FLORA, FAUNA, AND PALEOECOLOGY OF THE
Brazil Formation of Indiana

Southwestern Indiana provides a window on a Middle Pennsylvanian coastline in the equatorial tropics about 310 million years ago.

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THE PRIMEVAL FORESTS FIRST APPEARED in the Late Devonian and Early Mississippian and reached the peak of their development during the Middle Pennsylvanian. From above, the lowland coastal regions of the Pennsylvanian Period might not have looked much different from parts of modern Sumatra or Borneo. However, an observer on the ground would find a world very different from today's, one populated by strange plants and animals. By the end of the Middle Pennsylvanian, these great primitive forests and their animal inhabitants were on the brink of final destruction. A series of climatic changes beginning at the transition between the Middle and Late Pennsylvanian induced widespread extinctions. We discuss a portion of this ancient landscape in what is now southwestern Indiana, a window on a Middle Pennsylvanian coastline in the equatorial tropics about 310 million years ago.

Paleoecology

PALEONTOLOGY AND THE EXPLOITATION of natural resources, particularly coal and limestone, have an old and firmly established connection. This is especially important in deposits of Pennsylvanian age, where coal mining has helped to fill the collection drawers of museums and universities across North America and Europe. Unlike most natural exposures, those created by mining frequently reveal whole trees, forests of tree stumps, and enormous complete fronds of ferns and fernlike plants, preserved where they fell in muds that covered dying peat-swamp forests. So much information is preserved in these kinds of exposures that they provide paleontologists with an extra measure of insight into the past. Not only can the species that lived at that time be identified, but also the structure and even some element of the dynamics of ancient ecosystems can be reconstructed.

Paleoecology is a growing and increasingly important part of studies of terrestrial plants and animals. The time element afforded paleoecology permits the study of ecosystems over long periods of time. As a result, the response of these ecosystems to climatic change, changing sea levels, or the appearance of new kinds of organisms can be studied empirically. This has led to a series of test cases for theories and predictions of modern ecology that are based on extrapolations from short intervals of time. Such tests are extremely important. Today's society may have initiated a major global climate change, and paleontology may be able to provide insights into the likely outcome of biological events attendant on changing physical conditions.

The Brazil Formation

The rocks of the Brazil Formation are from the middle of the Middle Pennsylvanian (upper Westphalian C in European stratigraphic terms), about 310 million years old. At this time Europe and North America were part of a single continent straddling the equator. The Illinois Basin coal field, including Indiana, was in the southern hemisphere,

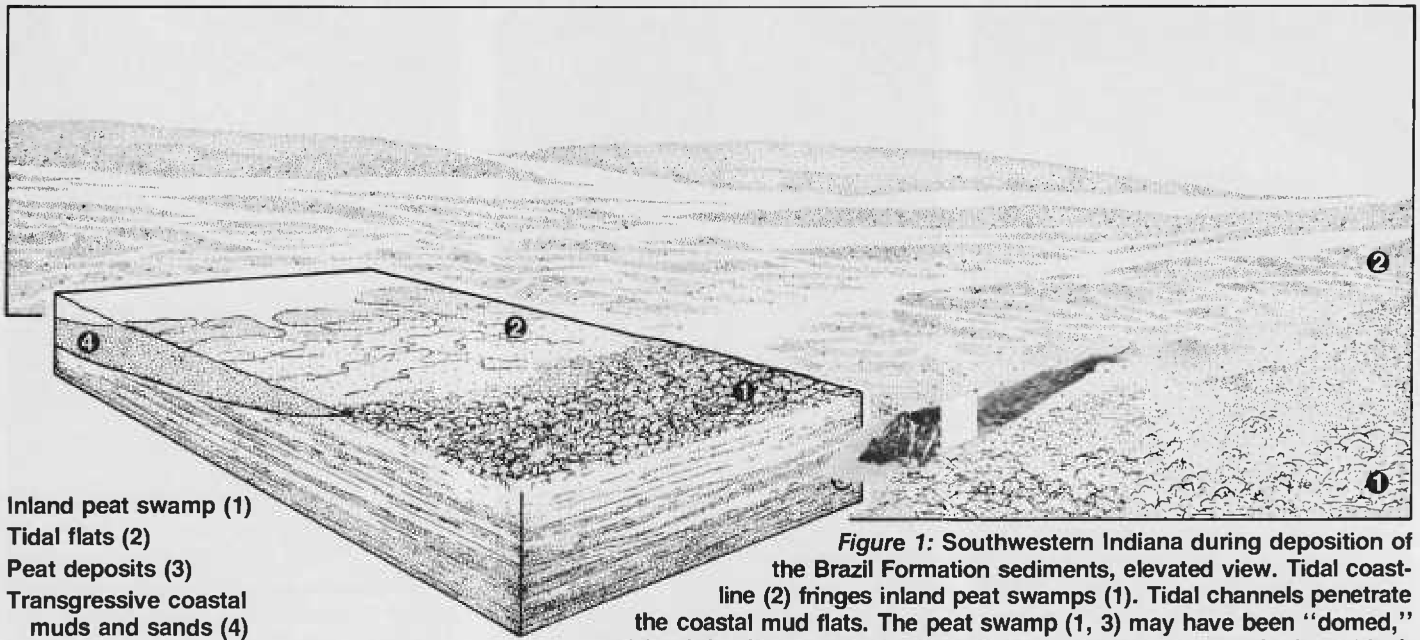

Figure 1: **Southwestern Indiana during deposition of the Brazil Formation sediments, elevated view. Tidal coastline (2) fringes inland peat swamps (1). Tidal channels penetrate the coastal mud flats. The peat swamp (1, 3) may have been "domed," raising it in elevation above the seaward coastal muds (4). The inset block diagram illustrates the transgression of the peat swamp (1, 3) by the tidal flats.**

within a few degrees of the equator. This was a time of changing climates in the Euramerican tropics. Studies by Tom Phillips and Russell Peppers of the University of Illinois and the Illinois State Geological Survey (1984) and by Blaine Cecil and coworkers at the U.S. Geological Survey (1985) suggest that the tropics were changing from a region of nearly year-round rainfall to one dominated by seasonal rainfall.

Reconstructing the ecological interactions of an ancient ecosystem requires several kinds of data. It is important to know the environment of deposition, from which it is possible to reconstruct the general habitat occupied by the flora and fauna, or at least to interpret the extent to which some of the components of the biota have been transported. Detailed descriptions of the plants and animals are also very important; because of the possibility of transport, the physical condition of each specimen must be examined in order to determine whether abrasion, corrosion, or other types of damage have occurred. Detailed study of the plants and animals is necessary in order to understand how they resemble and differ from modern relatives and to begin to interpret the ecology of each kind of organism represented. Once the habits and behaviors of the individual taxa are interpreted, it is possible to reconstruct the interactions and dynamics between them, giving a picture of the entire forest community.

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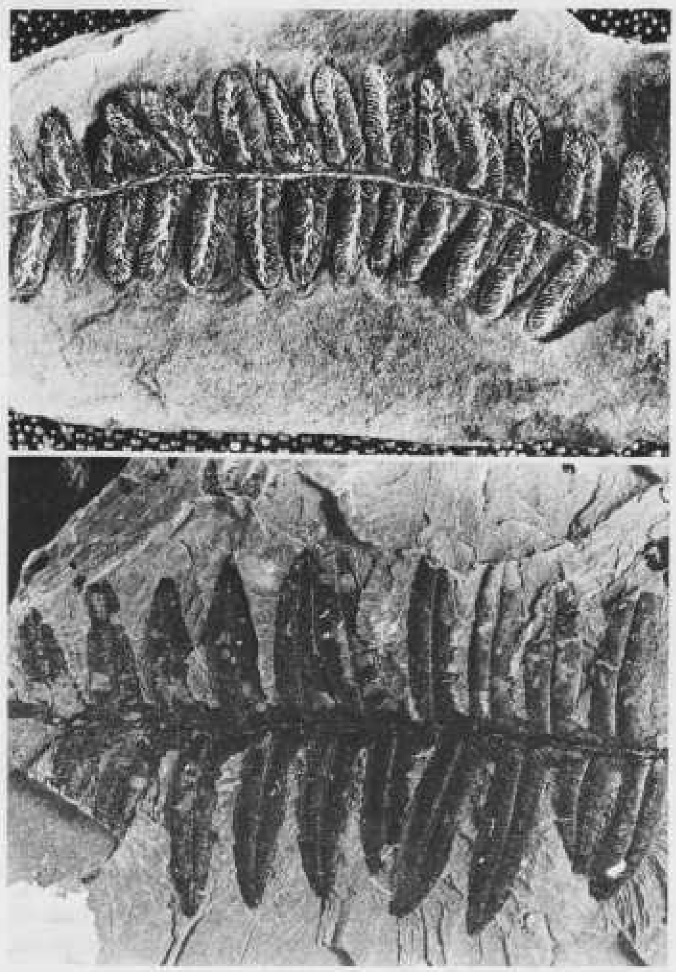
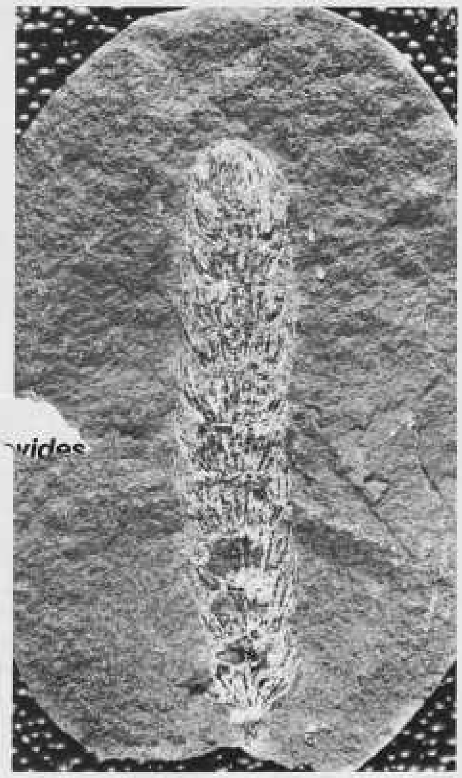


Figure 2: **Two species of *Alethopteris*, foliage of seed ferns. The upper specimen is preserved in a siderite nodule (plate 6, figure 1 of Wood, 1963); the lower is preserved as a compression in gray clay-shale. These and all illustrated specimens are from the shales above the Lower Block coal.**

Figure 3: Samaropsis, **seed of a cordaite, a coniferlike plant; siderite nodule (plate 11, figure 11 of Wood, 1963).**



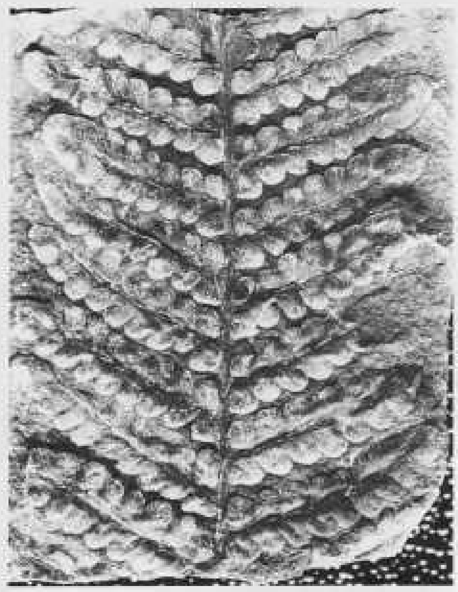


Figure 5 (above): Pecopteris, **foliage of a tree fern; siderite nodule (plate 8, figure 1 of Wood, 1963).**

Figure 4 (left): Calamostachys, **cone of a calamite, close relative of modern horsetails; siderite nodule (plate 4, figure 6 of Wood, 1963).**

Habitat and Environment of Deposition

Three hundred ten million years ago southern Indiana lay near the margin of a shallow, epicontinental sea covering most of the midcontinental United States. Africa was colliding with Euramerica, raising the Appalachian Mountains. As the mountains became higher, they interfered with global atmospheric circulation patterns, creating a rain shadow that changed the climate of Euramerica drastically. It was during the early part of this climatic change that the Brazil Formation was deposited on a shallow shelf bordering the eastern side of the Illinois Basin. Because the mountains were only beginning to alter the climate, rainfall still weathered the uplifts. Rivers carried the muds, silts, and sands to the edge of the epicontinental sea, where they were deposited. Oscillation of the shoreline across the shelf is recorded in the sequence of coals and shallow, nearshore muds and sands that make up the Brazil Formation. These rocks preserve the remains of the coastal margin flora and fauna that lived in several environments bordering the sea.

The finest biota of this time is preserved in finely laminated clays immediately above the Lower Block coal, a thickness of about 50 cm to 1 meter. In some places the plants and animals are preserved as compressions and impressions in siderite (iron carbonate) concretions, the type of preservation characteristic of the famous Mazon Creek biota of northeastern Illinois. However, most of the fossils, largely plants, are preserved as black carbonized compressions in the dark gray claystone. Many of these plant fossils are quite large and well preserved, suggesting that they were buried in mud very near their site of growth. In rare instances, upright trees have been found rooted in the top of the coal seam, undoubtedly representing the final drowned forest of the peat swamp.

The rocks containing the plant fossils, if broken at right angles to the bedding surfaces, reveal very fine rhythmic laminations or layers. Above the plant-rich clays, the rocks become siltier and even sandy. The distinct laminae remain, however, and can be traced widely across exposed surfaces in mines. Erik Kvale of the Indiana Geological Survey and Allen Archer of Kansas State University have been studying the deposition of these rocks. They recognize not only the very distinct laminations but also a periodicity in the thickening and thinning of laminae, indicating a regular cyclicity. By counting laminae vertically they infer a periodicity conforming to that of the lunar cycle—tides! It appears that the rocks above the Lower Block coal were deposited in a transgressive sequence; that is, they reflect the encroachment of the sea onto the land surface. Sand-filled channels, also showing the distinct laminations, buried trees up to 5 meters tall, and lateral changes in the relative abundance of silt, sand, and clay suggest a complex of mud flats, embayments, and tidal channels along a coastline seaward of peat swamps.

As sea level rose slightly, this complex of coastal sedimentary environments was pushed back over the peat swamps, drowning and burying them. The plant-bearing claystones immediately above the coals probably represent muds of mud flats or lagoons that buried the vegetation fringing the peat swamp. Only the occasional upright trees, rooted in the top of the coal and often found in the bottom of tidal channels, allow us to see the swamp vegetation. The height of some of these trees indicates rapid burial, suggesting accumulation of the rocks between the Lower and Upper Block

Figure 6: Pecopteris bearing reproductive organs (sporangia) that give pinnules a bumpy appearance; shale compression.

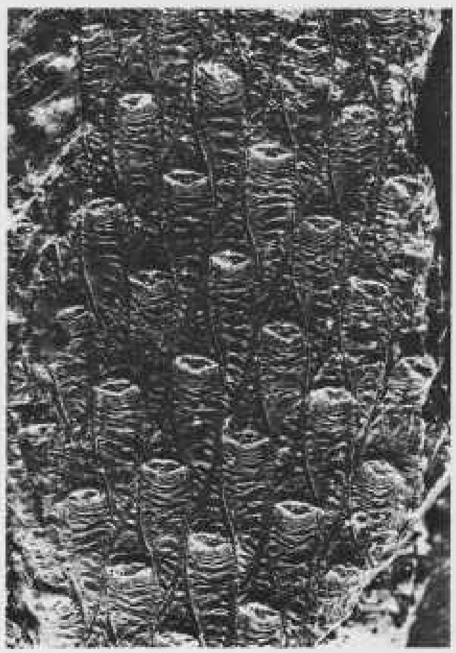


Figure 7: Lepidodendron wortheni, bark of a lycopod tree, also known as scale trees, which have no modern descendants of comparable form; shale compression.

Figure 8: Millipede in a siderite nodule. Several kinds of millipedes occur in siderite concretions in the Brazil Formation. This one was able to enroll completely, much like the "pill bugs" living today.

The authors continue to collect floras in active strip mines, mostly southeast of Terre Haute, and have found dominant shale compressions and occasional siderite nodules.

coals during a relatively short period of time, perhaps less than one thousand years. Kvale and Archer believe that compaction of the peat by the weight of the accumulating silts and sands provided most of the space for the clastic sediments. If this assumption is correct, only a small relative rise in sea level would have been necessary to initiate the drowning and transgression process. Once muds covered the surface of the swamp, the peat would have begun to compact, providing space for ever greater amounts of sediment. When peat compaction was complete and space was filled, the coastal fringe and its vegetation again prograded seaward, ultimately forming the Upper Block coal, now about 8–10 meters above the Lower Block.

The Flora

The major and only synthetic work on the flora of the Brazil Formation was published by Joseph M. Wood in 1963. The publication was the culmination of years of collecting from strip mines in Greene County, Indiana, by Wood and his associates at Indiana University. G. K. Guennel (1958) studied the spores and pollen from the Block coals. Several papers have described compression floras from Parke County, Indiana, near Turkey Run State Park, including cuticular or paper shales, which are thought to be the same age as those from the Brazil Formation farther south. The authors continue to collect floras in active strip mines, mostly southeast of Terre Haute, and have found dominant shale compressions and occasional siderite nodules.

The large collection of siderite nodules studied by Wood (1963) formed the basis of his classic and still definitive study of this flora in southern Indiana. The illustrated specimens are now housed at the Smithsonian Institution. The flora consists of about fifty species—give or take a dozen or so to allow for taxonomic uncertainties—and vagaries of paleobotanical organ taxonomy (the practice of giving different names to different parts of the same plant). All major groups of Pennsylvanian lowland "coal-measures" plants are represented, including lycopods (scale trees), tree ferns, sphenopsids (horsetails and their relatives), pteridosperms (seed ferns), and cordaites (coniferlike plants with strap-shaped leaves). Occasional odd elements are also included, such as *Megalopteris* (probably *Lesleya* in this case), a component of "upland" floras in the Early Pennsylvanian.

The dominant components of the flora, as well as overall taxonomic diversity, vary greatly over remarkably short distances, apparently reflecting slight changes in depositional environment. In our collecting, we have seen assemblages consisting almost entirely of *Lepidodendron wortheni* change in less than 20 meters to fern and sphenopsid dominance. Ferns, pteridosperms, and sphenopsids are most abundant in the collections we have made over the last ten years. Occasional local forests of *Sigillaria* tree stumps or large pieces of fern foliage with intact spore-producing or-

Figure 9: **Anthracomartid, a spiderlike animal in a siderite nodule.**

Figure 10 (above): **Whip spider in a siderite nodule. Whip spiders are important predators In some modern ecosystems.**

Figure 11 (right): **Wing fragment of a protorthopteran in a siderite nodule. Protorthopterans were important herbivores in Pennsylvanian ecosystems.**

gans are found serendipitously. In a typical day of collecting one might expect to encounter the most common genera, including *Lepidodendron, Annularia, Asterophyllites, Sphenophyllum, Alethopteris, Pecopteris,* and a few examples of fertile fern foliage, winged seeds, and perhaps cones of lycopods or sphenopsids.

The Fauna

The fauna of the Brazil Formation is known only from siderite concretions from the shale above the Lower Block coal. This fauna, consisting of insects, arachnids, millipedes, horseshoe crabs, shrimp, and sharks, is the only diverse Westphalian C nonmarine fauna known from North America. Many of the animals lived in freshwater ponds and swamps. The horseshoe crabs lived among the leaves of the lycopods that had fallen into the water and scuttled along the bottoms of the swamps looking for bits of organic detritus. The shrimp lived in the same environments, and they and the horseshoe crabs had to be wary of the freshwater sharks cruising through the waters.

On the land, arthropods lived everywhere. A variety of millipedes crawled along the forest floor. Smooth-backed millipedes may have burrowed among the forest litter, but the spiny millipedes (including small forms that could enroll and others that were almost a foot long) were probably confined to the surface of the litter. The mouthparts of these extinct millipedes are poorly known, but we can infer that they probably ate decaying plant materials, although they also may have fed upon some of the living plants.

Several kinds of arachnids (spiderlike animals) lived in the Pennsylvanian forests of southern Indiana. Whip scorpions may have hunted under fallen trees, while whip spiders either shared this habitat or crawled on the trunks of living trees. Both whip scorpions and whip spiders have large prey-catching appendages that dispatch their victims efficiently. Another group of arachnids, the extinct anthracomartids, were probably predatory, but we know virtually nothing else of their behavior.

Regardless of *where* they lived, the arachnids were probably eating insects. The Brazil Formation gives us merely a glimpse of the diversity of insects present 310 million years ago. Only three specimens, representing two orders of insects (both extinct), have been recovered. The Palaeodictyoptera have no living relatives, but we know from their mouthparts that they may have been feeding on sap. The other group, the Protorthoptera (relatives of grasshoppers, crickets, and katydids) had mouthparts that allowed them to consume the abundant vegetation of the ancient forests. European deposits of this age were teeming with many kinds of insects, and the slightly younger Mazon Creek biota includes more insect species than any other Pennsylvanian fauna. The three insects from above the Lower Block coal are therefore clearly an underestimate of the original diversity.

Although amphibians and reptiles were unknown in southern Indiana, we know from other localities that they lived at this time and appear to have been almost exclusively carnivorous, eating arthropods or each other.

A Carboniferous Ecosystem

Turning a list of plant and animal names into a living forest requires knowledge of growth habits, patterns of species co-occurrences, and the sedimentary context of the deposits. Not all these data may be available from any single locality, so it is important to be able to synthesize data from other similar deposits. The plant fossils from above the Lower Block coal came from a heterogeneous coastal vegetation. Some of the deposits that preserve tree trunks in place suggest that "forest" may be a misnomer for these ancient plant communities. The spatial distribution of the slender trunks of pteridosperms, calamites, and lycopods suggests patchy vegetation with an open or broken canopy. *Sphenophyllum* and small ferns were very abundant locally, particularly in association with pteridosperms and calamites, indicating areas of thick, possibly tangled ground cover. These plants fringed the coastline; their preservation in clay-rich tidal rhythmites suggests a position between lagoons or mud flats and peat-forming swamps further inland. Patches of low-stature dense undergrowth, spatial heterogeneity, and variably open canopies present us with a landscape quite unlike that of "coal-age" museum dioramas and emphasize the complexity that existed in lowlands during the Pennsylvanian.

The co-occurrence of multiple plant and animal fossils is uncommon in Pennsylvanian deposits. In this case, they reaffirm that modern ecosystems are a poor analog for those of the distant past. The plants accounting for most of the biomass of these early ecosystems are extinct, and their closest living relatives are so different that using them as analogs presents a distorted picture.

Food webs were complex in these ecosystems. Many arthropods in Pennsylvanian communities were detritivores, animals that eat dead plant material. Probably all the arachnids, reptiles, and amphibians were predators, although we do not know the details of the interactions between these predators and their prey. Although many of the Pennsylvanian animals were similar to modern animals, using living species as analogs presents difficulties due to evolution during the past 310 million years.

Herbivority and other kinds of plant-animal interactions, especially by insects and tetrapods, have significant effects on modifying the dynamics of plant competition, population structure, reproductive patterns, and community ecology in today's world. This herbivore influence was much different during the Pennsylvanian Period. Solid evidence of herbivorous vertebrates is unknown until the middle of the Permian, millions of years after deposition of the Brazil Formation. Conrad Labandeira, of the University of Illinois, who has been studying mouthparts of insects throughout their entire geological history, has found that many of the feeding groups represented among modern insects evolved several times as environments and available resources changed. He has also found that Pennsylvanian insects could have utilized plants as a food source in most of the same ways we see today but that many of the specific kinds of interactions were different. As a result, the "rules" of interaction among plants were probably different from what they are today. So although there were Pennsylvanian "forests" that were superficially similar to some modern ones, the mechanisms influencing the development of these ancient systems appear to have differed significantly from those we can study in modern lowland communities.

***Figure 12: Palaeoxyris*, egg capsules of early sharklike fishes, are the only vertebrate remains from the lower Brazil Formation. These egg capsules were originally thought to be seed capsules of contemporary plants.**

Summary

The Lower Block coal biota joins the slightly younger Mazon Creek deposit as one of the few well-studied siderite-concretion assemblages in the United States. Unfortunately, the Indiana fossils have never really been accessible to dedicated private collectors due to the limited number of natural exposures or accessible mine spoils. Thus, although the potential importance of these fossils is great, there is much more to be learned. Only extensive new collecting can provide the needed information. Through study of fossil biotas such as that of the Lower Block coal, we gain insight not only into what lived during the past, but also into how past worlds were organized and how they functioned. These "vignettes" of the past, together with the time perspectives that only geology can provide, permit us to look into the future and imagine how plants, animals, and the ecosystems of today might respond to changes in climate, to species extinctions, or to the appearance of new forms. We have great need of such insights now as our planet enters a period of human-induced environmental change and global extinctions. By joining paleontology to present-day biology, we will perhaps be able to solve some of our dilemmas.

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