THE CARPATHIAN–BLACK HILLS CYCADEOID PARALLEL.

G. R. WIELAND.

ABSTRACT, A friendly and scientific European view and interest in the so-called FOSSIL CYCAD NATIONAL MONUMENT of the southwestern Black Hills "Rim" has led to repeated loans or gifts to the author of historic and invaluable petrified cycadeoids. These have mainly come from the Capellini Museum of Bologna; the Jardin des Plantes and Ecole de Mines, Paris; the Stone Quarries (Company) of the Isle of Portland; also Alfred J. Mew of Shanklin Isle of Wight; the Zwinger Museum of Dresden, the Natural History Museum, Stockholm; and the Physiographic Museum at Cracow. From the latter collection comes the very handsome flowerbud here described as cut from the long known Carpathian type *Cycadeoidea niedzwiedskii* (Plate I, Figs. A and B) once more illustrating the exceedingly close parallel between the Carpathian and Black Hills cycadeoid series. Several of the latter are also figured as recovered *in situ* at the Monument Mesa in November 1935. There is also shown the stem of the free-flowering variant *Monanthesia magnifica* (Plate IV), from the upper Cretaceous (Mesaverde=approximate Senonian) of the San Juan Basin, New Mexico. In THE AMERICAN JOURNAL OF SCIENCE for March-May 1899 was given the first definite account of the floral features and foliage of the Cycadeoids. Many subsequent notes followed.

AS briefly commented on in my account of the historic petrified cycadeoid stem "Raumeria" of the Zwinger Museum of Dresden, in the course of the past two centuries four fairly distinct "species" referable to the Buckland genus *Cycadeoidea* have come from the northerly flanks of the Carpathians. Of these the "Raumeria," *Cycadeoidea reichenbachiana*, has the longest museum record of any member of the stately and cosmopolitan Mesozoic group to which it belongs. It was first named by Goeppert in 1844. Description with illustration came in 1857 along with a figure and short account of "*Raumeria schulziana*," a smaller, related stem from near Gleiwitz in Silesia.

The third of the Carpathian types is the upper two-thirds of a medium-sized obovate stem long in the museum at Cracow, and in the year 1893 correctly named by Maryan Raciborski, *Cycadeoidea niedzwiedskii* (Plate I, Figs. A and B). The fourth type, also a true simple-stemmed Cycadeoidea bearing the lateral fruiting axes, is the only one of its group recently found. It was named *Cycadeoidea polonica* by K. Wallisch in 1928. This isolated specimen comes from the more or less forest-clad

terranes of the valley of the San, an affluent of the Vistula in the vicinity of Kamien, or about 100 miles east-northeast of Cracow.

In addition to these four Carpathian types it is certain that a few lesser specimens long since noted are now utterly lost to view. One such is seen in the drawing given by Walch in 1771. Hence despite this limited occurrence or recovery of specimens from the outer northerly slopes of the "Beskids" of the Carpathian mountains along an east-west distance of about 160 miles of Mesozoic terrane, there has been brought to light a noteworthy fossil record. The silicification is beautiful, the substance dark and clear. The horizon has been thought to lie somewhere in the so-called "Hornstein Schichten." Whether

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PLATE I.

Fig. 1. A. *Cycadeoidea niedzwiedskii.* Longitudinal thin section through bract enveloped young seed cone 8 millimeters in diameter. Summit cut away by transverse section cut to locate flowerbud. At D, wilted disk insertion, traced all round base of seed cone. At S, lowermost interseminal scales which tend to separate from the receptacular insertion line. Compares nearly with the seed cones of the Cycad Monument species *Cycadeoidea painei.*

B. *Cycadeoidea ingens.* Restoration of flower (in glass).

PLATE II.

Fig. 1. *Cycadeoidea colossalis.* Height 72+ centimeters. Columnar wholly unbranched stem with summit partly broken away. From base to summit many half-grown seed cones. This is one of the specimens obtained by direct excavation at Fossil Cycad National Monument, Nov. 1935 Cf. (Plate III).

PLATE III.

Fig. 1. *Cycadeoidea colossalis.* Height 85+ centimeters. A striking bifurcate trunk obtained *in situ* near the specimen of preceding Plate II, November 1935. In same fruiting stage. Seed cones more abundant toward the summit; numerous, in much the same stage of growth, and well silicified. There can be no doubt that this specimen is of identically the same species as that of Plate II.

PLATE IV.

Fig. 1. *Monanthesia magnifica* Wieland. A cotype in the collection of the American Museum of Natural History. An immense stem with base and summit missing. In life at least one meter in height. Over the entire surface of the armor a fruit stalk is seen in the axilla of every old frond base without exception. Young seed cones seem for much the greater part to fail of preservation, but a culminant or monocarpic condition is indicated.

This specimen is from the Mesaverde Upper Cretaceous of the San Juan Basin, about thirty miles northerly from Gallup, New Mexico. It came from an unrecorded point near the old "Mexican Springs" trading station.

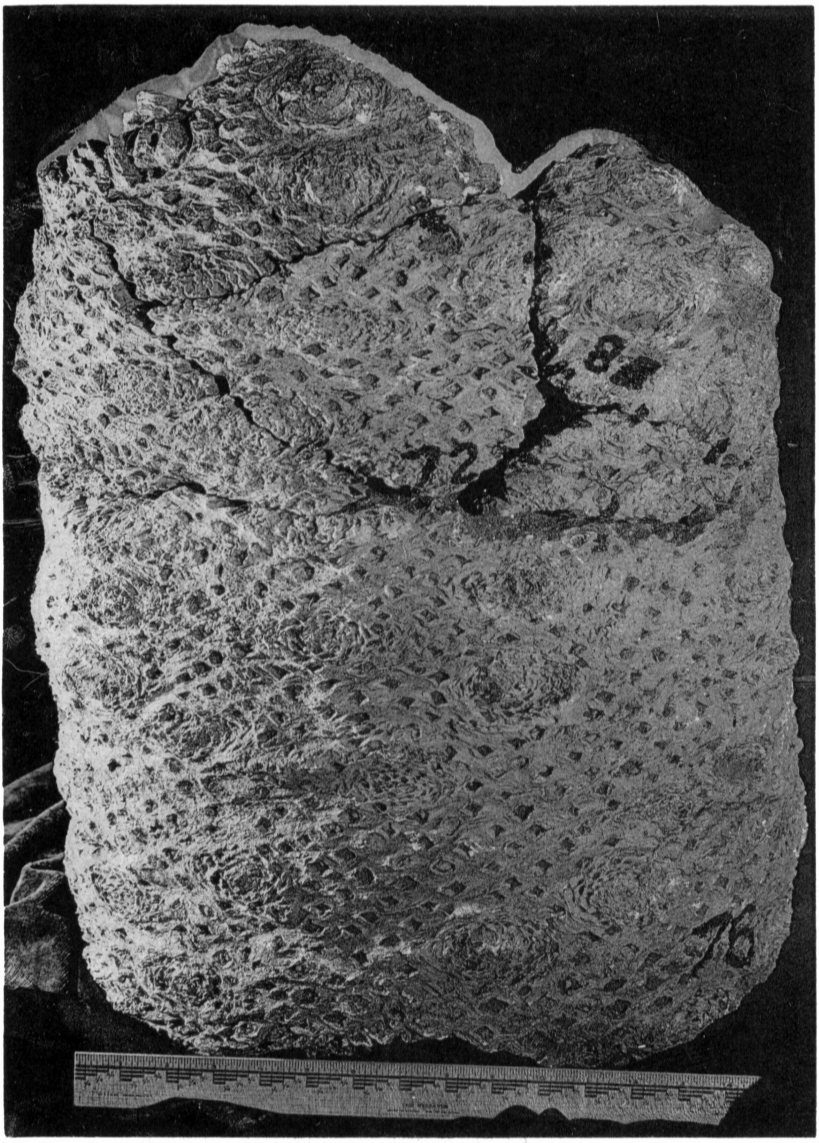

FIG. I

Cycadeoidea colossalis unbranched. About x1/6.

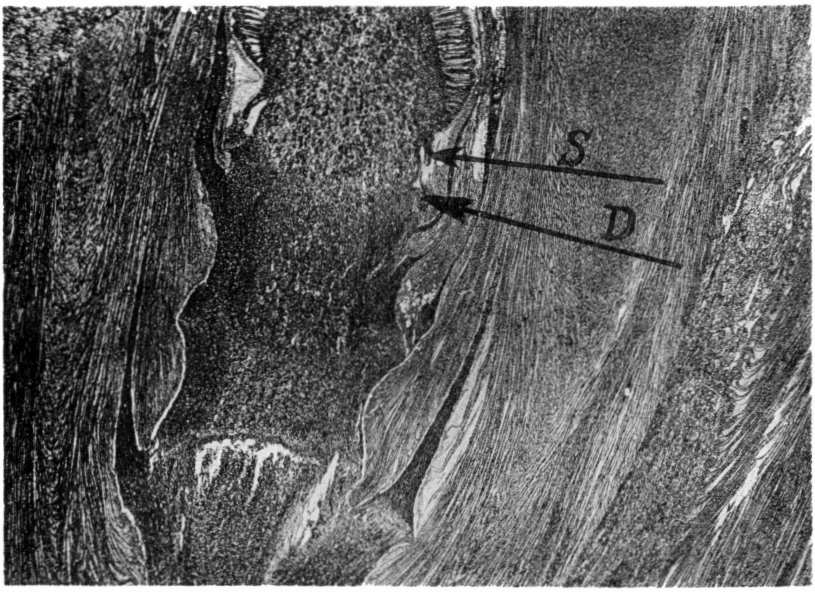

FIG. I A.

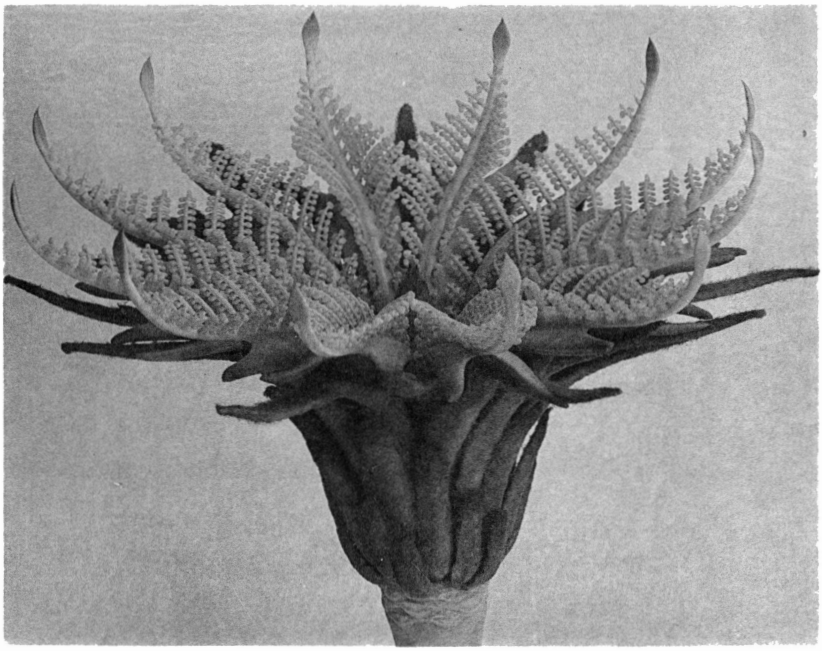

FIG. I B.

ABOVE. *Cycadeoidea medzwiedskii* x3.
BELOW. Glass-flower model of Cycadeoidea ingens. Near natural size.

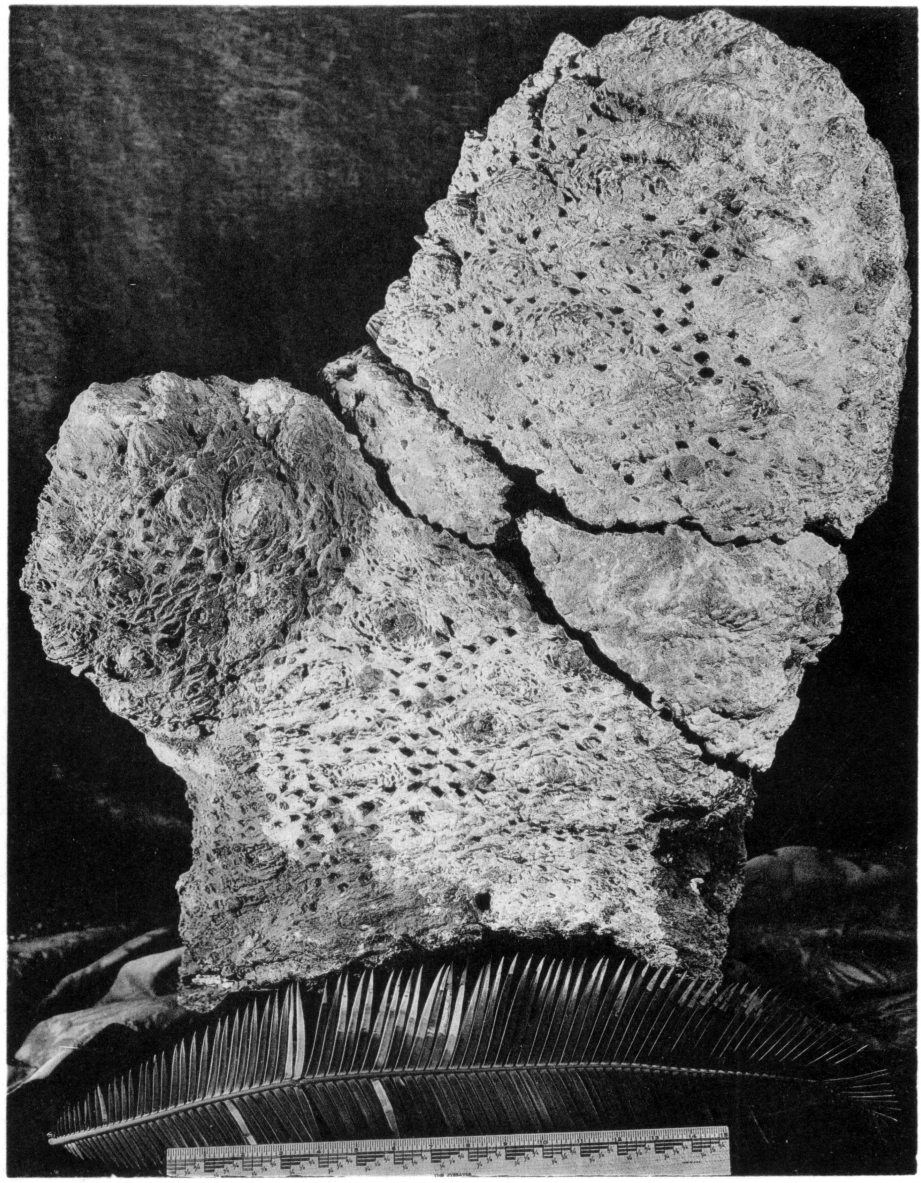

FIG. I

Cycadeoidea colossalis. About x1/6.

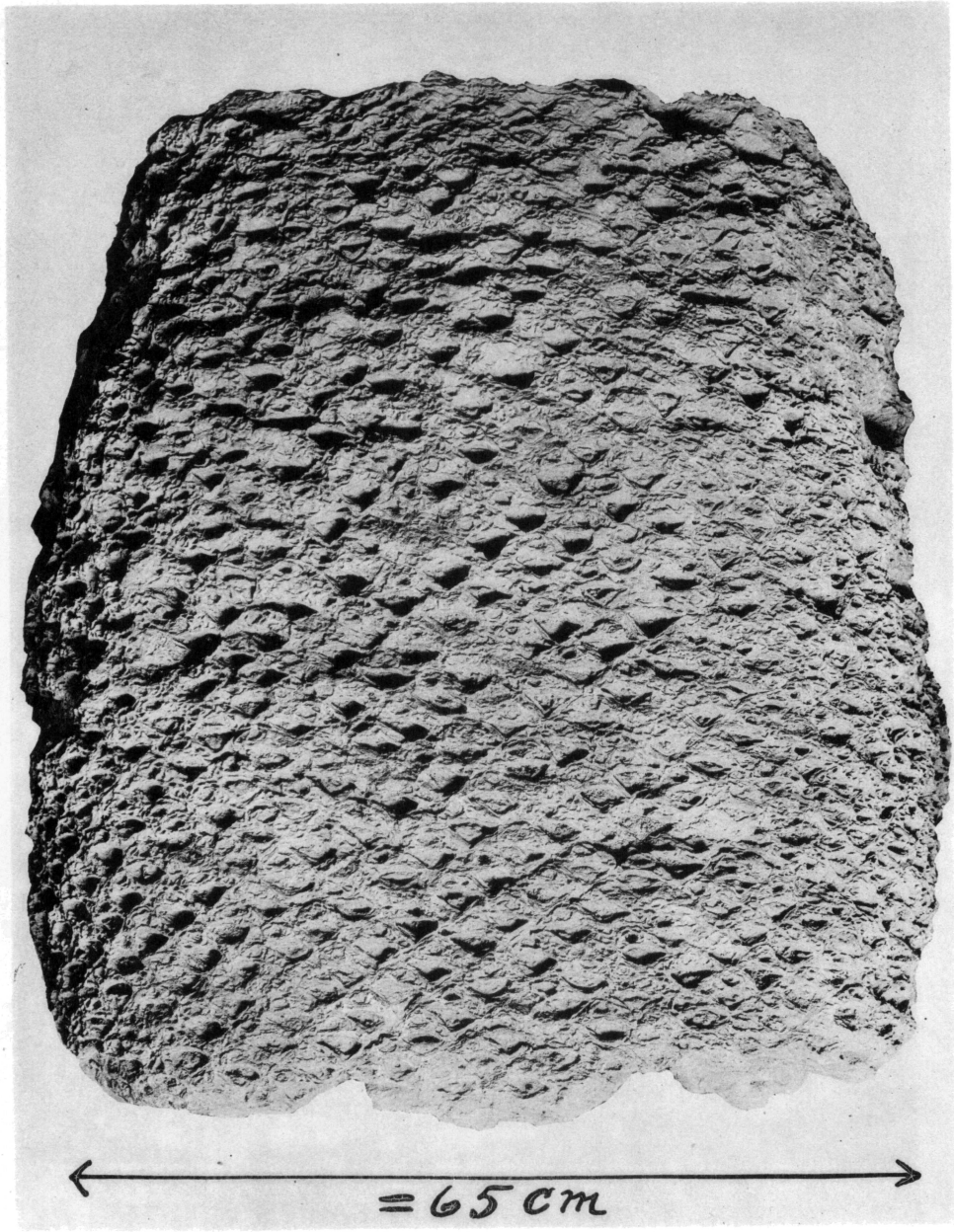

FIG. I

Monanthesia magnifica. x1/6.

there is some vertical range in the occurrence remains uncertain. There is in preservation and type a remarkably close parallel to the "Fossil Cycad National Monument" series of the Black Hills, which occurs low in the Cretaceous. Final decisions of age might here be left in abeyance for some time to come. I believe this was also the virtual view of the geologists Wegemann and Wilson who worked with me in the course of the making of the large and distinctive *in situ* collections of November 1935 at Cycad Monument . . .

The near certainty is that there lie hidden somewhere in the outer Carpathians the localities which must yet yield a far more varied record than that now in view. So outstanding is this fact that search in the field carried out persistently is of even more present importance than structural study. It is the view, too, of Professor Bertrand of Lille that he would like to join in a serious search in the Carpathians. For the present, however, there is added a needed further note on the fruiting of the third of the Carpathian types, *Cycadeoidea niedzwiedskii* (See Plate I). This is in the first instance due to Dr. J. Lilpop of the Cracow Museum. He suggested cutting out from the type *Cycadeoidea niedzwiedskii* (Plate I, Figs. A and B) a core carrying one of the lateral axes of fructification for sectioning here at Yale and closer comparison with our Black Hills types. This plan has been carried out.

FRUITING IN *Cycadeoidea niedzwiedskii*.

(Plate I, Figs. A and B.)

The axis selected by Doctor Lilpop is I believe the one seen as a low bud to the left of the stem apex in Raciborski's original figure. The drill core as cut is about six centimeters in diameter and includes, as seen in thin section, a somewhat slender peduncle bearing a small and young seed cone enveloped in its heavy husk of inclosing hairy bracts. The appended Plate I, Fig. A, shows these features to be all clearly silicified. The better to locate this axis a transverse slice was first cut out.

It was hoped that the stamens might prove to be present. But there is merely to be seen the insertion line basal to the seed cone, it not being absolutely sure that there was a maturation of stamens before the first event in the course of fossilization. Probably there was, with but a short interval before that

course began. Here, as in most, but not all, cycadeoid floral axes, the presence of complete flowers appears certain. Also, a main flowering stage is indicated much as in "Raumeria." There three periods of flowering are attested by: (1) scattered old peduncles, (2) the main series, then (3) a few younger axes; while in the *C. niedzwiedskii* there are also many bract areoles—a fact suggesting a very distinct main season of fruit growth. The condition in these Carpathian species is of much interest in connection with the difficult question as to whether the monocarpic condition or tendency, so remarkably developed in *Cycadeoidea dartoni* and certain other species, is ancient and primitive or merely a secondary specialization.

The seed cone, Plate I, Fig. B, belongs to the cycadeoid cone series with slightly elongate instead of convex receptacular cushions. But it is to be noted that as such cones grew forward, somewhat rounded or obovate outlines were always reached, this being the form seen in most petrified cycadeoids and also in the Yorkshire *Williamsonia gigas* and in *W. mexicana*.

The Carpathian group of Species.

While this group of four species forms a close-set unit there is no present need to question their taxonomic validity. The *Cycadeoidea reichenbachiana* is of large columnar form. Its flowers are so nearly like those of *Cycadeoidea dacotensis* (Plate VI, Figs. A and B) that, taking floral features alone, even a specific variation is little in evidence. The other three Carpathian species appear to be merely lesser related types which can vary but little. If we knew the flowers of all, some difference in the number of stamens to the disk might be found. Not one of these forms shows the least indication of vegetative branching. However, the *in situ* series from the Fossil Cycad Monument includes a large unbranched stem of the species *Cycadeoidea colossalis* (See Plates II and III), and another large associated stem clearly of this same species which bifurcates. These, as shown on Plates II and III, are both remarkably handsome plants bearing a full series of seed cones not yet mature.

Note then that the transition from simple-stemmed, squat, or columnar types is very easy, so easy in fact that it seems strange that not once in all the European series referable to

the genus *Cycadeoidea* can a single branched specimen be cited. And this absence of branched types is again seen in the case of most American occurrences. A few minor instances of branching occur in the Trinity Beds of Texas, a few in the Como of Wyoming, but none in the Arundel series of Maryland. Among all the scattered localities of the globe yielding the silicified types more or less certainly referable to the genus *Cycadeoidea*, only at Fossil Cycad National Monument does branching become the conspicuous and varied feature. There the alignment is seen almost in reverse; columnar stems are present, but few in number. On the contrary, only sixty miles to the north in the Piedmont-Black Hawk sector of the rim of the Black Hills, and in rocks slightly younger than the Monument strata, there is present one of the most striking series of well marked low to columnar cycadeoid species yet found in any single locality on the globe; not one of these branches.

We see that the Carpathian series also falls closely within the limits of the original *Cycadeoidea* of Buckland. Hence three questions arise. May not branched types yet be found in the Carpathians where the occurrence, the terranes, and the type of preservation is most similar to that in the Black Hills? Can the branched types be included in the genus *Cycadeoidea* of Buckland, 1888? And where are the Carpathian dinosaurs?

Certainly more varied types are to be awaited in the Carpathians if the collector is persistent enough! And certainly the branched series of petrified cycadeoids might be held as a subgenus. Then the actual transition toward the branched forms would be exemplified by types from the Isle of Portland such as *Cycadeoidea portlandica*, and *C. microphylla*. In these species the peduncles are not only numerous but very large with some of the bracts even approaching the size of fronds. By far the greater bulk of the so-called "armor" is made up of the very large *fertile branches*, and some of the bracts are pinnatiform.

While therefore it may be for a time at least preferable to consider *Cycadeoidea* as an inclusive inter-continental genus like *Quercus*, which has many species varying from the greatest forest trees to small bushes, there is no need to obscure the fuller evolutionary significance of branching in any of the cycadophyte gymnosperms. The Cycadophyta certainly came up from somewhere within the seed ferns. If that origin does

not explain the pines too, then the pines had a separate and distinct lepidophyte ancestry. Let botanists face that dilemma! In few words, the cycadeoids are the group-extraordinary of Permo-Mesozoic time. They are to that plant world what the dinosaurs are in the animal world, their range in geologic time much the same.

Knowledge of the dinosaurs and cycadeoids goes back over one hundred years to the splendid illustrations and text of Buckland in the Bridgewater Treatises. The crucial dates are for the Dinosauria (Owen, 1839): 1825, first formal account of a carnivore, the *Megalosaurus* by Buckland; also 1825, the account of the herbivore *Iguanodon* by Mantell. But while Buckland understood the dinosaurs, by some strange fatality such as may ever and anon beset the course of Science, the clearing of the associated cycadeoids over and above excellent illustration awaited for sixty-six years the discovery and initial investigation of the more vast American series.

In noting these dates emphasis must be placed on results next reached through new methods of study developed by the keen student Nathorst in bringing to light for the first time the small-flowered, small-stemmed, much-branched but related cycadeoids of the Rhaetic of southern Sweden, mainly seen as carbonized impressions of difficult but singularly significant material. Study of similar Yorkshire Jurassic types by both Nathorst and Hamshaw-Thomas followed. Startling as are the petrified types, they would be too remote of feature, too strange to our seeing to carry their full evolutionary weight were it not for these later discoveries of the small-stemmed types indicating a group that, taken in all its features, at last comes near to the floral and stem structures which might be awaited in the forerunners of the Angiosperms.

The Free-flowering Habitus.

So far, perhaps, the most recondite feature brought into view in the entire course of cycadeoid study is the profuse flowering seen in the series of silicified columnar types strongly tending toward and actually reaching monocarpy. Until recently these peculiar forms were placed in the genus *Cycadeoidea*, six species being so assigned—each based on but a single specimen and of widely different age or locality. In only one of these, the type first called *Cycadeoidea dartoni*, one of the most remark-

able monocarpic plants of all time, was the fructification clearly seen. Agreement with the *Cycadeoidea* cone type was obvious and no vegetative variations were noted beyond mere minor ones on which fossil species may be based. So stood this closely set group which appeared on both sides of the Atlantic. Then came into view the long series of monocarpic or sub-monocarpic stems from the Mesaverde Cretaceous of the San Juan Basin of New Mexico, mainly recovered in the years 1928 and 1929. Three new species appeared to be indicated. The seed cones were found to hold again to the cycadeoid type. Because the monocarpic series of assigned species had risen to nine in number, it seemed that a separate generic name should be sought out, *Monanthesia* (Plate IV) being finally, if somewhat arbitrarily assigned. In using this generic name it was not meant that there was but a single anthesis throughout, but that this condition was reached in a few of the species with a tendency toward it in all. There might be the variation from the single anthesis to several periods of active floral growth in one and the same species.

With wide distribution and with a geologic range at the very least from the closing Jura to high up in the Upper Cretaceous, the genus *Monanthesia* (Plate IV) may be an old and primitive, instead of merely a terminal type. In any case the habitus suggests not merely some early trend of change towards more modern plants but yet other analogies to some of the inflorescent features of the older gymnosperms. Very easy might be the transition from these giant types toward or from microphylly and microflory. We may well await the type in the Carpathians. Here also may be set with near certainty the splendid type of Seward, *Cycadeoidea gigantea* from 17 feet above the "dirt-bed" of the Isle of Portland.

All in all a great range of variation is both seen and possible in the cycadeoids as a group cosmopolitan to all of Mesozoic time. The seed cones conform to a single simple type but are primitive. The structures are not far from those found in the ginkgoid Cordaites.

Perhaps more than any others, Scott has lain much stress on the fact that the cycadophytans are a great group of the Mesozoic about which we have only begun to learn. Certainly there must have been far more floral diversity than has been as yet visualized. While exactly in *Monanthesia* (Plate IV)

there is suggested easy transition into small-stemmed and inflorescent types much branched and small flowered as fairly well seen in *Williamsoniella* and *Wielandiella*. At first view *Monanthesia* seems far removed from a type like *Cycadeoidea microphylla*; but though appearing so squat of form *C. microphylla* is really nothing more than a small columnar stem bearing a great mass of relatively very large fruiting branches. The bracts of these are nearly as full grown as the fronds borne directly on the main stem. Transition from the latter to the bract condition is thus easy. Also, the laterally borne fruiting stalks, which make up fully three-fifths of the entire bulk of the plant, could easily take on a more vegetative function, with fruiting thus relayed forward to the true secondary branching. These are by no means involved conceptions; they are simple.

Moreover, considering the general alignment of the cycadophytans, it is well to hold in view the likelihood of the existence and the ultimate discovery of small-flowered, freely branched, larger forest types, not yet well seen because probably much subject to bacterial decay with scanter fossil preservation. The need to widen and extend cycadophyte discovery is severe. If on the one hand the cycadeoids include some of the most remarkable plant types known, on the other the evidence gained is new and strange to our thinking. It is as yet seen only as if from afar. The types seem either little known or far apart after a very slow, and now century-long, course of study. It is as if, in some far view of the dicots, there were known only an older leaf record of *Casuarina* plus various species of *Tamarix*, along with certain huge petrified magnolias and a few oaks. The limits may not soon be set for a group of small-leafed, much-branched types like the species *Cycadeoidea minima*, *C. nana*, and the *C. protea* which has many branches that in some specimens seem even to form a root-stock. (Plate V, Figs. A and B.) With all this variation in stem and fruiting habitus, with at least some foliar plasticity, with the likelihood of a much more varied wood structure than has as yet appeared to view, neither the antecedent nor the sequent relationships of the Cycadophyta may be seen in more than the most general outlines. None the less, the field for renewed study is well defined. The Triasic areas of Virginia and North Carolina, the Dockum Beds of Texas, the Sonoran Trias, the Triasic-Liasic-Oolitic terranes of the Mixteca Alta of southern

Mexico, and a long series of singularly rich Rhaetic beds extending along the eastern foothills of the Andes, mainly in West Argentina, are occidental regions of first importance. Then come the Gondwanas of India.

Silicification in the Cycadeoids.

Scarcely secondary to the biologic interest of the Cycadeoids as a dominant group of the Mesozoic, is the problem of the siliceous replacement of vegetal tissues. Probably no other group presents as striking and favorable a foreground for the study of this long-unsolved problem. With all organs highly developed, these plants, of species no more than specifically separable in such far set bounds as the Beskids of the Carpathians and the Black Hills, the favorable point of attack is seen. In both regions there seems to have occurred as the initial event following silting in, an upwelling along fault lines of magmatic waters carrying orthosilicic acid and a much lesser iron content. The part iron had in replacement is not clear. In the Carpathian "Raumeria" there are flecks of a very resistant iron taking a high polish, while in one specimen of the Black Hills *Cycadeoidea dartoni*, such of a larger area may be seen, extending to even several centimeters across. In both regions small, yellow included pyrite occurs, but inclines to be very rare. There are also present other specimens in which the original plant suffered minor faulting after replacement had set in. Spheno- and sphærocrysts are a further guide to the course taken during and after replacement. While the changes ending in the final replacement seem to have gone on very slowly, there is little doubt but that in the laboratory an end result could be much hastened by the use of specially devised autoclaves with the right diluent matrix under temperature-controlled pressures holding carbon dioxide in liquid form.

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YALE UNIVERSITY,
NEW HAVEN, CONNECTICUT.

PLATE V.

Fig. 1. A. *Cycadeoidea nana* (?). No fruits being here present the exact species remains in some doubt. This squat five-branched stem with very small frond bases has a habitus even suggesting tendency towards growth like a rootstock. The group of branches is about 35 centimeters across. National Parks and Monuments specimen obtained *in situ* at Fossil Cycad National Monument at the same time as the specimens of Plates II and III. Branches are numbered I-V in order of growth. No. V arises from IV.

Fig. 2. B. *Cycadeoidea nana* (?). A companion specimen to that of Fig. A, and obtained at the same time. A pre-fruit stage of growth is seen, no bract areoles as yet appearing at the armor surface.

PLATE VI.

CYCADEOIDEA DACOTENSIS—Transdissection of flowerbud.

Fig. 1. A. Above. By inspection the ascending and decurved limbs of the staminate rachides may be separated in the mid-region of the flower with accuracy, as is done in this view. (Dotted line DD.)

Fig. 2. B. Below. Exceptionally beautiful section cut transverse near the extreme ends of the decurved frond tips eight to nine in number (for the entire disk 16 or 17).

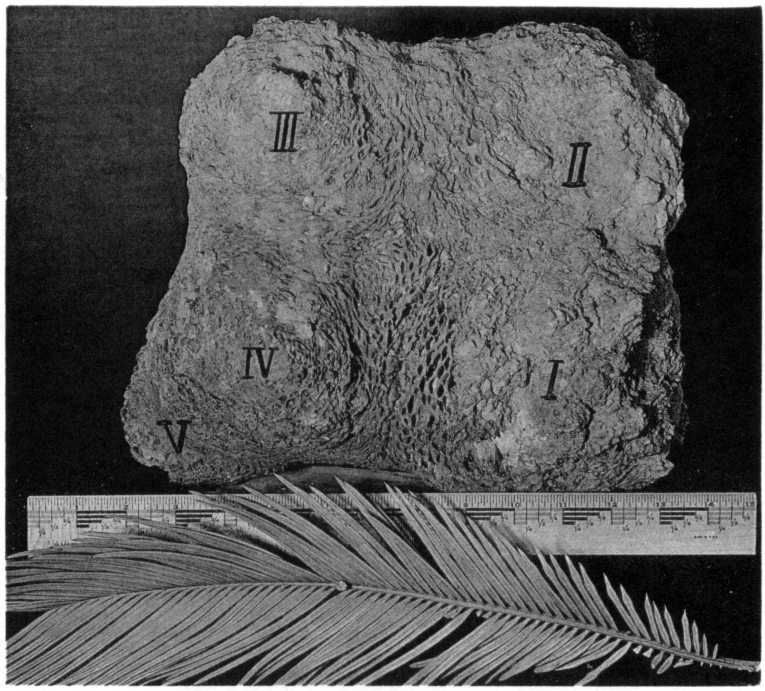

FIG. I A. x1/5

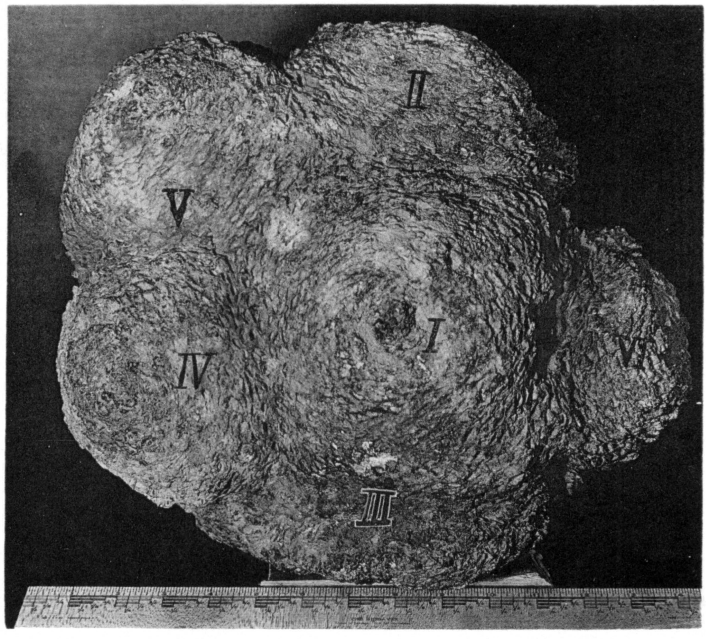

FIG. I B.

Cycadeoidea nana (?). About x1/5.

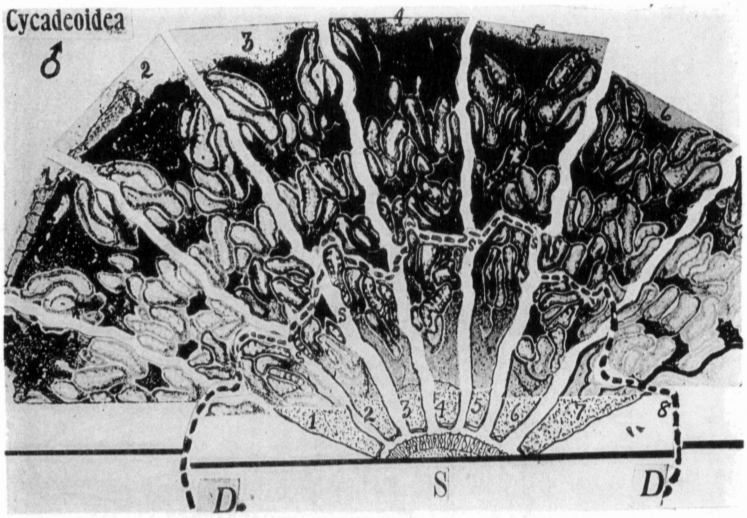

FIG. I A.

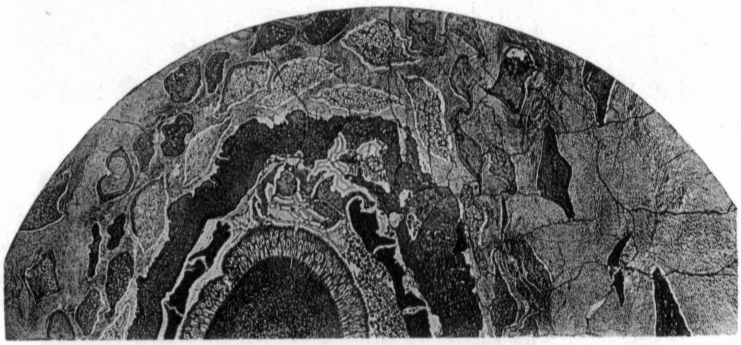

FIG. I B.

ABOVE. *Cycadeoidea dacotensis* flowerbud (enlarged).
BELOW. Section through seed cone and frond disk. x3.