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THE LIVING CYCADS

CHARLES JOSEPH CHAMBERLAIN

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THE LIVING CYCADS

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THE LIVING CYCADS

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TO MY FATHER AND MOTHER

PREFACE

The living cycads are fernlike or palmlike plants and are the surviving remnants of a line reaching back through the Mesozoic into the Paleozoic. The title *The Living Cycads* was chosen to contrast with *The Fossil Cycads*, a work in two large volumes by Professor G. R. Wieland, of Yale University, dealing with the extinct cycads of the Mesozoic.

A study extending over more than fifteen years has necessitated trips to Mexico, Cuba, Australia, and Africa. All the genera and many of the species have been studied in the field, and material has been preserved for later study in the laboratory. In addition to investigations by the author, studies upon this material have been published by Dr. R. Thiessen, Dr. Sister Helen Angela, and Dr. F. Grace Smith, and studies by Mr. Ward L. Miller and Miss LaDema Langdon are in progress.

Part I is an account of the distribution, general appearance, and field conditions of the cycads, together with some of the experiences which come to one who attempts an investigation involving so much travel in distant and varied tropical countries. Technical terms are avoided except in the names of plants.

Part II presents the life-history of the group and is based largely upon my own observations in the field and in the laboratory. Wherever statements are made which have not been confirmed by my own observation the authority is quoted. Several technical terms are used, but they are explained as they occur. It is hoped that this section will be appreciated, not only by those who are interested in general science, but also by teachers who feel the need of a rather complete account of the life-history of a gymnosperm.

Part III is devoted to the evolution and phylogeny of the cycads, the opportunity for such a study being exceptionally favorable because the ancestry can be traced back through geological periods, and because the extinct predecessors of the living cycads are the best known of all fossil plants.

A much more extended account, technical in character, will be published later.

CHARLES J. CHAMBERLAIN

CONTENTS

PART III. THE EVOLUTION AND PHYLOGENY OF THE GROUP

LIST OF ILLUSTRATIONS

INTRODUCTION

The name cycads is likely to sound strange to those who are not botanists, but the group itself is represented in greenhouses by some of our most familiar decorative plants. The sago palm, *Cycas revoluta*, whose rigid fernlike leaves are in such demand on Palm Sunday and on funeral occasions, is the best-known representative, and many regard it as the most beautiful.

For an introduction to the cycad family nothing would serve better than the Mexican *Dioon edule* (Fig. 1). The short, stocky trunk, covered by an armor of old leaf bases and surmounted by a crown of dark-green leaves, is characteristic and makes the plant look like a small tree fern or palm. By the natives the various cycads are usually called palms, so that we have the sago palm, bread palm, Dolores palm, and other palms; but to the botanist, who knows that they are intimately related to the ferns and not even distantly related to the palms, they look more like ferns. And they deserve to look like ferns, for they have retained the fern leaf of their ancestors from the Paleozoic age down to the present. The scientific name of the family is Cycadaceae, but botanists generally call the plants cycads.

The genus *Cycas* was called the "sago palm" because the stem and seeds contain so much starch; but all the genera contain an abundance of starch, and some of them have been exploited commercially. The growth, however, is extremely slow and must always prevent them from being recognized as an important source of food.

FIG. 1.—Female plant of *Dioon edule* on rocky hillside at Chavarrillo, Mexico. The trunk is about 5 feet in height. The plants underneath are small but fully grown oaks.

I was attracted to an investigation of the group partly by its great antiquity and partly because so little was known about it. The scanty information was due to a distant and scattered geographical distribution, coupled with the fact that those likely to be interested could not afford such extensive journeys, or at least could not afford them until they became too old for such strenuous collecting.

My earlier trips were financed by the Botanical Society of America, with such additions as my own slender purse would allow. The most extensive journey was financed, in large part, by the University of Chicago.

The first thing in the investigation was necessarily to obtain material, and practically none of it could be sent for. Besides, one who knows his material only in the laboratory or greenhouse is sure to get inadequate and often distorted ideas of his subject. The "norm" of a plant can be determined only by studying it thoroughly in its natural surroundings, and consequently I have devoted considerable space to field studies and the collection of material.

PART I

COLLECTING THE MATERIAL

In geological times the ancestors of the cycads were numerous and widely distributed, but now there remains only a single family with nine genera and about a hundred species, all confined to tropical and subtropical regions. The geographical distribution is very peculiar. Of the nine genera, four belong exclusively to the Western Hemisphere and five to the Eastern; all the western genera, except one, are north of the equator, and this one ranges from Florida to Chile; all the eastern genera, except one, are south of the equator, the exceptional genus ranging from Japan to Australia.

Even in the warm regions, to which the cycads are confined, their distribution is very restricted. Of the western genera, one has been seen only in the province of Pinar del Rio in Cuba; two are not known, with certainty, outside of Mexico; the fourth, as we have remarked, extends from Florida to Chile. Two of the eastern genera are confined to Australia, two belong to South Africa, while the other reaches from Japan to Australia. Even in these places the plants occur singly or in small patches, so that collecting is slow and more or less uncertain.

Without regard to possible interrelationships we shall consider first the cycads of the Western Hemisphere and then those of the Eastern.

CHAPTER I

THE WESTERN CYCADS

For convenience, the four western genera, *Zamia*, *Microcycas*, *Dioon*, and *Ceratozamia*, will be treated separately. All four occur in North America, but, as far as we know, *Zamia* is the only one which is found in South America. *Ceratozamia* and *Dioon*, however, are popular decorative plants and would grow in the open throughout most parts of Central America and a large part of South America. It is certain that in some cases erroneous reports with regard to geographical distribution have been due to exotic specimens.

ZAMIA

Zamia, the only genus found in the United States (Fig. 2), has about thirty-five species, more than a third of the whole family. It is represented in Florida by two species, there are several species in Porto Rico and other islands of the Caribbean Sea, some in Mexico and Central America, while others extend across the northern part of South America and down the Andes into Chile.

Zamia is a small plant with a turnip-like stem which rarely appears above ground, and a crown of leaves which seldom reach a length of more than two feet. The cones are borne in the center of the crown and sometimes are nearly as large as the stem. Starch is very abundant in the underground portions of the plant, and it is often used for food. The stem is pounded to a pulp and washed in a straining-cloth to remove a poison which is found in most cycads. During the Civil War several

Fig. 2.—Female plant of *Zamia pumila* at Hawks Park, Florida. The plant is about 18 inches in height and bears two large female cones.

soldiers died from eating the root before the poison had been washed out; but the meal, when properly prepared, makes a fairly palatable cake or pudding. Some species in Eastern Cuba are being used for the manufacture of starch, but *Zamia* does not grow fast enough to give it much commercial importance.

Comparatively speaking, this genus lies at our door, since we have typical representatives in Florida. Consequently field studies and collections are not difficult; besides, it is so little damaged by transportation that it can be sent by parcel post or express to any part of the United States and arrive in good condition for study or for transplanting. Some plants sent to Cape Town, South Africa, survived the journey and are now growing in the Kirstenbosch Botanical Gardens. Naturally *Zamia* was the first of the western genera to receive attention.

MICROCYCAS

The Cuban genus was named *Microcycas* from a few small leaves which seemed to resemble the Japanese *Cycas*, except that they were smaller (Fig. 3). As a matter of fact, only two species in the entire family reach a greater height, and some exceptional individuals have the greatest girth ever recorded for any cycad. There is only one species and not many individuals, so that the genus could very easily become extinct. The best specimens are in the mountains of Pinar del Rio, where they form a narrow patch a few miles wide, not extending much beyond Herradura on the north or Consolacion del Sur on the south, so that *Microcycas* is the most restricted genus of the family.

Next to *Zamia*, *Mycrocycas* is the easiest genus to reach from the United States. Eight hours from Key West brings you to Havana, and three hours more, through a beautiful country with thousands of magnificent royal palms, brings you into the midst of some small *Zamias* and within easy walking distance of

Fig. 3. Male plant of *Microcycas calocoma* on El Tigre Plantation near Pinar del Rio, Cuba. The trunk is about 10 feet in height.

Microcycas. The larger plants are ten to thirty feet in height, and the dense crown of glossy, dark-green leaves mark them off from the numerous small palms, so that they are not difficult to recognize. Cones are not abundant, but when they do occur they are easy to find, since they sometimes reach a length of two feet.

Everywhere the people were hospitable and ready to help me in my collecting. A very inadequate knowledge of Spanish occasionally caused some delay, but the Cubans must be credited with an ability to recognize seriously mutilated fragments of their language, if accompanied by appropriate gestures; besides, many of the Cubans speak English, and there are many Americans in the western part of the island.

Although the cycads are peculiarly free from plant diseases and are not likely to carry diseases to other plants, the various quarantine regulations of our Department of Agriculture cause such delays that it is practically impossible to get living material by mail or express before it has become unfit for microscopic study. Consequently I have depended principally upon my own collections, generously supplemented by important stages furnished by my former colleague, Professor Otis W. Caldwell, who gave to the scientific world the first adequate account of the genus and the only account of its life-history.

DIOON EDULE

The two genera which may be confined to Mexico (Fig. 4) are *Dioon* and *Ceratozamia;* but several species of *Zamia* also occur there. The general appearance of *Dioon edule* has already been shown in Fig. 1.

The name *Dioon* means "two eggs" and refers to the fact that each scale of the female cone bears two seeds, a feature which is common to all the cycads except one genus. There are three species of *Dioon*, and some think that there are four or five.

One of the species, called *Dioon edule*, because the Mexicans make "tortillas" from a meal obtained from its seeds, was the object of my first visit to Mexico, undertaken in the spring of 1904. The systematic

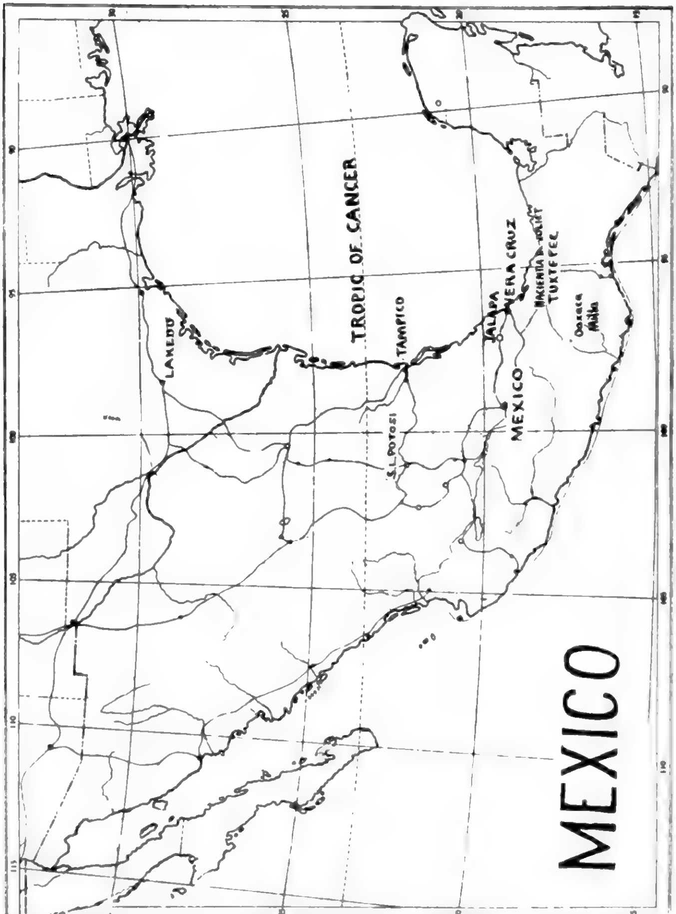


Fig. 4.—Map of Mexico

diagnosis based upon the leaf, cone scales, and seeds proved to be accurate enough for an identification but gave little idea of the plant or its surroundings. The life-history had never been studied, and the location indicated by the phrase "arbuscula Mexicana" seemed rather vague to one whose time and money were limited. However, Professor George Karsten had mentioned to me that he had seen *Dioon* somewhere near Banderilla; and the late Professor George Pringle wrote me that he had seen large specimens two or three stations east of Jalapa.

With this rather scanty information I laid the matter before the Botanical Society of America and received a grant sufficient to cover the railway fare from Chicago to Jalapa and return. I also obtained a fine letter of introduction from President William R. Harper to our ambassador in the City of Mexico, who gave me an embarrassingly cordial introduction to the governor of the state of Vera Cruz, Teodora A. Dehesa, who used his powerful influence in furthering my investigations. His broad scholarship and deep interest in education was best expressed in the system of schools which he had devised and developed, consisting of excellent graded schools, a normal school, and a technical school, adapted to the needs of his people. His private secretary, Mr. Alexander M. Gaw, an American, thoroughly familiar with Mexico, not only helped me while I was there but sent material at frequent intervals for nearly ten years. With directions furnished by Governor Dehesa I found *Dioon edule* in great abundance at Chavarrillo, a small station on the International Railway about an hour's ride east of Jalapa.

The plant grows in the blazing tropical sun and is a prominent feature of the landscape, although its stocky trunk seldom reaches a height of more than four or five feet. But even at this height it towers above fully grown oak trees which remind one of the artificially dwarfed evergreens of Japan. Some other associates are wild pineapples, cacti, and various peculiar ferns which are able to survive under such dry conditions. The region, while interesting to the botanist, does not look very cheerful; but during the rainy season the dried-up ferns take on a rich green, and numerous brightly colored flowers relieve the severity.

I visited this region twice in the dry season and twice in the rainy season, each time making a stay of several days, collecting material, making notes, and taking photographs.

Between the *Dioon* locality and Jalapa lies a wonderful region for botanical study. Even during the dry season the vegetation is luxuriant; or it would be more nearly correct to say that there is no dry season here, for streams and cataracts formed by the ever-melting snows of Orizaba and Perote cause an abundant rainfall. The forest is dense and varied, and botanists will understand the richness of the fern flora from the fact that six out of the seven time-honored families may often be found within a ten minutes' walk. Ferns cover the ground and hang from the trees, while magnificent tree ferns with trunks twenty or thirty feet high and leaves ten or fifteen feet long are not uncommon. This rich collecting-ground has furnished material for several investigations by students of our department, besides an abundant supply for illustrative purposes. The place is almost ideal for a tropical botanical station. It is never much warmer than Chicago; it is never too cold for oranges, coffee, and bananas; and it is only a few miles from Jalapa, the capital of the state of Vera Cruz. The great coffee plantations of the Arbuckles give only a hint of its agricultural possibilities.

DIOON SPINULOSUM

Another species is called *Dioon spinulosum*, because the leaflets are spiny. Seedlings of *Dioon edule* have spiny leaflets, but this character is not found in plants with stems more than a few inches in height, the margins of all leaflets of older plants being quite smooth. Some would call this an instance of recapitulation—ontogeny recapitulates phylogeny, or the history of the individual is the history of the race—and would claim that *Dioon edule* is the offspring of *Dioon spinulosum*, since the older stock is obviously the one which is being recapitulated.

This species was practically unknown when I began my studies. There were two descriptions, both based upon a few small leaves of young plants, and in the only localities given, Progreso in Yucatan and Cordova in the state of Vera Cruz, the plant does not occur at all. Both descriptions were from potted plants, but the gardener at Cordova believed that his specimen came from Tuxtla.

During my second trip, in 1906, I saw a small potted specimen in the park at Vera Cruz, but I received only the vague information that it grew somewhere farther south. After returning to Chicago I sent Governor Dehesa a photograph of the Vera Cruz specimen and, together with Mr. Gaw, he began a series of inquiries which finally resulted in locating the plant in the mountains beyond Tuxtepec, more than a hundred miles south of Vera Cruz.

Two years later, fully provided with directions and introductions, I started for Tuxtepec. At Vera Cruz I chanced to meet a man who was quite sure that plants like the potted plant in the park could be found near Tierra Blanca, a town which I should have to pass on my way. Accordingly I got off at that place and after an hour's ride on horseback was rewarded by my first view of *Dioon spinulosum*, not the small plants which descriptions had led me to expect, but splendid specimens several feet high with leaves three or four feet long. I was informed that plants were larger and more abundant a few miles farther south, and so I turned in that direction and soon found that the information was correct, for on the immense hacienda of the Joliet Tropical Plantation Company, a plantation owned by people in Joliet, Illinois, magnificent specimens are abundant (Fig. 5). Mr. J. C. Dennis, superintendent of the plantation, generously furnished horses, guides, and the hospitality of his palatial home, while I explored the mountains and secured photographs and material.

Although *Dioon spinulosum* grows on the prevailing limestone rocks which have given the name Tierra Blanca to the region, it is well shaded by a forest of Spanish cedar, mahogany, ceiba, various kinds of rubber, and occasionally ebony. Orchids, bromeliads, ferns, and other plants weigh down the branches of the trees until they break off, so that one may collect this epiphytic vegetation without the labor of climbing. In some places vines are so luxuriant that it is impossible to get through on horseback, and even on foot one makes his

FIG. 5.—*Dioon spinulosum* on the Hacienda de Joliet, near Tierra Blanca, Mexico. The tallest specimen is about 32 feet in height.

way slowly, constantly slashing about with his machete. There is no anxiety about getting lost, for the trail is so evident that even a tenderfoot need not miss it.

With the exception of one Australian species, *Dioon spinulosum* is the tallest of all the cycads. Plants ten to thirty feet tall are not uncommon, and I measured one fine specimen which had reached a height of thirty-five feet. My colleagues Dr. Barnes and Dr. Land visiting the hacienda a few months later, found specimens fifty feet in height.

The female cones are very large, reaching a length of more than twenty inches and a weight of more than thirty pounds. At first the cone is erect, but as it grows its stalk elongates, and the great weight makes it hang down below the crown of leaves, often bending the trunk of the plant, as shown in Fig. 6. The big cone may contain two or three hundred seeds, about an inch and a half in length, which furnish meal for tortillas, as in the case of *Dioon edule;* while the dry, stony coat of the seed, with a hole cut in both ends, is a popular plaything for children.

The male cones are much smaller, and not being heavy enough to hang down below the crown of leaves they are harder to find.

Of course, in such a country there are interesting animals as well as plants. The jaguar, "big tiger," and ocelot, "little tiger," are abundant, but deer are also so abundant that their otherwise dangerous neighbors cause the natives little anxiety. Monkeys and parrots are common, and some of the snakes are large enough to make their skins worth removing. Some small, inconspicuous animals make their presence felt before they are seen. "Ticks" are everywhere, and the itching they excite is most distracting. The pests are fond of

FIG. 6.—Female plant of *Dioon spinulosum* on the Hacienda de Joliet, bearing a large female cone.

cattle, but cattle have friends. One may see a dozen blackbirds on a cow's back and others hopping up from beneath to get the ticks; and besides the cattle are driven into the rivers where the fish pick off every tick in sight.

The hacienda had afforded a far more extensive study than I had dared to anticipate when I left Chicago, but I had a ticket to Tuxtepec and an introduction to its "Hefe Politico," an official who seemed to have the combined powers of mayor, police, and judge. I arrived in the morning, presented my credentials, and indicated that I was ready to start. My knowledge of Spanish was inadequate, and the "Hefe" knew less about English, but I made him understand that I wanted to start at once, and he made me understand that I could not start until tomorrow. Later I found that the governor had made him personally responsible for my safety, and as a precautionary move he had immediately sent to the mountains, twenty miles beyond, for a guide who knew both the people and the region which I wished to visit.

The country beyond Tuxtepec is full of botanical opportunity. The Papaloapan River at that place is as wide as the Mississippi River at St. Louis, and the vegetation along its banks is rich and varied. Leaving the river, one comes into a fairly open forest, which can be traversed on horseback. Several species of *Zamia* were encountered before we came to the object of our journey. *Dioon spinulosum* is so abundant that in some places it is almost the only large plant, and it would not be exaggerating to speak of a *Dioon* forest. The plants were of the same size and appearance as those at Tierra Blanca but grew in denser stands. The whole region should be studied. It is practically untouched botanically. No one had ever seen a botany can or a plant press, and they said that no one but the Indians had ever collected plants there, even for medicine. Lack of time and money prevented me from making an adequate study. I collected *Dioon* and dug up an unfamiliar *Zamia*—now growing in the University of Chicago greenhouse—which proved to be a new species, secured a few ferns, and determined to make another visit. I did so two years later, in company with Dr. Land; but that was in September, 1910, while the Madero revolution was trying to break out. We had a hard time getting started from Tuxtepec, were led astray in the forest, and finally made our way back with scarcely any study of the locality.

CERATOZAMIA

The other Mexican genus is *Ceratozamia*, so named because each cone scale bears two rigid spines, or "horns" (Fig. 7; see also Figs. 46 and 47).

During my first visit I made repeated but unsuccessful efforts to locate *Ceratozamia*, wandering about for days in places where I guessed, from taxonomic accounts, that it might occur. Before leaving for home I paid my respects to Governor Dehesa, thanking him for his assistance in making the study of *Dioon edule* so successful and mentioning the fruitless search for *Ceratozamia*. He wanted to know what the plant looked like, and when I told him that there was a specimen in the park near his palace, he said he would find where it came from, if it grew in his state. In about a month some splendid cones came to my desk in Chicago. I learned from

Mr. Gaw that police were stationed at the plant in the park, with directions to ask people coming in from the

Fig. 7. *Ceratozamia mexicana* growing on a steep mountain side, opposite Naolinco, near Jalapa, Mexico.

country whether they knew where the plant grew. After a couple of weeks they found a man who knew. Cones were then sent at intervals, and two years later, in company with Dr. Barnes and Dr. Land, I visited the place under the guidance of the man who knew. Another

FIG. 8.—The extinct volcano Naolinco seen from across the valley. *Ceratozamia* is abundant on the precipitous slopes on both sides of the valley.

visit in 1908 added much to my data and material. Anyone can find *Ceratozamia.* A three hours' walk along the military road toward the extinct volcano Naolinco brings one to a broad valley, lying two or three thousand feet below the road along which one has come. Standing in the military road and looking straight ahead, one has a fine view of Naolinco, while the precipitous descent to the valley abounds in *Ceratozamia* (Fig. 8).

The plant seldom reaches a height of six feet, and specimens three or four feet high may be regarded as very large. It grows in such deeply shaded places that a brand of photographic plates which gave full exposures in one-fifth of a second in the *Dioon edule* locality required three minutes to yield a similar negative of *Ceratozamia*. The epiphytic vegetation is very rich, and there is a peculiar *Begonia* with leaves three feet across. The whole region would be worth investigating, particularly the mountain slopes on the other side of the valley, where two waterfalls, perhaps a thousand feet in height, look like slender white ribbons at the left of Naolinco.

CHAPTER II

THE AUSTRALIAN CYCADS

There are only two regions in the world where three genera of cycads may be found growing naturally—Mexico, with *Dioon*, *Ceratozamia*, and *Zamia*, and Queensland in Australia, with *Macrozamia*, *Bowenia*, and *Cycas*.

On the way to Australia I made only steamer stops at the Sandwich Islands and Fiji Islands, which have no native cycads; but at New Zealand, which is also entirely lacking in cycads, I spent a month in general study and collecting, since it is well known that it has a remarkable flora. The month was well spent. A. P. W. Thomas, professor of botany in the University College at Auckland, immediately put me into contact with the rich flora of that region and went with me on some trips to point out small but important things which might be overlooked. He also gave me directions for reaching and studying the taxad forests of Ohakune and the peculiar hot-springs district about Rotorua. The Kauri Timber Company entertained me for a week in their camp at Owharoa, where I secured an abundance of material and many photographs. Meanwhile various invitations to musical and literary entertainments impressed upon me the fact that, although New Zealand is a very young, a very wealthy, and a very practical colony, she is not neglecting the humanities.

An American naturally thinks of New Zealand and Australia as near neighbors, doubtless because the maps

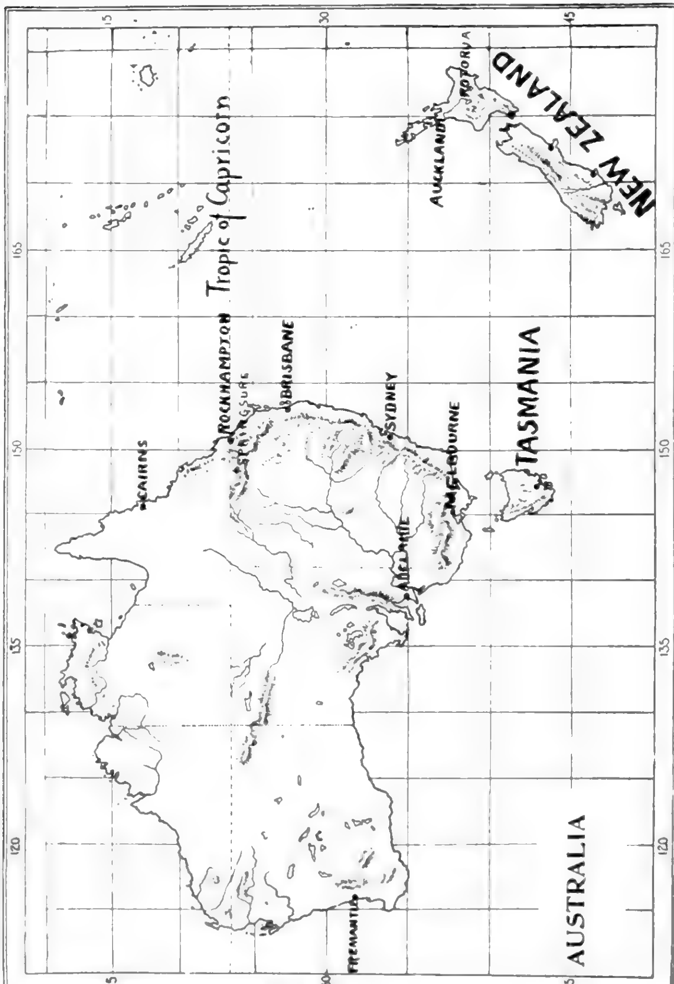


FIG. 9.—Map of Australia

of school geographies show the United States on a large scale and other countries on a small scale. As a matter of fact, it is a 1,200-mile trip from Auckland to Sydney, and the boats, not being Atlantic liners, require four days for the passage.

Sydney has a population of 600,000 and claims the finest harbor and docks in the world. Of course the botanical garden was the first object of interest, and its well-known director, Professor J. H. Maiden, gave me every facility for study and directions for reaching the cycad localities of New South Wales, besides introductions to the botanists of Queensland.

In this magnificent garden all the genera of cycads, except the Cuban *Microcycas* and the Queensland *Bowenia*, were growing in the open under natural conditions. Practically all the cycads of New South Wales are represented, and there are fine specimens of African forms. A week was well spent in making notes and photographs and in gaining familiarity with forms not seen in American greenhouses.

Two genera, *Macrozamia* with about a dozen species and *Bowenia* with two species, are confined to Australia, and *Cycas*, the genus which extends from Japan to Australia, is represented by four species.

MACROZAMIA

The name *Macrozamia* was doubtless intended to mean "the big Zamia," and one of the species, *Macrozamia Hopei*, is the tallest of the cycads, reaching a height of sixty feet, so that the name is not inappropriate.

Some of the species have tuberous, subterranean stems seldom appearing above the surface; others have a short, stocky trunk, while the one just mentioned is tall and slender. No other cycads look so much like palms as do some of the species, like *Macrozamia spiralis* and nearly related forms. The genus is identified by a single spine, sometimes rather long, terminating the scales of both male and female cones.

Macrozamia spiralis, one of the species with tuberous stems, sometimes grows in such profusion that it forms dense thickets, a rare thing for a cycad. Some species are small and scattered, so that they are likely to be overlooked.

A beautiful species, *Macrozamia Denisoni*, grows on Tambourine Mountain, west of Brisbane. Mr. J. F. Bailey, at that time director of the botanical garden at Brisbane, but now director of the botanical garden of Adelaide, went with me, fearing lest in my limited time I might not be able to find the plant. It reaches a height of twenty feet, and the long, graceful leaves are very glossy and have a peculiar tinge of reddish purple.

Returning to Brisbane, I told Mr. Bailey that I had heard that the "staghorn fern," *Platycerium*, was abundant in the vicinity, but that I had seen only a few small specimens. He kindly arranged another trip, which proved to be one of the most delightful experiences in all my travels. After an hour's journey by rail a young man who had been sent to meet us with a carriage took us for a couple of hours' ride through the Australian bush and brought us to the coast. We started in a rowboat for a little island about a mile offshore but were soon met by a launch and taken to the island, "Tabby Tabby Island," owned by William Gibson, who, with his family, occupied the only house. As a quiet, restful, interesting place it could not be surpassed. For two days Mr. Gibson with his launch took us to neighboring islands, especially Stradbroke Island, where the "staghorn fern" surpassed anything I had ever seen or read about. Great specimens five or six feet across were not uncommon (Fig. 10). In some places a score of plants could be seen growing on a single tree, and often the increasing weight of the growing ferns broke or overturned the trees.

To me the most interesting species of the genus is *Macrozamia Moorei*, which is abundant at Springsure, about two hundred miles west of Rockhampton, just on the Tropic of Capricorn (Fig. 11). It has a massive trunk, seldom more than eight or ten feet in height, but often fifteen inches or even two feet in diameter. The region is extremely dry; when I was there in November, 1911, they said that there had not been a rain for eight months. The grass was dry and brown, but the cycads looked fresh and vigorous, with dark-green leaves and a wonderful display of cones. The position of the cones, as we shall note in a later chapter, is identical with that in the fossil cycads (Bennettitales) of the Mesozoic age.

Unfortunately the leaves of cycads contain a poison which has a disastrous effect upon cattle, and in such a dry place anything green is likely to prove attractive. The cattle eat the leaves, especially the young leaves, and soon show a kind of paralysis which the cattlemen call "rickets." The hind legs begin to drag, giving the animal a peculiar gait, and when it can no longer move about it dies of starvation rather than from the direct effect of the poison. The government is trying to exterminate the plant by poisoning it with arsenic. A notch is cut in the side of the stem, and the arsenic is

FIG. 10.—The staghorn fern, *Platycerium grande*, on Stradbroke Island, off Brisbane, Australia.

inserted (Fig. 12). The plant soon dies, its leaves droop, and the stem becomes so brittle that the first strong wind completes the ruin. When the war broke out steps were being taken to create a small reservation and thus prevent a plant of such scientific importance from becoming extinct.

FIG. 11.—*Macrozamia Moorei*, at Springsure, Queensland, Australia. The plant in the foreground is about 10 feet in height.

It seemed nothing short of vandalism to destroy such splendid plants, but since the destruction was in full swing and I was encouraged to do all the damage possible, I cut into buds and trunks, securing material and information which would have been impossible under other conditions. A couple of plants of modest size were sent to Chicago, and later the St. Louis

Botanical Garden and the Brooklyn Botanical Garden secured specimens from this region

BOWENIA

The western genera of cycads, except *Microcycas*, are fairly well represented in the greenhouses of the

FIG. 12.—*Macrozamia Moorei:* a poisoned specimen

botanical gardens of both hemispheres; and the eastern genera, except *Bowenia*, are similarly represented. When I started on my trip there was not, as far as I know, a single living specimen of *Bowenia* in America. I did not see one in Africa and had not seen one in Europe, although I had visited most of the large botanical gardens.

All the rest of the cycads have pinnate leaves, the leaflets being arranged along the sides of the midrib, as in the well-known "Boston fern." *Bowenia* has twice pinnate leaves, each leaflet being pinnate, as in the "maidenhair fern" (Fig. 13).

FIG. 13.—*Bowenia spectabilis*, at Babinda, near Cairns, Queensland, Australia. The plant is a little more than 3 feet in height.

Bowenia is really hard to find until you get into its immediate vicinity. I was told that it could be found at Cooktown, in the northern part of Queensland. As we approached Cairns, about a hundred miles south of Cooktown, I could see, from the boat, fine specimens of *Cycas* in the scanty *Eucalyptus* bush on the hillsides; besides, passengers said that tree ferns and even larger ferns without any trunks grew in the dense, rainy forest west of Cairns. So I alighted at Cairns and started for the forest. With three Australian bushmen—the first I had seen—armed with axes and carrying boomerangs, I managed to move around some in the midst of tall trees, almost impenetrable undergrowth, and spiny hanging vines which they call "lawyer vines" on account of the exasperating tangles. In places roads had been cut by lumbermen, and along these one could get photographs and a wider view of the surroundings.

The immense *Lycopodium Phlegmaria*, the "tassel fern," with tassel-like clusters of cones, and *Ophioglossum pendulum*, the "ribbon fern," were the most interesting features of the epiphytic vegetation of the treetops. If a tree with such specimens was a foot or less in diameter the bushmen were likely to cut it down; if larger they would climb; but when they found that fine, uninjured specimens were worth three pence or even six pence, a climb of eighty feet was not at all objectionable. As I was leaving, they showed their appreciation of the tips by presenting me with a varied assortment of boomerangs.

The big ferns were all that had been claimed. The tree ferns belonged to the genus *Alsophila*, familiar in all large conservatories. The "larger ferns without trunks" proved to be *Angiopteris* and *Marattia*, the most primitive of living ferns. Their gigantic leaves, with a midrib as large as a man's arm, reached a length of seventeen feet.

While collecting material of these ferns I accidentally came upon a specimen of *Bowenia*, and when the bushmen, who spoke no English, noticed that I was much pleased with it, they took me to a place where there were scores of fine plants, some of them bearing cones. It was the typical *Bowenia spectabilis*, by some botanists regarded as the only species in the genus. I made photographs and notes and secured material. The beauty of the glossy, dark-green leaves gave the specific name *spectabilis* to this species. Some leaves which had been removed from the plant and had been lying in the blazing tropical sun for three days still looked fresh and green. It would be a popular hothouse plant if gardeners could only learn how to grow it.

When I returned to Rockhampton, Mr. Simmons, director of the botanical garden of that place, gave me directions for reaching a variety of *Bowenia spectabilis* which could be found at Maryville and Byfields, about twenty miles from Yeppoon, a small town east of Rockhampton. There was only one house at Maryville, and only one man lived in it; but at Byfields there were two houses and three bachelor brothers who lived as comfortably as people could under such circumstances. *Bowenia* was abundant, not scattered specimens, as at Cairns, but thousands forming a prominent feature of the floor of the scanty *Eucalyptus* forest. Both stem and leaf differ so decidedly from those of *Bowenia spectabilis* that I have no hesitation in calling the plant a distinct species, *Bowenia serrulata*, from the serrate margin of the leaflets, the margins in the other species being quite smooth. Cones were very abundant, so that it was easy to secure material.

Although the plant seems to baffle gardeners, in its native surroundings it has a remarkable hold on life. Along the river, where the current had washed nearly all the soil from the stem and roots, plants were putting out fresh leaves, and I saw plants which had been entirely dislodged and had rolled down to the dry bed of the stream, where they looked like round stones as large as one's head; and yet they were sound, and some of them were forming leaves. Mr. Edward Meilland, one of the three bachelor brothers, told me that a large, underground stem, lying in the path near the door, had been tramped over for twenty years, but when the house and the path had been abandoned, vigorous new leaves began to appear. Plants from this vicinity are now growing in the greenhouse at the University of Chicago, at the St. Louis Botanical Garden, and at the Brooklyn Botanical Garden.

The most interesting animal of the region is the kangaroo. Some are large and some are small, but all are amazing jumpers.

Raising cattle is the principal occupation, and the great ranges are in striking contrast with the small farms of New Zealand, where nearly 90 per cent of the land is in holdings of less than three hundred acres.

CYCAS

Cycas, the genus which extends from Japan to Australia, is represented in Queensland by four or perhaps five species (Fig. 14). I saw it first at Rockhampton, where it is very abundant within an hour's drive from the town. I spent several days at the home of Mr. Sydney Snell, who was thoroughly acquainted with the plants of the vicinity and knew the distribution of *Cycas* not only in that region but throughout the Bersirker ranges. I secured material and arranged with Mr. Snell to collect cones at frequent intervals and also to send plants to Chicago.

The species growing here is *Cycas media*, reported to be the tallest of the cycads, Eichler's account in Engler and Prantl's *Die natürlichen Pflanzenfamilien* giving it

FIG. 14.—Female plant of *Cycas media*, on the plantation of Mr. Sydney Snell, near Rockhampton, Queensland, Australia.

a height of twenty meters, or sixty-five feet. This is certainly a mistake. Dr. F. M. Bailey, in his *Queensland Flora*, states that the species reaches a height of eight to ten feet and sometimes twice that height. Directors of botanical gardens said that twenty feet was the limit. Mr. Snell, who had lived and hunted in the *Cycas media* region for many years, showed me the tallest specimen that he had ever seen, and it measured a few inches less than twenty feet in height. I saw the species at various places over a range of 700 miles, and the tallest specimen examined measured a little more than twenty-two feet in height. The person who started the mistake may have confused meters and feet or, more likely, may have applied to *Cycas media* the height of *Macrozamia Hopei*, which really reaches a height of sixty feet.

Cycas is the only genus in which the male and female cones, in their external appearance, show any marked difference except in size. The male cone looks about like that of other cycads, but the female consists of a large number of reduced leaves bearing seeds on their margins and not crowded together into a compact cone as shown in Fig. 14. The earliest seed plants, as far back as the Paleozoic age, bore their seeds on the margins of more or less modified leaves, so that in this respect *Cycas* shows the most primitive condition to be found in the plant kingdom. In all the cycads the "scales" of both male and female cones are modified leaves, but all have digressed farther than *Cycas* from the primitive condition.

The genera have been treated separately, but in many places two genera were often growing together. At Rockhampton, *Cycas* and *Macrozamia* were almost constantly associated, so that one could get both on the same photographic plate; at Byfields, *Bowenia* and *Macrozamia* were similarly associated, and at Cairns *Cycas* and *Bowenia* were growing together.

There are no cycads in Victoria, although they thrive in the open in the botanical garden at Melbourne. There are none in the vast desert of the central part. There is one species of *Macrozamia* in the western part near Perth, but the steamer stop was too short to risk a

FIG. 15.—Albatross

visit, and I could not wait a month for another boat. Besides, I had already secured photographs and several collections of cones and seeds through correspondence with a local botanist. Consequently, after leaving Sydney I made steamer stops only at Melbourne and Freemantle and then started on the long voyage across the Indian Ocean to Africa.

Throughout the voyage, fourteen days out of sight of land, we were accompanied by a large flock of albatross. The crime of the "Ancient Mariner" must still linger in the albatross mind, for not one of the birds ever alighted on the ship. They are built along monoplane lines, or rather the monoplane is built along albatross lines. They circle round and round the ship, sometimes a mile ahead, sometimes a mile behind, sometimes so close that you can see their eyes, but always without apparent effort, often flying a mile without a perceptible flexing of the wings (Fig. 15).

CHAPTER III

THE AFRICAN CYCADS

Durban, the port at which one arrives from Australia, has a large botanical garden with nearly all the African cycads, some of them represented by

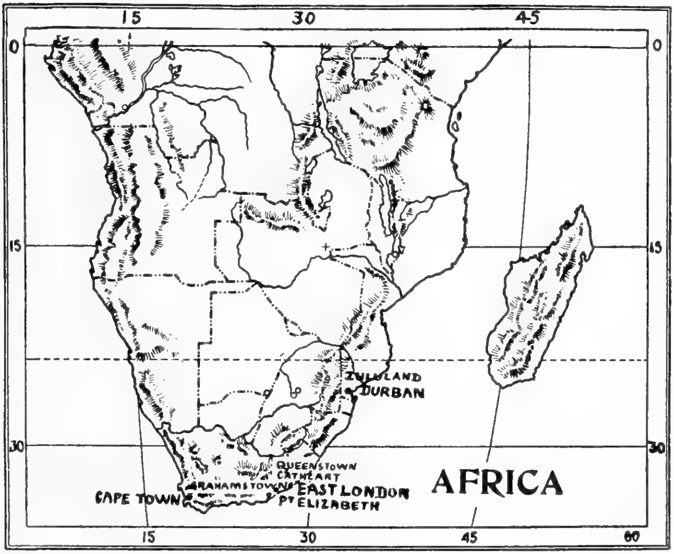


FIG. 16.—Map of South Africa

numerous specimens of various sizes. Mr. Wylie, director of the garden, was particularly interested in the group and was able to give me directions for finding many of them and introductions to local botanists who might be of service.

Only two genera, *Stangeria* and *Encephalartos*, occur in Africa, both of them strictly African and confined to the southeastern part of the continent. A week was well spent at Durban in gaining familiarity with *Stangeria* and the various species of *Encephalartos*, since at that time the Durban garden had the largest collection of *Encephalartos* in the world. Two of the species have found great favor as decorative plants, and beautiful specimens adorned the lawns throughout the city. In any town of Southeastern Africa the lawns are likely to indicate what cycads are to be found in the vicinity, for all the species find favor, on account of either their beauty or their peculiarity.

The first field work was done in Zululand. Starting with a Zulu guide from Mtunzini, about a hundred miles north of Durban, a few hours' tramp brought us into the midst of the cycads.

STANGERIA

Stangeria paradoxa is abundant in Zululand (Fig. 17). It is the most fernlike of all the cycads; in fact it was described originally as a fern, and the mistake was not corrected until the cones were discovered. The genus was named in honor of Mr. Stanger; the specific name was given because the plant looks like a fern but is really something very different.

The stem is entirely subterranean, and there are usually only one or two, sometimes three or four, leaves. The variation in the leaves has led some to suggest that there may be more than one species. That its general habit, as it appears in the field, is extremely variable is beyond question; and that under cultivation in conservatories and botanical gardens it becomes quite different from the wild form is also apparent. In both Australian and African gardens *Stangeria* produces leaves and cones more freely than in the field, so that the cultivated specimens become much larger and more

FIG. 17.—*Stangeria paradoxa*, near Mtunzini, Zululand, South Africa.

beautiful. In the field *Stangeria* presents two forms, one growing on the open grass veldt and the other in the shade of bushes or trees, the shaded form being much larger and resembling more nearly the cultivated specimens. I dug up several specimens from the grass veldt and sent them to the University of Chicago, where, after five years of the usual unnatural conditions, they are producing leaves and cones as large as those of the bush veldt form.

In Zululand the grass veldt stretches for miles, rolling and hilly, broken by huge rocks of granite and gneiss, and occasionally with exposed surfaces covered only with lichens and a peculiar little lycopod called *Selaginella rupestris*.

It was January when I visited the place in 1912. At this season, which is midsummer in the Southern Hemisphere, the grass is dry and yellowish, so that the green leaves of *Stangeria* form a striking contrast, making the collecting much more expeditious than it would be with greener surroundings.

The plants are fairly abundant, as many as twenty being in sight at one time; but the specimens are scattered, with no crowded masses like the thickets of *Macrozamia spiralis* and *Bowenia serrulata* in Australia. In January the male cones have either rotted or dried up, and the female cones are falling to pieces.

On the Mtunzini grass veldt only a few seeds were secured, and in the bush, which is particularly dense and rich in ferns, the plants of *Stangeria* were few in number but much larger than those growing in the open. Not a single cone or seed was found in the bush. It is said that baboons are very fond of the seeds and carry them away as soon as the cones reach their full size.

Zululand is near the northern limit for *Stangeria*, but the range extends southward as far as East London and doubtless even to Port Elizabeth. I made my most extensive study at East London, but I did not see a single plant west of that place. However, Mr. George

Rattray, principal of Selborne College at East London, who is interested principally in the classics but knows more about cycads than anyone else in Africa, told me that he had seen specimens at Port Elizabeth, and that he regarded this as the western limit.

Stangeria is abundant about Kentani in the Transkei. My friend Mr. Walter Saxton, who has published various papers on African gymnosperms, and who was then at the South African College at Cape Town, later at Gujarat College, Ahmedabad, India, and who is now an officer in the British Army, arranged to have material collected and fixed for me. Miss Sarah Van Rooyen, of Kentani, has done this work for five years, collecting such a close series of stages that my study has been scarcely handicapped by the great distance.

ENCEPHALARTOS

The other African genus is *Encephalartos* (*ἐν κεφαλῇ ἄρτος*), very appropriately called the bread palm, because the natives made meal from the starchy seeds. It has about a dozen species, one of which is found as far north as the equator, but most of which are south of Zululand, while two or more are found farther west than Port Elizabeth, so that the range is more extensive than that of *Stangeria*, with which it is often associated.

The first field studies were made in Zululand, where *Encephalartos brachyphyllus*, a species with a tuberous, subterranean stem and rather short leaves, is abundant, associated everywhere with *Stangeria*. Since the cones had not quite reached the stage most approved by baboon and monkey epicures, it was easy to secure material and to distinguish male and female plants, insuring both genders for the collection in the botanical garden at the University of Chicago.

About twenty miles from Mtunzini, in the midst of the *Stangeria* and *Encephalartos brachyphyllus*, stands a single specimen of another species of *Encephalartos* more than ten feet in height. They say that it is the only cycad, with a trunk, within a distance of fifty miles. There had been three trunks, doubtless derived from buds at the base of an old plant which had fallen hundreds of years ago, but one of the trunks had been cut off and taken to Durban, where it is now one of the finest cycads in the botanical garden. The species has been called *Encephalartos Altensteinii bispinosa*, and has also been called *Encephalartos Woodii*, but to me it seemed to come within a reasonable range of variation which should be expected in *E. Altensteinii*. My Zulu guide, the son of a Zulu chief, was thoroughly familiar with Zululand and had been well coached by Mr. Wylie; otherwise there would have been little likelihood of finding such an isolated specimen in a hilly country, with numerous stretches of forest and bush.

The principal studies were made in the vicinity of Queenstown, Cathcart, East London, Grahamstown, and Port Elizabeth, a region lying between the Drakensburg ranges and the coast, and between Durban and Cape Town, and containing nine species of *Encephalartos*, besides several good *Stangeria* localities.

One can go by boat from Durban to East London, but I wanted to visit Queenstown, about one hundred and fifty miles north of East London, and Cathcart, about fifty miles farther south; besides, I had seen enough of the Indian Ocean and did not want to miss the remarkable and varied flora of Cape Colony. So I took the train by way of Ladysmith, Bloemfontein, and Springfontein, a country dotted with cemeteries and monuments reminding us of the Boer War.

At Queenstown I met Mr. E. E. Galpin, F.L.S., a banker, whose knowledge of South African plants and whose extensive collections had made him a Fellow of the Linnean Society. He went with me to the rugged dolerite ridges near the town and not only showed me scores of large plants of *Encephalartos Friderici Guilielmi* (*venia sit nomini*), a species little known to botanists, but gave me such information with regard to its behavior as only a botanist could give after years of observation (Fig. 18). His warning prepared me for the striking variation which this species displays in different localities, and guarded me against confusing it with a nearly related species which closely resembles it and is associated with it in some places.

This species has a massive trunk surmounted by a crown of forty or fifty leaves which have a pale-green, almost gray, color. The trunk is seldom more than five or six feet in height, and the taller specimens are likely to have the leaning position shown in Fig. 18. The tallest specimens measured less than ten feet and were prostrate; but new crowns continue to appear, and the tip of the stem turns up, while new plants develop at the base from buds which are likely to form on any wounded portion of a cycad stem. When two or three plants are found with their bases united, they are almost sure to mark the site of an old trunk which had fallen and decayed, perhaps hundreds of years before.

I found the same species on the Windvogelberg overlooking the town of Cathcart and made a rather extensive series of notes and photographs.

From this place I made a carriage trip to Junction Farm, a few hours' ride from Cathcart. The farm takes its name from the fact that it lies at the junction

Fig. 18.—*Encephalartos Friderici Guilielmi*, at Queenstown, South Africa.

of the Zwart Kei and White Kei rivers, which unite to form the Great Kei River. The country is called the Transkei.

Three cycads are abundant on Junction Farm, *Encephalartos Friderici Guilielmi*, *E. Lehmanni*, and *E. villosus*. I was particularly interested in the second one and in comparing it with the first. The third I had already seen, and I knew that I should find it again.

Encephalartos Lehmanni, as it occurs on Junction Farm, looks so much like *E. Friderici Guilielmi* that even a botanist might not notice that there are two species, since both have the massive trunk and crown of very pale leaves. In both the leaflets usually have smooth margins, but in *E. Lehmanni* there are occasionally one or two small spines. This might not seem to be an important characteristic, were it not for the fact that in other localities the spines become larger and more numerous, until the plant looks so different that even a layman could not confuse it with the Kaiser's cycad. There is really a series whose extremes are easily recognizable species between which are intergrading forms that could hardly be identified by leaf or stem characters. However, the male cone of *E. Lehmanni* is not very hairy and has a distinct reddish color, while the other has a cone so densely covered with long, light-brown hairs that the solid portion—a dull green when the hairs are removed—is entirely hidden.

At Grahamstown, about a hundred miles southwest of Cathcart, *E. Lehmanni* has such jagged leaves that one risks injury to hands and clothes in getting material. The leaves also have little of the grayish color so characteristic of the Queenstown and Cathcart specimens.

Professor Shönland, formerly director of the Albany Museum at Grahamstown, but now professor of botany in the Rhodes University of that place, gave me the benefit of his extensive acquaintance with the cycads of the vicinity. It also increased the value of the field study to have associated plants pointed out and named with such authority.

One of the most interesting species, *Encephalartos latifrons*, was found at Trapps Valley, between Grahamstown and the coast. It reaches a height of five or six feet and has a dense crown of rather short leaves with very broad and extremely jagged leaflets. Field studies are laborious, since the plants are isolated, usually half a mile or even a mile apart. However, the ground is not very uneven, and with a good pair of binoculars one can make efficient use of his limited time. I was particularly gratified to find this species, since it is almost unknown to botanists.

Its growth is extremely slow. In Grahamstown I had heard of a row of "bread palms" in front of a house at Trapps Valley, and it was not difficult to find the place. There are five plants in the row, three of them *Encephalartos Altensteinii* and the other two *E. latifrons*. A pleasant, gray-haired lady told me that they had been set out when she came to that house as a bride forty-six years before. She said that the *E. Altensteinii* may have grown a foot in the forty-six years, but that the *E. latifrons* did not seem to have grown any, although they always had green leaves.

Before I left Chicago I had heard that there were cycads at East London but could get no definite information. However, on the voyage between the Sandwich Islands and New Zealand I met an elderly gentleman and his wife and, incidentally mentioning my difficulty in getting into contact with anyone at East London, was delighted to find that he had been mayor of that city for ten years, and that his wife was interested in decorative plants and was familiar with the *Stangeria* and *Encephalartos* localities. They gave me letters to

Mr. George Rattray, principal of Selborne College, and to their son, the collector of customs, who relieved me of any annoyance which the unusual and rather extensive baggage necessary in such an expedition sometimes occasions. But I have no complaints to make about tariff regulations, for throughout the British colonies the customs officials were always gentlemanly and considerate.

There are four cycads at East London, *Stangeria*, *Encephalartos Altensteinii*, *E. villosus*, and *E. cycadifolius*, all within easy distance from the city.

I had already studied *Stangeria*, but I made photographs and spent some time in comparing the specimens growing on the exposed grass veldt and in the shaded bush veldt. Several specimens were dug up and sent by parcel post to Chicago, where they are now growing luxuriantly.

Encephalartos Altensteinii, one of the most popular cycads in botanical gardens throughout the British colonies, is abundant along the rocky banks of the Buffalo and Nahoon rivers.

Very few specimens reach a height of six feet, and they seldom measure more than a foot in diameter; but the crown is large and vigorous, making the plant so attractive that it is in great demand for lawns and parks. It grows in the open and consequently is not hard to find. I saw only one specimen growing in the deep, shady bush, and Mr. Rattray told me that the bush was a recent growth of not more than fifty years' standing. The cycad was about six feet in height and certainly as much as a hundred years old. It had become established before the trees appeared and had continued to grow as the shade developed.

The leaves of young plants are very spiny, and even on the largest plants one can usually find leaflets which have two or three spines; but a careful examination is likely to show some leaves on which all the leaflets have entire margins. Such leaves the taxonomist is sure to identify as *Encephalartos caffer*, and local botanists have amused themselves by sending entire and spiny leaves to European herbaria, to trap the taxonomists into identifying two species from the same plant. The scheme has succeeded so well that one should look with considerable suspicion upon herbarium specimens identified only by the leaf.

Another cycad in the East London region is *Encephalartos villosus*, the most widely cultivated and most popular species of the genus. In nature it grows in shaded localities, but it thrives on lawns and in parks if well watered, and in greenhouses it reaches a size and luxuriance not likely to be found where there is any struggle for existence.

The stem is entirely subterranean. The leaves, which reach a length of ten feet, have a bright-green color and a graceful curve which give this species its decorative value. It is very easily grown. A stem about as large as one's fist was sent to me in 1908 from Cape Town, simply wrapped in a piece of burlap. It was potted, but for two years did not produce a single leaf. It is now a magnificent specimen in the greenhouse at the University of Chicago, with a dozen leaves ten feet long.

The other cycad of the East London region is *Encephalartos cycadifolius*. It is very rare, and the cones have not been described. The leaves have a peculiar, twisted appearance which make the plant easy to recognize, but which bear so little resemblance to those of any species of *Cycas* that it is difficult to imagine what suggested the specific name. I secured one plant and a fully grown female cone. Since the plant at the University of Chicago has produced a male cone, the description of the species can now be completed.

While the opportunity to study four cycads in one locality was unusual, it was no more valuable than the opportunity to talk with Mr. Rattray with regard to the various South African species. Although a teacher of the classics, he had studied nearly all the African species and had made copious notes, which he should have published. However, he had studied the cycads as he had studied many other African plants, and he was glad to give me freely the benefit of his extended observations. The late Professor Pearson had already acknowledged his indebtedness to Mr. Rattray. I am under even deeper obligation.

The next stop was at Port Elizabeth, on the coast about one hundred and thirty miles west of East London. In this region I wanted to study *Encephalartos caffer* and *E. horridus*.

No South African cycad causes more disagreement among local botanists than *Encephalartos caffer*, and so I was eager to see it in its type locality at Van Staadens, about thirty miles inland from Port Elizabeth. The mayor, Mr. A. W. Guthrie, who is interested in cycads and has some fine specimens growing on his lawn, kindly sent a big touring car to my hotel, with the director of the botanical garden, Mr. J. T. Butters, and

Mr. L. Drege, a local botanist, and also with an ample basket, since Van Staadens has no restaurant or store. Thus provided for, we soon reached the cycad locality and began our observations.

Mr. Rattray had told me that if I got to Van Staadens I might feel an intuition that *Encephalartos caffer* was a good species, but that I would not be able to give a good reason for the feeling. He was entirely right about the intuition, and I tried to find out what could be responsible for it.

The stout trunk, seldom more than six or eight feet in height, with its crown of very rigid leaves, makes the plant look like *E. Altensteinii*, but there seemed to be something a little different. The leaves often curve at the ends instead of curving uniformly throughout the entire length, thus giving the plant a characteristic aspect, but many specimens do not show this feature. The margins of the leaflets have caused nearly all of the discussion. A study of the seedlings of the Mexican *Dioon edule* had prepared me for a considerable difference in leaf margins in plants of different ages, and it was not difficult to find that the plant under consideration was showing a similar behavior. The leaflets of seedlings and young plants are uniformly spiny, but as the plants become older the spiny character gradually disappears, and in plants two or more feet in height there is scarcely ever a spine.

Encephalartos Altensteinii is characterized, in the manuals, by its spiny leaflets, but in the East London region plants more than three or four feet in height are likely to show this character sparingly, and, as we have already noted, some leaves do not show it at all. As far as the diagnosis is concerned, a young plant forty or fifty years old might be labeled *E. Altensteinii*, while the same plant, fifty years later, would be diagnosed as *E. caffer*. However, it must be admitted that the plants at Van Staadens lose the spiny character much earlier than do the typical specimens of *E. Altensteinii* in the East London district. Here again local botanists have amused themselves by selecting leaves from a single plant of *E. Altensteinii* and sending them to large European herbaria for identification. Carefully selected leaves of either *E. Altensteinii* or *E. caffer* will satisfy the diagnostic requirements of both species. The joke simply shows that, in some cases at least, diagnosis should be based upon a study of plants in the field.

The young cones look alike in the two species. A prolonged study of mature cones might show something distinctive, but here again the baboons carry away the cones before the seeds are ripe, and I did not see a single mature female cone in the field, although there were hundreds of plants. Having found a nearly mature cone not far from the waterworks which supply Port Elizabeth, I arranged to have it covered, and to have seeds sent to Chicago when they were ripe. I finally received a photograph of a man with a rifle in his hand and a big baboon propped up beside him. The accompanying note informed me that the seeds were inside.

The female cones are huge, and the larger plants frequently bear two or three at a time. Three large cones from a single plant in the botanical garden had a total weight of more than one hundred and forty pounds. Mr. Butters said that when there is a single cone it may reach a weight of ninety pounds, the largest cone known in cycads or any other plants. The great difference in the size of cones borne singly and of those borne in groups, together with some differences in cone scales caused by crowding, would account for most, perhaps all, of the diagnostic distinctions between *Encephalartos Altensteinii* and *E. caffer*, as far as they concern the cones.

If baboons would let the cones alone and thus permit the collection of material for a study of critical stages in the life-history, it could probably be determined whether there are two species or only one; and if there are two, it could be determined which has given rise to the other, for there can be no doubt that the forms are intimately related.

As it is, with only field observations and a study of superficial characters available, one has an intuition but not decisive evidence that *Encephalartos caffer* is a good species, and that it is the offspring of *E. Altensteinii*.

The last of the African cycads to be studied in the field was *Encephalartos horridus*. This species, specimens of which can usually be found in any large conservatory, is scantily represented at Despatch, an hour's ride from Port Elizabeth. Its terrible leaves give it a clear title to its name (Fig. 19).

While *Encephalartos horridus* is well named, the genus as a whole has suffered from the bad habit which taxonomists have of naming plants after each other, so that we have *E. Altensteinii*, *E. Lehmanni*, *E. Woodii*, *E. Vroomi*, *E. Ghellinkii*, and, worst of all, *E. Friderici Guilielmi*. How much better christened are *E. brachyphyllus* with its short leaves, *E. villosus* with its hairy leaf stalks, *E. latifrons* with its broad leaflets, and *E. horridus* with its fierce, spiny leaves! Appropriate descriptive names like these might have been given instead of the meaningless commemorative ones, for *E. Altensteinii* might have been called *E. pachyphyllus* on account of its very thick leaflets, *E. Lehmanni* might

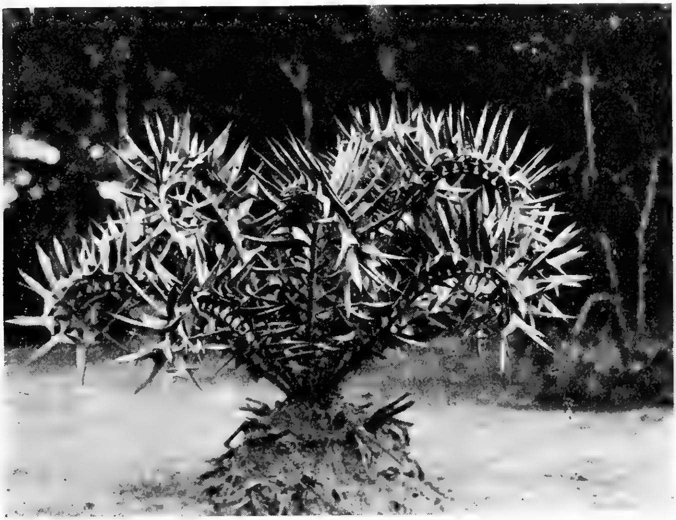


FIG. 19.—*Encephalartos horridus*, near Port Elizabeth, South Africa

have been *E. albus* from the pale color of the leaves, and *E. Friderici Guilielmi* might have been *E. tomentosus* because the buds and cones have a dense covering of hair. Almost any cycad might claim a specific name like *sanguineus*, *rubus*, or *coccineus*, because the rigid and often spiny leaves are likely to draw the blood of anyone who attempts to collect material.

Before starting for the *E. horridus* locality I was advised to wear old clothes and to carry safety pins, for not only the cycad but many other plants in its neighborhood have spines or thorns. There are scarcely any trees or even large shrubs in the vicinity, but there are numerous specimens of *Aloe ferox*, which also got its specific name on account of its ferocious leaf, and of *Aloe africana*, both of which look like agaves (century plants) on tall stems. Some of the small, thorny bushes are weighted down by large mistletoes, and the general thorniness is increased by occasional cacti from Mexico. The region is very dry, and a better place for a study of succulent plants could hardly be imagined.

Throughout this series of collections from Queenstown to Despatch one of the most interesting plants is *Euphorbia*. On our tennis courts we often find the small, milky, prostrate "spotted spurge," called *Euphorbia maculata* on account of a purplish spot on the leaf. Some of these African *Euphorbias* are small, some are like cushions, a couple of feet in diameter and a foot tall, but the most striking species are large trees twenty or thirty or even fifty feet in height (Fig. 20).

Many of our most popular cultivated flowers are native here, like *Gladiolus*, many species of *Geranium* (*Pelargonium*), scores of immortelles (*Helichrysum*), and magnificent *Crinums*. Many beautiful plants, not native, easily gain a footing and run wild, like *Canna* and the *Calla*. Early one morning I counted more than three hundred flowers on a single plant of the "night-blooming cereus" growing on a tree by the roadside.

Some of our native trees, like the larch (*Larix americana*) and the white pine (*Pinus Strobus*), are being introduced on an extensive scale by the forestry department of South Africa. In this mild climate these trees grow nearly twice as fast as they do in Ohio or Michigan. It looks as if large portions of the grass veldt would become forested. I was told that very probably large tracts of the grass veldt had originally been covered with forests, but that the natives had

FIG. 20.—*Euphorbia grandidens* on Junction Farm, near Cathcart. South Africa. The largest plants may be nearly 60 feet in height.

destroyed the trees, partly to clear ground for cultivation, but largely from a childish desire to see things burn.

A botanist could hardly be expected to know much about the zoölogical features of a country, but some things are too obvious to be overlooked. In Zululand there may still be found an occasional hippopotamus in the river, big boa constrictors in the bush, and even more dangerous little snakes in the grass. A medical missionary told me that the bite of the green "momba," not larger than our black snake, is fatal within fifteen minutes, and that of the brown "momba" is fatal within half that time. Early in the trip, when I was trying to impress upon my guide, who spoke no English, that I was not afraid of snakes, he patted my heavy leather leggings and then patted his own bare shins, indicating that he should observe a reasonable degree of caution. Some birds protect their eggs and young by building their nests on slender twigs hanging over the water, so that snakes can neither crawl down the twig nor rise far enough out of the water to do any damage. Along the rivers it is not rare to see scores of such nests on the drooping twigs of a single tree.

The southern part of the *Stangeria* range is a great ostrich country. Wild ostriches are numerous, and ostrich farming, with modern incubators and scientific breeding, is a leading industry. I was surprised to learn that in a country where ostriches still run wild a pair of thoroughbreds bring as much as a thousand dollars, and that high-grade feathers are worth, at the farm, as much as $200 a pound. Xenophon in his *Anabasis* noted the speed of the great bird. In South Africa people sometimes ride them as they would horses. The birds often race with railway trains, and the tales one hears would fill a book.

The secretary bird is scarcely less interesting. It is held in great respect because its principal diet is snakes, even the most venomous ones. This bird is a fighter, a finished boxer. It does not swoop down from above but stands on the ground, facing the snake, striking a single chopping blow with its foot, and then jumping back, dodging blows from its adversary and alertly seeking the opportunity for a knockout. They say that the bird practically always wins. The snake is swallowed whole.

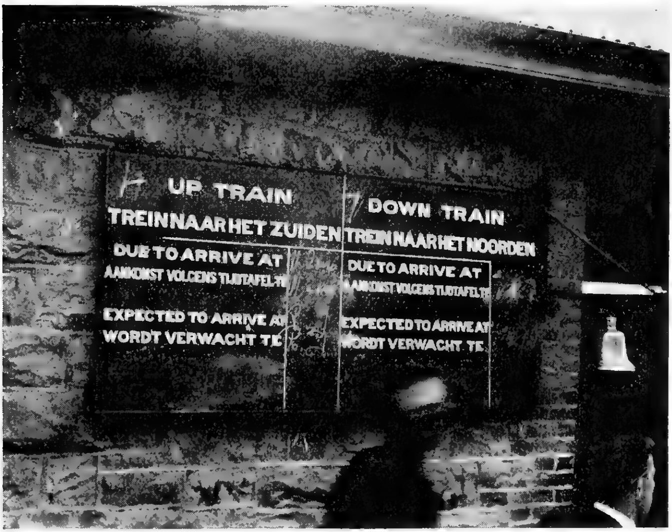


FIG. 21.—Train bulletin. All official notices must be in both English and Boer languages.

One result of the Boer War is constantly thrust upon the traveler in South Africa. All official notices and documents are bilingual (Fig. 21). Every official document must be published in the Boer language as well as in English. Bulletins from experiment stations must be in both languages. Professor Pearson told me that he was often asked for the Boer equivalent of such words as *Spirogyra*, *Erica*, and *Helichrysum*, and that translators seemed disappointed to find that scientific names, like Arabic numerals and musical notation, are common to all languages.

With the cycad collecting at an end, I came by rail to Cape Town to take the boat for London and home.

Educational institutions are well developed in South Africa, there being excellent schools at Durban, East London, Port Elizabeth, and particularly at Grahamstown, where there is also a first-class conservatory of music. But Cape Town, with the South African College, the name of which has recently been changed to the University of Cape Town, and with Stellenbosch and Hugenot College within a short distance, is the chief educational center.

The department of botany in the University of Cape Town had three teachers of international reputation, Professor H. H. W. Pearson, Dr. Edith Stephens, and Mr. Walter Saxton, but Professor Pearson died in the autumn of 1917, and Mr. Saxton has gone to war, so that only Dr. Stephens is left. The botanical laboratory is nearly as large as that at the University of Chicago, and it is well equipped.

Professor Pearson was deeply interested in establishing a botanical garden on the slopes of Table Mountain, and he had it well under way before he died. Plants addressed to the garden are carried free by the railways from any part of South Africa, and in consequence no garden in the world has ever developed so rapidly. Within three years all the known species of African cycads had been sent in, some of them represented by more than a score of specimens. Other plants are also well represented. The vertical range of this garden, nearly 3,000 feet, gives it a great advantage over any of the other great gardens of the world.

While the garden existed only in Professor Pearson's mind when I was at Cape Town, the park contained a good collection of cycads, so that I was able to get some final photographs, notes, and material before starting for Chicago.

During these trips to Mexico, Cuba, Australia, and Africa all the nine genera of cycads, with about thirty of the species, were studied in the field, notes and photographs were secured, material was carefully selected for later microscopic study, arrangements were made with people in cycad localities to send collections at suitable intervals, and living plants were sent to Chicago for that prolonged and critical observation which is impossible when time is limited.

The following chapters will describe the life-history of the cycad, the description being based upon field notes and a laboratory study of the abundant material.

PART II

THE LIFE-HISTORY

The life-history of a plant, like that of a person, is a cycle—birth, childhood, middle age, reproduction, and death—but since it is a cycle botanists begin sometimes at one place and sometimes at another and trace the history until they come around to the point from which they started. Theoretically it might be best to begin with the fertilized egg, then study the development of the embryo, the seedling, the adult plant, the appearance of sperms and eggs, and then the fertilization of the egg, the stage with which we started; but we shall begin with the adult plant, then study the reproductive features leading to fertilization, the development of the embryo, and finally the seedling, which gradually reaches the adult stage.

CHAPTER IV

THE VEGETATIVE STRUCTURES

It is convenient to treat separately the vegetative and reproductive phases of a plant's life-history; but as a matter of fact vegetative structures often reproduce the plant, and reproductive structures do vegetative work. We shall consider first the typically vegetative structures, the trunk, or stem, the leaf, and the root; and then the typically reproductive structures, the cones and gametophytes, which lead up to the formation of seeds.

THE STEM

It is the unbranched trunk and the crown of leaves which make the cycads look like tree ferns or palms. The remote ancestors of the cycads, now entirely extinct but fairly well known from leaf impressions and fossils of the Paleozoic age, are called the Cycadofilicales, the name indicating a combination of cycad and fern characters. The leaves of these ancient forms were so identical with those of ferns that botanists called the Paleozoic the "Age of Ferns," until it was found that most of the leaves belonged to these primitive seed plants. In many cases it is not yet known whether a given leaf is that of a fern or of one of these remote ancestors of the cycads. The leaves look like those of ferns, they have the same internal structure, and it is beyond dispute that the plants are simply ferns which have developed the seed habit. For the sake of convenience we have made a definition separating the ferns from the seed plants, although the series, like that often existing between two species within a genus, is one with easily recognizable extremes, but with intergrading forms which can be classified only arbitrarily.

During the Mesozoic the aspect of the group became more like that of the living cycads, so that they were no longer mistaken for ferns, but were mistaken for true cycads, and botanists characterized the Mesozoic as the "Age of Cycads." Technically most of the Mesozoic cycads, now represented only by fossils, are called the Bennettitales (Fig. 78).

In general appearance the living cycads would not be easily distinguished from some of their Mesozoic ancestors, for both have the armored trunk surmounted by a crown of leaves. The distinctions are found in the reproductive structures and in details of internal structure. There is little difficulty in applying names, since all the Bennettitales are extinct, and all the living cycads are called Cycadales, so that extinct members of the Cycadales are the only ones which could cause confusion. While there must be such extinct members in the Mesozoic, very little is known about them.

In the living cycads there are two types of stem, one subterranean and tuberous, the other aërial and columnar.

The tuberous type is represented in both hemispheres; in the Western by *Zamia*, and in the Eastern by *Bowenia*, *Stangeria*, and by some species of *Macrozamia* and *Encephalartos*. This stem varies in size from an inch in diameter and a few inches in length in *Zamia pygmaea*, to a foot in diameter and two feet in length in *Macrozamia*. In some cases the bud and leaf bases are above ground, but in others even the bud is below the surface. The armor of leaf bases is likely to be poorly developed or entirely lacking in these underground stems.

For various reasons the columnar type of stem has received more attention. It is more conspicuous, can be seen without digging, its armor of leaf bases is an interesting feature, and it is the type which has been retained from its fossil ancestry.

The tallest of all cycads is *Macrozamia Hopei*, of northern Queensland, which occasionally reaches a height of sixty feet; *Dioon spinulosum*, with an occasional specimen fifty feet in height, comes next; and the Cuban *Microcycas*, with here and there a specimen over thirty feet in height, is third. But these are all exceptional figures, even for these species; very few of them get beyond twenty feet. Among the remaining columnar forms any plant reaching a height of ten feet must be regarded as very tall.

The leaning habit, shown in Fig. 18, is common among the taller specimens, outside of the three very tall species just mentioned. The explanation is not hard to find. The root system is not very extensive, and the plants are very heavy; consequently, as soon as they become tall enough to be much affected by the wind they begin to lean and finally become prostrate. The main root seldom breaks, but the tissues at the base of the trunk become ruptured, and from these wounded portions buds arise and develop into new plants. Gardeners propagate some species of cycads by wounding the stem and thus causing the development of buds which can be potted. The bud at the apex of the prostrate trunk may become erect and produce crown after crown for more than a hundred years; but it often happens that the trunk dies as soon as the bud has exhausted the food materials stored in the ample pith and cortex.

It is well known that some of the mammoth *Sequoias* of California have reached an age of 3,000 years, perhaps even 4,000 years. The Big Tree of Tule, a cypress near Oaxaca, Mexico, has a trunk fifty feet in diameter and may be even older than the big trees of the Yosemite. But these are very large trees. The cycads are comparatively insignificant in size, and yet a *Dioon* with a trunk not more than a foot in diameter and six feet in height may have reached an age of 1,000 years. The plant shown in Fig. 1 is about 1,000 years old.

In the big trees the age is determined by counting the annual rings; in the cycads it is estimated by a study of the armor of leaf bases.

The duration of a crown of leaves varies with the species and with conditions, the leaves persisting one year, two years, three years, or even longer; but after a while the leaflets fall off, the midribs decay, and finally there comes a clean break leaving an inch or more of the leaf stalk, so that the trunk is completely covered by these leaf bases which constitute the "armor" (Fig. 22).

The clean break just referred to is like that which occurs in the case of our familiar shrubs and trees whose leaves fall in the autumn; a peculiar protective tissue develops at the base of the leaf long before the leaf is to drop, so that the wound is healed before it is made. In the cycads this tissue keeps reappearing, scaling off in thin, papery flakes, thus gradually reducing the diameter of the trunk until the diameter of the lower portion may become less than that of the upper.

Since the armor, in the columnar forms, persists throughout the life of the plant, it is possible to determine within reasonable limits the number of leaves

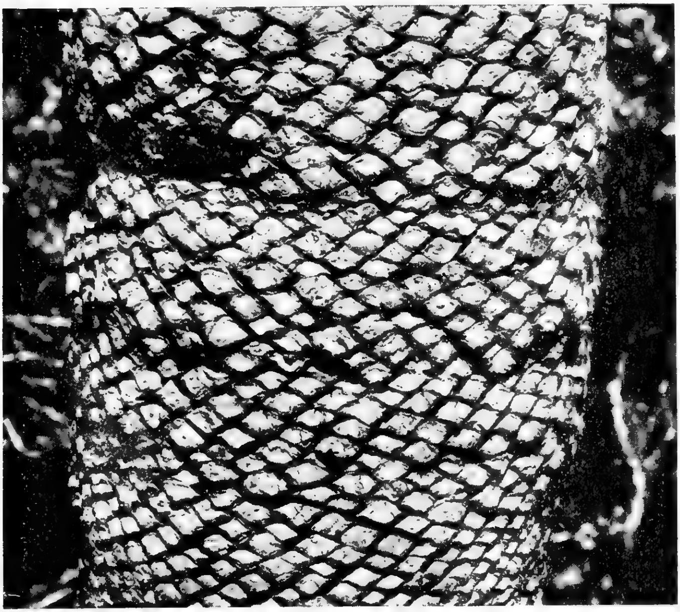


FIG. 22.—Portion of the trunk of *Dioon edule*, showing the armor of persistent leaf bases; also showing three zones marking prolonged resting periods.

which it has produced. To determine the age it is necessary to count the number of leaf bases and to know the average number of leaves produced in a year. This yearly average can be determined only by observations extending over a considerable period of time. A simple case may be used for illustration. The Mexican *Dioon edule* forms a new crown every other year, and there are about twenty leaves in a crown, so that the average is ten leaves a year. If there are ten thousand leaf bases the plant is about one thousand years old. A glance at Fig. 22 will show that the counting of leaf bases can be done with considerable accuracy.

This method of estimating the age is very conservative, for seedlings have only one or two leaves the first year, and at ten years they are not likely to produce more than four or five leaves at a time, and crowns are not likely to contain as many as twenty leaves until the plant is at least fifty years old. Besides, when a cone is produced there may be no new leaves in that year. And further, after bearing a cone the plant may be exhausted and may go into a prolonged resting period of three or four years, during which neither cones nor leaves are produced. It is evident that estimates made in this way will be lower than the actual age of the specimens under consideration.

It would not be safe to apply this method indiscriminately in estimating the age of columnar cycads, for some develop a new crown every year, a few may develop two crowns in a single year, and in some cases the interval between crowns is more than two years. In greenhouses a crown of *Dioon edule* may keep bright and fresh three times as long as in the field, and prolonged resting periods are not so likely to occur.

In Mexico individual plants of *Dioon edule* were observed in 1904, 1906, 1908, and 1910, and it was determined that the duration of the crown is two years. Professor Luis Murrillo, who was the botanist of the

State Normal School at Jalapa when I made my first trip, had made a record extending over eleven years of every leaf produced by a specimen of *Dioon edule* in his garden, and had found that a crown is formed every other year. Estimated by the method just described, this plant, which was less than five feet in height, was 970 years old. Another specimen of the same species, about eight inches in height, was known to have been under cultivation for forty years and was presumably a fine specimen when brought in from the field.

In addition to the leaf bases, which look like leaf scars, many species show a distinct "ribbing" caused by the alternation of small scale leaves and large foliage leaves, the zone representing the foliage leaves having a larger diameter than that of the scale leaves (Figs. 3 and 5). The ribs are conspicuous in the upper part of the trunk, but lower down they become less and less evident, and in very old plants it is practically impossible to identify any trace of the alternation in the lower part of the trunk. The number of ribs shows the number of crowns and thus indicates the age wherever the ribs can be counted and the duration of the crowns is known.

In some forms, like *Dioon edule*, there are zones which are not due to the alternation of scale leaves and foliage leaves but to prolonged resting periods. The trunk shown in Fig. 1 has about a dozen of these zones, some of which can be recognized in the figure. Four such zones are shown in Fig. 22, indicating that there have been four prolonged resting periods during the growth of this portion of the trunk.

Branching in a cycad is rather rare, but it sometimes occurs both in the subterranean and the columnar types.

In *Stangeria* it is easy to find branching specimens, but in the other tuberous genera the phenomenon seldom appears. In the columnar forms branching specimens are recognized at a glance when they are found.

In the tuberous type the branching may be due to injuries caused by contact with sharp stones, since cycad localities are generally rather dry and stony. In the columnar type much and perhaps all of the branching may be due to injuries or to the germination of seeds.

An injury to the stem often results in the formation of a bud, and a strong bud developing successive crowns of leaves becomes a vigorous branch. Such branching is seldom profuse, more than one, two, or three branches being extremely rare. The most extreme cases occur in *Cycas revoluta* in some of the Japanese gardens and temple grounds, where the branching has been induced artificially.

In some cases a severe injury, like the burning of the upper part of the plant in the fires which often occur during the hot, dry season, may completely destroy the crown and bud. After a long resting period a new bud may appear in the cortex and develop a new trunk which is really a branch from the old stem.

In South Africa the top of the bread palm, *Encephalartos*, is sometimes cut off for the sake of the abundant starch. A bud may then appear in the cortex and develop a new stem, as in the case of burned specimens. In the Cathcart region I saw such branches which must have reached an age of five hundred years or more.

Still another method, which is likely to result in the formation of several branches, is due to the germination of seeds in the nest formed by the crown of leaves. As the cone decays the seeds are covered by the decaying portions and germinate. The roots grow into the soft tissue of the main bud and become established. When several small crowns are found at the top of a vigorous trunk they are almost sure to have developed in this way. This behavior was not seen in any plants bearing male cones.

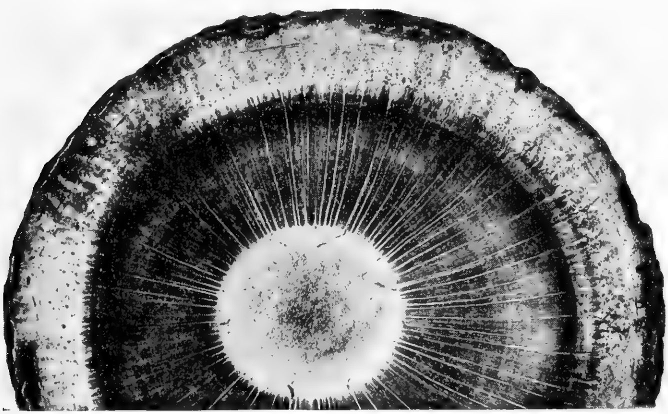


FIG. 23.—*Dioon spinulosum:* transverse section of trunk, showing large pith and cortex. The zone of wood is the broadest ever described for any cycad.

The internal structure of the trunk is as characteristic as the external. A transverse section shows a large pith, a comparatively narrow zone of wood, a broad cortex, and a zone of persistent leaf bases constituting the armor (Fig. 23).

The pith and cortex contain a large amount of starch, and the whole trunk has a large proportion of water, so that a piece immediately sinks when thrown into water;

but after a thorough drying it becomes extremely light, even lighter than the dryest white pine.

Growth rings, which are such a conspicuous feature of woody plants, were supposed to be entirely lacking in the cycads, until they were found in *Dioon*. In *Dioon spinulosum* these rings are formed whenever a new crown of leaves is produced; but in *Dioon edule* a ring marks the alternation of growing periods and prolonged resting periods, the mere alternation of rainy and dry seasons not being sufficient to cause any noticeable inequality of growth. If crowns of leaves are formed every other year, the number of growth rings in *D. spinulosum* would indicate half the age of the plant; in *D. edule* they would give no clue to the age of the specimen, since the number of rings does not correspond to the number of crowns or the number of cones, but to the number of prolonged resting periods, which probably come at irregular intervals. A plant of *D. edule* about one hundred years old showed twenty growth rings.

In most cycads the growth of the woody zone is continuous, but in *Cycas*, *Macrozamia*, and *Encephalartos* the growth of the woody zone ceases, and after a time a new zone appears in the cortex, and this phenomenon may be repeated, so that the result looks like a few enormously large growth rings. These successive zones of wood doubtless mark the alternation of growing periods and periods of prolonged rest.

A puzzling feature of some cycad stems is the "cone dome." Inside the main zone of wood some genera, like *Dioon*, *Ceratozamia*, and *Stangeria*, show a small zone which, lower down, becomes connected with the main zone. This small zone is called the cone dome. In these genera a cone is apparently terminal on the main axis, and the first cone is really terminal; but in the production of a cone the embryonic tissue at the apex of the plant is used up, and the growth of this axis is thus brought to an end. However, a new embryonic region develops at the base of the cone stalk and thus establishes a new axis, which continues to bear crowns of leaves until its life is brought to a close by the production of a cone, and this sequence is continued as long as the individual lives. Consequently the trunk, which appears to be unbranched, is really nothing but a series of branches which can be seen internally, but which do not appear on the surface. Each cone dome, for the time being, is the apex of the plant (Fig. 24).

The trunk of the columnar forms is easily cut with an ax, but it is almost impossible to saw off a large plant. It is like sawing a mass of tough cloth. An examination of the microscopic structure reveals the cause of the difficulty.

A transverse section of the woody zone shows nothing unusual (Fig. 25). There are the ordinary thick-walled cells which one expects to find, and occasionally a few thin-walled cells. The figure shows one of the growth rings, the larger cells alternating with slightly smaller ones.

Longitudinal sections, cut along a line from the pith to the cortex, are more characteristic. The elongated wood cells show very numerous pits of the bordered type (Fig. 26), and near the pith the pits are so elongated that they are long narrow slits producing a ladder-like effect, so that the cells are called scalariform tracheids.

The most characteristic view is seen in longitudinal sections cut at a right angle to a line from the pith to the cortex (Fig. 27). Such sections show a lattice effect caused by the association of very long wood cells and the shorter cells of the "rays" which extend from the

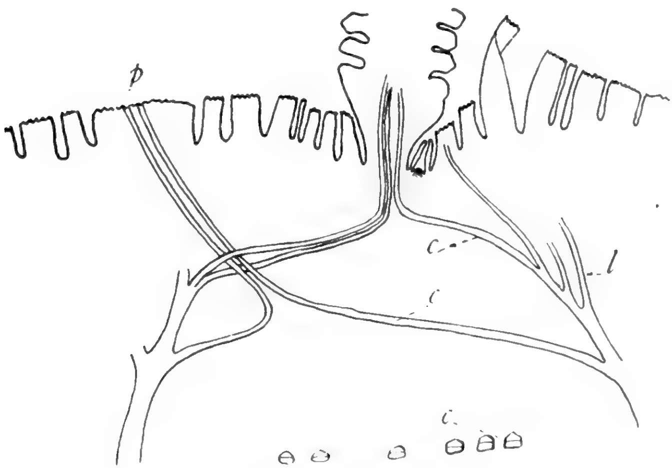


FIG. 24.—*Zamia floridana:* longitudinal section of the apex of a large plant, showing three cone domes (*c*), the lower with bundles in transverse section, the middle with bundles running to the peduncle (*p*) of a mature cone, and the upper with bundles running to a young cone; the new growing-point is at the right of the young cone; several leaf traces (*l*) are shown. About $2\frac{1}{2}$ times natural size.

pith to the cortex. These rays are full of starch and crystals of calcium oxalate and are alive, while the long, empty wood cells are dead. It is this arrangement of long woody cells and shorter starchy cells which makes the stem hard to cut with a saw. However, when the stem becomes thoroughly dry and seasoned, it can be cut and polished.

THE LEAF

The beautiful crown of leaves is the feature which gives the cycads their popularity as decorative plants. Even the seedlings would be popular if they were better known, for a seedling of *Dioon spinulosum* three or four years old has four or five graceful leaves, and the plant is easy to keep, even in a steam-heated house.

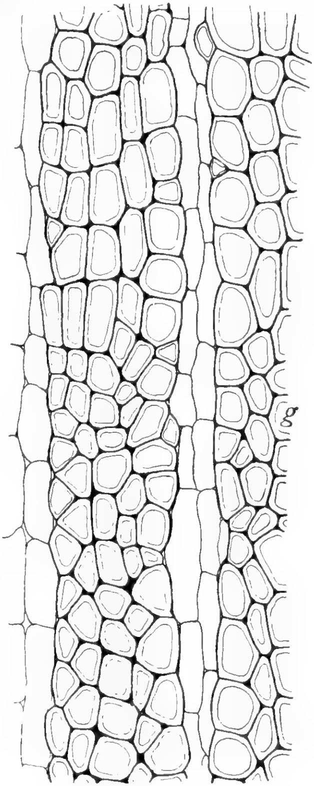


FIG. 25.—*Dioon spinulosum:* transverse section of mature wood, showing a growth ring (*g*).

The young leaves are very delicate and susceptible to injury during the rapid growth, but after they have attained their full size the tissues harden, and they become extremely strong and resistent to extremes of dryness and moisture. The mature leaves of older plants become very tough and leathery, and their structure is such that very little moisture is lost from the inner tissues, so that leaves of some species keep bright and green for a couple of weeks after they have been removed from the plant. Leaves of *Bowenia spectabilis* lying on the veranda of a hotel in the blazing, tropical sun of Northern Australia still looked fresh after three days.

Crowns, as we have already noted in considering the age of plants, are produced at rather regular intervals in the field, but in the greenhouse the leaves last much

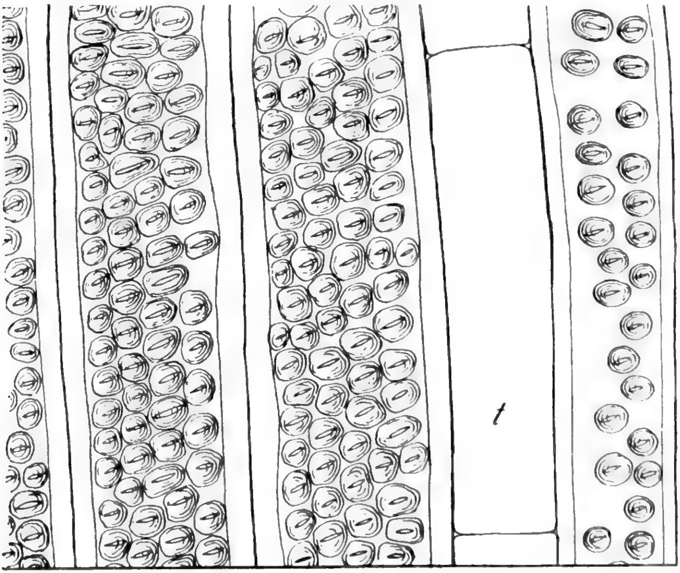


FIG. 26.—*Dioon spinulosum:* radial longitudinal section of mature wood, showing the numerous pits; a thin-walled cell (*t*) in the wood is also shown.

longer. *Dioon spinulosum,* in the field, may produce a crown every year, and *Dioon edule* every other year; but in the greenhouse the interval may be four or five years.

In the field *Dioon edule* generally has one bright, fresh crown and a gray-green crown, the lighter color being due, in some degree, to tiny lichens which do not attack the leaves until they are about a year old. When the leaves first break through the bud scales they are

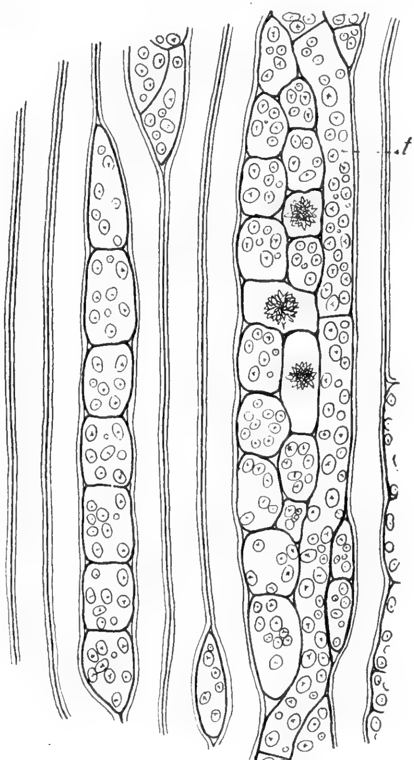


FIG. 27.—*Dioon spinulosum:* tangential longitudinal section of mature wood, showing elongated woody fibers (tracheids) and four rays.

perfectly erect (Fig. 28), but soon spread out into an oblique position, which they maintain for a year or more; afterward they begin to droop but may retain their leaflets for some time. The leaflets then fall off, and the naked leaf stalks become more and more reflexed, and finally they decay, and their bases form the characteristic armor. Most of these features may be seen in Fig. 1, which shows a crown of vigorous leaves rising

FIG. 28.—*Dioon edule:* seedling about twelve years old, grown in greenhouse: the straight, erect young leaves of a new crown are shown in the center; next are the leaves of the preceding crown, rising obliquely; below these are three leaves of a still earlier crown, now beginning to droop.

obliquely, a crown of two years before, with leaves beginning to droop, and some leaf stalks of a still earlier crown, from which nearly all the leaflets have fallen. In *Encephalartos Friderici Guilielmi* the leaf stalks hang on for several years after the leaflets have fallen (Fig. 18).

In *Cycas* the leaflets have a midrib but no side veins; *Stangeria* has both a midrib and numerous reticulated side veins, while in all the rest there is no midrib, but a series of veins parallel with the long axis of the leaf. Taxonomists, having in mind the type of venation seen in grass and lilies, describe these veins as "parallel"; in

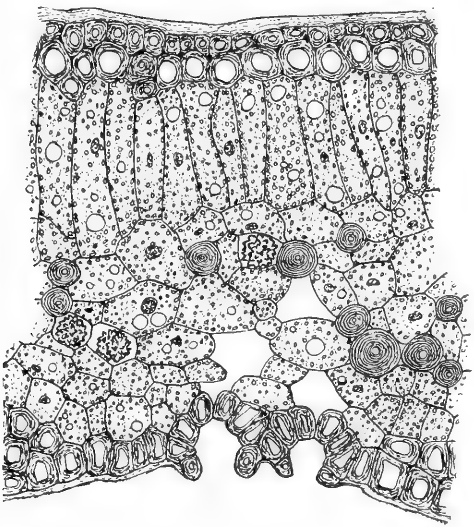


FIG. 29.—*Dioon edule:* portion of a transverse section of a leaflet

reality they show the forked or "dichotomous" method of branching which they have retained from their fern ancestors of the Paleozoic age.

The section of the leaf shows a structure which affords effective protection against the hot, dry weather of most cycad localities (Fig. 29). The highly cutinized surface is almost impervious to water, and the stomata, or pores, on the under side of the leaf have a form well adapted to keeping the opening closed except when the air is full of moisture. Long, narrow cells with thick,

FIG. 30.—*Dioon spinulosum* at Tierra Blanca, Mexico; plants growing on rocks with little soil, showing exposed roots; at the right the base of a trunk with an exposed root (+) nearly as large as the trunk itself.

corky walls are abundant, and they give the leaf a maximum of rigidity combined with elasticity.

THE ROOT

No extensive study of the cycad root has been undertaken. There is a main tap root which tapers gradually and extends down to a great depth, so that small amounts of water are brought up even when the surface soil is very dry. Lateral branches are usually small and weak. When plants are growing on exposed rocks where there is little soil, the root development is remarkable (Fig. 30). In the specimen shown in the figure the upper part of the roots is entirely exposed. Sometimes such roots may extend along the exposed rock for many feet before entering the soil. In an extreme case a root was exposed for forty feet before it finally entered the soil.

A peculiar feature of the root has attracted much more attention and investigation than the normal structure itself. The small, lateral roots often become infected by "bacterioids" which cause a swelling accompanied by a profuse dichotomous branching, and besides the roots begin to grow up instead of down, soon emerging above the surface of the soil in dense coralloid masses (Fig. 31). After the infection by bacterioids, a blue-green alga (*Anabaena*) enters and causes still more distortion. The zone occupied by the bacterioids and alga lies in the cortex between the vascular cylinder and the epidermis, where it is easily visible to the naked eye, appearing in a transverse section as a bluish-green ring. The function of these novel roots is problematical. Some have suggested that they may be aërating organs. They are found in all the genera and are much more abundant in the greenhouse than in the field, and more abundant in young plants than in adult specimens.

Fig. 31. *Cycas revoluta:* coralloid masses of root tubercles on the erect roots.

CHAPTER V

THE REPRODUCTIVE STRUCTURES: THE FEMALE CONE AND THE FEMALE GAMETOPHYTE

Cycad plants are strictly male and female, cones of both sexes never being borne upon the same individual (Fig. 32). Even in branching specimens cones on all the branches are of the same sex; and plants developed from buds are of the same sex as the main axis.

The conspicuous reproductive structures are the cones. The female cone produces spores, called megaspores; and the male cone produces smaller spores, called microspores. The megaspore upon germination produces a "female gametophyte," which finally gives rise to eggs; and the microspore produces a "male gametophyte," which gives rise to sperms.

THE FEMALE CONE

The female cone of the cycads, called the seed-bearing cone, the ovulate cone, or the ovulate strobilus, is borne at the apex of the stem, or is lateral just below the apex. Usually the cones are borne singly, but occasionally two or three are found, especially in *Macrozamia* and *Encephalartos*.

Some of the female cones are the largest known in either living or extinct plants. The cones of *Encephalartos caffer* and *E. Altensteinii* frequently attain a weight of more than forty pounds when two or three are borne at the same time. In the botanical garden at Grahamstown, South Africa, a specimen of the latter species bore three cones in 1912. One of the cones had shed about half of its seeds, but the other two were just ready to open. They weighed forty-six and forty-eight pounds, and presumably the third cone was at least as heavy, since such cones are not quite simultaneous, and

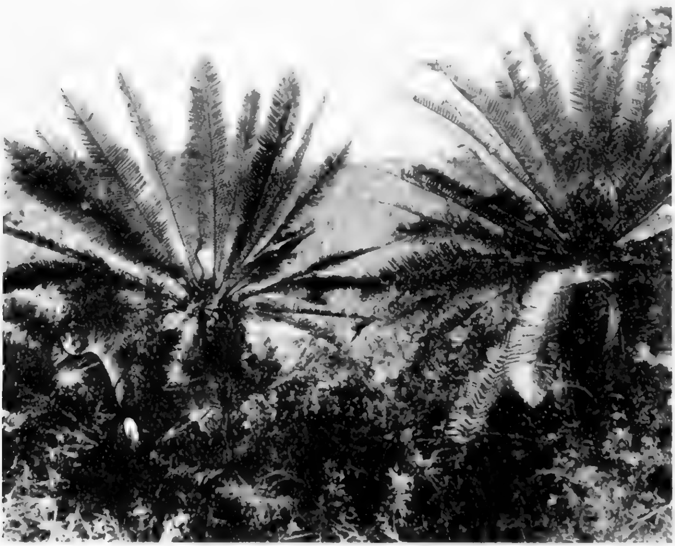


FIG. 32.—*Dioon edule:* two male plants with cones at the left; a female plant with a large cone at the right, Chavarrillo, Mexico.

the first to appear is likely to be the largest and most vigorous, so that the combined weight must have been more than one hundred and forty pounds. When there is only one cone it may be much larger. Mr. J. T. Butters, director of St. George's Park at Port Elizabeth, told me that in such cases the cone may reach a weight of eighty pounds, and in one case a cone weighed more than ninety pounds. These cones are somewhat egg-shaped.

In *Macrozamia Denisoni* the cones are about two feet long and have a diameter of nearly a foot at the base, tapering to six inches at the top. They weigh from fifty to seventy pounds, and contain two hundred to three hundred seeds so large that they are cut through the middle, provided with hinges and a clasp, and used as match boxes.

In other cycads the cones are smaller, that of *Dioon spinulosum* weighing twenty to thirty pounds; *Microcycas*, according to Caldwell, up to twenty pounds; *Dioon edule*, ten to fourteen pounds; while others range down to less than an ounce in *Zamia pygmaea*.

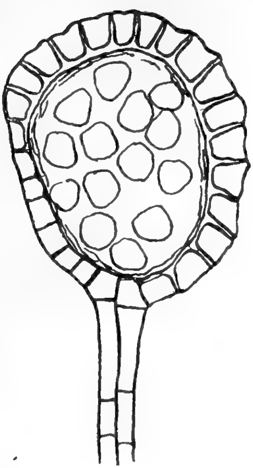
The female cone is composed of a large number of modified leaves called sporophylls, which are arranged spirally upon an axis. In *Cycas* these sporophylls are quite leaflike and are loosely arranged, so that they behave like a crown of leaves, and the axis which produced them continues its growth, producing crowns of foliage leaves and occasionally a crown of sporophylls. Many do not like to call this crown of sporophylls a cone. It is true that *Cycas* is the only cycad in which the axis is continued through the crown of sporophylls, but the same phenomenon is frequently found in highly developed cones of lycopods and conifers. However, the transition from the *Cycas* type to a highly developed cone in which the sporophylls bear little resemblance to foliage leaves is not abrupt, for there is an instructive series in the evolution of the compact cone from a crown of loosely arranged sporophylls. Various stages in this evolution are described and illustrated in chapter ix.

In the Paleozoic ancestors of the cycads the ovules were borne on leaves with little or no modification from the vegetative type, and from this condition there has been a gradual reduction from sporophylls closely resembling foliage leaves to those so profoundly modified that such resemblance is nearly obliterated. If the living cycads could be arranged in a genetic line, on the basis of this single character, the line would begin with *Cycas* and end with *Zamia*.

The sporophyll in *Cycas* bears several ovules, but in all the other genera there are regularly just two ovules, one on each side of the stalk.

It is impossible to understand the ovule, which in its later development is called the seed, without noting a couple of stages in its fern ancestry, for the ovule is the lineal descendant of the sporangium, or "spore case," of the ferns. The sporangia of a common fern, like the "Boston fern," contain many spores, all of which look alike and at maturity fall upon moist soil, where they give rise to green "prothallia," which finally give rise to structures bearing eggs and sperms (Figs. 33–36).

In *Selaginella*, one of the fern allies which can be seen in any greenhouse, the development starts just as in the common fern, but only four of the prospective spores develop, the others becoming abortive and serving as nutritive material for the four, which become so large that they are called "megaspores." When they germinate, the prothallium does not come out and become green but remains within the megaspore, and the megaspore itself may remain within the sporangium until the eggs are produced, or even longer (Figs. 37 and 38). In the common fern the prothallium usually produces



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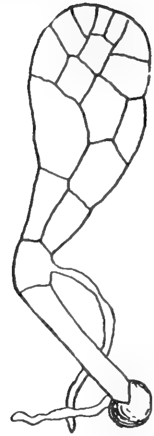

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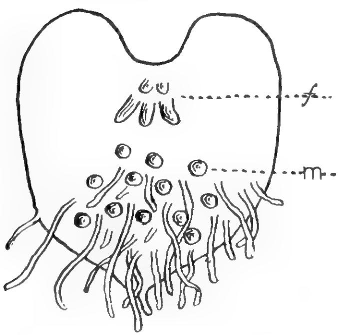

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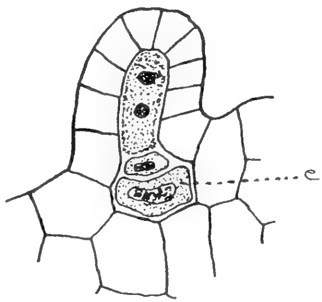

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Figs. 33–36.—Some features of the life-history of a fern: Fig. 33, a sporangium containing spores; Fig. 34, young prothallium (gametophyte) arising from the germination of the spore (shaded), which is still visible at the bottom; Fig. 35, mature prothallium, showing the female organs (archegonia) at the top (*f*) and male organs (antheridia) at the bottom (*m*); Fig. 36, a section of a single archegonium, showing the egg (*e*) immediately above it, the ventral-canal cell, and above this the neck-canal cell with two nuclei. Highly magnified.

both eggs and sperms; in *Selaginella*, the sporangium shown in the figure is a "megasporangium," producing only megaspores which give rise to prothallia bearing eggs but no sperms. There is a corresponding "microsporangium," with "microspores" which give rise to prothallia bearing the sperms. Both kinds of spores are borne upon the same plant but not in the same sporangium.

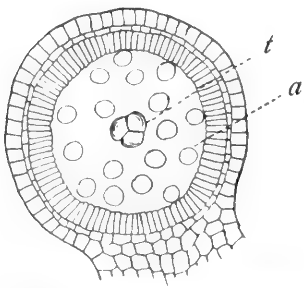


FIG. 37. *Selaginella:* a megasporangium, showing one megaspore mother-cell which has divided, forming a tetrad (*t*) of four spores, three of which are shown The rest of the spore mother-cells (*a*) are abortive. Highly magnified.

THE FEMALE GAMETOPHYTE

The ovule of a cycad is strictly comparable with the megasporangium of *Selaginella*. At an early stage of development it contains four megaspores, three of which begin to abort as soon as they are formed, while the other germinates, as in *Selaginella*, without escaping from the megasporangium. To the uninitiated this plant—variously called the "endosperm" or prothallium, or female gametophyte—looks like a part of the tissue of the ovule itself (Figs. 39 and 40).

Ovules vary in size from that of *Cycas circinalis*, which sometimes reaches a length of more than two inches, down to that of *Zamia pygmaea*, less than an eighth of an inch in length.

The structure varies in details, but the principal features are rather uniform: there is one integument closely applied to the "nucellus"; the integument, with parts of the ovule below it, becomes differentiated into three characteristic layers, the outer and inner fleshy, with a stony layer between; the outer fleshy layer finally decays and disappears, while the inner gives up

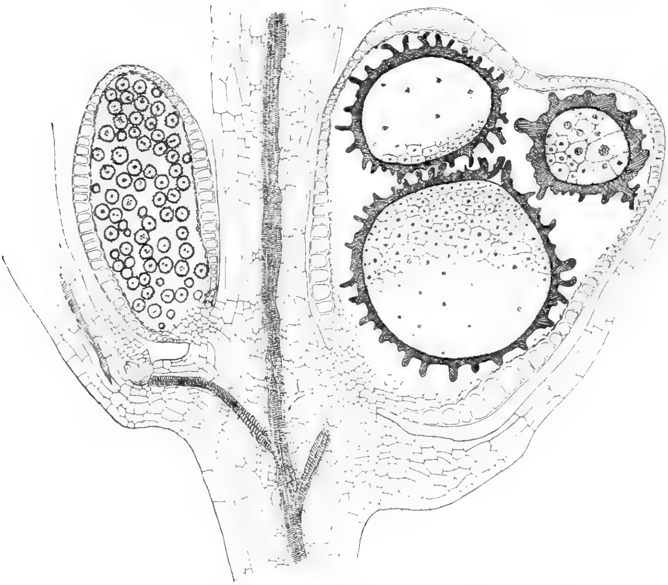
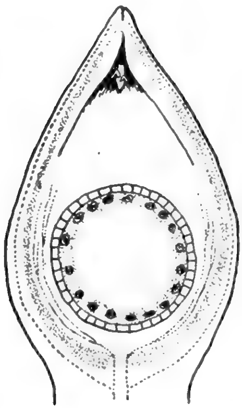


FIG. 38.—*Selaginella:* longitudinal section of a portion of the cone, showing a microsporangium with microspores at the left and a megasporangium with three of its four megaspores at the right; the female gametophyte is shown within the spore. Greatly magnified.

its nutritive substances to the prothallium—or female gametophyte—growing within, until the fleshy layer becomes reduced to a thin, dry membrane; the stony layer becomes as hard as a hickory nut.

The ovule is supplied with an extensive vascular system. Two vascular strands from the sporophyll enter the base of the ovule, and each strand forks, one part going to the inner fleshy layer where it branches repeatedly, and the other going to the outer fleshy layer, the outer series branching only a few times and



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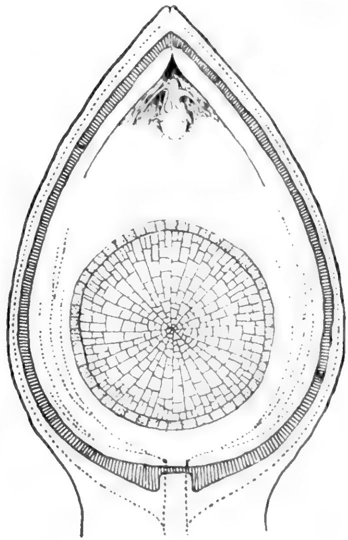

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FIGS. 39-40.—*Dioon edule:* two stages in the development of the ovule and female gametophyte: Fig. 39, soon after pollination, the female gametophyte consisting of a layer of protoplasm with numerous free nuclei; Fig. 40, later, the female gametophyte, having become cellular throughout. Magnified.

only at the base of the ovule, so that there are about a dozen straight, unbranched vascular strands extending from the base of the ovule to its apex. Most of these features, at a stage before the inner fleshy layer has become thin and dry, are shown in Fig. 40.

The plant developed from the spore of an ordinary fern is almost always called the prothallium, but the plant developed from the germinating megaspore of *Selaginella* is just as regularly called the *female gametophyte*, although it is strictly comparable with the prothallium of the fern. In the cycads the plant developed from the megaspore is usually called the *endosperm.* It is unfortunate that there should be so many names for the same thing; one name would be sufficient for all three cases. Since the plant developed from the spore bears the gametes—as the eggs and sperms are called—we prefer the term gametophyte, and we shall call the plant developed from the megaspore the female gametophyte, and that developed from the microspore the male gametophyte.

The development of the female gametophyte is more easily illustrated than described. At the very beginning a point which many fail to realize is that the megaspore is really a spore like that of the fern or *Selaginella*, and that instead of falling out from the sporangium (or ovule) it remains within, germinates there, and never escapes. It is this retention of the megaspore and the female gametophyte developed from it that distinguishes the seed plants from the ferns and their allies. However, *Selaginella* shares this seed-plant character to such an extent that no definition has yet been devised which will include all seed plants and exclude some species of *Selaginella.*

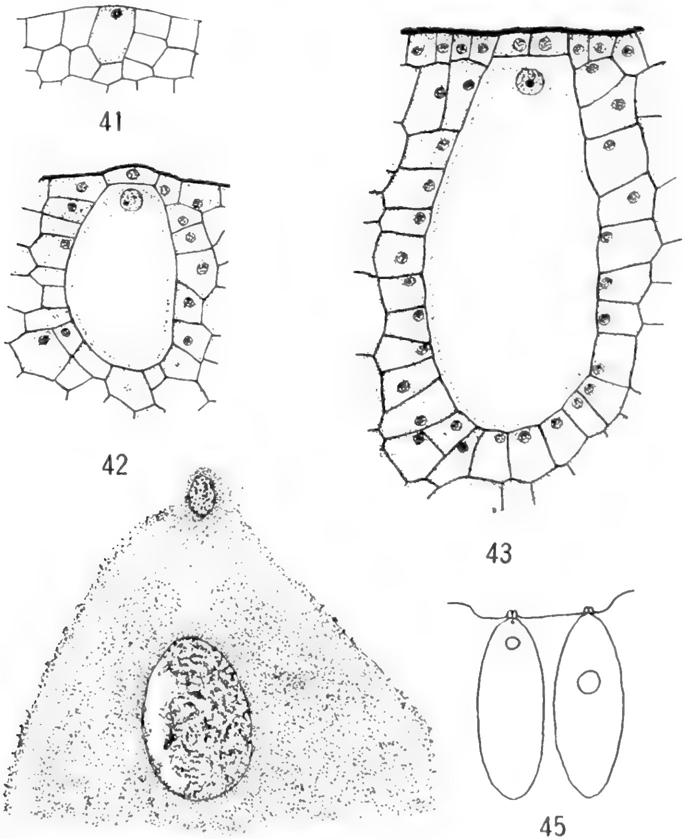
When the megaspore begins to germinate it does not form a cellular tissue, but its nucleus divides without the formation of a wall, the two resulting nuclei divide, the four thus formed divide, and the process continues until there are a large number of nuclei—in *Dioon* as many as a thousand—not separated from each other by cell walls but lying in a common mass of protoplasm (Fig. 39). The growth of the megaspore is so rapid during this stage that the mass of protoplasm does not keep pace with the increasing size, and consequently a large, central vacuole appears, so that the protoplasm, with its numerous nuclei, forms a thin layer pressed against the wall of the megaspore, as shown in Fig. 39.

Cell walls then appear at the periphery, the increase in the mass of protoplasm keeping pace with the increase in size and then even exceeding it, so that the protoplasm encroaches upon the central vacuole, which becomes smaller and smaller, until it finally disappears. Meanwhile the formation of cell walls proceeds from the periphery toward the center, until the entire female gametophyte consists of cells, each cell with its own nucleus (Fig. 40).

In *Dioon edule* the female gametophyte is about an eighth of an inch in diameter when it reaches the stage at which it has become cellular throughout; but the cells continue to divide, enlarge, and divide again, until the length is an inch or even more. In *Dioon spinulosum*, *Cycas circinalis*, and some species of *Macrozamia* the length may be twice as great. During this growth various foodstuffs, but principally starch, are stored in the cells, the materials for growth being brought in largely by the vascular system. Immediately surrounding the gametophyte is a jacket, one or two cells in thickness, and in this the nutritive substances undergo more or less modification before they pass into the gametophyte. The jacket is very prominent during the earlier stages but is itself soon absorbed by the encroaching gametophyte, which then draws upon the inner fleshy layer until all its nutritive substances have been appropriated, and only a dry membrane composed of the vascular strands and some dead cell walls remains.

At an early stage in the development of the female gametophyte in *Dioon edule*, when it is about an eighth of an inch in diameter, a few of the outer cells in the upper portion become noticeably larger than the rest. These cells are called "archegonium initials," because they develop into the archegonia which produce the eggs (Fig. 41).

Soon after the archegonium initial appears it divides, forming two very unequal cells, the upper being much smaller. This upper cell then divides, and the two resulting cells are called neck cells (Figs. 42 and 43). The lower cell, which is called the "central cell," does not divide but increases greatly in size, sometimes reaching a length of an eighth of an inch. During this growth, which extends over a period of several months, the protoplasmic content of the central cell increases, and in the later stages of its growth various food materials accumulate. These come from the neighboring cells of the female gametophyte and are passed into the central cell by a layer of modified cells called the "jacket," which surrounds the central cell just as a jacket, previously referred to, surrounded the entire gametophyte. After the central cell has reached its full size and has become filled with nutritive materials, its nucleus divides, but no wall is formed between the two resulting nuclei. The upper nucleus, called the ventral-canal nucleus, immediately disorganizes, but the lower increases immensely



Figs. 41–45.—*Dioon edule:* development of the archegonium: Fig. 41, the archegonium initial; Fig. 42, the archegonium initial divided, forming a primary neck cell and a central cell; Fig. 43, the primary neck cell divided, giving rise to the two neck cells; Fig. 44, the central cell divided, giving rise to the ventral-canal nucleus (the smaller nucleus at the top) and the egg, with the larger nucleus; Fig. 45, the archegonia at a later stage, showing the depression (archegonial chamber) above the archegonia. Figs. 41–44 highly magnified; Fig. 45 much less magnified.

in size and finally becomes the largest nucleus ever observed in plants, having—in extreme cases—a diameter of one-fiftieth of an inch. This is the nucleus of the egg. Practically, the central cell is an egg, but we do not use the term egg until the division has occurred which results in the formation of the egg nucleus and the ventral-canal nucleus (Fig. 44). Immediately after the division the egg nucleus moves down into the central part of the egg, while the ventral-canal nucleus disorganizes and disappears (Fig. 45).

The egg is now ready for fertilization. Although numerous archegonium initials may be formed, only a few finally produce eggs, the number of eggs usually ranging from four to ten. *Microcycas*, which was investigated by Caldwell, is very exceptional in this respect, having scores and sometimes hundreds of eggs.

CHAPTER VI

THE REPRODUCTIVE STRUCTURES: THE MALE CONE AND MALE GAMETOPHYTE

The male reproductive structures are the male cones with their microsporangia and male gametophytes. The microsporangia produce microspores, which, upon germination, give rise to male gametophytes, and these produce the sperms.

THE MALE CONE

The male cones, also called staminate cones or staminate strobili, are much smaller than the female and are usually comparatively slender, but the number of sporophylls is larger (Fig. 46). In a few cases, like *Encephalartos villosus*, the two cones are not very different in size or external appearance. In some species the female cones reach a weight of ninety pounds, while weights of seventy, fifty, and thirty pounds are not rare, but any male cone weighing ten pounds must be regarded as very large.

Just before the microspores (pollen grains) are to be shed, the axis of the cone elongates considerably, thus separating the sporophylls and facilitating the dispersal of spores. In this elongated condition the cone of *Cycas circinalis* may reach a length of more than two feet; while at the other extreme the cones of some species of *Zamia* may not measure more than one or two inches at this stage.

The male cone consists of an axis bearing numerous modified leaves, called microsporophylls, which show little or no trace of the pinnate character of the leaves from which they have been derived. On the under surface the microsporophylls bear numerous microsporangia arranged in groups called sori (Figs. 47–49).

The grouping of sporangia into sori is characteristic of ferns, but the number in a sorus is very much larger than in cycads. In the more primitive cycads, like *Cycas* and *Dioon*, the predominant numbers in a sorus are the five's, four's, and three's, while at the other end of the series scarcely any five's are found and four's are scarce, the usual numbers being the three's and two's. Occasionally the sorus consists of a single microsporangium. The cycads show a steady tendency to reduce the number of microsporangia in a sorus.

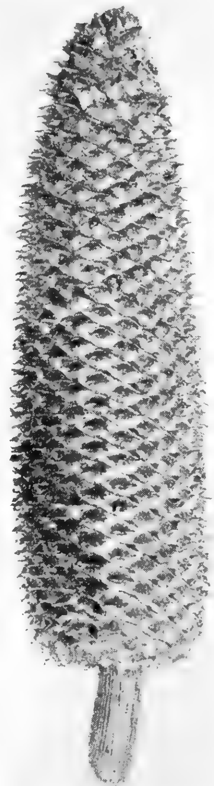
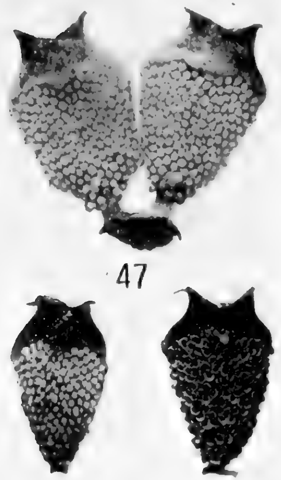


FIG. 46.—*Ceratozamia mexicana:* male cone; the entire cone, with stalk, is 9 inches in length.

There is also a persistent tendency to reduce the total number of microsporangia on a sporophyll. A large number of sporophylls of *Cycas circinalis* and *Dioon spinulosum*, representing the more primitive cycads, showed an average of more than 700 microsporangia to the sporophyll, *Encephalartos caffer* has about 500, *Dioon edule* about 300, *Ceratozamia* about 200, *Stangeria* 150, *Bowenia* 50, and *Zamia* 25.



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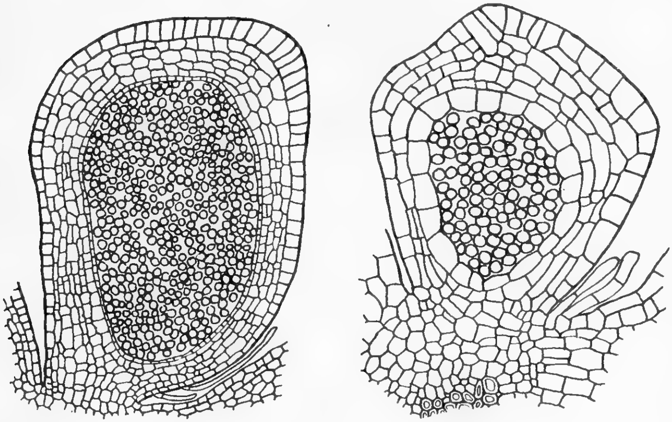
FIGS. 47–49.—*Ceratozamia mexicana:* male sporophylls with microsporangia: Fig. 47, the sporangia not yet opened; Fig. 48, the sporangia on the upper half of the sporophyll opened, but the pollen not yet shed; Fig. 49, the sporangia, having shed their pollen. The arrangement of sporangia in three's and four's is easily seen. The two "horns" at the top of the sporophyll give the name to the genus; about 1½ times natural size.

The structure of the microsporangium is interesting. In the case of the megasporangium, or ovule, the structure has been so profoundly modified that its relation to the sporangium of its remote fern ancestors is established only by the details of development and by the evidence of comparative morphology; but the microsporangium bears such a close resemblance to its fern prototype that the novice may have great difficulty in distinguishing them. The similarity will be appreciated by comparing the sporangia of *Dioon* and *Angiopteris*, a primitive fern (Figs. 50 and 51). In both there is an outer layer of thick-walled cells, then several layers of thin-walled cells, and beyond these a layer of modified cells called the "tapetum." The interior is occupied by the spores.

Throughout the plant kingdom the male structures are far more conservative than the female, so that the microsporangium of the cycads is only an illustration of a general phenomenon. The megaspore never escapes



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FIGS. 50–51.—A comparison of the sporangia of a cycad and a fern resembling the ferns of the carboniferous: Fig. 50, longitudinal section of microsporangium of *Dioon edule*, with numerous spores; Fig. 51, similar section of a sporangium of *Angiopteris*.

from the megasporangium, but the microspore is shed, as in its remote fern ancestors. Other features which the male structures of cycads have persistently retained have been mentioned in the preceding paragraphs.

THE MALE GAMETOPHYTE

The microspore is the first cell of the male gametophyte, but leading up to its formation there is a series of stages strictly comparable with those leading up to the formation of sperms in animals. At a very early stage in the development of the microsporangium one or more cells just beneath the epidermis become somewhat larger than their neighbors and richer in protoplasm. They divide several times, all dividing at once, so that each division doubles the number of cells. After a while these divisions cease, the cells separate from each other and become spherical, at which stage they are called "microspore mother-cells," because each one, by two very peculiar divisions, gives rise to four microspores. It is during these two divisions that the number of chromosomes is reduced, and the plant returns to the original gamete-bearing, or gametophyte, generation. The counterpart is the sporophyte generation, which begins with the fertilized egg and constitutes all we can see of any flowering plant, except by means of the microscope. These two generations alternate, the sporophyte producing the gametophyte, and the gametophyte in turn producing the sporophyte. Such an alternation is a necessary consequence of fertilization in plants and, we believe, in animals also.

The microspore then is the first cell of the male gametophyte. In the megasporangium (ovule) only four spores are produced, and only one of these functions, but in the microsporangium the number of spores is very large, even larger than in any living ferns. In *Dioon edule* the number of spores may reach 30,000, in *Encephalartos villosus* 26,000, in *Ceratozamia mexicana* 8,000, and in *Zamia floridana* 500.

The microspore consists of a single cell with a wall differentiated into two distinct layers, the outer called the *exine* and the inner the *intine*. The exine is hard and dry, but the intine consists largely of cellulose and is capable of extreme growth. There is one nucleus, an abundance of protoplasm, and some starch (Fig. 52).

Germination begins within the spore before it is shed. The first division results in the formation of two very unequal cells, the one nearest the base of the spore being much smaller. This small cell, called the "prothallial cell," is strictly comparable with the prothallium of a fern, and also with the female gametophyte of the cycad,

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FIGS. 52–53.—*Dioon edule:* Fig. 52, microspore, showing inner and outer spore coats, several starch grains, and a large nucleus; Fig. 53, later stage, showing prothallial cell at the bottom, immediately above it the somewhat larger "generative cell," and at the top the large tube nucleus. Very highly magnified.

which consists of millions of cells. The prothallial cell increases in size but does not divide. The larger cell divides unequally, forming a small cell called the generative cell, and a larger cell called the tube cell (Fig. 53). At this stage the male gametophyte is ready to be shed from the sporangium. At the shedding stage the male gametophyte, not only in cycads but in all flowering plants, is called the pollen grain.

As soon as this three-celled stage is reached the axis of the cone elongates, so that the microsporophylls become widely separated, the pollen grains fall out from the sporangia and are blown about by the wind, and those happening to reach female cones sift in among the cone scales, which are rather loose for a few days, while the male cones are shedding their pollen.

At just this period, while the pollen is sifting in, some cells at the tip of the ovule are breaking down and secreting a clear, mucilaginous substance which oozes out as a sparkling droplet. As the droplet dries, whatever pollen has fallen upon it is drawn down into the chamber, called the pollen chamber, formed by the disintegration of the cells which produced the mucilaginous droplet. Within the pollen chamber the development of the male gametophyte continues for several months before it finally results in the formation of sperms. The details of spermatogenesis and sperms, which are more complex in cycads than in any other group of plants or in animals, will now be considered.

As soon as the pollen grain arrives in the pollen chamber the interrupted germination is resumed. The exine at the apex of the pollen grain is ruptured, and the intine protrudes, forming a long tube called the pollen tube, which penetrates deeply into the tissues surrounding the pollen chamber, while the chamber itself continues to enlarge by disintegration of adjacent tissues (Fig. 54). Almost immediately after the pollen grain reaches the pollen chamber the generative cell divides, giving rise to a "stalk cell" in contact with the prothallial cell, and a "body cell" which will finally produce two sperms; but several months elapse between the formation of the body cell and the division by which it produces the sperms.

During this long period the pollen tube behaves like a parasitic fungus, drawing food materials from the nucellus, as the region containing the pollen chamber is called. As the tissues are used up the pollen chamber becomes larger and larger until it finally extends entirely through the nucellus, so that nothing remains between the female gametophyte and the pollen tubes. The

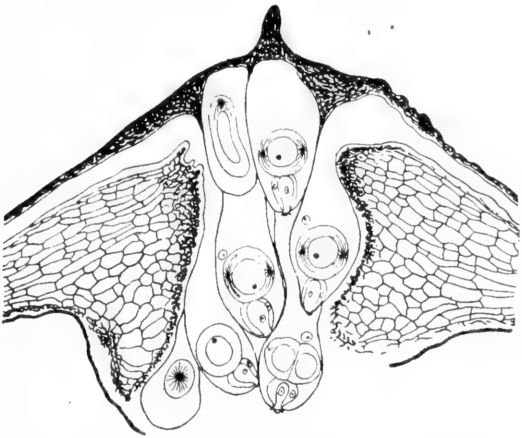
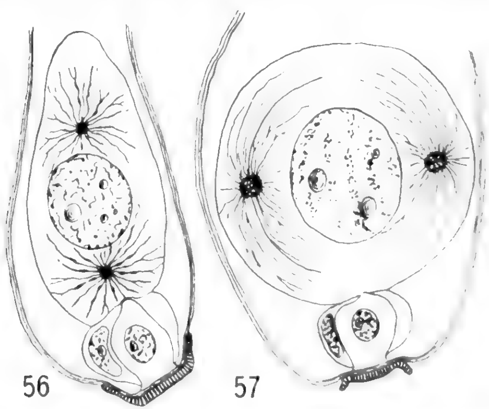


FIG. 54.—*Stangeria paradoxa:* nucellus of ovule with pollen tubes with the body cell, except the lower tube, in which the body cell has divided, forming the two young sperms. Highly magnified.

appearance of the nucellus, the pollen chamber, and the pollen tubes just before the sperms escape is shown in Fig. 55.

Meantime the body cell undergoes a remarkable development; it increases in size, and two small, spherical bodies, called "blepharoplasts" because they produce cilia, make their appearance. Long, slender, threadlike strands radiate in every direction from the blepharoplasts, which, at first scarcely visible with the best

FIG. 55.—*Stangeria paradoxa:* nucellus of ovule with pollen tubes, in three of which the two sperms are shown. Highly magnified.



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FIGS. 56–57. *Dioon edule:* two stages in the development of the pollen tube and body cell: Fig. 56, December condition, body cell elongated and the blepharoplasts arranged in the long axis of the tube; Fig. 57, several months later, the blepharoplasts having rotated until they are transverse to the long axis of the tube. In both figures the outer spore coat of the pollen grain is easily seen; the inner spore coat has developed into the pollen tube. Highly magnified.

microscopes, keep pace with the growth of the body cell and finally reach a diameter of one one-thousandth of an inch, so that they can be seen with an ordinary pocket lens. In the earlier stages the body cell is elongated in the direction of the long axis of the pollen tube; later the free end of the pollen tube hanging in the pollen chamber becomes swollen, and the body cell gradually assumes a nearly spherical shape (Figs. 56 and 57). While the change in the shape of the body cell is taking place, the blepharoplasts rotate 90°, so that their position becomes transverse to the long axis of the pollen tube.

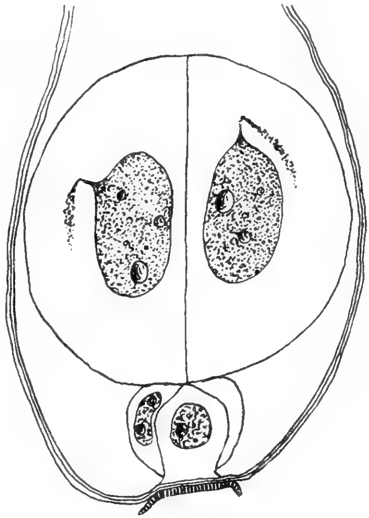


FIG. 58.—*Dioon edule:* end of pollen tube, showing the two young sperms resulting from the division of the body cell. A beak of the nucleus has become attached to the mass of granules derived from the blepharoplast. This is the beginning of the spiral band. Highly magnified.

The growth of the pollen tube and of the structures within it is slow and steady up to this point, but the final stages, the division of the body cell and the formation of two extremely complicated sperms, take place with astonishing rapidity. The two cells resulting from the division of the body cell are shown in Fig. 58. Within each of these cells a sperm is formed.

The blepharoplast, shortly before the division of the body cell, has reached its maximum size. During its growth it becomes increasingly vacuolate, until it is a mere shell with such large vacuoles that the interior looks

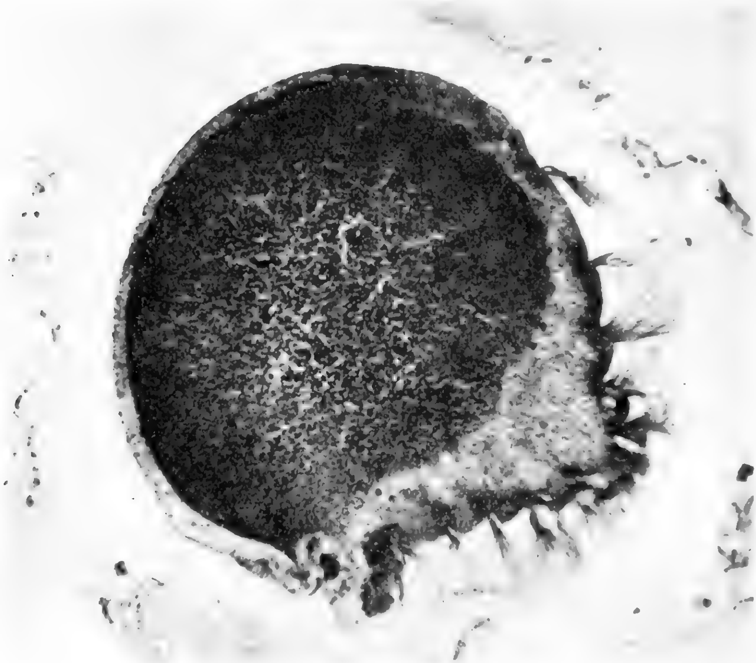


Fig. 59.—*Ceratozamia mexicana:* photomicrograph of a section of a sperm, showing the very large nucleus, with a thin sheath of protoplasm and numerous cilia. Highly magnified.

frothy. Even before the division is completed the blepharoplast begins to break up into innumerable small granules which become more or less flattened and adhere to each other and then are drawn out into a long, spiral band. This band, lying in the protoplasm between the nucleus and the periphery of the sperm, develops thousands of long, slender cilia which pierce through the protoplasm and extend some distance beyond it (Fig. 59). The cilia are the motile organs of the sperm, and they enable it to swim with considerable vigor.

A constant and striking feature in the pollen-tube structures of all of the cycads is the behavior of the prothallial cell. From an early stage it continues to press up into the stalk cell, until it finally looks as if it were entirely surrounded. The function of these two cells is not very well understood, but, like the rest of the tube, they are abundantly supplied with starch, and much of this is used up by the body cell and the sperms derived from it.

CHAPTER VII

FERTILIZATION

It is easy to write a chapter heading "Fertilization," but it is not so easy to determine just what should be included in that chapter. Some writers would define fertilization as the union of definitely organized male and female elements; but in many of the lower plants, where the essential features are the same as in the flowering plants, the two gametes, as the two uniting elements are called, are certainly not definitely organized as male and female elements. Even where the gametes are different in appearance, so that it is perfectly correct to call them sperms and eggs, some investigators believe that half of the sperms are really female and half of the eggs male. And even if these uncertainties with regard to the gametes were cleared up, there still remains a difference of opinion as to what constitutes union. Some begin to speak of fertilization as soon as the sperm touches the surface of the egg; some regard the entrance of the sperm into the egg as the beginning of fertilization; many think that the fusion of the two gamete nuclei is the essence of the process; but in some gymnosperms, including the cycads, the nuclei of the two gametes do not form a resting nucleus when they come together. In short, we may define fertilization as the union of gametes, but any attempt to make a more restricted definition, at the present stage of our knowledge, is likely to satisfy only the definer and his friends.

All agree that the two most important features of fertilization are a stimulus to development and a transmission of hereditary characters. We shall take more latitude than any definition is likely to allow, and shall begin by describing associated structures and the behavior of the sperm and egg before they come into contact. Since we have made our most detailed observations upon *Dioon edule* we shall use this species as a type. The principal features are about the same in other forms which we have studied.

The relations of the various structures at the time of fertilization are shown in Fig. 60. The outer fleshy coat of the ovule is highly differentiated, the stony layer has become so hard that it is difficult to cut it with a pocketknife, and the inner fleshy layer has been reduced to a thin, papery membrane, which in the figure appears as a dark border lining the inner surface of the stony layer. The nucellus, with its conspicuous beak and pollen tubes, has begun to sag. The tissue of the female gametophyte has become quite firm, while the depression above the archegonia, called the archegonial chamber, has reached its maximum depth, and the nucleus of the central cell of the archegonium has divided to form the egg nucleus and the ventral-canal nucleus.

Sperms within the pollen tube measure about 200 μ[1] in diameter and about 275 μ from apex to base. After leaving the tube they increase somewhat in size, reaching a diameter of 230 μ and a length of 300 μ. Consequently they are easily visible to the naked eye, appearing as

[1] The micron, μ, is $\frac{1}{1,000}$ of a millimeter, about $\frac{1}{25,000}$ of an inch. All measurements of microscopic objects are expressed in microns.

FIG. 60.—*Dioon edule:* upper part of ovule at time of fertilization. The pollen tube on the left shows the body cell still undivided; in the one on the right the body cell has just divided; the one in the middle shows two sperms in the swimming condition; two empty pollen tubes, with wavy margins, have shed their sperms; a sperm is about to enter the egg at the right; at the left a sperm has already entered and can be seen in the top of the egg. Magnified about 400 diameters.

tiny, whitish points in the nearly colorless fluid which fills the pollen tube.

The living sperm, as seen under the microscope, has a very large nucleus, surrounded by a thin and almost colorless sheath of protoplasm, which is somewhat thicker at the forward end containing the spiral, ciliated band.

The movements of the sperms are easily observed by mounting the piece of the ovule containing the pollen chamber with the pollen tubes, so that the enlarged ends of the tubes are uppermost. The upturned ends of the pollen tubes are so transparent that they scarcely obscure the view. The cilia begin to move sluggishly while the sperms are still fast together, and this movement is accompanied by pulsating and amoeboid movements which continue for an hour before the sperms separate. After the separation they swim for half an hour or more in the constantly enlarging body cell before they escape into the main portion of the tube. Occasionally the sperms are still attached to each other after they have escaped into the general cavity of the tube, and in such cases their movements are awkward, because they naturally try to move in different directions. When they become free from each other the principal movement is straight ahead, with a rotation on the long axis. The sperms swim up and down the tube, going up as far as the diameter of the tube will permit and then coming back. The amoeboid movements of both the protoplasm and the nucleus are quite noticeable, especially while the sperm is changing its direction. Most of the changes in direction occur when the sperm bumps against the wall of the tube. At the apex, where the protoplasmic sheath is thickest, the amoeboid movement is most conspicuous and may be so rapid that it is more like spasmodic twitching. How long the sperms might swim in the pollen tubes under natural conditions it would be impossible to determine; but under artificial conditions, in a sugar solution, the movements have continued for five hours.

After the sperms begin to move there is a rapid increase in the turgidity of the tube, which sooner or later ruptures at or near the exine of the pollen grain. Most of the starch and liquid contents of the tube escape with a spurt, unless one of the sperms is immediately drawn into the opening. The first sperm may escape in two or three seconds, but the other may be half a minute in getting out, probably because there is not so much pressure behind it. The rupture is often not more than 50 μ in diameter, while the average sperm is four times as broad. But however much the sperm may be constricted in getting out, it promptly regains its form and begins to swim.

Efforts to keep the sperms alive after their escape from the pollen tube were not very successful. In weak sugar solutions they immediately break to pieces, almost explode; in a 10 per cent solution they simply die; in a 12 or 15 per cent solution they live a few minutes; in a 20 to 25 per cent solution they live a little longer, but this is about the maximum, for solutions stronger than these were less and less satisfactory. Of course the behavior under natural conditions could not be determined.

When the pollen tubes begin to discharge, the archegonial chamber is moist but contains no free liquid.

The amount of liquid discharged by a single pollen tube is small in comparison with the size of the archegonial chamber, and if the liquid should spread evenly it would not be sufficient to cover the sperm; however, it behaves somewhat like a drop of water on a greasy surface, not spreading much, but moving until it comes into contact with the neck of an archegonium.

What causes the sperm to enter the egg? In ferns it has been shown that the sperms are strongly attracted by certain chemical substances in the neck of the archegonium and are thus drawn to the egg. My own experiments and those of the Japanese botanist Miyake prove that there is no such chemical attraction in the cycads, even the material of the egg failing to exert any stimulus.

In *Dioon*, *Stangeria*, and other cycads, just before fertilization, numerous preparations show a little protoplasm about the necks of the archegonia, and for a long time I assumed that it had been squeezed out of the egg by the pressure of the knife, as a square piece containing the archegonia was being cut out from the top of the endosperm for the purpose of making thin sections for detailed microscopic study. It was also noted that when material near the fertilization period is dropped into water or into some preservative a small bubble appears at the neck of the archegonium.

These phenomena suggested an explanation of the presence of the protoplasm about the necks of the archegonia, and also suggested how the sperm might get into the egg.

The drop of liquid discharged from the pollen tube has a very high osmotic pressure, and when it comes into contact with the extremely turgid neck cells these lose so much of their contents that they appear more or less shrunken. The pressure within the egg has been increasing until the contents are retained only by the rigidity of the turgid neck cells, and consequently even a slight decrease in the turgidity of the neck cells would allow the escape of a small portion of the protoplasm of the upper part of the egg, together probably with some gas. In this way there is formed at the apex of the egg a vacuole, which may be of very short duration. We suggest that this series of conditions would result in drawing the sperm into the egg, the cilia merely keeping it oriented, for sperms just within the egg always show the apex in advance.

While the whole sperm enters the egg, the nucleus soon slips out from the protoplasmic sheath and moves toward the egg nucleus, leaving the sheath with its ciliated band in the upper part of the egg. The sperm is very large in proportion to the neck of the archegonium, and it may be that the constriction of the sperm during its entrance into the egg loosens the sheath so that the nucleus slips out more easily. When more than one sperm enters the egg, as is frequently the case, the nucleus of the second sperm does not slip out from the sheath, but the whole sperm remains intact in the upper part of the egg. Doubtless the first sperm opened the neck of the archegonium so that the second suffered little constriction, and the protoplasmic sheath was not loosened.

The protoplasm of the sperm gradually mingles with that of the upper part of the egg, and the two soon become indistinguishable, but the spiral band with its cilia maintains its identity much longer and may be distinguished throughout the early development of the embryo, but it finally merges with the protoplasm of the egg.

As the sperm nucleus moves toward the egg nucleus, it enlarges somewhat, and the two nuclei soon come into contact (Fig. 61). At the time of contact both nuclei are in the resting condition, and this condition continues even after the nucleus of the sperm has become more or less imbedded in that of the egg. From this point the development must be exceedingly rapid, for the next stage observed showed the division of the nucleus formed by the fusion of the two nuclei of the egg and sperm, the first division in the sporophyte generation. This stage is illustrated by Fig. 62 in the next chapter. The fact that this division, at the stage represented in the figure, shows only half the number of

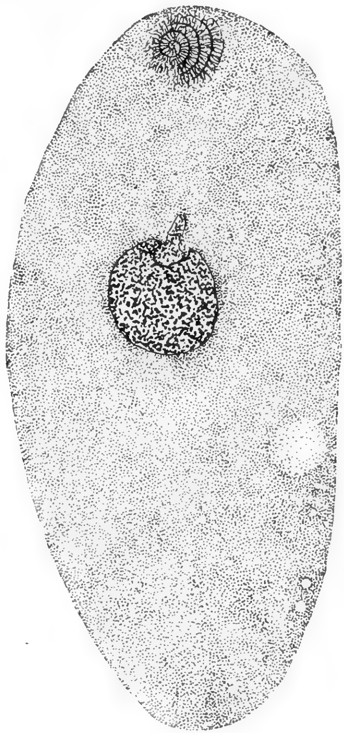


FIG. 61.—*Stangeria paradoxa*, showing fertilization; the sperm nucleus is entering the nucleus of the egg; the spiral, ciliated band of the sperm remains at the top of the egg. Highly magnified.

chromosomes characteristic of the sporophyte, together with the fact that nuclear divisions in immediately subsequent stages of embryogeny show the anticipated double number, indicates that the chromosomes contributed by the sperm and egg are pairing. Such a phenomenon has been described by Dr. A. H. Hutchinson for *Abies balsamea*, the balsam fir.

For a study of this phase of fertilization the cycads are unfavorable, since events are very rapid, material is hard to secure, and the ovules are so large that almost endless time is needed for making preparations. Such stages as we have secured, especially in *Stangeria*, confirm Dr. Hutchinson's account.

An interesting feature common to all cycads is the long interval between pollination and fertilization. Fifty years ago the two phenomena were confused, or rather it was not recognized that there were two phenomena. The term fertilization was applied to pollination, as in Darwin's *Fertilization of Orchids by Insects*, and botanists were not devoting much attention to subsequent stages.

In *Dioon edule* the pollen is shed late in September or early in October, and fertilization occurs late in April or early in May, so that the interval between pollination and fertilization is about seven months. During most of this period there is a gradual growth of the pollen tube, but near the close of the period there is a rapid development of the sperms with their spiral, ciliated bands.

The long interval, however, is not unique, for more than a year elapses between pollination and fertilization in the pines, and in the oaks the interval is still longer; but in most flowering plants it is only a few days.

CHAPTER VIII

THE EMBRYO AND SEEDLING

THE EMBRYO

The fertilized egg is the first cell of the sporophyte generation. The earlier stages in the development of the sporophyte, while it is still within the seed, are generally referred to as the embryo; subsequent stages, as the embryo breaks through the seed coats and becomes established in the soil, constitute the seedling; later the seedling is called the plant. Attempts to apply these terms too strictly are like applying the terms baby, child, boy, and man. We know what is meant, but the process is continuous, and attempts to make a strict definition of embryo, seedling, and adult must be arbitrary, like making the age of twenty-one years the dividing line between the boy and the man.

As the nucleus formed by the union of the egg and sperm nuclei enters upon the first division it is surrounded by a great display of fibrous protoplasmic structures contrasting sharply with the granular contents of the rest of the fertilized egg (Fig. 62). It is not at all surprising that a nuclear figure so small in proportion to the mass of protoplasm fails to divide the fertilized egg into two cells. No wall is formed between the two nuclei resulting from this first division, but the two nuclei divide simultaneously; the four resulting nuclei again divide simultaneously, and such free nuclear divisions continue without the formation of any cell walls, so that the embryo, without any perceptible increase in size, contains successively 1, 2, 4, 8, 16, 32, 64, 128, 256, and in some cycads 512 and 1,024 nuclei before walls begin to appear (Fig. 63).

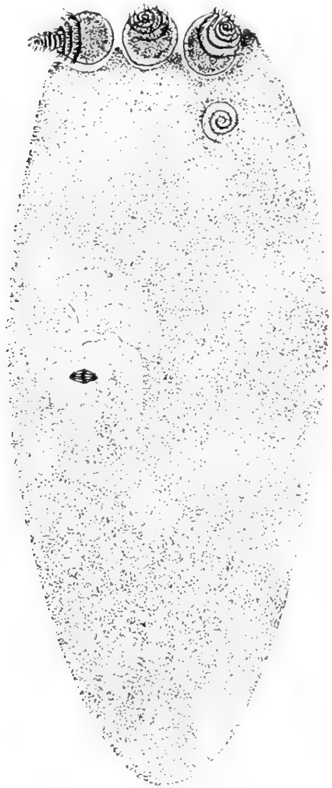


FIG. 62.—*Stangeria paradoxa:* first division of the nucleus of the fertilized egg; the spiral, ciliated band is still visible at the top of the egg. Three sperms which passed through the neck but did not get into the egg are shown at the top. Highly magnified.

These nuclear divisions follow each other in such rapid succession that there is little growth between divisions, and consequently the nuclei become smaller and smaller as they become more numerous. After the number of nuclei reaches 128 the mathematical regularity begins to diminish, because a nucleus here and there, especially in the upper part of the embryo, fails to divide, and such nuclei become more numerous as development proceeds. However, the proportion of such nuclei is not large, and there is no uncertainty in determining whether one is dealing with approximately 256, 512, or 1,024 nuclei.

The free nuclear period is common to all cycads, and the earlier divisions seem to be nearly identical in all the species I have been able to investigate; but after the

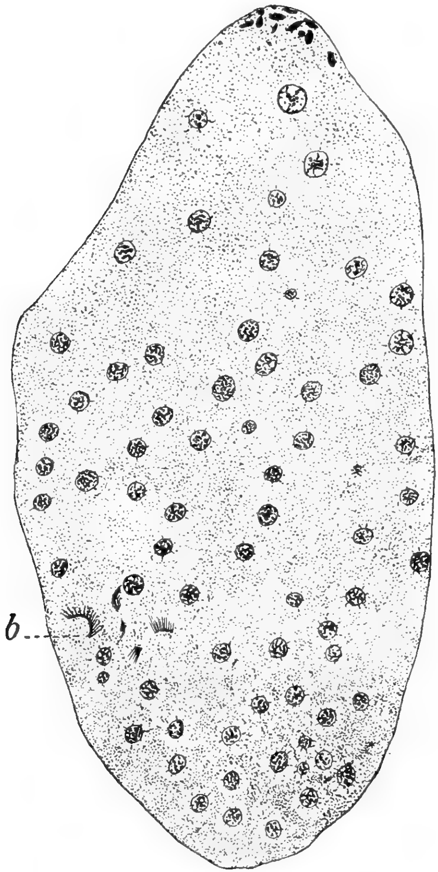


FIG. 63.—*Dioon edule:* a late free nuclear stage in the development of the embryo. The remains of the ciliated band are shown at *b*. Highly magnified.

sixth division, resulting in the formation of 64 nuclei, various differences which seem to be characteristic of the species begin to appear.

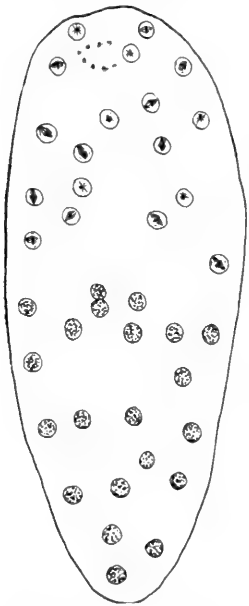


FIG. 64.—*Stangeria paradoxa:* free nuclear stage in the development of the embryo, showing simultaneous nuclear division in the upper part and resting nuclei in the lower. Highly magnified.

In *Stangeria*, even with the fifth division, resulting in the formation of 32 nuclei, digressions frequently occur. There is often a distinct polarity, half of the nuclei being in the upper third of the embryo and half in the lower third, while the protoplasm of the middle third has no nuclei at all. The two groups may behave alike, dividing simultaneously, or they may behave independently, one group dividing while the other remains in the resting condition, the latter case causing a wide variation from the regular series of numbers (Fig. 64).

In *Stangeria* and *Cycas*, after the period of general simultaneous division has come to a close, a hundred or more nuclei at the extreme base of the embryo divide once or twice more, the dividing region being marked off sharply from the region above, in which all the nuclei are in the resting condition. The entire plant, root, stem, and leaves, is organized from the restricted lower region which has divided again (Fig. 65).

In *Dioon* and *Stangeria* there is an evanescent segmentation of the protoplasm of the entire embryo before any permanent cell walls appear. The mechanism for the formation of walls seems to be present all the time, but the nuclear divisions follow in such rapid succession that it does not get into operation. As the number of nuclei increases, the amount of protoplasm surrounding

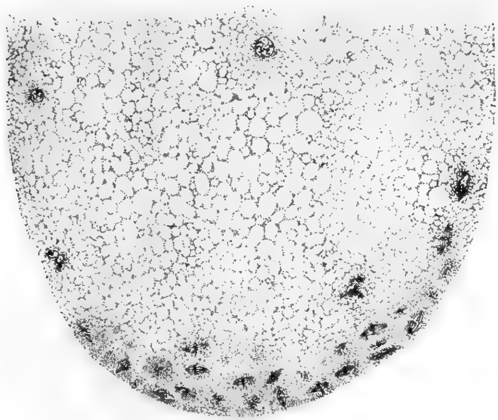


Fig. 65.—*Stangeria paradoxa:* free nuclear stage in the development of the embryo, showing simultaneous free nuclear division below and resting nuclei above. The root, stem, and leaves come from the dividing nuclei; all the rest serve as nutrition. Highly magnified.

each one becomes less and less, and the intervals between successive divisions become greater, so that the ever-present tendency to form walls begins to express itself. The appearance of these evanescent walls is shown in Fig. 66.

In *Dioon* and *Stangeria* the walls disappear completely except at the base of the embryo. In *Macrozamia* and *Encephalartos*, the walls persist throughout the embryo, although the plant is built up exclusively from the lower portion, the larger upper region serving only as food material.

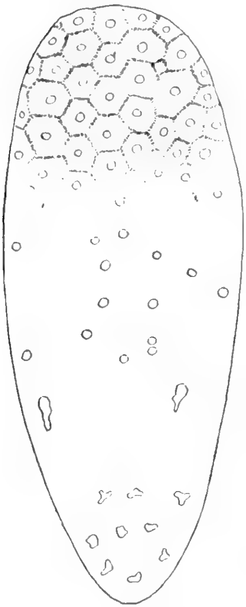


FIG. 66.—*Stangeria paradoxa:* free nuclear stage in the development of the embryo, showing evanescent segmentation at the top. Highly magnified.

With the ninth or tenth division, in all cases which we have observed, the period of free nuclear divisions without the formation of cell walls comes to a close. Some conclusions with regard to the origin, cause, and evolution of the free nuclear period will be found on page 155.

The first permanent walls at the base of the embryo are formed simultaneously, since they result from a simultaneous division of the nuclei (Fig. 67). Subsequent divisions are not simultaneous, doubtless because each nucleus is now inclosed in its own cell, and the nuclei are no longer exposed to the uniform conditions which prevailed when they were in one common mass of protoplasm.

Almost immediately after permanent walls begin to appear the cells become differentiated into three regions: the upper, in contact with the large mass of protoplasm and nutritive materials, consisting of cells which become more or less haustorial in function; the lower, consisting of smaller cells with rich protoplasmic contents; and the middle region, consisting of rapidly elongating cells with very little protoplasm (Fig. 68). The upper region ceases to function as soon as it has absorbed and passed on the nutritive materials stored above it. The middle region, which is called the "suspensor," elongates

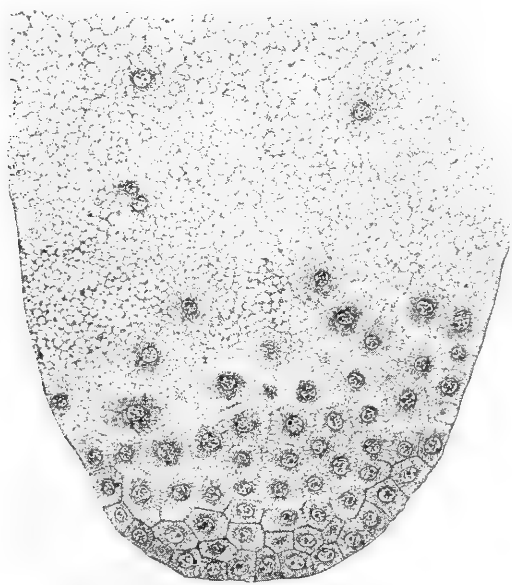


FIG. 67.—*Stangeria paradoxa:* early wall formation in embryo. Highly magnified.

enormously, so that it becomes coiled and twisted and packed in the disorganizing upper part of the endosperm. This suspensor, which is the longest known in plants, when stretched out as far as it can be stretched from its packed and cramped condition reaches a length of two or even three inches. The lower region, below the suspensor, gives rise to the root, stem, cotyledons, and

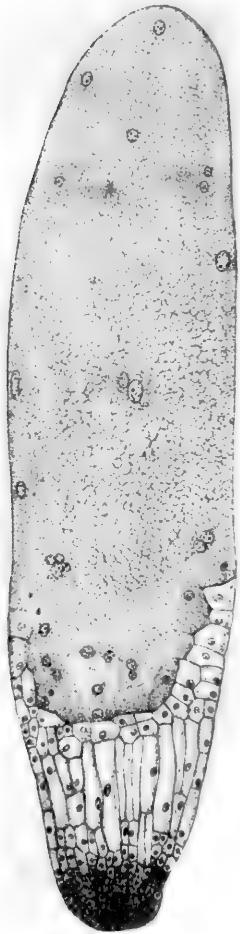


FIG. 68.—*Zamia floridana:* young embryo. Free nuclei are shown in the upper part; the elongated cells beneath will give rise to the long, twisted suspensor; the root, stem, and leaves will come from the small, deeply shaded cells at the bottom. Highly magnified.

leaves of the plant. Consequently only a small portion of the fertilized egg takes part in the formation of the plant, the greater portion being used as nutrition and in the formation of the suspensor and haustorial cells.

The region at the tip of the suspensor, which might be called the embryo proper, since it will give rise to the root, stem, cotyledons, and leaves, advances into the endosperm, partly by digesting and absorbing the surrounding cells, and partly by the crushing thrust of the big suspensor. Cell division proceeds rapidly, so that the advancing embryo soon consists of thousands of small cells.

Differentiation of the embryo takes place imperceptibly. It is soon noticed that the rapid growth is becoming somewhat retarded at the extreme apex, while the growth of the region about it not only continues but is even accelerated, thus causing a depression surrounded by a ring of tissue. The ring is not entirely complete, consisting of two equal crescentic portions nearly touching each other at their ends. The depressed area is the stem tip; the two crescentic portions represent the beginnings of the two cotyledons. The origin of the root is difficult to detect, but converging rows of cells soon indicate that the root region has been established (Fig. 69). Even at the stage shown in this figure the "dermatogen," which gives rise to the single-layered epidermis, has not become differentiated, as those who are students of morphology will recognize from the periclines in the outer layer of cells.

Soon after the two cotyledons are outlined, the ring of rapidly growing tissue surrounding the stem tip becomes complete, so that the two cotyledons are carried up on a "cotyledonary tube." The growth of the tube does not continue long, but the cotyledons grow rapidly, and when the seed is mature the length of their free portion is several times that of the tube. The two cotyledons are closely applied to each other by their

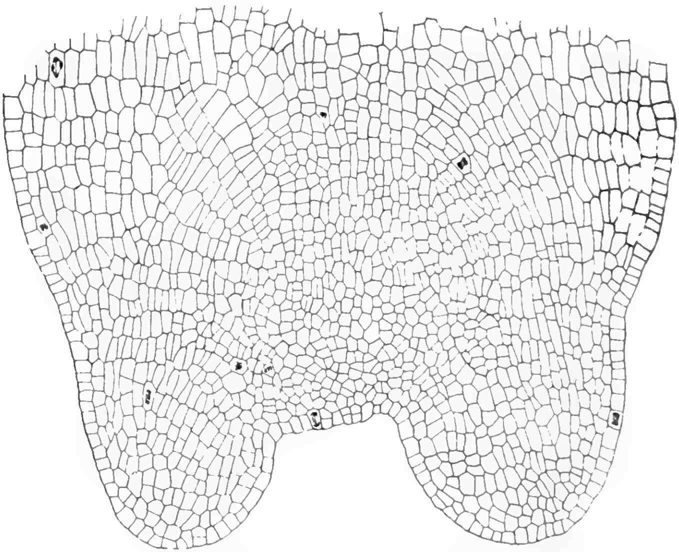


FIG. 69.—*Dioon edule:* later stage in the development of the embryo, showing the flat stem tip, the beginning of the two cotyledons, and farther back a swollen region which marks the beginning of the coleorhiza. Highly magnified.

edges throughout nearly their entire length, but at the tip they bend outward, in some species slightly, and in others so decidedly that many cycads could probably be distinguished by their cotyledons.

It is some time after the appearance of the cotyledons that the stem tip gives rise to any leaves. Several of the first leaves, whose embryogeny looks promising, are destined to form nothing but protective scales. When the seedling has completed its intraseminal development, as the development before it breaks through the seed coats is called, it usually has one foliage leaf well started and the rudiments of one or two more are easily distinguishable.

The root structures of the cycad embryo are rather complex. At the stage shown in Fig. 69 there is a conspicuously swollen portion just back of the cotyledons. This portion is called the "coleorhiza," because it acts as a protecting shield for the tender root until the stony layer of the seed coat has been ruptured.

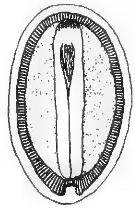


FIG. 70.—*Dioon edule:* section of mature seed, showing the embryo with two cotyledons, the endosperm (dotted), the stony layer of the seed coat (shaded), and the outer fleshy layer. Natural size.

Some features of the mature seed are common to all cycads (Fig. 70). There is an outer fleshy layer, which may persist for months after the seed begins to germinate; a middle stony layer, which is as hard as that of a hickory nut but at the same time slightly elastic; and an inner fleshy layer, which is thin, dry, and membranous. The endosperm is firm but cuts easily with a knife. Its cells are richly stored with starch but contain other materials, some of them doubtless the poisonous elements which have made so much trouble.

THE SEEDLING

The term seedling is applied for an indefinite period beginning with the rupture of the seed coats. As a matter of fact the cycad, under favorable conditions, has no resting period, development being continuous from fertilization to old age and death, with only such temporary dormancy as may result from exhaustion after the cone-bearing stage has been reached.

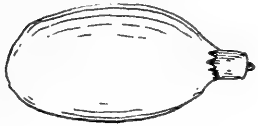
As the embryo within the germinating seed elongates, the hard coleorhiza presses against the stony layer of the seed coat with such force that an irregular fracture is produced, through which the basal part of the embryo protrudes more and more. As soon as the coleorhiza gets through the fracture, the tip of the root partly digests and partly tears its way through the coleorhiza and then begins to turn down into the soil.

Practically all cycad seeds are longer than broad, and consequently the long axis of the embryo lies nearly parallel with the surface of the ground. In nature most of the seeds germinate on the surface of the soil, so that it is easy to observe the appearance of the fracture, the emerging coleorhiza, and the young root (Figs. 71–73).

The young seedling continues to back out until the coleorhiza, the root, the cotyledonary tube, and a small portion of the cotyledons are outside the seed coats, but the principal part of the cotyledons remains inside the seed, absorbing the endosperm and passing it on to the growing seedling. After all the endosperm has been used, the nutritive material within the cotyledons themselves is absorbed, and they wither away. The stony seed coat and the withered cotyledons inside it may cling to the seedling for a year or two.

Usually the emerging seedling shows only one leaf, the next leaf not appearing for a month or more. Leaves continue to appear, one at a time, for a few years, the intervals between leaves being much shorter in greenhouses than in places where there is any marked alternation of wet and dry seasons.

After the young plant has reached an age of five or six years the leaves begin to appear in crowns; at first



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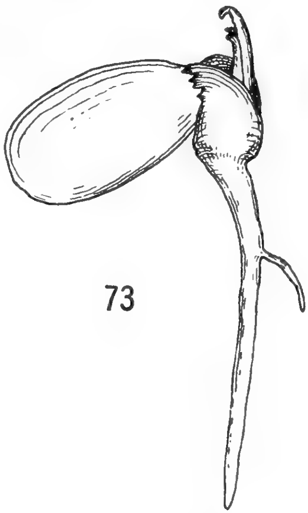

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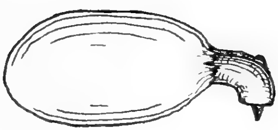

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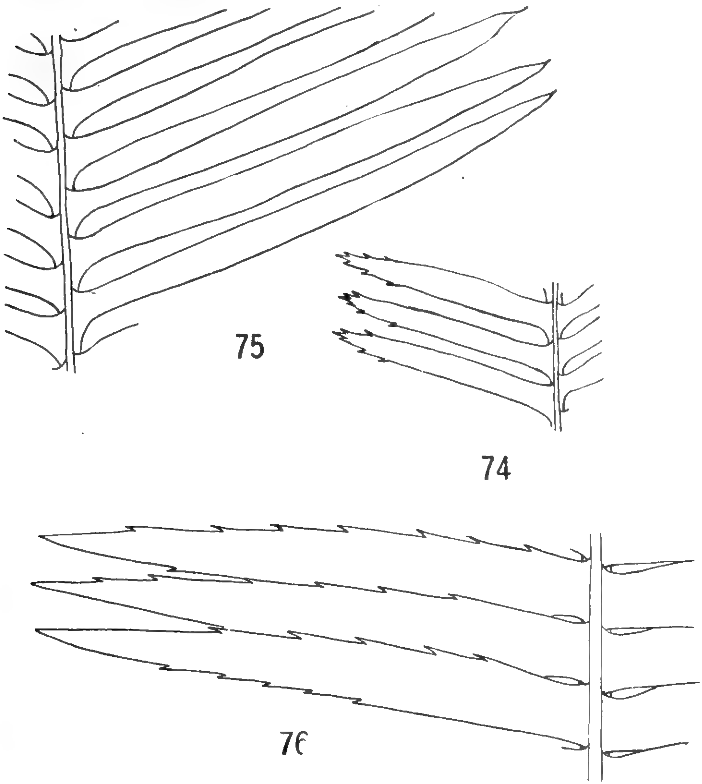
FIGS. 71–73.—*Dioon edule:* early stages in the development of the seedling: Fig. 71, coleorhiza breaking through the stony seed coat and tip of root breaking through the base of the coleorhiza; Fig. 72, later stage, showing tip of first leaf emerging between the two cotyledons; Fig. 73, the root is well developed and three leaves are seen between the two cotyledons. Natural size.

there are only a few leaves, perhaps only two or three in a crown, but as the plant gets larger the number of leaves in a crown gradually increases, until it reaches the approximate number characteristic of the species.

The leaves of seedlings differ decidedly from those of the adult plant. Naturally they are smaller, the first leaf of the seedling in some cases not reaching more than a tenth of the length of the leaves of adult plants. The number of leaflets is smaller. In *Ceratozamia* the first leaf usually has four leaflets, while the leaves of large plants may have as many as a hundred leaflets. The number of leaflets increases steadily as the plant becomes larger, until, in this respect as in the case of the number of leaves in a crown, it attains the approximate norm of the species.

In seedlings the margin of the leaflet often differs strikingly from that of the leaflet of an old plant. *Dioon edule* may be taken as an example (Figs. 74–76). The leaflet in the seedling has a spiny margin, the spiny character being most conspicuous during the first four or five years; the number of spines then diminishes slowly but does not disappear completely until the plant has reached an age which may be estimated at twenty or thirty years.

In this connection it is interesting to note that the seedling leaves of *Dioon spinulosum* have the same spiny character, but that the plant retains it as long as it lives. Many would regard this as an illustration of recapitulation—ontogeny recapitulates phylogeny, or the history of the individual is the history of the race—and would claim that *Dioon edule* is the offspring of *D. spinulosum*, and that *D. edule* in its earlier development is passing through a stage which characterized its ancestor. In the case of *Encephalartos Altensteinii* and *E. caffer* a difference in leaf margins is enough to confuse a taxonomist in his diagnosis. *E. Altensteinii* has leaflets with spiny margins, and the character is supposed to persist throughout the life of the individual. *E. caffer* shows the spiny character in young plants, but it is rather uniformly absent in plants more than fifty years old. As



FIGS. 74–76.—Parts of leaves showing character of leaflets: Fig. 74, *Dioon edule:* leaflets of seedling showing spines near the tip; Fig. 75, leaflets of adult plant with no trace of the spiny character; Fig. 76, *Dioon spinulosum:* spiny leaflets of the adult plant.

far as this character is concerned an individual might begin its career as *E. Altensteinii* and end it as *E. caffer*.

The lower leaflets of the seedling differ from those of the adult in many species. In *Dioon spinulosum* the lowest pair of leaflets is nearly as large as any of the rest

FIG. 77.—*Dioon spinulosum:* young plant with new leaves, showing reduced leaflets at the base and leaves of the previous crown with no reduced leaflets.

until the plant reaches the age of eight or nine years, and during this period the part of the midrib below the lowest pair of leaflets is about as long as the part bearing the leaflets. After this age the new leaves appear with leaflets throughout nearly the entire length of the midrib, the lowest leaflets being merely spines, above which the leaflets gradually increase in length (Fig. 77).

Ferns are characterized by their circinate "vernation," the term meaning that in the bud the tip of the leaf is rolled in so that it looks like crozier. Many cycads, like *Cycas*, show this type of vernation, which was characteristic of their remote Paleozoic ancestry; but in others, like *Dioon*, the leaves lie perfectly straight in the bud.

The anatomy of the seedling has been studied chiefly by Thiessen and by Sister Helen Angela, both of whom have traced the development of the vascular system from its first appearance up to a stage in which the seedling has several leaves. Here again there are lingering structures retained from the remote fern ancestry. The peculiar "girdling" of the numerous bundles which supply the leaves is present even in the first leaf of the seedling, but the bundles start straight, the girdling being due to the great radial growth of the leaf base.

It would be interesting to know the anatomy of the seedlings of the Paleozoic Cycadofilicales and the Mesozoic Bennettitales, but this information is not yet available.

The vascular anatomy of both the seedling and the adult plant deserves more attention than we have given it, but the extensive technical vocabulary which seems necessary in dealing with this subject has led us to omit much of this important source of evidence.

The seedling develops gradually into the adult plant, the stage of the life-history with which we started.

PART III

In any investigation there is a temptation to indulge in speculation and philosophy. I have tried to keep the preceding chapters largely descriptive, thinking it best not to mix actual observations with theoretical considerations. In the following pages I have drawn some conclusions which seem to be warranted by the facts, and have ventured cautiously into the domain of theory.

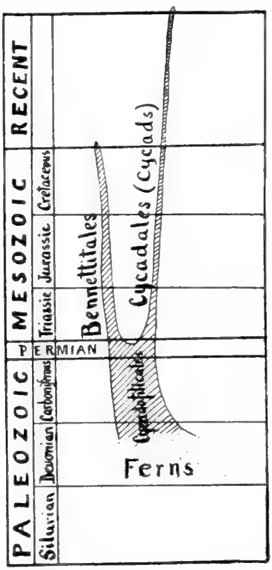


FIG. 78.—Diagram of geological horizons.

Since many organs, like the sporophyll, can be traced from the Paleozoic through the Mesozoic, and through the living forms, trends in evolution can be studied with more confidence in the cycads than in groups not favored with such long and well-known geological records. A diagram of the geological horizons, together with the position of the cycads and their ancestors, and also the Bennettitales (the "fossil cycads" of Wieland) will help those who are not familiar with paleobotany (Fig. 78).

CHAPTER IX

THE EVOLUTION OF STRUCTURES

Nearly every feature of the cycads shows enough range in development to make it worth a study from the standpoint of evolution, but we shall consider only a few which seem to be particularly suggestive.

THE EVOLUTION OF THE CONE

Even the living cycads afford an excellent opportunity to study the evolution of the cone; but, taken together with an encouraging amount of information with regard to the Paleozoic Cycadofilicales and the Mesozoic Bennettitales, it is possible to state with considerable confidence how the most compact cone of the cycads has been evolved from a group of fernlike leaves bearing scarcely any resemblance to a cone.

The ferns of the Paleozoic, like those of today, bore their sporangia on the back or on the margin of the leaf. In some cases the leaves bearing reproductive structures looked just like the ordinary foliage leaves, and their vegetative functions were probably not very much curtailed; in other cases the leaves with sporangia were considerably smaller than the foliage leaves and probably died soon after the spores had been shed. Both types are common in the living ferns. The unmodified foliage type is undoubtedly the more primitive and has given rise to the other, which, through various modifications, has given rise to the cone.

Even after the spore-bearing leaf, or sporophyll, has become modified, the spores may still be uniform in size; but when the spores become differentiated into two sizes, some remaining small while others grow larger, a long step toward the seed habit has been taken. The small spores and large spores are in different sporangia. The small spores, microspores, are male and are comparatively little modified; the large spores, megaspores, are female and become more and more modified and in the course of evolution pass into the seed condition by such imperceptible gradations that it is impossible to construct even an arbitrary definition that would include all seeds and exclude the most advanced megaspores. Plants which have microspores and megaspores are called heterosporous, to distinguish them from their homosporous ancestors, in which all the spores were alike.

An extremely idealistic view, which might pass for a Devonian or Carboniferous heterosporous fern ancestor of the Cycadofilicales, or for one of the Cycadofilicales themselves, is shown in Fig. 79. The large outer leaves are strictly vegetative. Just within the crown of vegetative leaves is a crown of smaller leaves bearing microsporangia on the under surface; and in the center is another crown of small leaves bearing megasporangia upon their margins. The inner leaves, bearing megasporangia, have become modified, the modification consisting in a reduction in size and a simplification of the outline. The microsporophylls, the leaves bearing microsporangia, represent the first stage in the evolution of the cone. The inner leaves, the megasporophylls, show a distinct advance toward a structure which can be recognized as a cone. This is as far as the Paleozoic predecessors of the cycads have advanced in the evolution of the cone.

The Mesozoic Bennettitales, commonly called "fossil cycads," illustrate a stage in our series. A somewhat diagrammatic figure, borrowed from Professor Wieland, will illustrate the general condition of the Bennettitales

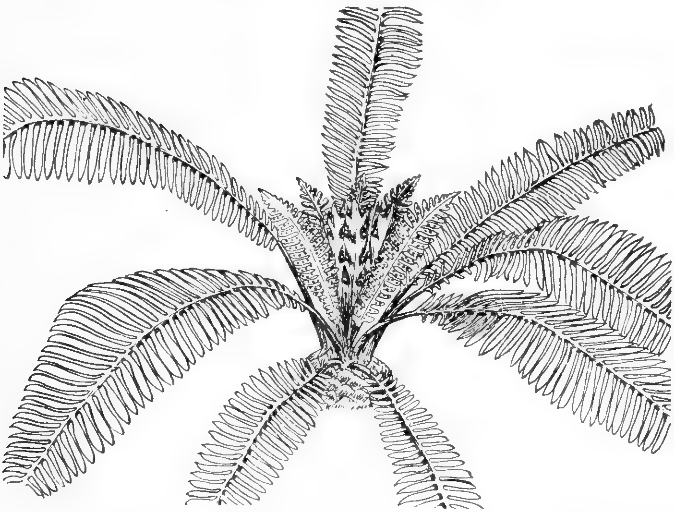


FIG. 79.—Idealistic view of a primitive seed plant such as may have given rise to both the fossil and the living cycads.

of the later half of the Mesozoic (Fig. 80). The microsporophylls, one of which is shown expanded and the other recurved in the bud, are considerably modified, but they still show the pinnate character of the foliage leaf, which was many times the length of the much-reduced sporophyll. The microsporangia are borne on the under side of the leaflets of the sporophyll. This is as far as the male structures of the Mesozoic forms approach the formation of a cone.

The female sporophylls, however, have not only become grouped into a cone, but the cone has departed

FIG. 80.—*Cycadeoidea*, the best known of the "fossil cycads" of the Mesozoic, showing the female cone in the center, on the left a male sporophyll still recurved as in the bud, and on the right a male sporophyll fully expanded; outside of these are the hairy, protective scale leaves of the bud. After Wieland.

so far from the condition shown in the Paleozoic Cycadofilicales that speculation seems unprofitable. If the earlier half of the Mesozoic were as rich in fossils and had been as thoroughly studied as the later half, it is probable that some missing links would have been found. As it is, the female cone of those Bennettitales which have been described could not have given rise to the cones of any of the living cycads. As far as the living cycads are concerned, the Bennettitales of the later Mesozoic must be regarded as a line which ends blindly, becoming extinct without leaving any progeny.

However, the Bennettitales illustrate some features in the evolution of the cone. The male and female sporophylls are borne upon the same plant and are close together upon the same axis, a condition which is undoubtedly more primitive than that shown by the living cycads, in which the male and female structures are borne upon different plants. The male sporophylls of the Bennettitales doubtless represent a stage which existed in the ancestors of the living cycads.

The female cone.—The female cone of the living cycads is easily derived from the condition known to exist in some of the Cycadofilicales and represented very diagrammatically in Fig. 79. This condition differs little from that shown by the female sporophylls of *Cycas*, and it is as certain as anything can be in matters of phylogeny that *Cycas* has persistently retained this primitive type of female sporophyll which characterized the most ancient seed plants.

In *Cycas* the female sporophylls are really a crown of modified leaves bearing seeds on their margins, usually only on the margins of the lower part of the sporophylls. The apex of the stem does not become converted into sporophylls, but grows, producing crowns of foliage leaves and sometimes crowns of sporophylls. The general appearance of this crown of sporophylls is shown in Fig. 14, and a closer view is shown in Fig. 81. The sporophylls still show the pinnate character of the vegetative leaf from which they have been derived.

The cone of *Dioon edule* illustrates a distinct step in advance (Fig. 82). The axis of the stem has become suddenly and greatly elongated and has produced a

FIG. 81.—*Cycas revoluta:* crown of female sporophylls not grouped into a compact cone.

large number of sporophylls which have lost almost entirely the pinnate character of the foliage leaf but still retain unmistakable evidences of their foliar origin. Even the apex of the axis has become converted into sporophylls, and consequently the growth of that axis is brought to an end. But the checking of the growth of the cone axis results in the formation of a growing-point near the base of the cone stalk, and thus there is established another stem axis, which is really a branch, but which assumes the erect position, crowding the cone aside and producing crowns of leaves, until it finally

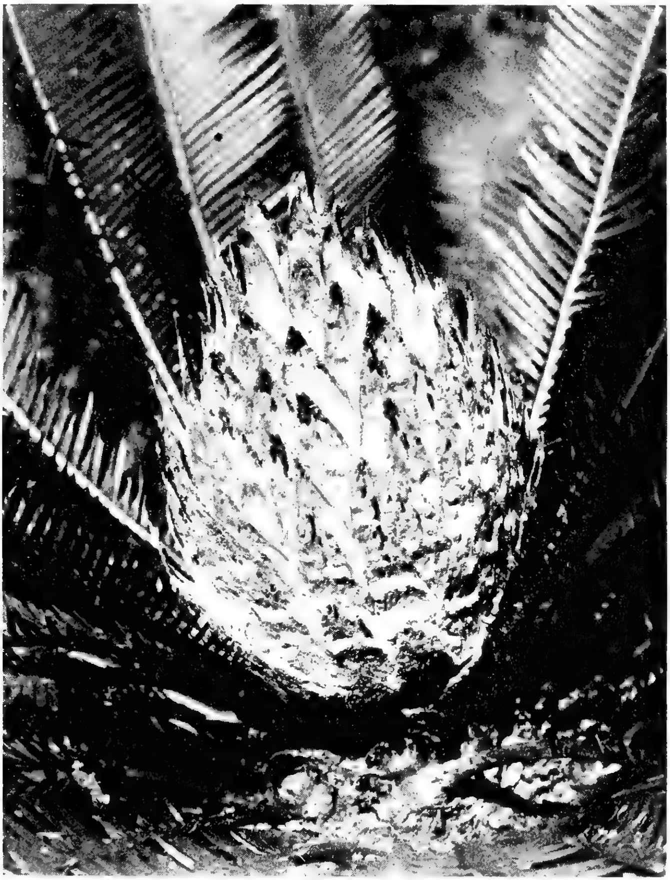


FIG. 82.—*Dioon edule:* top of plant with large female cone

becomes transformed into a cone which is, in turn, pushed aside by the next growing-point. This behavior is found in all cycads with terminal cones. In *Macrozamia* and *Encephalartos* the cone comes from the axil of a leaf, and the original axis persists throughout the life of the plant, as in the female plant of *Cycas*.

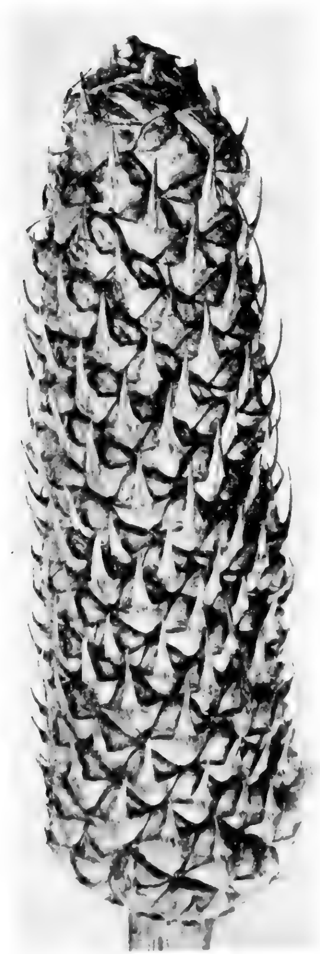


Fig. 83. *Macrozamia Miquelii*: female cone.

The cone of *Dioon spinulosum* is more compact, the tips of the sporophylls being closely appressed; but the sporophylls still show very clearly their foliar character.

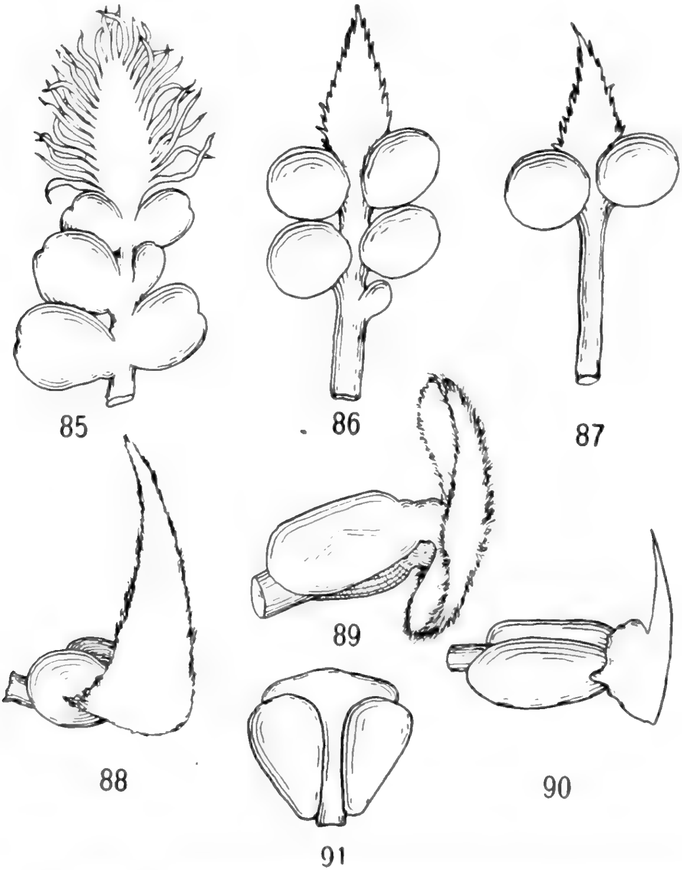
In *Macrozamia* the female cone has reached the maximum of compactness, but the midrib of the sporophyll is prolonged into a spine which at once identifies the genus (Fig. 83).

Beyond this the only advance is the elimination of even the spines which represent the midrib or its lateral leaflets. In *Zamia*, not only has the cone reached the maximum of compactness, but the sporophylls bear so little resemblance to foliage leaves that their nature is established by the evidence of comparative morphology rather than by their own appearance (Fig. 84).

In the series just described stress has been laid upon the cone as a whole, and we believe that the evidence shows conclusively that even the most compact cone has been derived from a crown of sporophylls differing little, or not at all, from the foliage leaves. It seems worth while to present a series of sporophylls, beginning with those which show unmistakable leaf characters and ending with those in which the resemblance to leaves is lost most completely. Such a series, like most evolutionary series in the family, begins with *Cycas* and ends with *Zamia*.

FIG. 84.—*Zamia floridana:* female cone

In *Cycas revoluta* the sporophyll shows clearly its derivation from the foliage leaf (Fig. 85). It is shorter than the foliage leaf, has fewer leaflets, and the midrib region is broader and somewhat thickened, the appearance suggesting that some of the broadening has been due to a coalescence of the lower portions of the leaflets. There are usually six or eight ovules on each sporophyll.



FIGS. 85–91. Series of female sporophylls, showing reduction from the leafy condition to the reduced sporophyll of the most compact cone: Fig. 85, *Cycas revoluta;* Fig. 86, *Cycas circinalis;* Fig. 87, *Cycas media;* Fig. 88, *Dioon edule;* Fig. 89, *Dioon spinulosum;* Fig. 90, *Macrozamia Miquelii;* Fig. 91, *Zamia floridana.*

In *Cycas circinalis* the broadening of the midrib region has progressed farther, so that only the tips of the leaflets remain free (Fig. 86). The number of ovules is about the same as in the preceding case.

Cycas media shows several features in the reduction. The midrib region has broadened until the leaflets appear only as spines, giving the upper part of the sporophyll the appearance of a serrate leaf; the number of ovules may be as high as eight, but usually not more than six, often four, and occasionally only two (Fig. 87). This latter feature is important, since all the other genera have two ovules.

In *Dioon edule* there remains scarcely any external evidence of lateral leaflets, but the broadened portion of the sporophyll is rather thin and tapering and still preserves something of the contour of the foliage leaf (Fig. 88). The basal part has become very thick, and it may not be clear to the layman that the two ovules have the same morphological position as in *Cycas*.

Dioon spinulosum has a shorter and thicker sporophyll and furnishes an easy transition from the preceding examples, in which the contour of the leaf blade is more or less preserved to the rest of the series, in which such a contour has nearly or entirely disappeared (Fig. 89).

In *Macrozamia* the basal thickening noted in *Dioon edule* has become extreme, but the midrib is prolonged as a spine and thus leaves the sporophyll this vanishing trace of its leaf character. In some species of *Macrozamia* the spine is very long, reaching a length of four inches in *Macrozamia Fraseri;* but in some other species the spine has become so short that the sporophyll looks like that of *Encephalartos* (Fig. 90).

The final stage in the reduction is well illustrated by *Zamia* (Fig. 91). There is no indication of leaflets or a midrib, and the whole structure has become so flattened that the two ovules seem to be borne on the under side of a peltate expansion of the stalk; but even in this most reduced condition the internal structure shows that we are dealing with a leaf bearing ovules on its margin.

The whole series shows conclusively how the compact cone has been derived from a crown of sporophylls which in their most primitive condition closely resemble foliage leaves.

Some may object to this statement and claim that in phylogeny the spore-bearing function appeared long before there were any sporophytes with foliage leaves. This we readily admit. We do not know how the foliage leaf originated, but in the Devonian it was already as highly developed as in our living ferns. Beginning at this point the sporophyll has been derived from the foliage leaf and has become more and more modified, until it has reached an extreme form in compact cones like those of most of the cycads.

The male cone.—The male cone is comparatively uniform throughout the group. There are differences in size and shape, but the sporophylls are alike in being more or less flattened, in showing no indication of leaflets, and in bearing groups of sporangia upon the under surface. Even in *Cycas*, which has the loose crown of female sporophylls, the male cone is as compact as in *Zamia*.

There is a reduction as we pass from the *Cycas* end of the group to the *Zamia* end, but the reduction consists in a diminution in the size of the sporophylls and in a gradual lessening of the number of sporangia and the number of spores in the individual sporangium. There are no sporophylls with leaflets like the microsporophylls of the Mesozoic Bennettitales.

The megasporophylls are so characteristic that an artificial key based upon this single character will identify the nine genera, but it would be difficult or impossible to construct a usable key based upon the microsporophylls. This emphasizes the fact that the microsporophylls are comparatively conservative, reminding one of the rather uniform appearance of the antheridia of liverworts or mosses.

While it would be an evolutionary impossibility to derive the female cone of the cycads from the female portion of the cone of any known member of the Mesozoic Bennettitales, it is perfectly easy to derive the male cone of the cycads from such a loose crown of microsporophylls as Wieland has described for *Cycadeoidea*, the most completely known member of the upper Mesozoic Bennettitales.

THE EVOLUTION OF THE FEMALE GAMETOPHYTE

The female gametophyte presents considerable uniformity throughout the group, and at present we do not see any evolutionary tendencies which would prompt us to claim that one genus is more primitive than another in this feature, except that *Microcycas* has advanced far beyond all the other genera.

In all cases there is a well-developed megaspore membrane, a survival of the thick spore coat of some extinct fern ancestor which gave rise to the less ancient Cycadofilicales of the Paleozoic. The persistent retention of the spore coat, a structure which was so necessary in the case of spores which were shed, so long after the shedding habit has been lost and the necessity for protection has ceased to exist, is not easy to explain. In other groups of gymnosperms the gradual reduction and disappearance of the spore coat can be traced, and consequently it seems to be, not a necessary structure, but one which has been retained by heredity long after it has ceased to perform its original function.

The germination of the megaspore throughout the group begins with a period of free nuclear division which is more or less prolonged, according to the size of the ovule. The formation of the cell walls and the later development of the female gametophyte are very uniform in all the genera except *Microcycas*, in which the cells often have more than one nucleus. The general character of the mature gametophyte is quite uniform, a firm, white, ovoid body with an abrupt depression, the archegonial chamber, at the top. The number of archegonia varies, within narrow limits, ranging from three to ten, except in *Microcycas*, which often has more than a hundred, not always grouped at the top, but often scattered over the whole surface. The development of the individual archegonium is quite uniform, there being two neck cells, a ventral-canal nucleus, and an egg. The failure to form a wall between the ventral-canal nucleus and the egg nucleus is an advanced feature, so that in this particular the cycads have advanced farther than the pines, firs, and spruces, which always form a wall at this point, as did their very remote fern ancestors.

The free nuclear stage, with the subsequent formation of walls, is an interesting phase in the evolution of the female gametophyte. We venture to hazard a guess at missing links in the phylogeny and believe that the guess is not far from what would actually be found, if fossils of early heterosporous pteridophytes and the earliest gymnosperms could be secured. That the heterosporous condition, with its large female spores and smaller male spores, has been derived from the homosporous condition, in which the spores are all alike and small with no differentiation of sex, is too obvious for argument. When such spores fall upon a moist substratum they germinate, developing a gametophyte which immediately protrudes from the spore and takes on a green, flattened form producing eggs and sperms. But when the spores are differentiated into larger female and smaller male spores there is little or no protrusion at germination, the gametophyte developing within the spore and having necessarily a more or less spherical form. Being protected from light by the thick spore coat, there is little or no development of chlorophyll, so that the gametophyte is nearly colorless. The spore is large in comparison with the nucleus and is densely packed with food material. The large size of the spore would make it difficult for the nucleus to segment the large mass into two cells, and the food material would shorten the interval between nuclear divisions. As a result of the large mass and the rapid sequence of divisions, walls might very naturally fail to be formed, and nuclear divisions without accompanying cell walls—free nuclear divisions—would continue until the mass about each nucleus became small enough to be segmented; then walls would begin to appear, and the gametophyte would become cellular. We believe that this has been the origin of the free nuclear habit. This habit of free nuclear division in the early stages of the female gametophyte, having been acquired, has never been lost even in the higher seed plants, which have very small gametophytes.

While we should not attempt, within the cycads themselves, to trace an evolutionary line based upon the female gametophyte, the preceding argument indicates that in phylogeny the green gametophyte, cellular throughout its entire existence, was the original form, and that the free nuclear habit was a secondary development due to the increasing size of the spore and the rapid succession of nuclear divisions. The fact that the free nuclei are in a homogeneous mass of protoplasm and nutritive substances would account for the well-known fact that the nuclei divide simultaneously until the period of wall formation is initiated.

THE EVOLUTION OF THE MALE GAMETOPHYTE

In some respects the male gametophyte presents an almost startling uniformity throughout the entire group: the pollen grain at the time of shedding consists of three cells, a prothallial cell, a generative cell, and a tube cell; the pollen-grain end of the tube remains free in the pollen chamber, while the opposite end grows out into the nucellus and acts as a haustorium; the generative cell divides just once, forming a stalk cell and a body cell; the body cell divides just once, except in *Microcycas*, producing two sperms bearing numerous cilia upon a coiled band.

However, in spite of this remarkable uniformity, there are small but constant differences, like the small number of turns in the spiral band of the sperm in *Cycas*, the large number of sperms in *Microcycas*, the basal haustoria of the pollen tube of *Ceratozamia*, and other equally definite features which would enable one to make a fairly reliable, although impractical, key to the genera based upon pollen-tube structures alone.

As far as the male gametophyte is concerned, we cannot trace any series like the reduction of the sporophyll during the evolution of the female cone. The pollen tube of *Microcycas*, with its numerous sperms, is undoubtedly nearer the fern condition than any of the rest, but the other genera seem so uniform that we have not attempted to construct an evolutionary series within the group.

However, there is no doubt that these male gametophytes are highly specialized, and that the pollen-tube habit is a comparatively late development. It is practically certain that the male gametophytes of the Paleozoic seed plants had no pollen tubes. The pollen grains of these ancient forms, as far as they have been observed, indicate that the male gametophyte developed within the pollen grain and consequently had no green, independent cells. The transition from a green, independent male gametophyte protruding beyond the spore to the colorless, dependent gametophyte included within the spore took place in the ancient heterosporous ferns which preceded the earliest seed plants. The earliest pollen tubes were mere haustoria and did not carry the sperms.

EMBRYOGENY

In the development of the embryo from the fertilized egg some prominent features are common to all the genera, but there are differences which enable one to see an evolutionary sequence.

In all cases the development begins with simultaneous, free nuclear division; later, walls appear throughout the entire egg or only at the base; and finally the embryo proper, with its suspensor, root, stem, and leaves, is developed from a comparatively small group of cells at the base of the egg. It is an excellent example of what is called meroblastic embryogeny.

The embryos of homosporous ferns, which have given rise to the heterosporous ferns and, through them, to the early seed plants, have no free nuclear stage in their development. Every nuclear division was followed by the formation of a wall. The free nuclear habit arose, as in the case of the female gametophyte, when the mass of the egg became large in proportion to the size of its nucleus. In all the known ferns, both homosporous and heterosporous, the egg is rather small, and its first division is followed by the formation of a cell wall. It is known that some of the Cycadofilicales had very small seeds and therefore still smaller female gametophytes and eggs. In such eggs it is quite possible that walls were formed at every nuclear division, and that the entire egg participated in the formation of the embryo. As the seeds became larger it is known that the gametophytes and eggs also became larger. We believe that when the egg reached a certain size the mechanism of the dividing nucleus became inadequate to divide the increased mass, so that the two nuclei resulting from the division were left free in the protoplasm, where they again divided, and so continued to divide until the mass of protoplasm about the individual nuclei became comparatively small. It is to be remembered that in free nuclear division in female gametophytes and embryos the mechanism for the formation of walls is present. The nuclear divisions simply occur in such rapid succession that the mechanism does not get into operation.

Although my series of stages in the embryogeny of *Cycas*, *Encephalartos*, and *Macrozamia* are not yet quite complete, it seems safe to say that at the close of the free nuclear period normal cell walls are formed throughout the egg, just as in the well-known Ginkgo, or maidenhair tree. In *Stangeria* and *Dioon* evanescent cell walls appear throughout the egg but almost immediately disappear, leaving the nuclei free again, except at the base, where the embryo proper is to be organized. In *Zamia* and perhaps others there is not even an evanescent formation of walls in the main body of the egg, the only walls coming late and at the base. I have no doubt that three stages in the phylogeny of the cycad embryo are represented in these three illustrations, which may be typified by *Cycas*, *Dioon*, and *Zamia*, with *Cycas* as the most primitive and *Zamia* as the most modified type of embryogeny.

Tracing the evolution of embryogeny is not a simple matter. As far as the free nuclear period is concerned, we believe that it has become more and more prolonged as the egg has increased in size, reaching its maximum in eggs like that of *Dioon edule*, where the egg is usually an eighth of an inch in length, and occasionally reaches a length of more than three-sixteenths of an inch. Here there may be a thousand free nuclei before any walls appear. In *Stangeria* there are about five hundred nuclei before walls appear, and in some species of *Zamia* about two hundred and fifty. Doubtless the very small *Zamias*, like *Zamia pygmaea*, would show a still smaller number of free nuclei.

This reduction in the number of free nuclei before walls appear is significant, if we compare the Coniferales, the group to which the pine, fir, cypress, yew, and other familiar evergreens belong. The eggs are smaller than in the cycads, and the number of free nuclei is correspondingly smaller, in *Taxus* 32, in *Podocarpus* 16, in *Thuja* 8, and in *Pinus* 4. In *Sequoia*, the mammoth tree of California, there is no free nuclear period, a wall following the first division of the nucleus of the fertilized egg, which is very small, and this condition is found in all the higher plants.

Thus it is seen that there has been a rise of the free nuclear period accompanying an increase in the size of the egg, and a decline as the size of the egg became more and more reduced. The series begins and ends with small eggs in which a wall followed the first division of the nucleus, the rise and decline of the free nuclear period coming between. In determining whether a certain form is primitive or advanced with respect to the free nuclear feature, it is obviously necessary to note whether one is dealing with a small number of nuclei in an increasing or in a decreasing series.

The similarity between this embryogeny and the development of the female gametophyte—both having a free nuclear period followed by the formation of cell walls—often confuses students. The causes of the phenomena being the same in the two cases, it is not strange that both should show a rise and decline of the free nuclear period. In the embryogeny, as we have just stated, the series begins with small eggs in which a wall follows the first nuclear division, and the series ends with the same condition; but in the gametophyte, while the series begins with a condition in which a wall follows the first nuclear division, then shows a gradually increasing free nuclear period, and then a decline of the free nuclear period, the decline never quite reaches the starting-point of the ascending series, for even in the highest flowering plants with exceedingly small gametophytes there is no formation of cell walls until a secondary development resulting from fertilization is initiated.

THE LEAF

The fern type of leaf has been maintained with remarkable persistency throughout the entire phylum, from its earliest appearance in the Paleozoic, through the Mesozoic, and in all the living genera. Some cycads still show the circinate, or coiled, arrangement of the leaf as it unfolds from the bud, a striking fern character. The forked veins, so characteristic of ferns, appear in all the living genera except *Stangeria*, and this exception is one which also occurs in ferns, so that the leaf of *Stangeria* may be as conservative as any of the others. On the basis of the leaf we should not attempt to decide whether one cycad is more advanced than another.

THE STEM

The stem affords a few characters which may indicate the trend of development. The columnar stem, covered by an armor of leaf bases, we should regard as the primitive type, the disappearance of armor being more or less correlated with the development of the tuberous, subterranean habit so that, in this respect, genera like *Cycas* would represent the beginning of the line, and *Stangeria* the most extreme reduction.

The course of the leaf bundles in the cortex is direct in the Cycadofilicales and Bennettitales, while most of the cycads are characterized by the girdling of these bundles. Consequently cycads like some species of *Macrozamia*, which show a direct course of the bundle in the adult plant, and *Bowenia*, which shows a similar arrangement in the seedling, are nearer the fern condition in this respect. In the microscopic structure of the wood *Stangeria*, with its scalariform tracheids, seems to present the least divergence from the fern habit.

THE ROOT

Comparatively little is known about the roots of the living cycads, and practically nothing is known about the development of the roots of their Mesozoic and Paleozoic predecessors.

The building up of a root from the segments of a single apical cell is characteristic of ferns, but no such cell has yet been described in the cycads, the root developing from a group of cells, as in the highest flowering plants. We should not be surprised to find the single apical cell in the Cycadofilicales, but at present we could only guess at conditions in Paleozoic, Mesozoic, and even most of the living members of the phylum. Growth by the single apical cell is doubtless the primitive method, and growth by a group of cells has been derived from it, but in this character the cycads seem to present such a uniformity that no trend is distinguishable.

CHAPTER X

LINES OF EVOLUTION

A prolonged comparative study of any group would probably bring an investigator to some conclusions with regard to the evolution of structures and relationships. In the cycads, where a structure like the sporophyll can be traced not only through the living group but through Mesozoic and Paleozoic predecessors, mistakes in judgment are not so likely to occur as in the case of groups known only through their living representatives. The real tendency of evolution is most reliably recognized when the development of a structure within a living group can be compared with the same structure in fossil groups, and where the same organ can be recognized in related plants of various geological horizons, a reliable interpretation of the organ in living forms becomes quite possible.

One of the most satisfactory evolutionary series was described in the beginning of chapter v, dealing with the evolution of the compact cone from a loose crown of sporophylls. The most primitive sporophylls most nearly resemble the foliage leaves, and from this point there is a shortening of the sporophyll, a reduction of the leaflets, and a thickening of the midrib region, until the series closes with a sporophyll which is little more than a thickened, short-stalked expansion bearing two ovules. With respect to this single character it is not hard to arrange the genera in order, and taxonomic keys are based largely upon this series. *Cycas* is first, *Dioon* second, and *Zamia* is the final genus. There is no difficulty in reading the series, for a sporophyll, having once lost the leaflet character, would never regain it. Of course we recognize reversions and similar phenomena but regard them as restricted manifestations of heredity, whose influence does not extend over any very great period of time. For example, if some Paleozoic character should suddenly appear in a living species, we should not attribute it to the influence of some long dormant force of heredity but should regard it as a freak, in no way due to the fact that some remote Paleozoic ancestor may have had a similar feature. If we are right in this opinion the living cycads could not have been derived from the Bennettitales, like *Cycadeoidea*, because the female sporophyll in these Mesozoic forms had already lost more of the leaf character than have the cycads of today.

The reduction in the number of microsporangia on a sporophyll and the reduction in the number of spores in a sporangium furnish good illustrations of evolutionary series.

Embryogeny affords one of the strongest illustrations of the drift of evolution within a group. *Cycas* and *Encephalartos* both have a complete or nearly complete segmentation of the egg during the early embryogeny, but this does not mean that either inherited it from the other; in fact, it seems probable that there was no such inheritance in this case, but that both are still retaining a type of embryogeny which characterized the ferns. Other cycads, whose ancestors doubtless had this type of embryogeny, have diverged from it to a greater or less extent. Here again the superficial investigator is likely to make a mistake and assume that a form with this latter type of embryogeny is necessarily related to the one with the more primitive type. The two may or may not be closely related. If related, the one with the more complete segmentation of the egg is the ancestor and the other the offspring, for we could hardly expect reversions of generic rank in genera so widely separated as those of the cycads.

These illustrations which we have partly recalled from earlier chapters and partly restated, together with others which have been described in various parts of the book, show very clearly that evolution does not progress at equal rates in all the organs of a plant. In *Cycas* the female sporophylls are quite leaflike, but the male sporophylls have lost entirely the pinnule character and have become grouped into a compact cone. On the other hand, in the Mesozoic *Cycadeoidea* the male sporophylls are leaflike and form a loose crown, while the female sporophylls have lost all resemblance to foliage leaves and are grouped into a cone. Both were doubtless derived from a form in which both female and male sporophylls were leaflike and in loose crowns. *Cycadeoidea* has retained the primitive male sporophyll, and *Cycas* the primitive female sporophyll.

In *Dioon* the female sporophyll is much more leaflike than in *Encephalartos*, but in the embryogeny *Encephalartos* shows a much more extensive segmentation of the egg. *Dioon* has retained more persistently the primitive sporophyll character, while *Encephalartos* has retained the more primitive embryogeny.

Contrasts are very striking in *Microcycas*. The male gametophyte is undoubtedly the most primitive yet described for any seed plant, its swimming sperms being more numerous than in some of the ferns; but the female gametophyte is the most advanced yet described for any cycad, approaching the condition shown by *Welwitschia*.

It used to be assumed that characters indicating relationship would be found only in those plants which are near the place where the branch originated from the main stock, and no doubt this is a good place to examine. But the same assumption would lead to the conclusion that a plant in a side branch having an important character, which it has inherited from the main stock, is necessarily near the place where the branch originated.

Such a conclusion would often be incorrect. Botanists now quite generally agree that the monocotyls have been derived from the dicotyls, and that the point of origin is the order Ranales, of which the buttercup, anemone, and crowfoot are familiar examples. It is true that dicotyls with one cotyledon and monocotyls with two are rather frequent near this supposed origin of the branch; but some of the most striking examples of monocotyls with two cotyledons are found as far up in the monocotyl series as the lilies, which in other features have diverged most widely from the dicotyl type.

In typical dicotyls the wood is in a zone surrounding the pith, while in monocotyls the woody strands are scattered, as in a cornstalk; but here again there are some species in the lily family which have the wood in a compact zone surrounding the pith. These species have persistently retained this dicotyl feature, while they have diverged in others.

Various illustrations could be added showing that evolution along some lines has been more rapid than along others. This is not a new idea, for it is well known that plants show a progressive increase in the complexity of the sporophyte, accompanied by an equally regressive simplification of the gametophyte; but the tracing of such lines of evolution should be of the greatest importance in determining relationships.

In our opinion a cycad in which the embryogeny has progressed so far that there is no complete segmentation of the egg could not give rise to one with such a complete segmentation. This character alone would show that *Zamia* could not have given rise to *Encephalartos.* As far as sporophylls and embryogeny are concerned, *Cycas* might have been the ancestor of *Dioon;* but the reverse could not have been true, for *Dioon* has the more advanced sporophyll and the more advanced embryogeny. Of course there is a theoretical possibility that some ancient *Dioon* with pinnate sporophylls and complete segmentation of the egg may have given rise to *Cycas* and then proceeded more rapidly than its offspring to reduce its sporophylls and simplify its embryogeny; but all available facts indicate that *Dioon* is more recent. The genus *Cycas*, as it exists today, could not have been derived from any known *Dioon;* but *Dioon* could have arisen through a modification of *Cycas.*

The predecessors of the cycad line were ferns, and from the ferns there emerged those primitive seed plants, the Cycadofilicales, which looked like ferns and were long believed to be genuine ferns. There can be no doubt that the Mesozoic Bennettitales came from the Cycadofilicales; but whether the cycads came from the

Bennettitales or developed directly from the Cycadofilicales cannot be determined until we know more about the extinct forms of the lower Mesozoic. The university zone of the Northern Hemisphere has been studied with considerable care, and the amount of Triassic material obtained has not been encouraging; but the tropics and Southern Hemisphere may yield material which will solve the whole problem. The immense amount of fossil material secured by Wieland in the Mixteca Alta of Southern Mexico, although not in a condition to be sectioned, leads us to hope that the missing links will be discovered.

For many years the author has been preparing a much more extended technical account of the living cycads. The work has been delayed by the more important work of these imperative times, but, when completed, we hope that the results will be of interest to those who are investigating the evolution and phylogeny of the gymnosperms.

INDEX

INDEX

[Many features are indexed only under the generic names. Italics indicate illustrations.]