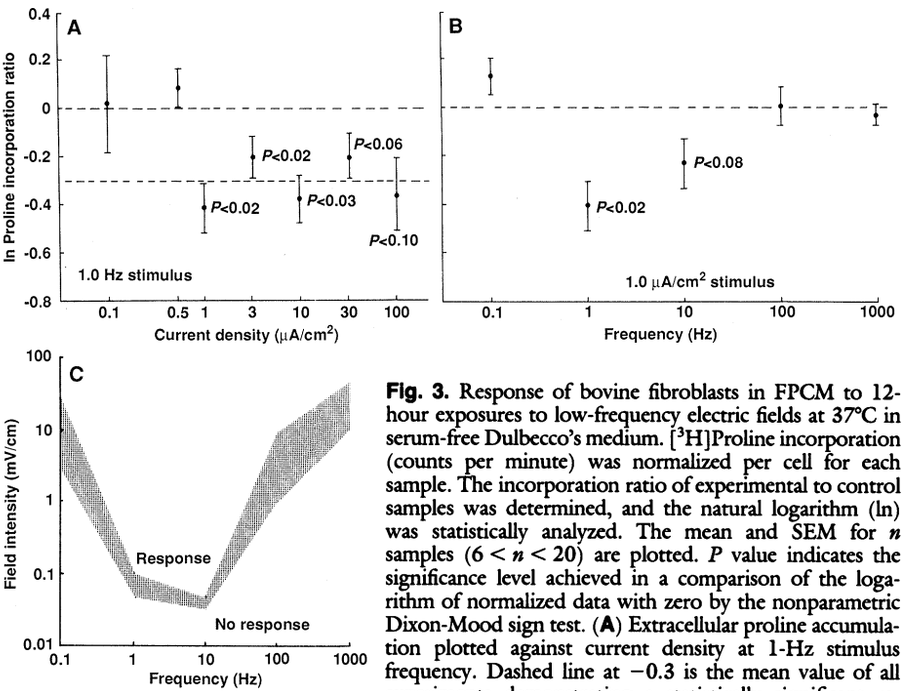

Fig. 3. Response of bovine fibroblasts in FPCM to 12-hour exposures to low-frequency electric fields at 37°C in serum-free Dulbecco's medium. [^{3}H]Proline incorporation (counts per minute) was normalized per cell for each sample. The incorporation ratio of experimental to control samples was determined, and the natural logarithm (ln) was statistically analyzed. The mean and SEM for n samples ($6 < n < 20$) are plotted. P value indicates the significance level achieved in a comparison of the logarithm of normalized data with zero by the nonparametric Dixon-Mood sign test. (**A**) Extracellular proline accumulation plotted against current density at 1-Hz stimulus frequency. Dashed line at -0.3 is the mean value of all experiments demonstrating a statistically significant response. (**B**) Normalized extracellular proline accumulation plotted against frequency for 1.0 $\mu A/cm^2$. (**C**) Minimum field intensity for a detectable response. Summary of results for all tested frequencies and current densities. Current densities were converted to peak field intensities by using the measured media resistivity of 65 ohm-cm. The lower boundary of the gray region represents the highest field intensity at which no significant change in extracellular protein accumulation was detected; the upper boundary represents the lowest intensity evoking a statistically significant change ($n = 6$).

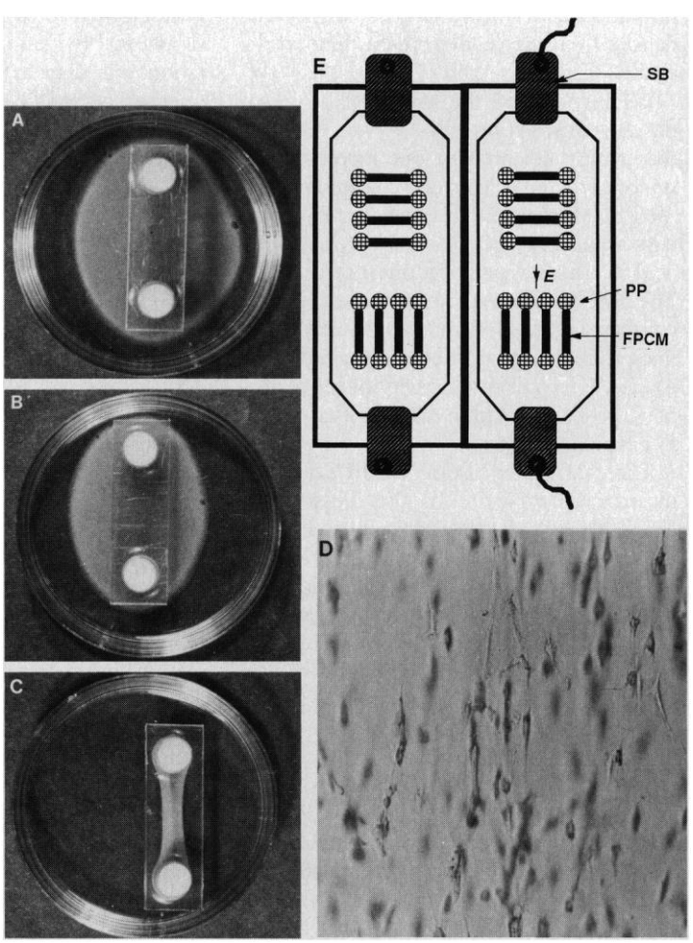

Fig. 4. Contraction and formation of oriented FPCM. Fibroblast populated gels cast into 60-mm petri dishes with two polyethylene posts (PP) held at a fixed separation. (**A**) Hydrated gel after 24 hours of contraction, (**B**) intermediate stage, and (**C**) 72 hours, the condition at which the oriented FPCMs were utilized. (**D**) Bright-field photomicrograph (×100) of FPCM showing cellular alignment. (**E**) Diagrammatic representation of control and exposure chamber (with electric field E) for oriented FPCM samples. Each chamber holds eight samples, four oriented parallel and four perpendicular to the applied field. Current density is dictated by media depth for a constant current source. SB, salt bridge.

field. For nonspherical cells, a maximum imposed membrane potential occurs when the major axis of the cell is aligned in the direction of the imposed electric field. This alteration in transmembrane potential may mediate the cellular response to low-frequency extracellular electric fields.

One test of this hypothesis makes use of the nonspherical shape of the cells used in this study. Fibroblasts, in the collagen lattices, took on a bipolar morphology that has been previously described (*17*). The maximum length of these cells was approximately 150 μm, which is seven to ten times the length of their minor dimension. If the depression in incorporation is mediated by a change in the membrane potential, then cells exposed to fields parallel to their major axes should exhibit a different threshold intensity than cells with their major axes perpendicular to the applied electric field. Of course, other, probably significant, parameter changes occur with changes in the cells' orientation. The plasma membrane area over which the maximum transmembrane potential alteration occurs is reduced when cells are aligned with the field. Also, the interaction of the electric field tangential to the plasma membrane with the cell surface will change with cell reorientation. Despite these complicating factors, such an orientation-dependent effect provides further evidence of a response dependent only on the electric field.

We investigated the role of cell orientation by constructing FPCMs with cells predominantly oriented in one direction. To uniformly align cells in the collagen matrix, the FPCMs were allowed to contract over 3 days around two porous polyethylene posts held at a fixed separation distance of 2 cm. The FPCMs contracted with the cells and collagen aligned along an axis defined by the line passing through the porous posts (Fig. 4). The electrical conductivity of the media-filled posts was within 10% of that of the free media solution.

Three days after casting, the FPCMs were placed in the exposure chamber illustrated in Fig. 4. In each chamber, half of the FPCMs were installed with the major axes of the cells parallel to the applied electric field, while the other half were installed with cells oriented perpendicular to the direction of the electric field. Current was passed through the experimental samples for 12 hours. After the exposure period, the center sections between the posts were removed and analyzed for proline incorporation with the same protocol as used for the FPCMs with random cell orientation.

Because the cells were most sensitive to 10-Hz fields, we used this frequency to examine the effect of orientation on the field

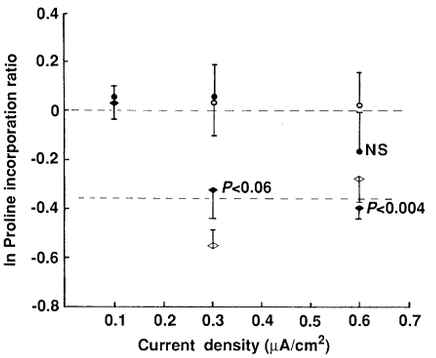

Fig. 5. Normalized extracellular proline incorporation (closed symbols) and intracellular proline incorporation (open symbols) plotted against current density for oriented FPCMs at 10 Hz. Samples with cells oriented parallel to field (diamonds) demonstrate a threshold current density below that seen in the samples of randomly oriented cells, whereas samples with cells perpendicular (circles) show no depression of proline incorporation at a current intensity above the threshold level for randomly oriented samples. Data points (n = 6), dashed lines, and probabilities are as defined in the legend to Fig. 3A. NS, not significant.

intensity threshold. For the randomly oriented FPCMs, a current density of 0.3 μA/cm^2 produced no significant effect on the rate of proline incorporation. However, when cells aligned with the electric field were exposed to the same current density, a significant reduction in proline incorporation was detected. In contrast, the cells oriented perpendicular to the field did not respond. Cell alignment with respect to the electric field modulated the intensity threshold (Fig. 5). Cells parallel to the field responded at 0.3 μA/cm^2, whereas cells perpendicular to the field did not show a significant depression in protein secretion at 0.6 μA/cm^2. Therefore, at 10 Hz cells with their major axes aligned with the field detected a field intensity as low as 20 μV/cm. This corresponds to a maximum membrane potential perturbation of less than 0.5 μV.

Our study has demonstrated that protein production in FPCMs is more sensitive to electric fields over the physiological frequency range than was previously shown for connective tissue cells. If the cells are equally sensitive in vivo, mechanically induced fields in connective tissue may be able to trigger cell-mediated changes in tissue repair and remodeling as proposed by Bassett (*18*). Similarly, fibroblasts in vivo may also be sensitive to other endogenously or exogenously generated electric currents.

The strong frequency dependence of the response suggests two modes of electrically mediated control of tissue composition. In the presence of a constant frequency current, a change in biosynthetic activity could follow an increase in local current density. Alternatively, if the frequency of local electrical currents were altered, for example, through a change in the mechanical loading rate on the tissue, then a biosynthetic response could be triggered even at constant current amplitude. Through either pathway, endogenously generated currents might be used as a feedback signal for tissue remodeling and repair.

Other cell types have been shown to have frequency-dependent responses to electric fields. The action potential firing rate of *Aplysia* ganglion cells was modified by tissue current densities as low as 2 μA/cm^2, and a distinct frequency sensitivity was established with a peak sensitivity near 0.5 Hz (*19*). The heart rate of frogs was found to be depressed at current densities above 500 μA/cm^2 with a peak sensitivity near 0.5 Hz (*20*), and the respiration rate of cats decreases at current densities as low as 1 μA/cm^2, with a peak sensitivity at 2 Hz (*21*).

The molecular mechanisms through which weak electric fields trigger a biosynthetic response are unknown. Because a variety of cell types (*22*) also exhibit extreme sensitivity to electric fields, this capability may be a primitive one and may serve a fundamental role in the interaction of living systems with their environment.

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Pollen and Spores Date Origin of Rift Basins from Texas to Nova Scotia as Early Late Triassic

ALFRED TRAVERSE

Palynological studies of the nonmarine Newark Supergroup of eastern North America and of rift basins in the northern Gulf of Mexico facilitate correlation with well-dated marine sections of Europe. New information emphasizes the chronological link between the Newark basins and a Gulf of Mexico basin and their common history in the rifting of North America from Pangea. Shales from the subsurface South Georgia Basin are shown to be of late Karnian age (early Late Triassic). The known time of earliest sedimentation in the Culpeper Basin is extended from Norian (late Late Triassic) to mid-Karnian, and the date of earliest sedimentation in the Richmond and Deep River basins is moved to at least earliest Karnian, perhaps Ladinian. The subsurface Eagle Mills Formation in Texas and Arkansas has been dated palynologically as mid- to late Karnian. The oldest parts of the Newark Supergroup, and the Eagle Mills Formation, mostly began deposition in precursor rift basins that formed in Ladinian to early Karnian time. In the southern Newark basins, sedimentation apparently ceased in late Karnian but continued in the northern basins well into the Jurassic, until genesis of the Atlantic ended basin sedimentation.

THE TRIASSIC-JURASSIC FAULT-bounded basins of the eastern United States and Canada (Fig. 1) contain nonmarine clastic rocks, minor tholeiitic extrusive igneous rocks, and diabase plutons and dikes, now referred to the Newark Supergroup (*1*). The basins themselves are commonly called the Newark basins. Because these rocks contain no marine fossils, their correlation with European sections was long problematic, although abundant vertebrate and megafossil plant fossils are found at various localities throughout the basins. When it was discovered that abundant fossil spores and pollen occur not only in the coals and other relatively rare carbonaceous rocks in a few of the basins, but also in gray shales found among the prevailing red sandstones and shales of all of the Newark basins (*2*), the possibility of correlating with European sections containing both palynofloras and marine fossils was realized. The original broad-scale palynostratigraphy suggested for the major basins has held up quite well since its proposal a decade ago (*3*). More recently, because the palynomorph forms were well known from previous study of the floras in the basins just mentioned, it has also proved possible to date shales from the Cow Branch Formation of the Danville–Dan River Basin of Virginia–North Carolina as mid- to late Karnian, despite the poor state of preservation of the palynomorphs (*4*). The Fundy Basin of Nova Scotia and New Brunswick, Canada, has yielded only a few palynoflorules, largely because aeolian red beds predominate, but nevertheless palynoflorules have provided enough information to date most of the sedimentary rock of the basin as ranging from at least as old as mid-Karnian to Pliensbachian (Early Jurassic) (*5*).

As a result of recent palynological studies (*6*) considerably more information about the correlation and dating of the sedimentary rocks of these basins has become available. Newly discovered palynologically productive localities in the Culpeper Basin of Virginia and Maryland have extended the known age of the oldest rocks of this basin downward to mid-Karnian (Fig. 2). Extensive investigation of the Taylorsville, Richmond, and Deep River basins (*7*) has extended the age of their sediments to at least earliest Karnian, possibly late Ladinian (previously, none older than mid-Karnian was

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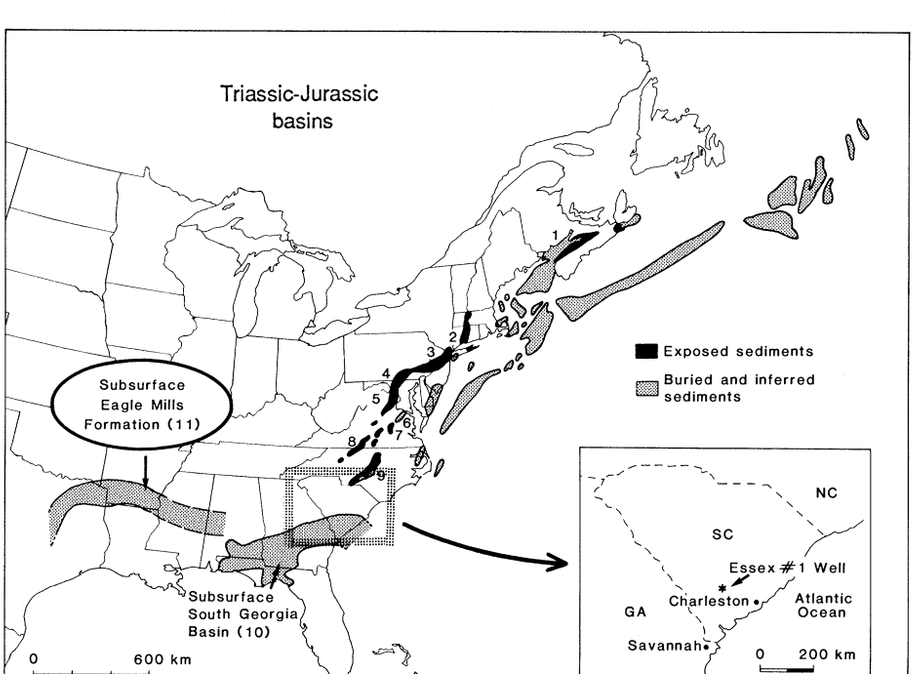

Fig. 1. Outcropping and buried Mesozoic fault-bounded rift basins of the eastern and southern margins of North America: the location of the newly dated sediments of the South Georgia Basin is indicated by the inset. The basins treated in this report are numbered: 1, Fundy; 2, Hartford-Springfield-Deerfield; 3, Newark; 4, Gettysburg; 5, Culpeper; 6, Taylorsville; 7, Richmond; 8, Danville–Dan River; 9, Deep River; 10, South Georgia; and 11, Eagle Mills (*17*).