The Stem

The stem of cycads may be either aerial and columnar (arborescent) or subterranean and tuberous. An arborescent stem is characteristic of all species of Cycas, Dioon, Microcycas, and Ceratozamia. In Macrozamia and Encephalartos the stem is aerial in some species and subterranean in others. In Zamia a tuberous underground stem occurs in most of the species, an aerial one being found in only a few. Both Stangeria and Bowenia have a tuberous subterranean stem. The tallest cycads are Macrozamia hopei, reaching a height of 18 m., and Dioon spinulosum, reaching 16 m. Microcycas calocoma becomes nearly 10 m. tall, while Encephalartos laurentianus, with a prostrate stem, attains a length of 15 m. Most arborescent cycads are much smaller, few species exceeding 3m. and many being less than 2 m. in height. The smallest of all cycads is Zamia pygmaea, with a stem less than 25 cm. long and only 2-3 cm. in diameter.

Typically, cycads have an unbranched stem, but wherever they are abundant, one can usually find an occasional branching plant. Often the branching is obviously the result of injury. At van Staadens, near Port Elizabeth, Union of South Africa, are many plants of Encephalartos longifolius like the one shown in Fig. 1. The soft terminal part of the stem had been cut off, perhaps a hundred years ago, to make Kaffir bread, a practice which gave the genus its common name, Bread Palm, and its scientific name, Encephalartos.

Young plants frequently arise from the base of an old one, especially if the old plant has a leaning stem, as in Dioon edule. The large crown of leaves on a cycad about a meter in height offers such resistance to the wind that the stem may lean or even be blown down. Any slight crack at the base may result in the formation of a bud which develops into a branch. When formed close to the soil, such buds become rooted and established as independent plants when the old plant dies. The most conspicuous cases of branching are seen in plants of Cycas revoluta growing in temple grounds or on old estates (Fig. 2). Here branching has been induced by making cuts in the stem, a method still employed by nurserymen, who pot the resulting buds. Sometimes branches become hundreds of years old and must be supported by props. Branching is very common in subterranean stems. When growing in stony ground, the stems are often cut or scratched, and a bud arising from the wound becomes a branch (Fig. 3).

An entirely different type of branching may appear in another way. When a cone breaks down, some of the seeds may be held in a kind of basket formed by the crown of leaves. Here they sometimes germinate and the seedlings grow down into the soft tissues of the stem apex (Fig. 4). At Chavarrillo, Mexico, I saw a plant of Dioon edule with thirty-five buds at the top forming a circle that replaced the normal crown of leaves. Five of the buds had four to ten green leaves; the others were still covered by bud scales. At least some, and perhaps all, of the thirty-five buds were seedlings.

Other plants in the vicinity showed three to five crowns, some of which were almost certainly a result of the germination of seeds at the stem apex. In Zamia floridana seedlings often grow down into the tissues of the stem apex and produce what appear to be branches. Such a young plant, becoming established and looking like a true branch, might bear a male cone, while the older plant might be female. The finder of such a specimen might claim that cycads are sometimes monoecious.

Another type of branching, which is internal and may never reveal itself externally, takes place regularly when a terminal cone is produced. When a cycad produces its first cone, the apical meristem is used up, but a new meristem is soon formed at the base of the peduncle (Fig. 5). This develops leaves and pushes the cone aside. Although really a lateral branch, it continues the growth of the main stem. When another cone is produced, the process is repeated, but externally the stem still seems to be unbranched. However, a longitudinal section of the stem shows a series of cone domes, each of which was terminated by a cone (Fig. 6). If two meristems should appear at the base of the peduncle, as they probably sometimes do, one might remain vegetative for several years and build up a branch; while the other, producing a cone, would form a new meristem. Although externally alike, one branch would show a cone dome, while the other would not.

In the female plant of Cycas, the original meristem continues throughout the life of the individual, producing successive crowns of foliage leaves, scale leaves, and sporophylls (Fig. 7). A longitudinal section of the stem does not show any cone domes. The male plant has terminal cones and a longitudinal section shows a cone dome for every cone the plant has produced except the first one.

Where several cones are produced, the stem may or may not contain cone domes. *Zamia* has a complicated system of cone domes, and when a new meristem appears at the base of each peduncle, a profusely branched stem results. A plant of *Zamia latifoliolata* in our collection has produced as many as 60 male cones at one time. Even externally, it is much branched. A dissection of the stem would doubtless reveal a complicated anatomy that would probably be of the cone-dome type, with more than one meristem appearing at the base of a peduncle.

Encephalartos friderici-guilielmi frequently has a circle of cones appearing in the axils of leaves (Fig. 8). The cones are lateral structures, the terminal meristem continuing the growth of the stem. Cone domes are absent. In *Macrozamia moorei* male cones are usually numerous, with 10 to 20 not rare and sometimes as many as 100 being present (Fig. 9). These cones are strictly lateral, arising from the leaf axils. A tangential section of the stem resembles a section of the extinct *Cycadeoidea*, of the order Bennettitales. Ovulate cones are not so numerous, usually only two or three being present, but in one plant eight were counted, all fully grown and weighing about 15 kilos each. Both male and female plants of *Macrozamia moorei* have no cone domes.

In *Stangeria* and *Bowenia*, which have subterranean stems, an abscission layer develops at the base of the petiole and cuts off the leaf cleanly, leaving only an inconspicuous scar that finally becomes unrecognizable. In other cycads with subterranean stems, as in most species of Zamia and in some species of Encephalartos and Macrozamia, an abscission layer does not appear so early. Instead, the leaf dies, the leaflets are shed, and the rachis and petiole disorganize. In Zamia an abscission layer is formed after several years, the base of the petiole then breaking off cleanly. Consequently, the top of the stem is covered with a temporary armor of leaf bases. After the leaf is cut off, the scar may be visible for a long time (Fig. 10), but usually soon disappears, leaving the stem as smooth as in Stangeria or Bowenia, and a normal phellogen is continuous around the entire cortex. Those species of Encephalartos and Macrozamia having subterranean stems, or stems raised only slightly above the ground, have an armor less conspicuous than in arboreal types but one that may persist throughout the life of the plant.

Cycads with aerial trunks have a conspicuous armor of persistent leaf bases, Dioon edule affords a good example (Fig. 11). In its first year the young crown of leaves is obliquely erect; in its second year it becomes depressed, so that the leaves are almost horizontal; in its third year the leaflets fall off; during the next two or three years, the rachis and petiole disorganize and only 8 or 10 cm. of the petiole remain. Finally an abscission layer forms, not at the base of the petiole but farther out, so that 2 or 3 cm. of the base of the petiole remain as a permanent armor. The end of the remaining part is suberized. Even trunks a thousand years old are completely covered by these petiole bases, which are more or less diamond-shaped as seen from the surface. In such an old trunk, the diameter near the top is usually greater than at the base, for there is almost no increase in the width of the xylem of the stele. On the other hand, there is often a decrease in the diameter of the trunk, for one abscission layer after another forms at the outer ends of the leaf bases, cutting off thin flakes that finally reduce the diameter of the trunk. In extremely old trunks of Encephalartos latifrons this process goes on until no trace of the armor remains.

In trunks of rapid growth - rapid for cycads - a distinct alternation of large and small leaf bases occurs. The large bases, forming a rib, belong to foliage leaves, while the small ones, forming the depression between two ribs, belong to the bud scales. Microcycas calocoma and Dioon spinulosum furnish good illustrations of such ribbing (Fig. 12). The successive cork cambiums are much more vigorous in the bases of the foliage leaves, which form the ribs. Consequently, the ribs become reduced, and at a distance of a couple of meters from the top, the trunk becomes even, with no distinction between ribs and depressions. In very old trunks the abscissions continue until they not only remove the armor but invade the cortex, so that the diameter of the trunk is noticeably less at the bottom than at the top (Fig. 13).

In Dioon edule one might imagine an obscure ribbing; but here the buds scales are hardly recognizable except near the tip. Each of the big groups which might be mistaken for ribs is made up of the bases of foliage leaves and consists, not of the bases of one crown but of several crowns, perhaps as many as twelve. When a plant produces a crown of leaves every other year and a cone every other year, or even every year, it becomes exhausted and goes into a dormant state, looking dead and producing neither leaves nor cones for several years. A fire may sweep through the patch and thus initiate a dormant stage or an animal may initiate it by eating a young crown. When the plant comes out of the dormant state, an unusually large number of bud scales makes a slight constriction. The number of such constrictions on a stem doubtless denotes the number of times the plant has become dormant. In Dioon edule a growth ring resembling an annual ring is formed as the plant comes out of the dormant state. Such a growth ring, in this species, may be formed every 20 or 30 years. The dormant periods are too irregular to make the rings of much value in estimating the age of a plant.

In Dioon spinulosum the successive abscission layers in the leaf bases are so frequent that, at the bases of plants 6 or 7 m. high, there is not only no distinction between ribs and depressions, except in the upper part of the trunk, but even the diamond-shaped markings are obliterated. Thus any estimate of the age of the plant on this basis is extremely indefinite. In this species the width of the xylem of the stele increases considerably, the diameter of the stem being greater at the bottom than at the top. Except during dormant periods, a crown is formed every other year, and with every new crown a growth ring appears in the wood. In trunks 10 m. high the ribs are easily recognizable in the upper 3 m. Consequently, the age of this upper part, making no allowance for possible dormant periods, is just twice the number of ribs. A plant of D. spinulosum 16 m. high would probably not be half as old as one of D. edule 1 m. high. In the lower part of such trunks, where leaf bases or ribs are indistinguishable, one might make a guess from the growth rings, making the number of years twice the number of rings.

Some records of very old cycads are available. In the grounds of the temple of Gokokuji, at Takaido, Japan, is a plant of Cycas revoluta that is known to have been growing in the same place for over 650 years, and it was probably 100 years old when transplanted from the field. One of the largest specimens of C. revoluta in Japan is in the temple grounds of Shokuji, at Hiji-Cho, Oita Prefecture. The stem is 9.15 m. tall and 1.75 m. in diameter. It has 90 branches and the area covered by them is about 100 square meters. The age is said to be about 500 years.

At Chavarrillo, Mexico, large plants of Dioon edule produce a crown of about 20 leaves every other year, an average of 10 a year. Some specimens not more than 1.5 m. in height have 10,000 leaf bases, indicating an age of about 1,000 years (Fig. 14). Such an estimate is conservative because a plant is not likely to produce 20 leaves in a crown until it is nearly 100 years old; also no account is taken of dormant periods. In conservatories both Dioon edule and D. spinulosum may retain their leaves for 2, 3, or 4 years, or even longer, or crowns may appear two years in succession, the duration being so irregular that the method of determining the age of field specimens is of little value when applied to plants in cultivation.

Transverse sections of adult cycad trunks show two distinct types of vascular structure, the monoxylic and the polyxylic, the former having a single zone of wood and the latter two or more zones separated by parenchyma (Fig. 15). Most cycads have the monoxylic type of stem. In *Cycas* all species which have been examined are polyxylic, while in *Macrozamia* and *Encephalartos* some species are monoxylic and some polyxylic. In *Cycas revoluta* and *C. media* plants 1.5 m. in height seldom show more than 3 or 4 zones. The greatest display of zones which has come to our attention is in *Cycas pectinata*. A piece of stem 20 cm. in diameter, collected by Sir Joseph Hooker in 1848, in the Great Rungeet Valley, Sikkim, shows 14 zones, all rather narrow but very distinct. (Fig. 16) The zones are formed at irregular intervals of, probably, many years, and may indicate the number of times the plant has had a prolonged dormant period.

In adult plants of *Zamia floridana* having a stem diameter of 8 cm., the xylem zone is about 2 mm. wide and the phloem zone the same. In exceptionally large specimens with a diameter of 12 cm., the xylem zone is about 3 mm. wide and the phloem zone about 2 mm. Growth rings are absent. It is evident that growth of the woody cylinder is very slow. A plant of *Ceratozamia mexicana* near Jalapa, Mexico, with a trunk 30 cm. high and 15 cm. in diameter, had a zone of xylem only 3 mm. wide. A plant of *Microcycas calocoma* near Consolación del sur, Cuba, was about 2.5 m. high and about 20 cm. in diameter at 50 cm. above the ground. The diameter of the pith at this level was 10 cm., the width of the xylem zone 1.5 cm., the phloem 1 cm., the cortex 2.2 cm., and the armor 0.5-1 cm.

A plant of *Dioon edule* at Chavarrillo, Mexico, with a trunk about 60 cm. high and 21 cm. in diameter, had a pith 8.7 cm. in diameter, a xylem zone 5mm. wide, phloem zone 5 mm., cortex 2 cm., and zone of leaf bases 3.6 cm. A specimen about 1 m. in height but with no greater diameter had a pith 6.9 cm. in thickness, a xylem zone 15 mm. wide, phloem zone 8 mm., cortex 3.2 cm., and zone of leaf bases 1.5 cm. *Dioon spinulosum* has the widest zone of xylem ever recorded for any cycad. A specimen at Tierra Blanca, Mexico, with a stem 6 m. high and 33 cm. in diameter, had a pith 8 cm. in diameter, a xylem zone 10 cm. wide, phloem zone 1.4 cm., cortex 2.5 cm., and armor 0.5-1 cm. (Fig. 17).

Leaves

The leaves of cycads are produced in crowns, except that in Stangeria, which often has only one leaf and rarely more than two or three in a season, the term crown is not very appropriate. But even in Stangeria, whose leaves often live two or three years, particularly in gardens and conservatories, the foliar display might be called a crown. The leaves of all cycads do not appear simultaneously but in succession along a low spiral. Consequently, the leaves in a crown are of such different lengths that the oldest may be several times as long as the youngest (Fig. 18). In some species of Macrozamia, such as M. moorei and M. miquelii, the crown may contain as many as 100 leaves, but in most cycads the number is much less, seldom exceeding 20 or 30, and often being fewer than 15.

The duration of the crown varies with the species and with conditions. The young crown is erect until the leaves reach at least half their mature length (Fig 19). At Chavarrillo, Mexico, where Dioon edule is very abundant, crowns are produced every other year. During the first year the crown is bright green and the leaves extend obliquely upward. During the second year, partly because of the presence of a small grayish lichen, the leaves are not so bright and become horizontal or even droop slightly. During the third year the leaflets fall off, the petiole and rachis hang down and decay, beginning with the tip, and still later an abscission layer appears 2 or 3 cm. from the cortex, making a clean cut that leaves the base of the petiole on the trunk (Fig. 14).

As nearly as could be determined, the production of new crowns seems to be the same in Dioon spinulosum as in D. edule. At Trapps Valley, near Grahamstown, South Africa, Encephalartos altensteinii produces a new crown every year, but E. latifrons does not. Cycas circinalis usually bears a new crown every year, but at Townsville, Queensland, Australia, lying at sea level in a hot and wet region, a plant in the botanical garden is said to produce two crowns a year. This is a ~~very~~ unique case. Probably in no other cycad are the successive crowns more sharply marked than in Encephalartos friderici-guilielmi, where the tomentum is extremely abundant, covering the scale leaves and making the foliage leaves very abundant. In this species a new crown appears every year and remains green for two years.

The vernation in Dioon, Macrozamia, and Encephalartos is perfectly straight (Figs. 18, 19, 20A). In Cycas it is as circinate as in any fern, both in the rachis and leaflets (Fig. 20B). In Zamia, Ceratozamia, and Microcycas the rachis is circinate and the leaflets straight (Fig. 20C). In Stangeria the rachis is distinctly curved, sometimes appearing circinate and sometimes conduplicate, while the leaflets are straight (Fig. 20D). In Bowenia the bipinnate leaf has the tip of the main rachis and side branches curved, but the leaflets are straight.

When a new crown has broken through the bud scales, growth is very rapid. The following measurements were made in the greenhouse, where growth is likely to be faster than in the field. But the rates of growth at various periods in the development of the leaf, and comparative rates of growth of the different regions, are probably the same as in the field. All the plants measured, except Stangeria and Bowenia, were grown from seed and were not more than 35 years old.

	Number of days	Increase in length	Average rate per day
Dioon spinulosum	6	28 cm.	4.6 cm.
D. edule	6	21 cm.	3.5 cm.
Cycas circinalis	48	146 cm.	3.0 cm.
Ceratozamia mexicana	55	61 cm.	1.1 cm.
Encephalartos villosus	50	110 cm.	2.2 cm.
Stangeria paradoxa	31	88 cm.	2.8 cm.
Bowenia serrulata	30	83 cm.	2.7 cm.

The leaves of all cycads are pinnate except those of Bowenia, which are bipinnate or even tripinnate. They range in length from 5 or 6 cm. in some mature specimens of Zamia pygmaea to as much as 3 m. in Cycas circinalis, Dioon spinulosum, and Macrozamia denisonii. The leaves of Encephalartos villosus sometimes reach a length of 5 m. while E. laurentianus, of tropical Africa, is reported to have leaves reaching 6 m. in length. About 1 m. is a very common length for a cycad leaf and this is reached or surpassed in all the genera and in many of the species.

The pinnate leaves, arranged in crowns, make the cycads look like ferns. Stangeria paradoxa was long thought to be a fern and was included in the tropical genus Lomaria until the discovery of its cones proved it to be a seed plant. Zamia pseudoparasitica looks so much like Polystichum acrostichoides that, without cones, it might be mistaken for that well-known fern. On the other hand, some of the ferns resemble cycads. At a distance of 50 m. the South African Cyathea dregei could easily be mistaken for a cycad. In the tropical rain forest south of Tuxtepec, Mexico, one must often dismount from his horse for a closer look before he can decide whether a plant is a cycad or a fern. Sometimes it is a Zamia, but usually only a fern. Bowenia, with its bipinnate leaves, is so fern-like in appearance that, without cones, one might pass it by without even suspecting that it is a cycad.

Most cycad leaves are differentiated into a petiole and rachis. In some species the lower leaflets are gradually reduced to spines that often extend to the base of the leaf, so that a distinct petiole seems to be lacking. Such spines, generally occurring in a row along each of the two sides of the petiole, are seen in most species of Cycas, in Dioon spinulosum, and in some species of Encephalartos, such as E. villosus. In many species of Macrozamia the lower leaflets are reduced in size but, with only a few exceptions, are not spine-like. In Ceratozamia, except C. kuesteriana, and in many species of Zamia, the petiole is spiny, but the spines are irregularly scattered and do not intergrade with the leaflets; in fact, they are frequently borne on the rachis as well. In Stangeria, Bowenia, and Microcycas the petiole is entirely without spines of any kind.

In Dioon spinulosum, where in older plants the reduced leaves extend to the base of the petiole as spines, seedlings and young plants, as well as buds from older plants, have very long unarmed petioles and the lower leaflets are nearly as large as those higher up (Fig. 21). Such leaves are called juvenile leaves and many students of phylogeny regard them as evidence in favor of the recapitulation theory. In Ceratozamia, also, the first leaves of the seedling have unarmed petioles, the spiny condition developing gradually as the plant becomes older. In some species of Cycas, on the other hand, where the leaves of mature plants have few or no spines on the petiole, numerous spines occur on the petioles of young plants. Because the degree of spininess often depends on the age of the plant, too much stress should not be placed upon it, especially since nearly all taxonomic descriptions of cycads have been written by botanists who have never studied the plants in the field.

In nearly all herbarium specimens leaves are cut off above the base, the extreme lower portion being lost. In Zamia stipules are as prominent as in the Rosaceae. In Ceratozamia the stipules are thick and fleshy, forming an important part of the armor that covers the stem; in C. latifolia they develop so early that the growing leaf breaks through the stipule as the root tip of a cycad embryo breaks through the coleorhiza. In this species the stipules are so closely applied to the cortex that the trunk is smooth, making it easy to distinguish C. latifolia from C. mexicana by this feature alone.

Since Zamia and Ceratozamia have highly developed stipules, it seemed desirable to examine representatives of all the other genera. In no others are the stipules as prominent as in Zamia, but in every one there is a distinct widening at the base. In Dioon, while the widening could hardly be called a stipule, there is a wedge-shaped edge from which a dense mat of tomentum extends in a thin layer, making the whole structure resemble a wing. In Microcycas, Stangeria, Macrozamia spiralis, Encephalartos hildebrandtii, and E. latifrons the wings may very well be called stipules; and in some other species of <u>Macrozamia</u> and <u>Encephalartos</u> the broad thin wing, while not quite as stipular in appearance, is doubtless the same morphologically. In <u>Cycas</u> and <u>Bowenia</u> also, the broad thin wing is morphologically a stipule. In old leaves of some cycads the thin stipule or wing weathers off at the tip and what remains becomes so closely applied to the leaf that it may be overlooked, or if noticed, as in <u>Encephalartos latifrons</u>, may be called a "collar".

It would not be worth while to ask those who collect large leaves to cut them far enough down so as to show the lowest part, for it is difficult to make such a cut and there is danger of damaging the plant. Moreover, in leaves such as those of <u>Macrozamia moorei</u>, the fleshy base is so broad and thick that it does not make an attractive herbarium specimen.

The leaflets are arranged in two rows that arise laterally from the upper edge of the rachis. They are usually spread out horizontally in one plane; sometimes they bend upward but rarely to such an extent that they are erect. On older plants of <u>Microcycas calocoma</u> the leaflets bend downward. The leaflets are definitely articulated with the rachis in <u>Zamia</u>, <u>Ceratozamia</u>, and <u>Microcycas</u>, but not in the other genera. In <u>Dioon</u> the base of the leaflet is as broad as its widest part; in the other genera the leaflets are more or less attenuated toward the base, the insertion being sometimes quite narrow. In most species of <u>Cycas</u> the leaflets are decurrent at the base, often to the next leaflet below. The leaflets may be either opposite or alternate along the rachis, but often the arrangement is not constant for an individual species; in fact, frequently it is not the same at the apex of a leaf as at its base.

In seedlings the first leaves have only a few leaflets, the number increasing each year until the plant reaches maturity. In an adult plant the leaflets range from as few as 5 on each side in Zamia pygmaea and Z. ottonis to as many as 100 or more on each side in Cycas circinalis, Dioon spinulosum, and Macrozamia denisonii. The leaflets of most cycads are linear-lanceolate, but vary from ovate in Zamia pygmaea and a few other species to very narrowly linear in Zamia angustissima and Encephalartos ghellinckii. Forked leaflets are found in Cycas micholitzii and Macrozamia heteromera. In length the leaflets vary from 1-3 cm. in Zamia pygmaea to as much as 50 cm. in some specimens of Z. wallisii and Ceratozamia mexicana. The leaflets of Zamia angustissima, only 1-2 mm. wide, are the narrowest in the Cycadaceae, while those of Z. wallisii, up to 25 cm. wide, are the broadest.

Some genera are characterized by leaves having an entire margin. These are Cycas, Stangeria, Macrozamia, Microcycas, and Ceratozamia. In Bowenia, Dioon, Encephalartos, and Zamia some species have entire leaflets, while others have leaflets that are more or less toothed. Sometimes the degree of serration depends upon the age of the plant. Thus, Encephalartos altensteinii and Dioon edule have spiny leaflets when young and entire leaflets when mature.

The venation of the leaflets is dichotomous, a condition inherited from the Cycadofilicales and, still farther back, from the ferns. However, most of the forking is so near the base of the leaflet that taxonomists describe the venation as parallel. In *Dioon* no forking takes place except at the base, but in most of the other genera close examination will reveal dichotomous branching of the veins throughout the leaflet. This is particularly apparent in species with broad leaflets, such as *Zamia skinneri*, which has very conspicuous veins. *Cycas* and *Stangeria* are the only genera with a midrib. In *Cycas* the leaflet is without any side veins, the midrib being the only vein present. In *Stangeria* lateral veins extend out from the midrib at right angles to it. In the other genera all the veins are equivalent.

See chapter on fossil cycads for discussion of epidermal and stomatal characters.

Cones and Sporophylls

All cycads are strictly dioecious. Their sporophylls are borne in spiral succession on an elongated axis and are generally organized to form compact strobili that are apparently terminal or nearly so. In *Cycas*, however, the megasporophylls form a loose crown at the apex of the stem. At first they are tightly pressed together, but later separate and finally hang down (Fig. 34). After the seeds ripen, the original meristem of the stem resumes its activity, forming successive crowns of scales, foliage leaves, and megasporophylls. When a male cone is formed in *Cycas*, the original meristem is used up and a new one forms at the base of the peduncle. When growth of the stem is resumed and a new crown of leaves appears, the cone is pushed to one side. The same condition prevails in the formation of both male and female cones in all the other genera except *Macrozamia* and *Encephalartos*. In these two genera the original meristem is not used up in the formation of a cone but later contributes to the elongation of the stem; the cones are lateral structures, arising close to the stem apex in the axils of young leaves.

Some cycads produce cones almost simultaneously. That they really appear in succession is revealed by their difference in size during early stages; but, as they mature, they reach about the same size (Fig. 140). In a group of male cones the oldest sheds pollen somewhat earlier than the others; in a group of female cones the oldest cracks apart a little earlier; thus the pollination period is prolonged. More than a single male cone may be produced in *Macrozamia*, *Encephalartos*, and *Zamia*, whereas in the other genera the male cones are generally solitary. The female cones may occur in groups of two, three, or more in *Macrozamia* and *Encephalartos*; elsewhere they are usually borne singly.

Where multiple cones are produced, the origin of each may involve the apical meristem of the stem, as where only one cone arises. This appears to be the situation in *Zamia*. In *Macrozamia* and *Encephalartos*, on the other hand, the cones appear in the axils of leaves and the apical meristem continues the growth of the stem. *Macrozamia moorei* presents an extreme case in that as many as one hundred male cones, all of which are axillary, may appear on a single plant (Fig. 9).

Although the sporophylls are always borne spirally, their arrangement is so regular in the male cones of *Dioon* and in both the male and female cones of *Bowenia*, *Microcycas*, *Ceratozamia*, and *Zamia* that, in surface view, they seem to stand in vertical rows. The microsporophylls of all cycads are borne in definite cones, but the megasporophylls of *Cycas*, as previously noted, form a loose crown, while those of *Dioon* are in a rather loose cone. In the other genera the megasporophylls form a compact cone. The male strobilus is usually smaller than the female, expecially in thickness, and has a greater number of sporophylls. In *Bowenia* and *Zamia* both kinds of cones are smaller than in the other genera.

The smallest cones in the family are found in *Zamia pygmaea*, where the male cones are only 3 cm. long and 1 cm. in diameter, the female cones 4.5 cm. long and 2.5 cm. in diameter. Among the largest are those of *Macrozamia denisonii*, where the male cones are 24-40 cm. long and 10-15 cm. in diameter, the female cones 40-60 cm. long and 30 cm. in diameter. Exceptional male cones in this species reach a length of 80 cm. and exceptional female cones a length of nearly 1 m., the latter weighing 38 kilos. Exceptional female cones of *Encephalartos longifolius* are not so long but may weigh as much as 45 kilos.

The microsporophylls of cycads may be flat, as in *Cycas*, or peltate, as in *Zamia*. In both cases there is a stalk-like basal portion and a sterile apex. The abaxial surface bears the microsporangia, which are generally grouped in sori of 2-6. The microsporangia range from over 1,000 per sporophyll in some species of *Cycas* to a comparatively few in *Zamia*, the lowest number in the family, 10-14, occurring in *Z. pygmaea*. The microsporangia may form a continuous group or, as in *Zamia* and some species of *Macrozamia*, may be separated into two groups by a sterile median line.

The megasporophylls of cycads exhibit a striking reduction series, ranging from pinnate types with as many as 8 or 10 ovules to peltate types with only 2 ovules. The most primitive condition is seen in *Cycas revoluta*, where the megasporophylls are 20-30 cm. long and distinctly leaf-like (Fig. 26). The lower portion, or petiole, is slender and stalk-like, while the rachis consists of a narrow fertile portion that is expanded above into a broad sterile blade. The fertile portion bears several ovules, most commonly 3, along each lateral margin, while the sterile blade bears a number of reduced leaflets up to 5 cm. long. In the other species of *Cycas* the leaflets of the megasporophyll become smaller and smaller, finally being represented by mere serrations, as in *C. circinalis* (Fig. 35). The ovules are reduced to a single pair in *C. cairnsiana* and *C. normanbyana*, the number characteristic of all the other genera.

The megasporophylls of *Dioon* are without serrations, but the sterile blade is long and acuminate (Fig. 56). In *Macrozamia* the blade is reduced to a median spine that is particularly conspicuous in *M. miquelii* (Fig. 78). In *Encephalartos* and *Ceratozamia* the terminal part of the blade is suppressed, but the leaflets are often represented by serrations. Reduction has gone still farther in the other genera, the megasporophyll being a thick peltate structure with scarcely any resemblance to a leaf. Reduction of the sporophylls reaches its extreme in *Zamia*.

no section on "seeds"?