PÁL GREGUSS

XYLOTOMY OF THE LIVING CYCADS

WITH A DESCRIPTION OF THEIR LEAVES AND EPIDERMIS

Pál Greguss :

XYLOTOMY OF THE LIVING CYCADS WITH A DESCRIPTION OF THEIR LEAVES AND EPIDERMIS

This volume is a direct continuation of the author's monograph "Identification of Living Gymnosperms on the Basis of Xylotomy", a highly esteemed work in professional circles. This new book describes, with illustrations on 98 tables containing 950 original microphotos, the wood anatomy of 83 of the 107 to 130 species belonging to 10 Cycad genera living or becoming extinct in the tropics. The structure of the leaves is illustrated on 10 tables. 75 leaflet drawings and several epidermis photos on 77 tables complete the work.



AKADÉMIAI KIADÓ

Publishing House of the Hungarian Academy of Sciences

Budapest

XYLOTOMY OF THE LIVING CYCADS
with a Description of Their
Leaves and Epidermis

XYLOTOMY OF THE LIVING CYCADS

WITH A DESCRIPTION OF THEIR LEAVES AND EPIDERMIS

by

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950 microphotos and 79 drawings on
185 plates, 80 figures and a map



AKADÉMIAI KIADÓ, BUDAPEST 1968

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Printed in Hungary

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INTRODUCTION

Paleontological research deals with an ever increasing multitude of fossil plant remains, stems, flowers, fruits, pollen grains, etc. These finds very often resemble living plant forms, in their finest details as well as in their principal traits. Their determination is greatly facilitated by comparison with the living forms; but that, of course, requires a thorough knowledge of the latter.

According to a fundamental hypothesis of natural history, the living flora is a continuation of the vegetation of past geological times; it could not have come to exist in its present form without its fossil precursors. During the long periods of its evolution, it bore throughout the stamp of its ancient heredity, acquiring as it progressed new facilities of adaptation to prevailing external conditions. However, the new influences never wrought changes so deep as to completely efface the ancient, primitive features. Therefore the ancient, extinct forms are in a number of respects similar to the living ones. For example the *Pinaceae* that lived in various geological periods are in a number of anatomical properties highly similar to and sometimes even identical with the recent *Pinaceae*, so much so that the copious information available about the living forms permits the fossils to be readily determined or to be placed, at least approximately within the genetic system of plants.

It was with this purpose in view that the present author wrote a book on a xylotomical basis (Greguss 1955a) to assist researchers in determining the trunks of the fossil *Gymnospermae* of various geological epochs. In that work, the author gave a xylotomical description of living species of *Gymnospermae*; from the other class of the Gymnosperms, the Cycads, only a single type was presented. The survey of the rest in a separate book had been set aside for a later time. So far, the literature of this branch of science has produced no comprehensive work on the xylotomy and leaf epidermis of the living Cycads that would have been apt to serve as a basis for the anatomical examination of extinct Cycads. This is why the author decided to compose, as a continuation and on the basic principles of his work on *Gymnospermae*, a xylotomical manual of the living Cycads. Recognizing, however, that *epidermology* has by today become a new discipline, likewise indispensable in the determination of fossil finds, he wished to facilitate research of leaf imprints by giving descriptions of the leaf epidermis of the living forms.

The present work covers all the ten genera of living Cycads; more precisely, it deals with the xylotomy of about 40 of the 83 species recognized so far and with the leaves and epidermal structure of 83 species or varieties. Completeness in any work of this kind is a somewhat elusive goal; it is particularly so in the case of the Cycads which thrive widely scattered on both sides of the Equator, for the most

part in tropical regions, far away from human habitations; the rare accessible specimens are carefully guarded treasures of botanical gardens and institutions; to acquire a sample suitable for analysis of the often sole, non-branching stem, or of the leaves, is difficult, if not impossible. The author, however, most kindly assisted by a number of scientific institutions, succeeded in collecting material of all the ten genera, and of nearly all living species and varieties. Most valuable are the trunks and leaves of the exceedingly rare *Stangeria* (Africa), *Bowenia* (Australia) and *Microcycas* (Cuba), without which the work would have remained a torso.

When writing a comprehensive monograph it is in no way satisfactory for the author to collect and treat the data contained in the literature. A systematic survey requires ready evidence in the form of adequate comparative material. Beside its paleontological significance, the anatomy of the living Cycads is highly important in another respect. The trunks and leaves exhibit many traits suggestive of phytogenetical relationships. It was these anatomical traits that allowed to put forward the hypothesis, gaining an ever broader acceptance, that the Cycads represent a transition between some groups of pteridophytes (*Filicinae*, *Pteridospermae*) and angiosperms (*Monocotyledoneae*). On the other hand, except for their gymnospermy, they show very little semblance, particularly as regards their anatomy, to the other great living class of gymnosperms, more closely: the conifers. Their systematic examination is thus desirable also from the phylogenetic viewpoint.

Anatomically, the Cycads exhibit several peculiar properties in most typical form, such as the gradual transition of the transfusion cells into the tracheids, the origin of pith rays, the pitting of the tracheids, the appearance of perforations in the tracheids, the origin of the vessels, etc.

This work could hardly have been completed without assistance from many quarters. The author wishes to express his sincere gratitude to all who by sending samples of trunks, leaves and photographs greatly contributed to its composition. The generous contributors are enumerated in the following list: R. H. Anderson, Sidney, Australia; J. Barna, La Habana, Cuba; J. Bedford, Pretoria, Union of South Africa; R. de Belder, Kalmthout, Belgium; H. M. Burkill, Singapore; H. Callens, Kisantu, Congo; Centre de Recherches, Division de Botanique, Ineac, Yangambi, Congo; R. W. Davis, Miami Beach, USA; Department of Agriculture, Beltsville, USA; Forest Research Branch, Ibadan, Nigeria; Forest Research Inst., Bogor, Indonesia; M. B. Foster, Orlando, USA; H. Gottwald, Reinbeck, German Federal Republic; L. R. Holdrige, San José, Costa Rica; Instituto Botanico, Caracas, Venezuela; Jardin Botanique, Montreal, Canada; D. M. A. Jayaweera, Paradeniya, Ceylon; P. G. Jordaan, Stellenbosch, Union of South Africa; B. W. J. Kean, Ibadan, Nigeria; Prof. J. Lebrun, Louvain, Belgium; T. R. N. Lothian, Adelaide, Australia; Ponce de Leon, Habana, Cuba; E. Salisbury, Kew, England; Benjamin R. Seda, Santurce, Porto-Rico; Singh, Lucknow, India; P. H. Soewarsono, Bogor, Indonesia; The Forestry Dep., Limbe, Nyassaland; Universidad de Los Andes, Merida, Venezuela; W. Wilkes, Brisbane, Australia; R. A. Dyer, Pretoria, Union of South Africa; L. A. S. Johnson, Royal Botanic Garden, Sydney, Australia; Australian News and Inf. Bureau, Canberra, Australia; K. N. Kaul, Lucknow, India.

The treatment of the material is in this work the same as in the previous books by the author; it can thus be regarded as a direct continuation of the Conifer monograph. The examination of the material collected over many years was carried out for the most part by the author in person. In preparing the nearly 3000 xylotomical sections and the several hundred epidermal preparations he was assisted by Research Assistant L. Siprák. The 950 or so microphotos of the 185 Plates were prepared almost without exception by the author himself; in preparing copies of the photos and in typing the text, Research Assistant Mrs. György Róbert, Mrs. M. Holtz and my wife Dr. Therese Greguss lent a helping hand. The drawings after nature of the leaflets praise the talents of Dr. Margit Szabados; the drawings and photos in the text were adopted from various textbooks. For these too the author wishes to express his sincere gratitude. He also wishes to extend his thanks to all who have furthered in any way the composition of the present work.

Thanks are due to my colleagues, Professors Dr. Gábor Andreánszky and Dr. Árpád Haraszty who read the manuscript and assisted the author with their valuable advice.

The author further wishes to extend thanks to the Hungarian Academy of Sciences which made possible the preparation and publication of the present work, and to the Publishing House of the Hungarian Academy of Sciences for the beautiful presentation of the book.

Szeged, December 31, 1967.

The Author

A SURVEY OF THE EXAMINED FAMILIES, GENERA AND SPECIES

Serial number	Species examined	Stem		Leaf		Epidermis		
		Number of plates	Description on pages	Number of plates and drawings	Description on pages	Number of plates	Description on pages	Number of figures
	I. CYCADACEAE							
1	*Cycas beddomei*	XVII, XVIII	35	—	—	—	—	—
2	*Cycas celebica*	—	—	XCVI. 13	151	CVII	174	—
3	*Cycas circinalis*	XIX, XX	36	XCVI. 9	151	CVIII	174	1
4	*Cycas media*	XXI, XXII	39	XCVI. 15a	151	CIX	175	2
5	*Cycas neocaledonica*	XXIII, XXIV	42	XCVI. 15b	151	CX	176	3
6	*Cycas normanbyana*	XXV, XXVI	—	—	—	—	—	—
7	*Cycas revoluta*	XXVII, XXVIII	47	XCVI. 7	151	CXI	177	4
8	*Cycas rumphii*	XXIX, XXX	49	XCVI. 11	151	CXII	177	5,5a
9	*Cycas seemannii*	—	—	XCVI. 10	152	CXIII	178	—
10	*Cycas siamensis*	XXXI, XXXII	53	XCVI. 14	152	CXIV	179	6
11	*Cycas taiwaniana*	—	—	XCVI. 8	152	CXV	179	51
12	*Cycas thouarsii*	—	—	XCVI. 12	152	CXVI	180	52
	II. STANGERIACEAE							
13	*Stangeria eriopus*	—	—	XCV. 3	159	CXVII	182	53
14	*Stangeria paradoxa*	XXXIII, XXXIV	55	CIV. 76	159	CXVIII	183	7
	III. ZAMIACEAE							
15	*Lepidozamia hopei*	XXXV, XXXVI	57	XCVII. 19	157	CXIX	184	—
16	*Lepidozamia peroffskyana*	—	—	XCVII. 18	158	CXX	184	54
17	*Macrozamia communis*	XXXVII, XXXVIII	60	XCVIII. 24	158	CXXI	186	8

Serial number	Species examined	Stem		Leaf		Epidermis		
		Number of plates	Description on pages	Number of plates and drawings	Description on pages	Number of plates	Description on pages	Number of figures
18	*Macrozamia douglasii*	XXXIX, XL	62	—	—	—	—	—
19	*Macrozamia fawcettii*	—	—	XCVIII. 25	158	CXXII	187	—
20	*Macrozamia macdonnelli*	XLI, XLII	64	XCVII. 20	158	CXXIII	187	9
21	*Macrozamia miquelii*	XLIII, XLIV	67	XCVII. 22	158	CXXIV	188	—
22	*Macrozamia moorei*	XLV, XLVI	69	XCVII. 21	158	CXXV	189	10
23	*Macrozamia pauli-guilielmi*	XLVII, XLVIII	71	XCVIII. 27	158	CXXVI	190	—
24	*Macrozamia secunda*	XLIX, L	73	XCVIII. 26	158	CXXVII	191	—
25	*Macrozamia spiralis*	—	—	XCVIII. 23	159	CXXVIII	192	55
26	*Encephalartos altensteinii*	LI, LII	75	C. 40	153	CXXIX	193	11
27	*Encephalartos arenarius*	—	—	C. 37	153	CXXX	194	56
28	*Encephalartos barteri*	LIII, LIV	78	CI. 49	153	CXXXI	195	—
29	*Encephalartos bubalinus*	—	—	CI. 53	153	CXXXII	195	—
30	*Encephalartos caffer*	—	—	XCVIII. 28	153	CXXXIII	196	57
31	*Encephalartos cycadifolius*	—	—	XCVIII. 31	154	CXXXIV	197	58
32	*Encephalartos eximius*	—	—	C. 46	154	CXXXV	199	—
33	*Encephalartos ferox*	—	—	XCIX. 36	154	CXXXVI	199	59
34	*Encephalartos friderici-guilielmi*	—	—	CIV. 72	154	CXXXVII	201	60
35	*Encephalartos gratus*	LV, LVI	80	CI. 52	154	CXXXVIII	202	—
36	*Encephalartos hildebrandtii*	—	—	CI. 54	154	CXXXIX	203	61
37	*Encephalartos horridus*	—	—	C. 38	155	CXL	204	62

Serial number	Species examined	Stem		Leaf		Epidermis		
		Number of plates	Description on pages	Number of plates and drawings	Description on pages	Number of plates	Description on pages	Number of figures
38	*Encephalartos humilis*	—	—	C. 43	155	CXLI	205	63
39	*Encephalartos inopinus*	LVII, LVIII	82	C. 45	155	CXLII	206	12
40	*Encephalartos latifrons*	—	—	CI. 51	155	CXLIII	207	64
41	*Encephalartos laurentianus*	—	—	XCIX. 32	155	CXLIV	208	65
42	*Encephalartos lebomboensis*	—	—	CI. 48	155	CXLV	210	66
43	*Encephalartos lehmannii*	LIX, LX	84	CI. 50	155	CXLVI	211	13
44	*Encephalartos longifolius*	—	—	XCIX. 34	156	CXLVII	212	67
45	*Encephalartos manikensis*	—	—	CIV. 73	156	CXLVIII	213	—
46	*Encephalartos natalensis*	—	—	C. 39	156	CXLIX	214	68
47	*Encephalartos poggei*	—	—	C. 44	156	CL	215	69
48	*Encephalartos princeps*	—	—	CIV. 74	156	CLI	216	70
49	*Encephalartos septentrionalis*	LXI, LXII	87	CI. 55	156	CLII	217	14
50	*Encephalartos tegulanus*	—	—	XCIX. 35	156	CLIII	218	—
51	*Encephalartos transvenosus*	—	—	C. 42	157	CLIV	219	71
52	*Encephalartos trispinosus*	—	—	CIV. 75a,b	157	CLV	220	72
53	*Encephalartos umbeluziensis*	—	—	CI. 47	157	CLVI	222	73
54	*Encephalartos villosus*	LXIII, LXIV	89	C. 41	157	CLVII	223	15
55	*Encephalartos woodii*	—	—	XCIX. 33	157	CLVIII	223	74
56	*Dioon edule*	LXV,LXVI	91	XCV. 6	152	CLIX	225	16,17
57	*Dioon pectinatum*	—	—	XCV. 5	152	CLX	226	—
58	*Dioon spinulosum*	LXVII, LXVIII	95	XCV. 6a	152	CLXI	226	18

Serial number	Species examined	Stem		Leaf		Epidermis		
		Number of plates	Description on pages	Number of plates and drawings	Description on pages	Number of plates	Description on pages	Number of figures
59	*Microcycas calocoma*	LXIX, LXX	96	XCV. 4	159	CLXII	228	19
60	*Ceratozamia kuesteriana*	—	—	XCVII. 16	150	CLXIII	228	—
61	*Ceratozamia mexicana*	LXXI, LXXII	99	XCVII. 17	150	CLXIV	229	20
62	*Ceratozamia robusta*	—	—	XCVIII. 30	151	CLXV	230	—
63	*Zamia angustifolia*	LXXIII, LXXIV	102	CIII. 69	159	CLXVI	231	21
64	*Zamia fischeri*	—	—	CIII. 65	159	CLXVII	232	—
65	*Zamia floridana*	LXXV, LXXVI	104	CIII. 71	160	CLXVIII	232	22
66	*Zamia furfuracea*	—	—	CII. 59	160	CLXIX	233	75
67	*Zamia gutierrezi*	LXXVII, LXXVIII	106	CII. 56	160	CLXX	234	—
68	*Zamia kickxii*	—	—	CIII. 67	160	CLXXI	235	76
69	*Zamia latifolia*	—	—	CII. 58	160	CLXXII	236	—
70	*Zamia latifoliata*	—	—	CIII. 70	160	CLXXIII	237	77
71	*Zamia lindenii*	—	—	CII. 62	160	CLXXIV	238	78
72	*Zamia loddigesii*	—	—	XCVIII. 29	161	CLXXV	239	79
73	*Zamia media*	—	—	CIII. 68	161	CLXXVI	240	—
74	*Zamia muricata*	LXXIX, LXXX	108	CII. 57	161	CLXXVII	241	23
75	*Zamia obidensis*	LXXXI, LXXXII	110	—	—	—	—	—
76	*Zamia ottonis*	—	—	CII. 60	161	CLXXVIII	242	80
77	*Zamia portoricensis*	LXXXIII, LXXXIV	112	—	—	CLXXIX	243	—
78	*Zamia pumila*	LXXXV, LXXXVI	114	CIII. 63, 64	161	CLXXX	244	24
79	*Zamia pygmaea*	—	—	CIII. 66	161	CLXXXI	244	—
80	*Zamia silicea*	LXXXVII, LXXXVIII	116	CII. 61	161	CLXXXII	245	—
81	*Zamia skinneri*	LXXXIX, XC	117	—	—	—	—	—
82	*Bowenia serrulata*	XCI, XCII	119	XCV. 1	150	CLXXXIII	246	25,26
83	*Bowenia spectabilis*	XCIII, XCIV	122	XCV. 2	150	CLXXXIV	247	27a,b 28

PLACE OF THE CYCADS IN THE SYSTEM OF PLANT TAXONOMY

The modern plant systems regard the living Cycads (*Cycadinae*) as a separate class in the subphylum *Gymnospermae* of the phanerogamous plants:

Subphylum I. *Gymnospermae*

Class 1. *Pteridospermae*
Class 2. *Cycadinae*
Class 3. *Bennettitinae*
Class 4. *Cordaitinae*
Class 5. *Ginkgoinae*
Class 6. *Coniferae*

Of these, the classes *Cycadinae*, *Ginkgoinae* and *Coniferae* are represented among the living plants; the *Pteridospermae*, *Cordaitinae* and *Bennettitinae*, which had first arisen in the Palaeozoic, had disappeared already in the Mesozoic, and their place was gradually taken by the Angiosperms.

At present, about 130 species of living Cycads are known. Although all these are rather similar in external habit, in the appearance and structure of the flowers, in being all dioecious, and also in their anatomical structure, it is easy to classify them into smaller or larger natural groups. They include quite dwarfed, almost epiphytic (*Zamia pseudoparasitica*) and fern-like forms (*Stangeria*, *Bowenia*) but also trees 20 metres tall. To illustrate their size range, let us cite *Zamia floridana* (barely 15 cm high), *Dioon edule* (almost 1 m), *Cycas revoluta* or *Dioon spinulosum* (10 m), and *Lepidozamia hopei* which may exceptionally grow to the height of 20 metres. Their stem is cylindrical, unbranched or dichotomous; the low trunks are carrot- or egg-shaped, creeping in the soil, or erect and slender; they remind frequently of the palms whose unbranched or exceptionally dichotomous trunks also bear terminal crowns of leaves. The class *Cycadinae* (2.) is divided according to Johnson (1959) into three families:

Class 2. *Cycadinae*

Family I.	*Cycadaceae* L. C. Rich (1807)	
	Genus 1.: *Cycas* L. (1737)	(14 species) (12)
Family II.	*Stangeriaceae* L. Johnson, n. fam. (1959)	
	Genus 2.: *Stangeria* T. Moore (1958)	(2 species) (2)

Family III. *Zamiaceae* Reichenb. (1837)

Tribus a.: *Encephalarteae* (Miq.) L. Johnson. n. comb. (1959)

Genus 3.: *Lepidozamia* Regel (1876) (2 species) (2)
Genus 4.: *Macrozamia* Miq. (1842) (12 species) (9)
Genus 5.: *Encephalartos* Lehm. (1834) (28 to 40 species) (30)

Tribus b.: *Dioeae* (Schuster) L. Johnson n. comb. (1959)

Genus 6.: *Dioon* Lindl. (1843) (3 species) (3)

Tribus c.: *Zamieae* Reichenb. (1837)

Genus 7.: *Microcycas* (Miq.) A.D.C. (1868) (1 species) (1)
Genus 8.: *Ceratozamia* Brongn. (1846) (4 species) (3)
Genus 9.: *Zamia* L. (1753) (28 to 40 species) (19)
Genus 10.: *Bowenia* Hook. (1863) (2 species) (2)

Of a total of 107 to 130 species the author elaborated 83

The first number in parentheses after the name of the genus indicates the year of first description; the second is the approximate number of species in the genus; the third is the number of species and varieties treated in this book. From the latter enumeration it appears that in the face of considerable difficulties, the author succeeded in obtaining material from every living genus and was thus in a position to supply a fairly complete image of the anatomy of the trunk and the leaf epidermis of the living Cycads.

In the following, our concern shall be mainly with the structure of the trunks and leaf epidermis of the Cycads since in the determination of most fossil finds it is these two aspects that enter into consideration. This does not mean, however, that in the determination of the fossil Cycads the knowledge of flowers, pollen grains or seeds is of no importance.

GEOGRAPHICAL DISTRIBUTION OF THE LIVING CYCADS

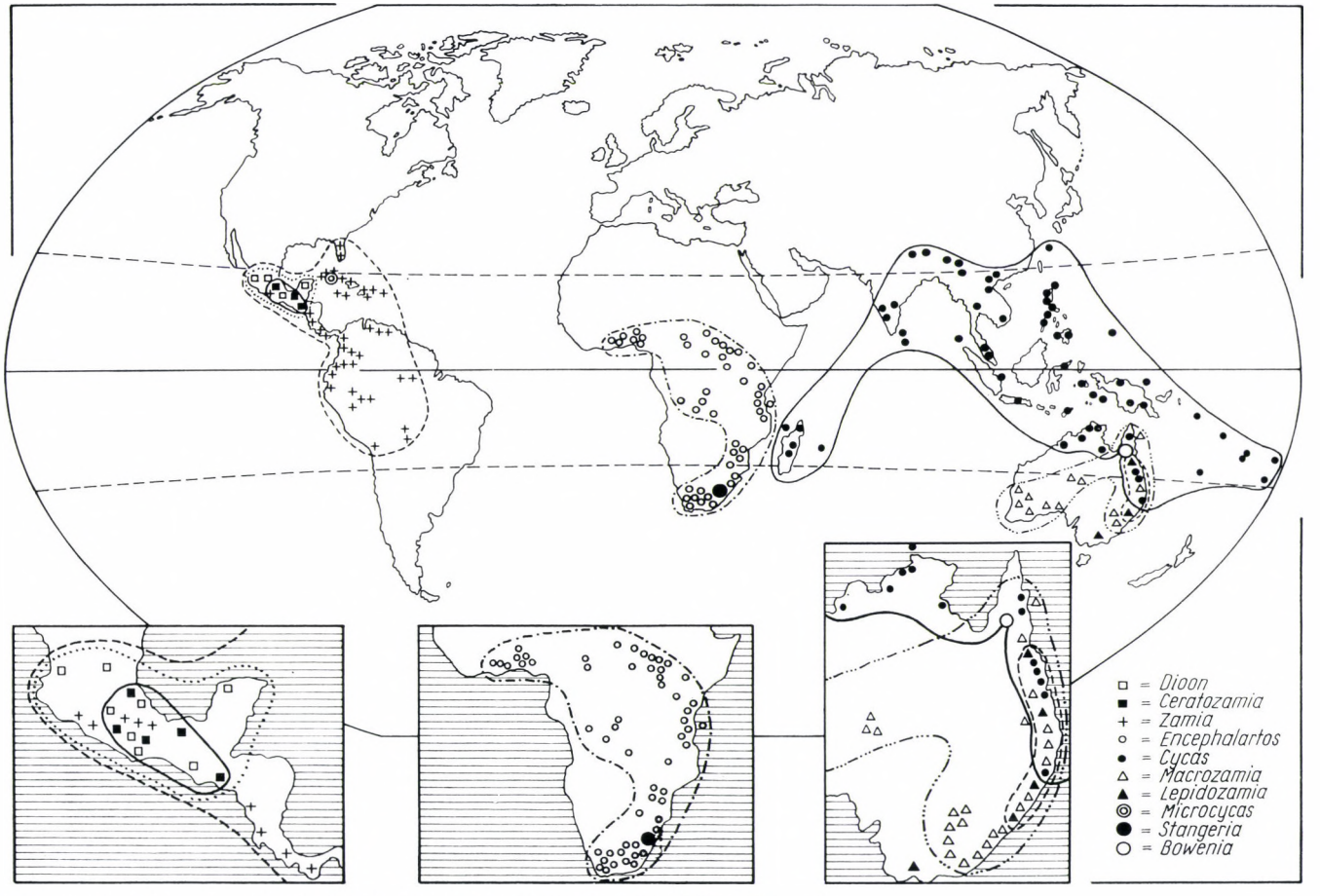
Most Cycads inhabit the tropical zone. In the Mesozoic, they were widespread also in the northern hemisphere, in the temperate zone of the Europe of today. At present they generally live in the equatorial region, in the zone between the Tropics of the Capricorn and of the Cancer. They nowhere form continuous closed stands, but occur sporadically, at most in smallish groups, in the savannah regions and partly in the virgin forests of the mountains. In our days, not a single *Cycas* species is living in Europe, and on the other continents, too, the class is restricted to the tropical regions.

These morphological differences are reflected also in the geographical distribution, since *Encephalartos*, e.g., lives only in Central and South Africa (see Map); also, *Stangeria* lives in a single South African site. *Cycas* occurs from the island of Madagascar through South Asia to the northern coastline of Australia, while *Macrozamia* thrives only in Australia, mainly along the east and west coast. The same holds for the two species of *Bowenia*, while *Microcycas*, *Zamia*, *Ceratozamia* and *Dioon* are restricted to the northern regions of Central America.

Examining in more detail the distribution of the 10 Cycad genera we may state as a general relationship that, on the continents named above, they are found in about equal numbers north and south of the Equator. Indeed, according to the available literature, Cycads are known from 117 sites on the northern hemisphere. This general relationship does not, of course, hold within the individual continents, since in Africa e.g. *Encephalartos* occurs much more frequently (in 42 sites) south of the Equator than north of it (21 sites).

A comparison of the number of sites in Africa and America yields a highly interesting result relevant to Wegener's theory of continental drift. According to this theory, Africa and South America were in the Mesozoic close to each other and drifted apart only in subsequent times. The present geographical spread of the Cycads and the number of the individual sites do not seem to wear out this theory for the following reasons.

The different number of sites of *Encephalartos* north and south of the Equator in Africa has already been mentioned. Another remarkable fact is that while *Encephalartos* extends north of the Equator only to the 10th degree of latitude (to Nigeria), in South Africa it occurs as deep down as 37–38° lat. S. (i.e. to the Cape). In South and Central America the situation is the other way round. In Central America and in South America north of the Equator, *Zamia* is known from about 45 sites; in the southern hemisphere from 11 sites only (see above). Now if, in the Mesozoic, South America and Africa had been in close vicinity, then the



Map showing the geographical distribution of the living Cycads. (After Schuster)

Cycads could have spread more or less evenly on both sides on the Equator, and this distribution should have remained, at least in general outlines, also after the separation. Some Cycads ought to occur on the east coast of Brazil, as well as in Ghana and Nigeria. On the other hand, on the west coast of North Africa, in the region which was supposedly in direct connection with Central America, at least some Cycads should have remained, as Cycads still thrive in many places in Central America. It should be further noted that not a single *Encephalartos* species occurs either in Central or in South America; conversely, not a single *Zamia*, *Ceratozamia*, *Dioon* or *Microcycas* species is found in Africa. The present spread of Cycads in Africa and South America thus contradict the theory of continental drift.

In Central America (Mexico and Cuba), *Ceratozamia* is represented with 2, *Dioon* with 3 species; there occurs also monotypic *Microcycas*; the latter three genera seem to be dying out while *Zamia* still boasts 26 species.

The main range of the genus *Cycas* is southern Asia and the South Asian Archipelago from Madagascar to the Fiji Islands. In Madagascar and the neighbouring islands there is the only genus *Cycas*; none of the *Encephalartos* species of the African continent are encountered there. Although on the African continent there are specimens of *Cycas* near Moçambique bay, these were imported in historical times. On the other hand, the southern part of Madagascar, Ceylon, South-East India, the Malay Peninsula, Vietnam, Japan, Taiwan, Java, the northern and eastern coastline of Australia, Celebes, New Guinea and the Fiji Islands bear only the genus *Cycas*: these scattered sites may once upon a time have been portions of a vast Gondwana continent.

It was probably after the development of the Australian continent and the break-up of Gondwana that the *Macrozamia* species spread in the eastern and mainly in the western coastal region of Australia. In the north-eastern corner of Australia there thrives also monotypical *Bowenia*.

In the geographical spread of the Cycads, the most remarkable fact is that each of the 4 great genera occupies an almost completely isolated area, mixing only in the easternmost and westernmost narrow coastal regions of Australia.

PART ONE

XYLOTOMY OF THE TRUNK

Although different in a number of respects such as external form, development, of flowers, foliage etc., the 10 genera of the class *Cycadinae* have a number of common xylotomical traits which differ fundamentally from those of all other Gymnosperms, first of all of the conifers in the strict sense of the term. In the following, however, we shall attempt to emphasize just those anatomical properties which make it possible to distinguish the individual genera.

CROSS-SECTION STRUCTURE

(Plates II–XI)

Common traits (see Plate I). The most characteristic common features of the trunks of all Cycads are the well-developed pith system (1), the comparatively narrow conductive bundle system (5, 6, 7), the equally well-developed cortical zone (8), and the mucilage canals meandering in pith and cortex (2). All these features are apparent on macroscopic, and partly on microscopic, examination.

In the various Cycad species, the pith is of different bulk as compared with the conductive bundle system and the cortex.

Genus	Height	Overall diameter	Diameter of			
			pith	xylem	phloem	cortex
Ceratozamia mexicana	0·3–2 m	15 cm	5·7 cm	3 mm	2 mm	1·5 cm
Zamia floridana	15 cm	6 cm	1·3 cm	2 mm	2 mm	2 cm
Dioon edule	0·6–1 m	21 cm	6·9–8·7 cm	0·5–1·5 cm	5–8 mm	2–3·2 cm
Dioon spinulosum	6–12 m	33 cm	8 cm	10 cm	1·4 cm	2·5 cm

(After Schuster)

1. THE PITH

(a) *Ground tissue. Thin- and thick-walled parenchyma cells.* The pith invariably occupies the central part of the stem (Plate II, Photos 1, 2, *Stangeria paradoxa*; 3, *Macrozamia douglasii*) and consists largely of thin-walled parenchyma cells (Plate II,

Photo 1). The parenchyma cells are isodiametrical, polygonal, mostly close-packed, but sometimes with minor or major intercellular ducts between them. Although their walls are in most cases thin and smooth, in some species they bear small circular or elliptical pits permitting communication between the cells (Photo 4, *Encephalartos lehmannii*). These thin-walled cells usually contain lots of starch which is used by some tropical tribes to produce sago and other nutrients ("kaffer bread").

In the pith of some species there are scattered solitary cells (idioblasts) fundamentally different in wall structure and pitting from the directly adjacent thin-walled parenchyma cells, although they are of the same size and shape (Photos 5, *Encephalartos altensteinii*; 7, *Lepidozamia hopei*). The pits are always simple and never bordered; consequently, the idioblasts cannot be transfusion cells the pitting of which can always be traced back to bordered pits (Photo 6, *Macrozamia macdonnelli*). Where the parenchyma cells of the pith, penetrating between the xylem bundles, substantially lengthen radially, the idioblasts also elongate, while retaining their simple pitting and parenchymal structure (Plate II, Photo 9, *Encephalartos altensteinii*).

(b) *Transfusion cells* (Plate III, Photos 1–12). *Encephalartos altensteinii*. Distinctly different from the thick-walled idioblasts are the transfusion cells which generally occur adjacent to the vascular bundle rings, at the edge of the pith. Shape and size of these transfusion cells agree with those of the adjacent thin-walled parenchyma cells, but their walls are thick and invariably exhibit bordered pits or scalariform thickening (Plate II, Photos 4, 8, *Macrozamia pauli-guilielmi*). Sometimes they are sporadic especially in the external part of the pith (Plate III, Photos 1, 6, *Cycas neocaledonica*); in other cases they form clusters in the pith, e.g. in *Macrozamia macdonnelli* (Photo 2) and particularly in *Cycas neocaledonica* (Photo 3), *Zamia obidensis* (Photo 10) and *Zamia floridana* (Photo 9) (Plate III, Photos 3, *Encephalartos lehmannii*; 5, *Cycas rumpfii*; 11, *Encephalartos barteri*; 12, *E. septentrionalis*).

These transfusion cells are so typical of the various species and genera that their structure may be taken as a criterion in the determination and distinction of the species (Plate IX, Photo 8).

(c) *Mucilage canals* (Plate IV, Photos 1–9). Another characteristic feature of the pith of the Cycads is that it is interwoven with tubular mucilage canals. The canals are in most cases scattered in the pith or form a more or less elliptical, loose ring directly within the vascular bundle rings of the xylem (Plate VII, Photo 1g, *Zamia pumila*). In places in the longitudinal sections they are seen to pass through the broader primary pith rays into the cortex and from there into the leaves. The mucilage canals are of schizolysigenous origin. They are surrounded by so-called peripheral cells while their interior is lined with papilliform cells secreting a mucous substance (Photos 2, 3, *Stangeria paradoxa*; 9, *Zamia floridana*). Their diameter varies between 130 and 550 μ, similarly to those of the mucilage canals in the cortex (Photos 4, *Encephalartos lehmannii*; 5, *E. villosus*; 6, *E. altensteinii*; 7, *E. gratus*; 8, *Ceratozamia mexicana*).

The function of the mucilage canals is in all probability connected with the water household: during spells of drought they may function as water reservoirs; after injuries, they produce protective substances preventing the penetration of bacteria causing rot.

(d) *Proper bundles* (Plate V, Photos 1–5). In the pith of most genera there are interconnected collateral tracheid bundles, meandering along at random but without passing through the pith rays into the vascular bundle ring or into the cortex (Photo 2a, *Encephalartos altensteinii*). In these bundles there are only a few tracheid rows; the phloem portion is similarly underdeveloped. The collateral structure, however, is obvious (Photo 3).

In this respect, *Dioon edule* is of particular interest as in its pith – at least in the specimen examined – there are no pith parenchyma cells, their place being taken up by a dense tangle of conductive bundles. In the interior of these bundles, the central xylem is surrounded by a narrow phloem bundle followed by a narrow cortex and, remarkably, by a periderm covered with cork cells (Plate V, Photos 2, 3, *Encephalartos altensteinii*; 4, *Dioon edule*). Thus their structure agrees with that of the undeveloped stem or of the root penetrating into the soil (see also Photo 4).

It is improbable that this skein of roots entered the pith subsequently, since these "pith roots" reach rather far up into the higher regions of the stem. That these are really the true bundles of the pith, is probable, because they are quite easy to move about in the pith, not being surrounded by any ground-tissue parenchyma. Their thickness may attain 2 mm. The assumption that they are true roots is borne out by their rather thick periderm and cork layer (Photos 1, 4, 5).

(e) *Common vascular bundles* (Plate V, Photos 4, 5, *Dioon edule*). *Encephalartos* and *Macrozamia*, e.g. have common conductive bundles. The common bundles differ from the proper bundles – to which they are highly similar in structure – only in that they issue from the pith through the primary pith rays into the cortex and from there continue as leaf-scar bundles into the leaves. The common bundles are generally accompanied by the mucilage canals which as a rule run on the phloem side of the conductive bundles.

(f) *Calcium oxalate crystals* (Table V, Photos 6–9). In the parenchyma cells of the pith, calcium oxalate crystal druses are rather frequent which generally fill out the parenchyma cells alone (Plate V, Photos 7, *Dioon spinulosum*; 8, *Encephalartos barteri*). The crystal druses are of the same form and structure in all Cycad species. In some species, they tend to concentrate in the external part of the cortex, near the vascular bundles and mucilage canals.

Besides the crystal druses, the pith parenchyma cells of some Cycads contain rhombohedral crystals, singly or in minor or major clusters (Plate V, Photos 6, 9, *Cycas circinalis*).

2. CONDUCTIVE BUNDLE LAYER

The extensive pith is surrounded by a conductive bundle layer which belongs to either of two types: the monoxylic type (Plate VI, *Microcycas*: Photo 1, *Ceratozamia*: Photo 2, *Zamia*: Photo 3, *Dioon*: Photo 4, *Stangeria*: Photo 5, *Bowenia*: Photo 6) and the polyxylic type (Plate VII, *Encephalartos*: Photo 1, *Cycas*: Photo 2, *Macrozamia*: Photo 3, *Lepidozamia*: Photo 4).

(a) *Monoxylic type* (Plate VI, Photos 1–6). In this type there is a single vascular bundle ring which consists of two layers: the xylem and phloem (Plate IX, Photo 1, *Zamia skinneri*). Their thickness is but a few millimeter, being greatest in *Dioon spinulosum* where the xylem may measure 10 cm, the phloem 1·4 cm (Plate IX, Photo 7).

Both layers are divided up by the primary pith rays into collateral bundles (Plate V, Photo 2, *Encephalartos altensteinii*; Plate IX, Photo 1h, *Zamia skinneri*); these larger units are further dissected by the secondary, uni- or biseriate pith rays.

The primary pith rays are the direct continuation of the pith parenchyma (Plate IX, Photos 1, *Zamia skinneri*; 4, *Cycas circinalis*). At the beginning of a pith ray there is practically no difference between the parenchyma cells of the pith and of the ray (Photo 4). At the edge of the pith, the pith ray cells begin to lengthen radially as they enter between the xylem bundles, but remain unchanged in structure and wall thickness; subsequently running along with the narrow cambium layer of the primary rays, they penetrate between the phloem bundles; then, as a consequence of dilatation, they slightly spread out and pass almost imperceptibly into the parenchyma cells of the cortex the size and structure of which agree with those of the pith parenchyma cells. This structure of the primary pith rays also bears out the hypothesis that the pith rays of the Cycads derive from the pith parenchyma (Photos 1, *Zamia skinneri*; 4, *Cycas circinalis*).

In the primary pith rays there are frequent conductive bundles and mucilage canals, running as a rule close to each other (Plate XII, Photo 6, *Cycas neocaledonica*). Among the thin-walled pith ray cells there occur in places some thick-walled parenchyma cells, and transfusion cells as well, mostly side by side with the tracheids (Plate II, Photo 7, *Lepidozamia hopei*).

Both the primary and secondary pith ray cells are distinctly different in size from the adjacent more or less isodiametric xylem and phloem parenchyma cells: the latter are almost invariably smaller, but their walls are as thin and smooth as those of the pith ray cells (Plate X, Photo 2, *Macrozamia miquelii*).

Xylem bundles. The collateral bundles between the primary pith rays form a ring around the pith (Plate VIII, Photo 1, *Zamia skinneri*). On the side facing the pith of the xylem bundles there are in most cases protoxylem elements in fours or fives or in clusters. They are followed by the radially arranged tracheids of the xylem bundles (Plate IX, Photos 4, *Cycas circinalis*; 5, *Encephalartos villosus*; 6, *Encephalartos septentrionalis*).

The cross sections of the tracheids of the xylem are generally square or rectangular but their lumina are invariably rounded (Photos 3, *Macrozamia hopei*;

5, *Encephalartos villosus*; 7, *Dioon spinulosum*). Close packed as a rule, they are in places separated by one or two thin-walled xylem parenchyma cells in direct or indirect contact with the parenchyma cells of the pith rays (Plate IX, Photo 5, *Encephalartos villosus*).

A few xylem parenchyma cells among the tracheids are filled out with calcium oxalate crystal druses.

Most xylem bundles are only 2 or 3 tracheids wide (Plate IX, Photos 4, 5) but some attain the width of 8 to 10 tracheids. *Dioon spinulosum* is exceptional in that its xylem is not dissected into smaller collateral bundles but forms a continuous ring, interrupted here and there by pith rays uni- or biseriate (Photo 7).

Phloem bundles (Plate X). The phloem bundles are as a rule separated from the xylem by a cambium consisting of 2 or 3 cell layers (Photo 1, *Cycas rumpfii*). Thence they proceed outward, one phloem bundle corresponding to each xylem bundle, until, gradually and conically tapering, they end near the cortex, separated in most cases from this latter by the primary phloem elements. The phloem ring is divided up by the primary pith rays into wider or narrower phloem bundles in the same way as the xylem ring; the phloem rings are likewise further dissected by the uni- or biseriate secondary pith rays. The individual phloem segments are at most quadriseriate and most often only biseriate (Photos 2, *Macrozamia miquelii*; 3, *Cycas media*; 4, *Dioon edule*).

The phloem bundles consist of (1) phloem fibres, (2) phloem parenchyma cells and (3) sieve tubes.

The *phloem fibres* (Photos 2–9) occur either singly or in clusters, sometimes even in the form of parallel plates, which latter frequently alternate with parenchyma plates. The phloem elements are square or rectangular in cross section; their lumina are circular or slit- or pin-prick-like. Their walls are invariably thick (Photos 5, 6).

Among the phloem fibres there are *phloem parenchyma cells.* In some species, phloem parenchyma is rather subordinate (Photo 3, *Cycas media*), in others there are hardly any fibres among the parenchyma cells (Photo 4, *Dioon edule*). In the parenchyma cells of the phloem, calcium oxalate crystal druses and single rhombohedral crystals or clusters of such are rather frequent.

Sieve tubes. Beside the above-mentioned elements of the phloem bundles there occur in the phloem some rare sieve tubes, easy to recognize by their cross-field-like sieve structure. In cross section, they are much larger than the fibres or parenchyma cells. A sieve plate may contain 30 to 40 sieve holes (Plate X, Photo 7, *Cycas media*).

Occasionally fibres of much larger cross section than the normal phloem fibres are observed: although remarkably thick walled, these nevertheless have invariably wider lumina than the normal fibres (Photos 8, *Encephalartos lehmannii*; 9, *Cycas siamensis*).

(b) *Polyxylic types* (Plate VIII, Photos 3, 4, *Encephalartos altensteinii*). In the polyxylic types there is a succession of vascular bundle rings (cd) replacing the single one of the monoxylic types. It is known from literature that e.g. in a specimen of *Cycas rumphii* (Plate VII, Photo 2) of 8·5 cm diameter, 22 vascular bundle

rings were counted; in a specimen of *Encephalartos tombifolius*, 24 successive rings had developed. In the polyxylic types, the vascular bundle rings succeeding the first ring are often termed abnormal rings, although their structure completely agrees with that of the first ring. These abnormal rings are so formed that on the external part of the previous ring, in the region of the pericycle, the parenchyma cells of the cortex are transformed into a meristem which produces xylem elements inwards and phloem elements outwards. Between the vascular bundle rings there are frequent transfusion cells, the pitting of which fully agrees with that of the tracheids of the xylem rings, favouring the assumption that the tracheids developed from these transfusion cells. The tangential section reveals almost step by step how the initially isodiametric transfusion cells gradually lengthen and turn into true tracheids (Plate III, Photos 9, *Zamia floridana*; 10, *Z. obidensis*; 11, *Encephalartos barteri*).

The abnormal vascular bundle rings are, however, in no way related to annual rings. The xylem of Cycads exhibits no definite annual rings as does e.g. that of the conifers. In a *Cycas* 100 or 150 years old there are at most 20 or 25 such rings. At the apex of the stem there is originally no bundle ring at all; the first one develops somewhat below the apex.

The finer longitudinal structure and pitting of the xylem fibres in the tracheids of the vascular bundle ring will be described in detail in the chapter on the longitudinal section.

3. CORTEX

(Plate XI, Photos 1–9).

The structure of the cortex is largely similar in all Cycads; size, pitting and wall thickness of the cortical parenchyma cells essentially agree with those of the ground tissue cells of the pith. It is at most near the periphery of the cortex that they flatten and radially shorten while lengthening tangentially (Photos 1–6).

Calcium oxalate crystals are much frequent in the cortex than in the pith, actually forming layers at the cortical periphery of some specimens (Photo 4, *Macrozamia macdonnelli*). The number of the mucilage canals in the cortex is somewhat larger (Photos 3, 5, 6, *Zamia skinneri*) and the canals are particularly near the external vascular bundle ring, arranged to form a ring (Photo 3, *Dioon edule*). This, however, is no general rule.

Cortical bundles (Plate VIII, Photo 4, *Encephalartos altensteinii*; Plate XI, Photo 3, *Zamia skinneri*). The cortical bundles agree in structure with the common bundles of the pith. The cortical bundles are also collateral and accompanied by mucilage canals, as a rule on the phloem side. The cortical bundles meander to and from in the cortex and subsequently emerge as leaf scar bundles into the leaves where in the leaf base they are mostly arranged in a ring. One such common bundle consists of 100 to 150 tracheids and almost as many phloem parenchyma cells and fibres (Plate V, Photo 3).

4. PERIDERM

(Plate XI, Photos 1–6).

On the stems, or at least on those parts of the stems where the leaf bases remain on the stem for a long time and form an armour over its surface, there is no periderm in the strict sense of the term; the parenchymatic structure of the cortex passes almost imperceptibly into the leaf base which initially remains on the stem as a leaf stump (Plate XI, Photo 7, *Ceratozamia mexicana*). On the older stem sections, however, or on species which soon lose the leaf stumps, a cork cambium develops in the leaf base or in the external part of the cortex. Giving rise to suberized cells, this cork cambium or phellogen gradually develops a phellom which in a suitable stage of ontogeny becomes the impermeable covering of the stem. This process of abscission may last several years.

In the species whose stem creeps in the ground, the foliage leaves get soon detached from the surface of the stem. Before the abscission of the leaf, a thicker or thinner periderm layer is developed. On the external part of the cortex a phellogen, i.e., a meristematic cork cambium develops (Plate XI, Photo 6); actively dividing, it gives rise externally to suberized cells which cover the surface of the stem in various thickness. This external armour may attain on some older stems a thickness of 10 cm. In *Stangeria*, *Lepidozamia* and *Zamia* the leaf bases rather soon fall off and the exterior of the periderm becomes quite smooth (Plate XI, Photo 9, *Lepidozamia hopei*).

The multitude and meandering of the vascular bundle rings in the cortex and the abundance of calcium oxalate crystals largely contribute to the strength of the stem which is mostly composed of parenchyma cells. *Zamia* and *Stangeria* which mostly develop underground stems have comparatively few conductive vessels; also, their vascular bundle ring is one-layered only. As a contrast, in the tall species the mass strengthening xylem bundles is much better developed.

5. LEAF SCARS

(Plate XI, Photo 8, *Encephalartos septentrionalis*)

When the leaves and leaf stumps fall, they leave behind cicatrices or leaf scars on the surface of the stem. The cicatrices are, in conformity with the cross section of the rachis, mostly rhomboidal. The subsequent thickening of the tree causes these marks to disappear gradually and at last their place is occupied by a more or less smooth periderm.

TANGENTIAL STRUCTURE

(Plate XII, Photos 1–9)

1. THE PITH

As was to be expected after the comparative monotony of cross-sectional structures, the stem of the Cycads exhibits no great variety of tangential structures either.

(a) *Ground tissue.* The cells are also here more or less isodiametrical. No particular lengthening in the direction of the longitudinal axis is observed. The mucilage canals and the conductive bundles are seen to meander also from this side. All variety is restricted to the structure of the conductive bundles.

(b) *Pith ray* (Plate XII, Photos 1–8). The pith-ray system is characteristic of the Cycads inasmuch as the pith rays may be uni- and multiseriate up to 10 cells wide. The uniseriate rays are generally 1 to 10 cells high, whereas the primary rays may attain the height of 40 cells. The sections of the pith ray cells are in most cases upright, elliptic and very seldom procumbent (Photo 7, *Encephalartos villosus*). In the cells of the broad pith rays, calcium oxalate crystal druses are frequent (Photos 2, 3, *Dioon spinulosum*). Some rays include also thick-walled parenchyma cells (Photo 1, *Cycas media*).

The vertical xylem and phloem bundles are in lateral contact in those sections where there is no intercalated ray between them (Photo 6, *Cycas neocaledonica*). From the vertical bundles, lateral bundles branch out, penetrating into the cortex and emerging as leaf scar bundles into the leaves (Plate V, Photo 5, *Dioon edule*). Thus the conductive bundle system issuing from the pith and breaking through to the cortex in the form of primary pith rays and the secondary bundles reaching the cortex and the leaves form a coherent system which supplies with nutrients all parts of the plant.

In the stems of the species creeping in the soil the conductive bundles are considerably underdeveloped. These are mostly monoxylic species nearer in our opinion to the ferns, i.e. of more primitive type. As a contrast, in the species of tall and thick stems the conductive tissues are more developed. These are the more modern forms of the polyxylic type.

The uni- and multiseriate pith rays are flanked on either side by bundles of meandering tracheids. A bundle may include as many as 10 tracheids but in other cases each pith ray is flanked by 1 or 2 tracheids only (Plate XII, Photos 4, *Encephalartos altensteinii*; 5, *Cycas neocaledonica*; 6, *Lepidozamia hopei*; 7, *Encephalartos villosus*; 8, *E. barteri*). This structure depends of course on how far off-centre the tangential section intersects the xylem and the phloem.

(c) *Transfusion cells.* The tangential section shows how the transfusion cells adhere to the tracheids and how the initially more or less isodiametric transfusion cells gradually elongate into tracheids (Plate III, Photos 4, *Macrozamia pauli-guilielmi*; 8, *Zamia floridana*; 9, *Z. obidensis*). The pitting of these transfusion cells is exactly as that of the tracheids. This gradual transition confirms the idea that the tracheids originate from transfusion cells and the latter from parenchyma cells.

2. CONDUCTIVE BUNDLES

(Plate XII, Photos 3–5)

(a) *Xylem bundles.* In the xylem bundles, the tangential walls of most longitudinal tracheids are entirely smooth but some portions may be covered with tiny araucarioid bordered pits (Photo 3, *Encephalartos gratus*). There is, however, no uninterrupted bordered pitting in the tangential walls of the tracheids. On the other hand, in the tracheids of the species whose radial walls exhibit scalariform thickening (Photo 1, *Stangeria paradoxa*), the tangential walls are also thickened that way (Photo 7, *Encephalartos gratus*).

Among the longitudinal tracheids, some xylem parenchyma cells may also occur (Photo 2, *Cycas revoluta*).

(b) *Phloem bundles.* In the phloem bundles, the structure of the pith rays is as in the xylem bundles. The pith rays are also here uni- or multiseriate, up to 10 cells wide (Plate XII, Photo 8, *Encephalartos barteri*). The difference between the two kinds of bundle is that the pith ray cells are somewhat larger and wider between the phloem bundles than between the xylem bundles. Of special interest is the phenomenon that where the endings of the phloem bundles taper off conically the primary pith rays flare out almost trumpet-like. In such cases, the pith ray cells lengthen tangentially until their radial dimension becomes much less than the tangential (Plate X, Photo 6).

In the tangential sections of the phloem bundles, the structure of the fibres, of the phloem parenchyma cells and very exceptionally of the sieve tubes is seen.

The *fibres* are thick-walled phloem elements the lumen of which can be slit-like or somewhat wider (Plate XIII, Photo 8, *Ceratozamia mexicana*). The *phloem parenchyma cells* among them have essentially the same structure as the pith ray cells, at most they are somewhat elongated vertically. Their walls are thin and completely smooth.

The plates of the sieve tubes (or sieve cells) are seen only in the rare case when the plane of the section by chance coincides with the sieve plate.

3. CORTEX AND PERIDERM

In tangential section the arrangement and finer structure of the tissues appear essentially the same as in cross section, with the difference that the cells of the cortex are seen to be somewhat elongate longitudinally.

RADIAL STRUCTURE

(Plate XIII, Photos 1–8)

1. THE PITH

(a) *Pith rays.* From the radial side it is the structure of the pith rays, the composition of the conductive bundles, the shape, size and finer structure of the pith ray cells that deserve particular attention. In radial view, the pith ray cells are generally square, rectangular or polygonal, rather often hexagonal (Photo 1, *Zamia*). As a rule they are upright but square pith ray cells are rather frequent, too. Their size is varied, their wall invariably thin and smooth.

(b) *Cross fields.* Where the pith ray cells contact the axial tracheids, cross fields arise (Photos 2, *Cycas revoluta*; 3, *Encephalartos gratus*; 4–6, *Cycas beddomei*; 7, *Encephalartos gratus*). The cross fields are sometimes well marked, in other cases less conspicuous. Generally speaking, wherever thin-walled pith ray cells contact tracheids in whose walls the bordered pits follow the araucarioid pattern, the cross fields tend to include more araucarioid pits. The number of pits is varied but always rather high: 5 to 35 per cross field (Photos 2–7). Their apertures are linear or slit-like, almost extending beyond the outline of the pit border. Frequently the apertures of two adjacent pits are coalescent (Photo 3); occasionally three pit apertures may coalesce, and then this common aperture nearly reaches clear across the wall of the tracheid. Several such coalescent apertures above each other give rise to scalariform thickening, so characteristic of some Cycads, particularly of *Zamia* and *Microcycas*. Locally there are third apertures intercalated from the side between two such coalescent ones resulting in an alternation of shorter and longer apertures in the tracheid wall.

Where the pith ray cells contact tracheids with exclusive scalariform thickening, there develop no explicit cross fields nor pits (Photo 1). Such are the *Zamia* or *Stangeria* species of subterranean stem. In such cases the pitting is interrupted in certain sectors of the tracheid walls, namely in those places where the horizontal wall of the pith ray cell contacts the tracheid wall. This phenomenon may be interpreted to mean that the tracheids and pith ray cells communicated by the slits of the scalariform thickening rather than by bordered pits.

(c) *Thick-walled pith ray cells.* Among the thin-walled pith ray cells there are in places pith ray cells of the same shape and size but of substantially thicker wall. These cells bear a simple pitting and cannot consequently be regarded as radial tracheids but rather as idioblasts. In some of them the walls are so much thickened that the lumen is contracted almost to a pin-prick (Plate XII, Photo 1, *Cycas media*).

2. CONDUCTIVE BUNDLES

The *elements* of the xylem are the tracheids. Their length may amount to a few millimeter; the so-called short tracheids are only a few hundred μ long.

(a) *Short tracheids.* These fully agree in pitting with the long tracheids; perpendicular to the stem axis, their transverse walls bear 2 or 3 large bordered pits through which vertical communication takes place (Plate XVI, Photo 3). The short tracheids are particularly conspicuous in *Zamia skinneri.*

(b) *The tracheids* (Plates XIV–XVI). In the walls of the tracheids of the Cycad genera, bordered pits and scalariform pitting are most common. There are genera, e.g. *Cycas*, whose tracheids bear almost exclusively bordered pits in three or four longitudinal rows, in close-packed alveolar or araucarioid arrangement (Plate XIV, Photos 1, *Encephalartos gratus*; 2, *Lepidozamia hopei*). In the *Encephalartos* species this arrangement is much looser, the borders of the pits are wider spaced, with minor or major gaps between them; in some places the pits are quite sparsely scattered, forming in the simplest case a unique longitudinal row (Plate XIV, Photos 3, *Cycas media*; 7, *Zamia skinneri*).

The apertures of the bordered pits are linear or slit-like, mostly included. Frequently too, the apertures are arranged crosswise on opposite walls of the tracheids (Photo 3, *Cycas media*).

Pitting sometimes exhibits a number of transitions in one and the same species forming an araucarioid pattern in one tracheid, the pits are coalescent in the next. In such cases the coalescent aperture is horizontal (Plate XIV, Photo 1, *Encephalartos gratus*), while in other cases this gradual transition passes into scalariform thickening (Photos 5, *Zamia furfuracea*; 6, *Encephalartos barteri*). Beside a mere bordered pitting tracheids with an overall scalariform thickening may thus occur. Different variants and degrees of the pitting of tracheids are presented in Plate XVI, Photo 3, *Cycas media*). The so-called modern pitting is, however, invariably absent from the Cycads, as a further argument for a lineage different from that of the conifers.

(c) *Perforations.* An interesting variety of the pitting of tracheids is when the tracheid walls bear simple or definitely scalariform perforations (Plate XIV, Photos 2, 3, *Lepidozamia hopei*).

Primordia of simple perforations. Very seldom there are at some points of the tracheid walls, as a rule near the ending of the tracheid, three or four smaller or larger bordered pits forming an elliptical or circular cluster in a pattern greatly suggestive of the development of perforations in *Ephedra* and *Gnetum.* To all probability, this primitive form of perforation occurs also in other Cycads (Plate XIV, Photo 10, *Cycas beddomei*).

Much more interesting is the phenomenon when on the one radial face of a tracheid there are decidedly bordered pits close-packed in the araucarioid pattern whereas on the other face the apertures of one-time bordered pits, substantially widened, reach over the wall from one edge to the other. This phenomenon is repeated several times in the axial sense; as a result, steps as high as the transverse

ladder intervals between them come to exist. This structure is exceedingly similar to the perforations connected with scalariform thickening of the Monocotyledons, particularly of the palms and Pandanus (Plate XV, Photos 1, *Cycas siamensis*; 2, *Encephalartos gratus*; 3, 4, *Zamia skinneri*; 5, *Encephalartos villosus*; 6, *Zamia muricata*; and Plate XVI, Photos 1, *Zamia obidensis*; 2, *Zamia muricata*; 3, *Zamia skinneri*).

The steps may in places number 15 to 20, in others even 50 to 60. The observation that there may be two different structures in the walls of the same tracheid is proved by the fact that, between the steps, the bordered pitting in the wall behind is readily visible in every case (Plate XIV, Photo 2, *Lepidozamia hopei*).

According to this observation, vascular structures may occur not only in some Pteridophytes (Pteridosperms, Chlamydosperms) but also in the Cycads.

(d) *Phloem elements*. The longitudinal structure of the phloem elements, their wall thickness, width of lumen etc., was discussed already when dealing with the tangential section, so that we need not further pursue this subject here (Plate XIII, Photo 8, *Ceratozamia mexicana*).

3. CORTEX AND PERIDERM

On the radial section, the structure of cortex and periderm is essentially the same as shown in the cross and tangential section; this makes further discussion superfluous.

XYLOTOMY OF THE SPECIES

1. CYCADACEAE

In his monograph on the *Cycadaceae*, Pilger (1926) distinguished 15 species within the genus *Cycas*; Schuster in 1932 reduced this number to 8 (*Cycas cairnsiana*, *C. circinalis*, *C. media*, *C. micholitzii*, *C. nathorstii*, *C. revoluta*, *C. rumphii* and *C. siamensis*). Some species enumerated by Pilger are regarded as varieties by Schuster: e.g. *C. beddomei* and *C. neocaledonica* are considered as variants of *C. circinalis*. In the present volume we shall deal with five out of Schuster's 8 species, beside *C. beddomei*, *C. normanbyana* and *C. neocaledonica*, i.e. with a total of 8 species or varieties of the genus *Cycas*.

All the *Cycas* species examined are polyxylic, i.e., their stems include several xylem and phloem rings. This repetition is two- or threefold in most stems; it is fivefold in *C. rumphii*. In the older stems this number may probably increase up to 10 while in the young ones only a monoxylic ring could develop. All species feature the well-developed pith characteristic of the Cycads which in some cases may amount to one-fourth or one-third of the outside diameter of the xylem. The pith is interwoven with mucilage canals and collateral bundles which as a rule emerge

through the primary pith rays into the cortex whose structure is similar to that of the pith.

A common anatomical property is the araucarioid pitting of the tracheids but various transitions toward scalariform thickening are also rather frequent.

Another common trait is that the cross fields always include several (4 to 20) pits and that the horizontal or oblique apertures of the pits are slit-like in most cases.

Cycas beddomei Dyer (1883)

(Plates XVII, XVIII, Photos 1–12)

Although this species is regarded by Schuster only as a variety [*C. circinalis* var. *beddomei* (Dyer) Schuster], on the basis of its anatomy it deserves specific rank, as was stated also by Pilger. In its histological structure it does not resemble either *C. circinalis* or *C. revoluta*, although it was in 1869 described as *C. revoluta* by Beddome. Its area of distribution is South India (the State of Madras) and Java. Its occurrence in these regions is probably due to human activity. The stem samples examined were presents from the Royal Botanic Gardens in Kew.

Macroscopical examination. On the cleaned and polished surface of the specimen the characteristic structure of Cycads could be immediately observed (Plate XVII, Photos 1, 2, 3). The diameter of the pith is 4 to 4·5 cm (a); the thickness of the double xylem and phloem ring (c, d) is 2 cm; that of the cortex (e) plus periderm (f) is 2·5 to 3 cm. The exterior of the stem bears the bases of fallen leaves. Both in the pith and in the cortex, the dark spots and lines represent mucilage canals (g) and vascular bundles.

Microscopical examination. Cross section. The pith consists largely of thin-walled parenchyma cells whose interior is rich in starch. The cell sections are circles or somewhat flattened ellipses of 110 to 120 μ diameter but locally they become angular owing to compression. At the edge of the pith the mucilage canals are arranged in a sort of ring; their diameter is 510 to 520 μ (Photos 2, 7g [$\times$ 100]). Their interior is lined with epithelial cells. Besides this mucilage canal ring, there are in the interior of the pith also solitary mucilage canals. The members of the external mucilage canal ring are generally arranged in the same sectors as the primary xylem bundles. In the pith there are also sporadical solitary vascular bundles which in most cases emerge into the cortex through the primary pith rays.

Vascular bundle ring. On the border of pith vascular bundle ring there are in places clusters of transfusion cells (Photo 1b [$\times \frac{2}{3}$]), which continue towards the vascular bundles. In some places, however, protoxylem elements may be arranged inside the xylem bundles.

Pith rays. The pith sends outwards primary pith rays that pass between the xylem bundles. The cells of the primary pith rays are somewhat elongate radially. The xylem bundles between the primary pith rays are subdivided by the secondary uni- to triseriate pith rays (h) into finer tracheid sections (Photo 5 [$\times$ 100]), 1 to 3 cell

layers wide, including some scattered xylem parenchyma cells. The tracheids of the xylem bundles are never quite axial but meander in all directions; this is why it is practically impossible to get a faultless cross-section picture (Photo 5). The tracheids are square (Photo 5c) or polygonal in cross section; their radial dimension is 40 to 50 μ, their width about the same or somewhat less. The cambium, 1 or 2 cell layers thick (Photo 2 [$\times$ 3], between c and d) separates the xylem bundles and the phloem bundle (d). In the phloem bundle, the fibres are either solitary or paired, but nowhere grouped into fibre plates (Photos 2, 3 [$\times$ 100], 4 [$\times$ 200]); most of the phloem consists of parenchyma. The walls of the phloem fibres are thick, their lumina point- or gask-like (Photo 4).

First abnormal ring. The phloem ring is immediately followed by the first abnormal xylem and phloem ring; the structure of this abnormal ring fully agrees with that of the first (normal) ring, so that its detailed discussion can be dispensed with.

Tangential section (Photos 8 [$\times$ 100], 9 [$\times$ 100]). The pith rays are uni-, bi- or multiseriate (h). The uniseriate rays are 1 to 5 cells high, the biseriate rays attain a height of 10 to 12 cells, while the multiseriate rays may be up to 40 cells high. The height of the pith ray cells is 60 to 70 μ, their width 40 to 50 μ. The cells in the multiseriate rays are somewhat lower. In the broader rays, vascular bundles and mucilage canals run from the pith towards the cortex. In places, the tracheids are joined by transfusion cells; here and there the transfusion cells are seen to elongate substantially and to change gradually into tracheids (Photo 8).

Tracheids. The tangential walls of most tracheids are smooth, but some bear bordered pits, scattered or in rows (Photo 7 [$\times$ 100]).

Radial section. There are upright, square and procumbent pith ray cells. All cell walls are thin and smooth. The contact between axial tracheids and ray cells gives rise to cross fields (Photos 10–12) including 8 to 10, sometimes even 20 pits. The pit apertures in the cross fields are mostly horizontal. The chambers and apertures of some pits may be elongate horizontally, in some cases to the point that two adjacent apertures coalesce (Photos 11 [$\times$ 300], 12 [$\times$ 600]).

Tracheids. In the tracheid walls the bordered pits are generally arranged in the araucarioid pattern (Photos 11, 12). The chambers of most bordered pits are, however, horizontally somewhat elongate and in very rare cases even coalesce from the one tangential wall to the other, which gives rise to a structure suggestive of scalariform pitting. Definite scalariform thickening does not, however, occur in this species. On the other hand, the tracheid walls locally bear clusters of 4 or 5 bordered pits which look like primordia of primitive perforations (see top centre of Photo 10 [$\times$ 300]).

Cycas circinalis L. (1753)

Plates XIX, XX, Photos 1–14; Fig. 1

Area of distribution South India, Ceylon, Java, Sumatra, Taiwan and the Philippines.



Fig. 1. *Cycas circinalis* (after Graf)

A tree reaching a height of 5 to 6 m, it bears at its top a tuft of leaves 2 to 2·5 m long. The leaflets of the compound leaves are 30 cm long and 1 to 1·5 cm wide. The material has been received from India.

Macroscopic examination. On the smoothly cut cross section, the typical extensive pith and polyxylic structure of the Cycads is conspicuous. In the stem of about 10 cm diameter, the pith (Photo la [×1·5]) is about 4 cm wide, the polyxylic xylem-phloem ring 2 cm thick and the cortex even in its dried-out condition about 3 cm thick.

Microscopic examination. Cross section. The pith largely consists of more or less isodiametrical thin-walled parenchyma cells circular or of some similar cross section, whose interior is filled with starch. Their walls bear randomly scattered simple pits. In the parenchymatous ground tissue there are comparatively few mucilage canals lined with thin epithelial cells meandering in various directions (Photo 2g [×8]). Their diameter ranges from 330 to 370 μ; the epithelial cells 40 to 50 μ in diameter are much smaller than the surrounding parenchyma cells.

Pith rays (h). At the edge of the pith, the parenchyma cells pass imperceptibly into the primary pith rays, at the beginning of which the cells fully agree in shape and size with the parenchyma cells of the pith. The primary pith rays dissect the xylem ring into minor and major (narrower and wider) collateral vascular bundles (Photo 2h). The pith ray cells between the bundles are substantially elongate radially; their radial dimension is 250 to 300 μ, their width 70 to 80 μ. The walls are also here invariably thin, unpitted. In the secondary rays and in

places also at the beginning of the primary rays – i.e. between the adaxial portions of the xylem bundles – the ray cells are tangentially lengthened to 140 or 150 μ; their radial dimension is much less (100 to 110 μ). The pith of the material examined contained neither proper nor common bundles. The cells of the secondary and primary rays contain octahedral or rhombohedral single crystals of calcium oxalate (Photos 5 [$\times$ 100], 7i [$\times$ 200]), but no crystal druses.

Vascular bundle ring (Photo 1c,d, c,d). *C. circinalis* is a typically polyxylic species. On the side facing the pith of the primary xylem ring, protoxylem elements are rare and transfusion cells wholly lacking. The vascular bundle ring generally begins with uniseriate rows of tracheids; there are farther outwards some rows having the width of 5 to 7 tracheids but most of them are only 3 or 4 tracheid wide. In cross section, most tracheids are rounded squares (Photo 5c). Their lumina are invariably rounded. Among the tracheids there occur a few scattered thin-walled parenchyma cells. The pith ray cells between the tracheid rows are of about the same size in cross section as the tracheids (Photo 5).

The primary xylem ring is followed by a narrow cambium ring and a phloem ring (Photo 3). Then there is a further xylem–phloem–xylem succession (Photo 2cd, cd, c).

Phloem rings (Photos 3d [$\times$ 50], 2d – d). The first cambium ring is followed by a phloem ring narrower than the first xylem ring. The phloem bundles correspond to the bundles of the xylem ring (Photo 2), being likewise interrupted by primary and secondary pith rays. The phloem consists largely of fibres (Photos 3d, 4d [$\times$ 100]) arranged in tangential plates, separated by layers of phloem parenchyma (Photo 4). The phloem fibres are thick walled, their lumen is slit-like. Near the periphery of the phloem there are the phloem primanei. In the ray cells (Photo 5h) and in the xylem parenchyma cells, octahedral or rhombohedral single calcium oxalate crystals (i) are rather frequent. The same structure repeats itself in the first and second abnormal vascular bundle ring (Photo 2cd, cd, c).

Cortex. Its structure completely agrees with that of the pith (Photo 6e [$\times$ 100]). The only difference is that there are many more mucilage canals and collateral leaf-scar bundles in the cortex. The diameter of the mucilage canals in the cortex is 150 to 180 μ, much less than in the pith (g). The parenchyma cells of the cortex are very rich in starch. The walls of the epithelial cells in the mucilage canals must be chemically different, as they readily take a stain with safranin whereas the walls of the parenchyma cells around them do not.

Periderm. The cortex is limited outwards by the close-packed suberized cells of the periderm (Photo 1f).

Tangential section. Most pith rays are also in this view uni- to triseriate, but the primary rays are often 10 to 15 cell layers wide (Photo 8 [$\times$ 100]). The height of the pith ray cells is 30 to 40 μ; their width is about the same. The cross section of most is circular, although other forms also occur, especially at the end of the rays. In the lower portions of the broad rays run the mucilage canals and above them the common bundles passing from the pith into the cortex. The tangential walls of the tracheids are pitted locally.

Radial section. In the radial walls of the tracheids between the pith rays, bordered pits are arranged in the araucarioid pattern, with 4, 5 and even 6 pits side by side within the width of a tracheid. The lumina of the bordered pits are slit-like and in most cases horizontal. In places, however, they are substantially elongate horizontally, almost forming a transition toward scalariform thickening (Photos 9 [× 300], 14 [× 600]). Among the tracheids there are a few axial parenchyma cells; the walls of these are quite thin and unpitted. To some tracheids slightly elongate transfusion cells are seen to adhere (Photo 10b [× 300]).

The cells of the pith rays are rectangular or square (Photos 9, 11 [× 300], 12 [× 300]), 50 to 60 μ in size; the longer side of procumbent cells ranges from 100 to 110 μ. In the cross fields 8 to 10 and in some cases even 20 bordered pits can be observed; (Photos 11, 12, 13 [× 300]). Their lumina are linear or slit-like, horizontal or oblique. Sometimes, however, there are no definite cross fields (Photo 9). Among the thin-walled ray cells, thick-walled ones rather often occur; their shape and size fully agree with those of the other ray cells.

Tracheids. In the tracheid walls, 2 to 4 rows of bordered pits exhibit the characteristic araucarioid pattern. Their lumina are linear, slightly included. Very seldom, however, the apertures of the bordered pits substantially elongate and reach over the width of the tracheids, giving rise to scalariform thickening (Photos 9, 14).

In connection with the tracheids, the trabecules should be mentioned which project radially across the lumina of some tracheids.

Cycas media R. Br. (1810)

Plates XXI, XXII, Photos 1–12; Fig. 2

The area of distribution of the species is the northern and north-eastern warm coastal zone of Australia. It is a tree reaching a maximum height of 5 m, whose leaves 50 to 120 cm long, form a tuft on the top of the stem. A compound leaf consists of about 120 leaflets of 6 to 25 cm length and 3·5 to 7 mm width.

The material examined was received from Prof. Gottwald of Hamburg who collected it on the spot.

Macroscopical examination. On the stem fragment received, the layers characteristic of the Cycads [the pith, the double vascular ring (cd, cd) and a portion of the cortex (e)] could be observed (Photo 1). Worsdell described a stem of *C. media* in which he found 12 abnormal rings.

Microscopic examination. Cross section. The pith. Unfortunately, our fragmentary sample carries but a very small portion of pith insufficient for a description of pith anatomy. Since the pith structure of the Cycads fully agrees with their cortical structure, the latter will be dealt with in rather more detail.

Vascular bundle rings. Both the xylem and the phloem of the first ring (Photo 1cd) are divided into collateral bundles by the primary pith rays. This structure repeats itself in the two abnormal rings. Hence, the wood is polyxylic as are the other Cycads (Photo 1cd, cd [× 5]).



Fig. 2. *Cycas media* (from Australian News and Information Bureau, Canberra)

Xylem ring. The xylem is twice to three times as thick as the phloem (Photo 2cd, cd [× 30]). The primary pith rays separating are 6 to 10 cell layers wide (Photo 1h). The ray cells are substantially elongate radially; their radial dimension is 200 to 220 μ, their width 30 to 40 μ. Among them, close-packed pairs, threes or fours of thick-walled sclereids are fairly frequent. Their walls consist of several layers, their lumina are narrow, almost slit-like (Photo 7 [× 100]). The normal ray cells are, on the other hand, thin walled and frequently contain calcium oxalate druses.

Occurring also in the uniseriate pith rays, these thick-walled sclereids are sharply distinct from the adjacent thin-walled ray cells.

The tracheid bands separated by the uni- and biseriate pith rays, are 3 to 8 tracheids wide. The cross sections of the tracheids are of about 50 to 60 μ diameter. Their lumina, as is the case with most tracheids, are square or slightly rounded polygonal (Photo 6c). The outline of the lumen does not follow that of the cell: the walls are triangular and somewhat thickened between the corners. Among the tracheids there are sporadic thin-walled axial parenchyma cells, most of which are in connection with the pith ray parenchyma (Photos 5 [× 200], 6 [× 200]).

Phloem. The xylem bundles are followed by 1 or 2 layers of cambium and then by the phloem bundles (Photos 2c, d, 3 c, d [× 50]). The latter are divided by the primary and also by the uni- or biseriate secondary pith rays into minor or major segments. The radial length of most pith ray cells is 80 to 120 μ, their width is 40 to 50 μ. The phloem bundle consists in its overwhelming majority of thick-walled fibres which, alternating with the phloem parenchyma cells, are arranged in plates or clusters (Photos 4 [× 100], 5). There are two types of phloem fibre, thin- and thick-walled ones. The walls of the former are 7 to 8 μ thick; those of the latter measure 12 to 14 μ. The lumina of the latter are circular or elliptical and but very seldom slit-like (Photo 4). The phloem parenchyma cells are thin walled.

At the end of the fibre bundles or near them the holes of sieve tubes can usually be observed; their diameter is 110 to 120 μ (see lower part of Photo 5). Also, there occur among them thick-walled sclereids whose number increases in the cortex (Photo 5, lower right corner).

Cortex. At the edge of the phloem ring, on the border of the cortex, the mucilage canals are arranged in a circle. Their diameter is 280 to 300 μ; their walls are lined with thin epithelial cells (Photo 7g). Around them, the parenchyma cells of the cortex are thin walled and loosely packed. Small and larger clusters of sclerenchyma fibres are rather frequent among the parenchyma cells. Their thick walls are in sharp contrast with the thin ones of the adjacent cortical cells (centre of Photo 7). The walls of most parenchyma cells are smooth and thin but some bear scattered simple pits. The thick-walled sclerenchyma fibres communicate through simple and reticular pits.

Cortical bundles. In the cortex, particularly near the mucilage canals, there are collateral vascular bundles which arrive from the pith by way of the primary pith rays. The xylem bundles may include up to 100 tracheids.

The periderm was missing from our specimen. Its structure agrees to all probability with those of the *Cycas* species examined up to now.

In the *tangential section*, most pith rays are seen to be either uni- or biseriate (Photo 8h [$\times$ 100]); broad primary pith rays are few and far between. The primary rays are 1 to 10 cell layers high; the biseriate rays are higher, and the multiseriate ones may be up to 60 cells high. The mean ray cell is 110 to 120 μ high and 30 to 32 wide. The exceedingly tiny pits arranged in axial rows in the tangential walls of some ray cells, being randomly scattered in other. Among the ray cells, exceptionally thick-walled sclerenchyma fibres occur (Photo 8h); their lumina are narrow or pin-prick-like, their walls layered. Among the ray cells, axial parenchyma cells are rather frequent; the walls of these are smooth and thin.

The walls of most tracheids are smooth but in places a definite spiral thickening, or what is more likely, a thickening resembling a scalariform perforation develops. This structure can be as readily observed in the tangential as in the radial view (right side of Photo 12 [$\times$ 600]). These exceedingly thin transverse lamellae are not sections of a spiral thickening but veritable ladder-steps, as proved by the circumstance that they flare out into a triangle before merging into the tracheid wall, which goes to show that these thin laths developed owing to the horizontal elongation of the bordered pits. On the opposite side of the tracheid, on the other hand, there are no laths but bordered pits, which fact also argues for the hypothesis just outlined.

Radial section. The pith ray cells are squares or upright rectangles; the height of the latter is 180 μ, their width 90 to 100 μ; the former are 70 to 80 μ square (Photos 9 [$\times$ 300], 10 [$\times$ 300], 11 [$\times$ 300]). Their walls are thin and unpitted. In the cross fields there are 6 to 12 simple pits, scattered or arranged in the araucarioid pattern; the lumina are slit-like or linear. In the pith rays, there are in places thick-walled parenchyma cells; in other places, no cross fields develop on the crossing of ray cells and axial tracheids.

Among the axial tracheids there are a few thin-walled parenchyma cells whose axial dimension is 250 to 300 μ; their width is 40 to 50 μ.

In the radial wall of the *tracheids* the bordered pits are arranged in 1, 2, 3 or 4 rows, partly in the araucarioid pattern, partly scattered. In such cases, the chambers are circular, the lumina linear or slit-like and the slits rather frequently placed crosswise (Photo 12).

This araucarioid pitting is almost invariably accompanied by the scalariform thickening of the radial walls, in which case the opposite tangential walls of the tracheids are connected by thin laths or broad bands creating the impression as if on the one side the tracheids communicated in their full length at least in certain sections through scalariform perforations. This structure, which can be observed not only in the tracheids in contact with the phloem but in the ones lying farthest from the phloem as well, is an interesting feature of *Cycas media*. Similar structures can be observed also in other Cycads, e.g. in *Lepidozamia hopei*. The right side of Photo 12 clearly illustrates this structure. In this photo the wall of the tracheid on the left shows araucarioid pitting while that of the adjacent one exhibits the scalariform perforation. On the distant wall of this latter tracheid, the arrangement of the bordered pits is clearly seen.

Another stem specimen of *C. media* was received from the Botanical Garden at Brisbane. Its diameter was 8 cm. From this, 2·5 cm fell to the pith, 1 cm each to the xylem and phloem ring and about 4 mm to the cortex.

The leaf bases remained on the stem whose surface was densely covered by the stumps. The width of the leaf scars was about 1·5 cm, their thickness about 5 mm. The specimen was during the long voyage attacked by mould fungi and the parenchymatous cells had rotted, but the xylem ring and the cortex remained in good condition so that sections suitable for examination could be prepared from them.

Cycas neocaledonica Linden (1881)

Plates XXIII, XXIV, Photos 1–12; Fig. 3

This species is regarded by Schuster as a form of *C. circinalis* although anatomically it differs from the latter. It is a tree 5 to 12 m high which on the top of its unbranched stem bears a tuft of leaves 1·5 to 3 m long. The leaflets are 15 to 30 cm long and 5 to 18 mm wide. The material examined was obtained from the Forest Research Institute of Indonesia, courtesy of Mr. Soevarsono.

Macroscopic examination. The diameter of the stem sample obtained is about 10 cm; it has probably come from the apex of the stem because when viewed in longitudinal section the xylem and phloem bundles are seen to converge slightly. In the stem (Photo 1 [$\times 2$]) the pith of about 5 cm diameter is conspicuous (Photo 1a); the thickness of the vascular bundle ring is 6 to 7 mm (Photo 1c, d), that of the cortex is 2 to 2·5 cm (Photo 1e). On the cortex the leaf scars are still distinct, but leaf stumps are no more present. On the cross section it is apparent even to the naked eye that both inside and outside the vascular bundle ring there are mucilage

canals forming almost full circles. Besides, mucilage canals occur also sporadically both in the pith and in the cortex. The meandering conductive bundles of the cortex are represented in the photo by black dots and dashes (Photo 1).

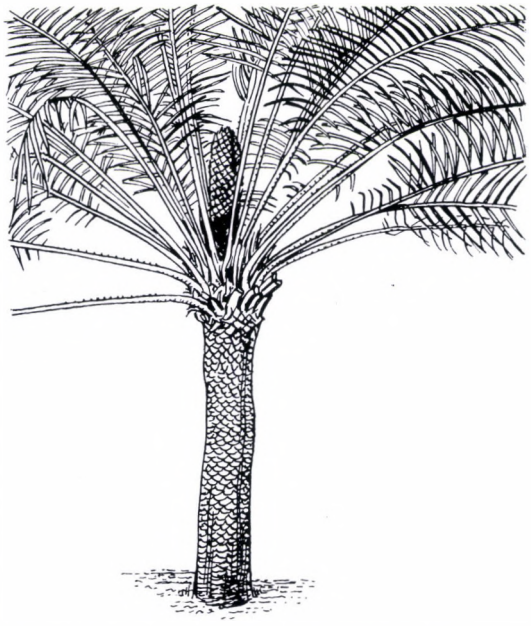


Fig. 3. *Cycas neocaledonica* (after Wieland)

Microscopic examination. The interior of the extensive pith consists largely of thin-walled parenchyma cells containing starch granules (Photo 6 [× 100]). Among the thin-walled parenchyma cells, idioblasts resembling them in size and shape are scattered. 180 to 200 μ by 90 to 110 μ in size, they are polyhedral and fit in so well among the cells of the ground tissue as to create the appearance of being modified parenchyma cells (Photo 6a). Their external appearance is suggestive of transfusion cells (Photo 6b). Their walls exhibit pitted and scalariform thickening (Photo 7b [× 200]). These idioblasts are often arranged as transfusion cells or protoxylem elements in rows joined to the ends of the vascular bundles. At the beginning of almost every vascular bundle there are such rows of idioblasts (Photos 6, 7b). Among the parenchyma cells there are the mucilage canals spaced at about equal intervals directly inside the xylem bundles (Photo 2g [× 15]). Their interior is lined with epithelial cells (Plate VI, Photo 8g [× 100]). The latter are much smaller (4 to 50 μ) than the surrounding parenchyma cells.

In the interior of the pith there are no vascular bundles in the section examined. In Photo 1 there are no dark spots in the pith but there are quite a few in the cortex.

Vascular bundle ring. The parenchymatous cells of the ground tissue form in some portions of the pith primary pith rays which penetrate into the xylem ring, dividing it up into minor or major segments (Photos 1, 2). The primary rays are substantially elongate radially, 300 to 350 μ long and 40 to 50 μ wide. The secondary and tertiary pith rays are only 1 to 3 cell layers wide (Photo 5).

Xylem bundle. At the beginnings of the xylem bundles, the idioblasts already referred to continue in 2 to 4 tracheid rows (Photo 2b). The xylem bundles are generally 2 or 3, exceptionally 4 tracheids wide (Photo 5c [× 100]), the sections of most are rounded squares or radially somewhat elongate rectangles or ellipses. Their lumina are always rounded. Among them there are a few scattered xylem parenchyma cells.

Cambium. At the edge of the xylem layer, very thin-walled cambial cells are arranged in 3 or 4 rows; they show a gradual transition towards the phloem ring (Photos 3 [× 100], 5c, d). To each xylem bundle corresponds a phloem bundle; the latter are, as the former, uni- to triseriate (Photo 3d). Among them there are idioblasts of the same shape and size as those of the pith.

The *phloem layer* consists of thick-walled fibres and thin-walled parenchyma cells (Photos 3, 4 [× 200]); the fibres form minor or major clusters including a few parenchyma cells. The walls of the phloem fibres are thick; their lumina are narrow slits or points (Photo 4d). In the thin-walled parenchyma cells and also in the pith ray cells, rhombohedral single crystals of calcium oxalate are rather frequent.

Cortex. Its structure fully agrees with that of the pith. The mucilage canals surround the phloem bundle in the shape of a ring (Photo 2g); their diameter is 300 to 320 μ; in their vicinity, there are the collateral bundles in which annular and spiral thickening predominates although in some cells the thickening is overwhelmingly scalariform (Photo 10 [× 300]). Besides them, transfusion cells are also frequent. They show a variety of transitions into tracheids (Photo 7). Near the external margin of the cortex, numerous thick-walled idioblasts form a continuous layer (Photo 6).

The idioblast layer is followed by a cork cambium 6 to 8 cells thick (Photo 2f), and subsequently by the cork which also consists of several layers, owing to the periodicity of its growth. The cork cells are rectangular and close packed radially.

Tangential section. In tangential view, the pith rays are uni- and multiseriate, up to 10 cell layers wide; the primary rays are even broader (Photo 9h [× 100]). The walls of the ray cells are exceedingly thin and unpitted; their height is 40 to 50 μ, their width 30 to 40 μ. Some contain calcium oxalate crystals (Photo 10). The rays contain sporadical idioblasts which become rather frequent next to the tracheids. The transition from the transfusion cells into the tracheids is in places readily observed. The primary rays include the mucilage canals and the conductive bundles. The mucilage canals are surrounded by isodiametrical parenchyma cells of the same forms as the idioblasts (Photo 8g); in the thickness of their walls, these cells definitely differ from the others. The tangential walls of the tracheids bear bordered pits in a close-packed araucarioid pattern.

Radial section. Pith rays. Most ray cells are upright rectangles but squares also occur. Their walls are quite thin and smooth; among them, the idioblasts known from the pith are sporadically observed. Cross fields are rare and not too well developed.

In the *tracheid* walls, bordered pits are arranged in 1 or 2 and even 5 rows; their chambers are crowded honeycomb-like (Photos 11 [× 300], 12 [× 600]); their lumina are horizontal slits. In some places, they exhibit sections corresponding to the horizontal walls of the ray cells. Sometimes 2 or 3 adjacent bordered pits coalesce, in which case the structure approaches the scalariform thickening (Photos 10, 12). Some tracheid rows are in places divided by transverse walls into short tracheids as it were; the transverse walls bear bordered pits through which the short tracheids communicate. Very seldom the cross walls may completely dis-

solve: this means that we are faced with actual vessel structures. It was to such vascular structures that Greguss (1958) called attention in connection with *C. revoluta*.

Sometimes the elongate apertures of the bordered pits reach across the tracheid wall to form a true scalariform thickening. These apertures considerably widen locally, getting roundish and becoming similar to scalariform perforation, as seen in Photos 10 and 12. This structure is highly suggestive of the scalariform perforation of the palms (Photo 12).

Cycas normanbyana F. Muell. (1874)

Cycas rumphii subspec. *normanbyana* (F. Muell.) Schuster (1956)

Plates XXV, XXVI, Photos 1–11

A dwarf tree living in Australia, mainly in Queensland. Its stem attains very seldom a height of 60 cm above the ground; its lower portion is subterranean. Its compound leaves measure 1·5 m; the leaflets are 18 to 20 cm long, 5 to 6 mm wide. I have received the specimen to be described from Brisbane, by the courtesy of Mr. Wilkes.

Macroscopic examination. The surface of the stem is covered by close-packed, protruding leaf-scar scales of 2·5 to 3 cm width, and 5 to 6 mm thickness. The diameter of the section examined was about 9 cm of which the pith made up 4·5 to 5 cm. It is apparent to the naked eye that the species is polyxylic, since beside the primary vascular bundle ring (Photo 1 [× 3]) there are solitary bundles arranged in 3 or 4 more rings (Photo 2 [× 3]). At the edge of the pith, the mucilage canals (black spots in Photo 3 [× 10]) are arranged in something like a circle mostly in front of the primary bundles.

Microscopic examination. The pith largely consists of more or less isodiametrical, thin-walled (1–2 μ) parenchyma cells of 140 to 170 μ size. Scattered among them, the thicker-walled parenchyma cells occur singly or in minor or major clusters. Their dark brown colour is in a marked contrast with the surrounding colourless thin-walled parenchyma cells; in their walls, tiny simple pits of 8 to 10 μ size are scattered. The number of the thicker-walled cells increases towards the primary pith rays; clusters are also more frequent. At the edge of the pith, the mucilage canals are arranged in the form of a ring; their diameter is 370 to 400 μ (Photo 6 [× 100]); their interior is lined with thin-walled epithelial cells of 35 to 40 μ size. Meandering about in various directions, at some places even horizontally, the mucilage canals are sometimes surrounded by 2 or 3 parenchyma-cell rings. The parenchyma cells contain much starch. In the primary pith rays, both the thin- and thick-walled parenchyma cells are considerably elongate radially.

Xylem rings. The xylem portion of most individual vascular bundles is dissected by uni- or biseriate secondary pith rays into smaller segments 1 to 3 tracheids wide. Most tracheids are quadrangular in cross section, more or less isodiametric; their

size is 35 to 45 μ, seldom 60 μ. Forming radial rows, they are fairly close-packed, becoming pentagonal or hexagonal in the more crowded portions (Photo 5 [$\times$ 100]).

Phloem rings. The xylem ring is followed by a thin cambium and then by a phloem ring; the radial dimension of the latter is only $\frac{1}{4}$ to $\frac{1}{5}$ of the xylem bundles (Photo 4 [$\times$ 100]). The pith rays between the phloem bundles are uni- or biseriate; the cells are much larger than the phloem parenchyma cells. In the phloem, the lumina of the thick-walled fibres are reduced to slits; the fibres occur as a rule either singly or in twos and threes; in places they form radial rows with thin-walled parenchyma cells among them. In the parenchyma cells, calcium oxalate crystals of rhombohedral or columnar shape are frequent. The primary pith rays flare out in the phloem. In cross section, the phloem fibres are generally oblong, 35 to 40 μ wide, and 15 to 20 μ high; the size of the adjacent ray cells is 110 to 120 μ (Photo 4). The size of the phloem parenchyma cells agrees with that of the fibres. Remarkably enough, fibres are rather scarce in the phloem.

Cortex. Its cross-sectional structure fully agrees with that of the pith, with the difference that the vascular bundles scattered in the cortex are absent in the pith; however, mucilage canals are present in both. Characteristically, calcium oxalate crystals grow more frequent in the cortex near the periderm; in the same zone, the parenchyma cells become smaller and flatter.

Tangential section. Most pith rays are 1 to 8 cells wide; some attain the width of 25 cells. Size of the ray cells is 60 to 100 μ; their wall is thin, unpitted; among them, there occur thicker-walled parenchyma cells. In some rays, the transformation of the transfusion cells into tracheids can be readily observed. In the broader rays, mucilage canals and in places also pith bundles are running from the pith into the cortex and from there as leaf scar bundles into the leaves (Photo 7 [$\times$ 100]). The tangential walls of the tracheids locally bear 2 or 3 rows of bordered pits; other walls are smooth; in yet other walls, the bordered-pit thickening gradually turns into scalariform thickening. The walls of the phloem fibres bear axial rows of oblique slits (Photo 8 [$\times$ 300]).

Radial section. The radial walls of the tracheids bear bordered pits close packed in the characteristic araucarioid pattern (Photos 9 [$\times$ 300], 10 [$\times$ 300], 11 [$\times$ 600]); the chambers of the pits are compressed, the aperture is as a rule horizontal. In the narrower tracheids there are 1 or 2, in the wider ones 3 or 4 rows of bordered pits side by side. Very exceptionally, the pitting of the tracheids almost turns into a scalariform thickening. The parenchyma cells of the pith rays are procumbent rectangles; their width is 180 to 200 μ, their height 70 to 100 μ; most are thin-walled, but among them, there are fairly numerous thick-walled cells with simply pitted walls. In the ray parenchyma cells, calcium oxalate crystals of rhombohedral form are rather frequent. There are no well-defined cross fields; at least, no such field was observed in the sections examined. Shape and size of the ray cells in the phloem agree with those of the parenchyma cells in the xylem. In the phloem there is a remarkable number of calcium oxalate crystals of rhombohedral shape. A distinctive feature of the wood is that in the phloem the fibres are generally solitary and comparatively scarce.

Cycas revoluta Thunb. (1784)

Plates XXVII, XXVIII, Photos 1–13; Fig. 4

The spread of this species covers South China, East India, Taiwan and the southern parts of Japan. It is grown everywhere in glasshouses. A tree attaining 5 to 8 m height, it bears on the top of its unbranched stem a leaf tuft consisting of composite



Fig. 4. *Cycas revoluta* (Cape Toi-raki, southern Kyushu, Japan)*

leaves 2 m long. The leaflets are 15 to 18 cm long, ending in bristles; after the falling off of the leaves the leaf base remains on the stem for a long time (Plate I, Photo 1 [×0·5]).

The sample examined originates from the Botanical Gardens of Cracow, from an old, dried out specimen. The diameter of the stem together with the leaf stumps is about 20 cm, that of the stem proper is 12 cm.

* By courtesy of Prof. U. Tatewaki.

Macroscopic examination (Photo 1). The cross section shows a polyxylic structure; the three characteristic main parts are clearly distinct. The diameter of the pith is 4·5 cm (Photo 1a), the thickness of the phloem and xylem rings, 16 mm each (cd, cd), that of the cortex, 2·5 cm (e). On the polished surface, the scattered light points represent mucilage canals both in the pith and in the cortical portion; the dark dashes and spots running axially represent the bundles of the cortex. The vascular bundle ring consists of two definite xylem rings and two phloem rings. Outside the first abnormal ring, a third xylem ring begins to develop in places.

Microscopic examination. Cross section. The pith. The pith consists largely of thin-walled isodiametric parenchyma cells (Photo 8c [× 100]). The average diameter of the cells is 140 to 150 μ. Among them, there are mucilage canals (g), their diameter in the pith is 300 to 350 μ. The epithelial cells lining them are much smaller than the surrounding cells of the ground tissue; the dimension of the epithelial cells ranges from 60 to 80 μ. The pith bundles of collateral structure generally run next to the mucilage canals. In the xylem of the pith bundles there are sometimes as many as 100 tracheids; the phloem is much less well developed.

The bundles in the pith are developed to various degrees; the less developed ones are probably the proper bundles of the pith; the more developed ones which are closer to the mucilage canals are the common bundles of the stem which run in the primary pith rays outwards into the cortex and from here as leaf scar bundles into the leaves. The cells of the ground tissue contain much starch.

Bundle ring (cd). Out of the pith there issue primary pith rays which divide the vascular bundle ring into broad segments (Photo 3h [× 25]). Thinner pith rays divide the broad segments into narrower ones (Photo 6h [× 100]). Among the broad pith rays, at the beginning of the tracheid rows, there are arranged wood primanei or transfusion cells (Photo 7b [× 200]). The cells of the primary pith rays passing between the xylem bundles are substantially elongate radially, their length at such places is 220 to 250 μ, their width 70 to 80 μ. The cells of the secondary pith rays are much shorter than these, 70 to 80 μ long and 35 to 40 μ wide (Photo 6h). Some cells contain octahedral or rhombohedral solitary crystals of calcium oxalate.

The cross section of the tracheids is generally rounded square, pentagonal or crowded polygonal; their inner lumina are always rounded; among them there occur sporadical thin-walled parenchyma cells (Photo 6c).

Both the primary and the secondary pith rays continue beyond the xylem bundle ring into the cortex (h – h). Across the border, their size and structure passes unchanged (Photo 6h). At the ends of the xylem bundles, however, there are several rows of thin-walled cambium cells and the phloem bundle continues thence in the same width as the xylem bundle (Photos 4cd [× 50], 5d [× 100]). The phloem bundle consists of thick-walled sclerenchyma bundles, parenchyma cells and sieve cells, which latter are difficult to observe (Photo 5d). The phloem fibres are thick-walled, their lumina are narrow slits (Photo 5). The rest of the phloem primanei is arranged on the outside of the phloem layer.

First abnormal ring. The bundle ring referred to above may repeat itself outside the phloem layer twice and even three times (Photos 1, 2 [× 10], 3cd, cd, cd). In the

external ring, the xylem bundles on the periphery do not occur everywhere in the prolongation of, and in the same thickness as the bundles of, the inner rings (Photo 1).

Cortex (e). Structure and arrangement of the ground tissue cells, of the mucilage canals and cortical bundles of the cortex agree with the corresponding features of the pith. In the cortex, the number of collateral bundles is multiplied, because the leaves require a large number of vascular bundles for their supply. The diameter of the mucilage canals is at some places 500 to 550 μ so that they are readily visible to the naked eye (Photo 8g).

Periderm. As on *C. revoluta* the leaf bases remain for a long time on the trunk and assume the role of periderm, no proper periderm develops except at most on the lower portions of old trunks, where a periderm develops before the leaf bases drop off the trunk (Photo 1).

Tangential section. The pith rays are 1 to 6, in extreme cases 15 to 20 cells wide (Photo 9h [$\times$ 100]). In section, the pith ray cells may be circular, elliptical, or crowded into hexagonal or polygonal shapes. Their length attains 80 μ, their width 35 μ. The broader pith rays include mucilage canals and vascular bundles.

Tracheids. The tangential walls are generally smooth, only rarely can any pitting be observed which probably reaches across from the radial side. Besides the tracheids, transfusion cells could also be identified in places (Photo 7b).

Radial section. Pith rays. Most pith ray cells are procumbent or upright rectangles (Photo 10 [$\times$ 200]), their size is generally 70 to 80 μ by 110 to 120 μ. Some pith ray cells contain solitary octahedral or rhombohedral calcium oxalate crystals.

Where the ray cells contact longitudinal tracheids, cross fields tend to develop. These include 10 to 20 and even as many as 25 simple pits, arranged according to the araucarioid pattern or loosely touching each other. The lumina of the pits are oblique, slit-shaped or linear (Photos 10, 11h [$\times$ 300]).

Transfusion cells. In places, transfusion cells are observed beside the pith rays, directly adhering to the tracheids. Their pitting agrees by and large with that of the tracheids but the lumina of the pits are much wider (Photo 7b).

Tracheids. In the tracheids, bordered pits are arranged in 1 to 3 rows in the araucarioid pattern or somewhat loosely (Photos 12 [$\times$ 300], 13 [$\times$ 600]). The lumina are oblique or horizontal slits, included in most cases but extended in some; adjacent lumina may coalesce to form in the tracheid walls horizontally elongate bordered pits, reaching almost full across the walls (Photo 11, above). However, no definite scalariform pitting occurs in this species.

Cycas rumphii Miq. (1839)

Plates XXIX, XXX, Photos 1–12; Figs 5, 5a

The range of this species includes the South-east Asian Archipelago, Timor, Celebes, New Guinea and the Polynesian Islands. A tall tree attaining a mean height of 8 m, exceptionally of 15 m, which on its top bears a tuft of leaves 1 to 2 m long.

The composite leaves consist of 50 to 100 lanceolate leaflets, 20 to 30 cm long and 2 cm wide.

Macroscopic examination. The stem sample of 10 cm diameter and 4 cm thickness was obtained from the Botanical Gardens of Singapore, courtesy of Director H. N. Burghill. On the polished surface, the three characteristic main parts of the Cycad stem can be distinguished with the naked eye. In the dried specimen, the diameter of the pith is 2 cm (Fig. 5a [× 1·5]); the vascular bundle ring is about 3 cm thick (cd); the thickness of cortex and periderm, 1 cm (c). The thick vascular bundle ring is composed of 6 xylem and 6 phloem rings, the thickness of the first xylem plus phloem ring is 6 mm, that of the second 8 to 9 mm, that of the others 5, 4 and 3 mm, respectively. The xylem rings alternate with much thinner phloem rings; this structure seemed at first sight to be a variety of annual rings. There is no such thing, however, in Cycads. No such multilayered xylem and phloem ring was found in any of the other Cycads examined, so that this wood is the most typically polyxylic type. The scattered dark spots in the cortex represent mucilage canals and vascular bundles (Fig. 5a [e, f]).

Microscopic examination. Cross section. The pith largely consists of thin-walled isodiametric cells between 150 and 200 μ in size whose section varies from circular to short elliptical. Their thin walls are most often continuous, but in places intercellular ducts develop between them. Some cells are filled out by single rhombohedral crystals of calcium oxalate. In contrast to other Cycads, there is not a single mucilage canal or vascular bundle in the pith. The walls of the parenchyma cells are smooth, lacking visible pitting. No darker or lighter spots are seen in the photo, either.

Pith rays. On the edge of the pith and at the issue of the bundles, the pith cells, radially elongate, penetrate between the xylem bundles as primary pith rays, dividing the xylem bundles into narrower or broader segments. The length of the radially elongate ray cells is 150 to 160 μ, their width 30 to 40 μ. The cells of the secondary rays are much shorter radially but invariably longer than the diameter of the tracheids (Photo 4 [× 100]).

Xylem bundles. Next to the inner side of the xylem bundles, short protoxylem elements are scattered, some of them assuming the form of transfusion cells (Photo 5b [× 200]). The xylem bundles are divided by the secondary and tertiary, mostly uniseriate pith rays into narrower segments (Photo 4h). The segments are generally uni- or biseriate but may be exceptionally 4 to 6 cell layers wide. In section, the tracheids have quadrangular, pentagonal or compressed irregular shapes (Photo 4c); their lumina are rounded, among them there are a few sporadic wood parenchyma cells (Photo 4c). Some parenchyma cells contain solitary rhombohedral calcium oxalate crystals.

Cambium. In the continuation of the xylem bundles there is the cambium consisting of one or two layers of cells (Photo 3c,d [× 100]) and the phloem bundles (Photo 2c,d [× 50]). In the phloem bundles, the fibres are scattered or arranged in tangential plates, between which the phloem parenchyma cells and the radially running pith ray cells are seen (Photos 2, 3c,d).

Second bundle ring. The first phloem ring is followed by another xylem ring, but the bundles of this second xylem ring are preceded by larger or smaller clusters of transfusion cells (Photo 5b). The transfusion cells generally bear a bordered pitting but in places this pitting passes into a scalariform thickening (Photo 5b). The first abnormal xylem ring is followed by a phloem ring of the same structure as described above. This structure repeats itself four or five times. The outermost phloem ring is in contact with the cortex (Photo 2e). In the phloem bundles, the fibres are solitary or congregated in smaller or larger clusters; among them, thin-walled parenchyma cells of similar cross-sectional size are arranged. The sections of the phloem fibres are elongate rectangles; their walls are thick, their lumina narrow slits or pinholes (Photo 3).

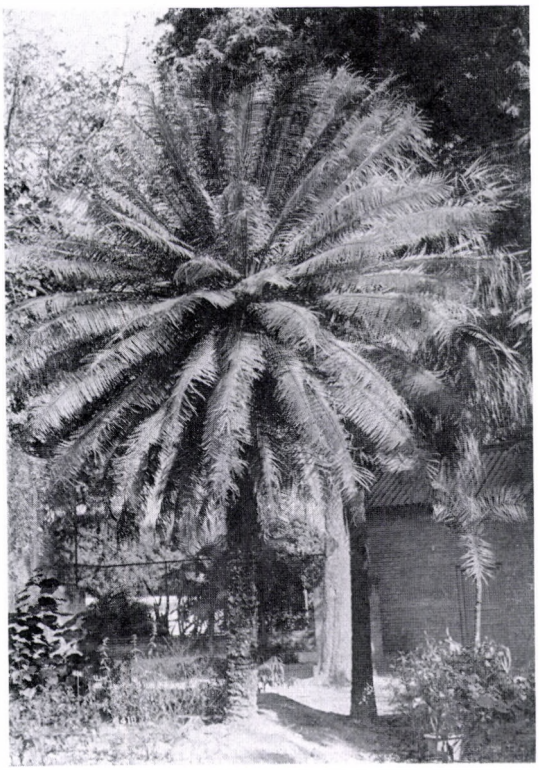


Fig. 5. *Cycas rumphii* (Lucknov, India; photo by Kaul)

The cortex (e). Its structure essentially agrees with that of the pith; the cells of the ground tissue are of the same size and shape (Photo 6e [× 100]). The only difference is that, in the cortex, mucilage canals are frequent and so are the collateral vascular bundles which to all probability originate in the cortex because no similar ducts or bundles occur in the pith. The mucilage canals are comparatively wide, 510 to 530 μ in diameter, and lined with thin-walled small epithelial cells (Photo 6g). The parenchyma cells of the cortex contain large numbers of calcium oxalate crystals which form veritable layers parallel to the periphery (Photo 5).

The xylem of the solitary bundles of the cortex may group 40 to 50 tracheids; beside and among them, transfusion cells are frequent, most of which exhibit scalariform thickening. The tracheids are also either spirally or scalariformly thickened. Araucarioid pitting is very rare in the tracheids of the cortical bundles.

Periderm (Photo 1f). The outermost part of the cortex is a cork cambium, 4 or 5 cell layers thick, which gives rise to cork cells, flattened rectangular cells covering the cortex in a thickness of 30 to 40 cell layers (Photo 6). The cork layer is made up

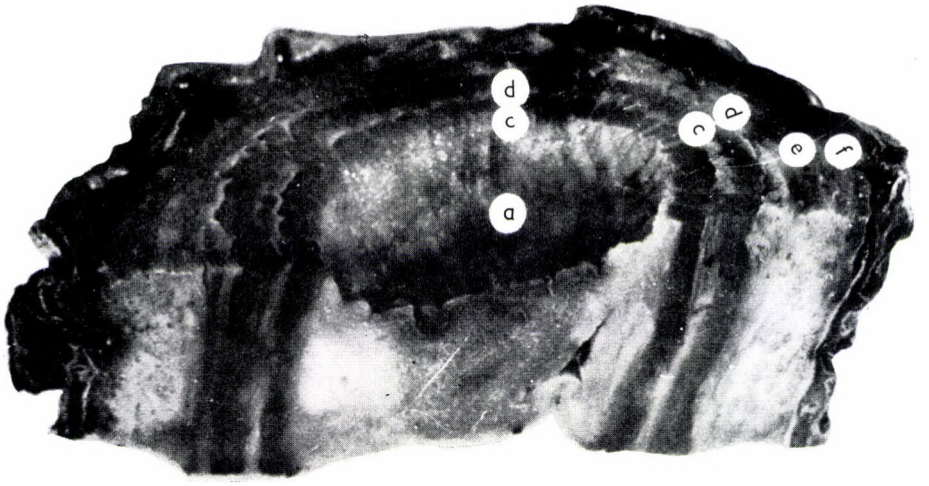


Fig. 5a. Surface view of a trunk section of the upper part of *Cycas rumphii*; (a) pith, (c) xylem ring, (d) phloem ring, (e) cortex, (f) periderm. (Natural size)

of thin and slightly thicker bands; this phenomenon is probably due to climatic changes.

Tangential section. Seen from the tangential side, most pith rays are uni- to triseriate (Photo 7h [× 100]). The uniseriate rays are 2 to 10, bi- and triseriate about 20 cells high, but there are also rays 10 to 15 cells wide which may be 80 to 100 cells high. The size of the ray cells is 70 to 80 μ by 40 to 50 μ; their walls are very thin and unpitted. In most broader rays there are vascular bundles meandering from the pith towards and into the cortex. The tangential walls of the tracheids bear numerous bordered pits.

At the edges of the pith rays, there are fairly numerous solitary transfusion cells, of manifold shape, sometimes substantially elongate and gradually transforming into tracheids (Photo 5b). The walls of these transfusion cells exhibit bordered or scalariform thickening, as well as various forms of transition. It is interesting to note that whereas some primary rays carry two or even three conductive bundles towards the cortex, they include not a single mucilage canal; hence, in this species, mucilage canals can develop only in the cortex.

Radial section. Pith rays. Most ray cells are rectangular or hexagonal (Photo 11 [× 300]), 70 to 80 μ by 50 to 60 μ in size. Where the outer ray cells contact the longitudinal tracheids, cross fields are developed, including 15 to 20 and even 50 pits (Photos 8 [× 300], 9 [× 300], 11). The pits are either arranged in the araucarioid pattern or somewhat scattered; their size is 7 μ, their apertures are linear and oblique. All walls of the ray cells are smooth, thin and unpitted.

In the tracheid walls the bordered pits form 1 to 4 rows, being packed alveolarly in the araucarioid pattern (Photos 9, 10 [× 300], 12 [× 600]). The apertures are linear, only rarely touching the outline of the pit border; their position is horizon-

tal or somewhat oblique. The width of the tracheids is 40 to 45 μ. In some rare cases the apertures are substantially elongate and the apertures of two adjacent pits may coalesce (Photo 9) but there is no scalariform thickening.

Cycas siamensis Miq. (1863)

Plates XXXI, XXXII, Photos 1–11; Fig. 6

Area of distribution: Burma, Vietnam and Cambodia. A squat tree of 30 to 180 cm height; the diameter of the trunk is 10 to 60 cm. The composite leaves are 60 to 120 cm long with 40 to 100 pairs of leaflets per leaf. The leaflets are 4 to 20 cm long and 55 mm wide. The stem sample examined originates from India.

Macroscopic examination. The specimen originally was of about 10 cm diameter, of which 4 cm was the diameter of the pith, and about 1·5 cm the thickness of the vascular bundle ring; cortex and periderm together are barely 1 cm thick.

Microscopic examination. The pith (Photo 1 [× 5]). During transport, the pith was somewhat crushed, so that only the bundle ring and the cortical part remained in a condition more or less suitable for examination. The structure of the pith, however, almost completely agrees with that of the cortex.

Bundle ring (Photos 2 [× 50], 3 [× 100]). The endings facing the pith of the larger bundles are rounded off. The bundle ring is divided into narrower and broader segments by broad primary pith rays. Each of the primary vascular bundles is about 4 to 5 mm wide, somewhat flaring out outwards, i.e. towards the cambium, whereas the phloem bundles grow slightly narrower towards the cortex (Photo 5h [× 100]).

Xylem bundle. The primary pith rays passing through the xylem ring are fairly wide-spaced, which gives rise to broad collateral vascular bundles (Photo 1). The xylem bundles are in their turn divided into minor or major segments, 2 to 10 tracheids wide, by uni- to triseriate pith rays (Photos 2, 3, 5c). The sections of the tracheids are rounded quadrangles or pentagons (Photos 3, 5c); their radial dimension is 40 to 50 μ; their width is about the same; the lumina are invariably rounded, circular or elliptical. The tracheids form long radial rows (Photos 2, 3, 5). Among them, parenchyma cells are very rare.

The normal xylem ring is followed by a very thin phloem (Photos 2, 3, 5d), whose thickness is no more than one-tenth of that of the xylem ring. Rather than forming a continuous ring, the phloem is found only at the outer ends of the xylem bundles (Photo 2d). The phloem consists largely of parenchyma with a few fibres (Photos 4 [× 200], 5d). In the arrangement of the fibres there is no regularity. In section, the fibres are circular, their lumina pinhole-like spots or very short slits (Photos 3, 4d). Their section is thus different from those of the phloem fibres of the Cycads described up to now. In cross section, the fibres are seen to be intensely luminous under the microscope.

The first abnormal ring hardly differs from the first normal one. It also contains pith rays but not always in the direct continuation of the primary pith rays of the normal xylem ring (Photo 1). Otherwise the tracheids perfectly agree in orien-

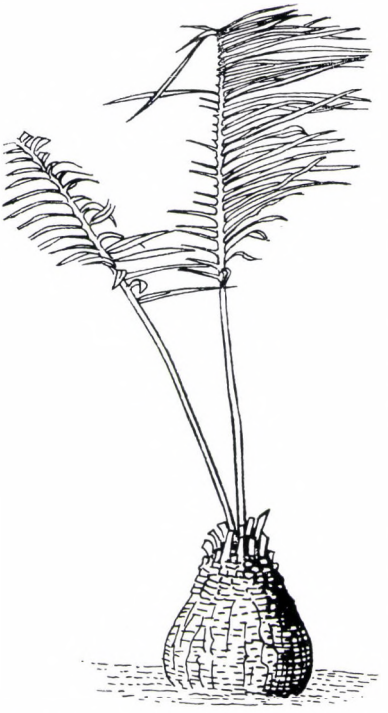


Fig. 6. *Cycas siamensis* (after Wieland)

tation, size and cross-sectional structure with those of the first normal ring.

The cortex (e) is directly attached to the bundle ring. In it, the parenchymatous cells are thin-walled, isodiametric, of a mean size of 150 to 200 μ (Photo 6e [$\times$ 50]). Some are filled out with calcium oxalate crystal druses. Among the cells there are mucilage canals (g) of 280 to 320 μ diameter whose inner walls are lined with epithelial cells. Next to the mucilage canals and vascular bundles, transfusion cells are frequent, most of which exhibit scalariform thickening.

Vascular bundles. In the cortex there is a remarkable number of cortical bundles. Some are axial, others meandering about, as proved by the fact that in the cross section the longitudinal structure of the tracheids is also visible. One such vascular bundle may include 100 to 200 tracheids. The phloem is subordinate, consisting of a few fibres and even less parenchyma.

The outermost part of the periderm (Photo 1f) consists of radially flattened cork cells; below the latter, thick-walled phelloderm cells are arranged. The cork layer consists of several bands which may be due to climatic, possibly seasonal, changes (Photo 1f).

Tangential section. Most pith rays are uni- or biseriate and may attain a height of 55 cells (Photo 7h [$\times$ 300]). The rays are 50 to 200 μ high and 35 to 40 μ wide. In some ray cells and in the rare xylem parenchyma cells calcium oxalate crystal druses occur. The walls of both the ray cells and the parenchyma cells are smooth and thin.

Tracheids. Their tangential walls are generally smooth but in places tiny bordered pits congregate into smaller or larger clusters or longitudinal rows arranged in the araucarioid pattern (Photo 8h [$\times$ 300]). The diameter of the pit chamber is 11 to 13 μ; the apertures are circular or short linear.

Radial section. In the radial walls of the tracheids, the bordered pits are arranged in a typically araucarioid pattern, in 1 to 5 rows. The pits in the uni- and biseriate arrangements are sometimes quite loose; in other cases they are crowded into contact. The apertures are more or less oblique, linear.

The walls of the ray cells are very thin and perfectly smooth (Photo 8h). Where the ray cells meet tracheids, cross fields are formed. The bordered pitting of the tracheids is visible through the thin translucent ray cell walls (Photos 8h, 9 [$\times$ 300], 10 [$\times$ 300], 11 [$\times$ 600]).

At the ends of some tracheids there are transverse lamellae suggestive of scalariform perforation. This structure reminds of *C. media* discussed before. This scalariform thickening occurs on one side only of the tracheid; on the opposite side, bordered pits are arranged in the araucarioid pattern. This suggests the perforation to be most probably unilateral.

The opposite walls of some tracheids are connected by trabeculae which may pass at the same level through 8 to 10 adjacent tracheids.

2. STANGERIACEAE

Stangeria paradoxa T. Moore (1853)

Plates XXXIII, XXXIV, Photos 1–13; Fig. 7

Its area of distribution is the region of Port Elisabeth in the province of Transvaal, South Africa, where it is found in forests and on prairies (see Map on page 18). It is extensively grown in glasshouses. The subterranean stem is tuberous (Photos 9 [× 100], 10 [× 300]) and continues in a thick taproot. Its surface is nearly smooth because the fallen leaves leave hardly any traces. The plant is fern-like not only in outside appearance but also in its structure, particularly in the stomatal structure of the leaves. Only two species are known, and the number of their varieties is also small. The material examined was obtained from the Division of Botany, Department of Agriculture, Pretoria, courtesy of Mr Bedeklinter.

Macroscopic examination. The stem sample examined comes from the upper part of an oldish specimen. Its diameter is 12 to 14 cm; pith diameter is 6 cm, bundle ring thickness 4 to 5 mm, thickness of the cortex about 3 to 4 cm. The polished section reveals a well-developed pith and cortex. On the other hand, the single ring is poorly developed, owing to the subterranean tuberous nature of the stem (Photos 1, 2 [nat. size]). In the interior of the pith, the dark spots represent the meandering vascular bundles, the light ones the scattered mucilage canals (g). The bundle ring is barely 4 to 5 mm wide (cd) and divided into several segments by broad pith rays. The bundle ring is surrounded by the cortex whose structure agrees with that of the pith (e). The exterior of the cortex bears a thin periderm (f) whose surface bears no leaf scars.

Microscopic examination. The pith consists of more or less isodiametric cells of rounded square, rectangular, circular or elliptical section (Photo 3a [× 50]). Their mean size range is 140 to 160 μ by 100 to 120 μ. They are thin walled and close packed, but there are sizable intercellular ducts between some. The walls of the parenchyma cells are thin simple circular or elliptical scattered pits; their interior is filled with starch. The mucilage canals running in the pith tissue are 200 to 220 μ in diameter. The inner epithelial cells are comparatively large, up to 70 μ; their orange-coloured content sharply differs from the adjacent parenchyma



Fig. 7. *Stangeria paradoxa* (Berlin–Dahlem; after Schuster)

cells which surround the duct in a ring (Photos 6 [× 100], 7g [× 100]). In their vicinity, there are sporadic xylem bundles which pass through the primary pith rays towards the cortex.

On the edge of the pith there is a ring of mucilage canals, clustering as a rule near the points of issue of the primary pith rays. The ray cells are considerably elongate radially and narrower than the cells of the pith. Their length is 200 to 220 μ, their width 50 to 60 μ. At the ends facing the pith of the bundles, no transfusion cells were observed.

Bundle ring. There are narrow vascular bundles between broad pith rays. These are comparatively underdeveloped, consisting of 25 to 40 tracheids radially and at most 8 to 12 tracheid transversally. In section, the tracheids are somewhat angular or rounded, square, rectangular, penta- or polygonal (Photo 5c [× 200]). Their radial dimension is 40 to 60 μ, their width 35 to 40 μ. Their walls are 5 to 6 μ thick. Among them there are a few sporadic xylem parenchyma cells, usually next to the pith rays (Photo 5). In the continuation of the xylem bundles, underdeveloped phloem bundles are seen (Photo 4 [× 200]).

The walls of the phloem fibres are comparatively thin, hardly different from the walls of the parenchyma cells in the ground tissue (Photo 4). In the phloem bundle, most fibres and parenchyma cells are scattered but some may be arranged in layers. The phloem parenchyma cells hardly differ in size from the neighbouring ray cells. The parenchymatous cells of the cortex are, however, much larger (Photo 8 [× 100]) than either the ray cells or the phloem parenchyma cells (Photo 4).

The parenchymatous cells of the cortex perfectly agree in shape and arrangement with the similar cells of the pith, but they are somewhat larger and wider. Some of the cortical bundles bend outwards into the leaves.

In *tangential section* (Photos 9, 10), the pith rays are 1 to 15 cells wide. The size of the ray cells varies between 70 and 120 μ. They are generally crowded, angular, more or less isodiametric.

Between the rays there are the tracheids whose thickening is scalariform without exception (Photos 9, 10); there is no araucarioid pitting in this wood. The height of ladder steps and step spacings is more or less the same; in an interval of 80 μ there are about 4 or 5 steps and as many step spacings. No calcium oxalate crystals were observed in this species.

Radial section. In the pith rays the ray cells are more or less isodiametric, square, upright rectangular or hexagonal (Photos 11 [× 300], 12 [× 300], 13 [× 600]).

Their height is 120 to 140 μ; their width is about the same. There are no cross fields; there is no periodicity in the tracheid wall, either.

In the phloem, the wall of the fibres is comparatively thin: 3 to 4 μ; the width of the fibres is 20 to 25 μ.

3. ZAMIACEAE

(a) LEPIDOZAMIA

Lepidozamia hopei Regel (1876)

Plates XXXV, XXXVI, Photos 1–12

In his monograph on the *Cycadaceae*, Schuster calls this species *Macrozamia denisonii* var. *hopei* (Hill) Schuster, while Johnson (1959) in his work places it as an independent species into the genus *Lepidozamia* established by Regel in 1876.

The *Lepidozamia* genus has two known species; *Lepidozamia hopei* occurring in a narrow area in the north-eastern corner of Australia and *Lepidozamia peroffskyana* in a narrow strip on the East Australian coast (see Map on page 18). The author obtained (courtesy of Mr Johnson) from the Botanical Gardens of Brisbane a dried-out stem sample of *Macrozamia hopei*, about 30 cm long and 12 cm in diameter. The surface of the stem lacked the traces of leaf scars; it was yellowish brown and uniformly smooth.

The stem of the *Lepidozamia* may reach a height of 20 m; on its peak the leaves, 2 to 3 m long, form a leaf tuft. A leaf consists of 160 to 200 pairs of leaflets. The female strobile may be up to 60 cm long with a diameter of 20 to 25 cm.

Macroscopic examination. From the dried-out stem a thin disk was cut. Its surface was cleaned after softening in water. Photo 1 [nat. size] shows this surface.

In cross section, the polyxylic structure of the stem is apparent. The diameter of the broad dark pith is 6·5 cm (a). In the ground tissue of the pith, proper and common vascular bundles and mucilage canals (dark spots in Photo 1) are scattered. Outside the pith there is the first, so-called normal vascular bundle ring (c, d); its xylem portion is 7 mm, its phloem portion 3 mm thick. The first abnormal xylem ring is somewhat thinner (4 mm); the phloem ring is barely 2·5 mm thick. These data agree with the statements of Worsdell made about 70 years ago. The double vascular bundle ring is surrounded by a thin cortex (e), and a periderm (d) hardly 1 to 2 mm thick.

Microscopic examination. Cross section. The pith largely consists of more or less isodiametric, thin-walled, loose parenchyma cells (Photo 5 [$\times$ 100]) whose interior contains remarkably large (35 to 40 μ), somewhat eccentric starch granules. Semi-composite starch is frequent among them. The walls of the parenchyma cells are very thin, even simple pitting is very rare in them. Among the thin-walled ground tissue cells thicker-walled idioblasts are arranged in places (Photo 6

[×300]). The vascular bundles of the pith are meandering to and fro and a regular cross-sectional picture can but seldom be made (Photo 2 [×7]). In them, the xylem consists of 35 to 40 tracheids; the phloem portion is subordinate and inconspicuous. A few parenchyma cells are filled with calcium oxalate crystal druses; sometimes there are even two druses in one cell. The mucilage canals usually occur close to the bundles (Photo 5). On the edge of the pith, at the ends facing the pith of the vascular bundles, no transfusion cells have been observed although such cells were described by Worsdell. There are at most a few thick-walled idioblasts at the endings of the xylem bundles. The diameter of the mucilage canals of the pith is 180 to 190 μ. Their inner walls are lined with epithelial cells (Photo 5).

The vascular bundle ring is divided into collateral vascular bundles by the primary rays issuing from the pith (Photo 1). The xylem portions of the broader vascular bundles conically taper toward the pith. The primary rays, 3 to 6 cells wide, include the common vascular bundles of the pith and usually also the mucilage canals (Photo 7 [×50]). In the primary rays, the ray cells are elongate ellipses or rectangles; their radial dimension is 370 to 400 μ, their maximum width 70 μ. The cells of the uniseriate rays are much shorter radially (50 to 100 μ); their width is about the same. The walls are exceedingly thin, without any noticeable pitting (Photo 4 [×100]). Some cells are filled with calcium oxalate crystal druses. Some pith rays include thick-walled sclerenchyma cells looking like septate fibres (Photo 7).

Xylem bundles. In the xylem, most tracheids are radially oriented; their walls are uniformly thick (7 to 8 μ), their radial dimension is 50 to 60 μ, their width about the same or somewhat greater. The lumina are invariably rounded (Photo 4), circular or elliptical, while the external outline is rounded polygonal. In the radial walls, bordered pits are readily visible but on the tangential side pits are very rare. Among the tracheids, a few thin-walled wood parenchyma cells are occasionally found (Photo 4).

Cambium. The xylem is in places flanked on its outer side by a cambium 3 or 4 cell layers thick (Photo 4). The cambial cells are smooth and thin walled.

Phloem bundles. Similarly to the xylem the phloem is dissected by primary and secondary pith rays (Photo 4). The structure of the pith ray cells is as in the xylem. The phloem consists for the most part of thick-walled fibres (Photo 4/1) whose lumina are narrow and invariably circular or elliptical. The layering of their walls is sometimes apparent. Among them a few thin-walled parenchyma cells are arranged (Photo 4/2). Very rarely, especially in the external part of the phloem, the holes of sieve tubes could be established (Photo 3 [×30]).

The normal xylem and phloem ring is surrounded by a second, so-called abnormal xylem and phloem ring (cd−cd), which agree in structure with the first ones although they are somewhat narrower (Photo 1).

Cortex. The cortex consists of ground tissue cells of the same structure as the pith. The solitary vascular bundles and the mucilage canals are also of the same structure and arrangement as those in the pith.

On the outer side of the cortex there is a rather broad layer of sclerenchyma cells (Photo 6). These are strictly speaking thick-walled idioblasts, loosely packed in some places and close packed in others. Locally they look like thick-walled twin fibres. In cross section, they are of two kinds: the one is thin walled, the other quite thick walled. The latter seem to be typical stone cells (Photo 6). It is this sclerenchyma layer which gives strength to the wood. The other cells of the cortex are thin walled and unpitted.

The periderm. The periderm cells are rectangular, suberized and close packed, as a rule in radial rows (Photo 1f).

Tangential section. The primary pith rays are multiseriate, 15 to 20 cell layers wide; the secondary pith rays are generally uni- to triseriate (Photo 7). The height of the ray cells ranges from 70 to 150 μ, their width from 50 to 60 μ. Their walls are very thin and smooth. In some pith rays, especially in the sites of corner cells, thick-walled sclerenchyma cells occur, easily recognized by their simple pitting (Photo 7/3). In the tangential walls of the tracheids, bordered pits are very rare. In the broader rays, mucilage canals and vascular bundles coming from the pith are seen (Photo 7/1,2). Among the thin-walled ray cells, thick-walled sclerenchyma fibres are rather frequent (Photo 7/3), which to all probability also pass from the pith into the cortex. All this is readily visible in Photo 7.

Radial section. Pith rays. Most pith ray cells are upright or square (Photo 11 [$\times$ 300]). Their height is 80 to 120 μ, their width 60 to 70 μ. Their walls are smooth and thin. Definite cross fields are but rarely observed. Between the tracheids and the ray cells there is sometimes what looks almost like scalariform perforation. The ladder steps form in places minor or major groups (Photo 10 [$\times$ 300]); in other cases the ladder covers the whole length of the tracheid (Photos 8 [$\times$ 300], 9 [$\times$ 300]). The pits occurring in some cross fields number 10 to 12; they are generally arranged in 2 or 3 longitudinal rows (Photo 11). Longitudinal parenchyma cells often adhere to the ray cells. Their height is 220 to 250 μ, their width 22 to 24 μ. In some broad rays, there occur some thick-walled ray cells among the thin-walled ones, in conformity with what we have seen in the tangential section.

Tracheids. The most characteristic property of the wood is the typical araucarioid pitting and scalariform perforation (Photos 8–12). In the broader tracheids the bordered pits are alveolarly arranged in 3 or 4 rows. Their apertures are linear, included. In other tracheids – sometimes in direct contact with the former – scalariform perforation and thickening are very frequent; to all probability, it only develops on the sides in contact with the pith rays. This is proved by the fact that in the opposite wall of the same tracheid, bordered pits are arranged in the araucarioid pattern (Photos 8, 12 [$\times$ 600]). Scalariform perforation or thickening mostly develops along the tracheids. In this respect there is a similarity – strange as it may sound – to the scalariform perforations of palms. No modern pitting has been observed. Such scalariform perforation has not been established up to now except in *Cycas media.* Scalariform thickening is not to be confused with spiral thickening. The helical ridges are of the same thickness in their whole

length while these ladder spokes widen at both ends, indicating that the space between them is due to the coalescence of bordered pits, i.e. that they derive from bordered pits.

(b) MACROZAMIA

Macrozamia thrives exclusively in Australia, mainly on the east coast (see Map on p. 18). In his latest work on the Australian Cycads, Johnson distinguished 14 species on the basis of external morphology, to wit, *Macrozamia communis* L. Johnson, *M. diplomera* (F. Muell.) L. Johnson, *M. fawcettii* Moore, *M. heteromera* C. Moore *M. lucida* L. Johnson, *M. macdonnelli* (F. Muell.) A. DC., *M. miquelii* (F. Muell. A. DC., *M. moorei* F. Muell., *M. pauli-guilielmi* W. Hill and F. Muell., *M. platyrachis* F. M. Bail, *M. reidlei* (Fisch.) C. A. Gardn., *M. secunda* C. Moore, *M. spiralis* (Salish) Miq., *M. stenomera* L. Johnson.

Of these species, the author has so far succeeded in procuring and treating specimens of seven, to wit, *M. communis*, *M. douglasii* – identified with *M. miqueli* by Johnson – *M. macdonnelli*, *M. miquelii*, *M. moorei*, *M. pauli-guilielmi* and *M. secunda*.

Macrozamia communis L. Johnson (1959)

Plates XXXVII, XXXVIII, Photos 1–12; Fig. 8

It occurs only in the narrow south-eastern coastal strip of Australia. Its stem is often creeping, subterraneous, sometimes rising to a height of 1 to 2 m; in the latter case its diameter is 30 to 60 cm. The leaves are 70 to 200 cm long. The examined material was received from Mr Wilkes in Brisbane. The stem sample probably originates from the apical region because the xylem rings are not complete yet and the collateral bundles are loosely arranged.

Macroscopic examination. The stem sample is of a diameter of about 8 cm. Pith diameter is about 2·5 cm; the xylem is 4 to 5 mm thick, the phloem somewhat less; the thickness of the cortical portion is about 2·5 cm (Photo 1 [nat. size]).

Microscopic examination. Even under a weak magnification it is apparent that the stem consists of a well-developed pith, a narrow xylem and phloem layer and a rather broad cortical portion (Photos 2 [× 30], 3 [× 15]).

The parenchyma cells of the pith are remarkably thin walled, isodiametric, unpitted. Among the parenchyma cells there are sporadic mucilage canals containing a yellow milk-like substance; their diameter is about 180 to 200 μ (Photo 7 [× 100]); their walls are lined with parenchymatous epithelial cells. They are scattered, but some of them constitute a sort of ring immediately inside the vascular bundle ring as a rule near the primary pith rays (Photo 4h [× 100]). The wide pith rays enter gradually between the collateral bundles, to melt outwards into the parenchyma cells of the cortex (Photo 5 [× 100]).



Fig. 8. *Macrozamia communis* (New South Wales; photo by Totterdell)

The xylem bundles are divided up by secondary and tertiary uni- or biseriate pith rays. In section, most tracheids are rounded polygons with a few thin-walled parenchyma cells scattered among them (Photo 6 [× 100]).

In the phloem bundle there are remarkably few fibres. Their walls are strongly thickened, their lumina often almost pinhole-like. The thin-walled parenchyma cells among them are in contact with the larger ray parenchyma cells. In the cortex, collateral bundles and mucilage canals are rather frequent. The cells constituting its external part contain rather many calcium oxalate crystal druses.

Radial section. In the tracheid walls, the bordered pits are generally arranged in the araucarioid pattern, in 4–5 alternating rows (Photos 8–11 [× 300]). Sometimes the chambers and apertures of 2 adjacent bordered pits coalesce and then the combined aperture becomes slit-like. In other cases the chambers and apertures of the bordered pits are considerably elongate transversely and span the cell walls; as a consequence, a thickening develops that is almost scalariform, but this is very rare. The ray cells are more or less isodiametric, their walls bear no pitting or definite cross fields (Photo 12 [× 600]).

Macrozamia douglasii W. Hill (1882)*

Plates XXXIX, XL, Photos 1–14

Its area of distribution is Australia, the province of Queensland where it sometimes grows in groups on sandy surfaces. Its stem is in most cases subterraneous, creeping; if it emerges above the ground it is 60 cm to 1 m high, its diameter may attain some 30 cm, and its exterior is tomentose. The leaves, 2 m long, are composed of 150 to 160 leaflets, 20 to 35 cm long, 3 to 11 mm wide. The material examined was received from the Department of Forestry, Brisbane (courtesy of Mr Horne and Mr Wilkes).

Macroscopic examination. The diameter of the stem sample received was about 12 cm including the leaf bases, and only 5 cm without them. The diameter of the pith was about 2 cm (a), the thickness of the double vascular bundle ring 3 to 4 mm (cd), that of the cortex, about 10 mm (Photo 1 [× 2]) (e). In the picture, the dark spots both in the pith and in the cortex represent solitary vascular bundles (e). The number of bundles decreases towards the exterior of the cortex and the cortex passes almost imperceptibly into the leaf base layer where the dark spots mark the cross sections of the vascular bundles running in the rachis. The leaf bases are covered on the outside with yellowish brown tomentose hairs.

Microscopic examination. The pith (Photo 6a [× 100]) consists of thin-walled, more or less isodiametric parenchyma cells most of which have a diameter of 100 to 120 μ. Their section is a circular or rounded polygonal. There are intercellular ducts between most pairs of neighbouring cells. The interior is filled with starch. The diameter of the mucilage canals (Photo 8g [× 100]) is 200 to 220 μ; their interiors are lined with tiny ephithelial cells. Here and there, vascular bundles occur, the number of tracheids in them ranges from 30 to 50.

* This species is identified by Johnson with *Macrozamia miquelii* but it differs so much in its anatomy as to justify separate discussion under this name.

The mucilage canals are generally arranged at the endings facing the pith of the xylem bundle ring or next to the protoxylem and transfusion cells, i.e. by and large in a circle parallel to the edge of the pith.

Vascular bundle ring. The cells of the pith gradually pass into the primary pith rays (Photos 2 [× 30], 5 [× 100]). Here the cells are strongly elongate and narrow. In the ray cells there is much starch; some are filled with calcium oxalate crystals.

Xylem ring. The primary xylem ring is comparatively narrow, 50 to 60 tracheids wide. The broader xylem bundles taper conically towards the pith. The broader xylem bundles are divided up by uni- and biseriate pith rays into bundles 1 to 3 tracheids wide (Photo 4 [× 100]). In section, the tracheids are rectangular, pentagonal or polygonal, with corners rounded off; so are also the cell lumina (Photo 4). The cell walls are 6 to 7 μ thick. Among the tracheids there are a few thin-walled parenchyma cells whose size agrees with that of the adjacent tracheids. On the other hand, the cells of the uni- and biseriate rays are invariably larger (h). The radial dimension of the tracheids is 40 to 45 μ; their width is about the same.

Outward of the xylem bundle ring there are a hardly perceptible cambium and a phloem bundle ring (Photo 2d). The phloem bundles lie in the continuation of the xylem bundles; they largely consist of thin-walled ray cells and phloem parenchyma cells (Photo 3 [× 100]).

Phloem fibres are sporadic and scattered; this may be due to the subterranean nature of the stem. The size of the phloem fibres is 30 to 35 μ; radially flattened rectangular of shape, they are comparatively thin walled; their lumina are flattened ellipses, sometimes almost slit-like. The ray cells are also in the phloem portion much larger than the adjacent xylem parenchyma cells (Photo 3d).

The first phloem and xylem bundle rings are embraced by the first abnormal ring. Between the first phloem bundle ring and the second xylem bundle ring there are remarkably many transfusion cells (Photo 7b [× 300]) which, congregated in clusters, gradually pass into the second xylem bundle ring. The transfusion cells are originally of the same size and shape as the parenchyma cells (Photo 7b), all the difference being in the thickening of the cell walls. The walls of the transfusion cells are as thick as those of the tracheids, their pitting is partly bordered. If, however, these transfusion cells elongate and turn into tracheids, they assume the simple pitting of the latter (Photo 13 [× 300]). This structure and pitting indicate that these transfusion cells derive from the parenchyma cells of the ground tissue.

The first abnormal xylem ring is much thinner than the normal xylem ring; the first abnormal phloem ring is also much thinner than the normal phloem ring. Outside the first abnormal phloem ring a new layer of transfusion cells develops which passes into the second abnormal ring (Photo 5). The cortex (e) follows outside this second or third abnormal bundle ring. Its cells are of the same size and structure as the pith cells. Among them there are mucilage canals of 280 to 300 μ diameter (g) lined almost ring fashion by thin-walled epithelial cells (Photo 8). The vascular bundles of the cortex are also apparent.

The parenchyma cells of the cortex gradually pass into the leaf bases whose parenchyma cells are basically of the same structure as the ground tissue cells of the pith or cortex. Since the exterior of the stem is densely covered by the leaf bases, there is no well-defined periderm on it. In the external part of the cortex, there are fairly numerous cortical bundles running parallel to the periphery which form a sort of webbing on the surface.

Tangential section. The pith rays are very rarely uniseriate, being mostly 2 to 5 and even up to 10 cell layers wide (Photos 9 [× 100], 10 [× 100]). The latter are the primary pith rays which, as a rule, carry mucilage canals and vascular bundles from the pith towards the cortex. The height of the ray cells varies from 80 to 100 μ.

In this species the abundance of transfusion cells is remarkable; these cells, locally forming minor or major clusters, gradually lengthen to assume the shape of tracheids (Photos 5, 7, 13 [× 300]). Their pitting is, similarly to that of the tracheids, bordered. Scalariform pitting is absent in both the tracheids and the transfusion cells.

The structure of the rays between the phloem and xylem bundles is alike. The walls of the parenchyma cells bear irregular patterns of smaller or larger simple pits.

Radial section. The pith ray cells are square or upright; their width is 80 to 100 μ, their height 110 to 140 μ (Photo 11h). Their walls exhibit at most the simple pitting observed in the axial parenchyma cells.

On the contact of pith ray cells and axial tracheids there are no conspicuous cross fields; there may be some periodicity of the tracheid walls where they contact the horizontal walls of the ray cells, inasmuch as in these places there are no bordered pits in the tracheid walls.

Tracheids. Their walls bear bordered pits only (Photos 11 [× 300], 12 [× 300], 14 [× 600]), arranged in 2 to 4 rows, in the araucarioid pattern; the chambers are alveolarly compressed, the apertures linear or slit-shaped, horizontal. Locally the apertures of two adjacent bordered pits may coalesce but this does nowhere result in scalariform thickening (Photo 12). In the phloem, fibres are comparatively thin walled with rather wide lumina.

Macrozamia macdonnelli (F. Muell.) A. DC. (1868)

Plates XLI, XLII, Photos 1–12; Fig. 9

This species is described by Schuster as *M. preisii* (Lehm.), by Johnson and Pilger as *M. macdonnelli* F. Muell. On the basis of the latest monograph by Johnson we shall adopt the name *macdonnelli* here. Its area of distribution is the central Australian desert where it is sporadically encountered. The stem is 1 or 2, exceptionally 3 m high, with a diameter of 60 to 80 cm; very often it lies prostrate on the ground. On its apex it bears a leaf tuft made up of 50 or 100 leaves 150 to 220 cm long; the length of the leaflets is 12 to 25 cm.

The stem sample examined was obtained from the Botanical Gardens of Adelaide (courtesy of director T. R. N. Lothian).

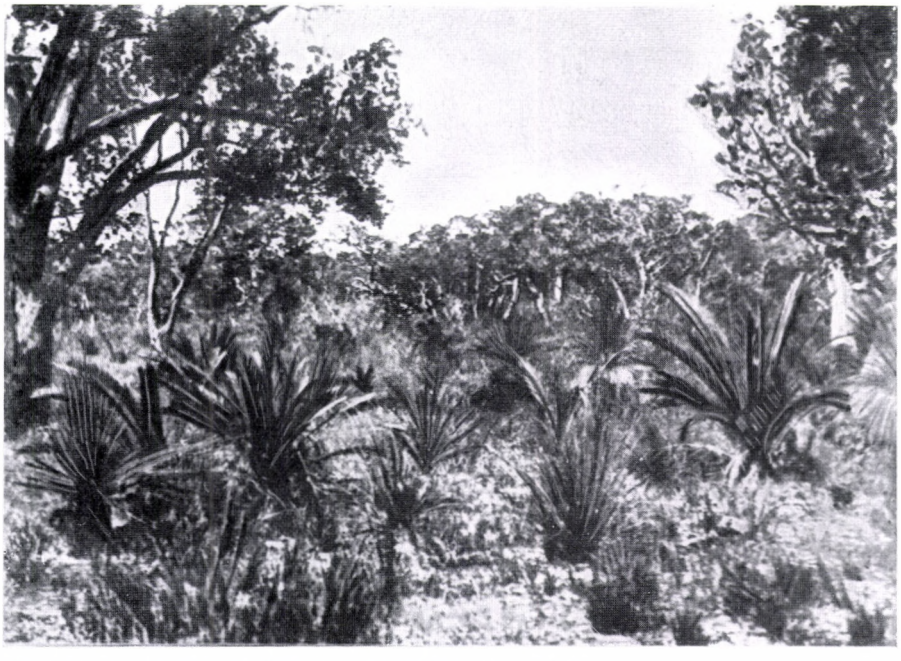


Fig. 9. *Macrozamia macdonnelli* (Australia; after Pritzel)

Macroscopic examination. One of the stem samples came from a quite young specimen of about 3 cm diameter which continued in a rhizome of about 50 cm length (Photo 1 [× 1·5]). The lateral roots branching from it carried root tubers characteristic of the Cycads; its surface bore traces of leaf scars, indicating that some leaves issued directly from the rhizome. A photograph of the rhizome reveals a peculiar structure (Photo 1). In the interior the bundles are either arranged in 2 or 3 rings or scattered about. There is no well-defined pith, its place having been taken up largely by the conductive bundles. The cortex includes no separate cortical bundles, nor any mucilage canals. Another piece of stem of similar thickness showed essentially the same structure (Photo 2 [nat. size]).

The lack of a well-defined pith in the stem sets apart *Macrozamia macdonnelli* from the Cycad species discussed up to now. The pith portion within the bundle layer is filled out with more or less isodiametric parenchyma cells.

Microscopic examination. The pith cells are of 110 to 130 μ size, of irregular, crowded shapes. Intercellular ducts are rare. Calcium oxalate crystal druses are remarkably numerous not only in the pith but in the pith rays and in the cortical cells as well. There are very few mucilage canals and as few conductive bundles in the pith. The primary pith ray cells are thin walled with tiny circular or elliptical pits. The interior of the cells is filled with starch.

Vascular bundle ring. The isodiametric parenchymatous cells of the pith grade almost imperceptibly into the broad primary pith rays (h) which are generally 6 to 10 cells wide. The ray cells among the xylem bundles are somewhat elongate radially, 110 to 120 μ long and 40 to 60 μ wide (Photos 3 [$\times$ 30], 5 [$\times$ 100], 7 [$\times$ 100]).

The xylem bundles are also comparatively narrow, bi- to quadriseriate as a rule (Photo 4 [$\times$ 50]). The pith rays between them are invariably much broader than the bundles (h).

In section, the tracheids are generally square, radially or tangentially elongate rectangular or polygonal (Photo 6 [$\times$ 100]). Among them there are a few scattered thin-walled xylem parenchyma cells whose size is the same as that of the tracheids. The adjacent ray cells are invariably larger than the xylem parenchyma cells themselves (Photo 4). The ray cells themselves are larger and wider near the cortex than near the pith.

The phloem bundles of the phloem ring correspond to the respective xylem bundles (Photo 4); they are uni-, or at most, biseriate and highly inconspicuous. The phloem tracheids are square or rectangular, in cross section thick walled, with pinhole- or slit-like lumina. This structure with underdeveloped xylem and phloem elements is due to the subterranean habit of the studied specimens.

The phloem bundle is embraced by a further xylem-and-phloem bundle ring in quite irregular arrangement (Photo 1). The finer structure of these perfectly agrees with that of the normal bundles referred to above. In the external part of the cortex, calcium oxalate crystals are very abundant, in places almost forming a full layer (Photo 8 [$\times$ 300]).

Near the periphery there are a few cortical bundles among the cortical cells; these continue through the cork cambium into the periderm. Their flattened cells form an alternating pattern resembling a brick wall (Photo 8). In places the exterior of the stem is detached in the form of a simple cortical scale (Photo 1).

In *tangential section*, some pith rays are up to 20 cell layers wide, but most are only tri-, quadri- or quinqueseriate. The bundles running between them have a width of at most 5 tracheids. The ray cells are 90 to 100 μ high and 50 to 60 μ wide. Their shape is upright, elliptical or elongate polygonal; they frequently contain solitary crystal druses of calcium oxalate.

The tangential walls of the tracheids bear close-packed bordered pits (Photo 9 [$\times$ 50]) arranged in 2 or 3 rows in the araucarioid pattern. Their apertures are linear or granulate, horizontal. As a rule, the apertures span the entire width of the walls in the very narrow tracheids (Photo 9), resulting in scalariform thickening. In the broader tracheids, however, 2 or 3 bordered pits may occur side by side. The ray cells are filled with starch.

Whereas in *M. pauli-guilielmi*, a species to be discussed later, there are numerous transfusion cells in contact with tracheids, transfusion cells are very scarce in *M. macdonnelli*. Those few which have been observed bear bordered pits which sometimes pass into scalariform thickening.

In the phloem, width and height of the pith rays are the same as in the xylem. The broadest pith rays carry conductive bundles from the pith towards the cortex.

Radial section. The ray cells perfectly agree, as to structure, with the parenchyma cells of the ground tissue. They are 100 to 150 μ high and 100 to 110 μ wide; their walls are smooth and thin.

Where the ray cells contact the tracheids there are no well-defined cross fields. The presence of such can at best be surmised from that in the tracheid walls, the rows of bordered pits are repeatedly interrupted where the horizontal walls of the ray cells contact the tracheids. One such cross field bears 15 to 20 or more pits.

In the tracheid walls, the bordered pits are arranged in 2 or 3 longitudinal rows, in the araucarioid pattern (Photo 10 [$\times$ 300]). The apertures of the pits are slit-like and horizontal. Sometimes the apertures of 2 or 3 adjacent pits coalesce to span the width of the tracheid wall; the bordered thickening then passes into a scalariform thickening (Photos 11 [$\times$ 300], 12 [$\times$ 600]).

Macrozamia miquelii (F. Muell.) A. DC. (1868)

Plates XLIII, XLIV, Photos 1–11

Its area of distribution is the narrow coastal strip of Eastern Australia. The stem is in most cases subterranean, rhizome-like, with 80 to 100 leaves of about 2 m length in a tuft on emerging apex of the stem. The leaflets are 23 to 36 cm long and 5 mm wide.

Macroscopic examination. The material was received from the Department of Forestry, Brisbane (courtesy of Mr Horne and Mr Wilkes). The stem of rhizome specimen examined was of 4 to 5 cm diameter. Photo 1 [$\times$ 2] shows the cross section of the rhizome. The stem substantially differs in its peculiar structure from those of the other Cycads and is greatly suggestive of the *Medullosae*, thus showing an archaic character. This is borne out also by the finer anatomical investigations. The rhizome is polystelic: in its interior, several separate steles are running. The diameter of the broadest bundle is 2 cm; that of the narrowest, 0·5 cm. The thick central xylem bundles are separated by phloem rings. The phloem layers surrounding the xylem bundles on the periphery merge on the outside to form a phloem ring and the whole is surrounded externally by a thin cortical layer (Photos 2 [$\times$ 30], 3 [$\times$ 50]).

The cortex bears no traces of leaf scars, perhaps owing to the fact that the portion of stem examined is actually part of a rhizome whose structure definitely differs from that of all Cycad stems.

Microscopic examination. There is no well-defined, separate pith. Although there are some parenchyma cells in the middle of the xylem, these cannot be regarded as a pith as known from other Cycads. Among them, there are neither mucilage canals, nor pith bundles and explicitly primary pith rays are also very rare. These parenchyma cells are comparatively small, of 30 to 40 μ size, and iso-

diametric. On the edge of the "pith", small tracheid clusters are arranged as protoxylem elements, it is from these that the tracheid rows issue radially. The rows are uniseriate at first, to flare out subsequently after 8 to 10 tracheids into xylem bundles of 2 to 6 tracheids width. The primary pith rays may be 15 to 20 cells wide; their cells are radially elongate, generally 60 to 70 μ long and 30 to 40 μ wide. Some contain calcium oxalate druses. The broad pith rays gradually taper towards the cambium while the xylem bundles flare out. Subsequently, however, beyond the cambium the rays flare out again in the phloem; as a result the spacing between the phloem bundles grows wider outwards (Photo 6 [$\times$ 100]).

The phloem bundles are in correspondence with the xylem bundles; their width equals the thickness of 2 to 4 phloem fibres. Their outer ends gradually taper until, similarly to the inner ends of the xylem bundles, they become uniseriate (Photos 4 [$\times$ 100], 5 [$\times$ 200]).

The phloem bundles consist of fibres and parenchyma cells; fibre plates alternate with plates or isolated cells of phloem parenchyma.

The phloem fibres are thick walled (8 to 10 μ) with lumina of about the same width or slightly narrower, circular or elliptical but not slit-like. Their sections are square, rectangular or polygonal.

The xylem parenchyma cells are thin walled, their size is about the same as that of the phloem fibres but invariably smaller than that of the ray cells. The thickness ratio of phloem to xylem is variable but the xylem is always thicker.

The cortex. The rhizome includes several steles so that the cortical portion is comparatively thin. This part of the rhizome includes no mucilage canals or cortical bundles, either.

The cortex is surrounded by a periderm whose suberized cells are crowded into a pattern resembling a brick wall.

Tangential section. Most pith rays are uni- to quadriseriate (usually bi- or triseriate). Broad pith rays are very scarce. The uniseriate rays can be 8 to 15 and even 20 cells high. The size of the cells in the uniseriate rays is 100 to 120 μ, exceptionally 200 to 300 μ, by 30 to 40 μ. All walls are smooth and thin (Photo 7 [$\times$ 100]).

Neither mucilage canals nor vascular bundles could be established in the broad pith rays; there are probably none. Some ray cells contain calcium oxalate crystals.

The tangential walls of the tracheids are smooth; pitting is restricted to the areas of contact with the parenchyma cells. The axial parenchyma cells are 250 to 350 μ long and, like the tracheids, 45 to 50 μ wide. All walls are thin and smooth.

Radial section. Pith ray. The height of the pith ray cells is 80 to 90 μ on an average; very exceptionally they attain the height of 300 μ; their width is 160 to 180 μ; they are invariably upright. Some such upright ray cells have the height of two adjacent ones; in such cases the number of the simple pits in the cross fields is also doubled. In the contact areas between ray cells and tracheids, there are cross fields whose height is the same as that of the pith ray cells. One cross field includes 10 to 18 pits, but definite pit fields do not develop everywhere (Photo 8 [$\times$ 200]).

In the tracheid walls, the bordered pits may be arranged in 2 to 5 rows; their chambers are compressed in the araucarioid pattern; their apertures are linear or slit-shaped, horizontal. Sometimes the apertures of two adjacent tracheids may coalesce but scalariform thickening is absent; hence, the tri- or quadriseriate araucarioid pitting of the tracheids is characteristic also of this species (Photos 9, 10 [×300], 11 [×600]).

Macrozamia moorei F. Muell. (1881)

Plates XLV, XLVI, Photos 1–13; Fig. 10

Macrozamia moorei occurs on the east coast of Australia. It is a tree reaching a height of 3 to 5 m. The diameter of the stem sometimes attains 1 m; the leaves are 2 to 3 m long (Fig. 10). The material received must have come from a tall stem, too, because the diameter of its pith is about 25 cm and the polyxylic ring system must have been at least 10 cm and the cortex at least 30 to 40 cm thick.

The excellent material for investigation was obtained by courtesy of Mr H. Wilkes, Department of Forestry, Brisbane.

Macroscopic examination. The polished cross section is shown in Photo 1 [×1·5]. In the extensive pith there are many pith bundles which pass in the form of primary pith rays through the cortex, from there into the leaf bases. Also the polyxylic structure of the wood is easy to recognize in cross section. The thickness of the first xylem ring is about 1·5 cm; it is surrounded by a narrow phloem ring of about 1 cm, which is surrounded in its turn by several alternating layers of xylem and phloem bundles. In places there are 4 or 5 xylem rings and as many phloem rings. In other places some rings coalesce, which reduces their number to 3 or 4 (Photos 1, 2 [×1·5], 3 [×5]).

The pith consists largely of thin-walled parenchyma cells of circular, elliptical, polygonal or rounded cross section; there are numerous intercellular ducts between them. In the pith there are comparatively few mucilage canals. Among the thin-walled pith parenchyma cells, thick-walled ones of the same size and shape are scattered. The thin-walled cells frequently contain calcium oxalate crystals. The diameter of the mucilage canals ranges from 180 to 260 μ; their inner walls are lined with epithelial cells. The thick-walled cells rather often cluster on the edge of the pith, at the points of issue of the vascular bundles, as if they were transfusion cells; their walls bear scattered pits some of which are slit-like. The mucilage canals are arranged in something like a ring, directly inside the first xylem bundle. They almost invariably occur in the places where the primary pith rays set out.

The primary pith rays are quadri- or quinqueseriate; the cells are radially elongated. The primary rays generally continue throughout the second, third and



Fig. 10. *Macrozamia moorei* (Sydney; photo by Johnson)

fourth ring. The xylem bundles between them are divided into smaller units by secondary and tertiary rays. The elements of the xylem bundle, the tracheids are arranged in one or two, rarely three contiguous rows; between the rows there are 1 to 3 layers of thin-walled parenchyma cells, mostly of rounded cross section and lumen.

The xylem bundle ring is embraced by a cambium ring 4 or 5 cell layers thick which is surrounded in its turn by a comparatively thick phloem ring, almost half as wide as the xylem ring. The phloem bundles too are divided into narrower or broader segments by the secondary and tertiary rays (Photo 5 [× 100]). The phloem bundles consist of fibres and parenchyma cells. In some phloem fibres, the walls are substantially thickened, the lumina are narrow; in others, the lumina are fairly spacious although the wall is somewhat thickened. Some thick-walled phloem fibres are solitary; other are arranged in radial or tangential rows (Photos 4 [× 100], 6 [× 300]). The thin-walled parenchyma cells among them differ only in size from the adjacent ray parenchyma cells.

In the cortex and periderm, shape and structure of the parenchyma cells, cortical bundles and mucilage canals (Photo 8 [× 100]) are as those in the pith, with the slight difference that towards the periderm the parenchyma cells become substantially flattened. The edge of the periderm could not be examined as this part was missing from the material received, but it is in all probability similar to those of the other *Macrozamia* species.

In the tangential section the various thickness of the pith rays is apparent. The pith rays are uni- to quinqueseriate (Photo 10 [× 100]); the uniseriate ones are 4 or 5 cells high, whereas the multiseriate ones, the primary rays in the first place, may attain the height of 30 to 40 cells. The sections of the ray cells are generally isodiametric, their walls are thin and calcium oxalate crystals are frequent in them (Photo 9 [× 100]). The tangential walls of the tracheids are generally smooth but at some places there are bordered pits arranged in minor or major clusters or in longitudinal rows. In the parenchyma cells, crystal druses are rather frequent.

Radial section. The pith ray cells are more or less isodiametric and thin walled. No pitting can be observed in them; hence, there are no definite cross fields, either. However, in those portions of the tracheid walls which contact the ray parenchyma cells the bordered-pit structure substantially changes inasmuch as the apertures of the pits coalesce and very often form slit-like pits which span the whole tracheid wall.

In the tracheid walls, the bordered pits are generally arranged in the araucarioid pattern, in 4 or 5 close-packed rows in which the pits occupy alternate positions (Photos 11 [× 300], 12 [× 300]). Sometimes the chambers and apertures of 2 or 3 adjacent bordered pits coalesce, forming oblique slit-like apertures. Annular or scalariform thickening is nowhere present in the tracheids of *Macrozamia moorei.* In some zones, however, of the tracheid walls the pits are missing; it is in these zones that the walls of the ray cells contact the tracheids. It is of course impossible for pits to develop in these zones; therefore Henes's hypothesis that these unpitted zones are bars of Sanio is untenable (Photo 13 [× 600]).

Macrozamia pauli-guilielmi W. Hill et F. Muell. (1859)

Plates XLVII, XLVIII, Photos 1–12

Its area of distribution is the easternmost part of Australia where, according to Johnson, three subspecies are living. Most plants develop a subterranean rhizome only but in some there is a short rising above the ground; a leaf tuft is then arranged at the apex of the stem, immediately above the soil. The short stem above ground is barely 20 cm long; it bears composite leaves about 1 m long whose bases are covered with dense brownish gray tomentose hairs. The material was received from the Department of Forestry, Australia (courtesy of Mr Horne and Mr Wilkes).

Macroscopic examination. The sample received is a portion of the above-ground stem, taken from the close vicinity of the subterranean rhizome. Its diameter is 3 cm, its height 10 cm. Its surface is covered by scars in its lower portion and by tomentose leaves in its upper portion (Photo 1 [nat. size]). The longitudinal section reveals the arrangement of the leaf bases, whereas the cross section shows the internal structure of the stem.

On the polished surface of the stem the various structural elements are readily visible even to the naked eye. The diameter of the pith is 2·5 cm; the first bundle

ring, including a phloem ring of 1 mm, is 2 to 2·5 mm thick; the first abnormal bundle ring is only 1 mm thick. Both in the pith and the cortex, the dark spots represent the proper and common bundles. The cortex of 5 to 6 mm thickness passes almost imperceptibly into the leaf scars which densely cover the surface of the stem.

Microscopic examination. The pith largely consists of thin-walled isodiametric parenchyma cells of 140 to 150 μ size. The smooth walls of the parenchyma cells bear smaller or larger circular or elliptical pits. The cells are close packed; still, intercellular ducts are rather frequent between them. Among the cells, there are remarkably large mucilage canals up to 500 μ in diameter. Their walls are lined with bulging epithelial cells. It is here that we encounter the scattered common bundles of the pith which emerge through the primary pith rays into the cortex.

Vascular bundle ring. At the edge of the pith, the parenchyma cells almost imperceptibly pass into the primary pith rays (h) where most of them are substantially elongated radially; leaving the phloem bundle and flaring out they just as imperceptibly pass into the isodiametric parenchyma cells of the cortex (Photos 2 [×20], 3 [×100]).

At the ends facing the pith of the bundle rings there are transfusion cells, singly or in clusters, which gradually pass into the tracheids of the vascular bundles (Photo 6b [×300]). The xylem bundles are uni- to quinqueseriate. Although in the beginning they are all uniseriate, most of them widen towards the cambium. Many xylem bundles remain, however, uni-, or at most, biseriate even directly before the cambium (Photo 5 [×200]).

The tracheids are rectangular, pentagonal-hexagonal or irregular in section. Their radial dimension is 40 to 50 μ. Among them there are a few thin-walled parenchyma cells of similar size, easily distinguished from the much wider pith ray cells of 80 to 90 μ size. They are procumbent rectangular, arranged more or less at right angles to the radial xylem bundles (Photos 3, 5). At the ends facing the cambium of the tracheids, transfusion cells are remarkably frequent. Outside the cambium, there is a phloem zone (Photo 4 [×200]) composed of subordinate phloem bundles and predominant rays (Photo 3). In section the phloem fibres are square or rectangular, of 18 to 20 μ diameter, thick walled, with slit-like or, more frequently, pinhole-like lumina.

The normal vascular bundle ring is embraced by an abnormal ring. The abnormal ring is much narrower than the normal one but agrees with the latter as to structure (Photo 2). It is remarkable, however, that outside the normal phloem ring there are abundant clusters of transfusion cells marking the passage into the xylem bundles (Photo 2). Transfusion cells are essentially squat tracheids with bordered-pitted thickening. The chambers of some pits are remarkably elongate, and so are their apertures; as a result, some transfusion cells exhibit reticular or scalariform thickenings (Photos 6, 7 [×300]).

The abnormal ring is surrounded by the parenchyma cells of the cortex which are much larger than those of the pith. Their tangential dimension is 400 to 420 μ, their radial dimension 100 to 120 μ. They gradually flatten outwards; in the

external portion of the cortex they become peridermal cells of flat rectangular shape. There is, however, no distinct periderm because the surface of the stem is for a long time densely covered by leaf bases. The cortex contains meandering mucilage canals and vascular bundles.

In *tangential section* the pith rays are seen to be 1 to 10 and even 20 cells wide (Photo 8 [×100]) with rather broad vascular bundles and mucilage canals. Xylem bundles in one of these primary pith rays may have 100 tracheids in a cross section. The size of the ray cells is 100 to 120 μ by 60 to 70 μ.

Beside the tracheids, transfusion cells (Photos 6, 11 [×300]) are very frequent. These sometimes form grape-like clusters which, undergoing a gradual lengthening, pass into tracheids (Photo 9 [×300]). They bear bordered pits exactly like the tracheids.

The radial walls of the tracheids bear bordered pits in 2 and even 3 rows. The horizontal apertures of the bordered pits may considerably elongate, sufficiently so to span the cell in the narrower tracheids; as a result, the pitting becomes almost scalariform (Photo 10 [×300]). Transfusion cells are particularly frequent between the phloem and xylem bundles.

Radial section. The ray cells are square or upright, their height ranges from 60 to 150 μ. Their walls are thin and perfectly smooth. In the zones where the axial tracheids meet thin-walled parenchyma cells there are hardly any cross fields; in most cases there is just a lack of pitting in the walls of the tracheids, in the sectors corresponding to the walls of the adjacent ray cells, whereas in some such zones there are 8 to 15 pits arranged in the araucarioid pattern. The apertures of the pits are generally horizontal; sometimes the horizontal apertures of 2 or 3 pits coalesce, giving rise to scalariform thickening in the tracheid walls (Photo 12 [×600]).

Macrozamia secunda C. Moore (1884)

Plates XLIX, L, Photos 1–12

This rare species occurs in South-eastern Australia, highly restricted in spread and numbers. One of its varieties was named var. *dichotoma* for the characteristic dichotomous branching of its stem. The stem sample examined was received from Mr Wilkes (Brisbane). Its diameter is 15 cm, that of its pith about 7 cm. It was probably taken from a younger stem because instead of the typical polyxylic structure of *Macrozamia* it possesses only a monoxylic ring and a rather substantial cortical portion. A younger stem is suggested also by the fact that the specimen examined bears all leaf bases.

Macroscopic examination. The cut surface reveals the well-developed pith (diameter 7 cm), the narrow xylem and phloem ring and the well-developed cortex. The external part of the cortex is covered by leaf bases (Photo 1 [×2]).

Microscopic examination. In the pith, the parenchymatous cells are isodiametric, varied of shape, sometimes elongate. The walls of some cells are quite

thin, those of the others are somewhat thicker, with tiny simple pits. The thicker-walled cells agree in shape and size with the surrounding thin-walled ones, they only differ in wall thickness and in their golden colour (Photo 5 [×200]). Among the parenchyma cells there are scattered mucilage canals of 300 to 340 μ diameter; their walls are lined with thin-walled epithelial cells (Photo 7 [×100]). Many pith cells contain calcium oxalate crystal druses (Photos 2 [×30], 3 [×100]).

The cells of the *primary pith rays* are almost the same from the pith to the cortex. A remarkable feature is the strong dissection of the *xylem bundles* whose single tracheid bundles are only bi- or triseriate. Even uniseriate tracheid rows are rather frequent. The tracheid sections are rounded-off polygons; the lumina follow the outlines of the cells.

Essentially the same applies to the *phloem bundles*, most of which lie in the continuation of the xylem bundles (Photos 3, 6 [×100]). Some phloem fibres are quite thick walled, with almost slit-like lumina; others have somewhat thinner walls and more spacious lumina (Photo 4 [×100]). The adjacent pith ray cells and the phloem parenchyma cells often contain calcium oxalate crystal druses. Towards the external part of the phloem bundle there are numerous transfusion cells which agree in shape and size with the surrounding parenchyma cells, differing from them only in their bordered pitting.

Tangential section. Most pith rays are 1 to 6 cells wide (Photos 8 [×100], 9 [×100]). Cell sections are isodiametric, some contain calcium oxalate crystals. In the broader rays, *common bundles* or mucilage canals are seen to run towards the cortex. In the tangential walls of some tracheids, the pits are arranged in longitudinal rows, but the tangential walls of other tracheids are perfectly smooth. In the thinnest tracheids, the chambers of some bordered pits are somewhat elongate transversally; their apertures then become almost slit-like.

Radial section. In the radial walls of the tracheids, the bordered pits are arranged in the araucarioid pattern, in 3 or 4 rows (Photos 10 [×300], 11 [×300]); the apertures of most of them are horizontal slits. Sometimes the chambers and apertures of 2 or 3 adjacent bordered pits coalesce, forming elongate horizontal slits.

Most pith ray cells are isodiametric, circular, hexagonal or octagonal. The zones where the horizontal walls of the pith ray cells contact the tracheids bear no pits at all. There is no definite annular or scalariform thickening (Photo 12 [×600]).

(c) ENCEPHALARTOS

About 35 species of the genus *Encephalartos* are known. The area of their distribution lies east of Ghana, the République Centre-Africaine, including Kenya, Tanganyika, Uganda and South Africa, particularly the former Cape Colony. They occur first of all in the arid and savanna areas, on the rocky slopes of mountains (see Map on page 18).

The author has succeeded in procuring and has treated stem samples of the following species: *E. altensteinii*, *E. barteri*, *E. gratus*, *E. inopinus*, *E. lehmannii*, *E. septentrionalis* and *E. villosus*.

In histological structure, the genus is far from being uniform, as shall be shown in some detail below.

Encephalartos altensteinii Lehm. (1834)

Plates LI, LII, Photos 1–12; Fig. 11

Its area of distribution is South Africa where it is found mostly on sunny hillslopes in the company of *Acacia* and succulents. Its sturdy cylindrical stem sometimes dichotomic attains a height of 4·5 m and a diameter of 30 cm. On its apex the leaves of 3 m length are arranged to form a tuft. The composite leaf may consist of up to 50 pairs of leaflets (Fig. 11). The material for examination was received from Mr R. A. Dyer, South Africa.

Macroscopic examination. The stem sample examined is a disk of about 22 cm diameter and 3 cm thickness. It includes a massive pith of about 12 cm diameter (Photo 1a [nat. size]). In the pith, the dark spots represent the proper bundles of the pith, the light ones the mucilage canals.

The pith is surrounded by a polyxylic conductive bundle ring (cd, cd) and a comparatively thin cortical portion (e); the thickness of the latter amounts to 1 or 1·5 cm. It passes gradually into the leaf base layer which densely covers the surface of the stem. Our stem sample bore no definite periderm layer because of the leaf bases. The latter were covered by dense brown hairs.

Microscopic examination. The pith largely consists of thin-walled, more or less isodiametric parenchyma cells of 200 to 230 μ size. They are circular, elliptical or compressed. The smaller ones are generally filled with calcium oxalate crystal druses. The walls are thin, bearing in places simple tiny pits. Among them there are a few scattered mucilage canals whose diameter attains 260 μ. They are lined with flat epithelial cells (Photo 7g [$\times$ 100]). Among the thin-walled parenchyma cells, thicker-walled ones of the same size are rather frequent (Photo 6a [$\times$ 300]), mainly near the origin of the vascular bundles. These are probably idioblasts. Their walls bear simple pits and therefore they can hardly be transfusion cells. Also in the pith there are some meandering vascular bundles whose xylem consists of barely 10 to 15 tracheids (Photo 2 [$\times$ 30]).

Vascular bundle ring (cd, cd). The isometric parenchyma cells of the pith (b) show almost imperceptible transitions towards the primary pith ray cells. In the rays, they gradually grow longer and narrower, and so do the thick-walled parenchyma cells (Photo 6). The length of these is 300 μ, their width 45 to 50 μ. Their pitting is the same as in the pith.

From the edge of the pith there issue xylem bundles conically flaring out outwards. Inside their endings one observes protoxylem elements forming minor



Fig. 11. *Encephalartos altensteinii* (left side) and *Encephalartos lehmannii* (right side) (Pretoria; photo by Dyer)

or major clusters and locally also separate tracheal rows which gradually pass into the xylem bundles. These latter have the width of 2 or 3, exceptionally of 6 tracheids (Photo 4 [× 100]); single xylem bundles wider than that are rare and tend to be split up by uni- and biseriate rays (h).

In cross section, most tracheids are square (Photo 4) or polygonal; their radial dimension is 50 to 60 μ, their width about the same. The lumina are invariably rounded. Wall thickness is 5 to 6 μ. The tracheids are close packed but there are among them some thin-walled xylem parenchyma cells of the same size whose radial walls are generally in direct contact with the ray cells. Some parenchyma and ray cells contain calcium oxalate crystal druses.

Phloem bundle ring (Photo 3 [× 100]). Outside the xylem bundle row there are a few rows of cambium embraced in their turn by the phloem bundle ring. The phloem bundles consist of thick-walled sclerenchyma fibres, phloem fibres and phloem parenchyma cells (d). In section, the sclerenchyma fibres are square or procumbent rectangular; their diameter is 35 to 40 μ, their radial dimension 28 to 30 μ; their lumina are small, almost pinhole-like and very seldom slit shaped. Their walls are 15 to 18 μ thick. The phloem fibres are single or arranged in axial rows or in tangential plates. Their size is the same as those of the sclerenchyma fibres, but their walls are much thinner. The sclerenchyma fibres are more numerous on the external side of the phloem bundles. Where phloem fibres and sclerenchyma fibres are seen side by side, the difference is quite striking.

Abnormal bundle rings. Outside the first phloem ring there are one or two cell layers of ground tissue, followed by the first abnormal xylem and phloem rings. These perfectly agree in structure with the normal vascular bundle ring. Outside this first abnormal ring, there is in places a third one in development. The conductive bundles of this latter are also separate and run as independent collateral bundles in the cortex. Outside the phloem ring, adjacent to the cortical border there are frequent mucilage canals corresponding to the vascular bundles, forming a loose ring in the cortex (Photo 5 [× 100]). The parenchymatic structure of the cortical ground tissue (e), the size of the mucilage canals (Photo 5g) and of the epithelial cells and the structure of the vascular bundles of the cortex (Photo 5cd) perfectly agree with those of the pith.

In the external part of the cortex (e), in the region of issue of the leaves, no periderm layer has developed as yet. The ground tissue cells of the cortex are seen to pass gradually into the parenchyma of the leaf bases (Photo 1e). In the leaf bases, on the other hand, more or less scattered leaf bundles are observed.

In *tangential section* (Photo 8), the pith rays are uni- to quinqueseriate; the primary rays may be up to 15 cells wide. The uniseriate rays are 6 to 10 cells high, the biseriate ones even higher and the primary rays may attain a height of 40 to 50 cell layers.

The height of the ray cells is likewise varied; the cells in the uniseriate rays are up to 150 μ high and 25 to 30 μ wide. In the multiseriate rays the height of the ray cells is generally less, 60 to 70 μ. The walls are thin and smooth. In some rays, thick-walled simply pitted parenchyma cells occur whereas the parenchyma cells in contact with the tracheids are invariably thin walled. The height of these is 220 to 240 μ, their width the same as that of the tracheids (30 to 40 μ).

The tangential walls of most tracheids are smooth (Photo 8 [× 100]). In places, however, there are clusters of tiny bordered pits of 8 to 10 μ size, with circular chambers. In cases where several such pits are close packed, the chambers tend to be hexagonal. The apertures are linear, horizontal or oblique. Some tracheid walls exhibit scalariform perforation which is, however, much more pronounced in the radial walls (Photo 11 [× 300]).

Radial section. The pith ray cells are square or upright rectangular. The height of the former is 90 to 100 μ, that of the latter 120 to 140 μ, their width 80 to 100 μ. All walls are smooth and thin. In the axial tracheids in direct contact with pith ray cells, cross fields are observed. These cross fields bear 8 to 15 pits arranged in the araucarioid pattern. The apertures of the pits are linear, in most cases included and oblique. In some rays there are quite distinct thick-walled and thin-walled ray cells.

Tracheids. In their walls the bordered pits form 2 to 4 rows arranged in the araucarioid pattern (Photo 10 [× 300]). The apertures are short, linear or slit shaped; in some cases, however, the slits are substantially elongate in the horizontal direction and even span the walls of the tracheids: the bordered pitting gradually passes into a scalariform thickening (Photo 10). In some tracheids, the scalariform thickening shows a peculiar modification, especially at, or near, the ends of the tracheids.

The pit apertures grow substantially wider, the chambers of the bordered pits elongate horizontally, resulting in veritable ladder steps (Photos 9 [×300], 12 [×600]). As behind these, on the opposite side of the tracheid, bordered pitting is readily visible, these ladder steps can be regarded as a true scalariform perforation (Photos 10, 11). The number of steps can be as large as 60 (Photo 11). This scalariform perforation-like thickening locally passes into true reticular thickening; similar structures can be observed exceptionally in some Monocotyledons, e. g. in palms.

Some tracheids fit together with horizontal, others with oblique end walls, communication being assured through the bordered pits in the said end walls, and, in the author's opinion, also through scalariform perforations (Photo 11, left and right side).

Encephalartos barteri Carruthers (1860)

Plates LIII, LIV, Photos 1–14

The species is known in Nigeria, Ghana, the Sudan, Uganda, Dahomey and Togo from about 8 localities in all. The stem sample examined was received from the Forest Research Department, Ibadan, Nigeria (courtesy of Mr R. W. J. Kean). The short ellipsoidal stem attains a height of 0·3 to 1·5 m and a diameter of 20 to 25 cm. The leaves are 100 to 165 cm long, the width of the leaflets is 15 to 26 mm.

Macroscopic examination. The specimen studied is a segment of a stem whose original diameter probably was 10 to 12 cm (Photo 1 [nat. size]). The pith portion is 3 cm, the vascular bundle ring 3 mm, the cortical part about 2 cm thick; the leaf bases adhering to the cortex cover the stem in about 3 cm thickness. It is apparent even to the unaided eye that the studied stem portion is monoxylic. The parenchyma cells both of the pith and of the cortex are filled with starch.

Microscopic examination. The pith largely consists of thin-walled isodiametric parenchyma cells of 150 to 200 μ size and rounded square or polygonal shape; intercellular ducts are rather frequent among them (Photo 9 [×100]). The walls of the parenchyma cells are thin and smooth, but some bear tiny scattered circular or elliptical simple pits. Some smaller cells contain solitary calcium oxalate crystal druses. Among the cells there are fairly numerous conductive bundles, some of which emerge in the primary pith rays through the vascular bundle ring into the cortex. One such bundle may include 15 to 20 tracheid rows. The pith further comprises comparatively narrow mucilage canals 150 to 180 μ in diameter, which are of the same structure as those in the cortex (Photo 9g). Their walls are lined with thin-walled epithelial cells. In some places on the edge of the pith, the pith cells almost imperceptibly grade into ray cells; among the vascular bundles the ray cells are considerably elongate radially, being of about 150 to 180 μ length and 40 to 45 μ width.

The xylem bundles taper conically towards the pith; at their ends facing the pith, transfusion cells or protoxylem elements are seen. The protoxylem elements change

gradually into tracheids (Photos 5 [× 100], 6 [× 100], 7 [× 100]). This gradual transition is particularly apparent in tangential and radial sections.

Vascular bundle ring. The xylem bundles are comparatively narrow, 2 to 4 tracheids wide (Photo 4 [× 100]). The lumina of the tracheids gradually widen towards the cambium; their radial dimension is 45 to 60 μ, their width about the same. Their wall thickness is 4 to 5 μ. Among the tracheids there are a few scattered parenchyma cells.

The xylem bundles are embraced by a cambium composed of a few cell layers and by a phloem bundle ring whose bundles correspond as a rule to the xylem bundles. The phloem bundles are broadest next to the cambium; they taper outwards, reducing near the cortex to a uniseriate row of phloem parenchyma or phloem fibre cells (Photo 3 [× 100]). In cross section, the phloem fibres are radially flattened, rectangular or irregular; they have comparatively spacious lumina and thin walls.

Between the phloem bundles, the rays flare out, their cells widen, which is partly due to dilatation. Their size is 80 to 100 μ, their sections are squares or radially flattened rectangles. In the ray cells and also in the phloem parenchyma cells, calcium oxalate crystals are frequent (Photos 3, 5).

The cortex. In the cortex, the shape and size of the parenchyma cells and the dimensions of the mucilage canals are the same as in the pith. On the edge of the pith, there are numerous conductive bundles some of which meander almost parallel to the periphery (Photo 2 [× 10]). In the external portion of the cortex, the cells of the ground tissue are radially somewhat flattened and tangentially elongate, being 300 μ long and 70 to 80 μ wide; some of them are filled with calcium oxalate crystal druses (Photo 8 [× 300]). The rectangular cells of the periderm are strongly crowded.

In *tangential section* (Photos 10 [× 300], 11 [× 300]), the rays are 1 to 6 cell layers wide both in the xylem and the phloem (h). Most primary pith rays are, however, 15 to 20 cells wide and 70 to 80 cells high. The cells of the uniseriate rays are generally 120 to 130 μ high and 40 to 50 μ wide. The smaller cells usually contain calcium oxalate crystal druses.

Along the margins of the xylem bundles, transfusion cells are frequent. At first these are of the same size and shape as the parenchyma cells and it seems as if they occupied the places of those; then, gradually lengthening, they grade into axial tracheids. This gradual transition is fairly often observed (Photos 5, 6, 7).

In the interior of the broader pith rays there are rather often conductive bundles running from the pith into the cortex and from there as leaf scar bundles into the leaves. The pith ray bundles are locally accompanied by mucilage canals. In the pith ray bundles, the xylem consists of a few tracheids, the phloem of a few phloem fibres and parenchyma cells. The walls of the phloem fibres are comparatively thin (5–6 μ) and even. Their size is 35 to 40 μ.

Radial section. The pith ray cells are generally 60 to 65 μ exceptionally up to 120 μ high. The squatter ones are mostly square, the taller ones upright rectangular; for a height of 110 to 120 μ their width is only 60 to 70 μ. All walls are smooth

and thin. In the ray cells contacting axial tracheids there are no cross fields. The pitting of the axial tracheids, faintly visible through the translucent walls of the ray cells, exhibits no interruption. In these cells, calcium oxalate crystal druses are abundant. Among the tracheids there are a few sporadic axial parenchyma cells.

Tracheids. Along the axial conductive bundles, transfusion cells are rather frequent, especially on the phloem side. They show a gradual transition from the isodiametric condition into the tracheid condition. Their walls bear a bordered pitting and reticular thickening. In the elongate, tracheid condition, either the one or the other pitting prevails; as a consequence, some tracheids exhibit a bordered pitting only, some a scalariform thickening only and some exhibit a mixed pitting, bordered and scalariform (Photo 13 [× 300]).

Encephalartos gratus Prain (1916)

Plates LV, LVI, Photos 1–13

The species thrives exclusively in Nyasaland on the slopes of Mlanji hill. The trunk of the female plant is slightly oval and 30 to 40 cm high; that of the male plant may be up to 120 cm high with a diameter of 60 cm. The leaves, 90 to 180 cm long, bear 30 to 70 pairs of leaflets; the latter are 30 to 45 cm long.

The material was received from the Forestry Department, Limbe, Nyasaland. On the stem sample, the polyxylic structure was visible to the naked eye (Photo 1 [nat. size]).

Macroscopic examination. The stem sample comprised a small pith portion only, followed by three or four vascular bundle rings of a total thickness of 3·5 cm (cd, cd); the cortical portion is 2·5 cm thick (e); the leaf bases covered the trunk in a thickness of about 3 cm. In the vascular bundle rings the primary pith rays and the collateral tracheid bundles are visible to the naked eye, and so are the solitary tracheid bundles and mucilage canals in the cortex.

Microscopic examination. The pith largely consists of isodiametric parenchyma cells of 140 to 150 μ mean size. Close packed in general, they locally include minor or major intercellular ducts. The cell walls are thin and smooth with occasional rows of smaller or larger circular or elliptical simple pits. Among the pith cells, there are mucilage canals of 280 to 300 μ diameter; their walls are lined with small epithelial cells (Photo 8e, g [× 300]). The pith further contains solitary scattered collateral conductive bundles which meander through the primary pith rays into the cortex.

Vascular bundle ring (Photo 2cd [× 10]). The bundles of the xylem ring issue at the edge of the pith, flaring out conically outwards. The broader bundles are separated by primary pith rays (h). In cross section, the tracheids of the xylem bundles are square, pentagonal or polygonal; their lumina, however, are invariably rounded and do not always follow the outline of the cell. In the fields of contact between tracheids and ray cells, the walls are somewhat thickened; intercellular ducts are rare (Photo 4 [× 100]).

Among the tracheids, thin-walled parenchyma cells are scattered whose shape, size and wall thickness agree with those of the ray cells. The xylem segments of 50 to 60 tracheids width between the primary rays are further dissected by uni- or biseriate secondary rays.

Phloem bundles (Photo 3d [×100]). The cambium limiting the xylem bundles consists of 2 or 3 cell layers. It is embraced by phloem bundles which correspond to the xylem bundles. The phloem bundles consist of thick-walled fibres and parenchyma cells. The sections of the phloem fibres are square, squat rectangular, polygonal or hexagonal; their lumina are very seldom slit-like, mostly ellipsoidal, or circular in the cells of square section. The wall thickness of the xylem fibres is 6 to 8 μ; the diameter of the lumen is as much or less.

The phloem bundles conically taper towards the cortex; at their ends, some phloem primanei can be observed.

The same vascular bundle ring structure may be repeated up to four times. The outermost phloem ring is surrounded by the cortex whose ground tissue generally consists of parenchyma cells of the same size and structure as those of the pith. The only difference is that, in the cortex, mucilage canals are much more numerous, their diameter, however, is also here around 300 μ. The number of xylem bundles is also much larger than in the pith.

Outside the last phloem bundle ring, there are in the ground tissue the tiny primordia of collateral bundles arranged in a ring. These primordia would presumably have developed into larger bundles. The structure of such a primitive primary bundle is shown in the upper part of Photo 2. The cortex is surrounded by the periderm whose structure by and large agrees with that of the other Cycad genera.

Tangential section (Photo 9 [×100]). Most rays are uni- or biseriate; the primary rays may attain a width of 10 to 20 cells. The cells of the uniseriate rays are 120 to 140 μ high and 22 to 24 μ wide. Those of the broader rays may be much squatter. They are of various shape, compressed, somewhat elongate longitudinally.

In the central portion of the broader rays there are conductive bundles passing from the pith towards the cortex.

Generally smooth, the tracheid walls locally bear loosely arranged bordered pits of 6 to 8 μ size, of linear or slit-shaped apertures. In a few rare cases of some tracheids a scalariform thickening develops in one of the walls, most often near one end of the tracheid; it closely resembles true scalariform perforation (Photo 11 [×300]).

Radial section. In the radial view, the pith ray cells are square, upright or procumbent rectangular (Photos 10 [×300], 12 [×300]). Their height is 70 to 80 μ. The procumbent ones are of the same height but 120 to 150 μ wide. Where the tracheids contact cells with bordered pits, their walls develop cross fields which may contain 16 to 30 simple pits arranged in the araucarioid pattern. The pit chambers are ellipsoidal, somewhat compressed, their apertures slit-like or linear, extended or included. There is no such pitting in the ray cells: only the bordered

pits of the tracheids are seen vaguely through the thin translucent walls of the ray cells.

In the tracheid walls the bordered pits are arranged in 3 or 4, exceptionally 6 rows, the chambers are alveolar, compressed (Photo 13 [× 600]). The apertures of neighbouring bordered pits tend to coalesce, forming gashes, but these gashes nowhere span the walls of the tracheids so that no true scalariform thickening develops. The scalariform structure described from the tangential side, which in all probability indicates the beginning of scalariform perforation, is a markedly different feature. Among the tracheids there are a few scattered thin-walled parenchyma cells of smooth and very thin walls.

Encephalartos inopinus Dyer (1964)

Plates LVII, LVIII, Photos 1–16; Fig. 12

The material examined was put at the author's disposal by Mr A. Dyer who described the new genus from South Africa.

Macroscopic examination. The diameter of the trunk sample is 18 cm. Its cross section shows the layers characteristic of a monoxylic Cycad. The diameter of the well-developed pith is 7 to 8 cm; the thickness of the xylem and phloem ring is about 1·5 cm; that of the cortical portion including the leaf bases is 3 to 4 cm (Photo 1 [nat. size]).

Microscopic examination. The pith is largely made up of thin- and thick-walled, more or less isodiametric parenchyma cells; the thick-walled cells differ only in wall thickness from the surrounding thin-walled ones. The thick walls locally bear simple pits (Photo 2 [× 100]). At the edge of the pith there are as a rule mucilage canals at the points of issue of the xylem bundles (Photo 3g [× 10]) accompanied by transfusion cells (Photo 4 [× 100]). Size and shape of these latter fully agree with those of the thick- and thin-walled parenchyma cells of the pith, except for the pitting. The transfusion cells form some sort of transition towards the tracheids; even their bordered pitting is like that of the tracheids (Photo 4). The two kinds of parenchyma cells turn up again in the cortex (Photos 3, 5 [× 30]). The mean diameter of the mucilage canals is 240 to 250 μ; the canal walls are lined with thin-walled epithelial cells. Most mucilage canals of the pith and cortex are axial but some meander to and fro (Photos 6 [× 100], 7 [× 100]). The size of the epithelial cells is 30 to 40 μ. The size of the pith parenchyma cells is about 150 to 160 μ; their shape is polyhedral as a result of crowding (Photo 2). The parenchyma cells at the edge of the pith are somewhat elongate in the direction of the primary rays, but not substantially so (Photo 8h [× 100]); some pith ray cells retain the thick walls and the simple pitting of the pith parenchyma cells.

Vascular bundle ring. The xylem ring is divided into narrow segments by dense uni- to triseriate primary rays; the xylem bundles are 2 to 8 tracheids wide, being broadest where they meet the cambium (Photos 7, 9 [× 30]). Xylem bundles wider

than 7 tracheids are very rare (Photos 8, 9). The sections of most tracheids are square, pentagonal or hexagonal; their radial dimension is 40 to 45 μ; their width is about the same (Photo 8). The walls are of uniform thickness. The xylem ring possesses in places a rather inconspicuous periodicity which is probably due to the life habits of the tree (Photo 6). Outside the xylem bundles (c) there is a thin layer of cambium; the phloem bundles (Photo 9d) gradually taper outwards while the uni- or biseriate pith rays become tri- and even quadriseriate towards the cortex, as a result of dilatation (Photo 10 [$\times$ 100]). The phloem consists of thick-walled fibres which as a rule form smaller or larger clusters or plates in threes or fives; among them, thin-walled parenchyma cells are scattered (Photo 10). No sieve tubes could be established. In cross section, the phloem fibres exhibit various types of thickening; the lumina of some are almost point-like, whereas in others the lumina are much wider and follow the outline of the cell. The size of the phloem fibres is 45 to 50 μ, being sometimes flattened radially to 35 to 40 μ.



Fig. 12. *Encephalartos inopinus* (Pretoria; photo by Dyer)

The structure of the cortex by and large agrees with that of the pith. Among the thin-walled parenchyma cells, thicker-walled ones are grouped in the form of tongues of flame pointing outwards (Photo 5); these groupings include mucilage canals and parenchyma cells containing calcium crystals. The number of the crystalliferous cells substantially increases towards the cortex; there are calcium oxalate crystals in nearly all cells of the periphery (Photo 11 [$\times$ 50]). It is interesting to note that there are sclerenchyma fibres arranged parallel to the periphery to strengthen, as it were, the outer portion of the cortex. Outside the sclerenchyma fibres the cortical cells gradually flatten and then pass into epidermis cells (Photos 5, 11).

Tangential section. There are rays 1 or 2 cells high and as wide but rays up to 3 cells wide are rather frequent, too (Photo 12 [$\times$ 100]). The cells of the broad pith rays are procumbent rather than perfectly isodiametric. The ray cells are, simi-

larly to the pith parenchyma cells, either thin or thick walled, they are somewhat smaller in the rays (80 to 90 μ) than in the pith. The tangential walls of the axial tracheids are generally smooth, but they bear in places tiny bordered pits (Photo 12). The phloem fibres are thick walled; some are septate. Near the cortex there occur among the tracheids and phloem fibres a few sporadic thin-walled xylem or phloem parenchyma cells.

In *radial section* the bordered pits in the tracheid walls are either arranged regularly in 4 to 6 rows in the araucarioid pattern, in which case their lumina are short horizontal slits (Photos 13–15 [$\times$ 300]), or the chambers of the bordered pits are flattened and often span the width of the tracheids. In such cases the aperture becomes slit-like and in some places spans the width of the tracheid, so that the wall becomes almost reticular with scalariform thickening (Photo 16 [$\times$ 600]). This gradual transition is occasionally exemplified by a row of neighbouring tracheids. The ray cells are either squares or upright rectangles. The size of the latter is 150 to 160 μ, their width 60 to 70 μ; their walls are thin, without pitting in the cross fields, although the elongate pits of the tracheids behind them may be visible through their thin translucent walls. Among the tracheids there are a few thin-walled parenchyma cells with rather narrow lumina, whose end walls are perfectly smooth and thin (Photos 14, 16). In some rays, the thick- and thin-walled parenchyma cells alternate, almost forming layers. The cells very often contain calcium oxalate druses (Photo 12).

Encephalartos lehmannii Ecklon (1834)

Plates LIX, LX, Photos 1–11; Fig. 13

Its area of distribution is South Africa, particularly the Transvaal, where it occurs on slopes covered with a rich humus soil. Its squat trunk is 30 to 50 cm tall and 30 to 40 cm thick. There are 10 to 25 leaves of about 1 m length on the top of the trunk. The composite leaf consists of 24 to 36 leaflets. It is an inhabitant of most botanical gardens. The material was obtained by the courtesy of Mr Dyer, Pretoria.

Macroscopic examination (Photo 1 [nat. size]). The trunk sample examined may have had a diameter of about 12 cm including the pith of 4·5 to 5 cm diameter (a), the double vascular bundle ring barely 1 cm thick (cd), the cortical portion 1 cm (e) and the leaf base layer, 2 cm (f). The surface at once reveals the polyxylic structure of the wood. In the photo, the dark spots both in the pith and the cortex represent the pith and cortical bundles, respectively; the light points arranged in a ring next to the vascular bundle ring both in pith and cortex represent mucilage canals (e). The cortical portion is covered almost armour-like by the dense leaf bases.

Microscopic examination. The pith largely consists of comparatively large, more or less isodiametric cells (Photo 2a [$\times$ 10]) of about 220 to 230 μ by 70 to 80 μ size and rounded square or polygonal, circular or elliptical shape. Their walls are



Fig. 13. *Encephalartos lehmannii* (South Africa; photo by Dyer)

thin and smooth, in places with irregularly scattered circular or elliptical simple pits (Photo 5 [× 100]). The diameter of the mucilage canals (g) is 220 to 230 μ; their interior is lined with tiny thin-walled epithelial cells.

There are also some conductive bundles which emerge through the primary pith rays into the cortex.

The cells at the edge of the pith penetrate as primary pith rays (h) between the xylem bundles, lengthening radially and becoming rectangular in the process. Their radial dimension is 180 to 200 μ, their width 65 to 70 μ. Among the tapering phloem bundles, the cells of these primary rays tend to elongate tangentially and to flatten out radially. Besides the primary pith rays, there issue from the pith much narrower, uniseriate secondary rays. Among the ray cells there are some thick-walled parenchyma cells; these are veritable idioblasts of 120 to 130 μ length and 100 to 110 μ width. Their walls bear simple pits.

Vascular bundle ring (cd). Directly inside the xylem bundles, the pith contains some protoxylem elements or transfusion cells (Photo 6 [× 300]). Similar elements occur after a slight interruption also in the xylem bundles, most of which are 2 to 4 tracheids wide. In sections, the tracheids are square, rectangular, polygonal or circular but their lumina are invariably rounded. The tracheids are close packed with sharp edges so that there is no place for wide intercellular ducts between them. Their radial dimension is 40 to 50 μ; their width is about the same (Photo 4 [× 100]). Between the tracheid rows there are parenchyma cells, mostly in contact with

the ray cells. The cells of the uniseriate rays are generally square or somewhat elongate rectangular.

Phloem bundles (Photo 3 [×100]). The uni-, bi- and triseriate xylem bundles continue in phloem bundles of identical width. The uniseriate phloem bundles are composed of rows made up of phloem parenchyma cells interrupted more or less regularly by solitary phloem fibres. In the external part of the phloem, the phloem fibres are slightly more numerous, forming smaller or larger clusters. In section, most phloem fibres are square or rectanguar; the tangential walls of the latter are often caved in; as a result, their lumina are substantially reduced. The ray cells are at least twice as wide and long as the adjacent phloem parenchyma cells (Photo 3). In the outermost portions of some phloem bundles, adjacent to the cortex, phloem primanei can still be observed.

Cortex. Shape and arrangement of the parenchyma cells, structure and size of the mucilage canals and structure of the conductive bundles are the same as in the pith. It is worth noting that outside the external bundle ring the mucilage canals are arranged in a ring (Photo 1) exactly as on the edge of the pith. The cortex is surrounded by a periderm.

Tangential section (Photo 7 [×100]). The rays are uni- to triseriate or multiseriate. Most uniseriate rays become bi- or triseriate at their ends and at their middle; they may attain the height of 15 cells. Cell size is 90 to 100 μ by 22 to 30 μ. All walls are smooth and thin. In the broad rays, the cells are somewhat lower and generally polygonal. In the very broad primary rays, the walls of some parenchyma cells are substantially thickened and simply pitted. In the primary rays there are numerous vascular bundles meandering from the pith towards the cortex. Mucilage canals occur in comparatively few rays.

Tracheids. The tangential walls of the tracheids are quite smooth, in some places with sporadic tiny bordered pits of 6 to 7 μ size and slit-like lumina. Among the tracheids or next to them there are thin-walled parenchyma cells with perfectly smooth and thin walls.

Radial section (Photos 8–10 [×300], 11 [×600]). The *ray cells* are square or upright. Their height is 80 to 90 μ, their width about the same or less. On the contact of the outside ray cells with the tracheids, cross fields are very rare. In them, 10 to 15 pits are arranged in 2 or 3 axial rows (Photo 8). The pits may be either close packed or loose. Their apertures are linear or slit-shaped and somewhat oblique. The apertures of neighbouring bordered pits sometimes coalesce and become gash-like but these gashes nowhere span the tangential walls so that there is no scalariform thickening (Photos 9, 10).

The *tracheids* bear exclusively bordered pits; in one tracheid wall, as many as 4 bordered pits may be placed side by side. The chambers are alveolarly compressed locally (Photo 9); elsewhere there are smaller or larger gaps among them. The lumina are slit-like, horizontal or oblique; the oblique ones sometimes cross those on the opposite wall.

Among the tracheids, axial parenchyma cells are rather frequent; their length is 370 to 400 μ, their width 35 to 40 μ. All walls are smooth and thin (Photo 10).

Encephalartos septentrionalis Schweinf. (1871)

Plates LXI, LXII, Photos 1–14; Fig. 14

The species is found in Uganda, the Sudan, the République Centre-Africaine and the Congo in a total number of 8 localities. For a height of about 2 m, the stem diameter is barely 30 cm. The leaves are 90 to 150 cm long, the leaflets are 20 to 28 mm wide; the tips of the leaflets are rounded and somewhat tomentose. The material for examination was received directly from the Congo. The sample was quite fresh and coloured white by its rich starch content. It is a portion of a trunk of 20 to 25 cm diameter.

Macroscopic examination. The photo of the smoothed surface (Photo 1 [nat. size]) reveals the very broad pith whose original diameter probably exceeded 15 cm (a), the vascular bundle ring of 3 to 4 mm thickness (cd) and the cortical ring, about 2·5 to 3 cm thick (e). In the photo, the dark spots in the pith and in the cortex represent the conductive bundles, the light spots the mucilage canals. The vascular bundle ring is divided into two double layers; the wood is consequently polyxylic. The dark dashes parallel to the periphery represent meandering vascular bundles.

Microscopic examination. The pith is largely composed of very thin-walled, more or less isodiametric parenchyma cells whose size ranges from 100 to 110 μ. They are not very closely packed; there are almost invariably triangular intercellular ducts among them. Their interior is filled with starch; among them, there are mucilage canals of 200 to 220 μ diameter. Their walls are lined with tiny, flattened, crescent-shaped epithelial cells, differing from the neighbouring cells in their yellowish colour. The cell walls of the ground tissue are slightly sinuous, with the waves on neighbouring cells fitting snugly into each other. The conductive bundles of the pith generally occur in the vicinity of the mucilage canals (Photo 2 [× 100]).

At the edge of the pith, the parenchyma cells of the ground tissue gradually, almost imperceptibly penetrate between the xylem bundles (h). The cells between the xylem bundles are radially elongate and narrow, 120 to 130 μ by 25 to 30 μ.

Vascular bundle ring (cd). The xylem bundles (c) are comparatively narrow, barely 20 to 25 tracheids wide, conically tapering toward the pith. At the endings especially of the broader pith rays, transfusion cells are seen to congregate (Photo 7b [× 300]). The walls of the transfusion cells exhibit bordered pitting and reticular thickening. The radial dimension of the tracheids is 60 to 70 μ in the external portion and 30 to 40 μ in the internal portion. Their sections are square, pentagonal or hexagonal; they are close packed with no intercellular ducts. Their lumina are always rounded, generally following the outline of the cell. Among them some sporadic xylem parenchyma cells occur (Photo 5 [× 100]).

Outside the xylem bundles there are a few cell-rows of cambium and the phloem bundles (d). In the phloem bundles there are hardly any fibres, they consist largely of parenchyma cells (Photo 3 [× 200]).



Fig. 14. *Encephalartos septentrionalis* (Congo; after Robyns)

In cross section, the phloem fibres are radially flattened rectangles, mostly with slit-like lumina. They are usually scattered but some congregate to form tangential plates (Photos 3, 4 [× 100]).

The phloem bundles correspond with the xylem bundles; the broader ones taper conically outwards (Photo 2).

The primary vascular bundle ring is surrounded by a second one, the bundles of which are much narrower and smaller. Among and beside them, mucilage canals are frequent. Directly outside the phloem bundles there are in places clusters of transfusion cells of scalariform or reticular thickening (Photo 7b). Outside the second bundle ring there are some scattered solitary bundles in the cortex (Photo 2).

The parenchyma cells of the cortex are somewhat smaller than those of the pith; they are generally rounded off, 70 to 80 μ in diameter; among them, triangular intercellular ducts are frequent.

The cortex is surrounded by a periderm. Unfortunately, from the sample received, the entire leaf base ring and most of the periderm were missing.

Tangential section. The rays are uniseriate or multiseriate up to 10 layers of cells. The multiseriate rays, the primary rays above all, can be up to 50 cells high. The size of the ray cells is 70 to 80 μ by 45 to 50 μ.

Among the pith rays, transfusion cells are rather frequent. Gradually lengthening and adhering to the other tracheids, these are gradually turned into tracheids themselves. Their walls exhibit bordered pitting or scalariform thickening (Photo 7b).

In the tangential walls of the tracheids, the bordered pits locally form minor or major clusters, or even 2 or 3 longitudinal rows. Their diameter is 7 to 8 μ; their apertures are horizontal and slit-like, but some portions of their walls are perfectly smooth (Photo 9 [× 100]).

Radial section. In the radial walls of the tracheids, the bordered pits are arranged in longitudinal rows, alveolarly and in the araucarioid pattern; the chambers are strongly compressed, the apertures slit-like and horizontal (Photo 10 [× 300]).

Some apertures coalesce but do not span the full width of the tracheid, whereas some other tracheids exhibit true scalariform thickening (Photos 12 [×300], 13 [×300], 14 [×600]). Among the two, transitions are very frequent; such thickenings sometimes grade into annular thickening. Sometimes even neighbouring tracheids show differences in structure; the one is pitted strictly according to the araucarioid pattern, with 3 or 4 close-packed pit rows while in the walls of the other, only scalariform thickening occurs; if the tracheids are angular, then in the adjacent walls the ladder steps and step spacings are seen to alternate (Photo 14). No xylem parenchyma was observed in the radial section.

The phloem fibres are 30 to 35 μ in diameter, thick walled, with narrow or slit-like lumina. Their walls closely fit those of the ray cells; as a result, they are corrugated rather than smooth. In some tracheid walls, bordered pits are arranged in 4 or 5 rows; the two adjacent tracheids may exhibit scalariform thickening while the next will again bear bordered pits: the pits are close packed in 5 rows (Photo 10).

Encephalartos villosus (Gaertn.) Lemaire (1867)

Plates LXIII, LXIV, Photos 1–9; Fig. 15

Its area of distribution includes South Africa, the south-eastern part of the former Cape Colony and Natal, further Uganda where it grows mainly on rocky slopes. Its trunk is low; the leaves are 2 m long; the rachis bears some 60 to 90 pairs of leaflets. The material was received from Mr Dyer, Pretoria.

Macroscopic examination. The diameter of the trunk sample examined (Photo 1 [nat. size]) is 6 to 7 cm, of which the diameter of the pith is nearly 5 cm (a); the vascular bundle rings occupy about 3 to 4 mm; the thickness of the cortical portions is 1·5 cm (cd); that of the leaf stump layer is about 3 cm (e). The dark spots in the pith are pith bundles some of which pass through the primary pith rays into the cortex. Both in the pith and in the cortex, the light spots represent mucilage canals. Instead of a periderm, the cortex is surrounded by leaf bases (e).

The pith (a). The pith largely consists of more or less isodiametric cells some of which are elliptic. Their length is generally 220 to 250 μ, their width 150 to 160 μ. The walls are thin, with scattered simple pits here and there. Their interior is filled with starch. The diameter of the mucilage canals (260 to 280 μ) is hardly greater than that of the largest cells of the ground tissue; their inner walls are lined with much smaller epithelial cells of 40 to 50 μ size. The tracheid bundles of the pith consist of cells exhibiting scalariform or spiral thickening.

Vascular bundle ring (cd). On the edge of the pith, inside the vascular bundle ring, the parenchyma cells of the pith almost imperceptibly grade into the primary rays which are 10 to 12 cells wide initially (h). At the point of issue of each primary ray there is as a rule one mucilage canal of 210 to 220 μ diameter, whose interior is lined with 8 or 9 epithelial cells in a ring.



Fig. 15. *Encephalartos villosus* (South Africa; photo by Dyer)

The cells of the primary rays (Photo 2h [×30]) are in places substantially elongate radially; their size is then 220 to 240 μ by 35 to 40 μ or less. The walls of most tracheids running in the primary rays exhibit scalariform thickening. Between the conically tapering phloem bundles, the cells of the primary rays are tangentially elongate or radially flattened. Their tangential dimension is 150 to 160 μ, their radial dimension 35 to 50 μ. More numerous than the broader primary pith rays the bi- and triseriate secondary rays also issue from the pith; their cells, however, are hardly elongate radially, being generally square of 50 to 55 μ size. The cells are thin walled: some contain calcium oxalate crystal druses.

The xylem bundles (cd) are comparatively narrow, bi- to quinqueseriate (Photo 2c). In section, the tracheids are rounded squares or polygons; intercellular ducts are fairly rare among them. Their radial dimension is 40 to 50 μ; their width is about the same. The tracheid rows are in places interrupted by xylem parenchyma cells of about the same size as the tracheids but invariably smaller than the parenchyma cells of the adjacent rays. Directly inside the xylem bundles there are a few sporadic protoxylem or transfusion cells.

Phloem bundles (d). After a cambium ring 3 or 4 cells wide there follow the phloem bundles which correspond to the xylem bundles (Photos 2, 3 [×100]). The broad rays separating the xylem bundles continue also in the phloem. The phloem bundles are very often only uni- or biseriate, composed of few fibres and phloem parenchyma cells. The fibres are rather loosely arranged (Photo 3). In section, the fibres are radially indented squares; their lumina are either slit-like or somewhat more spacious; their tangential dimension is about 40 μ, their radial dimension 22 to 25 μ. The phloem parenchyma cells are of about the same size. Most rays in the phloem ring are uni- or biseriate. In uniseriate rays (exterior part of the phloem), most ray cells are ellipses whose short axes are in the radial direction (Photo 3).

Cortex (e). Its parenchyma cells, mucilage canals and vascular bundles are as those of the pith. The length of the parenchyma cells is 220 to 230 μ; their width is about the same. Their fit is rather loose; tiny intercellular ducts are rather frequent between them. In the xylem bundles of the cortex, the tracheids exhibit scalariform thickening (Photo 4 [$\times$100]).

Periderm. As on the trunk sample examined, the leaf bases still adhere to the cortex, there is no separate periderm layer. A periderm probably develops only when the leaf bases fall off the trunk.

Tangential section (Photo 5 [$\times$100]). The rays are uni- to quinqueseriate. The uniseriate ones are 8 to 10 cells high; some of these flare out to become bi- or triseriate near their ends; some of their cells are 150 μ high for a width of only 30 to 35 μ. In the primary, broad rays (h), the cells are much smaller (30 to 80 μ), hexagonal or compressed polygonal in section. Among these thin-walled ray cells there are a few idioblasts, thicker-walled and containing a resin-like substance. In the central portion of the broader pith rays there is very often one mucilage canal and one vascular bundle, emerging from the pith through the primary rays into the cortex. The parenchyma cells of the rays contain a great deal of starch.

Radial section. The ray cells are generally square or upright. The size of the former is 90 to 120 μ; the height of the upright cells is about the same, their width ranging from 70 to 80 μ. In the ray cells contacting the tracheid walls, no cross fields develop. In the zones corresponding to the horizontal walls of the ray cells in the tracheid, there are shorter or longer unpitted bands (Photo 9 [$\times$600]).

Most tracheid walls exhibit a bordered pitting, with 3 or 4 rows of pits per wall (Photo 7 [$\times$300]). The apertures of the pits are invariably slit-like, spanning the pit chamber. In most cases, the chambers are horizontally elongate, and so are the apertures, which span the tracheid walls, giving rise to veritable scalariform and reticular thickening. In this species, this is the dominant feature although, as mentioned above, bordered pitting is also rather frequent (Photos 6 [$\times$300], 7, 8 [$\times$300]). Xylem parenchyma cells are rare; all the walls of these are smooth and thin.

In the phloem bundle, the structure of the fibres is the same radially as tangentially. The fibres are 30 to 35 μ wide, with walls 7 μ thick and spacious lumina (15 to 20 μ). Beside the tracheids, transfusion cells are rare.

(d) DIOON

Dioon edule Lindl. (1843)

Plates LXV, LXVI, Photos 1–13; Figs 16 and 17

The genus *Dioon* includes three species: *D. edule*, *D. spinulosum* and *D. purpusi*. Their area of distribution is Central and South Mexico. Of the three species *D. edule* Lindl. is best known.

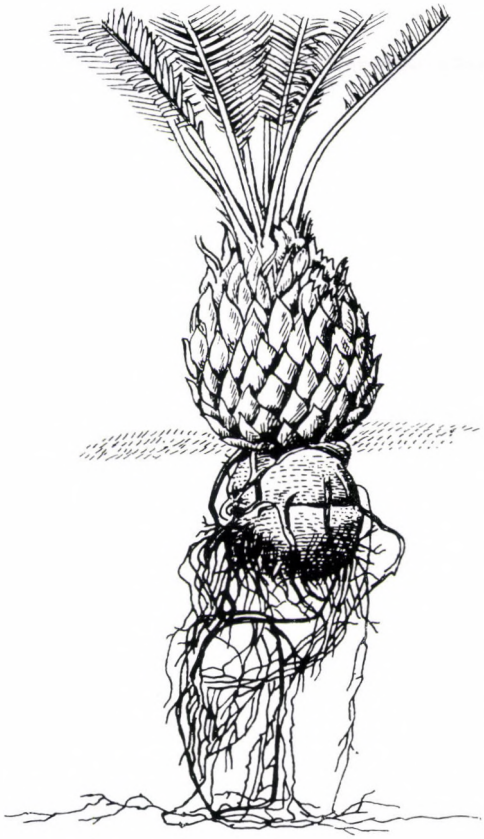


Fig. 16. *Dioon edule* (after Wieland)

The trunk of *D. edule* is usually 1 to 1·5 m high but may exceptionally attain 10 m; the tall trunks are usually bifurcate. The upper part of the trunk is covered by an armour consisting of the bases of fallen leaves. The composite leaves, 1 m long or shorter, consist of up to 100 leaflets of 13 to 17 cm length. The sample examined came from a trunk of about 10 cm diameter. Its surface is densely covered by the leaf bases. It was received from Mr R. de Belder, Kalmthout, Belgium.

Macroscopic examination. The trunk sample examined (Photo 1 [×0·5]) was conspicuous for the lack of a pith. The place of the pith cells was occupied by a skein of roots of 1 to 3 mm diameter. The roots bore the tubercles so typical of the Cycads. The surface of the vascular bundle ring was perfectly smooth; some roots however, apparently grew out of the inner wall of the cortex and probably anastomosed with it. Outside a vascular bundle ring of 7 to 8 mm thickness there was a cortical layer about 2 cm thick (e), surrounded in its turn by the ring of leaf bases (Photo 1).

Microscopic examination. The ground tissue of the pith was for the most part replaced by the skein of pith roots of 1 to 3 mm thickness. The cross-sectional structure of these pith roots proves them to be true roots (Photo 2 [×30]). In their interior secondary xylem bundles separated by uni- or biseriate pith rays are seen to issue radially from the protoxylem. The radial xylem bundles are 2 or 3 tracheids wide; among the tracheids there are some scattered thin-walled parenchyma cells. The xylem bundles are arranged concentrically about the centre. They continue in exact correspondence in narrow phloem bundles (d). The phloem bundles are also separated by uni- and biseriate radial pith rays. Outside the vascular bundle ring there is a thin cortical layer (e) and a comparatively thick periderm which consists of thin-walled cork cells (f).

The structure of such a pith root is illustrated in Photo 2. In the interior of the pith roots, the xylem tracheids exhibit bordered pitting, spiral, annular and in places even scalariform thickening. The ladder-like arrangement is generally most conspicuous at the endings of the tracheids, suggesting scalariform perforation

Otherwise, in tangential section, the structure of the rays, the size of the cortical cells and of the cork cells of the pith roots, agree with those of the trunk; these pith roots are of the same structure as the trunk itself but in the roots there are no pith cells; if there were any, they were absorbed subsequently. Such a pith root complete with tubercles is shown in Photo 1. Some pith roots adhere to the inner wall of the vascular bundle ring, but even the free surfaces of these are covered by the comparatively thick suberized cortex characteristic of the root (f). Thus their structure in no way differs from that of the roots penetrating into the soil. This exceedingly interesting structure raises the idea that these roots might have replaced the pith, at late stage all cells of a preaxisting pith having been diserganized in the process or oreviously. They may be, on the pther hand, simply the common bundles of the trunk as in the cortex bundles of ohe same cross-sectional structure can be found rather often. No such phenomenon has so far been observed in any of the Cycads.



Fig. 17. *Dioon edule* (Botanical Garden, Cracow)

Vascular bundle ring (cd). The xylem bundle ring (c) is divided by primary and secondary rays (h) in segments or collateral bundles 2 to 4 tracheids wide. In section, the tracheids are irregular squares or polygons of 45 to 50 μ size. The tracheid rows are locally interrupted by thin-walled parenchyma cells (Photo 5 [$\times$ 100]). The rays separating the xylem bundles are uni- to triseriate; their cells are larger than the neighbouring xylem parenchyma cells. They are considerably elongate radially; their radial dimension is 90 to 100 μ, their width 40 to 45 μ.

Phloem bundles (d). The cambium consisting of 3 or 4 cell layers is surrounded by phloem bundles which correspond to the xylem bundles. The phloem fibres and parenchyma cells are arranged in radial layers; most bundles consist of 1 to 3 such layers (Photo 4 [$\times$ 100]). The phloem fibres are of rounded square or irregular section, thick walled, with lumina following the outline of the cell; most lumina are square, indented on all four sides, but some are slit- or pinhole-like.

The ray cells are much broader in the phloem than in the xylem; they are approximately rectangular, their radial dimension is in most cases 100 to 105 μ; their width ranges from 70 to 100 μ (Photos 4, 6 [$\times$ 100]).

The vascular bundle ring is surrounded by a cortical layer among whose parenchyma cells mucilage canals and conductive bundles are seen to meander (Photo 3e [$\times$ 30]). Upon this ground tissue layer there follows a second vascular bundle ring whose structure agrees with that of the first one. The second conductive bundle ring is embraced by the cortex whose ground tissue cells are thin walled, of 180 to 200 μ by 65 to 70 μ size. The diameter of the mucilage canals is 140 to 150 μ; the size of the thin-walled epithelial cells lining them is 35 to 40 μ (Photo 7 [$\times$ 100]).

The conductive bundles of the cortex are in all probability the continuations of the pith roots, as proved by the fact that these bundles are rather thick, up to 20 cell layers wide, and covered with the same kind of cork layer (periderm) as the pith roots themselves (f).

The outermost part of the cortex is the periderm whose outer portion is a thick cork layer. The leaf bases adhere to this cork layer (Photo 8 [$\times$ 100]).

Tangential section (Photo 9 [$\times$ 100]). In tangential section, there are two kinds of pith ray, the ones 1 to 8, the others 15 to 20 cell layers wide. The latter carry the conductive bundles which, having to all probability issued from the pith, emerge into the cortex and continue as leaf scar bundles into the leaves. In their vicinity, mucilage canals are rather frequent. The tangential dimension of the pith ray cells is 90 to 100 μ, their width is 50 to 60 μ. Their walls are smooth and thin. The xylem bundles generally comprise 15 to 20 rows of tracheids. The same structure can be established in the phloem bundles. In the xylem, most tracheids exhibit scalariform thickening but bordered pitting also occurs.

Radial section. Most pith ray cells are square or upright. The height of the latter is 70 to 80 μ, their width 30 to 40 μ. The former are 70 to 80 μ square. The walls are thin and smooth. The pith ray cells in contact with axial tracheids do not usually develop well-defined cross fields; such fields being restricted to the ray cells contacting tracheids with bordered pitting (Photo 10 [$\times$ 300]). The scalariform tracheids exhibit at intervals (in most cases flush with the horizontal walls of the pith ray cells) broader cell-wall thickenings creating the impression of cross fields.

In the tracheid walls, the bordered pits are arranged in the araucarioid pattern (Photo 12 [$\times$ 300]).

The width of one tracheid includes as a rule 2 or 3 rows of bordered pits (Photo 11 [$\times$ 300]), their apertures are considerably elongate horizontally, usually slit-like (Photo 10). Considerably elongate locally, the slits gradually grade into scalariform thickenings. In some tracheids, scalariform thickening is exclusive (Photo 13 [$\times$ 600]).

In the ray cells, calcium oxalate crystal druses are rather frequent. One cell generally contains one druse only.

In the phloem, the fibres are 22 to 24 μ wide, the thickness of the walls is about 5 μ.

Dioon spinulosum Dyer (1883)

Plates LXVII, LXVIII, Photos 1–12; Fig. 18

The area of distribution of *Dioon spinulosum* is Oaxaca province, Mexico, and the Yucatan Peninsula. The trunk may attain a height of 2 to 16 m, for a diameter of 30 to 50 cm. The leaves in the leaf tuft are 0·5 to 2 m long, and comprise 40 to 120 pairs of leaflets. The latter are 8·5 to 20 cm long and 10 to 17 mm wide.

Macroscopic examination. The trunk sample obtained lacked pith and cortex. According to literature, *D. spinulosum* is the only Cycad species with several xylem rings of 8 to 10 cm thickness as distinct from the stem structure of all other known Cycads. The xylem reveals no traces of annual rings to the naked eye (Photo 1 [$\times \frac{1}{3}$]).



Fig. 18. *Dioon spinulosum* (Mexico; after Chamberlain)

Microscopic examination. Thetracheids form longitudinal rows; bundles of 2 to 10 rows are separated by uni- or biseriate (seldom triseriate) pith rays. Among the tracheids, a few xylem parenchyma cells are scattered. In the xylem parenchyma cells and in the ray cells, calcium oxalate druses are rather frequent (Photos 1, 2 [$\times 30$], 3 [$\times 100$]).

The radial dimension of the tracheids ranges from 40 to 60 μ; their width is about the same. The sections are square, pentagonal or polygonal but the lumina are invariably rounded. The cell walls are triangularly thickened along the lines of contact with the adjacent cells; hence intercellular ducts are quite rare. The walls are 7 to 8 μ thick.

The ray cells are of two sizes. The radial dimension of the smaller ones is 45 to 50 μ, their width 25 to 30 μ; the radial dimension of the broader pith ray cells is 100 to 110 μ, their width 60 to 65 μ; in fact, they are larger than the tracheids (Photo 3).

In its cross-sectional structure, with the 6 to 8 cm thick xylem and uni- to triseriate pith rays, this species is widely different from all other Cycads and also from any other Gymnosperm including *Ginkgo*. In its tangential and radial struc-

ture, however, the wood is like the other Cycads. The ray cells are thin walled. The horizontal walls bear tiny pits; some of these are irregularly scattered, but most of them form loose arcs parallel to the periphery. Their size ranges from 4 to 5 μ.

The cross section of pith, cortex and phloem will not, in the lack of suitable sample material, be discussed.

The *tangential section* (Photo 8 [$\times$ 100]) reflects the characteristic structure of the Cycads. The rays are uni- to triseriate, exceptionally quadriseriate. The solitary pith ray cells are 140 to 150 μ tall and 35 to 40 μ wide. The ray cells in the interior of the rays are lower, 70 to 80 μ high and 30 to 40 μ wide. They frequently contain calcium oxalate crystal druses. Their tangential walls locally exhibit tiny pit-like constrictions.

The tangential walls of the tracheids are smooth; pitting is rare and sparse; the size of the bordered pits is 7 to 8 μ; their apertures are linear and oblique.

Among the tracheids sporadic parenchyma cells of 400 to 420 μ by 30 to 35 μ are scattered. Their transverse walls are smooth and thin. The tangential walls of the tracheids bear tiny bordered pits only where they are in direct contact with parenchyma cells. Some bands of the tracheid walls show scalariform thickening; this perforation-like thickening was probably transferred from the radial to the tangential side by a twisting of the tracheids.

In *radial section*, in *D. edule*, most tracheids exhibit scalariform thickening. This phenomenon is also observed in some rare cases in *D. spinulosum* whose tracheids are, however, for the most part thickened by bordered pitting; the pits are arranged in the araucarioid pattern (Photos 7 [$\times$ 300], 12 [$\times$ 600]) loosely aligned in 1, 2 or 3 rows in some tracheids but alveolarly compressed in most.

The ends of some tracheids exhibit scalariform or annular thickening in some cases directly adjacent to tracheids with bordered pitting, creating the impression of scalariform perforations (Photo 6 [$\times$ 300]). Another difference between the two *Dioon* species is that while in *D. edule* cross fields are very rare owing to the frequent scalariform thickening, in *D. spinulosum* the tracheids contacting ray cells invariably present cross fields including 6 to 10 and even 16 pits, generally in 1, 2 or 3 longitudinal rows. The chambers of the pits are circular or more often elliptical; the oblique, linear and mostly included aperture coincides with the short axis of the ellipse (Photos 9 [$\times$ 100], 10 [$\times$ 200], 11 [$\times$ 300]).

Among the tracheids, there are axial parenchyma cells, all walls of which are smooth and thin (Photo 7).

(e) MICROCYCAS

Microcycas calocoma (Miq.) A. DC. (1868)

Plates LXIX, LXX, Photos 1–12; Fig. 19

Unique species of a monotypical genus, it occurs in the more elevated regions of Western Cuba. It may attain the height of 10 to 12 m (Fig. 19), but it is much lower in most cases. Its trunk is unbranched in most cases, dichotomously branching in

the others. The surface of the trunk is more or less smooth with conspicuous leaf scars. The apex of the stem bears a leaf tuft, the leaves are 60 to 100 cm long and paripinnate; there are 50 to 80 pairs of folioles. The strobile is 50 to 70 cm long and 13 to 16 cm thick (Fig. 19).



Fig. 19. *Microcycas calocoma* (Cuba, after van Hermann)

The material was obtained from Ponce de Leon, Havana. It was a disk 2 cm thick (Photo 1 [nat. size]). The dried-out sample was first immersed in water to swell. Two days later the whole surface was covered by mucus. On the cleaned surface, the macroscopic structure was readily visible.

In the trunk sample of 10 cm diameter, the pith was 2·5 to 3 cm thick (a). In it, the lighter spots indicate the mucilage canals. The pith is surrounded by a wide vascular bundle ring of 1 cm thickness (cd). It can be seen with the naked eye that the xylem (c) is somewhat thicker than the phloem (d). Our piece of stem included only one vascular ring but at the bases of older trunks there are several rings so that the species is polyxylic. Outside the unique vascular bundle ring, the cortex is 2 to 2·5 cm thick (e). The cortex is similar to the pith; on its outer side, a periderm of somewhat denser substance (f) is separated.

Cross section. The pith consists of thin-walled, isodiametric parenchyma cells, mostly close packed but locally separated by intercellular ducts. The size of the parenchyma cells is 150 to 200 μ. Their thin walls locally bear clusters of tiny pits (Photos 2 [$\times$ 50], 3 [$\times$ 8]).

Pith bundles scattered among the parenchyma cells of the ground tissue, the vascular bundles of the pith comprise loosely arranged 8 to 20 tracheids as well as some sporadic, very thin-walled xylem parenchyma cells and a very few thick-walled phloem fibres. These bundles may be the proper bundles of the pith of lateral branches of common bundles which pass through the primary rays into the cortex and from there as leaf scar bundles into the leaves.

The *mucilage canals* (g) of the pith are lined with thin-walled epithelial cells. Their diameter is 220 to 240 μ.

Transfusion cells (b). They form clusters on the edge of the pith near the points of issue of the xylem bundles or constitute rosary-like rows. Some are isodiametric, others more elongate, again others drawn out into veritable tracheids. Their walls exhibit reticular and scalariform thickening which can in places be traced back to bordered pitting. Their size is 100 to 250 μ, some are much longer. At some places they almost touch the tracheid bundles, as if the tracheids came to exist by elongation from these transfusion cells (Photos 6 [$\times$ 300], 7b [$\times$ 300]).

Vascular bundle ring (Photo 2). Outside the pith there is the single vascular bundle ring arranged. It is excellently visible in places that the xylem ring is divided into several smaller bundles of various size by the primary rays which can be up to 10 cells wide (Photos 2, 4 [$\times$ 100], 5 [$\times$ 100]).

Pith rays (h). The cells of the primary rays agree in structure and shape with the parenchyma cells of the pith and cannot be morphologically distinguished from them, clearly illustrating that the primary rays originate in the pith (Photos 3, 5).

Xylem bundles (c). The tracheid rows are either uniseriate or 2 to 8 tracheids wide, the latter constitute broader and continuous xylem bundles (Photo 2). In section, the tracheids are square, pentagonal or irregular polygonal of various shape and size. Their radial dimension is 40 to 60 μ, their width about the same. Among them, there occur some very thin-walled parenchyma cells, forming chains abutting at the pith ray cells from which they can hardly be distinguished morphologically and structurally (Photo 5).

Phloem bundles (d). The xylem ring is surrounded by 2 or 3 cell layers of cambium whose cells are slightly smaller than the ray cells and somewhat flattened radially. Both the broader primary and the narrower rays continue through the cambium into the phloem. The phloem bundles are as wide as the corresponding xylem bundles (Photo 4). In the phloem the thick-walled phloem elements may form smaller or larger clusters, or even tangential plates while in other cases they are scattered. In places, the perforated transversal walls of sieve tubes are rather small.

The cortex (e). The phloem ring is surrounded by the cortical layer whose thin-walled parenchyma cells are of the same structure as those of the pith. The mucilage canals (g) also agree in size and structure with the mucilage canals of the pith with which they communicate through the primary rays. The same holds for the common vascular bundles.

The periderm (f) consists of cork cells arranged in radial rows, in a brick-wall pattern. Their walls are thin and suberized. In some cells of the periderm calcium oxalate crystals are arranged in thinner or thicker layers. Mostly solitary, they locally cluster in twos and threes, exceptionally forming crystal druses (Photo 3f).

Tangential section. Pith rays (h). In the sections through the phloem, the rays seem to be 1 to 12 cell layers wide. The height of the pith ray cells is 180 to 200 μ, their width 70 to 80 μ. Some ray cells contain tiny calcium oxalate crystal druses (Photo 8 [$\times$ 100]).

Vascular bundles. The fibres composing the elongated phloem bundles are thick walled with narrow, slit-like lumina. The tracheids of the xylem bundles are also elongate, their walls usually exhibit scalariform thickening (Photo 8). Trans-

fusion cells are particularly abundant in the tangential view, being arranged between the phloem and the xylem bundles. Their walls show scalariform and reticular thickening (Photo 8, right side).

Radial section. Pith rays (h). The walls of the ray cells situated in the interior of the ray are smooth, whereas the walls contacting the tracheids bear smaller or larger pits in irregular scatter. These, however, do not form cross fields, because they do not correspond to the pitting of the tracheids behind them. This pitting of the ray cells definitely differs from the ray pitting of the conifers. These pits have no chambers because they have formed in the secondary cell wall. The height of the ray cells is 150 to 200 μ on this side; they are upright or rounded squares, forming close-packed rows. All in all, there are no pits in the cross fields of *Microcycas* (Photo 9 [$\times$300]).

Axial tracheids .The pitting of the tracheids is rather variable. In some tracheid walls there are only bordered pits while in others the thickening is scalariform or reticular. The tracheids bearing the different sorts of pitting are sometimes intermixed whereas in some places there are only scalariform (Photo 10 [$\times$300]) or only spiral tracheids. The ends of some tracheids join transverse walls which are pitted in the same pattern as the longitudinal walls. The bordered pits of the radial walls, however, invariably form the araucarioid pattern (Photos 11 [$\times$300], 12 [$\times$600]).

(f) CERATOZAMIA

Ceratozamia mexicana Brongn. (1846)

Plates LXXI, LXXII, Photos 1–13; Fig. 20

The area of distribution of *Ceratozamia* is South-Eastern Mexico. The best known of its three species is *Ceratozamia mexicana*. The trunk of this species is about 2 m long, and then comparatively thin, bent or procumbent. On its top it carries a tuft consisting of 10 to 20 leaves. The leaves are 1·5 to 2 m long, composed of 40 to 50 pairs of leaflets; these are coriaceous, lanceolate or falciform. The plant is cultivated in glasshouses, too.

In his monograph on the Cycads, Schuster distinguishes only two *Ceratozamia* species: *C. mexicana* Brongn. and *C. kuesteriana* Regel. Of the two species, the author has succeeded in obtaining a trunk sample from *C. mexicana*; R. de Belder, the proprietor of the Kalmthouth arboretum in Belgium cut off the upper part of one of his valuable specimens and put it at the author's disposal for examination.

Macroscopic examination (Photo 1 [$\times$0·5]). The diameter of the trunk is about 15 cm. Its cross section reveals even to the naked eye the typical structure of the Cycads; it is a monoxylic tree but even the single vascular bundle ring is incomplete, being interrupted on one side. Part of the ring penetrates into the pith where it continues at first as a continuous vascular bundle layer, but this layer soon breaks up so that there are independent bundles in the interior of the pith. Of

the trunk of 15 cm diameter, 8·5 cm are occupied by the pith (a); the vascular bundle ring is only 3 or 4 mm thick (cd); the thickness of the cortical portion is 2·5 cm (e). The latter is densely covered with leaf bases which cover also the growing point itself.

Microscopic examination. The pith largely consists of thin-walled isodiametric cells (Photo 2a [× 30]) of 200 to 220 μ size. Although the walls seem to be smooth, there are in places some faintly visible constructions (Photo 7 [× 100]). The pith further includes the proper bundles of the pith and the common bundles (lower part of Photo 2c,d) which emerge through the primary rays into the cortex and into the leaves. Such a collateral bundle is composed of 3 to 10 rows of tracheids and as many phloem rows (Photo 3 [× 100]).

A portion of the vascular bundle ring is seen almost to penetrate into the pith. This is definitely a fern character; similar arrangements have been observed in the rhizomes of some ferns. But it is also suggestive of the extinct *Medullosae*. In the cells both of the xylem and the phloem, calcium oxalate crystal druses are rather frequent. As the separate common bundles agree in structure with the bundles of the vascular bundle ring, they will be discussed together. The diameter of the mucilage canals occurring in the pith ranges from 250 to 300 μ; their inner walls are lined with tiny epithelial cells.

Vascular bundle ring (c, d). The isodiametric cells of the pith gradually pass into the primary rays where they somewhat lengthen radially (h).

The primary rays (h) divide the xylem ring (c) into narrower or broader xylem bundles. These latter 3 to 10 tracheids wide, are divided into even narrower segments by uni- and biseriate rays. At the ends facing the pith of the xylem bundles some xylem primanei or transfusion cells can be observed; considerably lengthened, these subsequently change into tracheids. The radial dimension of the tracheids is 40 to 60 μ; their width is about the same. In section, most cells are radially somewhat elongate squares or polygons, their lumina invariably rounded, but not perfect circles or ellipses: the shape of the lumen follows the outline of the cell (Photo 5 [× 100]).

The xylem is followed by a cambium layer of 3 or 4 cells layers thickness and subsequently by the phloem ring (d). Composed largely of thin-walled parenchyma cells, the phloem bundles correspond to the xylem bundles (Photo 2c, d). Phloem fibres are fairly scarce (Photos 3, 4 [× 100], 6 [× 100]). Their walls are comparatively thin, their lumina quadrangular rather than slit-like (Photos 4, 6). Radially flattened and tangentially elongated, the cells of the uni- and biseriate pith rays between the external portions of the phloem bundles become cylindrical (Photo 6). No sieve tubes could be observed.

Cortex (e). In shape, structure, size and pitting, the parenchyma cells of the cortex agree with the similar cells of the pith. Even the conductive bundles agree (upper part of Photo 2c,d) which proves that the conductive bundles of the cortex come from the pith through the primary rays.

In the cortex, the number of mucilage canals (g) (Photo 7) and the tiny collateral vascular bundles (cd) considerably increases toward the periphery, whereas the



Fig. 20. *Ceratozamia mexicana* (Botanical Garden, Szeged; photo by Gulyás)

size of the ground tissue cells gradually but substantially decreases; their size ranges from 100 to 150 μ. The diameter of the mucilage canals, however, hardly changes (g). The cells of the periderm form a brick wall pattern of radial rows. In the vicinity of the cortex, numerous xylem bundles meander parallel to the periphery. In them, the tracheids generally exhibit bordered pitting and scalariform thickening.

Tangential section (Photo 9 [$\times$ 100]). Most rays are uni- to triseriate, but the primary rays may have the thickness of 20 cells. In the uni- and biseriate rays, the cells are 80 to 120 μ high, their width is 50 to 60 μ. They are generally rounded with intercellular ducts in the lines of contact. The tangential walls of most tracheids are smooth but in some places there are a few pits shifted over from the radial side. The broader rays carry conductive bundles in their central portion. Some tracheids adhere to thin-walled parenchyma cells of 180 to 200 μ height and 30 to 40 μ width; other tracheids adhere to transfusion cells which may be shorter or longer than that; the longest ones are lengthened into tracheids (Photo 8b [$\times$ 300]).

Radial section. The ray cells are generally square or upright (Photo 12 [$\times$ 300]). The height of the squares is 70 to 80 μ, that of the rectangles, 90 to 110 μ. Their walls are smooth and thin. Where the ray cells contact the tracheids, in some tracheid walls develop cross fields corresponding in size to the ray cells in which there are 4 to 14 pits in the araucarioid pattern. The chambers of some pits just meet, in other cases they are alveolarly compressed, in yet other cases the apertures and

the chambers of the pits are horizontally elongate so that the aperture may span one-third or one-half of the tracheid wall. In other places, where the apertures span the full width of the tracheid, no such cross fields develop (Photo 13 [× 600]).

In the *tracheid* walls, bordered pits are generally aligned in 2 or 3 rows in the araucarioid pattern (Photo 10 [× 300]). Linear and horizontal or somewhat oblique (Photo 11 [× 300]), the apertures are considerably elongate locally; in such cases they reach across the walls of the tracheids and the bordered pitting gradually passes into scalariform pitting (Photos 11, 12). This pitting may be interrupted in the places corresponding to the horizontal walls of the ray cells.

The scalariform thickenings may locally split up Y-shape, as a result of the chamber of a bordered pit being inserted between two other bordered pits. In the tracheid walls, when the bordered pits are interlocked alveolarly in the araucarioid pattern, the linear apertures of the pits may be arranged crosswise (Photo 13).

(g) ZAMIA

About 25–26 species are living in the tropical and subtropical regions of America, in Florida, in Central America, in the West Indies, in South America down to Bolivia and Brazilia (see Map on page 18). There are species creeping in the ground and others rising above it; the short tuberose stems of the latter bear leaf tufts. From the anatomical viewpoint, one of their most prominent characteristics is that their tracheids bear no definite araucarioid bordered pits; in all tracheids, the scalariform pitting prevails. In some species the pitting of the tracheids is somewhat araucarioid, but nowhere alveolar; the chambers of the pits are horizontally elongate, their apertures are horizontal and slit-like. The author succeeded in procuring and examining stem samples of 9 species; it was on the basis of these that the anatomical features of the *Zamia* species were established. The species in question are: *Zamia angustifolia*, *Z. floridana*, *Z. gutierrezi*, *Z. muricata*, *Z. obidensis*, *Z. portoricensis*, *Z. pumila*, *Z. silicea* and *Z. skinneri*.

Zamia angustifolia (Jacq.) Schuster (1956)

Plates LXXIII, LXXIV, Photos 1–13; Fig. 21

Its area of distribution is Cuba, especially the eastern part of that island. Its rhizome is ellipsoidal, a few centimeter long and wide, not emerging above the ground. Its leaves are 4 to 25 cm long; the width of the folioles is 4 to 10 mm, their length 3 to 5 cm. The trunk sample examined was obtained by courtesy of Mr Barna, Cuba.

Macroscopic examination. The diameter of the trunk examined was 2 cm; the pith was 5 mm in diameter, the cortex together with the periderm was about 6 mm

thick; the thickness of the vascular bundle ring between the two was 1 to 1·5 mm. The trunk is typically monoxylic (Photo 1 [×4]). In the interior of the pith no conductive bundles can be observed with the naked eye; even in the cortex there are but a few cortical bundles, some axial, others parallel to the periphery. The periderm is narrow, in further evidence of the underground habit.

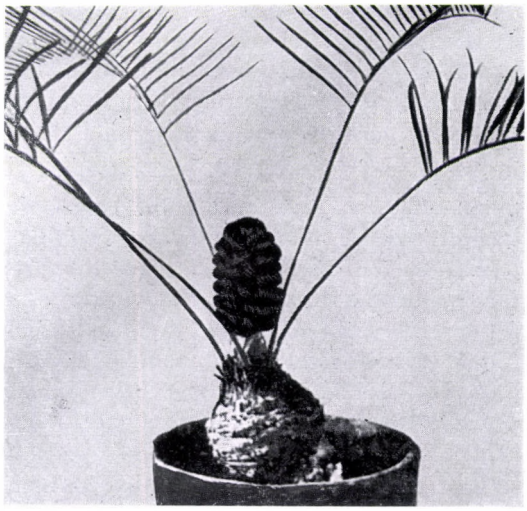


Fig. 21. *Zamia angustifolia* (after Graf)

Microscopic examination. Cross section. The pith largely consists of rounded, more or less isodiametric, thin-walled parenchyma cells, with rather spacious intercellular ducts among them. The cells are filled with starch. Among the parenchyma cells there are numerous mucilage canals (Photo 1) but no conductive bundles in the pith. The diameter of the mucilage canals is 330 to 350 μ; they are lined with thin-walled epithelial cells. Most mucilage canals occur on the edge of the pith, directly before the xylem bundles and the primary rays. The isodiametric parenchyma cells of the pith gradually, almost imperceptibly grade into the primary rays which in their turn grade beyond the vascular bundle ring into the parenchyma of the cortex. The radial dimension of most cells of the primary rays is 200 to 220 μ; their width is 110 to 130 μ (Photos 2–4 [×100]).

Vascular bundle ring. Facing the xylem bundles, there are at the edge of the pith protoxylem groups which continue into the xylem bundles (Photo 4). The vascular bundle ring is poorly developed, owing to the subterranean habit of the plant. In the xylem bundles, the tracheid rows are 2 or 3, sometimes 4 tracheids wide; broader xylem bundles are rare, because most are divided by the secondary rays into even narrower segments. The tracheids are angular in section; the lumina follow the outlines of the tracheids, although they are somewhat rounded. Among the tracheids, a few scattered thin-walled parenchyma cells are observed. Their size is the same as that of the tracheids.

The phloem bundle ring is poorly developed; the phloem portion consists of just a few fibres and phloem parenchyma cells (Photos 2, 3). The scarceness of fibres, i. e. of the strengthening tissue, is probably due to the underground habit. The sections of the tiny phloem fibres are angular, their lumina pinhole-like. Outside the phloem bundles, small clusters of phloem primanei are arranged in places (Photo 3).

Cortex. The phloem bundles penetrate among the parenchyma cells of the cortex. The mucilage canals meandering among them agree as to size and structure with those of the pith (Photo 5 [× 100]). There are a few sporadic cortical bundles which contain few tracheids and little phloem. The number of cortical bundles somewhat increases toward the periderm: they emerge as leaf scar bundles into the rachides. Their structure almost agrees with that of the solitary bundles of the vascular bundle rings; hence, they are collateral bundles, although in some of them the xylem is much more developed than the phloem (Photo 7 [× 300]).

Periderm. The parenchyma cells of the cortex gradually flatten towards the periphery and grade into the phelloderm produced by the phellogen. The cork layer of the phelloderm may be 25 to 30 cells thick. In the cells of the cortex, calcium oxalate crystal druses are frequent, arranged in places in 2 or 3 layers on the edge of the cortex (Photo 6 [× 100]). Among the cells containing the druses, there are in places some cells containing a rubber or resin-like substance, as revealed by their colouring.

Tangential section. The rays are uni- or multiseriate; the primary rays may be up to 10 cells wide (Photo 8 [× 100]). The walls of the tracheids adjacent to the rays exhibit a scalariform thickening; reticular thickening and bordered pitting are absent. In places, the gradual passage of transfusion cells into tracheids can be observed. Section, shape and structure of the ray cells agree with those of the parenchyma cells of the cortex.

Radial section. There are no definite pith ray plates and cross fields; in this respect, the species fully agrees with the other *Zamia*. The tracheids all show scalariform thickening (Photos 9–12 [× 300], 13 [× 600]). The ladder steps and step spacings are of nearly equal width. The steps generally spaning the tracheid walls are in such cases unbranched; in other cases they are bifurcate or reticular. If the tracheids happen to break up, this scalariform thickening assumes the form of a watch-spring or corkscrew. Bordered (i.e. araucarioid) pitting does not occur in this species, either; scalariform thickening is one of the most typical features of *Zamia*. In this respect they can be only compared with *Stangeria*.

Zamia floridana A. DC. (1868)

Plates LXXV, LXXVI, Photos 1–13; Fig. 22

Its area of distribution is Florida, the Biscayne Bay region where it lives on coral-reefs and in pine-woods. Its subterranean stem is beet-shaped, about 25 cm high and 6 cm in diameter (Fig. 22). Its rare branchings are dichotomous. The material examined was received from the Botanical Gardens, Rostock. The apex of the short stem bears 14 to 22 leaves. The diameter of the stem examined was 4·5 cm.

Macroscopic examination (Photo 1 [× 2]). On the cut and cleaned surface of the stem, the inner structure was visible to the naked eye. In the pith of 5 to 18 mm diameter (a) the dark spots arranged in a circle are proper bundles of the pith

or common bundles which through the primary rays emerge into the cortex. The light spots visible both in the pith and in the cortex represent mucilage canals. The pith is followed by a vascular bundle layer, 1 to 2 mm wide (c, d) and by the cortex, 10 to 12 mm thick (e). The outermost layer is the periderm of denser substance (f). Leaf bases are rare on the exterior of the cortex because the subterranean stem loses all leaves.

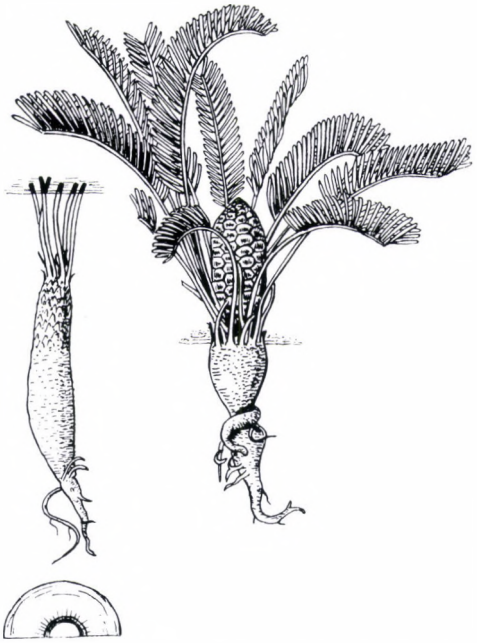


Fig. 22. *Zamia floridana* (after Wieland)

Microscopic examination. The pith (a) is largely composed of very thin-walled, more or less isodiametric parenchyma cells the size of which ranges from 140 to 150 μ. They are generally angular, close packed; along the lines of contact, there are intercellular ducts of various diameter; the walls do not even exhibit simple pitting.

Among the parenchyma cells there are mucilage canals (g) of relatively small diameter (140 to 150 μ), whose walls are lined with comparatively large epithelial cells.

The tracheid bundles of the pith are never quite axial, meandering to and fro in the pith and subsequently emerging into the cortex. In the parenchyma cells, calcium oxalate crystals are rather frequent.

On the edge of the pith, the mucilage canals form a more or less regular circle (Photo 2 [$\times$ 100]). The isodiametric cells of the pith gradually pass into primary ray cells, considerably lengthening radially and getting narrow in the process. Such cells may be 200 to 250 μ long and 70 to 80 μ wide.

Vascular bundle ring (Photo 4 [$\times$ 100]). The xylem bundles (c) penetrate conically between the primary rays. In their vicinity, calcium oxalate crystals are remarkably numerous. So are the transfusion cells at the points of issue of some pith rays and also among the tracheids, where the phloem bundles begin (Photos 5 [$\times$ 100], 6 [$\times$ 200], 7 [$\times$ 300]). Among the transfusion cells there are isodiametric, elongate and quite tracheid-like ones. Thickening is scalariform or reticular in all transfusion cells; bordered pitting is absent.

The tracheids can be rarely observed in cross section (Photo 4) because the vascular bundles are meandering rather than truly axial in the short stem. In section, the tracheids are angular, their lumina rounded. Their radial dimension is 50 to 60 μ, their width about the same. Among them, there are a few xylem parenchyma cells (Photo 4).

Phloem bundles (Photo 4d). The phloem bundles correspond to the xylem bundles but are much less developed. The phloem bundles mainly consist of parenchymatic elements; fibres are very rare and quite thin walled, hardly differing in wall thickness from the parenchyma cells. The phloem bundles taper and fade out towards the cortex. Their cells differ in size and arrangement from the adjacent ray cells, as the latter are radially compressed, oblong and almost perpendicular to the phloem bundles (Photo 4).

The cortex (e). The parenchyma cells of the cortex differ from the parenchyma cells of the pith only inasmuch as they are somewhat larger. Among the parenchyma cells there are mucilage canals and cortical bundles parallel to the periphery, meandering to and fro in the external part of the cortex (Photo 3 [× 100]). In the parenchyma cells, the abundance of the calcium oxalate crystal druses, almost forming layers locally, is remarkable; such layers may consist of rows of 15 calcium oxalate crystals (Photo 8 [× 100]).

The periderm (f) may consist of several layers. The specimen examined bears 3 such layers, each very rich in calcium oxalate crystals (Photo 8).

In *tangential section* (Photo 9 [× 100]), the rays are 1 to 5, sometimes 8 cell layers wide; some primary rays are even wider than that (h). The broader ones include as a rule vascular bundles. The ray cells are comparatively large, 110 to 120 μ high and 70 to 80 μ wide. The sections of most are circular; among some of them, intercellular ducts develop.

The tracheids adjacent to the rays invariably exhibit scalariform thickening. None of the tracheids bear bordered pitting.

Radial section (Photos 10–12 [× 300]). The ray cells are 110 to 120 μ high and about as wide. Some of them might, however, be twice as high. Where the ray cells meet the tracheids behind them, there are no cross fields. The pitting of the tracheids does not suggest the presence of cross fields, either, since no periodicity can be established in them. The walls of the ray parenchyma cells are smooth, thin and unpitted (Photo 11).

Tracheid (Photo 13 [× 600]). In this species there is only one kind of tracheid, with scalariform thickening. In most tracheids the ladder steps reach clear across the tracheid walls, but in some cases where the outside tracheids are arranged in a brick wall pattern, these scalariform thickenings only span one half of the tracheid, because its other half contacts another adjacent tracheid.

In the phloem bundle, the phloem fibres are thin walled with wide lumina. The diameter of the phloem fibres is 40 to 45 μ, the thickness of their walls 4 μ.

Zamia gutierrezi Sauvalle (1868)

Plates LXXVII, LXXVIII, Photos 1–13

Its area of distribution is Cuba, the Pinar del Rio and Baños San Vicente regions. The stem, barely 30 cm long and 2 cm thick, is about two-thirds underground. Its leaves are about 1 m long. The material was obtained from Mr Barna, Cuba.

Macroscopic examination. The rhizome examined was 18 mm thick. It included the pith portion of 4 mm diameter, the vascular bundle ring of 1·5 to 2 mm thickness and the cortex of 5 to 6 mm thickness. The pith contains no proper or common bundles, only a few mucilage canals, some scattered, others arranged on the edge of the pith, next to the vascular bundle ring. The cortex on the other hand contains numerous conductive bundles, some parallel to the axis, others to the periphery. The periderm bears no leaf bases: these are probably detached from the trunk when still in the ground.

Microscopic examination. Cross section (Photo 1 [× 4]). The pith largely consists of more or less isodiametric, thin-walled parenchyma cells the mean dimension of which is 110 to 150 μ. Among them, intercellular ducts are frequent. The cells are filled with starch (Photo 2 [× 50]). The mucilage canals among the cells of the pith parenchyma are 200 to 220 μ in diameter; their walls are lined with tiny, thin-walled epithelial cells (Photo 2). They are arranged for the most part on the edge of the pith, facing the xylem bundles, or at the points of issue of the primary pith rays. It is through these latter that the canals emerge into the cortex and further into the leaves; from the pith to the leaves, the mucilage canals constitute a connected system.

Vascular bundle ring. It is of the monoxylic type, composed of a xylem and a phloem portion. Directly inside the xylem bundles, some protoxylem elements can be observed which grade into xylem bundles of 1 to 3, exceptionally 4 tracheids width. The xylem bundles are separated by bi- and triseriate rays (Photos 3 [× 100], 4 [× 100], 6 [× 100]). The primary rays may be 5 to 6 cell layers wide (Photo 2). The parenchyma cells of the pith gradually pass into the primary rays, in which the cells are somewhat elongate radially. The primary rays almost imperceptibly pass into the parenchyma cells of the cortex (Photo 2).

The tracheids of the xylem bundles are usually close packed, their sections are more or less angular; their lumina invariably rounded, follow the outlines of the tracheids. Among them there are a few scattered xylem parenchyma cells invariably smaller than the neighbouring ray cells (Photo 6).

One or two layers or cambium are followed by the phloem bundles (Photo 5 [× 200]) which largely consist of phloem parenchyma cells; among them only a few sporadic phloem fibres are observed (Photo 5). Their sections are square or radially flattened rectangular; their lumina are narrow, pinhole- or slit-like.

The cortex. Outside the phloem bundles there are the parenchyma cells of the cortex with mucilage canals among them, similarly to the pith (Photo 8 [× 100]). The cortex contains also some few scattered conductive bundles; these consist only of a few tracheids and even fewer phloem elements. They meander to and fro in the cortex and pass as leaf scar bundles into the leaves.

Periderm. In the outermost portion of the cortex, the parenchyma cells gradually flatten into the phelloderm or periderm (Photo 7 [× 100]). The periderm is terminated outward by 15 to 20 or even more cork layers. Immediately inside the periderm there are cells with calcium oxalate crystal druses and idioblasts containing a latex- or resin-like substance, similarly as in *Zamia silicea* (Photo 7). On the basis

of their cross-sectional structure, it is almost impossible to distinguish the two species.

On the *tangential side*, most rays are uni- to triseriate, but the primary rays may be much wider (Photo 9 [× 100]). The size of the ray cells is 110 to 120 μ by 70 to 80 μ. The thickenings of the tracheid walls bordering the rays are exclusively scalariform or reticular; bordered pits do not occur even in traces.

In some of the broader primary rays there are beside the mucilage canals also conductive bundles which probably pass outward into the cortex and then as leaf scar bundles into the leaves. This assumption seems to be supported by the fact that beside these tracheids, transfusion cells with scalariform or reticular thickening are frequent. They locally form other in a knot and continue in the cortex as elongated tracheids (Photo 10 [× 100]).

Radial section. No definite pith rays and, accordingly, no cross fields are visible. The parenchyma cells corresponding to the ray cells are thin walled and unpitted.

The thickening of the tracheid walls is exclusively scalariform, as is the case with the other *Zamia* species. The ladder steps and the step spacings are of about the same width. Sometimes they bifurcate or form a reticulate pattern, as shown in Photos 11, 12 [× 300], 13 [× 600].

Zamia muricata Willd. (1805)

Plates LXXIX, LXXX, Photos 1–13; Fig. 23

Area of distribution: Central America, Mexico, Venezuela and Columbia. The rhizome is about 30 cm long, the stem about 15 cm high and 1·5 to 3 cm thick. The material was obtained from Caracas by courtesy of Dr Tobias Lasser.

Macroscopic examination (Photo 1 [nat. size]). The diameter of the stem sample examined is 37 mm, of which the pith occupies about 13 mm (a). The vascular bundle ring is 2 to 2·5 mm (c, d), the cortex (e) 10 mm thick (Photo 2 [× 50]).

In the cross section, the monoxylic structure is apparent on first sight to the naked eye. The trunk bears leaf scars, owing to the creeping habit of the plant.

Microscopic examination. The pith largely consists of more or less isodiametric parenchyma cells (Photo 3a [× 70]), whose size ranges from 150 to 260 μ. The cells are close packed; their section is consequently angular, but along the lines of contact, triangular intercellular ducts are frequent. Their thin walls are in places sprinkled with tiny simple pits. Among the parenchyma cells, there are mucilage canals of 250 to 300 μ diameter; their interior is lined with flat epithelial cells. It is interesting to note that there are no pith bundles in the pith.

Primary pith rays (h). The parenchyma cells of the pith gradually elongate in the direction of the primary rays. Beyond the phloem bundles, the rays flare out. The radial dimension of the ray cells near the pith is 180 to 200 μ, their width 35 to 40 μ whereas among the phloem bundles they are radially flattened and are perpendicular to the axes of the rays (Photo 4 [× 100]).

Bundles (c). On the edge of the pith, most xylem bundles begin with a few tracheids and then gradually widen into xylem bundles of 3 to 6 and even 10 tracheids width (Photos 2, 3). Their sections are angular, square, pentagonal or hexagonal (Photo 5 [× 100]); their radial dimension is 30 to 40 μ, their width about the same. Among the tracheids there are a few scattered parenchyma cells (Photo 5). Xylem bundles continue in corresponding phloem bundles (Photos 2, 3, 4d), which taper toward the cortex (Photo 4) and end in a single phloem fibre and phloem parenchyma row. The sections of the fibres are somewhat flattened radially (Photo 4d); their radial dimension is 20 to 25, their tangential dimension 35 to 40 μ. The dimensions of the adjacent phloem parenchyma cells are about the same.



Fig. 23. *Zamia muricata*
(Botanical Garden, Munich; photo by Bauer)

Cortex (e). The monoxylic bundle ring is surrounded by the parenchymatous layer of the cortex; the cells agree in shape and arrangement with those in the pith but perhaps they are slightly larger, and wider spaced. Also, the mucilage canals are somewhat wider, up to 400 μ in diameter (Photo 6g [× 100]). There are a few cortical bundles meandering in the cortex; these issue from the vascular bundle ring. Some transfusion cells closely adhere to them.

The lumina of the mucilage canals are somewhat narrower close to the edge of the cortex (Photo 7 [× 100]); the parenchyma cells are tangentially elongate. On the cortical edge, calcium oxalate crystals form an almost continuous layer. Beyond this layer there is a cork cambium of 10 to 15 cell layers (Photo 7f).

In the *tangential section*, most rays are uni-to quinqueseriate; the primary rays are even wider (Photo 8h [× 100]). Most ray cells are remarkably large, 110 to 120 μ high and of about the same width; there are, however, much smaller ones, too. Their sections are circular, elliptic or polygonal; there are intercellular ducts among them (Photo 8h). The tracheids beside the rays are either solitary or occur in pairs or threes. Their walls invariably exhibit scalariform, annular or flat-spiral thickening (Photo 9 [× 100]). Some are accompanied by transfusion cells (Photo 10 [× 100]).

Radial section (Photos 11 [×300], 12 [×300], 13 [×600]). In the rays, the ray cells are square or upright; their usual height is 70 to 120 μ, their width about the same.

In some rays, the cell walls are somewhat thicker and filled with a resin-like substance.

Most tracheid walls are scalariformly thickened. Some tracheid walls exhibit, however, various transitions from the bordered pitting to the scalariform or reticular thickening (Photo 12).

In some tracheids, the chambers of the bordered pits are horizontally elongate; alternating with the adjacent ones, these pits form something closely resembling a reticular thickening. If the lumina span the tangential walls, scalariform or perhaps annular or reticular thickening develops. Photo 12 shows this structure on the middle tracheid whose walls exhibit an almost annular thickening.

Characteristic araucarioid pitting with alveolarly crowded chambers is nowhere encountered in this species.

Where the ray cells contact the axial tracheids, there are no definite cross fields. This can be partly ascribed to the fact that the ray cells are arranged irregularly rather than in regular horizontal rows.

In the phloem bundle, the walls of the phloem fibres are comparatively thin (4 or 5 μ).

Zamina obidensis Ducke (1922)

Plates LXXXI, LXXXII, Photos 1–14

Its area of distribution is in Brazil, on the hilly slopes of the virgin forests of the Rio Branco. The material examined was obtained from the Museo National, Rio de Janeiro. The stem is strictly speaking a short rhizome; the leaf tuft develops directly above the ground; the older leaves remain on the stem for a short time only (Photo 1 [nat. size]).

Macroscopic examination. The material examined originates from a trunk 5 cm thick. In the surface photo, the monoxylic structure of the trunk is apparent.The diameter of the pith was 2 to 2·5 cm (a), the vascular bundle ring was 2 to 3 mm (c, d), the cortical portion (e) 1·5 to 2 cm thick. The darker spots in the pith and cortex represent bundles; the few light spots represent mucilage canals. The exterior of the cortex bears leaf scars near the apex (Photo 1).

Microscopic examination. The pith largely consists of very thin-walled parenchyma cells; most of these are isodiametric, but many are brick-shaped oblongs. Their size ranges from 70 to 120 μ, their walls are unpitted.

The diameter of mucilage canals in the pith may be considerable (350 to 400 μ). Their interior is lined with much smaller epithelial cells. The parenchyma cells of the pith are filled with starch. In the pith, there are comparatively few conductive bundles; some of these emerge through the primary rays into the cortex.

Primary rays (h). The isodiametric parenchyma cells of the pith gradually penetrate in the form of primary pith rays between the xylem bundles (Photo 2h [× 50]) where they considerably lengthen radially, their length being 180 to 200 μ, their width 35 to 40 μ. The primary rays flare out between the phloem bundles; the long axes of the cells are arranged almost perpendicularly to the axis of the phloem bundles; their size substantially differs from that of the adjacent phloem parenchyma cells.

Vascular bundle ring. Xylem bundles (c). The xylem bundles issue at the margin of the pith; initially 1 or 2 tracheids wide, they subsequently broaden towards the cambium, attaining the width of 5 and rarely 8 tracheids. These bundles are dissected into smaller sections by uni- to quadriseriate rays (Photo 2).

The sections of the tracheids are square, pentagonal or hexagonal; their lumina are invariably rounded. Their radial dimension is usually 45 to 60 μ; their width about the same (Photos 3 [× 200], 4c [× 100]).

Among the tracheids, at the margins of the rays there are parenchyma cells, communicating indirectly or directly with the ray cells running beside them.

Phloem bundles (d). Outside a few rows of cambium cells there follow the phloem bundles; corresponding to the xylem bundles, these gradually narrow down toward the periphery to end in a uniseriate row of phloem fibre and phloem parenchyma cells. In section, the phloem fibres are square, of 20 to 25 μ size; their walls are thick, their lumina pinhole- or slit-like. Most are solitary, but some congregate in threes, fours of fives. The adjacent parenchyma cells are of the same size as the phloem fibres, but very thin walled. In some cases, phloem fibres and phloem parenchyma cells are seen to alternate in sectors (Photo 3).

At the inner edge of the *cortex* (e), at the endings of the phloem bundles, mucilage canals (Photos 7 [× 10], 9g [× 70]) are rather frequent; their diameter is somewhat smaller here than in the pith (180 to 200 μ). Most cortical cells are rectangular, arranged in radial rows; they are rather varied in size, the largest ones being 140 to 150 μ long and 50 to 60 μ wide. Their walls are smooth and thin. In the smaller ones, calcium oxalate crystals are frequent (Photo 8i [× 200]). Gradually flattening, the cortical cells pass into the periderm (f).

In the *tangential section* (Photo 10 [× 100]), most rays are 1 to 7 cell layers wide; the primary rays, however, count 10 to 15 cell layers. In the interior of some primary rays there are vascular bundles.

The ray cells are highly varied in section and size. Some are 70 to 80 μ, others only 20 to 25 μ high. Their walls are smooth and thin. Some of them contain calcium oxalate crystals, also idioblasts filled with an oil-like substance; these are 150 μ long and 50 to 60 μ wide.

Transfusion cells (Photos 5 [× 100], 6 [× 200]). In the tangential section, beside and inside the tracheids, there are numerous transfusion cells which in most cases form smaller or larger clusters. Some are isodiametric; some others are elongate. The passage into tracheids is apparent (Photo 6). They contact with one end the tracheids, the other end or several faces are in contact with the adjacent parenchyma cells.

The tracheids exhibit without exception the scalariform thickening (Photo 8); it is rather seldom that 2 or 3 bordered pits occur in a row in the tangential walls of the tracheids. The apertures of these are slit-like, spanning one-third, one-half of the width or even the full width of the tracheid wall. No definite bordered pitting in the alveolar pattern is found in this species, either.

Radial section (Photos 11–13 [× 300], 14 [× 600]). The ray cells are aligned in radial rows; their height is unequal. Most of them are 70 to 80 μ high and of the same width, but the height of some attains 130 μ. Their walls are smooth and very thin, with no pitting.

In the zones of contact between the thin-walled ray cells and the axial tracheids behind them, no cross fields develop. Nor do the tracheid walls exhibit any such periodicity as would suggest the contact with the ray cell walls.

The tracheids (Photos 11–13 [× 300]) usually exhibit in their radial walls a scalariform thickening which is almost annular in certain respects. Thus the thickenings and pitting are rather varied.

Zamia portoricensis Urban (1899)

Plates LXXXIII, LXXXIV, Photos 1–12

Treated by most authors as an independent species, this plant is regarded by Schuster (1932) as a variety of *Zamia media* [*Z. media* var. *portoricensis* (Urban) Schuster]. Its area of distribution is the province of Guanica, Portorico, where it grows in the woods of the Ensenada mountains. Its trunk is low, cylindrical, partially subterranean. The material was obtained from the Division of Forestry, Santucce, courtesy of Mr R. Seda.

Macroscopic examination (Photo 1 [nat. size]). The diameter of the stem sample examined was 4 cm; on the cross section the principal layers were apparent to the naked eye. In Photo 1, the monoxylic structure of the wood is conspicuous. The diameter of the thick pith (a) is 1·5 cm; the vascular bundle ring (c, d) is 1·5 mm thick; the cortex (e) is 11 to 12 mm thick. The cortex bears a periderm (f), because the leaf bases fell off the stem, leaving almost no traces.

Microscopic examination. The pith (Photo 2a [× 50]) consists largely of circular, slightly crowded, more or less isodiametric parenchyma cells whose average size is 150 to 180 μ. In spite of the rather close packing, intercellular ducts are rather frequent. The walls are covered with a scattering of tiny elliptical or circular simple pits. Among the parenchyma cells, there are mucilage canals (g) of rather small diameter (180 to 200 μ), although some may be much wider (up to 600 μ). These latter can be seen with the naked eye. Their interior is lined with tiny, globular or conical epithelial cells of 30 to 40 μ size. In their vicinity, there are the vascular bundles of the pith, accompanied by a remarkable number of transfusion cells (Photo 6b [× 300]). The parenchyma cells are filled with starch. The mucilage canals are arranged in an almost regular ring at the edge of the pith, at the issue of the

primary rays, directly inside the vascular bundles, near the protoxylem (Photo 2). The cells of the pith gradually penetrate as primary ray cells (h) between the xylem bundles (Photo 3h [× 100]).

Vascular bundle ring (cd). The *xylem bundles* (c) begin in the pith with transfusion cells. Starting out uniseriately, they subsequently widen to become bi-, tri- or quinqueseriate, forming a more or less continuous xylem bundle (Photos 2, 3). Strongly crowded, their sections are angular but their lumina are always rounded. Their radial dimension is 30 to 35 μ, their tangential dimension 40 to 45 μ; near the cambium, they are radially somewhat flattened squares (Photo 3). Among them there occur a few scattered xylem parenchyma cells whose size agrees with that of the tracheids (Photo 4 [× 100]). The ray cells (h) running radially between the tracheids are remarkably large, 150 to 160 μ long and 70 to 80 μ wide (Photo 3), substantially different in size from the xylem parenchyma cells among the tracheids (Photo 4).

Phloem bundles. After a fascicular cambium one or two cell layers thick, the xylem bundles continue in corresponding phloem bundles which are comparatively narrow, bi- or triseriate (Photo 4). Between the phloem bundles, the cells of the rays are radially somewhat flattened, thus being approximately perpendicular to the radial direction (Photos 3, 4). In the phloem bundle there are comparatively few fibres (Photo 4) and few parenchyma cells. Phloem fibres alternate singly or in pairs with likewise single or paired parenchyma cells. The phloem fibres near the cortex are quite thin walled (Photo 3). The parenchyma cells near the cortex perfectly agree in shape, size and structure with the pith parenchyma cells (Photo 5 [× 100]). In the cortex, the mucilage canals run as in the pith (Photo 5g); however, their diameter is slightly greater, 330 to 350 μ.

The cortical parenchyma cells have the same kind of pitting as the pith parenchyma cells. There is no difference either in structure or shape between the two (Photo 5e).

In the external portion of the cortex, the cells gradually pass into the periderm developed by the cork cambium. The cells of the periderm are rectangular and thin walled (Photo 7f [× 100]).

In the *tangential section* (Photo 8 [× 100]), most rays are uni- to triseriate, but the primary rays can be 10 to 15 cell layers wide. The ray cells are relatively large, 120 to 140 μ high on the average and as wide. Some broader rays bear conductive bundles and mucilage canals.

In the tracheid walls, bordered pitting is rare but the walls of the solitary or clustered transfusion cells adjacent to the tracheids exhibit frequently enough an irregular bordered pitting; the pit apertures may coalesce in part of the wall, giving rise to scalariform or reticular thickening (Photo 6 [× 300]). In some cases, the outermost tracheids show the passage from more or less isodiametric transfusion cells through elongate, thin ones to tracheids with scalariform thickening.

The walls of the phloem fibres are thick, their lumina slit-like (Photo 9 [× 100]). At intervals the walls of the phloem fibres exhibit transverse displacements (Photo 9).

Radial section (Photos 10 [× 30], 11 [× 30], 12 [× 600]). The ray cells are also in the radial view square or rectangular. The height of most rectangles ranges from 140 to 150, their width from 60 to 80 μ.

In the tracheid walls, scalariform thickening is exclusive (Photos 10, 11, 12). Some ladder steps are seen to bifurcate (Photo 12), others pass into spiral thickenings as shown by the fact that the tracheids elongate or break up in the manner of a spring coil or a corkscrew (Photo 11, right side). The same structure can be observed on the other tracheids with scalariform thickening.

On the contact of the ray cells with the tracheid walls behind them, there are nowhere any definite cross fields. Hence, this species is, similarly to the other *Zamia*, characterized by the exclusive scalariform thickening of its tracheids.

Zamia pumila L. (1753)

Plates LXXXV, LXXXVI, Photos 1–13; Fig. 24

Its area of distribution is Cuba. Its underground rhizome is barely 10 to 15 cm long and about 8 to 10 cm thick. The stem is two-thirds subterranean; the leaves are about 1 m long, the leaflets 10 to 20 cm long and 2 to 4 cm wide. The material examined was received by courtesy of Dr Antonio Ponce de Leon, Director of the Botanical Gardens of the University of Havana.

Macroscopic examination (Photo 1 [× 2]). The stem sample examined was of a diameter of about 3 cm including 1 cm of pith (a), a single vascular bundle ring of 3 mm (c, d) and a cortical portion of 11 to 12 mm thickness (e, f). The trunk is covered by a thin periderm (f).

In the photo of the cross section, the few dark spots in the pith and in the cortex represent vascular bundles, the light spots are the sites of mucilage canals (g).

Microscopic examination. The pith largely consists of homogeneous, more or less isodiametric parenchyma cells (Photo 3a [× 70]) whose section is circular or polygonal, in most cases alveolarly hexagonal. Along the lines of contact, there are locally some narrow triangular intercellular ducts. The dimension of the cells is 200 to 220 μ. Their thin walls locally bear tiny scattered simple pits. Among the parenchyma cells there are mucilage canals (g) of 400 to 410 μ diameter; their interior is lined with thin-walled, conical epithelial cells. In the parenchyma cells, starch is accumulated. Xylem bundles are scarce in the pith.

Vascular bundle ring (c, d) (Photo 2 [× 30]). At the edge of the pith, next to the vascular bundle ring, there are numerous mucilage canals. Here the ground tissue cells gradually penetrate between the vascular bundles (h), elongating radially and becoming narrower in the process. The radial dimension of the elongate cells is 140 to 150 μ; their width is 60 to 70 μ. Between the phloem bundles, the broad rays flare out while the phloem bundles gradually taper from the cambium towards the cortex.

The *xylem bundles* (c), issuing at the edge of the pith, begin with protoxylem elements and continue in uniseriate tracheids, then in xylem bundles 6 to 8

tracheids wide and about 30 to 40 tracheids long (in the radial direction). In these bundles, the tracheids are angular; their average diameter is 30 to 40 μ (Photo 5 [$\times$ 200]). The broader vascular bundles are dissected by uniseriate rays. The bundles include thin-walled parenchyma cells which are invariably in indirect or direct connection with the rays referred to. The ray cells running beside the vascular bundles may be twice to three times and even five times as large as the xylem parenchyma cells among the tracheid cells, but their walls are of the same thinness.



Fig. 24. *Zamia pumila* (Hawks Park, Florida)

The *phloem bundles* (d) (Photo 4 [$\times$ 200]) correspond to the xylem bundles and are initially of the same width as those. Outwards, however, they gradually taper, ending in uniseriate phloem fibre and phloem parenchyma rows (Photo 3). The tangential dimension of the fibres is 30 to 35 μ, their radial dimension 17 to 18 μ. Their walls are thick, their lumina slit-like. Some congregate into minor or major clusters, but most are solitary.

Cortex. Its parenchymatous cells agree as to shape, arrangement and structure with the parenchyma cells of the pith (Photos 6 [$\times$ 100], 7); they are perhaps somewhat larger.

In the external portion of the cortex, the cells radially flatten; the surface of the stem is covered by a cork layer developed by the cork cambium (Photo 7f). In the cortex, there are beside the mucilage canals (Photo 6g) some thin tracheid bundles which emerge as leaf trace bundles into the leaves. Also here, the tracheid walls are spirally and annularly thickened.

Tangential section. The rays are 1 to 10 (Photos 8 [$\times$ 100], 9 [$\times$ 100]), the primary rays even 20 cell layers wide; the latter generally include tracheid bundles. The height of the ray cells is 110 to 130 μ on the average but the shape and size of the ray cells are very variable. Their interior is filled with starch (Photo 9). The thickness of the rays and the shape of the ray cells are more or less the same in the phloem portion as in the xylem but here the cells are somewhat larger as a consequence of dilatation (Photo 9).

Radial section (Photos 10–12 [× 300], 13 [× 600]). In the rays, the ray cells are square or rectangular. Their height is 120 to 140 μ, their width about the same. Their walls are smooth and thin, without any pitting.

In the ray cells contacting the tracheids, there are no cross fields; nor do the tracheids exhibit any periodicity which would suggest the development of cross fields. The tracheid walls bear exclusively scalariform thickenings and no araucarioid pitting. Some ladder steps are branched, locally even reticularly or furcately. The ladder steps are more or less of the same thickness (6 to 7 μ) as the ladder spacings. Among the tracheids, parenchyma cells are rare.

Zamia silicea Britton (1916)

Plates LXXXVII, LXXXVIII, Photos 1–13

Its area of distribution is in Cuba, on the shores of the river Mal. Its trunk is low, cylindrical, partly subterranean. Its greatest thickness is 7 to 8 cm, its height about the same. Its peak bears a tuft of leaves 35 cm to 1 m long. The material examined originates from Cuba and was obtained by courtesy of Mr F. Barna.

Macroscopic examination (Photo 1 [× 2]). The diameter of the trunk obtained for examination is only 2 cm, including the pith portion (0·5 cm), the monoxylous bundle ring (1 to 2 mm) and the cortical portion (6 to 7 mm). The structure of the trunk is typically cycadean. In the pith, there are few mucilage canals; there are more in the cortex where conductive bundles are also scattered. The cortical portion gradually passes into the periderm.

Microscopic examination. Cross section. The parenchyma cells of the pith are more or less isodiametric, angular or rounded, their size ranges from 140 to 160 μ (Photo 2 [× 50]). Along their lines of contact, intercellular ducts are rather frequent. Their interior is filled with starch. Among the cells of the pith parenchyma there are mucilage canals whose diameter varies between 180 and 500 μ. Their inner walls are lined with epithelial cells (Photo 2g) the size of which is 40 to 60 μ. Most mucilage canals are arranged on the edge of the pith (Photo 7 [× 100]), nearly always facing the xylem bundles or the primary rays (Photo 2g).

In the interior of the pith there are neither proper nor common vascular bundles. On the edge of the pith, usually between two mucilage canals, the parenchyma cells of the pith gradually pass into the cells of the primary rays, lengthening without any essential change (Photo 2h). The size of the ray cells is in these cases about 300 μ by 100 to 120 μ. Their interior is filled with starch grains.

Conductive bundle ring. At the edge of the pith, opposite the vascular bundles, there are protoxylem elements of narrower lumina which grade into the xylem bundles (Photo 4 [× 100]). In the vascular bundle ring, the single xylem bundles are rather wide spaced, their intervals being occupied by the rays (Photo 2). The xylem bundles are generally 1 to 5 tracheids wide; bundles of 8 tracheids width are very rare (Photo 4). The broader bundles are dissected by secondary rays into smaller segments. In general, the structure of the whole trunk reveals the subterranean

habit of the plant; the strengthening elements are hardly developed. The sections of most tracheids are angular; their lumina, invariably rounded, follow the general outline of the tracheids. Among the tracheid rows there are a few scattered xylem parenchyma cells (Photo 4).

Outward of the xylem bundles, beyond a few rows of cambium cells, the phloem bundles are in correspondence with the xylem bundles (Photo 3 [× 200]). In the phloem bundles there are hardly any fibres; they largely consist of parenchyma and ray cells. The phloem fibres are angular in section; their lumina are pinhole-like (Photo 8 [× 100]).

The bundles of the cortical portion usually issue at points between two collateral bundles, in the region of the primary rays. From there they run towards the periderm and continue as leaf scar bundles into the rachids.

The parenchyma cells and the mucilage canals of the cortex perfectly agree in structure with those of the pith (Photo 5 [× 100]). It is only towards the periphery that the cells of the cortex begin to flatten. In the cortical cells immediately inside the periderm, calcium oxalate crystal druses are frequent; some cells are filled with latex or resin-like substances (Photo 5). The cells of the many-layered periderm have suberized walls.

Tangential section. The rays are uni- to quinqueseriate; the primary rays are even wider (6 to 8 cell layers). In cross section, the ray cells are generally squat upright ellipses; their size is variable, ranging from 60 to 80 μ. The walls of the tracheids bordering the rays exhibit exclusive scalariform thickenings, no other kind of thickenings can be observed. The breadth of the rays changes according to whether the tangential section cuts the trunk nearer to or farther from the cambium. Frequently enough, spirally thickened transfusion cells adhere to the tracheids; in some places, there is a gradual transition between them (Photo 6 [× 100]).

Radial section. No definite pith rays are visible. In this species, as in *Zamia* generally, no definite cross fields develop; nor is there any periodicity in the walls of the tracheids contacting the rays.

The walls of most tracheids exhibit the scalariform type of thickening. Some ladder steps may bifurcate; in other cases, the scalariform thickening is combined with reticular thickening (Photos 10 [× 100], 11 [× 200]). In the protoxylem elements next to the phloem bundles the tracheid walls are spirally or possibly annularly thickened (Photo 12 [× 300]). In the parenchyma cells close to the tracheids, calcium oxalate crystal druses are rather frequent (Photo 13 [× 600]).

Zamia skinneri Warsz. (1851)

Plates LXXXIX, XC, Photos 1–16

This tree, attaining a height of about 1 m, thrives at present only in a few places in Panama and Costa Rica.

One of the samples examined was received from San José (Costa Rica), the other from Havana (Cuba). The diameter of both pieces was about 8 cm. One was

examined in the dried state, the other in fresh condition (Photos 1 [nat. size], 2 [nat. size]). The dried specimen was cut and polished; on the surface thus prepared, the details of the structure were just as visible as on the section of the fresh specimen. Both cross sections revealed the monoxylic structure of the tree.

Macroscopic examination. The diameter of the pith was about 2 to 2·5 cm (a). It included in both samples a remarkably large number of mucilage canals (g). In the older trunk, the xylem and phloem ring together were 8 mm, in the younger one 6 mm thick (c, d). The xylem and phloem rings were covered by a cortex about 2 cm thick (e); the latter was surrounded by a comparatively thin periderm (f).

Microscopic examination. The pith (a) largely consists of thin-walled parenchyma cells of 140 to 150 μ average size. The cells are isodiametric; their walls are slightly sinuous.

Mucilage canals (g). Among the cells of the pith, the cross sections of mucilage canals are frequently visible. The size of most is between 220 and 240 μ. A characteristic feature of the wood is that the longitudinal mucilage canals are arranged in a ring on the edge of the pith, next to the xylem bundles. Their interior is lined with thin-walled epithelial cells (Photo 9g [$\times$ 100]).

Pith rays (h). The pith continues radially in the primary pith rays. At first, the ray cells perfectly agree in structure and shape with the cells of the pith parenchyma but the cells among the xylem bundles are rectangular and somewhat elongate radially. Their radial dimension is then 180 to 200 μ; their width is 60 to 70 μ. They retain this shape and size even while bending out between the phloem bundles into the cortex (Photos 3 [$\times$ 50], 5 [$\times$ 10]).

Vascular bundle ring (c, d). It is dissected by the primary rays into several smaller or larger collateral vascular bundles (Photo 3). The xylem bundle between two primary rays is up to 40 tracheids wide, being dissected by uni- and biseriate, rarely triseriate rays into still smaller segments. Among the tracheids, xylem parenchyma cells are scattered. In section, most tracheids are polygonal; some are slightly elongate. Their walls are 10 to 12 μ thick; their lumina rounded (Photos 4 [$\times$ 100], 8 [$\times$ 100]).

Phloem bundle (Photo 7 [$\times$ 100]). Outside the xylem bundle ring there is the cambium composed of 2 to 5 layers of very thin-walled cells. The phloem bundles outside the cambium consist in their overwhelming majority of close-packed, thick-walled phloem fibres (Photo 3d) of point- or slit-like lumina. Thin-walled parenchyma cells are rather rare and sporadic among them. The mass of phloem fibres is only interrupted by the uni- and biseriate secondary rays (Photo 7).

The cortex (Photo 6e [$\times$ 100]). The parenchyma cells of the cortex agree in shape, size and simple pitting with the parenchyma cells of the pith and in structure and size with the cells around the mucilage canals. Nearly all cells of the periderm (f), except the outermost cork cells, contain calcium oxalate crystal druses.

Tangential section. Pith rays (Photo 10 [$\times$ 100]). In the phloem and xylem ring, the rays are 1 to 10 cell layers wide; the ray cells are exceedingly thin walled and unpitted. In the wide primary rays, *mucilage canals* and *conductive bundles* run toward the cortex. In some ray cells, large numbers of calcium oxalate

crystal druses are accumulated. The phloem fibres are thick walled with slit-like lumina.

Tracheids. The tangential section through the xylem bundle shows the highly varied fine structure of the tracheids (Photo 10). Most tracheids are annularly, spirally and even reticularly thickened. In places the thickening is suggestive of the annular and spiral thickenings of the Monocotyledons. The rays are 1 to 10 cell layers wide.

Radial section. Pith rays (Photo 12h [×300]). In the contact zones of tracheids and ray cells, no cross fields could be observed. The ray cells communicate with the adjacent tracheids only through their thin walls (and not by simple pits).

Tracheids. The radial walls of the tracheids exhibit in the overwhelming majority of cases scalariform or reticular thickening. A few cells, however, show bordered pitting (Photo 11 [×300]), although directly adjacent to tracheids with reticular thickening. Where the phloem and xylem bundles meet, the first tracheids have no walls with bordered pitting and it is only outside these that the first tracheids with scalariform thickening show up. However, this is no general rule, because also in the older tracheids, i.e. those farthest from the cambium, bordered pits may occur next to scalariform thickenings (Photos 13 [×200], 14 [×200]).

In some places in the wood, short tracheids occur whose end walls communicate partly through bordered pits and partly through reticular openings (Photos 13, 15 [×300]).

In *Zamia*, scalariform and reticular thickening is generally characteristic of the tracheids (Photo 16 [×600]); bordered pitting is much less frequent, being concentrated in the first place near the phloem. It is in all probability from these tracheids with bordered pitting that the tracheids with scalariform and reticular cell wall thickenings develop. Such a reticular annular thickening is presented in Photo 13.

(h) BOWENIA

Bowenia serrulata (W. Bull) Chamberlain (1912)

Plates XCI, XCII, Photos 1–12; Figs 25 and 26

Two species of the *Bowenia* genus are known: *B. serrulata* (André) Chamberlain and *B. spectabilis* Hook. Of the former, the author has received a small trunk sample from Mr Lothian, Director of the Botanical Gardens, Adelaide. *B. serrulata* has an underground stem (Fig. 25); only the leaf tuft and the flower rise above the ground. The leaves are 1 to 2 m, the pinnate leaflets 8 to 16 cm long. A very few specimens of *B. serrulata* are living today, in a single spot of Australia, near Brisbane.

Macroscopic examination (Photo 1 [nat. size]). The trunk sample of about 3 cm diameter was fully dried out when received. It was examined after softening. On

the smooth cut surface the three typical layers of the Cycads could be easily distinguished. The diameter of the pith (a) is about 1 cm, the monoxylic vascular bundle ring is of about the same thickness (c, d). The cortical portion (e) including the periderm (f) is thickest, about 1·5 cm.

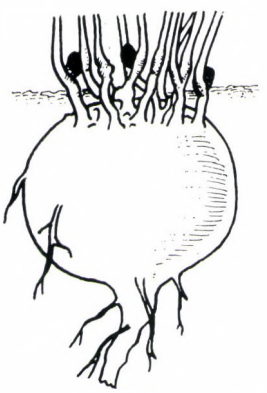


Fig. 25. *Bowenia serrulata* (a somewhat diagrammatic sketch of the stem being about 23 cm in diameter of a staminate plant; the dotted line is the ground line)

Microscopic examination. Cross section. The pith (a) largely consists of thin-walled isodiametric cells containing tiny starch granules accumulated; the cell walls bear scattered tiny pits. The cells are close packed, intercellular ducts being rare (Photo 3a [× 100]).

Among the thin-walled cells of the ground tissue, there are mucilage canals lined with epithelial cells. The diameter of the mucilage canals is 400 to 440 μ, so that they are visible in the cross section to the naked eye. The epithelial cells are much smaller than the surrounding ground tissue cells; their size is 30 to 40 μ, whereas the ground tissue cells may be up to 150 μ in diameter. In the pith there are very few proper or common bundles. In some parenchyma cells, calcium oxalate crystal druses are seen. In the arrangement of the mucilage canals and of the pith bundles there is no regularity.

Pith rays (h). From the pith, primary rays issue which divide the xylem ring and the phloem ring into wider or narrower collateral vascular bundles (Photo 2 [× 30]). The individual collateral vascular bundles are clearly separate (Photo 3). The parenchyma cells of the primary rays between the xylem bundles are radially elongate. At the edge of the xylem ring, the primary rays begin to flare out (Photo 2); the shape of the cells changes and their size increases. In the ray cells and in the xylem parenchyma cells, calcium oxalate crystals are frequent. The xylem bundles between the primary rays are dissected by the secondary and tertiary rays into further segments; these latter are usually 2 to 6 tracheids wide (Photo 3).

Tracheids. At the points of issue of the xylem bundles, protoxylem elements are almost invariably present, but transfusion cells are lacking. The primary tracheid bundles conically taper towards the edge of the pith. The tracheids are of varied sections, triangular, pentagonal or polygonal and crowded (Photo 3). Their size is 25 to 50 μ. Among them, thin-walled xylem parenchyma cells are rather frequent. In most cases these cells assume the communication between two neighbouring rays.

Phloem bundles. The broader rays dissect the phloem bundles similarly to the xylem bundles; hence, the phloem bundles correspond to the xylem bundles. In the phloem bundles there are comparatively few phloem fibres, owing to the subterranean habit of the plant. Among the scarce phloem fibres there are a few phloem parenchyma cells. No definite sieve tubes could be observed. The phloem primanei are arranged in the outermost portion of the broader phloem bundles (Photos 2, 3d).



Fig. 26. *Bowenia serrulata* (Australia, after Chamberlain)

Cortex (Photos 4 [× 100], 5e [× 100]). The histological structure of the cortex agrees with that of the pith. However, in the cortex the mucilage canals are much more frequent than in the pith and the cortical bundles, which are likewise collateral, are also more numerous. Also, the structure and size of the mucilage canals agree with those of the pith (Photo 4g). This is only to be expected as the two sets of mucilage canals are directly connected. Along the proper bundles, reticularly thickened transfusion cells are rather frequent.

Periderm (f). The cortex is limited outwards by the periderm (Photo 5). In the external portion of the cortex, near the periderm, the number of mucilage canals increases; some of these meander almost horizontally, parallel to the periphery. The outermost part of the periderm consists of thin-walled rectangular cork cells; the parenchyma cells of the cortex contain no calcium oxalate crystals.

The *tangential section* (Photo 6 [× 100]) exhibits the characteristic Cycad structure. Both in the phloem and in the xylem, the rays are uni- to quadriseriate or more (h). Most uniseriate rays are 1 to 5 cells high; the height of the ray cells is 100 to 110 μ, their width 30 to 40 μ (Photo 10 [× 300]). The broad primary rays are 8 to 10 cell layers wide; in them mucilage canals or tracheid bundles pass from the pith toward the cortex. The cells of the broad rays are particularly rich in calcium oxalate crystals. In the tangential walls of the meandering tracheids flanking the rays, the elongate bordered pits are locally arranged like the steps of a ladder.

In the tangential walls of some tracheids araucarioid pitting is observed, the alveolarly crowded pits are arranged in 2 or 3 rows (Photo 8 [× 300]).

Radial section. Pith rays. Most ray cells are upright or square, but some are hexagonal and alveolarly packed (Photo 10). The cross fields of the ray cells contacting the axial tracheids bear no explicit pitting, nor are there any interruptions corresponding to the ray cells in the tracheid walls; the ray cells are, in direct contact with the scalariform pitting of the axial tracheids, without any cross-field pitting. There are no definite cross fields even in the places where bordered pitting is present in the tracheid walls (Photos 9 [× 200], 10). In the ray cells, calcium oxalate crystal druses are rather frequent.

Tracheids. In the longitudinal walls of the tracheids, the bordered pits are either close packed in the araucarioid pattern (Photos 8, 9, 10, 11 [× 300]) or, considerably lengthened transversally, they grade into scalariform thickening in which case the ladder steps span the whole width of the tracheid (Photo 7 [× 300]). In other cases, the apertures of the bordered pits become slit-like and pass gradually into scalariform perforation (Photo 12 [× 600]). In the immediate vicinity of the phloem most tracheids bear a bordered pitting, whereas towards the cortex, scalariform thickening is prevalent.

Bowenia spectabilis Hook (1863)

Plates XCIII, XCIV, Photos 1–13; Figs 27a,b, 28

Samples of this second rare *Bowenia* species was received from Brisbane, by courtesy of Mr Watson and Mr Wilkes. The samples arrived in fresh condition so that the short rhizome, the leaves and the leaf epidermis could be readily studied.

In its external habit, *B. spectabilis* is very similar to *B. serrulata.* Its short trunk hardly rises above the ground; it is the above-ground portion that bears the leaves of 80 to 180 cm length (Fig. 28). On the thin rachis, elliptic leaflets of about 10 to 15 cm size are arranged alternatingly on both sides. The length of the short trunk and the connected beet-like root is 10 to 12 cm. One of the differences between the two species is that the short trunk and rhizome of *B. serrulata* are nearly globular whereas those of *B. spectabilis* are more beet-like, further, that the leaflet margin of *B. serrulata* is somewhat serrate, whereas that of *B. spectabilis* is entire. On the surface of the short trunk, the scars of the fallen leaves were visible. The thickness of the stem was about 4 cm (Figs 27a, 27b).

Microscopic examination. In cross section, the monoxylic nature of the species is apparent (Photos 1 [× 2], 2 [× 50], 3 [× 30]). The pith is a mass of isodiametric, thin-walled cells with spacious mucilage canals among them (Photo 8 [× 100]). In the walls of the parenchyma cells, simple pits of 6 to 7 μ size are scattered. The parenchymatic cells of the pith pass almost imperceptibly into primary rays of 4 to 8 cell layers width. Among the narrowing phloem bundles, the rays gradually flare out to pass almost continuously into the parenchyma cells of the cortex. In the

cortex, axial mucilage canals are frequent. In places they are seen to communicate through the primary rays with the mucilage canals of the pith (Photo 3).

The size of the mucilage canals is 260 to 300 by 220 to 230 μ. Their interior is lined with thin-walled epithelial cells (Photo 8). Among the parenchyma cells of the cortex, proper cortical bundles are rather frequent; there are no proper bundles in the pith. The cortex gradually passes into the periderm, whose suberized cells are compressed oblongs. In the cells of the cortex and particularly of the periderm, calcium oxalate crystal druses are frequent (Photos 6 [$\times$ 300], 7 [$\times$ 300]).

The primary ray cells are rectangular, their length is 100 to 110, their width 40 to 50 μ. In them, calcium oxalate crystal druses are frequent. The xylem bundles are dissected by secondary, tertiary rays (Photo 5 [$\times$ 100]). At the points of issue of the xylem bundles, on the edge of the pith, there are few transfusion cells; most such cells are arranged along the xylem or phloem bundles. Most tracheids are of angular, square, pentagonal or hexagonal section, but their lumina are usually rounded. In the continuation of the xylem bundles, there are phloem bundles tapering towards the cortex (Photo 4 [$\times$ 100]). The secondary and



Fig. 27a. *Bowenia spectabilis* (Australia; after Chamberlain)



Fig. 27b. *Bowenia spectabilis* (leaf and stem)



Fig. 28. *Bowenia spectabilis* (Australia; after Chamberlain)

tertiary rays continue in the phloem bundle; between them, the thick-walled phloem fibres are partly solitary and partly aligned tangentially, in plates of 3 to 6 elements (Photo 4).

The *tangential section* agrees with that of *B. serrulata*. Most primary rays are 2 to 10 cells wide (Photo 9 [×100]); in the ray cells, calcium oxalate crystals are rather frequent. The transfusion cells adhere to the axial tracheids and gradually pass into these. The transfusion cells exhibit bordered pitting; the apertures of the pits are elliptic, or slit-like as in the axial tracheids. Structure and width of the rays are the same as in the phloem. The walls of the phloem fibres are thick, their lumina slit-like.

Radial section. Most ray cells are isodiametric and smooth walled (Photo 12 [×300]). In the areas of contact with the tracheids, no cross fields develop, similarly as in *B. serrulata*. The tracheids and the rays cells communicate with each other only through the thin walls of the ray cells. In the tracheid walls, the bordered pits are arranged in the araucarioid pattern (Photos 10–12); in the width of one tracheid there are 2 to 5 bordered pits. Most apertures are horizontal slits; sometimes the chambers of neighbouring bordered pits coalesce. In yet other cases, the bordered pits are substantially elongate perpendicularly to the trunk axis, forming scalariform and sometimes even annular thickening (Photo 13 [×600]). Definite annular or scalariform thickening is, however, much more rare in *Bowenia* than e.g. in *Zamia*. Beside the tracheids, transfusion cells are rather frequent. Some of these gradually lengthen and turn into tracheids.

RELATIONSHIPS OF THE CYCADS ON THE BASIS OF THEIR XYLOTOMY

We have recognized above the most important xylotomical properties of the Cycads, of which the following are most essential:

1. All living Cycads – in contrast to the other Gymnosperms – have a well-defined, separate pith; polystely occurs, too.

2. The pith includes conductive xylem-phloem bundles and mucilage canals.

3. Directly outside the pith, there are one or several conductive bundle rings, dissected by primary or secondary rays into smaller or larger collateral bundles.

4. The conductive bundle rings are surrounded by a comparatively thick cortex and periderm.

5. In the cortex – similarly as in the pith – there are mucilage canals and conductive bundles composed of xylem and phloem.

6. In the parenchyma cells of the xylem, calcium oxalate crystal druses are very frequent; solitary and rhombohedral crystals are restricted to a few species.

7. Among the parenchyma cells of the pith, there are so-called transfusion cells which are nearly always in contact with the tracheids.

8. In the xylem, there are only tracheids, however, the endings of some tracheids or their lateral walls are very exceptionally perforated.

9. The phloem consists of phloem fibres, phloem parenchyma cells and a few scattered sieve cells.

10. Most tracheid walls bear bordered pits arranged in the araucarioid pattern. Rather frequently, however, the tracheid walls are scalariformly or reticularly thickened. The so-called modern bordered pits are absent from the wood of the Cycads.

All these anatomical features almost invariably occur together in the living Cycads examined, so they can be regarded as phylum traits.

Now the question arises whether all or some of these phylum traits occur also in other types of cauline plants (Cormophytes), and whether their presence or absence is suggestive of phylogenetic or evolutionary relationships.

The Cycads are gymnospermous seed plants (Spermatophytes) and as such represent a stage of transition between the spore-bearing Cormophytes in the strict sense of the term (*Psilophyta*, *Pteridophyta*) on the one side, and the seed-bearing Pteridosperms, Chlamydosperms and Angiosperms on the other.

On examining closely these evolutionary stages, we can distinguish in all of them several types substantially differing from each other. The simultaneous appearance of different types is very important, it may be construed to suggest a polyphyletic phylogeny of the Cormophytes. Thus, e.g. in one of his works, Remy distinguishes among the Psilophytes *Rhynia*, further *Protopteridium*, *Asteroxylon* and *Calamophyta*, first of all on the basis of their monopodial, dichotomous and verticillate branching.

The position is similar with the *Pteridophyta*, more evolved than the *Psilophyta*, where the phyla *Lycopsida*, *Pteropsida* and *Sphenopsida* can be clearly distinguish whereas among the extinct Pteridosperms the microphyllous *Lepidocarpon*, the macrophyllous *Miadesmia* and the verticillate *Calamocarpon* can be separated.

Within the Gymnosperms, the macrophyllous Cycads and *Ginkgoinae* sharply differ from the microphyllous strobilous Conifers in the strict sense of the term; similarly, within the Chlamydosperms the *Gnetales*, *Welwitschiales* and *Ephedrales* and finally within the Angiosperms the *Monocotyledones* and *Dicotyledones* are distinctly different.

The question now is whether, on the basis of their wood anatomy, the Cycads can be assigned to the above-enumerated types which represent various stages of evolution, i.e. whether the Cycads preserve in their present fairly highly evolved state such primitive anatomical properties which they carry in themselves since their most simple cormophytic condition or whether they possess properties which might have further evolved during the course of a phylogeny of several million years duration cropping up in the most developed Cormophytes (the Angiosperms) unchanged or slightly modified. It is rather difficult to answer these questions, as on the extinct simpler forms, it has not so far been possible to study all xylotomic features; therefore in establishing relationhips with these we are in a rather precarious position.

In spite of all these deficiencies we are already in the possession of several anatomical observations which permit some fairly well-founded conclusions as to the relationships of Cycads both downwards and upwards. The living Cycads bear a great many traits of wood anatomy the analogues of which occur both in the simplest Cormophytes and in the most evolved Spermatophytes. All this shall be conclusively proved in the following by comparison of drawings and photos.

Let us now review one by one the various stages of phylogenetic evolution.

Affinity relationships between Cycads and Psilophyta

The *Psilophyta* of the Devonian are divided by Remy (1959) into types of monopodial, dichotomous and verticillate branching. In their xylem, Henes (1959) distinguishes two main types on the basis of the structure of the tracheids. The one is represented by *Rhynia* and *Hornea*, which have a central stele (Fig. 29) and in which the tracheid wall is spirally or annularly thickened. In the Cycads, such thickening occurs at most in the protoxylem elements, but never in the secondary wood.

In the other type (*Asteroxylon*) there are already more xylotomical properties which suggest a closer affinity with the Cycads. The fact, that the young shoots of *Asteroxylon* are circinate, as are the young leaves of some Cycads (*C. circinalis*, *Bowenia*), and that in *Asteroxylon* the elements of the central xylem bundle (the tracheids) are arranged not asteroidally but essentially dichotomously (Fig. 29/3) (dichotomy being a further phylum trait of Cycads, not only as regards the branching of the trunk but also in the final branching of the leaf-veins), should not be left out of consideration when establishing the possible relationships (Fig. 29/3).

Besides these two interesting properties, the most important trait is the similar structure of the tracheids in *Asteroxylon* and Cycads. In *Asteroxylon*, the tracheid walls exhibit scalariform thickening as do those of many living Cycads, especially *Zamia* which, similarly to *Asteroxylon*, possess subterranean rhizomes. Figure 29/4 shows a specimen of *Asteroxylon*, while Fig. 29/5, of about the same magnification, shows living *Zamia muricata*. The similarity is so great that even the most rigorous comparison permits to conclude upon a close affinity.

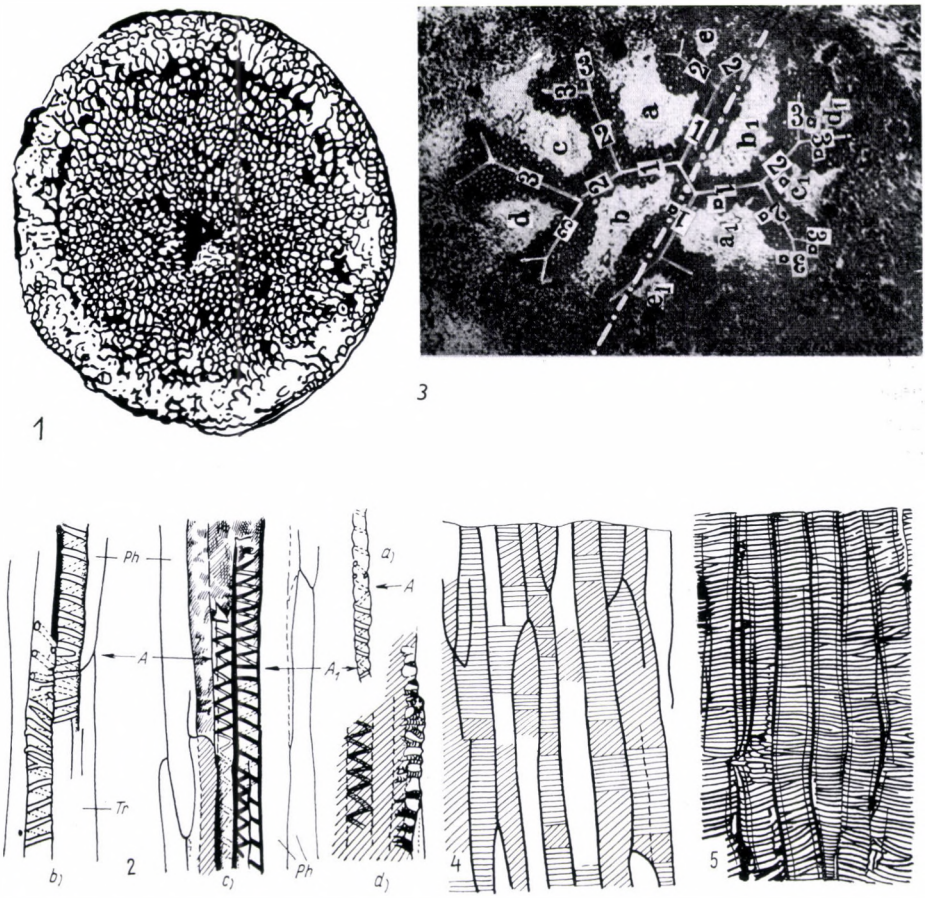


Fig. 29. 1. Central stele in the stem of *Rhynia* (after Zimmermann). 2. *Rhynia gwynne-vaughani* Kidston and Lang. Ring and spiral thickenings from protoxylem. Scalariform thickenings do not occur in these tracheids and therefore the sample differs essentially from *Asteroxylon* [×270] (after Henes). 3. *Asteroxylon mackiei* Kidston and Lang. In the interior of the little stem, the elements of the xylem bundles are not aligned stellately but dichotomously, which is a primitive trait of braching. Observe the direction of the white lines which shows the whole dichotomous arrangement of the elements. On the right and left side of the middle line the xylem and phloem bundles are the reflections of each other. Thus the ancestral dichotomous branching appears already in the vascular bundle arrangement of *Psilophyta* (after Zimmermann) [×70]. 4. *Asteroxylon mackiei* Kidston and Lang. Longitudinal section detail of the metaxylem. The tracheids show scalariform thickenings (after Henes). 5. *Zamia muricata*. The structure of wood is very similar and can be even regarded as identical to *A. mackiei* [×250]

The ladder steps are dichotomous both in *Asteroxylon* (Fig. 29/4) and in living *Zamia muricata* (Fig. 29/5) (Henes 1959). Similarly to living *Zamia*, *Asteroxylon* exhibits no so-called modern pitting either. All this does not prove that the Cycads

directly derived from the Devonian *Asteroxylon*; we only wish to call attention to the great similarity undoubtedly prevailing in the arrangement of the tracheids between *Asteroxylon* and the living Cycads. The assumption of a relationship between the Cycads and some types of *Psilophyta* is largely justified.

Relationship of the living Cycads and the living and extinct Pteridophyta and Gymnospermae

Within the three classes of *Pteridophyta* – not counting *Sphenopsida* – polystely is characteristic of *Lycopsida* and *Pteropsida*, although it does not appear in them in quite the same form. In *Lycopsida*, the steles in the procumbent stems are of a generally lamellar structure. In *Pteropsida* the steles (or better hadrocentric bundles) are very often scattered and in the central part of the stem there is sometimes even a rather well-defined pith system (*Isoetes*, *Stylites*). The tracheid walls exhibit scalariform thickening only, there are neither araucarioid, nor modern bordered pits.

As to the thickening of the tracheid walls, both *Lycopsida* and *Pteropsida* might be brought into a certain genetic connection with Cycads. This particularly applies to *Pteropsida* whose tracheids exhibit not only scalariform thickenings, but also scalariform perforations near their ends so that they essentially communicate as tracheae rather than as tracheids. In this respect the scalariform perforation of *Pteridium aquilinum* and of *Lepidozamia hopei* deserves interest. Let us add that within the *Pteridophyta*, the young leaves of the *Filicinae* are circinate, as are those of *Bowenia* or *Cycas circinalis*, further that the final branchings of the leaf veins are dichotomous in both and that in both there are multiciliate spermatozoids and no suspensors develop on the embryos at the time of development of the octants, etc. Hence, a relationship between *Filicinae* and Cycads may rightly be assumed.

This genetic connection is further corroborated by comparing the xylem of some Pteridophytes and Cycads of the Carboniferous, first of all of the tall *Sigillaria* (Figs 30–33). Most *Lepidodendrons* possessed central steles similar to those of the primitive shrub *Rhynia* (Fig. 29/1), that is, the xylem portion was arranged in the axis of the wood (Zimmermann 1959, Mägdefrau 1953). On the other hand, *Sigillaria* had a pith system exactly as developed as those of the recent Cycads.

Another similarity is that the trunks of some living Pteridophytes (*Alsophila*), of the recently discovered *Stylites* or of the extinct *Sigillaria* are and were unbranched, or if they branched – especially late in the life of the plant – they did so in a characteristically dichotomous way, exactly as some of the living Cycads or monocotyledonous *Cycas*, *Zamia*, *Dracaena*, *Yucca*, *Pandanus*, *Aloe*, etc.

The analogy is perfect also in that e.g. in *Sigillaria saullii* the tracheid walls are just as scalariformly thickened as in the living Cycads and especially in *Stangeria* and *Zamia* (Fig. 30).

As among the living Cycads several genera can be distinguished in which the structure of the wood and especially the pitting of the tracheids somewhat differ,

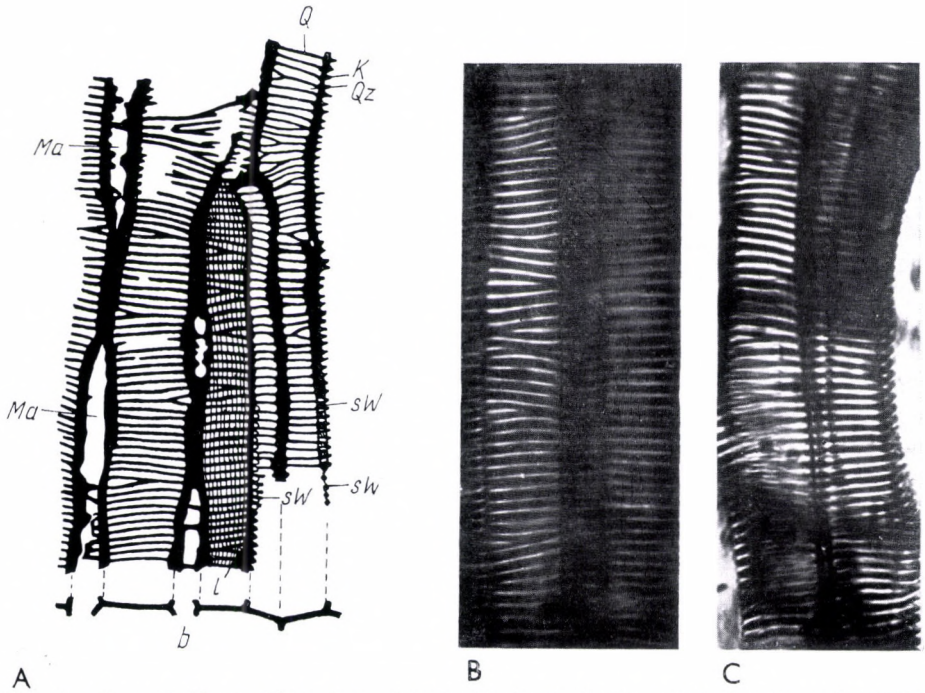


Fig. 30. **A:** scalariform thickenings of tracheids in *Sigillaria saulii* (After Henes [× 240]). **B:** scalariform and bifurcated cell-wall thickenings (*Zamia muricata*). **C:** scalariform thickenings of tracheids in *Stangeria paradoxa*. Tracheid structures highly similar, hard to differentiate. Similarity of such an exceeding degree may be supposed among relatives only. (**B** and **C** are original photos [× 300])

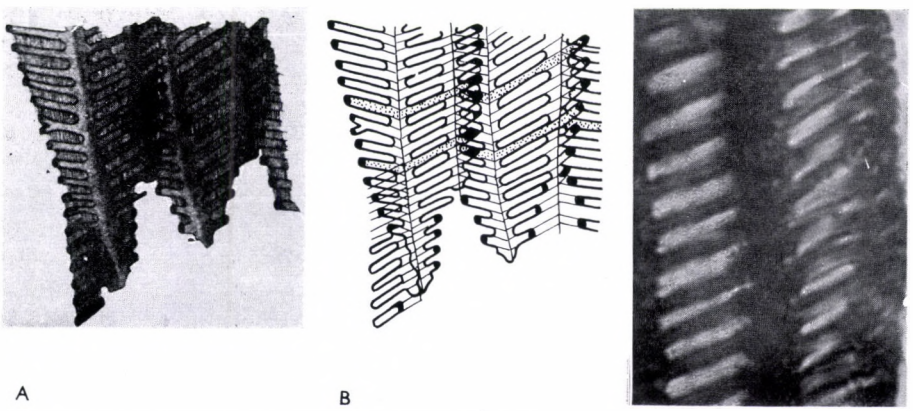


Fig. 31. *Sigillaria saulii* (explanation on p. 128)

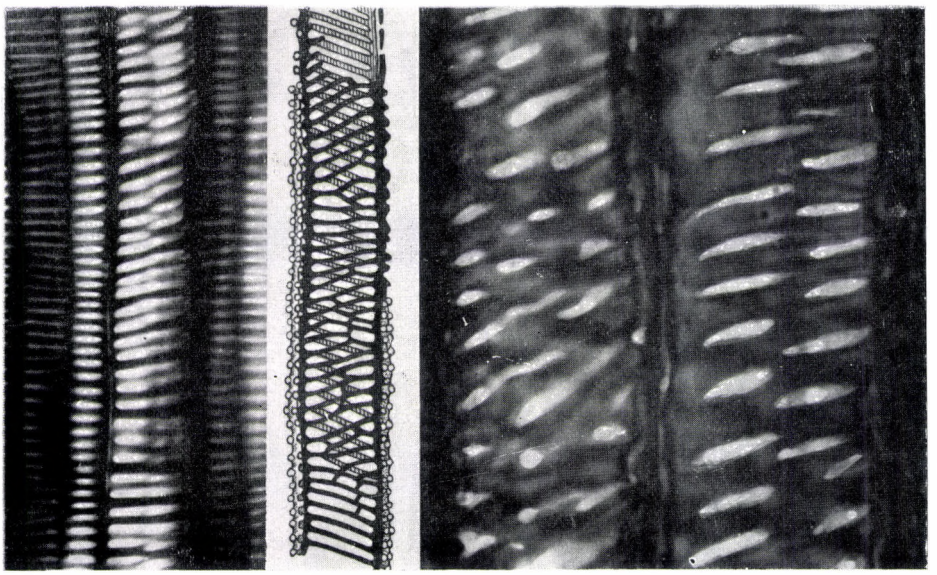


Fig. 32. Reticular thickening of the tracheid in (C) *Zamia portoricensis*, (A) *Sigillaria saulii* and (B) *Encephalartos* sp.

similar differences could exist between the Pteridophytes not only of the Carboniferous but also of the Permian. It is interesting, however, that the internal anatomy of some arborescent ferns – particularly as regards the pitting of their tracheids – is strikingly suggestive of some genera of living Cycads: comparing the two, it is difficult to decide which structure derives from a living Cycad and which from a Carboniferous or Permian fern. For example, the tracheids

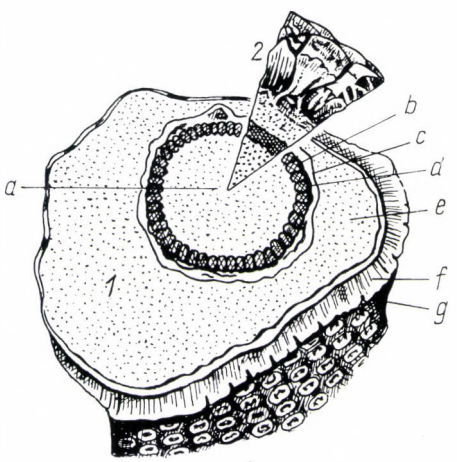


Fig. 33. *Sigillaria menardi* Brongn., of well preserved structure: (*a*) pith, (*b*) protoxylem and centripetal metaxylem, (*c*) secondary wood (centrifugal), (*d*) phloem, (*e*) middle cortex (destroyed), (*f*) periderm, (*g*) leaf scars (from Scott, after Brongniart). About half scale. 2. Stem of *Encephalartos* (*Cycadales*) in cross section showing two girths of bundles on the outer side of the bases of the leafs (original). Recent Cycads (2) have a stem structure similar to that of the *Sigillaria* of the Carboniferous (1)

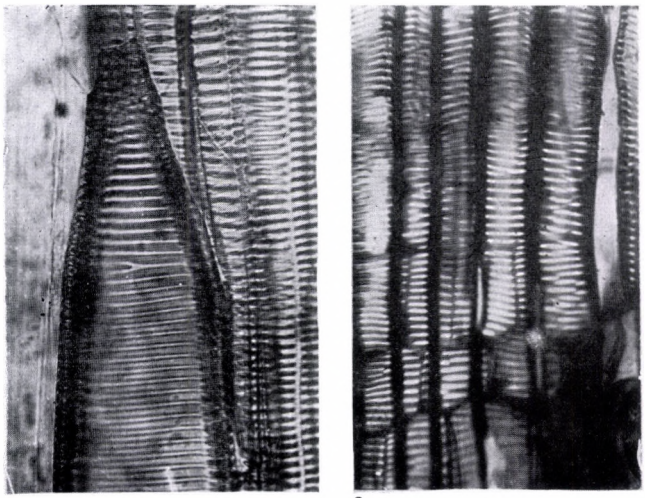


Fig. 34. Scalariform thickenings of the tracheid and scalariform perforation in (1) *Pteridium aquilinum*; similar thickening in (2) *Zamia skinneri*. (Original photos [× 300])

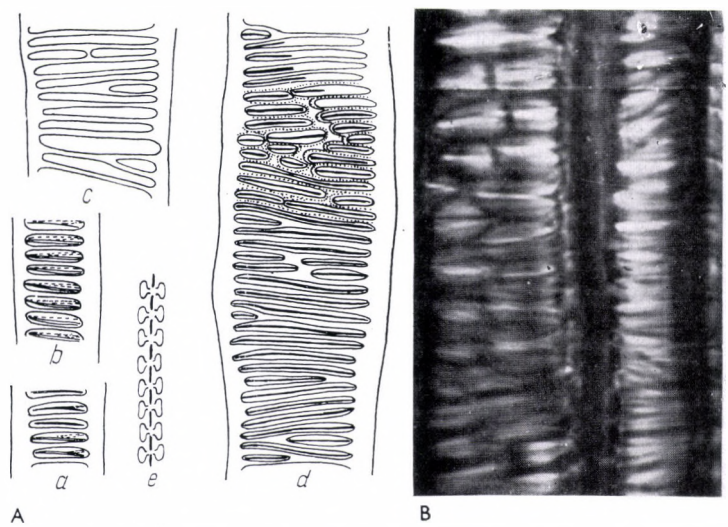


Fig. 35. Scalariform thickenings of the tracheid in (A) *Protopitys buchiana* and in (B) *Encephalartos gratus*. (A after Henes)

with scalariform thickening of *Sigillaria saullii* (Fig. 30), referred to above, almost fully agree with the tracheids, likewise of scalariform thickening, of the living Cycads *Zamia* and *Stangeria* (Fig. 30).

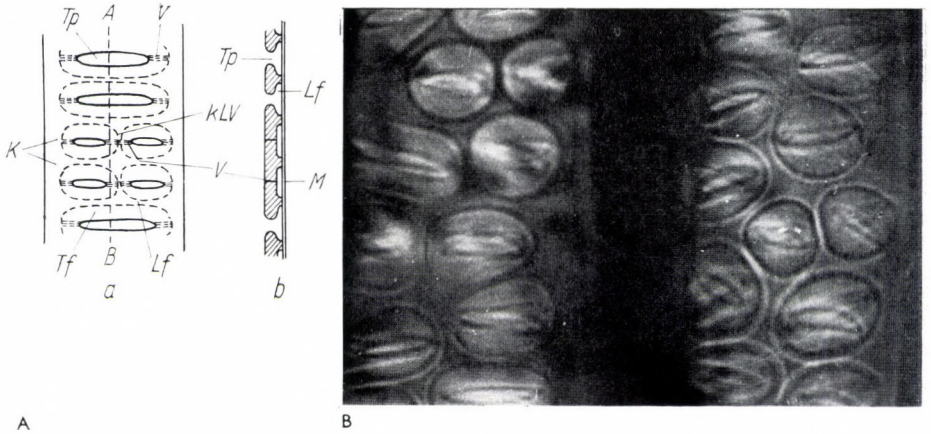


Fig. 36. **A.** As to shape and structure the bordered pits of tracheid wall in *Völkeliella* correspond entirely with those of *Encephalartos lehmannii* shown in **B.** (**A** after Henes)

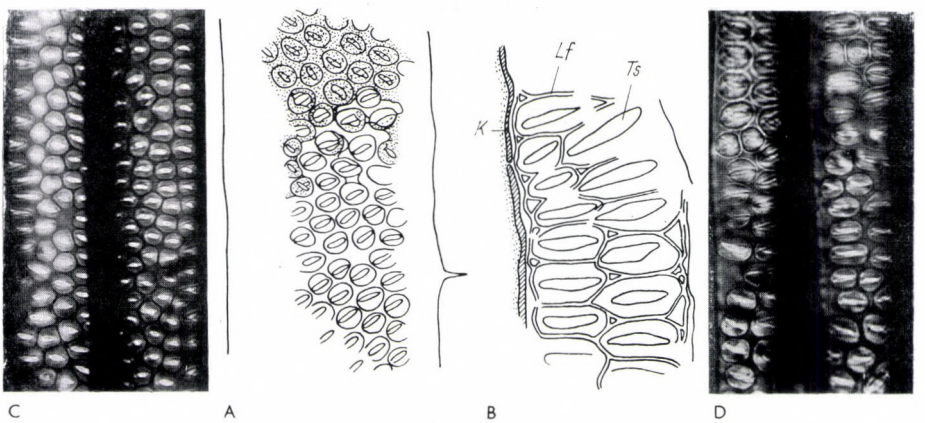


Fig. 37. *Lyginopteris oldhamium* (Binney) Seward. In the tracheids, the bordered pits are not closely but loosely arranged side by side, not in definite longitudinal rows (after Henes) [×350]. In the tracheids of the recent *Macrozamia* the shape and size of the bordered pits, the direction of their aperture and their position to one another are perfectly similar [×250]

In *Sigillaria saullii*, however, some tracheids could be thickened reticularly as well as scalariformly (Fig. 32), in the same way as in several living Cycads. This is by no means intended to state that the living Cycads derive from the extinct *Sigillaria*, but the common origin is evident.

Another example is the primitive fern *Protopitys buchiana* in which, in contrast to the above structure, the bordered pits in the tracheid walls are horizontally elongate, spanning the walls of the tracheids with a shorter third one inserted be-

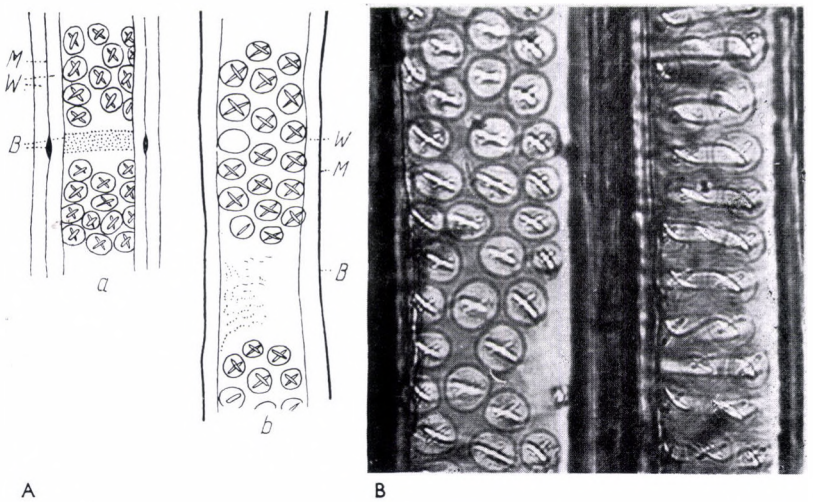


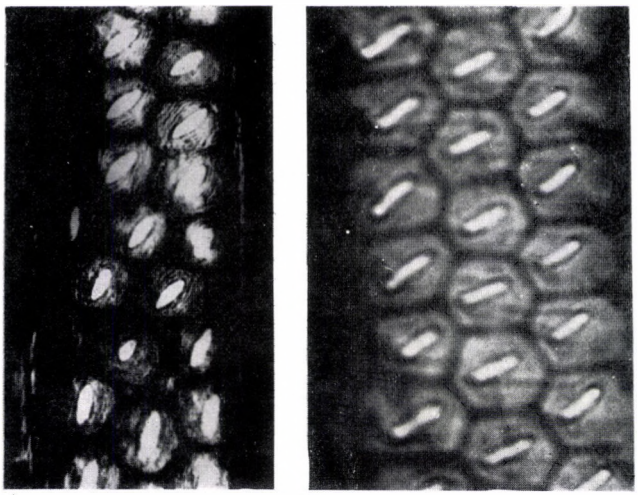
Fig. 38. **A** illustrates loosely arranged bordered pits of tracheids in the secondary xylem of *Callixylon* sp.; opposite apertures meet each other. According to the author, section at **B** is not a Sanio band [× 500] (after Henes). **B** reveals that in recent *Cycas media* the arrangement of bordered pits is entirely similar [× 600]

tween the two long ones; as a result dichotomous thickening has developed, similarly as in living *Encephalartos gratus*. This clearly indicates the transition from bordered pits to scalariform thickening. In the tracheids of *Völkeliella refracta* the bordered pits are somewhat compressed but not alveolarly crowded, similarly as in living *Encephalartos gratus* or *Encephalartos lehmannii* (Figs 35, 36).

In other spermatophylic ferns the bordered pits are not close packed; they form loose rows as in some Cycads, e.g. *Cycas beddomei*. Their apertures are arranged crosswise on opposite sides, exactly as in the tracheids e.g. of *Cycas media*. The photo of a tracheid of *Cycas media* (Fig. 38B) and a drawing of *Callixylon* (Fig. 38A) exhibit a striking resemblance.

Henes (1959) regards the zones where bordered pits are absent as bars of Sanio (Fig. 38A). In our opinion, these zones of interruption are the places where the horizontal walls of the ray cells meet the tracheids. In such places bordered pits cannot, of course, develop; and as a matter of fact, these unpitted zones always develop in the tracheid walls, in places corresponding to the height of the ray cells, so they have nothing to do with the bars of Sanio.

In the ancient Pteridophytes and spermatophytic ferns of the Carboniferous and the Permian, as well as in the Gymnosperms *Dadoxylon* and *Macrozamia*, the bordered pits in the tracheid walls are alveolarly packed in several rows (Fig. 39). In photos and drawings placed side by side, it is difficult to decide which pitting originated e.g. from a *Cordaites* of the Carboniferous or from a Permian *Dadoxylon* fossil and which from a living Cycad.



A B

Fig. 39. As to size, arrangement and aperture, the bordered pits of tracheids in (A) *Dadoxylon brandlingi* are similar to those of the tracheids in (B) *Macrozamia hopei* [×600]

However, the extraordinary similarity between the ancient Pteridophytes, gymnospermous *Callixylon*, *Cordaites* and the living Cycads, is not restricted to the fine structure of the tracheids; it extends also to the arrangement of the various elements. Figure 43B shows the cross section of a *Medullosa*; Fig. 43A the cross section of living *Macrozamia miquelii* in identical magnification. On the two pictures the structure of the wood is so similar that the two can hardly be distinguished. This identity of structure proves a close affinity between the Mesozoic *Medullosae* and the living Cycads.

In the arrangement of the elements, there are further points of similarity between the living forms and the Mesozoic ones. Figure 41 shows a living Cycads; the adjacent drawing presents the trunk of a pteridophytic *Cycadeoidea* (Fig. 41/1,2). Shape and arrangement of the cells of the ground tissue, orientation and width of the xylem bundles, structure of the primary rays are so similar that the drawing could have been made from the living *Cycas circinalis* and the photo from a fossil Cycadeoid extinct long ago.

Shape and size of the ray cells among the xylem bundles and the arrangement and wall thickness of the fibres in the phloem, and the lamellar arrangement of the thin-walled parenchyma cells among the fibres are so similar that there remains no doubt about a direct relationship between Triassic Cycadeoids and living Cycads.

All these traits are illustrated by Fig. 41/1–4 and the relevant photos and drawings.

There is also a striking similarity between the ray structure of the Devonian fern *Aneurophyton germanicum* and living *Dioon spinulosum*. The height of the ray cells

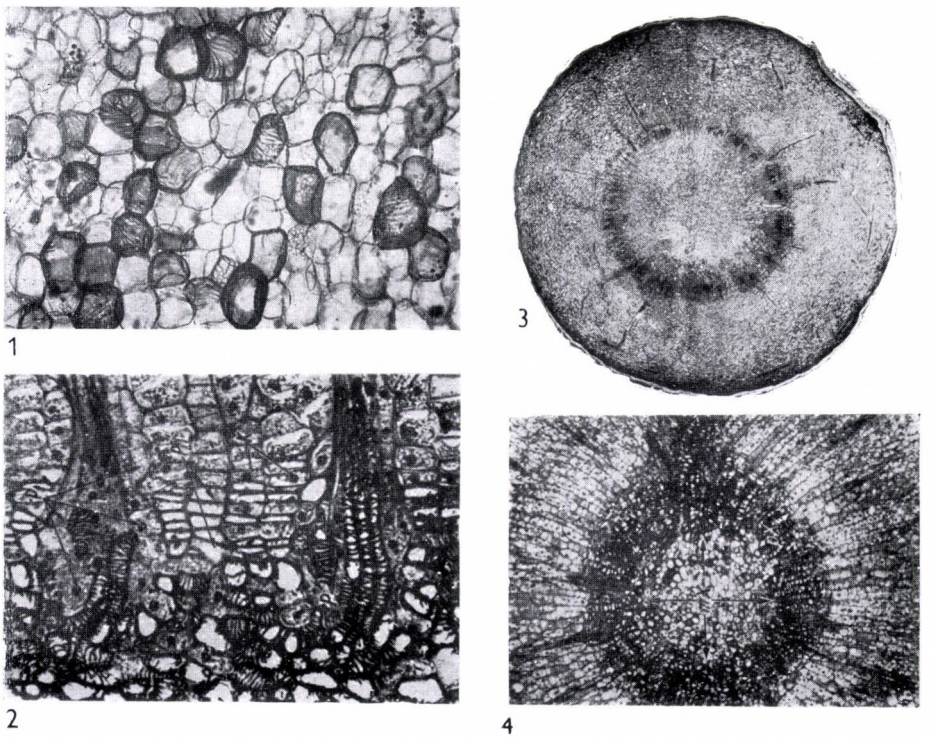


Fig. 40. Transfusion cells in the pit of (1) *Cycas neocaledonica*; scalariform thickenings of the transfusion cells in the pit of (2) *Stylites*; cross section of (3) *Zamia muricata*; cross section of the stem of (4) *Stylites*

and the pitting of the cross fields almost perfectly agree. The magnification of the photo of *Dioon spinulosum* is 150-fold (Fig. 42A, B), that of *Aneurophyton* is 160-fold (Fig. 42C), so that they agree even in the size of the elements.

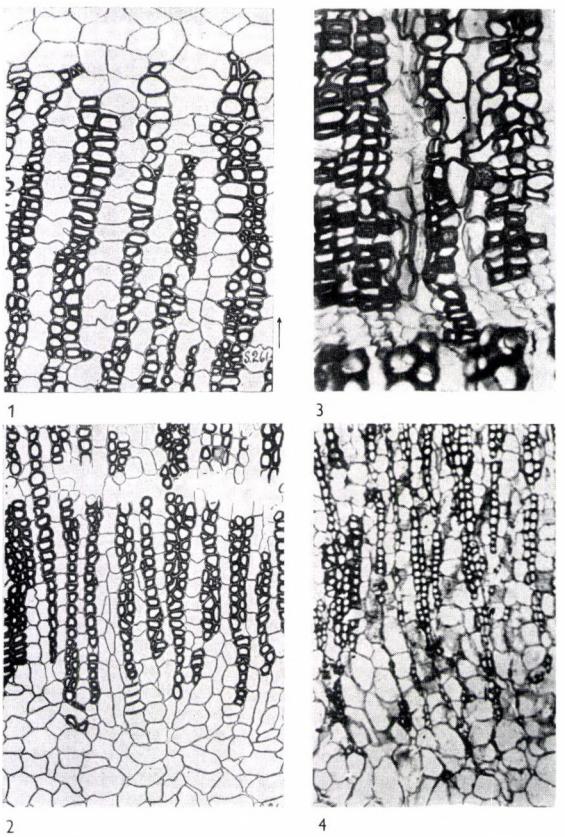
In discussing the affinity relationships of Cycads we must recall the relationship between the living Cycads and *Stylites* of the order *Isoetales*, discovered some years ago in Peru as well as the relationship between *Pleuromeia*, *Nathorstiana*. The genetic relations between *Sigillaria*, *Pleuromeia*, *Nathorstiana* and *Isoëtes* are recognized and emphasized by almost all geneticists. The question is whether or not the living Cycads are connected with these, with the *Isoëtales* in the first place.

According to the more exact anatomical and xylotomical examinations, *Isoëtes* and the closely related *Stylites* have a number of anatomical properties in common which preclude the belonging of the *Isoëtales* into the phylum *Lycopsida* and place them of necessity into the phylum *Pteropsida*. The short trunk of *Stylites* branches dichotomously, like that of Carboniferous *Sigillaria* or of some living Cycads. The ends of the adventitious roots issuing from the short trunk are also dichotomous. *Stylites* and *Isoëtes* have the same polyciliate spermatozoids as the Cycads.

Isoëtes and *Stylites* do no develop suspensors as do the forms belonging to the phylum *Lycopsida;* both develop further without suspensor, similarly to *Filicineae*, when the embryo is forming. In the short trunk of *Isoëtes hystrix* a centripetal wood develops, similarly to some Cycads. All these are phylum traits and not present by mere chance in the forms enumerated.

A further similarity between *Stylites* or *Isoëtes* and the Cycads is that all three include a rather extensive pith in the interior of the trunk and that, at the edge of the pith, transfusion cells are aligned which gradually pass into the tracheids and whose reticulate cell-wall thickenings agree with the thickenings of

Cycadeoidea (Jurassic) *Cycas circinalis* (recent)



1 3

2 4

Fig. 41. On pith border of a *Cycadeoidea* (1) phloem and tracheids (2) bundles line up in 1–2 rows to each other [× 100] (after Wieland). Arrangement and size of pith cells, primary medullary rays, as well as xylem (4) and phloem (3) bundles, in recent *Cycas circinalis* are entirely similar to the picture shown by (1) [× 100]

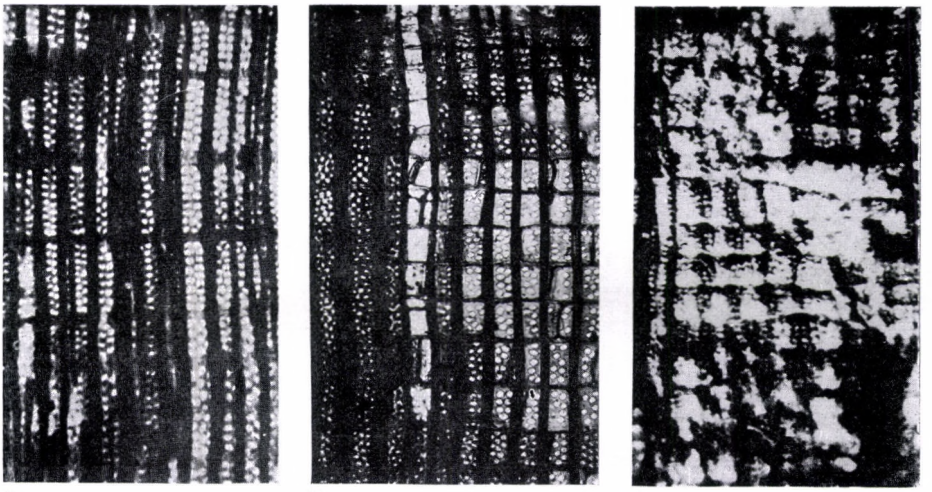


Fig. 42. Ray structure of (C) *Aneurophyton germanicum* and of (A, B) *Dioon spinulosum* (explanation on p. 134)

the similar transfusion cells of the Cycads. Transfusion cells of such structure only occur in the Cycads (e.g. in *Cycas neocaledonica*) or in *Ginkgo*.

Thus it may be established that besides the wood anatomy of the living ferns, first of all of the *Isoëtales*, as well as of the extinct *Sigillaria*, *Cycadeoidea*, *Callixylon*, *Protopitys*, *Medullosa*, etc., and of the living Cycads, there are many other morphological properties which permit to be concluded upon the close affinity of the enumerated groups.

Of the living or extinct Gymnosperms, *Dadoxylon* (*Cordaites*) is, in the first place – mainly on the basis of the araucarioid pitting of the tracheids – in some genetical relation with the Cycads (Fig. 44).

The Cycads have, in our opinion, no close genetical affinity to the strobilous conifers in the strict sense of the term. Only *Ginkgo*, *Araucaria* and *Podocarpus* might enter into consideration. In *Araucaria*, the bordered pits in the tracheid walls are perfectly similar, alveolarly close packed and aligned in 1 to 4 longitudinal rows, to those of some living Cycads, particularly the genus *Cycas*. It is certainly no mere chance that in the broad leaves of some *Araucariaceae* the ends of leaf-veins are dichotomous, as are those of some Cycads, and that recently in the pollen grains of some *Araucariaceae* similar traces of blepharoblasts, i.e. of polyciliate spermatozoids have been discovered as in the living Cycads and *Ginkgo*; this, however, is definitely a filicine feature.

Between *Ginkgo* and the Cycads too, some sort of genetical relationship may be assumed. In some tracheids of *Ginkgo* the bordered pits may form besides the uniseriate arrangement also 2 or 3 parallel rows, although these are not quite close packed and alveolar but rather loose, as in some *Encephalartos* species. If we add

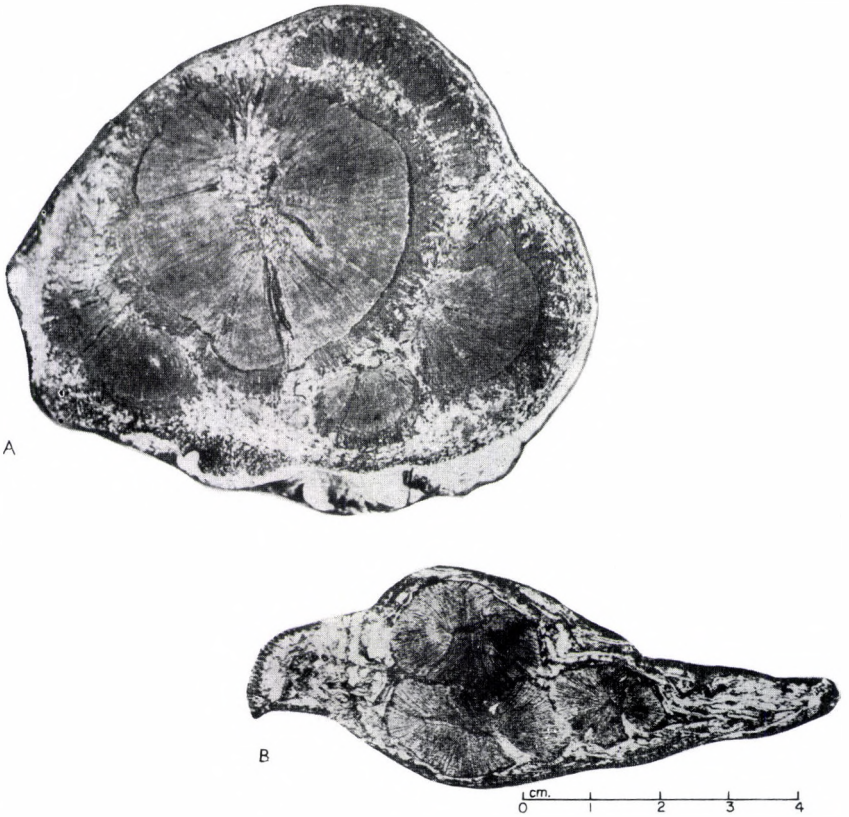
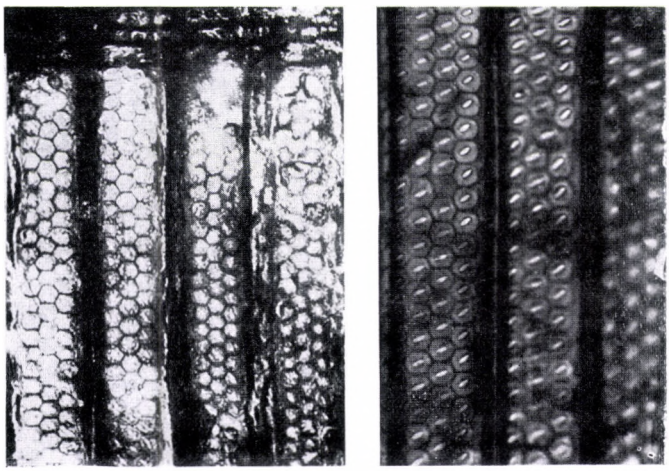


Fig. 43. The rhizome of recent (**A**) *Macrozamia miquelii* shows polystele [×3]. The arrangement and internal structure of stele is completely similar; corresponding with the stem structure of *Medullosa* (**B**). Even the cross section is similar in size (after Delevoryas)

that in the pollen grains of *Ginkgo* polyciliate spermatozoids are released on fertilization and that wood and leaves of young *Ginkgo* include similar mucilage canals, that in their dichotomous leaf blade the leaf veins exhibit a repeated dichotomous branching and that in *Ginkgo* exactly the same kind of calcium oxalate crystal druses occur as in the Cycads (while in the Conifers in the strict sense of the term, crystal druses never occur) a genetical relationship can rightly be assumed also between the Cycads on the one hand and *Ginkgo* and the *Araucariaceae* on the other.

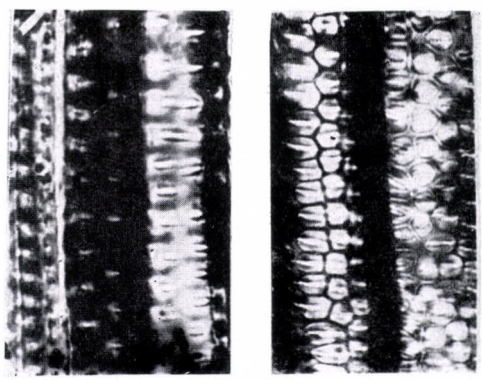


A B

Fig. 44. As to size, arrangement and aperture, the bordered pits of tracheids in (A) *Dadoxylon brandlingi* are similar to those of the tracheids in (B) *Macrozamia hopei* [×600]

Relationships between Chlamydospermae and Cycads

The living Cycads can be brought into affinity of a certain degree with some Chlamydosperms, first of all *Welwitschia* and *Bennettites*. In *Welwitschia* – although it has no developed pit system – the vessels are aligned in a definitely dichotomous pattern. In the vascular bundles, the phloem bundles corresponding to the xylem bundles are arranged in one or several rings. In the phloem bundles, the structure of the phloem fibres is similar to those of some Cycads. The similarity of the tracheids is enhanced by the fact that, in the vessels of *Welwitschia*, the bordered pits invariably form the araucarioid or Cycad pattern rather than the modern one, furthermore, the apertures of the bordered pits are horizontal as in the tracheids of many Cycads (Fig. 45). In the two foliage leaves of *Welwitschia* the leaf-veins



1 2

Fig. 45. (1) In the walls of the vessels of *Welwitschia mirabilis* the bordered pits are arranged according to the araucarioid pattern, often the apertures of two bordered pits merge in transverse direction. (2) The same phenomenon is frequent in the recent *Encephalartos* [×250]

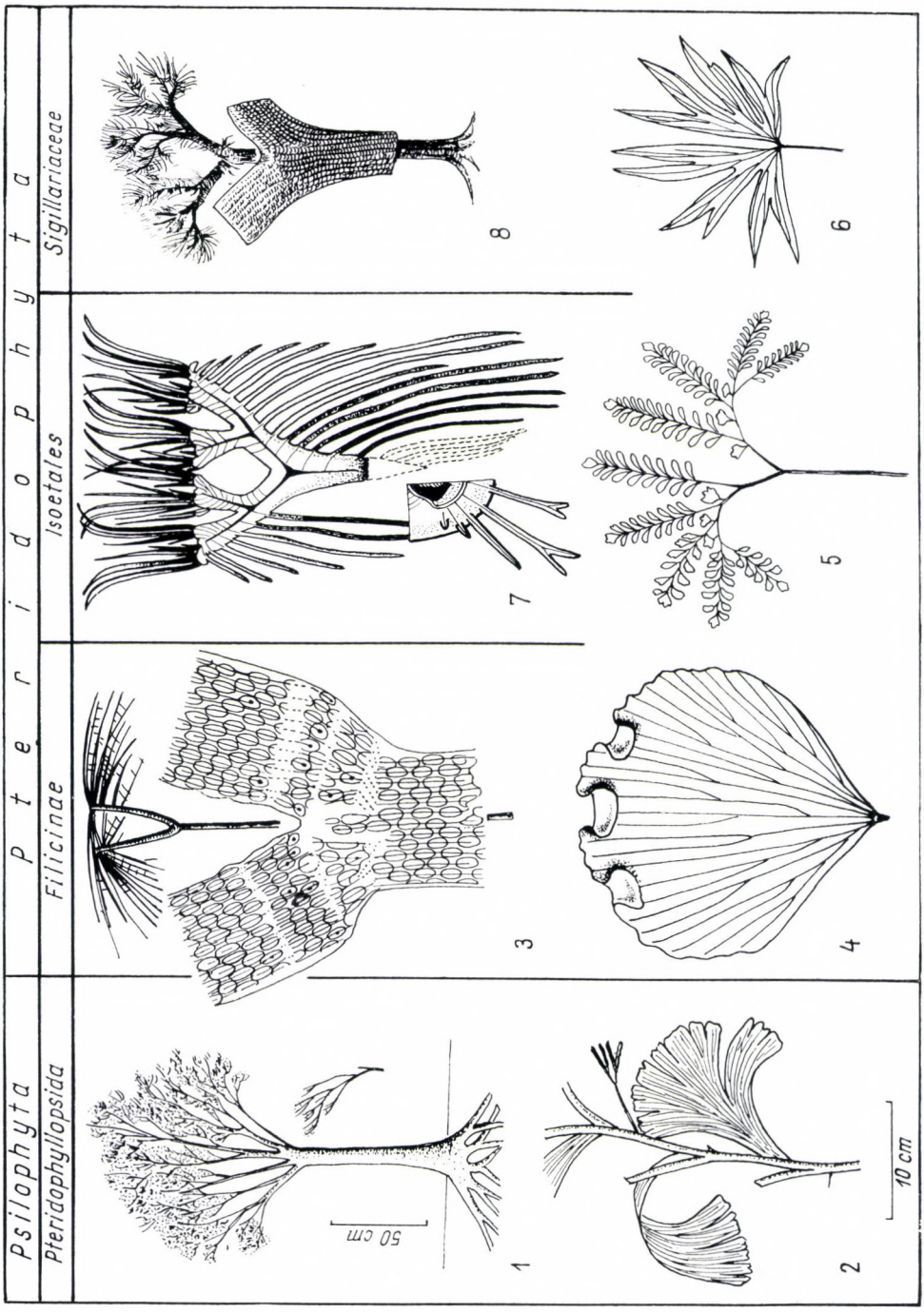


Fig. 47. Examples of dichotomous branchings.

(For caption see foot-note on p. 142)

Pteridospermae	*Gymnospermae*	*Chlamydospermae*	*Angiospermae*
Lyginapteridaceae	*Cycadales*	*Welwitschiales*	*Monocotyledones*



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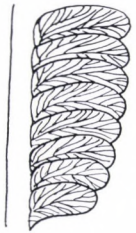

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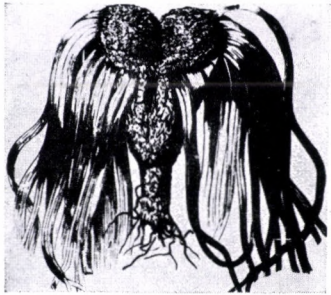

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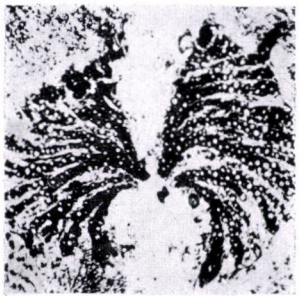

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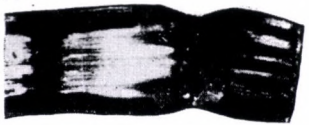

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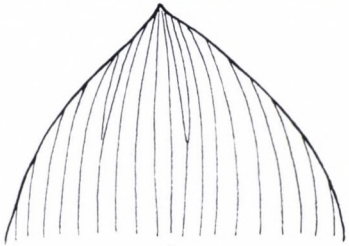

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18

are parallel which can be always traced back to dichotomous vein branching; the short trunk of the old *Welwitschia* invariably separates into two parts at the apex which can be also regarded as a somewhat recondite phenomenon of dichotomy.

Relationship between the living Angiosperms and the Cycads

Finally let us examine whether there are such related xylotomical characters in the living Cycads and the Angiosperms, which in the latter represent a heredity from the gymnospermous stage and which might suggest a relationship. Some monocotyledonous arborescent plants, e.g. *Hyphaena*, *Dracaena* or *Yucca*, always branch dichotomously, if at all, similarly to the Cycads. In the leaves of the Monocotyledons, the leaf-veins are parallel; this phenomenon can be traced back to dichotomous branching although as an abnormity also bifurcate branching occurs, etc.

The vessels are always annurarly, spilally, or scalariformly thickened (Fig. 46) but the so-called modern pitting hardly occurs. Their perforation is always scalariform; this phenomenon, as we have observed, occurs also in some Cycads. In our opinion, the Cycads show some affinity towards the Monocotyledons rather than the Dicotyledons, because in the latter the branching of the trunk (see upper row of Fig. 47) and the final branching of the leaf venation are always monopodial rather than dichotomous (see lower row of Fig. 47). There is no dichotomously branching dicotyledonous tree.

The branching of the root hairs, if any, of the Monocotyledons, is also invariably dichotomous* and never monopodial (Fig. 47). The true dichotomous branching,

* Dichotomous branchings shown in Fig. 47. 1. On the top of the short stem of the Psilophyte *Pseudosporochnus kreicii* the branches and their tips. 2. On the leaf-like branch or leaf of the Psilophyte *Enigmophyton superbum* and also on the leaf veins. 3. In Pteridophytes, on the stem of *Alsophila*. The perfect dichotomy is also verified by the arrangement of the cicatrices. 4. On the veins of the leaflet of *Adiantum capillus veneris*. 5. On the composite petioles veins in the leaflet of the fern *Adiantum pedatum*. 6. On the leaf blades and leaf veins of the petiole of the tropical fern *Dryopteris conjugata* (after Rauh). 7. On the short stem and at the root ends of the *Stylites*. 8. On the stem of *Sigillaria* of the Carboniferous. On the surface of the stem the number and direction of the cicatrices evidences perfect dichotomy. 9. On the climbing stem of the Pteridosperm *Lyginodendron oldhamium* and also on the leaf veins in the leaflets. 10. In the leaflet of the Pteridosperm *Neuropteridium imbricatum*, on the leaf veins. 11. On the stems both above and below the earth of the gymnospermous *Cycadales* (*Cycas revoluta*). 12. In *Zamia wallisii* at the initial running of the leaf veins, later parallel. 13. At the separation into two equal parts of the short stem of *Welwitschia mirabilis*. 14. In the stem of *Welwitschia mirabilis* where the xylem bundles are arranged, not only in their mass but also in their details. 15. In the leaves of *Welwitschia mirabilis* where the leaf veins are parallel. 16. On the stem of the monocotyledonous *Yucca arborescens*. (The same phenomenon occurs among the monocotyledonous *Palmae* and *Dracaena*.) 17. Sometimes on the veins at the ends of the leaf veins; (e.g. in *Funkia cordata*) the leaf veins of the Monocotyledons are generally parallel. 18. At the root hairs of the Monocotyledons (*Triticum vulgare*). Thus dichotomy as a phylum trait always existed from the simplest cauline plants, the Psilophyte, to the angiospermous Monocotyledons and as phylum trait remained also in the most developed phanerogamous plants.

however, is characteristic not only of *Filicinae* and *Pteridospermae* but also of the Cycads. It seems that this ancestral mode of branching (*Vaucheria dichotoma* is only one cell and even this branches dichotomously) of *Spermatophytes* appears even in the most evolved, always in the youngest organs and in the most distal branchings of these, that is, in the ultimate branchings of the root hairs and of the leaf veins, respectively.

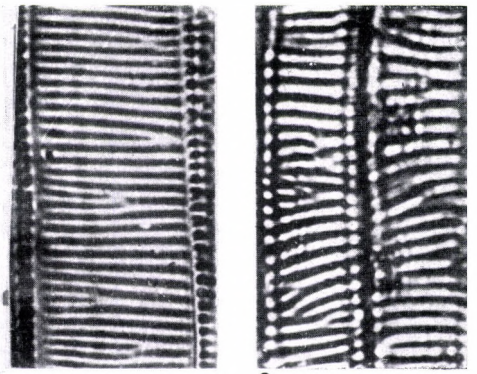

Fig. 46. (1) The walls of the vessels of Palms show scalariform thickening, the scales are furcately branched, e.g. in *Sigillaria*. (2) The pitting in the living *Microcycas* is also similar [×250]

Summarizing the above statements we may say that, on the basis of their anatomical and mainly xylotomical properties, the living Cycads are probably related among the Psilophytes of simpler structure first of all to *Asteroxylon*, *Protopteridium*, among the Pteridophytes to the *Eufilicinae* and particularly to the heterosporous *Isoëtes* and *Stylites*, among the Carboniferous plants to *Sigillaria*, *Pleuromeia*, *Nathorstiana*, among the Pteridosperms to *Medullosa*, *Lyginodendron*, the *Cycadeoideae*, *Williamsonia*, among the Gymnosperms to *Callixylon*, *Actinopodia*, *Völkeliella*, further to *Cordaites*, *Ginkgo* and to a certain degree to the *Araucariaceae*, *Podocarpus*; among the more developed Chlamydosperms, to *Welwitschia*, *Bennettites* and among the most developed Angiosperms to the *Monocotyledones* and by no means to the *Dicotyledones*. Author expounded this view for the first time as early as in 1918, and for the second time in 1964.

LITERATURE ON THE XYLOTOMY OF THE CYCADS

The detailed xylotomy of the Cycads has so far been dealt with by rather few authors. Although short descriptions of some species are available, there is no detailed comprehensive anatomical monograph.

Investigations into the xylotomy of the *Cycadaceae* were started about 130 years ago. Brongniart (1829) examined the anatomy of some Cycads with the methods of those times. Besides establishing some interesting facts, he asserted also some erroneous opinions. He did not, e.g. recognize the phloem beside the xylem and stated that in the stem of *Cycas revoluta* there is only a xylem. Disregarding these errors, notwithstanding, he was the first to recognize the gymnospermous features of the Cycad stem and to refute the old conception that the xylem of the Cycads is similar to that of the Monocotyledons.

In his paper, Hugo von Mohl (1832) already gave a rather rich collection of anatomical detail of two *Zamia* species (*Z. latifolia* and *Z. horrida*) establishing the presence of reticular bundles meandering in the pith of *Z. latifolia*, as well as bordered pits and scalariform thickening in the xylem elements, and stating that some of these pith bundles pass in the pith rays toward the cortex. He further established that beside the normal vascular bundle ring there are other bundle rings. It turned out, however, that the *Zamia horrida* examined by him was in fact an *Encephalartos horridus* which, as a matter of fact, tends to have abnormal rings, whereas in *Zamia* there occur no such rings.

Miquel (1842) established the parenchymatic nature of the pith and the pitting of the xylem elements, i.e. also of the tracheids.

Mettenius (1861) dealt with four species only: *Encephalartos horridus*, *Dioon edule*, *Zamia muricata* and *Cycas revoluta*.

Constantin and Morrot (1885) examined *Cycas siamensis*, particularly the structure of the pericycle, and stated that the site of the development of the abnormal rings should be looked for in the tissues of the cortex.

Solms-Laubach (1890) dealt in detail with the trajectories of the bundles and found that these, before getting attached to the xylem ring, severally cross each other in the pith. He did not observe any secondary thickening in the stem, and rightly so, because *Stangeria paradoxa* does not develop secondary vascular bundle rings.

Strasburger gave precise data on the conductive bundles of the genus *Cycas*, without extending his investigations to the other genera.

The xylotomy of the Cycads owes much to W.C. Worsdell (1898), who discussed rather fully the anatomy of several *Cycas* species, including young and older seedlings of *C. revoluta* and the stem of *C. media*. He found that, in a stem of 14 inch (35 cm) diameter, there were 12 vascular bundle rings, whose anatomy he described in some detail, illustrating his findings with excellent drawings. In the same paper, Worsdell described also the anatomy of the young seedling of *Macrozamia spiralis* and of the aged stem of *Stangeria paradoxa*. He gave a rather instructive drawing of the transfusion cells; in another paper, he discussed the presence and structure of transfusion cells in the rachis of *Cycas*.

Worsdell's (1896) study in which he examines a stem of 35 cm diameter of *Macrozamia frazeri* deserves special attention. It is an attempt to build upon the examination of this single specimen a general anatomical characterization of the stem of the Cycads, including the detailed discussion of pith, conductive bundles and cortex and a summary of the most typical traits of the Cycads. His observations are for the most part valid up to this day.

G. R. Wieland (1906) dealt in full detail with the xylotomy of living Cycads; his findings are still valued today. They were adopted by Lotsy (1909).

A useful compendium of knowledge on the anatomy of Cycads is the work of Pilger (1926).

An up-to-date review is J. Schuster's (1932) contribution to the series "Das Pflanzenreich" containing a copious list of references on morphology, anatomy

and physiology of the Cycads, on the structure of the flower, pollination, geographical distribution and paleontological aspects. So far there is no more comprehensive and useful work on the Cycads. Its morphological part, compiled from literature, is for the most part acceptable even today although the work has lately been sharply criticized by Johnson (1959) particularly from the viewpoint of nomenclature.

Johnson's above work is about the taxonomy and geographical distribution of the Australian Cycads and of the *Zamiaceae* in particular. It contains a map on the distribution of the Australian species and the results of recent examinations (e.g. on chromosome number). Unfortunately, anatomy is not even touched upon, although there were earlier studies concerning the anatomy of some Australian species (*Bowenia*, *Macrozamia*).

The same applies to R. Melville's paper (1957) which discusses the external morphology and geographical distribution of the 9 species occurring in Central Africa without any reference to histological structure.

Besides the anatomy of the living Cycads, a number of paleontological finds have lately been described in comprehensive monographs and in papers of various scope.

An outstanding work is G. R. Wieland's (1906) already mentioned above, in which the anatomy of the American finds is described and illustrated on 296 pages and 50 Plates. The cross and longitudinal sections of some of these fossils are strikingly similar to the stem structure of some Cycads to be discussed in this volume.

Arnold's paper (1953) established on the basis of the structure of the leaves and of some anatomical properties relationships between Paleozoic, Mesozoic and living Cycads.

In 1958, Greguss called attention to some xylotomical features common to the above three genera.

In 1961, Greguss described the xylotomy of *Microcycas calocoma* and *Lepidozamia hopei*, discussing the epidermal structure of their leaves.

Alfred Byrd Graf (1963) published a work with many beautiful habitat photographs of the Cycad genera.

R. A. Dyer (1965a) has published two important papers. In the first one he published two new and some *Encephalartos* species of South Africa.

His second work (Dyer 1965b) is more important. In it he gives a short review and a key of 26 living *Encephalartos* species of South Africa. He published also habitat pictures of these species, most of them in natural milieu. For the *Encephalartos* species this is a fundamental work.

Greguss (1964a, b) investigated the relationships of Cycads, based on their xylotomy, branching of stems and epidermology.

PART TWO

LEAF MORPHOLOGY OF THE CYCADS

Among the remains of fossil Cycads, especially of those that lived in the Mesozoic, leaves or leaf fragments are fairly frequent. Their determination, often difficult, is sometimes facilitated by their resemblance or identity to the leaves or leaflets of the living forms. The shape and size of the leaflets and the structure of their venation permit to conclude on possible relationships between Cycads living and extinct. In order to promote such comparatory work, the author has figured in the present volume the leaflets of 77 species of living Cycads, natural size. The drawings of course represent mean values only, because in the compound leaves of the Cycads the size, shape and indentation of the leaflets depend also on whether the leaflet is from the base, middle or end of the compound leaf; the venation pattern is, however, constant and typical. As a further help to visualization, the author has added also habit pictures, as far as such were available of the species discussed.

The drawings of the 77 Cycad leaflets are supplemented with a brief description of the leaf, to present a true image of the external morphology of the leaves and leaflets of the various Cycads. Paleontologists involved in the determination of Cycads leaves might also find these illustrations and descriptions useful. In establishing the diagnoses, Schuster's (1932) monograph on the *Cycadaceae* was of great help. Besides the external morphology of the leaves, the leaf epidermis, to be dealt with in the following, also possesses a substantial diagnostic value.

KEY TO THE GENERA OF CYCADACEAE ACCORDING TO THE EXTERNAL MORPHOLOGY OF THE LEAFLETS

(1) A single strong midrib in median of leaflet:
  (a) Blades linear, greatly tapering, entire . . . . . *Cycas*
  (b) Blades broad, serrate; secondary veins remarkably and severally bifurcate . . . . . *Stangeria*

(2) No midrib:
  (a) Blades thin, paper-like, 20 to 50 mm wide; apex tapering, sometimes dichotomous or lobate, margin entire (*B. spectabilis*) or serrate (*B. serrulata*); secondary veins bifurcate *Bowenia*
  (b) Blades thin, paper-like, at most 6 times as long as wide, elliptic, finely dentate near obtuse apex . . . . . *Zamia*

(c) Blades thicker, leathery:

(i) Blades oblong or broad, spinose on one margin or both, and on apex . . . . . *Encephalartos*

(ii) Blades long, linear, margin entire, with tiny spines on the margins or on the apex in some species; length of leaflet 8 to 40 cm; width 0·5 to 3·5 cm:

(*) Blades 8 to 23 cm long, 5 to 7 mm wide, margins entire, bases abruptly narrowing and thickening *Microcycas*

(**) Blades broad, decurrent, entire, bases widened; in one species (*D. spinulosum*), the margins bear tiny spines; blades 7 to 20 cm long, 7 to 20 mm wide *Dioon*

(iii) Blades 8 to 40 cm long, 0·5 to 3 cm wide; margins entire, at most some tiny spines at the apex in some species:

(*) Blade length 20 to 40 cm, width 1·8 to 3 cm . . . *Ceratozamia*

(**) Blade length 20 to 35 cm, width 5 to 12 mm . . *Lepidozamia*, *Macrozamia*

BRIEF DESCRIPTION OF THE LEAVES

(1) *Bowenia serrulata* (W. Bull) Chamberlain (Plate XCV, Drawing 1)
Folioles scattered, gradually widening from a narrow base; margin above the first quarter spinosely dentate; end of foliole gradually tapering and ending in several teeth. Veins parallel or severally bifurcating branching.

(2) *Bowenia spectabilis* Hook (Plate XCV, Drawing 2)
The rachis bears 6 to 20 pairs of folioles, oval or lanceolate; blade locally lobate or two-tipped, margin entire; blade decurrent, strongly narrowing at base. The length of the folioles is 6·5 to 16 cm, their width 16 to 50 mm; the number of veins, parallel or furcate, standing out on the undersurface, varies from 25 to 40.

(3) *Ceratozamia kuesteriana* Regel (Plate XCVII, Drawing 16)
The folioles are densely arranged, mostly of equal length, somewhat shorter, near the base of the rachis. Blades long narrow lanceolate, gently tapering above the base and at the end, somewhat falcate; margin entire, length 12 to 32 cm, width 8 to 13 mm, at the base 3 to 6 mm. Standing out on the undersurface, the veins number 6 to 12. The foliole is leathery.

(4) *Ceratozamia mexicana* Brongn. (Plate XCVII, Drawing 17)
The folioles are opposed or alternating, straight or mildly falcate, of various length, narrowly or broadly lanceolate or cuneiform from the base upward, entire. 3 to 11 mm wide at the base, they are on both sides of a lively, pale green or dark green colour, lighter on the undersurface; leaf scars 14 to 34 mm long,

1·8 to 7 cm wide; the veins standing out on both sides number 17 to 40. The younger folioles are short and wide.

(5) *Ceratozamia robusta* Miq. (Plate XCVIII, Drawing 30)
Folioles narrow, lanceolate, with unequal sides, gently tapering to acute tips 22 to 39 cm long, 1·8 to 3 cm wide; base 8 to 9 mm wide; the veins number 22 to 35; on the undersurface the ribs frequently exhibit dichotomous branching.

(6) *Cycas celebica* Miq. (Plate XCVI, Drawing 13)
Bases of the folioles tapering, decurrent. The narrow portion is 3·5 to 4 mm; blade width 11 mm, length 15 to 25 cm. Tip acute, tapering. In the mid-portion of the blade, the midrib stands out wedge-like on the upper surface.

(7) *Cycas circinalis* L. (Plate XCVI, Drawing 9)
On both sides of the rachis, 80 to 100 folioles are arranged alternately, rigidly and broadly fanning out at its distal end. Blades narrow lanceolate, margins parallel or somewhat broadening; slightly reclinate, not or hardly spinose, sometimes markedly tapering particularly at the base, more or less decurrent, 15 to 35 cm long, 5 to 18 mm wide; the proximal leaflets suddenly turn into bristles; in the mid-portion of the blade, the midrib stands out rather strongly, on the undersurface somewhat more than on the upper one.

(8) *Cycas media* R. Br. (Plate XCVI, Drawing 15a)
The folioles are linear, gently tapering at their base and tip, somewhat decurrent at the base. The midrib is marked on the upper surface, hardly noticeable on the undersurface. Blade length 10 to 16 cm, width 7 to 8 mm.

(9) *Cycas neocaledonica* Linden (Plate XCVI, Drawing 15b)
Folioles decurrent, 16 to 18 cm long, 4 to 5 mm wide and ending in a gradually tapering bristle; in the mid-portion of the undersurface a strong midrib stands out conspicuously; it passes into a gentle furrow in the distal portion. The secondary veins do not emerge either on the upper surface or on the undersurface.

(10) *Cycas revoluta* Thunb. (Plate XCVI, Drawing 7)
The folioles issue from a groove running along the rachis; their number on the large leaves may attain 125 in large fronds; they stand densely, the proximal ones short and opposed, the middle ones much longer and alternating, decurrent, straight, gently tapering both at the base and at the apex; margins recurved and thickened; midrib not particularly bulging; the undersurface paler than the upper one, the latter a shining, almost vernal, agreeable green.

(11) *Cycas rumphii* Miq. (Plate XCVI, Drawing 11)
The number of leaflets is 50 to 100 on both sides; blades somewhat acute, lanceolate, gradually tapering both at apex and base, somewhat decurrent, 20 to 30 cm long, 11 to 20 mm wide, slightly falcate; margins somewhat recurved.

(12) *Cycas seemannii* A. Braun (Plate XCVI, Drawing 10)
Folioles gently tapering; the undersurface paler than the upper one; both sides smooth; the uppermost and lowest blades are shorter than the middle ones; margins recurved or slightly undulating; blades green or bluish green, 5 to 28 cm long, 4 to 18 mm wide.

(13) *Cycas siamensis* Miq. (Plate XCVI, Drawing 14)
The number of the folioles is on both sides 40 to 100 or more, blades shorter near the base and tip of the rachis, all decurrent, gently tapering lanceolate; tips of the proximal folioles abruptly tapering into bristles; margins recurved, upper surface shining, almost greenish blue, undersurface paler; midrib furrowed on the upper, standing out on the undersurface; blades 4 to 20 cm long, 5 to 7 mm wide.

(14) *Cycas taiwaniana* Carruthers (Plate XCVI, Drawing 8)
The folioles are linear for some length, their lower end slightly tapering at the base, their tip ending in a pointed bristle. Length 14 to 20 cm, width 7 to 8 mm; in the mid-portion, the main rib stands out markedly on the upper surface less so on the undersurface.

(15) *Cycas thouarsii* R. Brown (Plate XCVI, Drawing 12)
The bases of the folioles are pinnately decurrent, opposed or alternating; their length is 16 to 22 cm, their width 9 to 11 mm. In the mid-portion, the midrib stands out markedly on the upper surface less so on the undersurface. The margins of the light green blades are perfectly entire and slightly recurved.

(16) *Dioon edule* Lindl. (Plate XCV, Drawing 6)
Folioles moderately lanceolate, at their tips almost spinose, tapering, 7 to 17 mm wide at their base, 6 to 17 veins are sunk in on the upper surface, standing out on the undersurface ribbed, with recurved margins; some bear 1 or 2 teeth with bristles near the apex, foliage very stiff, dense, locally more sparse; blades frequently a dewy blue on both sides. The folioles number 100 or more; they are 11 to 15·5 cm long, 4 to 8·5 mm wide. The distal leaves are short, the proximal ones even shorter, the last ones quite bristly. The young folioles are 2·8 to 4 cm long, 3 to 4·5 mm wide, with 6 to 7 veins, bearing 1 to 3 small spinose teeth at the apex and 1 or 2 on the margin.

(17) *Dioon pectinatum* H. Wendl (Plate XCV, Drawing 5)
The folioles are linear for some length, somewhat falcate, 20 to 25 cm long, 14 to 16 mm wide, gradually tapering upward of the lower third; base somewhat tapering before the articulation; 10 to 15 mm wide on contact with the rachis. Margin entire, recurved, the secondary veins number 12 to 14; veins marked on the undersurface parallel with frequent dichotomous branching.

(18) *Dioon spinulosum* Dyer (Plate XCV, Drawing 6a)
Folioles 8·5 to 20 cm long, 10 to 17 mm wide, lanceolate for some length, tip

acute, base tapering; with 5 to 9 little teeth bearing bristles 3 to 4 mm long, rigidly protruding; margin entire near the base; base on contact with rachis 11 to 22 mm wide; there are 11 to 24 veins, standing out on the undersurface and furrowed on the upper surface; blades rigid, flat, shiny green above, paler below. The proximal folioles are reduced to teeth; the distal leaves are also shorter. The number of folioles on the young plant is 11 to 22 on both sides.

(19) *Encephalartos altensteinii* Lehm. (Plate C, Drawing 40)
Folioles long, lanceolate, bases acute, tips tapering into a spine; blades asymmetric with 1 or 2 bristles on the proximal, 3 to 5 ones on the distal margin. The proximal folioles are short, 5 to 8, the median ones 15 to 20 cm long and 25 to 27 mm wide. The veins number 25 to 40; on the undersurface the ribs stand out about 1 mm apart, dichotomy is frequent.

(20) *Encephalartos arenarius* R. A. Dyer (Plate C, Drawing 37)
Folioles comparatively distant and alternating. The length of the proximal ones is 3 to 4 cm; their width is 10 to 15 mm. The median folioles are 12 to 15 cm long, 30 to 35 mm wide and asymmetric, the distal margins frequently entire or bearing only 1 or 2 small bristles; the proximal margin bearing 4 to 5 large, strong thorns; the base of these sometimes attains 10 to 12 mm, their length may be 20 mm. The number of the veins is 15 to 40, they run generally 1 mm apart, dichotomizing; standing out on the undersurface, but not on the upper surface. Base gradually tapering, 7 to 8 mm wide, diameter of leaf scar 10 mm.

(21) *Encephalartos barteri* Carruthers (Plate CI, Drawing 49)
Number of folioles 45 to 80 on both sides; blades alternate or opposite, straight or mildly falcate-lanceolate, base and apex tapering, apex ending in bristle; there are 3 to 6 bristles on some margins, while others are entire. Leaflets 7 to 15 cm long, 7 to 20 mm wide; number of veins 11 to 26, slightly standing out on the undersurface, lower folioles reclinate, those of the proximal third reduced to narrow bristles.

(22) *Encephalartos bubalinus* Melville (Plate CI, Drawing 53)
The median folioles are 8 to 10 cm long and 15 to 20 mm wide, elongate, lanceolate, sometimes slightly falcate; base narrowing (6 to 8 mm), apex gradually tapering from the middle. Distal margin entire, or very rarely slightly dentate; the proximal lower margin bears 5 to 6 projecting bristles. The veins, 15 to 30 in number, are barely 0·5 mm apart, frequently dichotomizing. The margin of the foliole is recurved.

(23) *Encephalartos caffer* Miq. (Plate XCVIII, Drawing 28)
The folioles stand quite close, 33 to 56 on the common rachis, blades straight, rigid, asymmetric, short or long, lanceolate, base and apex narrowing, apex ending in a shorter or longer bristle, folioles 5 to 15 cm long, 5 to 12 mm wide,

margins entire or bearing 1 or 2 tiny teeth. Upper surface sometimes tomentose. The number of veins is 9 to 20; the upper surface is furrowed, the undersurface is ribbed; the proximal leaves are somewhat shorter.

(24) *Encephalartos cycadifolius* Lehm. (Plate XCVIII, Drawing 31)
The proximal folioles are almost opposed and somewhat sparse, the others alternating, denser, erect, lanceolate, bristly; base somewhat narrower, apex acute, ending in a short point; 3 to 10 veins, standing out on the undersurface, covered with green hairs; the older leaves are glabrous; margins recurved, entire, blades of a greenish blue colour.

(25) *Encephalartos eximius* Verdoorn (Plate C, Drawing 46)
Folioles alternating; their length is 15 to 45 mm on young plants, their width 2 to 2·5 mm. The number of veins is 4 to 6. The folioles are of uniform width, with almost parallel sides tapering gradually to a short bristle; margin recurved, base somewhat narrowing.

(26) *Encephalartos ferox* Bertol (Plate XCIX, Drawing 36)
Folioles alternating or opposed, base acute, length of contact with rachis 6 to 8 mm, width 1 to 2 mm; blade length 3 to 10 cm, width 15 to 40 mm. Shape highly varied, asymmetrical, as a rule. Margins strongly dentate, recurved, bearing hard bristles, some of them 6 to 8 mm long. The number of veins is 15 to 45; on the undersurface, the ribs stand out and frequently dichotomize. The upper surface is shiny, the undersurface somewhat paler.

(27) *Encephalartos friderici-guilielmi* Lehm. (Plate CIV, Drawing 72)
Leaves fairly stiff, straight or curved, often spreading lower than crown when stem has cones, 1 to 1·2 m long; the leaflets somewhat bluish or silvery when young, and yellowish with age, closely spaced and overlapping in the upper half of the leaf and reduced in size towards apex and base; median leaflets 10 to 17 cm long, about 7 mm wide, with 7 to 9 prominent veins on undersurface.

(28) *Encephalartos gratus* Prain (Plate CI, Drawing 52) (from young plant)
The rachis bears 30 to 70 pairs of oblong oval lanceolate rigid folioles, which are sometimes falcately arched, 1·7 to 2·5 cm long, 2 to 3 cm wide; base strongly narrowing, apex tapering into a bristle, margins strongly indented; the number of the leaf-veins is 22 to 30; the upper surface is furrowed, the undersurface ribbed; some veins dichotomize.

(29) *Encephalartos hildebrandtii* A. Braun et Bouche (Plate CI, Drawing 54)
The number of folioles is 36 to 70 on both sides, increasing in size from the base to the mid-portion of the frond; blades asymmetric, lanceolate, 7 to 26 cm long, 1·4 to 2·2 cm wide, pointed, with margins bearing 1 to 4 straight, projecting bristles on both sides, with 2 or 3 teeth on the apex. The number of the veins is

15 to 22, they are mildly prominent below; the proximal folioles are shorter, spinose, the ones nearest the rachis are broad with 2 or 3 split apices. The folioles in the mid-portion are largest and widest.

(30) *Encephalartos horridus* (Jacq.) Lehm. (Plate C, Drawing 38)
The folioles are opposed or alternating; their shape is varied. The blade is divided into broad-based teeth. The divisions are as a rule bifurcate, the lobes tapering into hard bristles. Their size is varied, 6 to 16 cm in length, 3 to 4 cm in width; base width is 6 to 8 mm. The veins stand out on the undersurface and frequently bifurcate.

(31) *Encephalartos humilis* Verdoorn (Plate C, Drawing 43)
Folioles narrow, linear, slightly falcate; length 6 to 9 cm, width 4 to 5 mm; the veins number 8 to 10 and stand out on the undersurface.

(32) *Encephalartos inopinus* Dyer (Plate C, Drawing 45)
The folioles are alternating or opposed; their length is 12 to 18 cm, their width 8 to 10 mm; a narrow section precedes a broad base. The veins number 10 to 15 and stand out on the undersurface.

(33) *Encephalartos latifrons* Lehm. (Plate CI, Drawing 51)
The folioles are broad, 6 to 15 cm long, 6 to 7 cm wide, with wide lobes which end in rigid bristles; base acute. The veins number 40 to 60, standing out on the undersurface of the leaf and frequently dichotomizing at the base.

(34) *Encephalartos laurentianus* De Wilden (Plate XCIX, Drawing 32)
Folioles 20 to 45 cm long, 25 to 45 mm wide, elongate, lanceolate and slightly falcate, base acute, tip gradually tapering. Both margins bear 4 to 8 cm apart bristles, 4 to 5 mm long, narrow, hardly projecting thorns. The veins number 30 to 45 and stand out both on the upper and undersurface, dichotomizing particularly near the leaf base.

(35) *Encephalartos lebomboensis* Verdoorn (Plate CI, Drawing 48)
Folioles spaced on the rachis 2 to 8 cm apart, scattered and alternating; size varied, proximal blades scarcely 2 cm long, narrow, spinose; the median ones are longest (10 to 14 cm); the distal ones are 4 to 5 cm long and 8 to 18 mm wide. The margin is generally entire near the tip, but sometimes it bears 3 or 4 projecting teeth; nearer to the base, margin bears about the same number of projecting bristles. Base gradually narrowing (2 to 3 mm), 5 to 7 mm wide at contact with rachis, tip gradually tapering, ending in a bristle. The number of veins is 14 to 20; forming pronounced ribs on the undersurface, they mostly dichotomize near the base.

(36) *Encephalartos lehmannii* Ecklon (Plate CI, Drawing 50)
Folioles opposed or alternating; spaced 15 to 20 mm apart, they are 6 to 20 cm long, lanceolate, 10 to 15 mm wide; base somewhat acute, 6 to 8 mm wide on

contact with rachis, tip gradually tapering and ending in a bristle 6 to 8 mm long. The number of veins is 15 to 25; margin recurved and entire, tiny bristles on the margins being very rare.

(37) *Encephalartos longifolius* (Jacq.) Lehm. (Plate XCIX, Drawing 34)
Folioles 15 to 25 cm long, 2·5 to 3 cm wide, base tapering, 8 to 9 mm wide on contact with the rachis; blade of elongate oval shape, tip gradually tapering; the margin bears sparse spines; the veins number 20 to 40, standing out on the undersurface; on the upper surface, ribs and furrows are seen only near the leaf base. The veins are frequently dichotomous.

(38) *Encephalartos manikensis* Gilligand (Plate CIV, Drawing 73)
Leaflets 10 to 15 cm long, 2 to 4 cm wide, length narrow, on the other margin on the basis occasionally three thorns about 1 cm wide and long.

(39) *Encephalartos natalensis* Dyer et Verdoorn (Plate C, Drawing 39)
The length of the folioles is 20 to 35 cm, their width 25 to 40 mm; both margins are recurved and bear sparse projecting long bristles, the veins 35 to 45 in number, run about 1 mm apart, dichotomizing frequently enough. The ribs stand out on the undersurface, less so on the upper surface. The leaflets are shiny; the undersurfaces are paler.

(40) *Encephalartos poggei* Aschers (Plate C, Drawing 44)
Folioles 6 to 10 cm long, 7 to 13 mm wide, lanceolate, mildly arched, tips ending in a short bristle, base slightly tapering, 7 mm wide on contact with rachis, the margins bear 1 to 3 tiny teeth; the veins number 12 to 20, recessed on the upper surface standing out on the undersurface; the colour is a brownish green, paler on the undersurface.

(41) *Encephalartos princeps* R.A. Dyer (Plate CIV, Drawing 74)
Leaves 1 to 1·3 m long, fairly straight or recurved in the top third with often bluish or silvery bloom lasting for considerable period and pilose in early stage, leaflets reduced in size towards base, possibly to one prickle, mainly overlapping in the top third in V disposition; median leaflets about 15 cm long and 1·3 cm broad, pungent, entire or occasionally toothed on lower margin.

(42) *Encephalartos septentrionalis* Schweinf. (Plate CI, Drawing 55)
The folioles stand either densely or some distance apart, alternating or almost opposed; blades asymmetrical, lanceolate, with projecting teeth on the sides; tips gradually tapering into a bristle, sometimes bifurcate or trifurcate; base 6 to 9 mm wide; there are 10 to 30 veins, frequently dichotomous, forming conspicuous ribs on the undersurface.

(43) *Encephalartos tegulanus* Melville (Plate XCIX, Drawing 35)
Folioles 20 to 35 cm long, 20 to 40 cm wide, elongate, oval-lanceolate; base gradually narrowing, wide, preceded by 10 to 12 mm contact with rachis, a

narrower section of 6 to 7 mm width. Both margins bear a few projecting bristles of 5 to 8 mm length. There are 20 to 50 veins, unevenly spaced (1 to 1·2 mm), often dichotomous near the base, standing out markedly on the undersurface, not so much on the upper surface. The folioles are rigid, leathery, with recurved margins.

(44) *Encephalartos transvenosus* Stapf et Burtt Davy (Plate C, Drawing 42)
Folioles 8 to 15 cm long, 20 to 30 mm wide, of elongate oval shape, gradually tapering to 8 to 9 mm at the base bearing on their proximal half some bristles 5 to 6 mm long, jutting out at angles of about 40°; margins recurved. The veins frequently dichotomous, number 35 to 40, standing out slightly on the undersurface and even less on the upper one. Upper surface shiny, undersurface somewhat paler.

(45) *Encephalartos trispinosus* (Hook) R.A. Dyer (Plate CIV, Drawing 75a,b)
Leaves 0·7 to 1·25 m long, spreading-recurved and often twisted towards apex with a bluish bloom when young and without hairs; leaflets reduced in size and simple towards base, occasionally overlapping in the upper half; median leaflets often slightly curved to one side, 10 to 18 cm long, 1·5 to 2·5 cm broad, pungent, with 1 or 2 pungent, sometimes twisted lobes 1 to 3 cm long from the lower margin.

(46) *Encephalartos umbeluziensis* R.A. Dyer (Plate CI, Drawing 47)
Folioles 4 to 18 cm long, 8 to 12 mm wide, gladiate, somewhat falcate, base gradually or suddenly narrowing, tip gradually tapering; only toward the tip are there 1 or 2 rigid, short bristles; the tip always ends in 2 or 3 bristles, which are as a rule restricted to the proximal margin of the foliole.

(47) *Encephalartos villosus* (Gaertn.) Lemaire (Plate C, Drawing 41)
On both sides of the rachis there are 60 to 90 folioles, alternating or opposed, lanceolate, slightly falcate, narrowing at the base; tip pointed; both margins bear 4 to 9 teeth, somewhat wider spaced near the apex; blade 14 to 20 cm long, 10 to 20 mm wide; greatest width is at the lower third. The veins, numbering 20 to 25, stand out rib-like on the undersurface and often dichotomize.

(48) *Encephalartos woodii* Prain (Plate XCIX, Drawing 33)
The folioles are close spaced, opposed on the proximal, almost alternating on the distal end of the rachis; blades asymmetric, substantially widening in lower third; tip cuneiform, ending in a bristle. Base acute; margins sparsely dentate, teeth ending in bristles. Folioles 14 to 16 cm long, 3·5 to 7 cm wide; there are 25 to 50 veins, standing out somewhat on both sides. The distal folioles are much smaller than the median ones.

(49) *Lepidozamia hopei* Regel (Plate XCVII, Drawing 19)
Folioles are long, shiny, linear, somewhat falcate, 20 to 30 cm long, 12 to 23 mm wide, tip tapering; there are 10 to 18 veins, somewhat standing out on the undersurface, often bifurcate at the leaf base.

(50) *Lepidozamia peroffskyana* Regel (Plate XCVII, Drawing 18)
Folioles 12 to 32 cm long, 5 to 12 mm wide, lanceolate, tip very gently tapering; the number of veins is 7 to 15; they stand out on the undersurface; base wide but not thick, somewhat narrowing.

(51) *Macrozamia communis* L. Johnson (Plate XCVIII, Drawing 24)
The folioles issue at intervals of 1·5 to 2 cm on both sides of the rachis. Blades elongate, linear, tapering gradually to a thin bristle. Their length is 12 to 20 cm, their width at the middle 5 mm. There are 6 to 8 veins, standing out both on the upper and undersurface.

(52) *Macrozamia fawcettii* C. Moore (Plate XCVIII, Drawing 25)
Folioles long, lanceolate, with 2 to 4 short teeth on the gradually tapering tip and, on some blades, 2 or 3 tiny teeth on the margin. The length of the folioles is 13 to 27 cm, their width 7 to 17 mm. There are 8 to 13 veins, dichotomous near the base, standing out rib-like on the undersurface.

(53) *Macrozamia macdonnelli* (F. Muell.) A.DC. (Plate XCVII, Drawing 20)
The rachis bears about 70 close-spaced leaflets on both sides, the proximal ones alternating, the distal ones more opposed; blades elongate, lanceolate, gradually tapering; base narrow, somewhat thickened; there are 8 to 15 veins, forming a conspicuous ribbing on the undersurface, near the leaf base, dichotomy is frequent. The folioles are 23 to 24 cm long, 5 to 9 mm wide, the lowest ones are often remarkably small.

(54) *Macrozamia miquelii* (F. Muell.) A.DC. (Plate XCVII, Drawing 22)
Folioles comparatively long and narrow, vivid or pale green, scattered on the rachis; their length is 23 to 36 cm, their width 5 mm; blade narrowly tapering.

(55) *Macrozamia moorei* F. Muell. (Plate XCVII, Drawing 21)
45 to 50 folioles rigidly erect, fit into the grooves on the sides of the rachis, their length diminishing toward the apex. Blades lanceolate, 10 to 38 cm long, 3 to 9 mm wide, narrow at the base; acute tip ending in a bristle. There are 5 to 11 veins forming a conspicuous ribbing on the undersurface, dichotomous near the base.

(56) *Macrozamia pauli-guilielmi* W. Hill et F. Muell. (Plate XCVIII, Drawing 27)
The rachis is 7 to 9 mm wide; from its two sides there issue at intervals of 10 to 15 cm alternating linear folioles 18 to 35 cm long and only 3 to 5 mm wide; margins perfectly entire. There are 6 to 8 veins, strongly bulging on the undersurface but hardly visible on the upper surface.

(57) *Macrozamia secunda* C. Moore (Plate XCVIII, Drawing 26)
The folioles issue on both sides of the rachis at intervals of 3 to 4 mm; their length is 6 to 8 cm, their width 4 to 4·5 mm. Blades slightly falcate, gradually

tapering on both ends. The number of the leaf veins is 7 or 8, the undersurface bears a marked ribbing, the upper surface is smooth; the veins frequently dichotomize.

(58) *Macrozamia spiralis* (Salisb.) Miq. (Plate XCVIII, Drawing 23)
The rachis bears 20 to 50 straight or slightly arched, elongated folioles, narrowing toward the tip, somewhat constricted at the base. The apex sometimes bears 2 to 5 tiny teeth; the folioles are 10 to 35 cm long, 5 to 9 mm wide; the median ones are largest. There are 4 to 11 veins, slightly standing out on the undersurface and often dichotomous near the leaf base.

(59) *Microcycas calocoma* (Miq.) A.DC. (Plate XCV, Drawing 4)
Numerous folioles 50 to 80 or more on both sides issue alternately or in opposition from the rachis. Blades more or less falcate, long, narrow lanceolate, 9 to 23 cm long and 5·5 to 8 mm wide, tip obtuse, base somewhat thicker, margin entire, slightly recurved; veins parallel, cicatrice 4 to 5 mm in diameter, slightly flattened elliptic. Blades are widest in the lower third; the young ones are hairy, very seldom naked.

(60) *Stangeria eriopus* Nash. (Plate XCV, Drawing 3)
Issuing from the slightly pinnate rachis at intervals of 8 to 35 mm, the folioles are asymmetric, elongate, oval; tip narrowing, densely serrate. The proximal folioles have a short petiole (1 cm), the distal ones are decurrent on one side; their length is 13 to 18 cm, their width 30 to 32 mm; the proximal part of the folioles is lobate, the distal part entire. A number of dichotomous veins issue almost perpendicularly from the midrib. The midrib and the lateral veins stand out on the undersurface of the leaf.

(61) *Stangeria paradoxa* Th. Moore (Plate CIV, Drawing 76)
The number of the foliole pairs is 4 to 17; blades asymmetrical, long lanceolate, decurrent, 8 to 35 cm long, 20 to 70 mm wide, tip acute, margin dentate; there is a somewhat stronger mid-vein from which issue several repeatedly dichotomizing lateral veins.

(62) *Zamia angustifolia* (Jacq.) Schuster (Plate CIII, Drawing 69)
Alternating or opposed, the close-spaced folioles number 40 to 60 on both sides, being somewhat wider spaced near the distal end of the rachis. Blades narrow, margins locally bear tiny teeth; there are 1 to 3 teeth on the tip; base hardly narrowing; foliole sometimes arched, reclinate, rigid, sometimes falcate, 4 to 26 cm long, 1 to 6 mm wide; there are up to 10 veins, standing out on the undersurface.

(63) *Zamia fischeri* Miq. (Plate CIII, Drawing 65)
Folioles moderately lanceolate, acute and asymmetrical of tip, tapering of base; margins characteristically dentate near the tip with tiny, projecting teeth; there

are 10 to 20 veins, bifurcating; folioles 4 to 9 cm long, 7 to 15 mm, alternating or opposed, somewhat leathery.

(64) *Zamia floridana* A.DC. (Plate CIII, Drawing 71)
From the rachis there issue at angles of about 40° 12 to 22 pairs of folioles, mostly opposed. Blades straight, base tapering, tip obtuse, bearing 2 to 5 tiny teeth. There are 3 to 10 dichotomous veins, standing out on the undersurface. Upper surfaces smooth, undersurfaces slightly hairy; folioles 8 to 9 cm long, 3 to 12 mm wide, rigid.

(65) *Zamia furfuracea* L. fil. (Plate CII, Drawing 59)
Folioles alternating or opposed, 5 to 20 cm long, 18 to 45 mm wide, broadly lanceolate; base asymmetric, tip tapering from the middle of the leaflet, margin dentate with very short and close-spaced teeth or serrate; the tip bears obtuse teeth; there are 34 to 70 veins, often dichotomous; proximal and distal end of foliole ribbed on the under- and furrowed on the upper surface.

(66) *Zamia gutierrezi* Sauvalle (Plate CII, Drawing 56)
On both sides of the rachis there are 12 to 14 folioles of 7·5 to 21 cm length, 2 to 3·7 cm width; blade long elliptic or cuneiform; base gradually tapering; the lateral margin bears tiny teeth which are more frequent toward the tip; sometimes falcate; the dichotomous veins number 30 to 48.

(67) *Zamia kickxii* Miq. (Plate CIII, Drawing 67)
Folioles 4 to 5 cm long, 12 to 20 mm wide, shortly lanceolate, base strongly tapering, blade widest at the middle, tip asymmetrically obtuse; there are 10 to 30 dichotomizing veins, forming conspicuous ribs on the undersurface.

(68) *Zamia latifolia* Lodd. (Plate CII, Drawing 58)
Folioles elongate, elliptic, 10 to 14 cm long, 30 to 35 mm wide; base acute, tip rounded; there are tiny teeth at the endings of the veins. The number of the veins is 30 to 40; dichotomy is frequent near the base.

(69) *Zamia latifoliata* Prenleloup (Plate CIII, Drawing 70)
Folioles scattered on the rachis; blades obovate, tapering into petioles 1·5 to 2 mm long. Tip obtuse and obliquely truncate. Blade length 3 to 10 cm, width 25 to 30 mm. The tip bears 20 to 35 tiny teeth in the continuation of the veins. The veins stand out somewhat on the undersurface of the leaf, dichotomizing at the leaf base and spaced at intervals of 1 to 1·5 mm.

(70) *Zamia lindenii* Regel (Plate CII, Drawing 62)
The rachis bears 20 to 40 opposed folioles, elongate, lanceolate, 20 to 35 cm long, 2·5 to 3 cm wide; tip acute, base only 2 to 5 mm wide; blade sometimes falcate, with short, pointed, straight teeth on both margins from median to tip. The teeth are longer near the tip than on the margin. There are 20 to 30 veins,

often dichotomous, forming hardly noticeable furrows on the upper and a slightly prominent ribbing on the undersurface.

(71) *Zamia loddigesii* Miq. (Plate XCVIII, Drawing 29)
The folioles are of various shapes, lanceolate or oval, elongate, alternating or opposed, straight or somewhat falcate; tip gradually tapering, rather densely dentate, base acute; there are 7 to 25 veins frequently dichotomous, their lower side is sometimes tomentose.

(72) *Zamia media* Jacq. (Plate CIII, Drawing 68)
Folioles 6 to 25 cm long, 5 to 37 mm wide; there are 6 to 48 veins, standing out on the undersurface; blades broadly lanceolate, with tapering base and tip, sometimes falcate; tip conspicuously dentate, with tiny, dense teeth; the lower third of the foliole has entire margins.

(73) *Zamia muricata* Wild. (Plate CII, Drawing 57)
Folioles alternating or opposed, gradually widening from the base, widest at the middle, thence gradually tapering into a long point. In the distal half, the margins bear tiny teeth the density of which increases toward the tip; blades are 10 to 13 cm long, 12 to 18 mm wide, somewhat leathery, there are 27 to 57 veins, often dichotomous, forming prominent ribs on the undersurface.

(74) *Zamia ottonis* Miq. (Plate CII, Drawing 60)
Proximal folioles alternating, distal ones more opposed; blades broadly lanceolate or elliptic; margin entire up to upper third of blade; the upper third bears tiny close-spaced teeth; tip truncate, obtuse; folioles 5·2 to 11 cm long, 1 to 3 cm wide; the number of the generally dichotomous veins is 23 to 35; base cuneiform, tapering.

(75) *Zamia pumila* L. (Plate CIII, Drawings 63, 64)
Folioles alternating or opposed, 9 to 19 cm long, 9 to 20 mm wide, lanceolate, gradually widening, asymmetric; tip tapering, with many tiny teeth. Veins number 30 to 40; near the base, dichotomy is frequent; the undersurface bears a marked ribbing.

(76) *Zamia pygmaea* Sims. (Plate CIII, Drawing 66)
3 to 25 folioles alternating or opposed; the proximal ones are smaller, the median ones longest, 3 to 9 cm long, 10 to 23 mm wide. Veins number 21 to 43; base obliquely cuneiform, standing out and bifurcate on the undersurface, the obtuse tip bears tiny teeth.

(77) *Zamia silicea* Britton (Plate CII, Drawing 61)
The length of the folioles is 25 to 50 mm, their width 8 to 12 mm; blade elongate oval, base and tip gradually tapering; near the tip there are hardly visible tiny teeth at the endings of the veins, which number 15 to 22; on the undersurface, the dichotomous veins are readily visible.

LEAF EPIDERMIS OF THE CYCADS

GENERAL EXAMINATION

1. EPIDERMAL PREPARATIONS

In the study of fossil finds, more exactly of the cuticles of their leaves, comparison with living material is absolutely necessary. The present book is not intended to deal with the so-called "cuticular analysis" of fossil plants and its methods. A good guidance for that method can be obtained from Kräusel's (1949) practical book: Paläobotanische Untersuchungsmethoden. We shall only examine here the leaf epidermis of recent Cycads, both from the upper and undersurface of the leaflet, this being of primary interest in fossil determination.

Comparative epidermal preparations of living Cycads can be made not only from fresh but also from herbarium material. A portion of any leaf or petiole is suitable for the purpose. The rather thick leaves of most Cycads are difficult or impossible to study in transmitted light: the details of the cells on the surface are readily visible. This is why epidermal peels of leaves are utilized as these show not only the family traits but also the specific features.

The epidermis of the Cycads is covered on the outside by a cuticle layer of various thickness. Clear sight is rather strongly hindered even by this narrow layer. Hence, the leaves must be suitably prepared for examination, as follows.

First of all, one should inspect by means of a lupe whether the leaf surface bears any hair structures. If not, the leaves are washed in water by hand or with a brush to remove dust and dirt. Subsequently, about 1 sq. cm of the leaflet is cut out. If the leaflet is narrower it is advisable to cut straight the margin of the leaflet with a pair of scissors in order that the upper and undersurface of the leaflet may be spread out beside each other. The bits of leaflet are then placed in distilled water in a test tube, and warmed until the leaves are entirely soaked through. This lasts, depending on the quality of the leaflet, about 30 to 60 minutes. After proper soaking, the bits of leaflet are treated by Schulze's method (nitric acid + potassium chlorate).

The leaflet bits should be carefully boiled under a hood until the mesophyllum separates from both epidermis and the bit opens in two. To facilitate this, it is advisable to cut one margin of the leaflet before treatment.

When the mesophyllum has more or less disappeared and the leaflets have become almost translucent, the macerating liquid is poured off, the bits are placed into a Petri-dish filled and thoroughly rinsed two or three times with distilled water. After soaking for 2 or 3 minutes in dilute acetic acid, the bits are rinsed again in distilled water and placed in a Petri-dish filled with distilled water. Now the bits of leaflet are turned inside out so that the upper and undersurface

of the bit of leaflet come to lie on the bottom with the mesophyllum facing upwards. The mesophyllum is carefully removed with a soft brush. This operation is important because mesophyllum cells sticking to the epidermis layer greatly hinder clear sight.

After removing the mesophyllum, the preparation is put with the mesophyllum side downwards under the microscope to establish whether any mesophyllum cells still stick to the epidermis. Staining follows when there are no mesophyllum cells left.

Staining can be done in two ways. If we want to separate the lignified parts, the preparation is placed in a solution of phloroglucinol plus hydrochloric acid which stains the lignified portions a vivid sour-cherry red. This type of staining is particularly suitable to reveal the finer structure of the guard cells.

For a general staining, the selected material is placed first in 30 per cent, then in 70 per cent aethyl alcohol and kept in both for 5 minutes. After soaking in alcohol, the material is placed for half an hour in a 2 per cent solution of vesuvin or some other stain. Then, after adding a few drops of concentrated hydrochloric acid, the preparation is placed in 70 per cent aethyl alcohol (for 2 to 5 minutes) and then in 30 per cent aethyl alcohol (5 to 6 minutes), washed in distilled water and finally, when no more stain can be washed out, mounted and stabilized in glycerol gelatine previously heated in a water bath.

This method yields high-grade preparations, suitable for drawing and photography as well as for comparison.

2. STRUCTURE OF THE LEAF EPIDERMIS IN THE CYCADS

As stated above, most Cycads inhabit the tropical and subtropical regions, first of all the sunny savannas, with only a few species living in shady habitats or among the trees of closed forest stands. Accordingly, the leaves of the Cycads are generally of xerophytic character, mostly thick, leathery and covered with a thick cuticle; only the species growing in shady forests possess more fern-like leaves (*Bowenia*, *Stangeria*). Cuticularization can be considerable in some cases, whereas in others the leaflets carry a thin cuticular layer only.

The epidermal cells on the upper surface of the leaflet frequently differ in form and arrangement from those on the undersurface. Generally, however, the epidermal cells of both the upper and undersurface are elongated parallel to the rachis and only very exceptionally isodiametric.

The considerable variety of epidermal cells on both surfaces of the leaflets often provides marks by which certain species can be distinguished. Variety regards mainly the size and shape of the epidermal cells, the quality and pittedness of the lateral walls and their thickness. The epidermal cells of most Cycads are arranged in longitudinal rows parallel to the leaflet axis, placed end to end, whereas their long lateral walls touch the cells of the row alongside. Cell length ranges from 20 to 250 μ, cell width from 15 to 25 μ. Sometimes the fit is fibre-like, whereas in

other cases one observes mosaic-like patterns with sinuous walls. Wall thickness is not uniform. Very often quite thin-walled and thick-walled cells lie side by side. The thick walls are generally layered, sometimes 7 to 8 μ thick; their lumina are narrow, often slit-like (Plate CLVIII, Photo 2). Not more than 2 or 3 μ thick, the thin walls often bear simple pits; the interior of the thin-walled cells very often contain chloroplastids. In some cells, the pits are so small as to be hardly visible while in others comparatively large pits are aligned in the wall which appears almost perforated. This latter structure is restricted to the genus *Cycas*, so that its species can be directly separated from all other genera on the basis of this character alone. The more or less isodiametric cells generally have straight or slightly sinuous walls and only very seldom strongly undulating ones (*Stangeria*, Plate CXVIII). This trait definitely separates *Stangeria* from all other genera. The lateral walls are less sinuous e.g. in *Dioon* (Plate CLIX, Photos 6, 7), where both the end and side walls are seen to be sinuous but not as much as in the former case.

It is remarkable that there are no stomata among the epidermal cells of the upper surfaces of most leaflets. In some species, however, there are stomata both on the upper and undersurface: such leaves have to be regarded as amphistomatic (e.g. *Microcycas calocoma*, some *Encephalartos* species, and particularly *Macrozamia miquelii* and *Macrozamia moorei*). In the two latter species, the stomata are aligned in longitudinal bands both on the upper and undersurfaces of the leaflets, but on the upper surface the stomatal rows are fewer and the stomata in them much less close packed than on the undersurface.

Stomatal structure is in most cases the same on both surfaces of the leaf; it is but very seldom that there are no guard cells below the apertures on the upper surface, there being instead free apertures communicating with the interior of the leaflet. These apertures can be regarded as rudimentary stomata because the shape and arrangement of the accessory cells around them almost perfectly agree with those on the undersurface.

Some species bear tiny hair structures among the epidermal cells. Maceration erases most of these but the hair bases remain.

It is interesting to note that in *Stangeria paradoxa* the free surfaces of the epidermal cells are covered with projecting cuticular lamellae which as a rule issue radially and curl-like from the hair bases. This feature occurs exclusively in *Stangeria*. It is, however, highly reminiscent of the *Ctenis* species described by Florin so that a relationship between ancient *Ctenis* and living *Stangeria* can be rightly assumed.

On the undersurfaces of the leaflets, shape and structure of the epidermal cells mostly differ from those of the upper surface. This difference is largely due to the presence of stomata on the undersurface, whereas—as we have seen—there are seldom any on the upper surface.

There are two patterns of stoma arrangement. In the first, the stomata are randomly scattered, and the direction of their slits is also random. This is the case e.g. in the genus *Cycas*. In other cases the stomata are concentrated in longitudinal

bands separated by bands not containing any stomata. For these latter we shall employ the term *interband* in the following parts of the present work. The interbands usually correspond to the veins running in the leaflet; no stomata develop immediately above the veins. The width of the bands may vary even within the same genus. Shape, size and arrangement of the epidermal cells in the interbands generally correspond to those on the upper surface. In the bands, the cells are generally shorter and wider owing to the presence of the stomata; the structure of their walls and their content agree, however, by and large, with those on the upper surface.

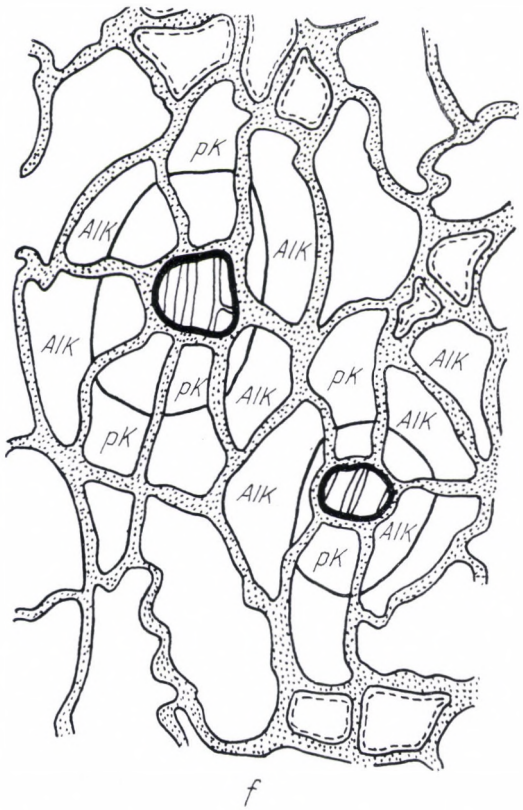

Fig. 48. Stoma structure of *Dioon edule* in surface view. (Explanation on p. 166)

A number characteristic of the undersurface of the leaflet is the number of stomata per sq. mm. In amphistomatic species this number is much smaller, often quite insignificant on the upper surface, sometimes only 2 to 6 (*Bowenia*), whereas in *Macrozamia* e.g. it is more or less the same as on the undersurface (25 to 35). On the other hand, on the undersurface of *Cycas neocaledonica*, the number of stomata per sq. mm can be as high as 100.

In stomatal structure, two main types can be distinguished among the Cycads. In the first type, the guard cells are flush with the epidermal cells or only slightly countersunk (Plate CIV, Photo 4). In the other type, the guard cells occur on the bottom of a stomatal pit of some depth. In this type, the guard cells are overarched by the cells above them (the so-called accessory cells). It is through this spacious pit that the stoma in the narrower sense of the word communicates with the outer world.

As the knowledge of the stomata of the Cycads is very important in the diagnosis of the species, it is desirable for the reader to get acquainted with the most important terms to bee mployed below.

In his treatise Florin (1931) elucidated the terms connected with the stomata of the Cycads as follows:

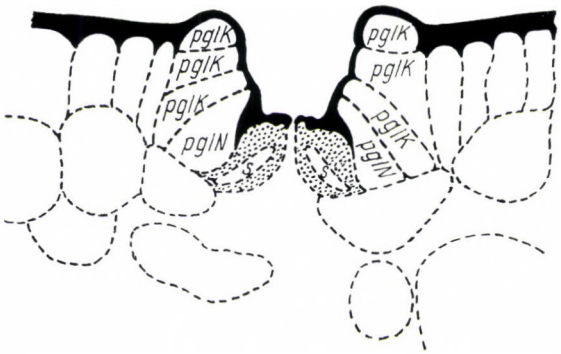

Fig. 49. Cross-sectional structure of the stoma and its surroundings in *Dioon spinulosum*. (Explanation on p. 165)

Guard cells. In a fully developed gaseous-interchange apparatus, those specific epidermal cells of peculiar shape and structure which flank the stomatal slit are called guard cells (Figs 48 and 49). They generally develop from the so-called stoma mother cell which is flush with the epidermis.

Neighbour cells (Nachbarzellen, N) are the cells flanking the fully developed guard cells and differing in structure, shape or position from the adjacent epidermal cells. There are so-called *lateral* and *polar* neighbour cells (l N, p N). Both cell types originate from the neighbouring mother cells; it is largely these which may develop differently in the various genera.

Accessory cells are the cells connected with the guard cells but provided with an elbow-joint, which otherwise (i.e. as regards the other cell walls) are similar to the neighbour cells (N). The accessory cells may develop also from the mother cells of the neighbour cells. Florin distinguishes lateral (l) and polar (p) accessory cells (Figs 48, 49).

From these cells Florin distinguishes so-called *coronary cells* which flank the stomatal apparatus in the shape of a wreath, lining in most cases the upper part of the stomatal pit. As a rule, these cells overarch the pit papilla-like, reducing its external aperture.

All these features are apparent in Figs 48, 49 on this basis, the arrangement of the various cells can be readily interpreted. Figures 48, 49 show e.g. the stomatal structure of *Dioon spinulosum* (after Florin). The leaflet is covered by a thick cuticle shown in black. The lignified walls of the guard cells (S) are stippled. Adjacent to these there are the perigenic lateral accessory cells (Pgl. N) and above these latter, in three storeys, the perigenic lateral coronary cells (Pgl. K).

The external aperture of the coronary cells is indicated by a heavy black line. Within this line, the two countersunk guard cells are seen, with a narrow slit between them. The stomatal pit is bordered on all sides by the coronary cells, two of which (pK, pK) are polar coronary cells. The two drawings offer an insight into the structure of such countersunk stomata.

In other cases where the stomata are more or less flush with the level of the epidermis, the situation is essentially the same but with the elements arranged in a

somewhat flattened fashion. This is the case e.g. in *Microcycas* where the guard cells are surrounded by accessory and coronary cells, namely by the so-called perigenic lateral accessory cells (Pgl. N) and the perigenic lateral coronary cells (Pgl. K) (Fig. 50).

In the guard cell itself, we distinguish a polar portion whose wall is thinner; this provides for the regulation of the opening; there is, however, also a thickened portion, whose external, bulging wall is called dorsal and whose other wall, adjacent to the polar portion, is called ventral. It is particularly the ventral part that exhibits considerable variety because its endings are either rounded or tapering swallow-tail fashion; also the angle subtended by the ventral parts of the two cells is varied, from zero (parallelism) through a right angle to obtuse angles. The surface of the lignified dorsal part is sometimes smooth; in other cases it bears various patterns and tubercles, most of which are almost radially aligned.

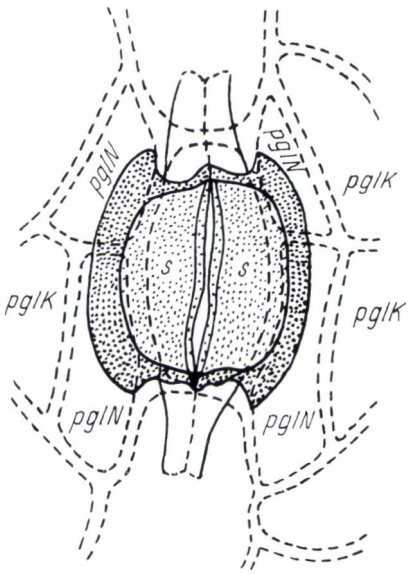

Fig. 50. Stoma structure of *Microcycas* in surface view. (Explanation on p. 166)

The shape of the guard cells as well as of the accessory and coronary cells is more or less similar in the various genera, but there are a number of rather variable details which provide a good orientation, specific as well as generic. The principal epidermal types of the Cycad genera are discussed below.

3. PRINCIPAL TYPES OF THE EPIDERMAL CELLS

As mentioned above, the living Cycads number 10 genera among them. These are: *Bowenia*, *Ceratozamia*, *Cycas*, *Dioon*, *Encephalartos*, *Lepidozamia*, *Macrozamia*, *Microcycas*, *Stangeria* and *Zamia*. These genera can be distinguished by and large also on the basis of their epidermal structures, by the shape and structure of the epidermal cells on the upper surface and by the arrangement and structure of the stomata on the undersurface of the leaflet.

There are several epidermal types which correspond by and large to the various genera. The main types are presented on Plates CV, CVI. Some of the characteristic traits are definitely characteristic of a single genus only. Such characters are e.g. the pittedness of the epidermal cells or the shape and arrangement of the stomata.

(1) The most typical feature of all species of the genus *Cycas* is – disregarding the shape and arrangement of the stomata – that both on the upper and undersurface of the leaflet, the secondary walls of the epidermal cells bear a simple pitting (Plate CV, Photo 1). Within the genus *Cycas*, shape and arrangement of the stomata fall into two types. In the first type, including *C. revoluta*, *C. taiwaniana* and *C. neocaledonica*, the stomata are on the bottom of a crater-like pit overarched by 8 to 16 accessory cells arranged in a pattern resembling lemon slices. Stomata of this type are restricted to a few *Cycas* species. In the second type the guard cells and the accessory cells are arranged more or less in the same plane although the crater-like structure exists also here to a certain degree (Plate CV, Photo 2a).

In all species of the genus *Cycas* the epidermal cells of both the upper and undersurfaces of the leaflets are more or less isodiametric; their walls are mostly straight, in other cases somewhat undulating, which is an ancient filicine feature.

(2) Another trait by which the genera can be distinguished is the sinuosity of the walls of the epidermal cells, accompanied by the presence of characteristic cuticular lamellae as e.g. in *Stangeria paradoxa* (Plate CV, Photos 4, 4a). In the genus *Stangeria*, the walls of the epidermal cells are strongly sinuous both on the upper and undersurfaces of the leaflets resembling the epidermal structure of some *Filicinae*. Another typical feature of *Stangeria* is the presence of curly patterns of parallel lamellae on the surface of all epidermal cells.

(3) Also *Bowenia* can be readily distinguished from the other genera by the stomata scattered on the upper surface and grouped in bands on the undersurface; their number is much lower on the upper surface. It should be noted, however, that amphistomatism appears also in other genera. Another typical feature of *Bowenia* is that the epidermal cells are mostly thin walled, in connection with the fern-like character and forest habitat of *Bowenia* (Plate CV, Photos 5a, b).

(4) A characteristic structure is that of the unique species of the genus *Mycrocycas*, *M. calocoma*. The upper surface bears no stomata, but on the undersurface the stomata are grouped in narrower or wider bands. Shape and structure of the stomata, arrangement of the accessory cells are typical enough to serve as a basis of distinction from the other genera.

(5) The genus *Dioon* includes three species: *Dioon edule*, *D. spinulosum* and *D. purpussii*. Of the three, the author succeeded in dealing with *D. edule* and *D. spinulosum*. It is a typical feature of *Dioon* that on the upper surface of the leaf, the epidermal cells are comparatively squat rectangles, arranged in longitudinal rows, joining transverse or slightly oblique end walls. The thickening of the walls is of two different types. The layered thicker walls are largely responsible for strength; the thin-walled parenchyma cells communicate among them through simple pits and perform the task of assimilation.

The most typical trait is, however, the shape of the stomata, the guard cells being overarched vault-like by the accessory cells: the walls facing the vault of the accessory cells are but very exceptionally rounded, being straight in most cases, so that the opening of the vault is either a regular hexagon or a slightly rounded one (Plate CV, Photos 6, 6a). No other living Cycad genus possesses a similar sto-

matal structure. However, among the extinct Mesozoic forms the stomatic structure e.g. of *Elatocladus punctatus* is perfectly similar to that of *Dioon*; some sort of genetic relationship may thus exist between living *Dioon* and the extinct *Elatocladus*.

(6) A different epidermal structure is found in *Encephalartos* of which the epidermis of 30 species have been examined. As to the arrangement of the stomata, two groups can be distinguished. Some species, e.g. *E. longifolius*, *E. septentrionalis*, *E. natalensis*, *E. lehmannii*, are amphistomatic, although the stomata are much sparser and of a somewhat different structure on the upper surface. On the upper surface of *E. longifolia* or *E. natalensis* there are no well-developed stomata with guard cells, only some apertures, the shape and arrangement of whose accessory cells, however, classes them definitely as stomata (see *E. lehmannii*, *E. longifolius*, etc.). The stomata are mostly grouped in bands, but the arrangement is different in *E. lehmannii*. Between the upper and undersurface of *E. septentrionalis* the only difference in the arrangement of the stomata is that the stomata on the upper surface generally form single rows while on the undersurface they form narrower or wider but always well-defined bands. Shape, size and arrangement of the epidermal cells, the distribution of thin- and thick-walled cell types show some differences among the species, so that, particularly after examination of the upper surface, the species are rather readily distinguished.

The same can be generally stated as to the arrangement of the stomata on the undersurface, and as to the shape, number and structure of the accessory cells. In some forms, e.g. *E. longifolius*, *E. natalensis*, *E. tegulanus*, *E. lehmannii*, *E. caffer*, *E. cycadifolius*, *E. bubalinus*, *E. hildebrandtii*, *E. transvenosus*, the guard cells are overarched by a lower or higher wall constituted by the accessory cells. In some other species, as *E. altensteinii*, *E. laurentianus*, *E. lebomboensis*, *E. poggei*, *E. septentrionalis* and *E. villosus* (Plate CVI, Photos 8, 8a), this overarching is not so conspicuous. On the upper surface, the variety in the shape of the epidermal cells is rather great, particularly in the species where the cell walls are considerably thickened. The cells are generally isodiametric and highly varied in form, whereas in the types with thinner-walled epidermal cells, shapes more or less substantially elongate in the direction of the leaflet axis are more frequent. Simple pitting is common in both the thin and the thick cell walls. Shape, size and arrangement of the epidermal cells seem to be at least approximate specific distinctive features. All these differences are visible in the photos of the various species.

(7) The two *Ceratozamia*, *C. mexicana* and *C. robusta*, have a highly typical structure. Difference between the two species is insignificant; it is rather difficult to tell them apart. It is characteristic both of the upper and undersurfaces of the leaflets of *Ceratozamia* that exceedingly thick-walled epidermal cells with narrow lumina, elongate fibre-like, are separated by rows of 8 to 15 thin-walled and much smaller epidermal cells. Such an arrangement of thin- and thick-walled epidermal cells is not encountered in any other Cycad genus.

The leaves are hypostomatic; the stomata of the undersurface of the leaflet are grouped in narrower or broader bands. Also the structure of the stomata is different

from that of the other genera. The number of the accessory cells is very often only two, more seldom 4; and the polar cells do not reach beyond the elliptic or circular periphery of the accessory cells. The very thick-walled epidermal cells suggest xerophytic habitats.

(8) A peculiar and rather characteristic epidermal structure is found in the two *Lepidozamia*, *L. hopei* and *L. peroffskyana*, already referred to by Cookson in connection with the discovery of *L. hopeites*. In both species, the epidermal cells of the upper surface are more or less isodiametric and arranged in longitudinal rows with 2 or 3 thick-walled and as many thin-walled epidermal cells alternating. A cellular arrangement of this type is restricted to *Lepidozamia*, *Macrozamia* and *Encephalartos*; this is why it is in many cases difficult to tell them apart on the basis of the epidermal cells alone. The epidermal structures of *Lepidozamia hopei* and *L. peroffskyana* are much alike but readily distinguishable on comparison. In *Lepidozamia* the stomata are generally surrounded and somewhat overarched by 4 to 6 accessory cells, but no definite pit structure is observed above the stomata.

(9) The leaf epidermis of 8 species of *Macrozamia* were examined. This genus can also be divided into several types on the basis of epidermal structure; in the first place according to whether the leaflets are amphistomatic or hypostomatic. *M. miquelii* and *M. moorei* are amphistomatic, whereas in the other species no stomata are seen on the upper surface.

The species of *Macrozamia* fall, however, into several distinct types according to the shape, size and arrangement of the epidermal cells on the upper surface of the leaflet. In several species, e.g. *M. pauli-guilielmii*, *M. pauli-guilielmi* var. *plurinervia*, *M. spiralis*, *M. secunda*, *M. fawcettii*, the epidermal cells of the upper surface are generally elongate, their length being a multiple of their width. On the other hand, the epidermal cells of *M. moorei*, *M. miquelii*, *M. denissoni* and *M. communis* are much shorter comparatively and much more varied in shape. The leaf-epidermis structure of *M. communis* differs from that of the others in that the end walls of the cells are sinuous as well as those of the side walls. In this structure, *M. communis* definitely differs from the other *Macrozamia*. All *Macrozamia* agree in that their epidermal cells are thickened in two different ways; the thin- and thick-walled cells are distributed more or less randomly. The thicker walls are uniformly thick, of layered structure and without pits; in the thin walls, numerous tiny simple pits and chloroplastids can be observed.

On the undersurface of the leaflets, the structure of the epidermal cells falls into two types, as was the case with *Encephalartos*, too. In both, the stomata are arranged in narrow or broad bands, but there are differences in the structure of the stomata. In *Macrozamia pauli-guilielmi* and *M. denissoni*, the accessory cells are more or less flush with the guard cells, i.e. there are hardly any crater-like pits, whereas the guard cells of the other *Macrozamia* species are overarched by 4 to 6, occasionally 8 accessory cells. The number of the accessory cells can be exactly determined by counting the faces of the stomatal pit. Another common trait of this structure is that the rounded end walls facing the stoma of the accessory cells are substantially thicker than their lateral walls. These accessory cells sometimes

bear a peculiar ornament of auricular shape below the endings facing the pit of the accessory cells.

The accessory cells can be easily distinguished from the adjacent thick-walled epidermal cells also in that the structure of their walls perfectly agrees with that of the thin-walled epidermal cells in pittedness as well as in the presence of chloroplastids.

In a general way, the epidermal cells on the upper surface of *Macrozamia* are substantially elongate in the direction of the leaflet axis; the stomata are surrounded by 4 to 6 accessory cells and the guard cells are placed on the bottom of a shallower or deeper stomatal pit.

(10) As regards the genus *Zamia*, the epidermal structures of 18 species were examined. All of these are characterized by that the stomata (more precisely, the guard cells) are not sunk in pits but are more or less flush with the epidermis. It is a further common trait that, although the epidermal cells are elongate in the direction of the leaflet axis, their length is only 3 to 8 times their width and there are hardly any more strongly elongate epidermal cells on the upper surface. There are, however, exceptions such as *Z. furfuracea* where the epidermal cells are only 2 to 3 times as long as wide.

The distribution of thin- and thick-walled epidermal cells is different in the diverse species. The thin-walled cells generally contain chloroplastids.

On the undersurfaces of the folioles, the stomata are without exception grouped in narrower or broader bands whose width depends on the spacing of the veins, since it is under the veins that the stomata are absent.

The guard cells are flanked by 4 to 6 accessory cells, frequently enough of trapezoidal shape, which in most cases overarch guard cells but slightly. The diameter of the stomatal pit is, however, in most cases smaller than the slit between the guard cells. It is generally circular or elliptical, elongate in the latter case in the direction of the leaflet axis. In the case of *Zamia furfuracea*, however, the stomatal aperture is an ellipse perpendicular to the leaflet axis, a specific feature permitting easy distinction from the other species. Shape, number and arrangement of the accessory cells is more or less varied according to the species. An interesting design of accessory cells is found in *Zamia muricata* where one of the accessory cells or a polar cell is lengthened as swallow-tail fashion; as a result the stomatal apparatus presents an aspect different from those of the other species (Plate CVI, Photo 11a).

Although the epidermal structure of the *Zamia* species is not very variegated, it presents some differences of almost specific rank, in the shape, size, arrangement and wall structure of the epidermal cells, especially on the upper surfaces. It must be borne in mind, however, that shape and size and, to a certain degree, also the structure of the epidermal cells depends on whether the sample studied was taken from the tip, mid-portion or base of the leaflet. The *Zamia* characters are, however, manifest in every portion of the leaflet.

4. TAXONOMIC KEY TO THE CYCADS ON THE BASIS OF LEAF-EPIDERMIS STRUCTURE

Plates CV–CVI; Photos 1–12a

1. Both on the upper and undersurface of the leaflet the secondary walls of the more or less isodiametric epidermis cells exhibit a pitted thickening and appear almost perforated; on the undersurface, the stomata are irregularly arranged; the lateral walls of the epidermal cells are sometimes slightly arched. (1, 1a, 2, 2a) . . . . . *Cycas*

1a. The superficial walls of the epidermal cells exhibit no conspicuous pitted thickening; the stomata on the undersurface of the leaflet are either grouped in narrow or broad bands or randomly scattered. . . . . .

2. The surface of the epidermal cells is covered by radially arranged cuticular lamellae (Photo 4); all walls of the epidermal cells are strongly sinuous; the height of the sinuosity may attain one-third of the diameter of the cell lumen; the stomata are randomly scattered over the undersurfaces of the leaflets. (4, 4a) . . . . . *Stangeria*

2a. The surfaces of the epidermal cells bear no projecting cuticular lamellae; the lateral walls are straight or scarcely sinuous; on the undersurfaces of the leaflets, the stomata are grouped in narrower or wider bands. . . . . .

3. Leaf amphistomatic; on the upper surface, there are 2 to 5 stomata per sq. mm randomly scattered; on the undersurface they are arranged in bands including 6 to 8 rows of stomata; the density of stomata in the bands is 55 to 60 per sq. mm. The epidermal cells, elongated in the direction of the veins, are 2 to 10 times as long as wide. (5, 5a) . . . . . *Bowenia*

3a. The stomata on the undersurface of the leaflet, and also on the upper surface if it bears any stomata, are grouped in bands of various width. . . . . .

4. On the upper surfaces of the leaflets, the thin- and thick-walled epidermal cells are generally squat, rectangular or ham-shaped, 2 to 5 times longer than wide; their lateral and transversal walls are slightly sinuous; the cells, joining transverse or oblique end walls, form rows parallel to the veins. The guard cells of the stomata are countersunk; the stomatal-pit apertures above them are circular or elliptical, in most cases perpendicular to the slit between the elongate hexagonal guard cells. The number of the thick-walled accessory cells is 4 to 6. (6, 6a) . . . . . *Dioon*

4a. On the upper surfaces of the leaflets, the epidermis cells are substantially elongate in the direction of the veins, or if more or less isodiametric, they constitute uniseriate longitudinal rows; the cell walls may be both thick and thin . . . . . .

5. The epidermal cells are 5 to 20 times as long as wide; their walls are very thick, their lumina sometimes slit-like; between 2 or 3 long thick-walled, there are rows of 3 to 7 quite short thin-walled cells of varied shape. The number of the accessory cells is generally 2 to 4, seldom 8; the stomata are sometimes amphicyclic. (9, 9a) . . . . . *Ceratozamia*

5a. The walls of the epidermal cells on both the upper and under-surfaces of the leaflets are generally thin or moderately thick, somewhat sinuous; the cells are 5 to 10 times as long as wide, of varied shape, arranged in a pattern of intertwinned wedges. The number of the accessory cells is in most cases 4; the endings of some are elongate, swallow-tail fashion. The guard cells are countersunk in some species. Some species are amphistomatic. (12, 12a) . . . . . *Zamia*

5b. The thin-walled epidermal cells are 2 to 5 times as long as wide; their lateral and terminal walls are slightly sinuous; the stomata are arranged in 1 to 5 longitudinal bands, the interbands are of about the same width as the bands. The guard cells are about twice as long as wide; their thick walls bear an ornament perpendicular to their long axis; the number of accessory cells is 2 to 4. (3, 3a) . . . . . *Microcycas*

5c. On the upper surface of the leaflet, the walls of the epidermal cells may be both thick and thin; the cells are generally short, having the shape of isosceles and equilateral triangles, squares, trapezoids and arranged in most cases in uniseriate longitudinal rows; other cells are 2 to 10 times as long as wide, walls comparatively thin walled; the stomata are sometimes countersunk, overarched by the accessory cells whose number is 4 to 6. Some species are amphistomatic. (10, 10a, 11, 11a) . . . . . *Macrozamia*
Lepidozamia

5d. The epidermal cells are generally isodiametric; only in some species are they 2 to 6 times as long as wide. In the first case, the cell walls are very thick; in the second case the walls may be both thin and thick. The stomata are grouped in narrower or wider bands; numbering 2 to 6, the accessory cells generally overarch the guard cells. Some species are amphistomatic. (7, 7a, 8, 8a) . . . . . *Encephalartos*

EPIDERMIS OF THE SPECIES

1. CYCADACEAE

Cycas celebica Miq. (1842)

Plate XCVI, Drawing 13; Plate CVII, Photos 1 to 4

Leaf typically hypostomatic. On the *upper surface* of the leaflet, most epidermal cells have the shape of short rectangles, lozenges, trapezoids or triangles with rounded vertices, whose longitudinal axes are randomly scattered in all directions. Sometimes 8 to 10 oblong epidermal cells of the same size are aligned side by side. The length of the cells is 40 to 80, their width 15 to 20 μ; their lateral walls are slightly undulous but not sinuous. The simple pits in their horizontal walls are either arranged in rows or scattered. There are simple pits also in the lateral walls, 6 to 7 μ long and 2 to 3 μ wide, the perforations are in most cases arranged in rows along the lateral walls. This type of upper epidermis is highly typical of the *Cycas* species.

On the *undersurface* of the leaflet, the stomata are scattered and the long axes of the guard cells almost never coincide with the direction of the veins. Shape, size and arrangement of the epidermal cells around the stomata perfectly agree with those on the upper surface. The length including the polar cells of the gaseous-interchange apparatus is 70 to 80 μ; its width is about the same (65 to 70 μ). The length of the guard cells is 50 to 55; the width of one guard cell is 15 to 17 μ. The walls facing the stoma of the accessory cells and of the two polar cells form a circle or a slightly flattened ellipse. The number of the accessory cells is generally 6; thin and perforated, their walls only thicken near the guard cells. The thicker-walled portion of the guard cells is 3 to 4 μ thick; the slit between them is as long as the guard cells themselves. Some epidermal cells contain chloroplastids.

Cycas circinalis L. (1753)

Plate XCVI, Drawing 9; Plate CVIII, Photos 1 to 4; Fig. 1

Leaf typically hypostomatic. On the *upper surface* of the leaflet, the arrangement of the epidermal cells is quite irregular; their long axes coincide but very seldom with the leaflet axis and then only above the veins (Photo 1). The cell walls bear numerous tiny pits so that the walls look almost perforated. The pits are partly aligned in parallel rows in the superficial and also in the lateral walls and partly scattered. The dimensions of the pits vary between 2 and 8 μ; their shape is circular or more or less flattened elliptical (Photo 2).

The sinuous walls of the epidermal cells are uniformly thickened and bear tiny pits. Two adjacent walls have a common diameter of about 3 μ; hence, the epi-

dermal cells are comparatively thin walled with wide lumina. Their length is generally 70 to 80 μ, their width 20 to 25 μ. They join sinuous lateral walls; the height of the waves nowhere attains $\frac{1}{5}$ of the diameter of the lumen. This structure is somewhat suggestive of the epidermal structure of ferns. The cells have the shapes of rectangles, lozenges or trapezoids, invariably elongate. They contain chloroplastids; hence, they are capable of assimilation just as the epidermal cells of ferns (Photo 2).

On the *undersurface* of the leaflet the stomata are irregularly scattered (Photo 3) with 20 to 22 of them to the sq. mm. The stomatal apertures are arranged in randomly varied directions (Photo 4). Size, shape and structure of the epidermal cells among the stomata perfectly agree with those on the upper surface, although they are somewhat smaller (50 to 60 μ) and their walls are slightly more sinuous. The guard cells are surrounded by 6 or 8 accessory cells and two polar cells are somewhat smaller than the rest. The external walls of the accessory cells are simply pitted as the other epidermal cells (Photo 4). The length of the gaseous-interchange apparatus is 70 to 75, its width, 65 to 75 μ; the stomatal aperture is 35 μ long and 14 to 15 μ wide. The length of the guard cells is 40 to 50 μ; the width of one is 10 to 12 μ. The base wall of the accessory cells is about 35 μ long; the length of their walls facing the stomatal pit is 17 to 18 μ. The slit between the guard cells is as long as the pit diameter. Pit depth is small (1 to 2 μ), but definitely noticeable owing to the different shades of the guard cells in Photo 4. The epidermal cells adjacent to the guard cells contain chloroplastids.

Cycas media R. Br. (1810)

Plate XCVI, Drawing 15a; Plate CIX, Photos 1 to 4; Fig. 2

This is an Australian species; in Queensland it thrives in the savanna and forest areas, singly or in small groups.

Leaf hypostomatic; the *upper surface* of the leaflet bears randomly scattered hair bases of 35 to 45 μ diameter. The epidermal cells exhibit the rows of close-spaced pits characteristic of the genus *Cycas*. The rows of elliptic and slit-like pits are generally parallel to the edges of the walls. Pit size is 3 to 4 μ by 1 to 1·5 μ. The shape of the epidermal cells is varied, triangular, quadrangular, oblong or trapezoidal. The walls are uniformly thick, strongly pitted, the joint diameter of two adjacent walls is 6 to 7 μ. The cells are 30 to 100 μ long and 10 to 40 μ wide. Sometimes 6 to 8 epidermal cells of equal length and shape are arranged end to end or side by side, whereas elsewhere most different shapes and sizes come together. The very scarce stomata as a rule overarch the veins.

On the *undersurface* of the leaflet, the epidermal cells are somewhat smaller than on the upper surface; they are mostly isodiametric of 30 to 50 μ size, although their shapes are highly varied. Among them the stomata are densely and irregularly arranged; in this respect, the plant reminds of *Cycas neocaledonica*. There are

85 to 100 stomata per sq. mm. The length including the accessory cells of the gaseous-interchange apparatus is 80 to 90 μ; their width is about the same. The number of the accessory cells is mostly 8 to 10; as a rule, accessory cells overarch the two countersunk guard cells. The lateral walls of the accessory cells are just as pitted as the other epidermal cells. The size of the stomatal pit is 28 to 30 μ by 18 to 22 μ. The length of the guard cells is 28 to 30 μ; the width of one is 17 to 18 μ; the thickened portion of the guard cell wall has a diameter of 3 to 4 μ. The position and orientation of the stomata or pit apertures exhibit no regularity.

Cycas neocaledonica Linden (1881)

Plate XCVI, Drawing 15b; Plate CX, Photos 1 to 4; Fig. 3

Leaf typically hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are of various shapes, in most cases squat rectangular or rhomboidal (Photos 1, 2). Their walls bear close-spaced simple pits, the size of which is at most 1·5 μ. The joint thickness of two adjacent walls is 7 to 8 μ. Scattered among the epidermal cells there are much smaller, rounded cells, probably atrophied stomatic primordia or hair bases. The walls of these special cells exhibit the same pinprick-like simple pits as those of the adjacent cells (Photo 2). Most epidermal cells are 20 to 60 μ long and 15 to 30 μ wide. In the walls, the tiny pits are generally arranged in rows parallel to the edges; in the broader walls, several rows side by side are rather frequent. The lateral walls of the cells are generally straight.

On the *undersurface* of the leaflet, the epidermal cells are much smaller than on the upper surface. Their length is only 20 to 35 μ, their width 15 to 30 μ; their lateral walls are 3 to 4 μ thick and finely pitted. The direction of the long axes of the cells is varied. There are 100 to 110 stomata per sq. mm.

The guard cells of the stomata are overarched by the accessory cells in such a way that 2 or 3 cells rise somewhat higher than the 2 or 3 accessory cells opposite (Photo 4). In other cases, however, the 6 to 8 cells rise to an even height; pit depth is then about 10 to 12 μ. The stomatal pit is, owing to the irregularly rounded walls of the accessory cells, mostly of irregular shape (Photo 4). The length of the gaseous-interchange apparatus is 55 to 60 μ; its width is 40 to 45 μ.

In the stomatal pit there are the two guard cells; their length is 35 to 40 μ, the width of one is 18 to 20 μ. The accessory cells are 30 to 35 μ long and 20 to 22 μ wide. The walls facing the pit of the accessory cells are substantially thickened in the form of a horseshoe, being definitely thicker than the other walls.

The accessory cells are underlain by a ring of much smaller and isodiametric coronary cells.

This structure, too, agrees by and large with that of *Cycas revoluta* and *C. taiwaniana* but can be readily distinguished from those in its finer details and in the size of the cells. The structure of the epidermal cells does not, consequently, bear out Schuster's hypothesis who identifies *C. neocaledonica* with *C. circinalis*; all in all, *C. neocaledonica* is to be regarded as an independent and valid species.

Cycas revoluta Thunb. (1784)

Plate XCVI, Drawing 7, Plate CXI, Photos 1 to 4; Fig. 4

Leaf hypostomatic. On the *upper surface* of the leaflet, the somewhat elongate epidermal cells are arranged randomly; in places, however, especially above the veins, the epidermal cells are arranged side by side in rows parallel to the leaflet axis. In the longitudinal rows the shape of the cells is highly varied, triangular, square, rectangular, rhomboidal, trapezoidal. There are thick-walled (3 to 3·5 μ) and thin-walled (1 μ) epidermal cells. The thick walls bear numerous tiny pits, hardly 1 to 2 μ in size, elliptic or slit-like (Photo 2). The longitudinal walls of the elongate epidermal cells are more or less straight, at most slightly undulous. Most cells are 25 to 70 μ long and 10 to 25 μ wide. Below the upper epidermis there is another layer, the fibrous cells of which are arranged perpendicularly to the cells of the upper layer.

On the *undersurface* of the leaflet, the stomata are arranged quite irregularly; there are about 50 to 60 per sq. mm. The epidermal cells among the stomata are somewhat smaller than on the upper surface (Photo 4); even the largest ones hardly attain 60 μ. Especially small are the marginal cells surrounding the stomata the diameter of which is hardly 20 μ. These tiny cells surround in a circle the accessory cells of the stomata; these latter are conical and rise above the surface of the epidermis, overarching the stomatal pit. Each stomatal pit is made up of 10 to 18 cells (Photo 1) of truncated cone shape (Photo 4). The shape of the pit aperture is varied, square, pentagonal, triangular, elliptic and rather often circular. Its size is generally 30 to 35 μ by 20 to 22 μ. Pit depth is 15 to 20 μ, rather much as compared with the size of the cells involved. On the bottom of the pit, below the level of the epidermis there are the two guard cells whose length (30 to 35 μ) nowhere attains the diameter of the pit. The width of one guard cell is 16 to 18 μ.

The cells of the pit differ not only in morphology but also chemically from the surrounding epidermal cells as they stain quite differently. The thickness of two adjacent walls of the projecting accessory cells is 7 μ; the walls bear sparse simple pits.

This epidermal structure substantially differs from that of *Cycas circinalis*; it looks as if it belonged to a different genus. This structure also proves that even within the genus *Cycas* there are substantial differences in the structure of the stomata.

Cycas rumphii Miq. (1839)

Plate XCVI, Drawing 11; Plate CXII, Photos 1 to 4; Figs 5 and 5a

The epidermal structure of this species is greatly suggestive of *Cycas circinalis* but the two can be distinguished in finer details.

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are somewhat elongate, sausage-shaped, square, rectangular, rhomboidal, etc. Of ir-

regular arrangement, the cells are not parallel to the veins or to the midrib (Photo 1). The size of most is 80 to 100 μ by 20 to 30 μ. They join gently undulous sides. The joint thickness of two adjacent walls is 3·5 to 4 μ. In the undulous walls, the simple pits of 6 to 7 μ by 4 to 5 μ size are arranged in rather close-packed rows; in most cases they are of lenticular shape. In the walls of the broader cells the simple pits are always aligned only along the margins of the walls; pits are very rare in the middle (Photo 2).

On the *undersurface* of the leaflet, the stomata are loosely scattered. There are 15 to 18 of them per sq. mm (Photo 3). Among them, the size and arrangement of the epidermal cells are more or less the same as on the upper surface, but the cells are somewhat smaller. The long axes of the cells are not parallel to the midrib of the foliole, exactly as on the upper surface.

The stomata are generally surrounded by 6 to 8 accessory cells, which are simply pitted, exactly as the other epidermal cells (Photo 4). The guard cells of the stomata are more or less flush with the leaf epidermis, so that no crater-like structure is developed. The size including the accessory cells of the gaseous-interchange apparatus is 90 to 95 μ by 70 to 80 μ; guard cells themselves are 45 to 50 μ long and one is 15 to 18 μ wide. The slit between the guard cells goes the full length of the cells. The orientation of the guard cells and stomatal apertures is uncertain because even the slits of adjacent guard cells are not parallel. The thickened walls of the guard cells bear no particular pattern (Photo 4).

Cycas seemannii A. Braun (1876)

Plate XCVI, Drawing 10; Plate CXIII, Photos 1 to 4

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are more or less isodiametric, at most twice or three times as long as wide, of highly varied shape, triangular, square, rhomboidal, trapezoidal or polygonal. Their orientation is random and the long axes of the cells are nowhere parallel to the veins. The lateral walls are somewhat sinuous; every cell contacts at least 3 to 5 adjacent cells. The walls are of uniform thickness (3 μ); there are no such differences as e.g. among the epidermal cells of *Ceratozamia* or *Encephalartos*. All horizontal cell walls are strongly perforated; the tiny perforations are generally arranged in rows parallel to the edge of the cell wall. The length of the perforations is 6 to 7 μ, their width is 2 to 3 μ; very often they are slit-like. Some epidermal cells contain numerous chloroplastids. The length of most cells is 40 to 70 μ, their width is 15 to 20 μ.

On the *undersurface* of the leaflet, the stomata are scattered irregularly; their long axes are not parallel to the veins. Shape, size, arrangement, perforation and relation to each other of the epidermal cells among the stomata perfectly agree with those on the upper surface of the leaf. The stomata are spaced about the length of two stomata apart. The number of the accessory cells is generally 6. The size including the accessory cells of the gaseous-interchange apparatus is 60

to 65 μ by 55 to 60 μ. The walls facing the stomatal pit of the accessory cells are considerably thickened; the other walls are not thickened at all. The length of the guard cells is 45 to 50 μ; the width of one is 15 to 18 μ; their wall thickness is 3 to 4 μ, the slit between them is longer than the pit diameter. Pit depth is 2 to 3 μ.

Cycas siamensis Miq. (1863)

Plate XCVI, Drawing 14; Plate CXIV Photos 1 to 4; Fig. 6

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are quadrangles or triangles of the most varied shape which nearly always join straight and rarely arched walls (Photo 1). Rather frequently they are aligned in rows parallel to the leaflet axis; the cells in the rows lie transversely. In places, the epidermal cells seem to be arranged radially around a cell, creating the impression as if these cells were hair bases or the primordia of stomata without function (see the darker patches in Photo 1). The length of most epidermal cells is 70 to 90 μ; their width is 20 to 30 μ. In their walls, the arrangement of the many small pits is irregular; only rarely are they found in rows parallel to the edges of the walls (Photo 2).

The pits are 1 μ or at most 1·5 μ in diameter and somewhat slit-like. The direction of slits is perpendicular to the long axis of the cell. Wall thickness is about 3·5 μ.

On the *undersurface* of the leaflet, size (45 to 50 by 10 to 30 μ), shape and arrangement of the epidermal cells definitely differ from those on the upper surface. The stomata are scattered quite irregularly; their long axis is rarely parallel to the leaflet axis (Photos 3, 4). There are about 45 to 50 stomata per sq. mm. The superficial walls of the cells around the stomata are finely pitted; their walls are about 3·5 μ thick. There are usually 6 accessory cells, but 5, 7 or 8 may occur, too (Photo 4). The endings of the accessory cells are slightly crater-like projecting toward the stoma, but the height of the crater is hardly 1 to 2 μ. The walls facing the stomatal pit of the accessory cells are rounded.

The size including the accessory cells of the gaseous-interchange apparatus is about 60 to 65 μ by 40 to 65 μ. The length of the guard cells is 35 to 40 μ; the width of one is 10 to 12 μ. The thickness of the lignified walls of the cells surrounding the guard cells is 3·5 μ. The slit between the guard cells reaches clean across the stoma. The size of the polar cells is 10 to 11 μ.

Cycas taiwaniana Carruth. (1893)

Plate XCVI, Drawing 8; Plate CXV, Photos 1 to 4; Fig. 51

Leaf hypostomatic. Suggestive in a general way of the epidermal structure of *Cycas revoluta* but definitely different from the other Cycads.

Upper surface. The shape of the epidermal cells is highly varied (square, rectangular, triangular, trapezoidal), but they are of nearly uniform size (Photos 1, 2).

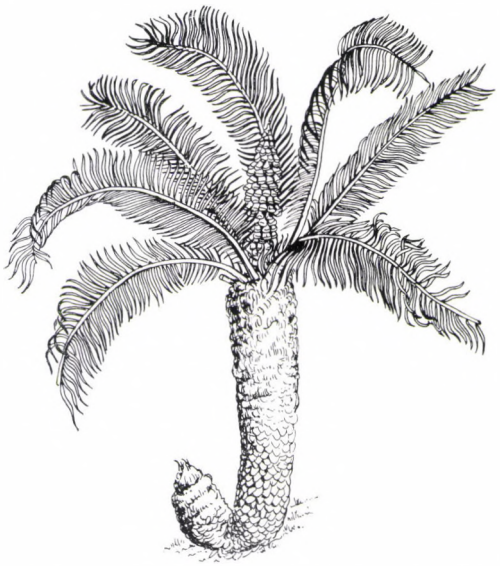

Fig. 51. *Cycas taiwaniana* (after Jisaburo)

Their average length is 50 to 70 μ, their width 15 to 20 μ. The walls of all epidermal cells are sprinkled more or less evenly with tiny simple pits distributed without any regularity. The thickness of their walls is about 2 to 3 μ. Straight or at most arched, their lateral walls communicate through simple pits. There are no intercellular ducts among them. In places, the traces of rudimentary stomata or at least simple forms resembling the stomatal pit could be detected. The cell walls locally bear tubercles.

On the *undersurface* of the leaflet, the structure of the stomatal pit above the guard cells is suggestive of *Cycas revoluta*. Some difference consists in that, in this species, the size of the stomatal aperture is generally much larger (35 to 40 μ) than in *Cycas revoluta*. The arrangement of the stomata is irregular; sometimes they are close packed, in other cases fairly loosely scattered. The stomata sometimes form rows that evidence a meandering pattern. In these meandering rows, the stomata are spaced more or less uniformly. There are 65 to 75 stomata per sq. mm. The length including the accessory cells of the gaseous-interchange apparatus is 100 to 120 μ, its width 80 to 90 μ. The outline of the stomatal pit is circular, more or less flattened elliptic or slightly compressed polygonal. The size of most is in the range of 60 to 65 μ by 40 to 45 μ. The pit is overarched by 8 to 12 cells. A further difference against *Cycas revoluta* is that the peripheral cells surrounding the accessory cells are of various size (Photo 4). On the bottom of the pit there are the two guard cells; the slit between them spans the pit. The length of the guard cells is 45 to 50 μ, the width of one is 18 to 20 μ. Pit depth 12 to 14 μ.

The epidermal cells around the stomata are generally smaller and more isodiametric than on the upper surface of the leaf. Their structure, however, perfectly agrees with those; their walls bear tiny pinprick-like scattered simple pits. The cells are generally 15 to 50 μ long.

Cycas thouarsii R. Brown (1810)

Plate XCVI, Drawing 12; Plate CXVI, Photos 1 to 4; Fig. 52

In the structure of its epidermal cells it considerably differs from *C. circinalis* and should thus be regarded as an independent species.

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are of highly varied shape, quadrangular, square, short or elongate rectangular, trapezoidal or rhomboidal (Photos 1, 2). The lateral walls are straight or slightly sinuous. Their orientation is varied; some are parallel to the leaflet axis; others are arranged perpendicularly. Sometimes 2 to 4 perfectly similar cells of equal size lie end to end. Their usual length is 80 to 100 μ, their width 15 to 25 μ. The joint thickness of two adjacent walls is 5 to 5·5 μ; the walls bear scattered simple pits, aligned generally in parallel rows. The pits are comparatively large, 8 to 9 μ by 3 to 4 μ, elongate, elliptical, lenticular or gash-like. The epidermal cells contain comparatively numerous chloroplastids: this is a feature suggestive of the *Filicinae*.



Fig. 52. *Cycas thouarsii*
(Botanical Garden, Munich; photo by Bauer)

On the *undersurface* of the leaflet, the stomata are scattered quite irregularly. There are about 30 to 36 of them to the sq. mm. The orientation of their long axes is varied; some are parallel, others perpendicular to the leaflet axis. Their size and shape differ somewhat from those on the upper surface; they are slightly shorter and are more likely to join sinuous walls (Photo 4).

The number of the accessory cells surrounding the stomata is generally 6 or 8; they overarch the guard cells crater-like. The outer peripheral walls of the accessory cells are thick (4 μ); their radial walls are, on the other hand, quite thin. The length of the guard cells together with the polar cells is 60 to 80 μ, their width 50 to 60 μ; without the polar cells, the length of the guard cells is 42 to 45 μ; the width of one is 12 to 15 μ. The slit between the guard cells is fully as long as the cells themselves. The width of the tapered portion of a guard-cell is 14 μ. The width of the accessory cells is 28 to 30 μ. The two guard cells are flanked by cells of such size. The walls of the accessory cells bear a simple pitting, just as the adjacent epidermal cells. The thickened portions of the guard cell walls exhibit no transverse striation; they look perfectly smooth.

2. STANGERIACEAE

Stangeria eriopus Nash (1909)

Plate XCV, Drawing 3; Plate CXVII, Photos 1 to 4; Fig. 53

On the surface of the leaf there are circular hair bases of 24 to 25 μ diameter. From them cuticular lamellae radiate in varied numbers, grouped in 4 or 5 sheaves with 4 to 7 lamellae per sheaf. The lamellae are substantially elongate in the direction of the veins. Below the laths, the walls of the epidermal cells are strongly sinuous. The height of the waves is 10 to 22 μ. The epidermal cells are generally elongate in the direction of the leaflet axis; above the veins they constitute narrower or broader bands of parallel cells.

On the *upper surface* of the leaflet, the present author has observed no stomata or similar structures although Pant and Nautiyal (1963) assert the presence of such. Hair bases are, however, rather frequent. The size of the epidermal cells varies in the range of 190 to 200 μ by 35 to 40 μ.

On the *undersurface* of the leaflet, the stomata are scattered in the fields between the veins. The length including the polar cells of the gaseous-interchange apparatus is 100 to 105 μ, their width, 65 to 70 μ. The length of the guard cells is 55 to 60 μ; the width of one is 17 to 18 μ, the length of the slit between them is 35 μ, its width 5 to 5·5 μ. The number of the accessory cells is 4 to 6, seldom 8; their shape is varied, their exterior margin finely dentate. At the apices of the guard cells, tiny pits can be observed. This structure substantially differs from those of all other Cycads. There are 20 to 22 stomata per sq. mm. Stomatal structure, as established already by Pant, permits to distinguish *Stangeria paradoxa* from *S. eriopus*, as revealed also by the comparison of our photos.



Fig. 53. *Stangeria eriopus* (South Africa; after Dyer)

Stangeria paradoxa T. Moore (1853)

Plate CIV, Drawing 76; Plate CXVIII, Photos 1 to 4; Fig. 7

The epidermal structure of this species substantially differs from those of all other Cycad genera. It somewhat resembles some of them in that the epidermal cells join strongly sinuous walls; there is, however, the substantial difference that the cuticle is thickened in the form of lamellae forming a wavy pattern and in various other ways. Such epidermal structures occur in no other genus except extinct *Ctenis* so that the question rightly arises whether there is a genetic connection between the two living *Stangeria* species and *Ctenis* of the Mesozoic.

The leaf is hypostomatic though a very few stomata (2 to 3 per sq. mm) occur also on the *upper surface* of the leaflet, especially near the leaf veins. There are hair bases around which the epidermal cells are arranged as around the stomata. Most cells are slightly elongate but there are also many isodiametric ones. The smaller cells are 25 to 36 μ long and of the same width, and even the largest ones hardly exceed 110 to 130 μ. Not only are the lateral walls sinuous, but terminal walls as well. The vertical walls are 7 to 8 μ thick; the horizontal walls bear parallel or meandering cuticular lamellae. The sinuous walls are not uniformly thick; in the troughs they are always thicker than on the crests, thus creating the impression as if they were composed of tiny hooks connected with each other. The distance between the crests is 9 to 10 μ. The shape of the cells depends somewhat on whether they occur above or between the veins. The walls of those above the veins are less sinuous, and the cuticular lamellae on them frequently follow the direction of the lateral walls of the cell while on the sinuous-walled cells they generally follow the waves of the walls (Photo 1a).

On the *undersurface* of the leaflet the stomata are generally scattered over the fields between the veins. There are 24 to 27 of them per sq. mm. The long axis of the stomata is only rarely parallel to the leaflet axis. The walls of the epidermal cells around them are always sinuous; the cells themselves are isodiametric or somewhat elongate, 80 to 90 μ long, 20 to 25 μ wide, perfectly alike in shape. On the undersurface there are somewhat more hair bases from which the cuticular lamellae are seen to radiate.

The length including the accessory cells of the gaseous-interchange apparatus is 100 to 120 μ, its width is about 90 to 100 μ. The guard cells are generally surrounded by 4 to 6 accessory cells. The shape of the latter is trapezoidal or rectangular. The length of the guard cells is 65 to 70 μ; the width of one is 16 to 17 μ. The slit between them is not as long as the cells themselves. The walls of the guard cells are thick and finely granulated, tubercular.

3. ZAMIACEAE

(a) LEPIDOZAMIA

Lepidozamia hopei Regel (1876)

Plate XCVII, Drawing 19; Plate CXIX, Photos 1–4

Leaf hypostomatic. The *upper surface* of the leaflet, the epidermal cells are arranged in more or less longitudinal, mostly uniseriate rows. The cells are slightly elongate; most of them subtend an angle of 45° with the leaflet axis; for some of them this angle is but 20–30°; yet others are perpendicular to the axis. The epidermal cells are arranged in different patterns above the veins and between them. Their shape is triangular, quadrangular, trapezoidal, rhomboidal, etc. Most of them, however, are isosceles triangles or similar forms. Their length is 30 to 35 μ, their width 15 to 20 μ. There are thick- and thin-walled epidermal cells (of 7 to 10 μ and 1 to 2 μ diameter, respectively). The former are of uniform thickness and very seldom pitted; the thin-walled cells communicate through simple pits and contain chloroplastids (Photos 1, 2). Their length is variable, 120 to 130 μ, their width 22 to 25 μ, but they can be somewhat larger and smaller, too.

On the *undersurface* of the leaflet the stomata number 20 to 25 per sq. mm; they are grouped in bands, 300 to 600 μ wide, separated by interbands of about the same width. Size, shape, arrangement and quality of the epidermal cells in the interbands perfectly agree with those on the upper surface so that a distinction is hardly possible. It could be mentioned as a slight difference that on the undersurface there are more cells subtending angles of 45–60° with the leaflet axis.

The stomata with the accessory cells are quite distinct from the adjacent epidermal cells. Shape and arrangement of the epidermal cells among the stomata and the relation of the thin- and thick-walled cells to each other substantially agree with those on the upper surface of the leaf. They number 6 accessory cells as a rule; they are generally rhomboidal in shape. The walls facing the stomatal pit of the accessory cells are 3 to 4 μ thick; that of their lateral walls hardly attains 1 μ. On the bottom of the pit there are the two guard cells; the length of the slit between them (21 to 35 μ) slightly exceeds the diameter of the pit. The thick walls of the guard cells are about 4 μ in diameter; pit depth hardly attains 4 μ. The walls of the accessory cells are finely tuberculate (Photos 3, 4). The size including the accessory cells of the gaseous-interchange apparatus is 80 to 90 μ by 25 to 30 μ; the length of the guard cells is 45 to 50 μ, the width of one is 17 to 18 μ.

Lepidozamia peroffskyana Regel (1857)

Plate XCVII, Drawing 18; Plate CXX, Photos 1–4; Fig. 54

Leaf hypostomatic. On the *upper surface* of the leaflet, some small scattered cavities are suggestive of rudimentary stomata, as the arrangement of the thin-walled epidermal cells around them is similar to the arrangement of the accessory cells



Fig. 54. *Lepidozamia peroffskyana* (i.e. *Macrozamia peroffskyana*) (Sydney; photo by Johnson)

around the stomata; their walls also contain chloroplastids. The epidermal cells are of varied shape and generally form parallel rows. These rows are in most cases uniseriate but sometimes there occur two cells side by side within the same row. Shapes include transverse oblongs, triangles or other polygons, some other cells are slightly elongate in the direction of the leaflet axis. The length of the cells is 50 to 160 μ, their width 15 to 20 μ; the width of the rows ranges from 20 to 140 μ.

There are thick- and thin-walled epidermal cells. Locally as much as 8 to 10 μ thick and layered, the thick walls exhibit no pitting; the width of the lumen depends on wall thickness. Scattered among the thick-walled cells there are the thin-walled ones, most of which contain chloroplastids; their walls 2 to 3 μ thick, bear many tiny simple pits. The thin- and thick-walled cells are irregularly distributed but in most cases 2 to 4, often 6 thin-walled cells and as many thick-walled cells are in contact with each other. The structure of the upper epidermis is greatly suggestive of *Lepidozamia hopei*.

On the *undersurface* of the leaflet, there are 20 to 22 stomata per sq. mm, in longitudinal bands of 400 to 500 μ width separated by interbands 300 to 400 μ wide. Size, shape and arrangement of the epidermal cells in the interbands and the relationship between thin- and thick-walled cells by and large agree with those on the upper surface. On the other hand, in the bands, among the stomata, the epidermal cells are owing to the close spacing of the stomata much shorter (40 to 100 μ) and somewhat wider than on the upper surface. The walls are also here thick

and layered; the thin-walled cells contain chloroplastids. The number of the accessory cells is generally 4 to 6 of which one or perhaps two are slightly elongate swallow-tail fashion. The accessory cells slightly overarch the guard cells; the size of the stomatal pit is generally 30 to 35 μ by 20 to 25 μ, the walls facing the pit of the accessory cells are somewhat thickened, but their other wall portions are as the walls of the thin-walled epidermal cells. The accessory cells here and there contain chloroplastids. The size including the accessory cells of the gaseous-interchange apparatus is 90 to 100 μ by 80 to 85 μ. On the bottom of the stomatal pit there are the two guard cells; the slit between them reaches beyond the pit aperture. Pit depth is 5 to 6 μ. Length of the guard cells is 50 to 52; the width of one is 17 to 18 μ.

(b) MACROZAMIA

Macrozamia communis L. Johnson (1959)

Plate XCVIII, Drawing 24; Plate CXXI, Photos 1–4; Fig. 8

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are generally elongate rectangles, trapezoids or lozenges, at most four to five times as long as wide. The lateral walls and sometimes even the terminal walls are slightly sinuous. Their usual size range is 30 to 90 μ by 15 to 30 μ. Mostly arranged in longitudinal rows, the cells meet end to end with transverse or oblique end walls. There are thick-walled (4 to 5 μ) and thinner-walled (2 to 3 μ) epidermal cells; the thicker walls are of layered structure. The two kinds of cell are arranged mosaic-like, with the convexity of the one snugly fitting into the concavity of the next. The thinner walls bear a pattern of very fine and more or less parallel cuticular lamellae, suggestive to a certain extent of the epidermis of *Stangeria*. The thin-walled epidermal cells communicate through simple pits.

Undersurface. 60 to 65 stomata per sq. mm are grouped in narrower or wider bands, each including 6 to 8 rows of stomata. The width of the bands is 400 to 500 μ; that of the interbands separating them is 200 to 250 μ. Shape, arrangement and mutual relation of the epidermal cells are more or less the same in the interbands as on the upper surface. There is a slight difference in that both the thick- and thin-walled epidermal cells are generally somewhat longer in the interbands. On the other hand, the thin- and thick-walled epidermal cells surrounding the stomata are more isodiametric, squat rectangular or polygonal. The stomata are generally overarched by 6 to 8 accessory cells which form a conical crater-like mound slightly rising above the epidermal surface. The length of the guard cells is 35 to 40 μ; their width is 18 to 20 μ. The walls facing the stomatal pit of the accessory cells are 3 to 4 μ thick; their lateral walls hardly attain 1·5 μ.The exterior surfaces of the accessory cells are finely tuberculate. Pit depth is 7 to 8 μ. The slit between the guard cells is longer than the outside diameter of the pit. The stomatal structure of *Macrozamia communis* perfectly agrees with that of the other *Macrozamia* species; it consequently represents a characteristic *Macrozamia* type.

Macrozamia fawcettii C. Moore (1884)

Plate XCVIII, Drawing 25; Plate CXXII, Photos 1–4

Leaf hypostomatic. On the *upper surface* of the leaflet, the cells are arranged parallel to the leaflet axis, joined end to end by oblique, transverse, rounded or tapering end walls or interwedged halfway between the two adjacent cells. Above the veins, the epidermal cells are somewhat longer and narrower but do not differ in structure from the other cells. Cells length is varied, 50 to 300 μ; width is 18 to 22 μ.

There are thick-walled (3 to 3·5 μ) and thin-walled (1·5 to 2 μ) epidermal cells. The thick walls are uniformly smooth, unpitted; the thin walls bear tiny simple pits. Containing chloroplastids, the thin-walled cells are somewhat wider, up to 24 μ (Photo 2).

On the *undersurface* of the leaflet, the stomata are arranged in longitudinal bands of 400 to 450 μ width separated by interbands 250 to 350 μ wide. Size, shape and arrangement of the epidermal cells are the same in the interbands as on the upper surface. Most bands include 4 to 7 rows of stomata, transverse rows (parasticha) are rare. There are about 40 to 45 stomata per sq. mm. The epidermal cells among the stomata are much shorter and much more varied in shape than those on the upper surface. Shapes include triangles, squares, trapezoids and a variety of other forms.

The length including the polar cells of the gaseous-interchange apparatus is 210 to 220 μ of which about 80 to 90 μ is taken up by one elongate polar cell whose width is 13 to 18 μ.

The number of the accessory cells is 4 to 6; their walls are thin and their surface finely pitted.

The end walls facing the stomatal pit of the accessory cells are slightly rounded and much thicker than the others which are perfectly smooth and unpitted. Similar in structure to the thin-walled epidermal cells, these accessory cells sometimes contain chloroplastids.

The endings of the accessory cells overarch the guard cells. Their length is 35 to 45 μ, their width 25 to 30 μ. On the bottom of the stomatal pit there are the two guard cells; the slit between them reaches beyond the circumference of the pit. The endings of the guard cells are tapering and more or less parallel. The length of the guard cells is 35 to 45 μ; the width of one is 16 to 18 μ. The thickened, lignified dorsal portion of the guard cell is 4 to 5 μ thick.

Macrozamia macdonnelli (F. Muell.) A. DC. (1868)

Plate XCVII, Drawing 20; Plate CXXIII, Photos 1–4; Fig. 9

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells, at most twice to 4 times as long as wide are frequently arranged in more or less regular longitudinal rows. Triangular, square, rhombic, trapezoidal or oblong in shape,

in most cases they meet end to end, joining transverse or oblique walls. Their lateral walls are frequently enough sinuous, the height of the waves not exceeding $\frac{1}{6}$ to $\frac{1}{10}$ of the width of the lumen. There are thin-walled (2 to 3 μ) and thicker-walled cells; the walls of the latter are usually of uniform thickness (4 to 5 μ) and of layered structure; their lumina follow the outline of the cell; the lumina of some elongate narrow cells are reduced to mere slits. The length of the thick-walled cells is 60 to 120 μ, their width is 15 to 30 μ; the thin-walled cells are shorter, 20 to 60 μ long and 15 to 30 μ wide. The rectangular cells are frequently elongate in the direction of the veins; in other cases they are quite squat, measuring e.g. only 15 μ in the longitudinal and 30 μ in the transverse direction. The surfaces of both the thick- and thin-walled cells are covered by very fine cuticles (Photos 1, 3); besides these they also bear tiny tubercles.

On the *undersurface* of the leaflet, the stomata occur in longitudinal bands of 400 to 550 μ width separated by interbands only 150 to 200 μ wide. Size, shape, structure and arrangement of the epidermal cells in the interbands agree with those on the upper surface. There are 80 to 85 stomata per sq. mm. In the bands, the stomata form 5 to 8 longitudinal rows on the one hand and almost transverse ones on the other. The almost isodiametric thin- and thick-walled epidermal cells among the stomata form a mosaic-like pattern. The guard cells of the stomata are overarched by 6 to 10 cells; the shape of the lateral and polar cells is so much alike that it is hardly possible to tell them apart. The walls facing the stomatal pit of both the polar and lateral cells are greatly thickened, their other walls are quite thin. The length of the stomatal pit is 35 μ; its width is about the same. The length of the guard cells is 35 to 40 μ, the width of one is 18 to 20 μ. Size and shape of the pit aperture vary in dependence on the number of accessory and polar cells. Pit depth is 7 to 8 μ; the slit between the two guard cells is longer than the outside diameter of the pit. This structure is somewhat suggestive of the stomatal structure of *Cycas revoluta*, but not without substantial differences. The size including the accessory cells of the gaseous-interchange apparatus is 80 to 100 μ by 60 to 70 μ; in other cases, the external walls of the accessory and polar cells form almost perfect circles, also reminding of *Cycas revoluta*.

Macrozamia miquelii (F. Muell.) A.DC. (1868)

Plate XCVII, Drawing 22; Plate CXXIV, Photos 1 to 4

Leaf amphistomatic. On the *upper surface* of the leaflet, the stomata are arranged in solitary, loose longitudinal rows. Some rows are farther apart than the others; these wider spacings probably mark the presence of the veins. There are 35 to 40 stomata per sq. mm. The epidermal cells in the bands between the stomatal rows are usually rectangular, rhombic, more seldom square or triangular, arranged end to end, joining transverse or oblique end walls. Their size range is 40 to 150 μ by 15 to 20 μ; their walls are comparatively thin (1 to 2 μ). Around the stomata,

however, the epidermal cells are largely thick walled (5 to 6 μ). The lumen mostly follows the outline of the cell, but it is reduced in places to a mere gash. The thin- and thick-walled cells communicate through tiny simple pits.

The guard cells are generally overarched by 6 accessory cells plus the two polar cells. The aperture of the stomatal pit is circular, elliptic, quadrangular or pentagonal depending on the shape and number of the accessory cells. Pit depth is 6 to 7 μ. Most accessory cells are trapezoidal or rectangular.

On the *undersurface* of the leaflet the stomata are grouped in bands including 4 to 6 rows rather than in solitary rows. There are 30 to 32 stomata per sq. mm. The width of the bands is 300 to 500 μ; that of the interbands separating them is 200 to 300 μ. Shape, size and arrangement of the epidermal cells are much the same as on the upper surface; this is also an amphistomatic character. Also on the undersurface, the stomatal pits are formed by 4 to 6 accessory cells whose size and shape almost perfectly agree with those on the upper surface. As a slight difference, the stomata may be more close spaced on the undersurface, and the walls of the epidermal cells among them are generally thicker. The length of the cells is 30 to 140 μ, their width 10 to 22 μ. The lumina of the strongly elongate thick-walled cells are very often slit-like. The length including the accessory cells of the gaseous-interchange apparatus is 80 to 100 μ, its width 70 to 80 μ. The length of the guard cells is 30 to 35 μ; the width of one is 15 to 20 μ.

Macrozamia moorei F. Muell. (1881)

Plate XCVII, Drawing 21; Plate CXXV, Photos 1–4; Fig. 10

Leaf amphistomatic. On both surfaces of the leaflet, the stomata are arranged in longitudinal rows, solitary on the upper surface and grouped in narrower or wider bands on the undersurface.

On the *upper surface* of the leaflet, there are 45 to 50 stomata per sq. mm. The solitary rows are generally spaced at distances of 140 to 150 μ. The rows themselves are 50 to 60 μ wide; in the intervals between them the epidermal cells are somewhat elongate in the direction of the leaflet axis, having the shapes of squat rectangles, lozenges, rhomboids or trapezoids and joined end to end, mostly with nearly transverse, in other cases with nearly longitudinal end walls. The length of the cells is 30 to 150 μ, their width 15 to 20 μ. The epidermal cells among the stomata are slightly shorter and of different shape.

There are thick-walled (5 to 6 μ) and thin-walled (2 to 3 μ) epidermal cells: the walls of the latter bear numerous simple pits. The thick walls are layered and unpitted: pittedness, and the width of the lumen are varied depending on the thickness of the cell wall. Shape, size and structure of the stomata in the solitary longitudinal rows perfectly agree with those on the undersurface.

On the *undersurface* of the leaflet, loosely parallel rows of stomata are grouped in broad longitudinal bands. The width of the bands is 100 to 600 μ. The bands of

600 μ width include 7 rows of stomata. The width of the interbands is 50 to 250 μ. There are 60 to 70 stomata per sq. mm.

Shape, size and structure of the epidermal cells in the band hardly differ from those of the similar cells in the interbands, except that perhaps the cells are shorter near the stomata. Here, too, there are thick- and thin-walled cells: the thick walls are layered; the lumina of the thick-walled cells do not always follow the cell outline. The thin-walled cells contain chloroplastids; there are many tiny simple pits in their walls.

The length of the stomata is 130 to 140 μ, including 60 μ for the two polar cells; their width, 65 to 70 μ. The guard cells are overarched by the accessory cells whose number together with the polar cells is generally 6. The walls facing the stomatal pit of the accessory cells are substantially thicker than their lateral walls (6 to 7 μ and 2 to 3 μ, respectively). The aperture of the stomatal pit is 25 to 30 μ by 18 to 20 μ. On the bottom of the pit there are two guard cells; the slit between them reaches beyond the periphery of the pit.

The length of the guard cells is 45 to 50 μ, their width is 15 to 18 μ; the endings of both guard cells are slightly tapering and elongate (7 to 8 μ); their internal walls are more or less parallel.

The thickened dorsal wall of the guard cells is 6 to 7 μ thick and bears thick transverse lamellae. Around some cells in the interbands, the thin-walled parenchyma cells are grouped as if they surrounded rudimentary stomata.

Macrozamia pauli-guilielmi W. Hill et F. Muell. (1859)

Plate XCVIII, Drawing 27; Plate CXXVI, Photos 1–4

Leaf hypostomatic. Highly elongate, the epidermal cells of the *upper surface* are arranged parallel to the leaflet axis, either end to end or interwedged with long oblique walls. The length of the cells is 300 to 400 μ; their width is as little as 15 to 20 μ. Their walls are 3 to 4 μ thick, their lumina are very narrow in consequence, sometimes almost slit-like. The walls of the thinner-walled cells measure 2 to 3 μ. There are a few twin epidermal cells: two cells alike in size and shape separated by a transverse wall. The walls are unpitted.

On the *undersurface* of the leaflet, 25 to 30 stomata per sq. mm are arranged in narrower or broader bands including 4 to 6 parallel rows of stomata. The width of the interbands is 200 to 250 μ, that of the bands is 600 to 800 μ. The stomata are surrounded by 4 to 6 accessory cells and 2 polar cells. The size including these cells of the gaseous-interchange apparatus is 90 to 110 μ by 65 to 70 μ. The length of the guard cells is 35 to 40 μ, the width of one is 12 to 15 μ. The walls facing the stomatal pit of the accessory cells are much thicker (3 to 4 μ) than their lateral walls (1 μ). The size of the aperture of the stomatal pit is 50 to 52 μ by 17 to 20 μ. The pit is sometimes constituted by three accessory cells only, one on one side only and two smaller ones on the other. The polar cells are always shorter than the other

accessory cells which are about 50 μ long and 30 to 40 μ wide. The slit between the two guard cells is as long as the diameter of the pit aperture. The thickened walls of the guard cells measure 3 to 4 μ.

It is an interesting feature of this species that one of the accessory cells is substantially elongate tapering, hereby impressing a peculiar design upon the environment of the stoma.

Among the guard cells there occur both thick- and thin-walled epidermal cells; the latter contain chloroplastids.

Macrozamia secunda C. Moore (1884)

Plate XCVIII, Drawing 26; Plate CXXVII, Photos 1–4

Leaf hypostomatic. On the *uppersurface* of the leaflet, the epidermal cells are elongate parallel to the leaflet axis, placed end to end with oblique or transverse with tapering ends, or interwedged. Their length is varied, generally 100 to 200 μ; their width is 12 to 15 μ. There are thick-walled (3 to 4·5 μ) and thin-walled (2 to 3 μ) epidermal cells. The thick walls are perfectly smooth; the thin walls bear simple pits; the thin-walled cells occasionally contain chloroplastids. Above the veins, the cells are somewhat more elongated and narrower but agree in structure perfectly with the other epidermal cells.

On the *undersurface* of the leaflet, the stomata are arranged in longitudinal bands of 300 to 450 μ width separated by interbands 250 to 300 μ wide. Shape, size and arrangement of the epidermal cells in the interbands perfectly agree with those on the upper surface. Solitary rows of stomata also occur, but most bands include 4 to 6 rows. Oblique parasticha are scarce, there are 35 to 40 stomata per sq. mm.

The length of the gaseous-interchange apparatus is, together with the elongate polar cells, about 120 to 130 μ. The length of the polar cells is 60 to 90 μ, their width, 14 to 15 μ. The length of the guard cells is 50 to 55 μ, the width of one is 18 to 20 μ; the aperture of the stomatal pit is about 15 to 20 μ wide by 30 to 40 μ long, its length is about the same as that of the slit between the guard cells. The pit is constituted besides the two polar cells by 4 to 5 accessory cells overarching the guard cells whose walls facing the aperture are substantially thickened (to about 6 μ). The width of one accessory cell is 18 to 20 μ.

The epidermal cells around the stomata are generally much shorter and slightly broader than those on the upper surface. The distribution of the thick- and thin-walled cells, however, is more or less the same as on the upper surface. Here, also the thin-walled cells contain chloroplastids. The lateral and peripheral walls of the accessory cells are as thin and pitted as those of the thin-walled cells and markedly differ from the thick-walled epidermal cells.

Macrozamia spiralis (Salisb.) Miq. (1842)

Plate XCVIII, Drawing 23; Plate CXXVIII, Photos 1–4; Fig. 55

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are arranged parallel to the leaflet axis, but no definite longitudinal rows can be distinguished. Some join transverse, others oblique walls. One frequently sees smaller epidermal cells sandwiched between two larger ones. The terminal walls of the cells placed end to end are often sinuous or obliquely truncated. Twin epidermal cells occur where two cells of equal height and shape are separated by a transverse wall. The length of the cells is 100 to 200 μ; their width is 15 to 20 μ. Thin- and thick-walled cells are interfingered to form a mosaic-like pattern. The thick walls measure 3 μ; they are of uniform thickness and totally unpitted. The lumina exactly follow the outlines of the cell. Having walls of 1 to 2 μ thickness, the thin-walled cells contain chloroplastids. The thin- and thick-walled cells slightly differ in colour (Photos 1, 2).

On the *undersurface* of the leaflet, the stomata are arranged in narrower or broader bands including 4 to 10 parallel rows of stomata. The width of the bands ranges from 300 to 800 μ; the width of the interbands between them is 200 to 300 μ. Shape and size of the epidermal cells in the interbands and the relation of the two kinds of cell to each other is much the same as on the upper surface; their length is 60 to 200 μ. In the bands, there are 30 to 35 stomata per sq. mm. Shape, size and structure of the epidermal cells adjacent to the stomata and their accessory cells are as on the upper surface. The apical portions of the accessory cells constitute a readily visible crater around the stoma. The length of the gaseous-interchange apparatus is 100 to 120 μ; its width is 80 to 90 μ. The length of the guard cells is 30 to 35 μ; the width of one is 15 to 16 μ. The number of the accessory cells is generally 5 to 6; they are of about the same size and approximately triangular. The height of the triangles is about 50 μ; the width of their base is 60 μ; the width of their truncate end facing the stomatal pit is about 10 μ. The walls facing the pit of the accessory cells is strongly thickened (4 to 4·5 μ), whereas their lateral walls



Fig. 55. *Macrozamia spiralis* (after Graf)

are only 1 to 1·5 μ thick. The slit between the two guard cells is longer than the diameter of the stomatal pit. The depth of the pit is 8 to 9 μ. One or another of the accessory cells is substantially elongate, cornucopia fashion. The surface of the accessory cells is finely tubercular. The thin-walled parenchyma cells contain chloroplastids.

(c) ENCEPHALARTOS

Encephalartos altensteinii Lehm. (1834)

Plate C, Drawing 40; Plate CXXIX, Photos 1–4; Fig. 11

Leaf hypostomatic. On the *upper surface* of the leaflet, epidermal cells are as a rule arranged in longitudinal rows. Shapes are highly varied, transverse rectangular, triangular, quadrangular or square. Uniformly thick, the walls of two adjacent cells measure 6·5 to 7 μ.

In the chemical composition of the cell-walls there must be some difference because the walls of some cells are dark brown whereas those of the adjacent ones are perfectly colourless. The walls of the latter are also somewhat thinner. Their size is 50 to 60 μ by 15 to 20 μ. The average width of the longitudinal rows is 30 to 35 μ. In the rows, the thinner- and thicker-walled cells follow in almost regular alternation; there are no exceptionally large cells.

On the *undersurface* of the leaflet, the stomata are arranged in narrower or wider longitudinal bands of 500 to 600 μ width. In some sections there are as many as 8 rows of stomata. The interbands are 250 to 300 μ wide. Shape and arrangement of the cells are much the same in the latter as on the upper surface, but the cells are somewhat smaller, 40 to 50 μ by 15 to 20 μ. The walls are uniformly thick; the lumen invariably follows the outline of the cell.

The stomata are in general surrounded by 4 to 6 accessory cells. The two largest accessory cells are always larger than the two polar cells. The accessory cells form a very low truncated crater cone around the stoma. The height of this cone is 3 to 4 μ above the plane of the epidermis; the stomatal pit surround by the crater is as long as the non-thickened portion of the guarded cells (26 to 27 μ); its mean width is 14 μ. The long axis of the pit is more or less parallel to the leaflet axis. The size including the accessory cells of the gaseous-interchange apparatus is about 70 to 80 μ by 50 to 60 μ; the external walls of the accessory cells form circles or slightly flattened ellipses.

The length of the guard cells is 25 to 30 μ; the width of one is 15 to 16 μ. The walls of the accessory cells are much thinner than those of the epidermal cells among the stomata; also, their stratification is markedly different.

Encephalartos arenarius R. A. Dyer (1965)

Plate C, Drawing 37; Plate CXXX, Photos 1 – 4; Fig. 56

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are generally somewhat elongate: their size range is 40 to 150 μ by 15 to 20 μ. There are thick-walled (2 to 2·5 μ) and thin-walled (1 to 1·5 μ) cells. The finely layered thick walls bear many irregularly spaced simple pits.

The thin-walled cells frequently contain chloroplastids. The distribution of the thick- and thin-walled cells is more or less uniform. Shapes of the cells are rounded triangles, lozenges or rectangles. The orientation of the rectangles is varied, sometimes quite irregular. In the horizontal walls there are in places very small pits suggestive of *Cycas*.

On the *undersurface* of the leaflet, the stomata (20 to 22 per sq. mm) are arranged in longitudinal rows in included narrower or wider bands of 400 to 450 μ width separated by interbands 150 to 200 μ wide. In the bands, the stomata follow oblique parasticha as well as orthosticha. Size, shape and arrangement of the cells are much the same in the interbands as on the upper surface of the leaflet. Twin epidermal cells are rather frequent. The cells generally meet end to end with rounded or obliquely truncate end walls or are wedged in halfway between the two adjacent cells.

On the undersurface of the leaflet, the thick-walled epidermal cells are much more numerous than on the upper surface. Slightly shorter and more isodiametric than those on the upper surface, the epidermal cells surrounding the stomata fall into two types of conspicuously different wall thickness. Finely layered, the thicker walls measure 7 μ. Sometimes almost slit-like, their lumina generally follow the outline of the cell. The stomata together with their accessory cells are rather distinct from the adjacent epidermal cells. The accessory cells generally number 4 to 6. The polar cells hardly differ in size from the accessory cells; their walls are thin, except for those facing and overarching the stomatal pit. The length of the gaseous-interchange apparatus is 90 to 100 μ, its width 70 to 80 μ. The size of the stomatal pit is generally 35 to 40 μ by 18 to 20 μ. Pit depth is 7 to 8 μ. The aperture between the guard cells is as long as or slightly longer than the pit aperture. The length of



Fig. 56. *Encephalartos arenarius* (South Africa; after Dyer)

the guard cells is 35 to 40 μ, the width of one is 18 to 20 μ. The accessory cells somewhat differ from the adjacent epidermal cells also in that their walls are thin and finely tuberculate.

Encephalartos barteri Carruthers (1868)

Plate CI, Drawing 49; Plate CXXXI, Photos 1–4

Leaf amphistomatic. On the *upper surface* of the leaflet, stomata occur only sporadically and then generally in solitary longitudinal rows. Substantially elongate in the direction of the leaflet axis, the epidermal cells are in general 5 to 10 times longer than wide (150 to 200 μ by 15 to 25 μ). There are thick-walled and thin-walled epidermal cells; the walls of the former measure 3·5 μ. The lumen of some thick-walled cells is in places almost slit-like; in others it is more spacious and follows the outline of the cell. The thicker walls bear sporadical simple pits. The stomata arranged in longitudinal rows follow each other loosely, the length of one or two stomata apart. Their structure perfectly agrees with that of the stomata on the undersurface of the leaf. The length of the guard cells is 42 μ, the width of one is 15 to 16 μ. The number of the accessory cells is 4 to 6. The two pairs of polar cells are thin walled.

On the *undersurface* of the leaflet, the stomata are arranged in longitudinal bands alternating with narrower interbands. Most bands include 3 to 6 rows of stomata, sometimes forming oblique parasticha as well as longitudinal orthosticha. The width of the bands is 200 to 350 μ, that of the interbands 150 to 200 μ. There are 50 to 55 stomata per sq. mm. The length of the gaseous-interchange apparatus is 160 to 180 μ, its width 90 to 100 μ. Shape, size and arrangement of the epidermal cells of the interbands agree with those on the upper surface. The epidermal cells in the bands, around the stomata, are somewhat narrower than those in the interbands. There are thick-walled and thin-walled cells. The number of the accessory cells is 4 or 6, less frequently 5; their radial walls are thin; those facing the stomatal pit are, however, substantially thickened. The aperture between the guard cells is longer than the diameter of the pit aperture. The length of the guard cells is 40 to 42 μ, the width of one is 15 to 16 μ. The size of the stomatal pit is 40 μ by 30 μ. The polar cells are thin walled. The ends of the two guard cells meet at an angle of 75°. The thicker cell walls are generally smooth and only very sporadically pitted.

Encephalartos bubalinus Melville (1957)

Plate CI, Drawing 53; Plate CXXXII, Photos 1–4

Leaf hypostomatic. On the *upper surface* of the leaflet, the more or less elongate epidermal cells of varied shape are arranged in uniseriate rows approximately parallel to the leaflet axis. Most of them are considerably elongate, rectangular or

triangular, the latter generally transverse, lying across the longitudinal rows. The width of the rows is 60 to 70 μ; the bases of the transverse triangular cells measure 20 to 25 μ, their height is 60 to 100 μ. Some cells are parallel to the leaf axis. This characteristic pattern of epidermal cells definitely differs from the epidermal structure of other genera and is at best only slightly similar to *Macrozamia* (Photos 1, 2). The walls of the cells are either thin or thick. Most thin-walled cells contain chloroplastids. The thick walls measure 4 to 5 μ; they are generally of uniform thickness but narrow down locally; their lateral walls communicate through simple pits.

On the *undersurface* of the leaflet, the stomata are arranged in longitudinal rows at a density of 40 to 50 of them to the sq. mm. The bands including these rows are 500 to 550 μ wide; the width of the interbands is 100 to 220 μ. There are 6 to 12 rows of stomata in each band. Among the stomata, thick-walled epidermal cells are remarkably frequent. Their walls are much thicker than on the upper surface (6 to 8 μ). The length of the cells is 60 to 100 μ, their width 20 to 25 μ. The size including the accessory cells of the gaseous-interchange apparatus is 110 μ by 70 to 80 μ. The accessory cells are 30 to 32 μ wide and 40 to 50 μ long. The stoma is generally surrounded by 4 accessory cells. The length of the two polar cells is 40 μ, their width 15 μ. The length of the guard cells is 35 to 40 μ, the width of one is 10 to 14 μ. The stomatal pit measures 30 to 32 μ by 20 to 22 μ. Its form is varied. Pit depth is 10 to 14 μ. The aperture between the two guard cells reaches clean over the pit.

Encephalartos caffer (Thunb.) Miq. (1842)

Plate XCVIII, Drawing 28; Plate CXXXIII Photos 1–4; Fig. 57

Leaf hypostomatic. On the *upper surface* of the leaflet, the shape of the epidermal cells is highly varied: they are arranged in rows parallel to the leaflet axis (Photo 1). In places, two rows merge and there the form of the cells is even more irregular. The length of most epidermal cells is 15 to 70 μ; their width is 20 to 25 μ. In places, there are 6 to 8 epidermal cells grouped around a single cell or cavity, as if they surrounded a stoma (Photo 2), but no stomatal structure can be recognized underneath. The walls of some cells are of uniform thickness, somewhat sporadically narrowing at some points. The width of the walls is 3 to 4 μ; the lumen exactly follows the outline of the cell. The walls of some other cells are somewhat thinner (2 to 3 μ); these cells contain choloroplastids. The thin- and thick-walled cells are easy to tell apart.

On the *undersurface* of the leaflet, the stomata are arranged in more or less well-defined bands parallel to the leaflet axis. But not definite. The stomatiferous bands are always wider (250 to 300 μ) than the interbands between them (100 to 200 μ).

The lateral cells of the stomata hardly differ from the adjacent epidermal cells. The latter are generally smaller and narrower than those on the upper surface.



Fig. 57. *Encephalartos caffer* (after Dyer)

Their length is 15 to 60 μ; their width, 20 to 25 μ. Their walls are 4 to 5 μ thick. The stomata in the bands form orthosticha and somewhat sinuous transverse parasticha. The size including the accessory cells of the gaseous-interchange apparatus is 100 to 110 μ by 70 to 80 μ; there are 45 to 50 stomata per sq. mm. There are usually 4 accessory cells and 2 polar cells. The latter are elongate, 25 to 30 μ long and 5 to 6 μ wide. The former are more isodiametric, 40 to 50 μ by 25 to 30 μ. The size of the guard cells is 40 to 45 μ by 12 to 14 μ. The stomatal aperture is generally rectangular, 20 to 22 μ by 10 μ. It is more or less flush with the epidermal surface, that is, there is no protruding crater around it. Pit depth is 3 to 4 μ. The thin-walled cells are randomly scattered among the thick-walled ones.

Encephalartos cycadifolius (Jacq.) Lehm (1934)

Plate XCVIII, Drawing 31; Plate CXXXIV, Photos 1–4; Fig. 58

Leaf hypostomatic. The *upper surface* of the leaflet (Photos 1, 2) bears no stomata, but there are some clusters of 4 or 5 cells arranged as if surrounding an intracellular duct. Elongate parallel to the leaflet axis, the cells form uniserial rows. Row width



Fig. 58. *Encephalartos cycadifolius* (photo by Dyer)

is 20 to 30 μ. Length and shape of the cells making up the rows are highly varied. Shapes include squat and more elongate oblongs, squares or equilateral and isosceles triangles, the latter perpendicular to the leaflet axis. Their length is 25 to 60 μ, their width, 15 to 20 μ.

There are thin-walled and thick-walled cells. The thick walls are 10 μ thick in some of their portions but no more than 2 to 3 μ thick elsewhere. In the thick-walled cells, the lumen does not always follow the outline of the cell, being substantially constricted in some cells and obliterated in the narrowest ones. The thin walls are 2 to 3 μ thick throughout. Slightly elongate in the direction of the leaflet axis and joined end to end by transverse walls, the thin-walled cells contain chloropastids. Their usual length is 25 to 30 μ, their width 15 to 20 μ. There are no traces of hair formations.

On the *undersurface* (Photos 3, 4), the stomata occur in relatively narrow but well-defined longitudinal bands of 300 to 320 μ width, separated by interbands of almost twice that width (500 to 600 μ). In the bands, there are usually 6 to 8 rows of stomata; moreover, the adjacent stomata of the rows tend to form straight or sinuous transverse rows. Shape, size and arrangement of the cells in the interbands fully agree with those of the cells on the upper surface. Also here, there are both thick-walled and thin-walled cells.

The stomata are usually loosely scattered in the bands but fairly close spaced locally with 55 to 60 of them to the sq. mm. The length of the gaseous-interchange apparatus is 55 to 60 μ; its breadth is 45 to 50 mm. The stomata are surrounded by 4 to 6 accessory cells slightly overarching the stomata. The walls facing the stoma-

tal pit of the accessory cells are much thicker (6 μ) than their lateral walls (2 or 3 μ). The pit aperture is 17 to 18 μ by 10 to 12 μ in size, pit depth is 5 to 6 μ. The rest of the epidermal cells around the stomata may be both thick walled or thin walled (6 to 8 μ or 2 to 3 μ, respectively). On the undersurface, the epidermal cells are somewhat shorter, 25 to 40 μ in length.

Encephalartos eximius Verdoorn (1954)

Plate C, Drawing 46; Plate CXXXV, Photos 1–4

Leaf hypostomatic. The *upper surface* of the leaflet bears occasional hair bases. Exhibiting a variety of shapes, the epidermal cells are elongate in the direction of the leaflet axis. The square or oblong cells are locally arranged in longitudinal rows. The side length of the square cells is 20 to 25 μ; that of the oblong ones may attain 150 μ. There are thick-walled and thin-walled cells. The thick cell walls measure 2 to 3 μ. The thickest-walled cells have no lumen and their surface bears longitudinal lamellae, some of which extend over the whole length of the cell. These laminated cells may locally form longitudinal rows, being irregularly scattered elsewhere. The thin-walled cells occasionally contain chloroplastids.

On the *undersurface*, the stomata are arranged in longitudinal bands 300 to 400 μ wide, separated by interbands of 150 to 200 μ width. There are 80 to 85 stomata per sq. mm. They form but seldom longitudinal rows; the diagonal rows are much easier to recognize. Size, shape and arrangement of the epidermal cells are much the same in the interbands as on the upper surface, but the cells in the stomatiferous bands are much squatter, more varied of shape and quite often isodiametric. The stomata are usually surrounded by 4 to 6 accessory cells; the two polar cells are usually longer than the accessory cells.

The length of the stomata, including the polar cells, is 100 to 110 μ; their width is 80 to 90 μ. The accessory cells are 30 to 35 μ in diameter. Their lateral walls are thin; their walls facing the stomatal pit are much thicker (4 to 5 μ). Their surface is usually covered with radially arranged cuticular lamellae in much the same way as the thick-walled epidermal cells of the upper surface. The length of a guard cell is 30 to 35 μ, its width is 16 μ. The pit wall rises markedly above the plane of the leaflet. The size of the pit aperture is 28 to 30 by 18 to 20 μ. Pit depth is 6 to 7 μ.

Encephalartos ferox Bertol. (1857)

Plate XCIX, Drawing 36; Plate CXXXVI, Photos 1–4; Fig. 59

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are 2 to 3 (at most 5) times as long as wide. Their length varies from 30 to 120 μ, their width between 15 and 20 μ. Highly varied in shape and arrangement, they locally form

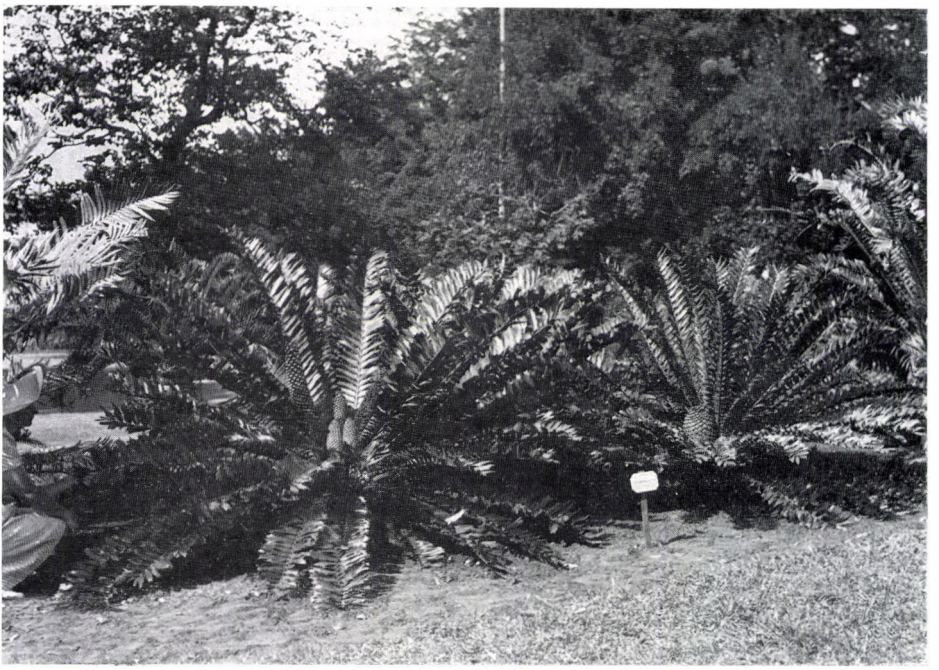

Fig. 59. *Encephalartos ferox* (Durban; after Dyer)

longitudinal or transverse rows. In this latter case, the transverse cells cover the ends of 3 or 4 longitudinal cells. The pistol-, ham-, sickle-, oblong-shaped, etc. cells are either thin or thick walled. The thinner walls measure 1 to 1·5 μ, the thicker ones 4 to 6 μ. The thicker walls are layered; the thinner ones bear many small simple pits. The thin-walled cells frequently contain chloroplastids.

On the *undersurface*, the stomata do not occur in well-defined longitudinal bands. The bands, 300 to 500 μ wide, and the interbands, 200 to 250 μ wide, can but occasionally be recognized. Size, shape and arrangement of the epidermal cells in the interbands agree in a general way with those of the cells on the upper surface. In the stomatal bands there are 2, 4, 6 or 8 parallel rows of stomata, with 34 to 40 stomata per sq. mm. The epidermal cells around the stomata are usually shorter and thicker-walled, with rare thinner-walled epidermal cells containing numerous chloroplastids. The gaseous-interchange apparatus including 5 or 6 accessory cells of 30 to 35 μ width and two markedly narrower polar cells of but 20 to 22 μ width has a size of 100 to 120 μ by 70 to 80 μ. The polar cells are not very elongate; as a result, the outline of the apparatus is a slightly flattened ellipse. The radial walls of the accessory cells are thin; their walls facing the pit are substantially thickened, however. The length of a guard cell is 35 to 40 μ, its width is 15 to 18 μ. In some instances, the joint width of the two guard cells somewhat exceeds their length. The pit aperture is circular, or more or less flattened, elliptical. The slit of

the stoma is longer than the pit diameter. The guard cells are thick walled (7 to 8 μ). The two guard cells join ends like opposed crescents; their ends are slightly rounded. The surfaces of the polar cells sometimes bear hardly visible cuticular lamellae.

Encephalartos friderici-guilielmi Lehm. (1834)

Plate CIV, Drawing 72; Plate CXXXVII, Photos 1–4; Fig. 60

Leaf to some extent amphistomatic, with groupings of cells suggestive of stomata irregularly scattered on the *upper surface* of the leaflet. At the middle of each such cluster of cells, there is a well-defined pit; indeed, around some such apertures, the cells are arranged in the fashion of the accessory cells of the stomata. Guard cells can but very seldom be observed under the apertures. The epidermal cells are usually isodiametric and but very seldom of a length of more than 4 to 5 times their width. Most such long cells (60 to 70 μ long and 20 to 25 μ wide) are very thin walled. The average cells are shorter, however. Highly varied in shape (triangular, quadrangular, oblong, trapezoidal or rhomboidal), most cells are arranged in rows parallel to the leaflet axis. The thick cell walls are 3 to 5 μ thick, pitted; the thinner walls are 1 to 2 μ thick. The thin-walled cells contain numerous chloroplastids. The walls



Fig. 60. *Encephalartos friderici-guilielmi* (South Africa; photo by Dyer)

facing the stomatal pit of the thin-walled accessory cells are considerably thickened. This, too, proves these pits to represent, in fact, modified stomata.

On the *undersurface* of the leaflet, the stomata occur in longitudinal bands of various width. There are 6 to 10 stomata in a row; the rows are longitudinal in the main, but somewhat oblique ones can also be recognized. The length of the gaseous-interchange apparatus is 100 to 110 μ; its width is 70 to 80 μ; there are 6 accessory cells on the average, plus two polar cells, all overarching the stoma. The walls facing the stomatal pit of the accessory cells are much thicker (6 or 7 μ) than their radial or tangential walls. 25 to 30 μ in length, 16 to 24 μ in width, the pit apertures are fairly varied of shape, sometimes polygonal in dependence on the number of accessory cells. On the bottom of the pit there are two guard cells of 35 μ length and 24 to 25 μ width. Their end walls are slightly arcuate. The walls of the epidermal cells between the stomata may be thick or thin, some attaining 4 to 5 μ, some being rather fine (1 to 2 μ). The thinner-walled cells usually form clusters of various size. The interbands, 20 to 30 cells wide, are generally wider than the bands themselves; in them, the walls of some cells are very thick and layered; the lumina of these are reduced to mere slits. Other cell walls are only 6 or 7 μ thick, and the thinnest ones are no thicker than 1 μ. Shape and arrangement of the epidermal cells in the interbands agree with those on the upper surface of the leaflet, although the cells are somewhat shorter.

Encephalartos gratus Prain (1916)

Plate CI, Drawing 52; Plate CXXXVIII, Photos 1–4

Leaf hypostomatic. The *upper surface* of the leaflet bears relatively short epidermal cells, elongate in the direction of the leaflet axis, but not arranged in well-defined longitudinal rows. They join tapering or truncate but always rounded tips.Twin epidermal cells are fairly frequent. Cell length ranges from 50 to 200 μ; cell width is 15 to 20 μ. The walls are usually of uniform thickness: there are no cells having exceptionally thick walls. Very thin-walled epidermal cells are also very scarce. The joint thickness of two adjacent walls hardy attains 6 μ; the walls are entirely smooth; pits are simple and very scarce.

On the *undersurface*, the stomata usually occur in wide bands separated by, but not very sharply bordered against relatively narrow interbands. The broader bands of 300 to 450 μ width may include as many as 6 rows of stomata. There are 35 to 40 stomata per sq. mm. The width of the interbands does not exceed 200 μ. Both in the bands and interbands, the shape, size and arrangement of the epidermal cells are about the same as on the upper surface of the leaflet. There are thin-walled and thick-walled epidermal cells. The length of the gaseous-interchange apparatus, including the polar cells, is 150 to 170 μ; its width is 75 to 80 μ. The pit aperture is usually surrounded by 4 accessory and 2 polar cells. The accessory cells frequently embrace the narrow polar cells. The size of the latter is 50 to 70 μ by 18 to 20 μ;

their side walls are thin; their walls facing the pit are, however, substantially thickened. The guard cells are 40 to 45 μ long and 15 to 18 μ wide; their walls are 8 to 10 μ thick. The pit aperture is usually a somewhat flattened ellipse of about 30 to 35 μ length. Pit depth is 4 to 5 μ. The slit between the guard cells usually reaches beyond the crater aperture.

Encephalartos hildebrandtii A. Braun et Bouché (1874)

Plate CI, Drawing 54; Plate CXXXIX, Photos 1–4; Fig. 61

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells stand close packed, in rows about parallel to the leaflet axis. The width of these rows is 20 to 25 μ; the cells themselves are 30 to 90 μ long. There are thick-walled and thin-walled cells. Both types bear relatively numerous small pits. The thin walls measure 2 to 3 μ; the thick walls measure 4 to 5 μ and exhibit a layered structure. Pits tend to occur in pairs wherever a thin-walled cell contacts a thick-walled one (Photo 2). The lumina of the thick-walled cells have about the same shape as the cell surface. The thin-walled cells contain chloroplastids which proves their assimilatory function; the rest of the cells serve to lend to the tissue the required strength. The cells are highly varied in shape (triangular, quadrangular, trapezoidal, rhombic or irregular); some cells are completely closed in by two adjacent ones (Photo 2).

On the *undersurface* of the leaflet, the stomata form ill-defined rows parallel to the leaflet axis. The rows occur in bands of various width (600 to 700 μ) separated by interbands 100 to 130 μ wide. In each band, there are 3 to 6 rows of stomata; each interband comprises 4 to 8 rows of cells. In the bands, there are about 30 to 36 stomata per sq. mm. The epidermal cells between the stomata are similar in shape, wall thickness and size to the cells on the upper surface of the leaflet. There are small differences in the shape and arrangement of the cells, modified by the presence of the stomata. The size of the gaseous-interchange apparatus including the accessory and polar cells is 90 to 100 μ by 60 to 70 μ. (There are usually 3 or 4 accessory cells and two polar cells.) The width of a polar cell is 18 to 20 μ, its length is also about 20 μ. The walls facing the stomatal pit of the

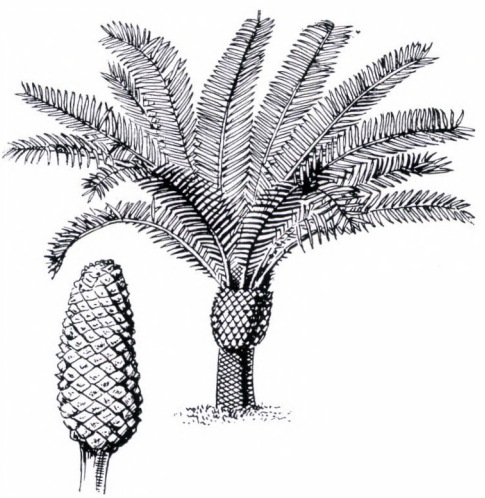

Fig. 61. *Encephalartos hildebrandtii* (after Wieland)

surrounding cells are thick; their other walls are much thinner. The walls of the accessory cells are always thinner than those of the adjacent thin- and thick-walled epidermal cells. The size of the accessory cells is 20 to 22 μ by 40 to 70 μ. Pit size is 30 to 35 μ by 18 to 20 μ. Beneath the pit, there are two guard cells: the slit between them is as long as the length of the pit or slightly longer. The length of one guard cell is 40 to 45 μ, its width is 18 to 20 μ. Thin- and thick-walled epidermal cells occur in about equal numbers around the stomata.

Encephalartos horridus Lehm. (1843)

Plate C, Drawing 38; Plate CXL, Photos 1–4; Fig. 62

Leaf hypostomatic. On the *upper surface* of the leaflet, most cells are seen to be arranged in rows parallel to the leaflet axis. The epidermal cells above the veins are slightly different in size and shape from the cells in between. Cell shapes are highly varied (square, oblong, rhombic, rhomboid, triangular, etc.). Cell junctions also exhibit a high degree of variety. There are thin-walled and thick-walled cells with walls measuring 1 to 2 μ and 2 to 4 μ, respectively. The cells communicate by simple pits in their side walls. The thinner-walled cells contain chloroplastids, indicating them to be capable of assimilation. The width of the longitudinal rows is 20 to 35 μ,



Fig. 62. *Encephalartos horridus* (photo by Dyer)

sufficient to contain one transverse cell or two longitudinal ones. The length of this latter kind of cell is usually 40 to 80 μ.

On the *undersurface*, the stomata are found in bands of 800 to 900 μ width which carry 40 to 45 stomata per sq. mm. The interbands are 250 to 300 μ wide. Shape, size and arrangement of the cells are much the same in the interbands as on the upper surface of the leaflet. Each band includes 8 to 12 rows of stomata, parallel to the leaflet axis. The length of the gaseous-interchange apparatus, including the polar cells, is 100 to 110 μ; its width is 80 to 90 μ. There are 6 to 8 accessory cells, rising crater-like above the rest of the epidermal cells. The stomatal pit is polygonal with arched sides; it is easy to tell the number of accessory cells by the number of the sides of the polygon. The walls facing the pit of the auxiliary cells are much thicker than their side walls. The length of the accessory cells is 30 to 35 μ; their outer side is of about the same length, whereas their side facing the pit is 10 to 12 μ long. Beneath the pit, there are two guard cells: the slit between them reaches far beyond the perimeter of the pit. The length of one guard cell is 35 to 40 μ; its width is 18 to 20 μ. Pit depth is 10 to 12 μ. The epidermal cells surrounding the apparatus are much thicker walled (6 to 7 μ) than the rest of the epidermal cells; their lumina do not always follow the outlines of the cells, being partly or completely obturated. The thin-walled epidermal cells joining these thick-walled ones have walls measuring 2 to 4 μ.

Encephalartos humilis Verdoorn (1951)

Plate C, Drawing 43; Plate CXLI, Photos 1–4; Fig. 63

Leaf hypostomatic. On the *upper surface* of the leaflet, bases of trichomes are fairly frequent. In Photo 1 the dark spots represent the vestiges of hair structures. Locally, there are epidermal cells substantially elongate parallel to the leaflet axis. Their length is 80 to 250 μ; their width is 15 to 20 μ. Their highly varied shapes include elongate crescents, ham and pistol shapes, oblongs, rhombs and triangles. Some are wedged together with rounded tips; others join end to end with oblique or transverse end walls. Cells fall, particularly near the seam of the leaflet, into two distinct types, the one thin, the other thick walled. The thin walls bear numerous simple pits; the thick walls are usually layered and the pits in them are reduced almost to slits. In the middle portion of the pinna, thick-walled cells are much less abundant.

On the *undersurface* of the leaflet, the stomatiferous bands are about as wide (200 to 250 μ) as the interbands between them. One sq. mm usually carries 60 to 65 stomata. Size, shape and arrangement of the epidermal cells are about the same in the interbands as on the upper surface, but the cells are slightly shorter (50 to 200 μ). These elongate cells of the interbands are rather thick walled, with slit-like lumina; the thin-walled type of epidermal cell is scarce. In this respect, the species is definitely different from all other known species of *Encephalartos*. Also between the stomata,



Fig. 63. *Encephalartos humilis* (after Dyer)

thick-walled cells are much more frequent than thin-walled ones. The stomata are usually surrounded by 4 accessory cells and a pair of elongate polar cells. The length of the gaseous-interchange apparatus including the polar cells is 220 to 230 μ; the length of a polar cell is 40 to 45 μ; its width is 15 to 17 μ. The width of the apparatus, including the accessory cells, is 110 to 120 μ. The guard cells are 40 to 50 μ long and 18 to 20 μ wide. The stomatal pit is somewhat lengthened in the direction of the leaflet axis, being 35 to 50 μ long, 25 to 30 μ wide and 4 to 5 μ deep. The accessory cells are usually trapezoidal in shape, with the short side of the trapezium facing the pit. Their walls are slightly thickened on this side. The slit between the guard cells reaches beyond the perimeter of the pit. Guard cell walls are 7 to 8 μ thick.

Encephalartos inopinus Dyer (1964)

Plate C, Drawing 45; Plate CXLII, Photos 1–4; Fig. 12

The *upper surface* of the leaflet bears apertures resembling stomata, surrounded by epidermal cells arranged much the same way as around the stomata: hence, the leaf is to be considered amphistomatic. The apertures are, in point of fact, gaseous-interchange pits lacking guard cells. They are 18 to 20 μ in diameter, circular, elliptically elongate parallel to the leaflet axis, or polygonal. They are usually surrounded by thin-walled epidermal cells rich in chlorophyll, forming longitudinal rows. There

are both thick-walled and thin-walled cells (measuring 6 to 7 μ and 3 to 4 μ, respectively). Cell length ranges from 30 to 110 μ; the majority is, however, 60 to 70 μ long and 10 to 15 μ wide. The rows of cells are 20 to 35 μ wide; the broadest cells are as wide as the row (about 30 μ). The thin- and thick-walled cells are arranged within the rows in a variety of patterns. Cell shapes include elongate oblongs, trapezia, lozenges and – most frequently – triangles. The outer surfaces of the cells often bear minute tubercles of circular section and various sizes. The thick cell walls are layered and bear a few simple pits.

On the *undersurface* of the leaflet, the stomata (30 to 32 per sq. mm) form conspicuous longitudinal rows and much less conspicuous transverse, slightly diagonal ones. There are 3 to 6 longitudinal rows in each stomatiferous band of 500 to 600 μ width. The width of the interbands is 250 to 300 μ. In them, epidermal cells 30 to 110 μ long are arranged in 10 to 14 longitudinal rows. The width of these cells (15 to 30 μ) is about the same as on the upper surface of the leaflet. Owing to the presence of the stomata, the cells in the bands are somewhat shorter (20 to 100 μ) than in the interbands. Among the thick-walled epidermal cells there occur also some thin-walled ones. Most of the slits of the stomata are arranged lengthwise, but some are oblique or even transverse. Length and width of the stomata are varied. The size of the gaseous-interchange apparatus including the accessory cells is 120 to 130 μ by 100 to 110 μ. The length of one guard cell is 70 to 72 μ; its width is 14 to 18 μ. Slightly elevated above the surface, the apertures of the stomatal pits are 20 to 25 μ long and 13 to 20 μ wide. There are 3 to 6 trapezoidal accessory cells: the base of the trapezium is 30 to 35 μ, its height is 25 to 30 μ. The surfaces of the accessory cells bear fine lamella of ecutin parallel to their radial walls: some cells exhibit single circular tubercles of 3 to 4 μ size. Pit depth is 5 to 6 μ.

Encephalartos latifrons Lehm. (1837)

Plate CI, Drawing 51; Plate CXLIII, Photos 1–4; Fig. 64

Leaf hypostomatic. The epidermal cells on the *upper surface* of the leaflet are usually isodiametric. Some portions of the leaf bear, however, bands consisting of oblong cells, 50 to 150 μ long, 15 to 35 μ wide. Epidermal cells are either thin walled (2 to 3 μ) or thick walled (3 to 4 μ): there is no striking difference between the thin and thick walls. The latter are of uniform thickness and layered structure, and bear no pits, whereas the thin walls often bear simple pits. The two kinds of cell differ also in light refraction (Photo 3). Most of the thin-walled cells are full of chloroplastids. The two kinds of cell form a mosaic-like pattern, but the thin-walled cells with chloroplastids are invariably in contact with one or more similar cells.

On the *undersurface*, the stomata are arranged in bands of various width. There are 45 to 50 stomata per sq. mm. The bands, 800 to 1000 μ wide, are separated by interbands of but 200 to 250 μ width. The epidermal cells in the interbands agree



Fig. 64. *Encephalartos latifrons* (photo by Dyer)

in size and shape with those on the upper surface. The only difference is that most cells are elongate parallel to the veins of the leaflet. There are 8 to 10 loosely ordered rows of stomata in each band. Some of the rows are rather sinuous, and the accessory cells of two stomata in adjacent rows may almost touch.

The more or less crater-like stomatal pits are surrounded by 4, 6 or 8 accessory cells. The aperture is a polygon of as many arcuate sides as there are accessory cells. The walls facing the aperture of these cells are much thicker than their other walls. Pit depth is 8 to 9 μ. The gaseous-interchange apparatus is usually surrounded by thick-walled epidermal cells having walls 6 to 7 μ thick, but the accessory cells themselves are thin walled (2 μ). The slit between the guard cells is much longer than the diameter of the pit aperture. The guard cells are 35 to 40 μ long and 15 to 18 μ wide. In the thinner-walled epidermal cells, scattered among the thicker-walled ones, chloroplastids are fairly abundant. Their walls bear numerous simple pits, which make some of them look like garlands. The length of the gaseous-interchange apparatus including accessory cells is 85 to 90 μ; its width is 65 to 70 μ. Fairly often, the accessory cells around the guard cells are asymmetrically arranged, e.g. with one cell on one side and two or three on the other. On the basis of its epidermal and stomatal structure, this species fits well into the genus *Encephalartos*.

Encephalartos laurentianus De Wild (1903)

Plate XCIX, Drawing 32; Plate CXLIV, Photos 1–4; Fig. 65

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells do not constitute well-defined longitudinal rows. Unlike the *Encephalartos* species described above, this one has most of its cells substantially elongated in the longitu-

dinal direction. Epidermal cells in transverse position are very rare. Cell length is 40 to 150 μ, cell width is 15 to 25 μ. Most of the cells are joined by oblique end walls, but transverse walls also occur here and there. Twin cells – two epidermal cells of about the same size joined by a transverse end wall – are also fairly common. There are both thin-walled and thick-walled cells; both kinds of cell bear simple pits. There is no striking difference between the walls, as the thick ones measure 3 to 4 μ, the thin ones 2 to 3 μ. The thinner-walled cells contain chloroplastids.



Fig. 65. *Encephalartos laurentianus* (Congo; after Robyns)

On the *undersurface*, the stomata occur in bands of various width, with 20 to 24 stomata per sq. mm. In the broader bands, the stomata form 3 to 6 loose longitudinal rows as well as slightly oblique transverse ones. The interbands are no more than 200 to 300 μ wide. The length of the gaseous-interchange apparatus including the polar cells is 110 to 120 μ, its width is 60 to 80 μ. The length of a guard cell is 40 to 50 μ, its width is 22 to 25 μ. There are 4 or 6 accessory cells whose ends, slightly elevated above surface of the epidermis, constitute the pit wall. The stomatal pit is usually flanked by two large accessory cells whose walls facing the pit are 3 to 4 μ thick, their other walls being much thinner (1·5 to 2 μ). All stomatal slits are invariably parallel to the leaflet axis. Some accessory cells have the shape of ordinary epidermal cells, but others are elongated swallowtail fashion.

Around the stomata there are both thin-walled and thick-walled cells, with walls measuring 4 to 5 μ and 2 to 3 μ, respectively. The cell lumen usually follows the outline of the cell, but in some cells it is constricted so much that the two opposite walls touch.

Encephalartos lebomboensis Verdoorn (1949)

Plate CI, Drawing 48; Plate CXLV, Photos 1–4; Fig. 66

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are strongly elongate parallel to the leaflet axis, but do not constitute well-defined rows. They are mostly arranged end to end, with transverse or slightly oblique end walls. The usual length is 60 to 150 μ, but cells as long as 200 μ also occur. The width of most cells is between 15 and 20 μ.

There are thick-walled as well as thin-walled cells: their respective walls are 2 to 3 μ and 1 to 2 μ thick.



Fig. 66. *Encephalartos lebomboensis* (photo by Dyer)

The cells communicate through simple pits. Although of various shapes all are arranged lengthwise; transverse cells are most rare. The irregularly alternating thick- and thin-walled cells form a highly typical pattern.

On the *undersurface*, the stomata occur in bands 500 to 800 μ wide, separated by interbands of 300 to 500 μ width. There are 3 to 5 loose rows of stomata in each band, with 20 to 22 stomata per sq. mm. The space between the stomata is filled out by epidermal cells resembling those of the upper surface, although of slightly smaller size. Their walls are of fairly uniform thickness, thin-walled cells being quite rare.

The length of the gaseous-interchange apparatus, including the polar cells, is 90 to 100 μ, its width is 80 to 90 μ. Some of this length may be due to the extra-

ordinary lengthening of one of the polar cells or of some of the accessory cells. The number of these latter is most often 2 or 3; only very seldom are there 4 or 5. Their shape is also varied. A single accessory cell on one side may be as large as the opposite two taken together. The pattern is almost invariably asymmetric, with more cells on the one side than on the other. Horn-shaped, elongate and arched accessory cells are fairly frequent. Accessory cells and polar cells surround a stomatal pit of 24 to 25 by 12 to 13 μ size, usually elliptic. Beneath the pit there are two guard cells, each 45 to 50 μ long and 15 to 18 μ wide. Their slit is as long as the pit. Pit depth is 7 to 8 μ. The pit wall hardly rises above the epidermal plane. The apparatus is usually surrounded by thick-walled (3–4 μ) epidermal cells communicating through simple pits.

Encephalartos lehmannii Ecklon (1813)

Plate CI, Drawing 50; Plate CXLVI, Photos 1–4; Fig. 13

Leaf amphistomatic. Scattered on the *upper surface* of the leaflet, there are among the cells cavities whose size and structure resemble those of the stomata. The dark spots in Photo 1 indicate stoma-like structures of this type. The pore is surrounded by the tapered, rounded ends of 5 to 8 accessory cells. Their walls facing the pore are substantially thickened (3 to 3·5 μ), whereas their other walls seldom attain a thickness of 2 μ. Having the overall outline of an isodiametric or slightly elongate polygon, each arcuate side of which corresponds to an accessory cell, the pore is about 22 to 20 μ long and as wide. The surrounding cells are usually 40 to 70 μ long and 30 to 35 μ wide. These pores may be vestiges of stomata or air ducts, as there are no guard cells beneath them. There are two or three such pores in a sq. mm. The other epidermal cells are aligned more or less parallel to the leaflet axis, constituting rows whose width, equal to that of the cells themselves, is usually 20 to 35 μ. Cell length is 30 to 120 μ. Of highly varied shape (square, longitudinal or transverse oblong, triangular, rhombic, trapezoidal, etc.) these cells are either thin or thick walled (2 and 3 to 3·5 μ, respectively). Their arrangement in the rows is also very varied. The thick cell walls are layered and almost never bear pits. If the cell wall is much thickened, the lumen is not always of the same shape as the outline of the cell, and in some cells it may almost disappear.

The *undersurface* bears no well-defined stomatiferous bands; the spread of the stomata is more or less uniform. There are about 38 to 46 of them per sq. mm. The long axis of the gaseous-interchange apparatus is more or less parallel to the leaflet axis. Its size including the accessory cells is 90 to 100 by 80 to 90 μ. The stomatal pit is 30 to 35 by 17 to 18 μ in size, circular, or elliptical with indentations on both sides. The guard cells are 40 to 45 μ long, 16 to 18 μ wide. There are usually 6 or 7 accessory cells, as shown also by the outline of the crater. They are more or less isodiametric or slightly elongate, 30 to 35 μ in length and 28 to 30 μ in width. The walls facing the pit are thick, the other walls are thin. Most of the

epidermal cells have layered walls 6 to 8, occasionally even 10 μ thick. In the latter, the lumen is very narrow, slit-like. The few thin-walled cells between them contain chloroplastids and have walls 2 to 3 μ thick. These cells communicate through simple pits.

Encephalartos longifolius (Jacq.) Lehm. (1834)

Plate XCIX, Drawing 34; Plate CXLVII, Photos 1–4; Fig. 67

The leaf might be called amphistomatic, as the *upper surfaces* of the leaflets carry very rare apertures which resemble stomata, although there are no guard cells beneath them. This and the arrangement of the thin-walled epidermal cells full of chloroplastids around them suggest these apertures to be the vestiges of stomata which have lost their function. Much more numerous are the broken stumps of cylindrical hairs. Most of the epidermal cells are isodiametric, but some are elongate parallel to the leaflet axis. Their length is 50 to 100, their width 25 to 35 μ. Their shape is varied; they either constitute an interwedging pattern or meet end to end with oblique end walls. There are thick- (3 to 4 μ) and thin-walled (1 to 2 μ) cells. The thin-walled ones contain numerous chloroplastids and have many simple pits in their walls. Layered and of uniform thickness, the thick walls are but very seldom pitted. The thick-walled and thin-walled cells are distributed in an irregular mosaic and tend to have sinuous side walls.



Fig. 67. *Encephalartos longifolius* (after Dyer)

Undersurface. The stomata occur in bands of varied width (500 to 600 μ) separated by interbands 300 to 400 μ wide. Size, shape and arrangement of the epidermal cells in the interbands almost agree with those of the cells on the upper surface. However, the under-

surface carries no traces of hair structures. Each band includes 6 or 7, or rows of loosely packed stomata, 35 to 40 per sq. mm. In the bands one encounters both the thin-walled and thick-walled epidermal cells known from the upper surface. The thin-walled epidermal cells contain numerous chloroplastids. The layered walls of the thick-walled ones measure 6 to 7 μ. There are 4 or 6 accessory cells, mostly trapezoidal, facing the pits with their short, very thick-walled sides. The other walls are much thinner. The size of the gaseous-interchange apparatus including the accessory cells is 80 to 120 by 70 to 100 μ. The guard cells are 35 to 40 μ long, 18 to 20 μ wide. The stomatal pit itself is 20 to 22 μ long and 10 to 12 μ wide. Its shape is an ellipse or a rounded hexagon, depending on the number of accessory cells. Its depth is 6 to 7 μ. The polar cells are about 16 to 18 μ in length and about as wide. The accessory cells frequently contain chloroplastids: their walls are finely tuberculate.

Encephalartos manikensis Gilligand (1949)

Plate CIV, Drawing 73; Plate CXLVIII, Photos 1–4

Leaf amphistomatic to some extent, because the *upper surface* of the leaflet bears clusters of what seem to be accessory cells around crateriform pores. There are usually six accessory cells and 2 elongate polar cells. These latter are thin walled; the walls facing the pore of the accessory cells are much thicker. Beneath some such crateriform pores, the slits of guard cells can be seen. On the upper surface of the leaflet, thin- and thick-walled cells occur in fairly conspicuously separated clusters. The thicker-walled cells usually form bands of various length. Not encountered in any other *Encephalartos*, this arrangement can well be considered a specific feature. The epidermal cells are highly varied in size and shape: as opposed to those of the other *Encephalartos* species, they are not often arranged in longitudinal rows. Decidedly layered and pitted, the thicker cell walls measure 10 to 12 μ; the thin walls are 1 to 3 μ thick and are also very finely pitted. The length of the cells is 35 to 40 μ, their width is about the same. The thin-walled epidermal cells contain numerous chloroplastids.

Undersurface. The stomata occur in longitudinal bands which are usually wider than the interbands between them. The bands are 20 to 25, the interbands 8 to 10 cells wide. In the interbands, the thin- and thick-walled epidermal cells occur in about equal numbers; they are somewhat longer and narrower than on the upper surface. They are oblong or tapering, triangular. In the bands, the stomata form longitudinal and sometimes diagonal rows. Between the stomata there are almost exclusively thick-walled cells; depending on the size of the cell, the small lumina are circular, elliptical or slit-like. The length of the gaseous-interchange apparatus is 95 to 100 μ, its width is 75 to 80 μ; pit size is 28 to 30 μ by 15 μ. The guard cells are 48 to 50 μ long and 20 to 21 μ wide. The ends of the guard cells constitute a kettle-shaped depression of 15 to 16 μ depth. The two polar cells do not jut out

beyond the elliptical perimeter of the apparatus. The exclusive occurrence of thick-walled cells between the stomata of the undersurface has not so far been observed in any other species of *Encephalartos* and can therefore be regarded as a specific feature. The cells in the interbands are 100 to 105 μ long and 24 to 26 μ wide. Their thick layered walls bear simple pit-pairs. Beneath the epidermal layer there are highly elongate thick-walled cells of 2000 to 3000 μ length and as little as 15 to 20 μ width, having narrow, slit-like lumina.

Encephalartos natalensis Dyer et Verdoorn (1951)

Plate C, Drawing 39; Plate CXLIX, Photos 1–4; Fig. 68

This is an atypically hypostomatic leaf. On the *upper surface* of the leaflet, there are scattered hair structures, indicated in Photo 1 by dark spots. There are a very few cavities between the epidermal cells, presumably representing the vestiges of one-time stomata or other kinds of gaseous-interchange apparatus. There is, however, no trace of guard cells beneath any of these apertures. The epidermal cells are, as in most species of *Encephalartos*, arranged in rows parallel to the leaflet axis, the mean width of the rows being 40 to 42 μ. The cells in the rows are square, oblong – transverse or longitudinal – or polygonal, usually arranged uniserially, but pairs of somewhat thinner cells may occur abreast locally. The length of the cells ranges from 20 to 70, their width from 20 to 25 μ. There are both thick-walled and thin-walled cells, with mean thicknesses of 5 to 6 and 2 to 3 μ, respectively. The thin-walled cells contain chloroplastids and usually communicate through

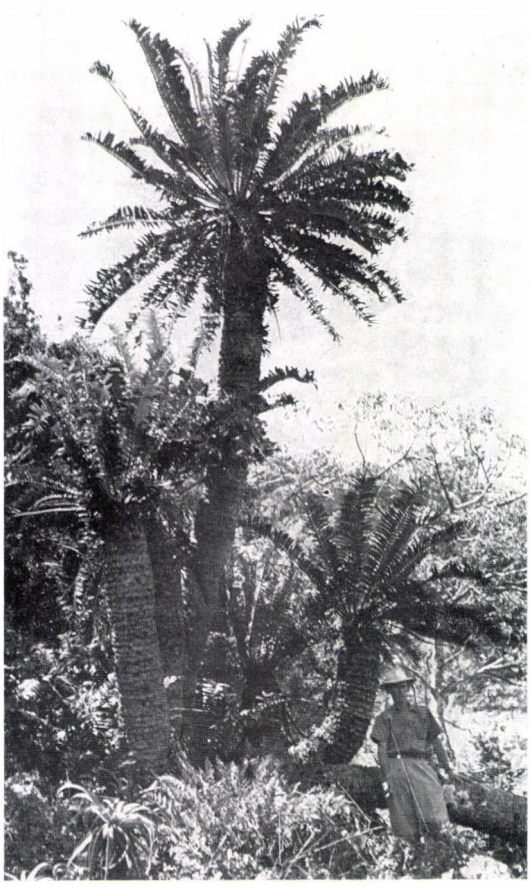

Fig. 68. *Encephalartos natalensis* (South Africa; photo by Dyer)

simple pits. The thick cell walls are layered and are but very seldom penetrated by simple pits.

On the *undersurface*, there are fairly broad stomatiferous bands, with 20 to 25 stomata per sq. mm. The breadth of the bands is 800 to 1200 μ; that of the interbands is 150 to 200 μ. Size, shape and arrangement of the epidermal cells in the interbands agree with those on the upper surface of the leaflet. Here, too, there are thick-walled and thin-walled cells. On the other hand, the epidermal cells between the stomata are mostly thin walled and shorter, squatter than the ones on the upper surface. The bands include up to 12 longitudinal rows of stomata, fairly close to one another. The thin-walled accessory cells of the stomata are sharply distinct from the thick-walled epidermal cells around them. The gaseous-interchange apparatus including the accessory cells is 70 to 80 μ long and about as wide. The size of the stomatal pit is 18 to 28 by 10 to 12 μ. Pit depth is 8 to 9 μ. The walls facing the pit of the accessory cells are not particularly thicker than their other walls. Beneath the pit there are two guard cells of 30 to 35 μ length and 14 to 15 μ width. The thin-walled epidermal cells around the accessory cells are relatively rich in chloroplastids. The cavities of the thick-walled cells are sometimes reduced to mere slits.

Encephalartos poggei Aschers (1878)

Plate C, Drawing 44; Plate CL, Photos 1–4; Fig. 69

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are substantially elongate parallel to the leaflet axis, without, however, constituting well-defined longitudinal rows. Some of the cells join obliquely truncated ends, but in some cases a third cell may be wedged in between the ends of two epidermal cells, thus giving, as it were, a fibrous appearance to the structure. There is no trace of any stoma on the upper surface of the leaflet. The epidermal cells are highly elongate oblongs of oblique ends or of some similar shape, of 50 to 150 μ length and 15 to 20 μ width. There are both thick-walled and thin-walled epidermal cells, the walls being 2 to 3 and 1 to 2 μ thick, respectively. The cells most often communicate through simple pits. Also in colour, the thick-walled ones differ somewhat from the thin-walled ones.

On the *undersurface* of the leaflet, the stomata are arranged in bands parallel to the leaflet axis. There are 30 to 35 stomata to the sq. mm. The width of the bands is 300 to 450 μ, that of the interbands is 200 to 250 μ. The interbands lie under the veins of the leaflet. Most bands include 4 or 5 rows of stomata. The stomata form at the same time also more or less conspicuous transverse rows. Size, shape and arrangement of the epidermal cells in the interbands are almost entirely the same as on the upper surface of the leaflet. One of the peculiarities of the stomata is that one or two accessory cells as well as one of the polar cells, of tapering shape, are much more elongate than the rest. The length of the gaseous-interchange apparatus



Fig. 69. *Encephalartos poggei* (Congo; after Robyns)

including the accessory cells is 120 to 130 μ; its width is 65 to 70 μ. The size of the stomatal pit is 36 to 40 by 15 to 17 μ. The aperture is usually surrounded by 2 or 3 accessory cells, one of which is invariably longer than the aperture itself. The walls facing the pit of the accessory cells are always thicker than their other walls (2 to 2·5 μ as against 1 to 1·5 μ).

The length of one guard cell is 35 to 36 μ; its width is 13 to 15 μ. The slit between the two is as long as the diameter of the pit. The accessory cells rise but slightly above the surface of the epidermis. Pit depth is 6 to 7 μ.

One of the differences between polar and accessory cells is that the former bear fine tubercles on their walls, whereas the latter do not. The thickened part of the guard cell wall is 5 to 6 μ thick and bears no particular pattern. The epidermal cells among the stomata are of the same size and shape as on the upper surface of the leaflet or possibly somewhat shorter and thicker walled. The adjacent walls of two thick-walled cells have a total thickness of 7 μ, while the total thickness of two adjacent thin cell walls is 1·5 to 2 μ.

The gaseous-interchange apparatus of this species differs from that of the species described so far inasmuch that the ends of the accessory cells are tapering, triangular, thus giving rise to a highly characteristic stomatal ornament.

Encephalartos princeps R. A. Dyer (1965)

Plate CIV, Drawing 74; Plate CLI, Photos 1–4; Fig. 70

Leaf hypostomatic. However, the *upper surface* of the leaflet bears some very rare arrangements of cells recalling the cell groupings around the stomata, with accessory and polar cells as on the undersurface. Indeed, in a very few cases, even the slit of the guard cells is visible on the bottom of the pit. The epidermal cells are mostly isodiametric, square, triangular, rhombic, oblong or ham-shaped. Somewhat elongate in the direction of the leaflet axis, the oblong and rhombic cells are about 80 to 90 μ long and 28 to 35 μ wide; they are arranged in rows roughly parallel to the leaflet axis, although this pattern is not always very conspicuous. There are thicker- and thinner-walled cells, randomly intermingled. The thin-walled cells contain chloroplastids. The thick cell walls are layered.

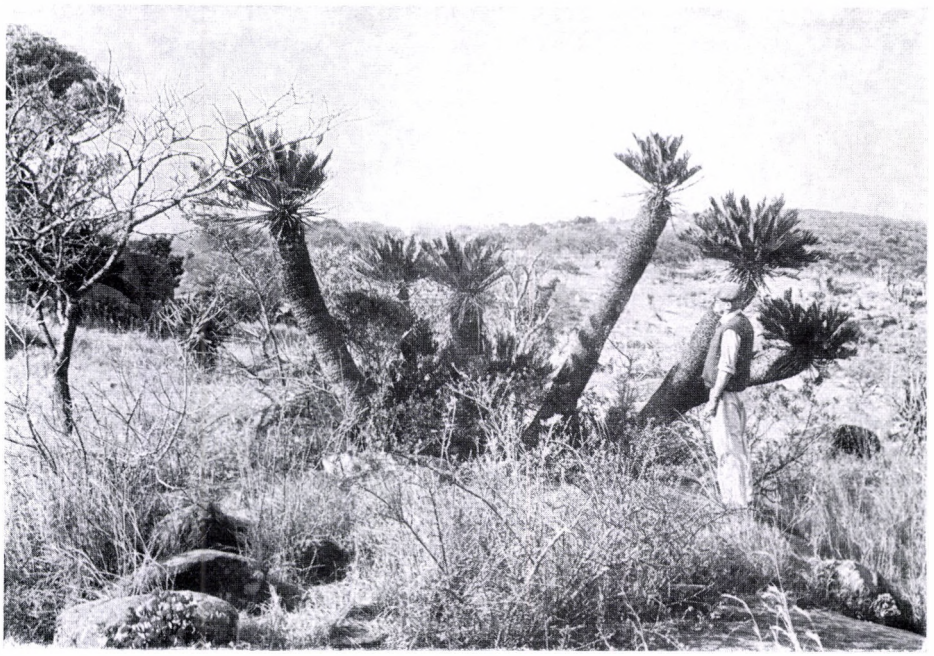

Fig. 70. *Encephalartos princeps* (photo by Dyer)

Undersurface. The stomata are arranged in bands of various width. Each band includes 6 to 16 rows of stomata, forming longitudinal and locally also diagonal parallel rows. The stomata are usually separated by thick-walled cells, although some thin-walled ones also occur between them. The length of the gaseous-interchange apparatus is about 115 to 120 μ; its width is about 80 to 90 μ. The stomatal pit is crateriform, with 4 to 6 accessory cells and two pairs of polar cells overarching the stoma. The radial and tangential walls of the accessory cells are thin. Pit size is 28 to 30 μ by 8 to 10 μ. Pit depth is 6 to 8 μ. The walls facing the pit of the auxiliary cells are considerably thickened. The length of a guard cell is 28 to 35 μ, its width 20 to 21 μ. The interbands are 8 to 10 cells wide: in shape and arrangement, the cells are as on the upper surface, only somewhat more elongate and arranged in slightly more conspicuous rows.

Encephalartos septentrionalis Schweinf. (1871)

Plate CI, Drawing 55; Plate CLII, Photos 1–4; Fig. 14

Leaf amphistomatic. There are no stomatiferous bands on the *upper surface* of the leaflet, but the stomata form nevertheless rows loosely parallel to the leaflet axis. The rows are sometimes fairly close together, sometimes quite far apart. There are

10 to 12 stomata to the sq. mm. The epidermal cells are elongate parallel to the leaflet axis. Most of them are 100 to 150 μ long and 15 to 20 μ wide. Their shape is highly varied, tapering triangular, wedge-shaped quadrangular, rhombic or trapezoidal. Some are transverse or diagonal; most of these are smaller than the rest (70 to 80 μ long), and triangular with a base length of 30 to 35 μ.

The size of the gaseous-interchange apparatus including the accessory cells is 250 to 260 μ by 110 to 120 μ. The guard cells are 60 to 70 μ long and 20 to 22 μ wide: the stomatal pit itself is 30 μ long and 20 μ wide. The usual number of accessory cells is 5 or 6: they surround the guard cells in arcuate arrangements. The polar cells are substantially elongate, 15 to 20 μ wide and up to 50 μ long. The epidermal cells around the apparatus are thick walled (6 to 8 μ): thin-walled cells are very scarce. Their lumina follow closely the outlines of the cells. There occur a few twin epidermal cells, i.e. pairs of cells of equal size and shape meeting end to end and separated by a transverse wall. Among the epidermal cells there are hair bases, indicated in the photo by small dark dots.

The *undersurface* of the leaflet bears stomatiferous bands of various width, containing 30 to 35 stomata per sq. mm. The bands are 500 to 800 μ wide; the interbands, situated below the veins of the leaflet, are 250 to 300 μ wide. Size, shape and arrangement of the epidermal cells fully agree with those on the upper surface of the leaflet. Also the structure and environment of the stomata are exactly as on the upper surface.

The guard cells are usually surrounded by 4 or 6, sometimes by 8 accessory cells. The accessory cells are oblongs or triangles with rounded apices. The length of the stomatal pit is 35 μ; its width is 16 to 17 μ. The walls facing the pit of the accessory cells are slightly thickened. Pit depth is 6 to 7 μ.

The polar cells are relatively small, 17 to 18 μ long and 10 μ wide. The accessory cells have a tendency, particularly near the polar cells, to end in conical papillae or to assume other unusual shapes, whereas the size, shape and wall thickness of the epidermal cells around the apparatus agree with those on the upper surface. The cells on the undersurface are perhaps somewhat shorter and smaller. They contain fairly numerous chloroplastids. The surfaces of the accessory cells are ornamented with a fine tuberculate pattern. This pattern is definitely different from the surface structure of the rest of the epidermal cells (see bottom part of Photo 4).

Encephalartos tegulanus Melville (1957)

Plate XCIX, Drawing 35; Plate CLIII, Photos 1–4

Leaf hypostomatic. The *upper surface* of the leaflet bears no stomata, although locally it appears as though there were small pores surrounded by rings of 4 or 5 cells. These arrangements may be either the vestiges of one-time gaseous-interchange apparatuses, or just random arrangement of cells. The cells are not usually

arranged in rows parallel to the leaflet axis, although some lengths of such rows are seen here and there. The rows often merge; also, one may locally observe shorter third rows intercalated between two longer ones. Either isodiametric or slightly elongate in the longitudinal sense, the cells are 20 to 70 μ long and 20 to 25 μ wide. Their shapes are highly varied, triangular, square, oblong, rhombic, trapezoidal, ellipsoidal, etc. Most of them are thick walled, but thin-walled cells are none too scarce, either. The thick walls measure 4 to 7 μ, the thin ones 2 to 3 μ. The thin walls bear numerous simple pits; the thick walls very seldom bear any. The thin-walled cells tend to contain chloroplastids. The thick walls are of quite uniform thickness; the shape of the lumen follows the outline of the cell. The lumina of highly elongate thick-walled epidermal cells are sometimes reduced to slits.

On the *undersurface* of the leaflet, the stomata occur in bands of various width parallel to the leaflet axis, containing 28 to 30 stomata to the sq. mm. The width of the bands is 500 to 550 μ; that of the interbands is 350 to 400 μ. One band usually includes 5 or 6 rows of stomata. Size, shape and structure of the epidermal cells in the interbands almost totally agree with those of the cells on the upper surface.

The stomata are relatively close spaced. The size of the gaseous-interchange apparatus including the polar cells is 120 to 130 μ; its width is 80 to 90 μ. There are usually 4 or 6 accessory cells. The walls facing the stomatal pit of the accessory cells are thicker than their other walls. Pit size is 25 to 40 μ by 10 to 15 μ. The length of one guard cells is 40 to 45 μ, its width is 18 to 20 μ. Pit depth is 6 to 7 μ. The epidermal cells around the stomata usually have thick, layered walls, with hardly any thin-walled parenchyma cells.

Encephalartos transvenosus Stapf. et Davy (1926)

Plate C, Drawing 42; Plate CLIV, Photos 1–4; Fig. 71

The leaf may be considered amphistomatic, because there are some stomata (2 or 3 per sq. mm) also on the *upper surface* of the leaflet. These might have lost their function, as suggested by the shape and arrangement of the cells surrounding them. At any rate, there are no guard cells beneath their apertures. Most of the epidermal cells are arranged in longitudinal rows. Their shapes are varied, triangular, quadrangular, trapezoidal: those of oblong shape are sometimes transverse to the direction of the rows. Their length is 70 to 80 μ, their usual width is 10 to 15 μ. As compared with the rest of the species of *Encephalartos transvenosus* possesses remarkably short and narrow epidermal cells which may be either thick or thin walled (3 to 5 and 1 to 2 μ, respectively). The thick walls are smooth, of uniform thickness and layered structure, and bear no pits. The thin walls, on the other hand, bear numerous simple pits. The thin-walled cells contain numerous chloroplastids. The thin- and thick-walled epidermal cells are distributed to form a mosaic-like pattern. Remarkably enough, the apertures are surrounded ex-

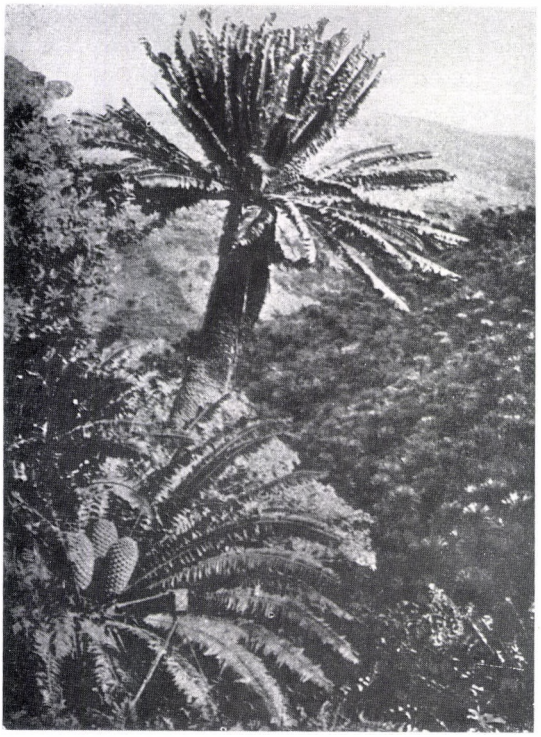

Fig. 71. *Encephalartos transvenosus* (South Africa; after Dyer)

clusively by thin-walled accessory cells rich in chloroplastids. The walls facing the aperture of these cells are thickened, thus proving that the apertures are indeed related in some way to stomata.

On the *undersurface* of the leaflet, the stomata occur in longitudinal bands of various width (350 to 450 μ) with interbands of 200 to 300 μ width between them. Each band includes 6 or 7 fairly loose rows of stomata, with 60 to 70 stomata to the sq. mm.

Size, shape and arrangement of the epidermal cells in the interbands are the same as on the upper surface. The epidermal cells among the stomata are slightly shorter, and their walls are more sinuous, as a result of their fitting in between the gaseous-interchange apparatuses. The epidermal cells have layered walls 6 to 7 μ thick; the walls of the thinner-walled cells measure 2 to 3 μ (e.g. on right side of Photo 4). The length of the gaseous-interchange apparatus including the accessory cells is 60 to 70 μ, its width is 50 to 60 μ. There are 4 to 6 accessory cells overarching the guard cells. The accessory cells are usually trapezoidal, with the short side of the trapezium bounding the stomatal pit which is usually 28 to 30 μ by 14 to 15 μ in size. The walls facing the pit of the accessory cells are slightly thickened. Pit depth is 4 to 5 μ. The guard cells are 35 μ long, 24 to 25 μ wide. The slit between them is as long as or longer than the pit diameter. The accessory cells are thin walled; some of them contain chloroplastids.

Encephalartos trispinosus (Hook) R. A. Dyer (1965)

Plate CIV, Drawings 75a,b; Plate CLV, Photos 1–4; Fig. 72

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are more or less isodiametric; cells 3 or 4 times as long as their own width are very rare. Usual length is 25 to 40 μ; usual width is 17 to 20 μ. Some transverse cells



Fig. 72. *Encephalartos trispinosus* (photo by Dyer)

are 10 to 15 μ high and 35 to 40 μ wide. Shapes are highly varied (square, oblong, trapezoidal, rhombic, isodiametric, etc.). Arranged in rows parallel to the leaflet axis, most epidermal cells have walls 3 to 5 μ thick, but they are interspersed with some thinner-walled ones. The thickness of the thick walls is not uniform; their layered structure is well visible in some instances. The thinner-walled cells contain chloroplastids.

Undersurface. The stomata are arranged in bands of various width including 5 to 15 rows of stomata and separated by interbands 8 to 10 cells wide. Size and shape of the epidermal cells in the interbands agree with those on the upper surface.

The walls of the epidermal cells between the stomata are not of uniform thickness; they are layered and pitted. The walls of the parenchyma cells scattered between them are very thin. These cells contain chloroplastids. The length of the gaseous-interchange apparatus is 105 to 110 μ, its width is 70 to 80 μ. The stoma is overarched by the accessory cells, 4 to 6 in number. The two polar cells do not reach beyond the accessory cells: their walls are thinner than the radial walls of these latter. The walls facing the stomatal pit of the accessory cells are thicker than their radial or outer walls. Pit size is 40 to 45 μ by 26 to 28 μ; pit depth is 6 to 8 μ. The shapes of the stomatal pits are rather varied, tetra-, penta- or hexagonal, depending on the number of accessory and polar cells surrounding them. The length of the slit between the two guard cells is 40 to 42 μ.

Encephalartos umbeluziensis R. A. Dyer (1951)

Plate CI, Drawing 47; Plate CLVI, Photos 1–4; Fig. 73

Leaf not entirely hypostomatic. Though there are no well-defined stomata on the *upper surface* of the leaflet, there are cell patterns which may be vestiges of stomata although there are no guard cells underneath. Most of the epidermal cells are elongate parallel to the leaflet axis, of 40 to 130 μ length and 20 to 25 μ width. There are thin-walled and thick-walled cells: the thin cell walls bear many simple pits. The thick ones are layered. The surfaces of some cells bear parallel cuticular lamellae. The outer surfaces of some are covered so densely by lamellae as to render the lumen invisible. These ribbed epidermal cells locally constitute longitudinal rows with the cells arranged end to end, sometimes joining oblique end walls.

The cells have the shape of more or less elongate oblongs, triangles, rhombs, crescents or pistols. Twin epidermal cells are fairly frequent. The cells near the margin are smaller, squatter and thicker walled than in the middle regions of the leaflet.

Undersurface. The stomata (26 to 28 per sq. mm) occur in bands of various width. Size, shape and arrangement of the epidermal cells in the interbands are more or less the same as on the upper surface of the leaflet. Both the bands and interbands are 500 to 600 μ wide. The cells around the stomata are somewhat shorter. Also the relative abundance of thin- and thick-walled cells is about the same as on the upper surface.



Fig. 73. *Encephalartos umbeluziensis* (Africa; photo by Dyer)

One of the most remarkable features of the stomata is that there are two different sizes of guard cell. The stomata with the bigger guard cells sometimes occur in groups and are easy to distinguish from the small stomata nearby. The length of the small guard cells is 33 to 35 μ; that of the big ones is 70 μ. The width of the

latter is 17 to 20 μ; the former are about half as wide. No Cycad species known so far exhibits such a marked differentiation in the size of the guard cells.

The usual number of accessory cells is 3, quite often 4; the one polar cell is sometimes lacking; the remaining one is narrow and very long. The walls facing the stomatal pit of the accessory cells are much thicker than their side walls. The elliptical pit aperture is 31 to 32 by 17 to 18 μ in size. Pit depth is 5 to 6 μ. The walls of the big guard cells are 15 μ thick, and the slit between them is longer than the pit diameter. The end walls of the two big guard cells meet at an angle close to 180°. The length of the end wall is 17 to 18 μ in the big and 5 to 6 μ in the small guard cells.

Encephalartos villosus (Gaertn.) Lemaire (1867)

Plate C, Drawing 41; Plate CLVII, Photos 1–4; Fig. 15

On the *upper surface* of the leaflet, the epidermal cells are arranged in longitudinal rows; the adjacent rows are not always clearly separate and one often sees shorter rows intercalated between two longer ones. Most cells are elongate, of 50 to 220 μ length and 15 to 20 μ width. Their shapes are highly varied (triangular, square, oblong, rhombic, trapezoidal).

On the *undersurface*, the stomata occur in bands of various width parallel to the leaflet axis. The width of the bands is 500 to 650 μ; that of the interbands is 400 to 500 μ. Most bands include 5 or 6 close-spaced rows of stomata. Size, shape and arrangement of the cells in the interbands are almost exactly as on the upper surface of the leaflet. The stomata are relatively close spaced (34 to 38 of them to the sq. mm). The length of the gaseous-interchange apparatus is, including the accessory cells, 120 to 130 μ; its width is 70 to 80 μ. The stomatal pit is usually surrounded by 4 or 6 accessory cells whose walls facing the pit are much thicker than the other walls. The size of the pit aperture is 28 by 16 to 17 μ. Beneath the aperture, there are two guard cells; the slit between them is longer than the pit diameter. Pit depth is 5 to 6 μ.

The epidermal cells between the stomata may be thick or thin walled. The thin cell walls bear simple pits; the thick ones are smooth and layered. Both kinds of cell are similar in shape and arrangement to those on the upper surface, but somewhat smaller in size.

Encephalartos woodii Prain (1914)

Plate XCIX, Drawing 33; Plate CLVIII, Photos 1–4; Fig. 74

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells, 20 to 80 μ long and 15 to 25 μ wide, are arranged in more or less parallel rows. The width of the rows is 15 to 35 μ. The cells are triangular, quadrangular, trapezoidal,



Fig. 74. *Encephalartos woodii*
(Botanical Garden, Durban; photo by Dyer)

rhombic or irregular in shape; those in the same row join transverse or oblique end walls. The triangular and quadrangular cells are often elongate in an oblique direction. There are thick-walled (3 to 5 μ) and thin-walled (1 to 1·5 μ) cells. Of uniform thickness and layered structure, the thick walls bear no pits. The thin-walled cells often contain numerous chloroplastids, and their walls bear simple pits. The thick- and thin-walled cells are arranged in a mosaic pattern, but the thin-walled ones always communicate with each other. This epidermal pattern resembles in certain features that of the *Macrozamia* and *Lepidozamia*.

On the *undersurface*, the stomata occur in bands of various width, in a density of 50 to 60 to the sq. mm. The bands are 500 to 650, the interbands 250 to 300 μ wide. The epidermal cells of the interbands are somewhat more elongate than on the upper surface, but the arrangement of the thin- and thick-walled cells is the same. Each band includes 3 to 8 longitudinal rows of stomata. Diagonal rows including about 45° with the leaf axis are also visible. The thin- and thick-walled epidermal cells among the stomata are shorter than the cells on the upper surface. The thin-walled cells sometimes contain chloroplastids. The length of the gaseous- interchange apparatus including the accessory cells is 100 to 110 μ; their width is about the same. The guard cells are overarched by 4 to 6 accessory cells and a pair of polar cells. The polar cells are about 18 μ square. The walls facing the stomatal pit of the accessory cells are much thicker than their fairly thin other walls. The surface of the accessory cells is very finely tuberculate.

Pit size is 22 to 25 μ by 13 to 14 μ. Pit depth is 4 to 5 μ. The slit between the guard cells is longer than the pit diameter. The guard cells are 35 to 40 μ long, 18 to 20 μ wide. The walls of the accessory cells are finely tuberculate,

unlike the adjacent thick-walled epidermal cells but resembling the thin-walled chloroplastid bearing ones.

(d) DIOON

Dioon edule Lindl. (1843)

Plate XCV, Drawing 6; Plate CLIX, Photos 1–4; Figs 16 and 17

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are oblongs parallel to the leaflet axis, or variously modified quadrangles. Most cells join transverse end walls, which results in more or less longitudinal rows of cells (Photos 1, 2). Cell surfaces are finely tuberculate and bear no well-defined pits: this is a generic feature not encountered in the rest of the Cycad genera. The longitudinal walls of the cells are somewhat sinuous locally. There are thin-walled (2 μ) and thick-walled (5 to 7 μ) epidermal cells. Most thick-walled cells are colourless, whereas the thick-walled ones contain a brown pigment. The thick-walled cells are usually longer than the thinner-walled ones. Their length varies from 25 to 140 μ, their width from 18 to 20 μ. The mean length of the thin-walled cells is 25 to 30 μ; their width is about the same. The sinuous side walls and longitudinally elongate cells constitute a characteristic epidermal pattern. Containing chloroplastids, the thin-walled epidermal cells are capable of assimilation. There is no chloroplastid in the thick-walled cells.

On the *undersurface*, the stomata occur in longitudinal bands of 320 to 350 μ width, in a density of 90 to 100 per sq. mm. The interbands are of about the same width. Most bands include 4 to 6 rows of stomata. Shape, orientation and structure of the cells are almost the same in the interbands as on the upper surface.

The stomata are surrounded by crater-like arrangements of cells. The number of accessory cells is 4 or 5, rarely 6. The stomatal pit is bounded by their arcuate end walls which are much thicker than their other walls. Pit depth is about 10 to 12 μ. The size of the gaseous-interchange apparatus including accessory cells is 110 to 120 by 70 to 75 μ. The guard cells beneath the pit are 50 to 60 μ long and 15 to 20 μ wide.

The shape of the pit is highly varied, depending on the number and shape of the accessory cells surrounding it. Usually, however, its long axis is more or less perpendicular rather than parallel to the slit between the guard cells.

The accessory cells are usually surrounded by thick-walled epidermal cells: there are hardly any thin-walled epidermal cells between the stomata. Layered parallel to the cell outline, the thick cell walls measure 7 to 8 μ. The cell cavity is apparently empty. The thick-walled cells are much smaller on the under- than on the upper surface, their length is about 50 μ at most.

Dioon pectinatum H. Wendl (1883)

Plate XCV, Drawing 5; Plate CLX, Photos 1–4

Leaf hypostomatic. The *upper surface* of the leaflet exhibits the bases of a few hair structures. The epidermal cells are of highly varied shape, but are somewhat elongate parallel to the leaflet axis. The length of these is 120 to 150 μ, but there are cells as short as 20 to 30 μ. Cell width is also varied: it is 10 to 15 μ for the longer cells and 20 to 35 μ for the shorter ones. These latter sometimes constitute short rows of 3 to 5 cells. Their side walls are invariably characteristically sinuous; even the end walls of some are like that. There are thick-walled (4 to 5 μ) and thin-walled (1 to 2 μ) cells. The latter usually contain fairly numerous chloroplastids. Both the thick and thin cell walls bear fairly numerous simple pits. The lumina of some of the narrower thick-walled cells are reduced to slits. Shape and arrangement of the epidermal cells are much like in *Dioon edule*, but *D. pectinatum* has more flattened oblong or trapezoidal thin-walled parenchyma cells.

On the *undersurface* of the leaflet, the stomata occur in longitudinal bands of various width, in a density of about 60 to 64 to the sq. mm. The width of the bands is 500 to 550 μ, that of the interbands is 200 to 300 μ. In the bands, the stomata form 5 or 6 longitudinal rows as well as diagonal ones. In the interbands, the epidermal cells are somewhat narrower and longer than on the upper surface of the leaflet; on the other hand, the epidermal cells between the stomata are much shorter, sinuous and of a greater variety of shapes, as a result of accommodation to the shapes of the stomata. Also here, there are thick-walled (3 to 4 μ) and thin-walled (1 to 2 μ) cells. The thin-walled cells often contain chloroplastids. The size of the gaseous-interchange apparatus including accessory cells is 115 to 125 μ; its width is 100 to 110 μ. Numbering 4, seldom 6, the accessory cells are relatively thin walled. The guard cells are 50 to 55 μ long; their width is 15 to 20 μ. The most typical feature of the stomata of the genus *Dioon* is that the long axis of the stomatal pit is perpendicular to the slit between the guard cells. The shape of the aperture is elliptical, circular or polygonal, depending on the number and shape of the accessory cells. The size of the pit is 18 to 20 by 14 to 16 μ. Pit depth is fairly great, 8 to 9 μ. The epidermal cells surrounding the stomata exhibit a variety of shapes; there is, however, no great difference in wall thickness between the thicker- and thinner-walled cells, the main difference being that the thicker-walled ones contain chloroplastids while the thinner-walled ones do not. The epidermal cells and particularly the stomata of *Dioon pectinatum* are so typical in shape that mistaking them for any other genus is practically impossible.

Dioon spinulosum Dyer (1883)

Plate XCV, Drawing 6a; Plate CLXI, Photos 1–4; Fig. 18

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are usually oblongs parallel to the leaflet axis, arranged end to end in longitudinal rows. The cells within a row are separated by transverse or slightly oblique walls.

The rows are but seldom interrupted by triangular or quadrangular, somewhat wider cells, most of which are transverse to the leaflet axis. There are thin-walled and thick-walled epidermal cells. Most of the thin-walled ones contain a dark-coloured pigment, although some are colourless. Most of the thick-walled cells are also colourless. The length of the cells is 120 to 150 μ, their width is 10 to 35 μ. The thick walls measure 4 to 5 μ, the thin ones 2 to 3 μ. There is, however, no sharp difference between thick and thin walls.

The lumina of most cells copy the cell outlines. Some adjacent cells communicate through simple pits. The cell surfaces are finely tuberculate, but lacking a conspicuous ornament. The thinner-walled cells usually contain chloroplastids, which proves that some at least of the epidermal cells are capable of assimilation. Among the epidermal cells there are some scattered round fields, presumably the basal cells of hair structures, surrounded by a radial pattern of 6 to 8 epidermal cells, looking like guard cells that have lost their function. There occur locally pairs of perfectly alike epidermal cells separated by a transverse wall, looking like septate twin cells.

On the *undersurface* of the leaflet, the stomata occur in longitudinal bands, in a density of 60 to 64 to the sq. mm. The width of the bands is 400 to 800 μ; that of the interbands is 250 to 300 μ. The epidermal cell in the interbands are much like on the upper surface, only slightly smaller. In most bands there are 4 to 6 longitudinal rows of stomata. The epidermal cells between the stomata are invariably smaller than those of the interbands, being 60 to 70 μ long and 20 to 22 μ wide.

The size of most stomatal pits is in the range of 20 to 25 μ by 10 to 18 μ. Beneath the pit there are two guard cells, usually perpendicular to the long axis of the pit aperture. The length of one guard cells is 35 to 40 μ, its width is 20 to 25 μ. The number of the accessory cells is normally 6. The length of the gaseous-interchange apparatus including accessory cells is 80 to 90 μ, its width is 55 to 60 μ. The width of the individual accessory cells is 12 to 15 μ, their length is about the same. No pitting is observed in their walls. The accessory cells are surrounded in their turn by much smaller cells which tend to contain chloroplastids. The shape of some the stomatal pits is a much elongate ellipse, 40 to 42 μ long and but 10 to 11 μ wide. In some apertures, the proportions may be widely different. The ends facing the pit of the accessory cells rise somewhat above the plane of the epidermis. Pit depth is 7 to 10 μ.

It emerges from the above description that the epidermal structure of *Dioon spinulosum* agrees in its fundamental traits with that of *Dioon edule*, so that it is very hard to tell them apart. On the other hand, these two species are easily distinguished from the rest of the Cycad genera.

(e) MICROCYCAS

Microcycas calocoma (Miq.) A. DC. (1868)

Plate XCV, Drawing 4; Plate CLXII, Photos 1–4; Fig. 19

Leaf hypostomatic. The *upper surface* of the leaflet bears epidermal cells elongate parallel to the leaflet axis, 5 to 10 times as long as wide (100 to 300 μ vs. 20 to 25 μ). Most cells are arranged in longitudinal rows, wedged together with tapering ends or joined end to end by transverse end walls. Their sides are slightly sinuous; their shapes are highly varied, although elongate oblongs or rhombs are most common. There are thin-walled and thick-walled cells. The thick cell walls are of uniform thickness and bear no pits. On the upper surface, there are no transversely elongate cells.

On the *undersurface* of the leaflet, the stomata occur in bands of various width, in a density of 36 to 40 to the sq. mm. Most bands include 3 to 5 longitudinal rows of stomata, but in some there is only one row. The bands are about as wide (150 to 200 μ) as the interbands (120 to 180 μ). Size, shape and arrangement of the cells in the interbands fully agree with those of the cells on the upper surface. On the other hand, size and shape of the cells in the bands are somewhat different, owing to the presence of the stomata. The cells are much shorter (30 to 100 μ), more varied in shape, and quite frequently isodiametric. In the bands, too, there are thick-walled and thin-walled cells.

The size of the gaseous-interchange apparatus including accessory cells is 65 to 90 μ by 50 to 60 μ. The length of one guard cell is 50 to 55 μ, its width is 15 to 20 μ. The size of the stomatal pit is most often 22 μ by 20 to 25 μ. There are 2 to 4 accessory cells. The slit between the guard cells extends rather far beyond the pit outline. The guard cells are thick walled; their end walls meet almost face to face. Their thick walls bear a sort of ribbing perpendicular to the long axis of the cell. This structure is definitely different from the stomatal structures of the other Cycad genera.

(f) CERATOZAMIA

Ceratozamia kuesteriana Regel (1857)

Plate XCVII, Drawing 16; Plate CLXIII, Photos 1–4

Leaf hypostomatic. On the *upper surface* of the leaflet, there are two types of epidermal cell, longer and shorter ones, both elongate parallel to the leaflet axis. The longer cells are thicker walled. (The joint thickness of two adjacent walls is 7 to 9 μ.) Their length ranges from 100 to 320 μ, the longer ones are sometimes divided into two or three by thin transverse septa. Their rounded ends interlace in a

wedge-like pattern. Some of their side walls are slightly sinuous. Their width is 25 to 30 μ. The lumen follows the outline of the cell. In the continuation of some of the long cells, or sandwiched in between them, there occur rows of 4 to 6, seldom 8 much shorter and thinner-walled cells of about 60 to 70 μ length. The thin- and thick-walled cells are markedly different. This is a typical ceratozamid epidermal structure much different from that of the rest of the Cycad genera. Some thin-walled cells contain chloroplasts.

On the *undersurface* of the leaflet, the stomata are seen to occur in bands of 500 to 600 μ width, separated by interbands 300 to 350 μ wide. There are 32 to 36 stomata per sq. mm. Most epidermal cells between the stomata are much shorter than those on the upper surface of the leaflet, being 60 to 160 μ long and 20 to 30 μ wide. The arrangement of the thin- and thick-walled cells is about the same as on the upper surface. The length including accessory cells of the individual gaseous-interchange apparatus is 120 to 140 μ, its width is 65 to 70 μ. The length of one guard cell is 35 to 40 μ, its width is 15 to 20 μ. The end walls of the guard cells converge at an angle of about 30 to 35°. There are 4 to 6 accessory cells. The polar cells are not particularly elongate. The thicker parties of the guard cell walls measure 7 to 8 μ. On the undersurface, twin epidermal cells are fairly frequent; twins consisting of two cells of similar size on either side of a separating wall. Pitting is restricted to the thinner cell walls.

Ceratozamia mexicana Brongn. (1846)

Plate XCVII, Drawing 17; Plate CLXIV, Photos 1–4; Fig. 20

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are arranged in longitudinal rows. The length of the thick-walled cells is about 350 to 400 μ; their width is but 20 to 25 μ. The cells are interlaced in a wedge pattern, with some cells wedged in between two others up to their middle; there are, however, other cells that meet end to end. The cell walls are thick (14 to 15 μ), but the width of the lumen is as little as 1 to 2 μ (a). It is only at the middle of the cell that the slit-like lumen expands slightly. Between the thick-walled epidermal cells, there are rows of thin-walled ones (b). The cells constituting these rows are much shorter (30 to 35 μ) and narrower (10 to 11 μ). Their walls are 3 to 4 μ thick. They contain a protoplast and chloroplastids. Hence, these cells perform an assimilatory function while the thick-walled ones lend strength to the leaflet.

On the *undersurface* of the leaflet, the stomata are arranged in bands of 800 to 900 μ width separated by interbands of 300 to 320 μ width. There are 25 to 30 stomata per sq. mm, and 8 to 10 rows of stomata per band. The interbands appear to correspond to the absence of 3 or 4 rows of stomata under the veins of the leaflet. The stomata are usually surrounded by thinner-walled epidermal cells, although locally thick-walled epidermal cells are also quite frequent in their neighbourhood. These are much shorter in the bands than elsewhere (60 to 250 μ);

also, they are somewhat wider and have more spacious lumina, thus differing in all their dimensions from the epidermal cells of the upper surface. In their thick (16 to 17 μ) and layered walls, simple and reticulate pits are fairly numerous. The thin cell walls measure but 3 to 4 μ.

Most stomata are surrounded by 4 to 6 accessory cells. The size of the gaseous-interchange apparatus including the accessory cells is 100 to 110 by 85 to 90 μ. The length of one guard cell is 42 to 45 μ; its width is 17 to 18 μ. The end walls of the two guard cells converge at about right angles. The parties facing the stomatal pit of the accessory cells are slightly elevated above the plane of the epidermis. Pit depth is 20 to 25 μ. The pit is elliptical or nearly circular; the long axes of some of the ellipses are transverse. The accessory cells are 20 to 26 μ wide and 22 to 24 μ long, but lengths of 32 μ combined with widths of 24 μ also occur.

In the interbands, shape and arrangement of the thin- and thick-walled epidermal cells are exactly the same as on the upper surface of the leaflet.

The epidermal structure of *Ceratozamia mexicana* is so typical as to render distinction from the other Cycad genera fairly easy.

Ceratozamia robusta Miq. (1848)

Plate XCVIII, Drawing 30; Plate CLXV, Photos 1–4

Leaf hypostomatic, resembling that of *Ceratozamia mexicana.*

On the *upper surface* of the leaflet, there are two sorts of epidermal cells, both elongate parallel to the leaflet axis. One sort is thick walled. The walls are finely layered and resemble phloem fibres, inasmuch as their ends are tapered and their lumina almost slit-like, expanding rather seldom near the middle of the cell. The length of these cells is 35 to 320 μ, their width ranges from 19 to 30 μ. Wall thickness is 8 to 10 μ. These cells interlace wedge fashion, some penetrating as far as the middle of the next cell, some meeting end to end.

Between the thick-walled cells there are rows of much shorter and thinner-walled epidermal cells. Their length is 35 to 150 μ, their width, 10 to 12 μ. They are separated partly by oblique, partly by transverse end walls, in which latter case they sometimes look like twin cells. The rows of thin-walled cells may include one or two thick-walled but very short cells. The thin-walled epidermal cells contain a protoplast and several chloroplastids. The rows of 10 to 20 thin-walled cells included between the long epidermal cells are spindle-shaped.

On the *undersurface* of the leaflet, the stomata occur in longitudinal bands each including 3 to 5 rows of stomata parallel to the veins of the leaf. There are 18 to 20 stomata per sq. mm. Within the rows, the stomata are rather wide spaced, with two stomata separated by the length of 5 or 6 stomata. They are usually surrounded by thin-walled epidermal cells whereas most of the interbands are made up of thick-walled cells. Both in the bands and interbands, the thick-walled cells are shorter than those on the upper surface of the leaflet. The

thick-walled cells communicate through simple pits. On the undersurface, the size of the thick-walled cells is 170 to 180 μ by 28 to 30 μ, whereas the length of the thinner-walled cells around the stomata ranges from 25 to 40 μ.

The outline of the stomatal pit as well as of the entire gaseous-interchange apparatus is circular or sightly flattened elliptical. The size of the apparatus including accessory cells is 80 to 90 μ and its width is about the same. The length of one guard cell is 45 to 50 μ, its width is 17 to 18 μ. The size of the pit is 32 by 21 μ. The guard cells are surronded by 4 to 6 or sometimes 8 accessory cells: the two polar cells are somewhat smaller than the rest. Pit depth is 10 to 12 μ. The slit between the guard cells is as long as the pit diameter.

(g) ZAMIA

Zamia angustifolia (Jacq.) Schuster (1956)

Plate CIII, Drawing 69; Plate CLXVI, Photos 1–4; Fig. 21

Leaf amphistomatic. On the *upper surface* of the leaflet, stomata are very scarce; there are no hair structures at all. The cells are loosely arranged in rows parallel to the leaflet axis and are densely wedged together. Their usual length ranges from 60 to 200 μ, their width from 16 to 20 μ. There are thick-walled (4 to 5 μ) and thin-walled (1 to 2 μ) cells. In the thick-walled ones the lumen does not always follow the outline of the cell: it expands substantially in some places to narrow down again almost to a slit. The thick cell walls are layered, smooth, with no pits; the thin ones bear many simple pits. The thin-walled cells contain several chloroplastids. These cells are sometimes arranged in longitudinal rows, in which case their length is 40 to 50 μ.

On the *undersurface* of the leaflet, the stomata occur in narrow bands, in a density of 60 to 62 per sq. mm. The width of the bands is 100 to 250 μ; that of the interbands is 200 to 250 μ. The number of rows per band is usually 3 to 6 but not infrequently just one or two. Size, shape, arrangement and wall thickness of the cells in the interbands are about the same as on the upper surface of the leaflet. The cells in the bands, between the stomata, are somewhat shorter, broader and more sinuous. This is due to the presence of the relatively close-spaced stomata. The cells are 50 to 140 μ long and 15 to 20 μ wide there.

The shape of the gaseous-interchange apparatus including the accessory cells is slightly flattened elliptical or circular. Its length is 50 to 60 μ, its width 40 to 50 μ. There are usually 5 or 6 accessory cells besides the polar cells. The shape of these latter is trapezoidal or triangular. The walls facing the stomatal pit of the accessory cells are thickened, the rest of their walls being of the same thickness as those of the thin-walled cells.

The length of one guard cells is 40 to 45 μ, its width is 12 to 15 μ, the size of the pit aperture is 18 μ by 13 to 14 μ. The thickness of the cell walls facing the pit is

5 to 5·5 μ. The slit between the guard cells is longer than the diameter of the pit. The end walls of the guard cells are slightly rounded and include an angle of about 90°. Pit depth is 6 to 7 μ. One or both of the polar cells frequently grow beyond the perimeter of the accessory cells.

Zamia fischeri Miq. (1845)

Plate CIII, Drawing 65; Plate CLXVII, Photos 1–4

Leaf hypostomatic. On the *upper surface* of the leaflet, the cells are substantially elongate parallel to the leaflet axis; some of them are arranged end to end, with end walls oblique at angles of about 45°, while some are wedged in far between the two adjacent ones. The cells are 40 to 160 μ long and 14 to 18 μ wide; their ends are rounded or slightly tapering. There are thick-walled (2 to 2·5 μ) and thin-walled (1 to 1·5 μ) cells. The walls of the thin-walled cells are very finely pitted. The walls of the thick-walled cells are of uniform thickness and bear no pits (see left side of photo 2). Twin epidermal cells are also fairly frequent. The ends of some cells are swollen like those of a bone, and these widened ends usually contact two narrower cells.

On the *undersurface* of the leaflet, the stomata occur in bands of various width (300 to 400 μ), separated by interbands of 150 to 250 μ width. Size, shape and arrangement of the cells in the interbands fully agree with those found on the upper surface of the leaflet. The stomata are arranged in loose, discontinuous rows, more or less parallel to the leaflet axis. The number of stomata in the transverse section of a band may attain 6, but in some places there are as few as two. There are 43 to 47 stomata to the sq. mm.

The stomata are usually surrounded by 4 or 6 accessory cells of trapezoidal or half-moon shape, the narrower ends of which constitute the stomatal pit. The walls facing the pit of the accessory cells are somewhat thicker than the other walls.

The length including the accessory cells of the gaseous-interchange apparatus is 90 to 100 μ; its width is about the same. The guard cells are 35 to 40 μ long and 14 to 16 μ wide. The size of the pit is 12 to 14 by 10 μ; pit depth is 5 to 6 μ. The thick wall sections of the guard cells measure 5 to 6 μ. The ends of the guard cells are obliquely truncated and meet at a somewhat acute angle. The epidermal cells between the stomata are somewhat shorter and exhibit a greater variety of shapes than those on the upper surface of the leaf.

Zamia floridana A. DC. (1868)

Plate CIII, Drawing 71; Plate CLXVIII, Photos 1–4; Fig. 22

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells, arranged parallel to the leaflet axis, are very narrow (15 to 18 μ) as compared with their length (150 to 400 μ). The individual cells usually taper to fairly acute tips wedged

in far between the next two cells. There are thin-walled (1 to 2 μ) and thick-walled (4 to 5 μ) epidermal cells. The thin-walled cells carry numerous simple pits. Cells placed end to end and separated by thin transverse walls are fairly frequent. The thick cell walls are of uniform thickness and bear no pits. The lumina of these cells exactly follow the outline of the cells.

On the *undersurface* of the leaflet, there are fairly wide stomatiferous bands separated by much narrower interbands. In the bands, there are about 50 to 65 stomata per sq. mm. The width of the bands is 500 to 600 μ; that of the interbands is 100 to 120 μ. The stomata are arranged in loose, more or less longitudinal rows, as well as in even more vague diagonal ones which include angles of about 45° with the leaflet axis. The size of the gaseous-interchange apparatus together with the accessory cells is rather varied (60 to 120 μ by 65 to 80 μ). The stomatal pit is constituted by 4 or 6 thin-walled accessory cells. The pit itself is usually circular or elliptical. Most accessory cells are trapezoidal; their base is 30 to 32 μ, their top side 15 μ long. Some, accessory cells are half-moon-shaped and are embraced by the two adjacent epidermal cells. The polar cells are usually 20 μ wide and sometimes 50 μ long, but most of them do not attain even half that length. The guard cells are 35 to 40 μ long, their width is 14 to 16 μ. The size of the stomatal pit is 15 to 18 by 12 to 13 μ. Pit depth his 5 to 6 μ. The slit between the two guard cells is longer than the pit diameter. The guard cell wall measures 6 to 7 μ where it is thickest. Its surface is covered by lamellae perpendicular to the slit. The walls facing the pit of the accessory cells are thick, the rest of their walls are fairly thin. The epidermal cells between the stomata are much shorter and broader than those on the upper surface of the leaflet. Among them, there are but a few thin-walled cells, but these are rich in chloroplastids (Photo 4). The length of the cells between the stomata ranges from 40 to 100 μ; their width is 20 to 22 μ.

Zamia furfuracea L. fil. (1789)

Plate CII, Drawing 59; Plate CLXIX, Photos 1–4; Fig. 75

Leaf hypostomatic. On the *upper surface* of the leaflet, the arrangement of the cells suggests at some points the vestiges of disappeared stomata. At more or less regular intervals, one observes the traces of hair structures. The epidermal cells are slightly elongate parallel to the leaflet axis; some meet end to end, some form an interwedged pattern. Their length (50 to 100 μ) is usually two to five times their width (15 to 20 μ). There is a variety of shapes (triangular, quadrangular, trapezoidal, lozenge, rhomboidal); the apices are invariably rounded. There are thin-walled (1·5 to 2 μ) and thick-walled (4 to 5 μ) cells. The smooth wall of the thick-walled cells is of uniform thickness and bears no pits. Scattered among these cells there are thin-walled ones which communicate through very small simple pits. Containing chloroplastids, these cells are capable of assimilation.

On the *undersurface* of the leaflet, the stomata are grouped in bands of 350 to 400 μ width, separated by interbands of 200 to 220 μ width. Size, shape and arrange-



Fig. 75. *Zamia furfuracea* (after Graf)

ment of the cells are exactly the same in the interbands as on the upper surface of the leaflet. The dark dots in Photo 3 indicate the bases of scattered hair structures. The stomata form 5 or 6 orthosticha per band and also constitute diagonal parasticha. The epidermal cells between the stomata are much shorter and exhibit a much greater diversity of shapes than in the interbands. Their length is 20 to 60 μ, their width, 15 to 18 μ. Triangular, quadrangular, trapezoidal and other shapes are common. The cells are usually thick walled, thin-walled parenchyma cells being fairly rare. The stomata are markedly different from the epidermal cells around them. Their size including the accessory cells is 70 to 75 μ by 65 to 70 μ. The usual number of accessory cells is 4 or 5. The polar cells are in most cases substantially elongate, sometimes 50 μ long. The guard cells are 28 to 40 μ long and 18 to 20 μ wide. Most frequent dimensions are 28 μ by 20 μ.

The thickened sections of the guard cell walls are 4 to 5 μ in diameter; the cells carry no particular ornament. Their end walls are rounded and meet at an angle which is more frequently obtuse than right. The stomatal pit is usually an ellipse flattened transversely to the leaflet axis, i.e. perpendicular to the slit between the guard cells. The long axis of the ellipse is 28 μ, the other axis is 16 to 17 μ long. This shape of the pit seems to be a specific feature which distinguishes *Z. furfuracea* from the rest of the *Zamia* species. Pit depth is 6 to 7 μ.

The walls of the accessory cells are thin (1 μ) and bear numerous simple pits, agreeing in this respect with the thin-walled epidermal cells. The walls facing the pit of these cells are not substantially thickened, either. The epidermal cells between the stomata are thick walled (4 to 5 μ). The accessory cells contain chloroplastids.

Zamia gutierrezi Sauvalle (1868)

Plate CII, Drawing 56; Plate CLXX, Photos 1–4

Leaf hypostomatic. The *upper surface* of the leaflet bears epidermal cells elongate in the direction of the leaflet axis: their length (60 to 200 μ) is several times their width (14 to 20 μ). Usual shapes are long tapering quadrangles or triangles. Third

cells are often wedged in between the tapering ends of two others, whereas in other cases the cells meet end to end with transverse walls. Twin epidermal cells are also fairly frequent: in this case, two epidermal cells alike in size and shape are separated by a transverse end wall.

There are both thick-walled (4 to 5 μ) and thin-walled (1·5 to 2 μ) cells. The thin-walled cells communicate through a large number of minute pits. The thick cell walls are smooth and bear no pits. The cells are somewhat longer and narrower above the veins of the leaflet.

On the *undersurface* of the leaflet, the stomata are grouped in bands of 300 to 400 μ width separated by narrow interbands, less than 100 μ wide usually. There are 3, 4 or 5 longitudinal rows of stomata per band, arranged in orthosticha and diagonal parasticha. The epidermal cells in the interbands fully agree in size and shape with those on the upper surface of the leaflet; the cells among the stomata are somewhat squatter, but their shape and arrangement are much the same as on the upper surface.

The gaseous-interchange apparatus including the accessory cells is circular or elliptical, 120 to 135 μ by 55 to 70 μ in size. There are 2 to 4 accessory cells, plus two polar cells which usually reach beyond the periphery outlined by the accessory cells. The latter are trapezoidal or pistol-shaped: their tapering ends constitute the stomatal pit. The size of the pit is 20 to 22 μ by 18 to 22 μ. Beneath the pit there are the two guard cells. The slit between them is longer than the pit diameter. The thickened section of the guard cell walls has a diameter of 6 to 7 μ. The guard cells are 55 to 60 μ long and 15 to 18 μ wide; their surface bears transverse lamellae perpendicular to the slit.

Zamia kickxii Miq. (1842)

Plate CIII, Drawing 67; Plate CLXXI, Photos 1–4; Fig. 76

Leaf hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are elongate parallel to the leaflet axis, with a mean length of 90 to 100 μ and a mean width of 20 to 25 μ. The cells are either aligned in the direction of the leaflet axis, or oblique, in which latter case they are often triangular, 40 to 180 μ in full length, whereas the base of the triangle is 50 to 60 μ. Cells placed end to end meet with obliquely or transversely truncated walls. Some twin epidermal cells also occur. There are thick-walled (1 to 2·5 μ) and thin-walled (1 μ) cells. The thick cell walls are smooth, without pits. Some thin-walled cells contain simple pits and chloroplastids.

On the *undersurface* of the leaflet, the stomata are arranged in bands of 400 to 450 μ width separated by interbands 100 to 200 μ wide. The interbands are under the veins of the leaflet. There are about 35 to 45 stomata per sq. mm. Size and orientation of the cells in the interbands fully agree with those of the cells on the upper surface; also, on the upper surface, the cells are somewhat more densely grouped above the veins.

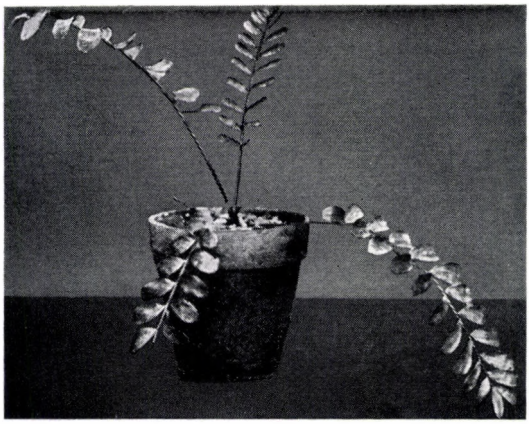

Fig. 76. *Zamia kickxii* (after Graf)

The accessory cells are markedly different from the epidermal cells around them. Most stomata are surrounded by four accessory and two polar cells. The former are mostly trapezoidal, with their short sides facing the stomatal pit. The walls of these sides are slightly thicker; the other walls are thin.

Beneath the pit there are the guard cells whose length is 30 to 35 μ and whose width is 12 to 15 μ. The slit between them is longer than the diameter of the pit. The pit is either circular or slightly flattened elliptical of 16 to 17 μ length and about the same width.

Size and shape of the epidermal cells between the stomata as well as the distribution and wall tickness of the thin- and thick-walled cells agree almost fully with those on the upper surface of the leaflet, except that the cells between the stomata are somewhat shorter and squatter.

Zamia latifolia Lodd. (1868)

Plate CII, Drawing 58; Plate CLXXII, Photos 1–4

Leaf typically hypostomatic. On the *upper surface* of the leaflet, the epidermal cells are substantially elongate parallel to the leaflet axis: their length ranges from 50 to 100 μ, their width from 25 to 30 μ. Cell walls are of fairly uniform thickness: most cells have tapering ends which interlace to form a wedge pattern with the similar ends of the other cells. Twin cells with transverse separating walls are also fairly common. The aggregate thickness of two adjacent cell walls is 3 to 4 μ. One often sees groupings of 3 or 4 somewhat thinner-walled cells between the thicker-walled ones. Some thinner-walled cells contain chloroplastids and have smooth walls which bear no pits. The epidermal cells above the veins are somewhat more elongate and thicker walled.

On the *undersurface* of the leaflet, the epidermal cells are somewhat shorter and wider owing to the presence of a large number of stomata. These latter occur in longitudinal bands of 350 to 400 μ width, separated by interbands 70 to 100 μ wide. There are 45 to 50 stomata per sq. mm. A band usually includes 1 to 5 rows of stomata. Most of the stomata stand alone, but some twin stomata are also observed. The usual size of the gaseous-interchange apparatus including the accessory cells is 75 to 80 μ by 65 to 70 μ. The length of one guard cell is 27 to

30 μ, its width is 17 to 18 μ. The guard cells are situated below the level of the leaflet epidermis, at the bottom of a pit. The long axis of the stomatal pit is 15 to 16 μ, its short axis is 12 to 14 μ. The usual number of the guard cells is 4 to 6, i.e. 2 or 3 on one side, but in some cases one on one side and three on the other have also been observed. Some stomata are slightly smaller than the others.

Zamia latifoliata Preneloup (1871)

Plate CIII, Drawing 70; Plate CLXXIII, Photos 1–4; Fig. 77

Leaf atypically hypostomatic: configurations looking like very scarce stomata are seen on the upper surface of the leaflet. The accessory cells surrounding these exhibit an arrangement similar to that of the accessory cells on the undersurface.

On the *upper surface*, the epidermal cells are substantially elongate in the direction of the leaflet axis, being 50 to 250 μ long and 20 to 35 μ wide. Cell shapes include highly elongate cylinders and trapezia, with the end of a third cell wedged in between the tapering ends of two adjacent cells. Elsewhere cells are seen arranged end to end, separated by transverse walls, constituting what look like twin cells. There are both thick-walled and thin-walled cells, randomly interspersed. The thin-walled cells contain a few sparse chloroplastids. The diameter of the thick walls is 7 μ on the average. The thick walls bear numerous simple pits.

On the *undersurface* of the leaflet, there are longitudinal bands of stomata, each band containing 3 to 5 longitudinal rows. Transverse rows, slightly oblique, can also be recognized. Band width is 200 to 300 μ, the width of the interbands is about the same. The thin- and thick-walled epidermal cells of the interbands are substantially elongate, being similar in size and arrangement to those on the upper surface of the leaflet. The thick- and thin-walled epidermal cells filling out the space among the stomata are much shorter. The length of a gaseous-interchange apparatus is 80 to 90 μ, the length of a guard cell is 55 to 60 μ. The trans-



Fig. 77. *Zamia latifoliata* (after Graf)

verse end of the pair of guard cells recalls two procumbent figure threes symmetrical about the stoma axis. The accessory cells number 3 to 5, seldom 6, the ends of some are elongate swallowtail fashion. Pit aperture size is 35 to 45 by 25 to 35 μ, pit depth is 6 to 7 μ.

Zamia lindenii Regel (1875)

Plate CII, Drawing 62; Plate CLXXIV, Photos 1–4; Fig. 78

Leaf hypostomatic. On the *upper surface* of the leaflet, cells of 50 to 200 μ length and 18 to 20 μ width are arranged in slightly sinuous rows more or less parallel to the leaflet axis. There are thicker- and thinner-walled cells: the diameter of two adjacent cell walls is 6 to 7 μ in the first case and 1·5 to 2 μ in the second. The thick cells have walls of uniform thickness that bear no pits. The lumina of these cells closely follow their outlines. The thin cell walls bear simple pits and the cells contain chloroplastids. Most cells are oblong, elongate in the direction of the leaflet axis, rhombic, trapezoidal or of some similar shape.

On the *undersurface* of the leaflet, the stomata occur in broad bands of 1000 to 1100 μ width, separated by interbands of 300 to 310 μ width. Size, shape and arrangement of the cells in the interbands are exactly as on the upper surface of he leaflet, particularly on those parts of that surface which overlie the veins. The stomata, forming 8 to 12 longitudinal rows not invariably parallel with the leaflet axis, do not stand very dense (45 to 50 of them to the sq. mm). Size, shape and arrangement of the epidermal cells between the stomata are slightly different from those in the interbands. Most of these cells are thick walled (3 to 4 μ). Thin-walled parenchyma cells are relatively scarce.



Fig. 78. *Zamia lindenii* (Botanical Garden, Munich: photo by Bauer)

The length of the gaseous-interchange apparatus including the two polar cells is about 120 μ. The length of the polar cells is 30 to 50 μ. The length of the guard cells is 55 μ; their width is 35 μ; their thickened wall sections measure 7 to 8 μ. The size of the stomatal pit is 30 μ by 15 μ. The slit between the two guard cells is longer than the pit diameter. The rounded end walls of the guard cells meet at a decidedly acute angle. The thickened wall section exhibits a dense transverse ornament. The number of accessory cells is 3 or 4, seldom 5; their lateral walls are very thin: their walls facing the pit are somewhat thicker. These cells which contain chloroplastids differ in their entire structure from the surrounding thick-walled epidermal cells.

Zamia loddigesii Miq. (1849)

Plate XCVIII, Drawing 29; Plate CLXXV, Photos 1–4; Fig. 79

Leaf hypostomatic. Elongate parallel to the leaflet axis, the epidermal cells of the *upper surface* of the leaflet form a densely interlaced pattern, each cell being in contact with the sides of 2 or 3 other cells. Their length ranges from 70 to 100 μ, their width from 15 to 20 μ on an average. Shapes are not too varied: one observes elongate oblongs, either with tapering ends or with obliquely or transversely truncate end walls, both types rounded. There are thick-walled (3 to 4 μ) and thin-walled (1 to 1·5 μ) cells; the thin cell walls bear numerous simple pits (see upper right corner of Photo 2). The thin-walled cells contain chloroplastids. The smooth thick cell walls are of uniform thickness and bear no pits. Thick- and thin- walled cells are about evenly distributed (Photo 2).

On the *undersurface* of the leaflet, the stomata, 55 to 60 to the sq. mm, are grouped



Fig. 79. *Zamia loddigesii* (Botanical Garden, Munich; photo by Bauer)

in bands of 300 to 350 μ width separated by interbands of 200 to 250 μ width. Size, shape and arrangement of the epidermal cells in the interbands more or less agree with those on the upper surface of the leaflet whereas the epidermal cells in the bands, between the stomata, are shorter (60 to 150 μ) and slightly broader (15 to 25 μ); also, owing to the presence of the stomata, their shape is much more varied. Most cells in the bands are thick; thin-walled cells are very rare here. The interbands have the width of 10 to 15 epidermal cells.

The stomata constitute longitudinal rows as well as oblique parasticha. The size including the accessory cells of the gaseous-interchange apparatus is 115 to 120 μ by 65 to 70 μ. The stomata proper are surrounded by 4 to 6 accessory cells, most of which are trapezoidal and whose walls facing the stomatal pit are thicker than the rest of their walls. The accessory cells differ from the surrounding epidermal cells not only in wall thickness but also in that they contain chloroplastids which makes them capable of assimilation.

The length of the guard cells is 35 to 40 μ, their width 12 to 15 μ. The size of the pit is 20 by 12 to 16 μ. The slit between the two guard cells is as long as the pit diameter. The thickened section of the guard cell wall measures 4 to 5 μ and exhibits an ornament of fine lines. The end walls of the guard cells are rounded and meet either at right angles or at an obtuse angle.

Zamia media Jacq. (1798)

Plate CIII, Drawing 68; Plate CLXXVI, Photos 1–4

Leaf hypostomatic. On the *upper surface* of the leaflet the epidermal cells are arranged parallel to the leaflet axis, end to end with rounded or obliquely or transversely truncate end walls. The ends of some epidermal cells are often wedged in rather far between the next two cells. Cell length ranges from 50 to 200 μ, cell width from 14 to 20 μ. There are thick-walled (2 to 2·5 μ) and thin-walled (1 to 1·5 μ) cells. The cells above the veins of the leaflet tend to be somewhat longer and slenderer. The thin cell walls bear very many simple pits. Smooth and of uniform thickness, the thick cell walls bear no pits at all. The thin-walled cells contain chloroplastids.

On the *undersurface* of the leaflet, the stomata occur in loose longitudinal rows grouped into bands of 400 to 600 μ width separated by interbands of 100 to 200 μ width. Size and shape of the cells of the interbands fully agree with those on the upper surface of the leaflet. The epidermal cells in the bands, between the stomata, are somewhat shorter (30 to 100 μ) and much more varied in shape. Their walls are not quite uniform in thickness. There are 4 or 5 trapezoidal or triangular accessory cells. Their walls facing the stomatal pit are somewhat thicker than their other walls. Some accessory cells contain chloroplastids. The two polar cells tend to be much larger than the accessory cells.

The size of the gaseous-interchange apparatus including the polar and accessory cells is 60 to 80 μ by 60 to 70 μ. The guard cells are 45 to 50 μ long and 15 to 18 μ

wide. The length of the stomatal pit is about 10 to 14 μ; its width ranges between the same limits; its shape is circular or slightly flattened, elliptical. Beneath the pit, there are two guard cells. The slit between them is as long as the diameter of the pit. The thickened section of the guard cell walls is 4 μ thick.

Zamia muricata Willd. (1805)

Plate CII, Drawing 57; Plate CLXXVII, Photos 1–4; Fig. 23

Leaf hypostomatic. However, on the *upper surface* of the leaflet there occur a few scattered groupings of cells which suggest vestiges of stomata. The cells are elongate in the direction of the leaflet axis and either join long oblique faces or shorter transverse walls. Cells of identical size fairly often constitute diagonal rows. The length of the cells is 60 to 130 μ, their width is 15 to 20 μ. There are thick-walled (2 to 3 μ) and thin-walled (about 1 μ) cells, often with 2 or 3 thick-walled cells surrounding a thin-walled one. The thin walls bear numerous simple pits: the thick ones are entirely smooth. The thin-walled cells contain chloroplastids.

On the *undersurface* of the leaflet, the stomata occur in bands of various width, 600 to 650 μ on the average, separated by interbands of 150 to 200 μ width. The stomata seem to be scattered in a random fashion over the band, with 28 to 36 of them to the sq. mm. Size, shape and orientation of the cells in the interbands fully agree with those on the upper surface of the leaflet; the epidermal cells are somewhat shorter and curved to fit the accessory cells of the stomata.

One of the remarkable features of the stomata is the substantial elongation, swallowtail fashion, or in some equally unusual form, of one or two accessory cells or a polar cell (see Photo 4). In this respect, *Z. muricata* differs from most *Zamia* species. Numbering 3 or 4, occasionally 5, the accessory cells are triangular, rhombic or trapezoidal, sometimes half-moon-shaped. The accessory cells differ in colour as well as in shape from the epidermal cells around them. Their short walls constitute the stomatal pit: these walls are somewhat thicker than the rest. Otherwise, the accessory cells are as thin walled as the thin-walled epidermal cells. The length of the gaseous-interchange apparatus including polar cells is 150 to 200 μ; its width is 60 to 70 μ.

The walls of the accessory cells bear several simple pits. The length of the guard cells is 35 to 40 μ, their width is 18 to 20 μ. The pit is 30 μ long and 22 to 25 μ wide; the slit between the guard cells is longer than the long diameter of the pit. The wall of the guard cell measures 5 to 6 μ where it is thickest.

Both the upper and undersurface of the leaflet bear some rare epidermal structures.

Zamia ottonis Miq. (1843)

Plate CII, Drawing 60; Plate CLXXVIII, Photos 1–4 ;Fig. 80

Leaf hypostomatic. On the *upper surface* of the leaflet, the cells are substantially elongate in the direction of the leaflet axis; their side walls are more or less sinuous; their end walls are oblique or transverse, sometimes rounded. Fairly often, one cell is wedged in far between the two adjacent ones. There are thick-walled (4 to 5 μ) and thin-walled (1 to 1·5 μ) cells. The latter contain numerous chloroplastids. The thin cell walls bear many pits; the thick ones are smooth and of uniform thickness. The cavity does not invariably follow the outline of the cells: it may be constricted or expanded in places. The distribution of thin- and thick-walled epidermal cells is fairly uniform. Their size ranges from 100 to 250 μ in length and from 15 to 20 μ in width.

On the *undersurface* of the leaflet, the stomata occur in bands of 300 to 400 μ width, separated by interbands about 150 to 200 μ wide. Density of stomata are about 50 to 55 per sq. mm. Size, shape and arrangement of the epidermal cells is the same in the interbands as above the veins on the upper surface of the leaflet. On the other hand, the epidermal cells between the stomata are markedly different from those in the interbands. Their usual length range is 40 to 200 μ, their width range, 18 to 22 μ. Thin- and thick-walled cells are intermingled just as on the upper surface. The thinner-walled cells contain chloroplastids and communicate through very small simple pits. In the bands the stomata form 3 to 8 loose longitudinal rows; diagonal or transverse rows can also be recognized occasionally. The number of accessory cells is 4 to 6, most often 4. The accessory cells are arranged as a quartet of trapezia round the stomatal pit. The walls facing the pit of the accessory cells are somewhat thicker; their other walls are just as thick as those of the thin-walled epidermal cells. The accessory cells thus differ markedly in wall thickness from the thick-walled epidermal cells around them.

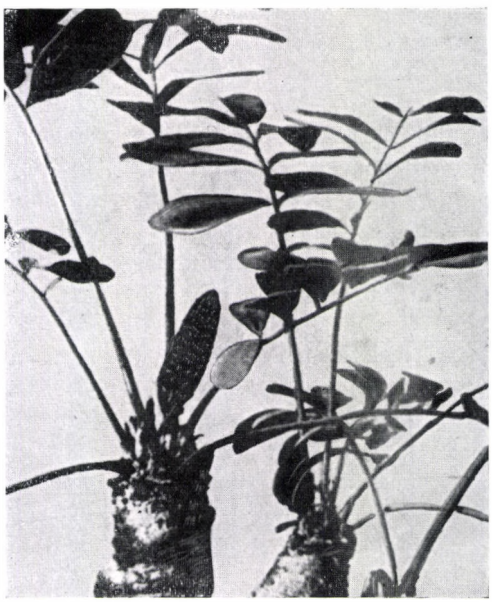

Fig. 80. *Zamia ottonis* (after Graf)

The length of the gaseous-interchange apparatus including the accessory cells is 75 to 80 μ by 65 to 70 μ. The length of the guard

cells is 30 to 32 μ, their width is 14 to 15 μ. The slit between them is slightly longer than the diameter of the stomatal pit. The thickened part of the guard cell wall measures 4 to 5 μ and bears no visible ornament. The rounded end walls of the guard cells meet at about right angles.

Zamia portoricensis Urban (1899)

Plate CLXXIX, Photos 1–4

Leaf hypostomatic. On the *upper surface* of the leaflet the epidermal cells are close packed and arranged parallel to the leaflet axis, without constituting conspicuous longitudinal rows. Some meet end to end with transverse or oblique end walls, some are interlaced in a wedge pattern. Fairly often one observes 2, 3 and even 4 cells end to end and separated by thin transverse partitions, much like segmented fibres. This phenomenon is largely restricted to thin-walled cells. The epidermal cells above the veins are much longer than the rest. There are thick-walled cells (2 to 2·5 μ) with smooth walls of uniform thickness and thin-walled ones (1 μ; at most 1·5 μ) containing chloroplastids, whose walls bear many simple pits. The size of the cells varies in the range of 80 to 250 μ by 15 to 20 μ.

On the *undersurface* of the leaflet, the stomata occur in bands of 500 to 600 μ width, separated by interbands of 150 to 200 μ width. There are 42 to 48 of them per sq. mm. In each band, the stomata constitute loose longitudinal orthosticha and parasticha; the epidermal cells between them are usually much shorter (35 to 70 μ long and 15 to 22 μ wide) and of a greater variety of shapes than the ones on the upper surface.

The shape of the gaseous-interchange apparatus including the accessory cells is circular or transverse elliptical. Its longitudinal dimension is 50 to 60 μ; its transverse dimension varies in the same range, a longitudinal dimension of 50 μ and a transverse one of 60 μ being the most frequent combination. Besides the two polar cells, there are 4, 5 or 6 accessory cells of crescent, triangle or rhombic shape. It is their somewhat thicker-walled short sides which constitute the bounds of the stomatal pit.

The accessory cells differ from the epidermal cells surrounding them firstly in colour, and secondly in that their surface is covered with a very fine tuberculate ornament. Some pits are surrounded by four rhombic accessory cells only, in which case the terminal walls of each pair of accessory cells lie in the continuation of the end walls of the guard cells.

The length of the guard cells is 25 to 30 μ; their width is 15 to 16 μ; pit size is 14 to 15 μ by 12 to 13 μ. The slit between the guard cells is longer than the pit diameter. The thickened section of the guard cell wall has a diameter of 4 μ and bears lamellae perpendicular to the slit.

Zamia pumila L. (1753)

Plate CIII, Drawings 63, 64; Plate CLXXX, Photos 1–4; Fig. 24

Leaf hypostomatic. On the *upper surface* of the leaflet, the cells are elongate parallel to the leaflet axis, arranged end to end with obliquely truncate end walls or interlaced with rounded ends to form a wedge pattern. Their size range is 150 to 250 μ in length and 15 to 25 μ in width. In the wedge pattern, the cells usually reach up as far as the middle of the two adjacent ones. There are thick-walled (4 to 5 μ) and thinner-walled (1·5 to 2 μ) cells. The thin-walled cells contain chloroplastids; their walls bear a dense arrangement of simple pits. The thick cell walls are layered; the lumina are irregular, reduced to slits in the narrower portions of the cell and expanded where the cell is wider. Twin epidermal cells are fairly common.

On the *undersurface* of the leaflet, the stomata occur in bands of 200 to 400 μ width separated by interbands 60 to 100 μ wide. There are 60 to 65 stomata per sq. mm. Size, shape, orientation and arrangement of the epidermal cells in the interbands fully agree with those of the upper surface, particularly of those portions of it which overlie the veins. In the bands, the cells are formed more squat (length 30 to 100 μ, width 14 to 20 μ) and more varied owing to the presence of the stomata. However, the cells in the bands may also be both thick or thin walled.

The stomata are surrounded by 4 or 6 accessory cells of trapezoidal quarter-circle or half-moon shape. The walls facing the stomatal pit of the accessory cells are somewhat thickened, the rest of their walls being as thin as those of the thin-walled epidermal cells.

The length of the stomata including the accessory cells is 120 to 140 μ, their width being 65 to 70 μ. The guard cells are 35 to 40 μ long and 15 to 16 μ wide. The size of the stomatal pit is 16 to 18 μ by 13 to 14 μ. Beneath the pit there are the two guard cells. The slit between them is longer than the diameter of the pit. The end walls of the guard cells are rounded and meet at right angles. Pit depth is 4 to 5 μ.

Zamia pygmaea Sims. (1815)

Plate CIII, Drawing 66; Plate CLXXXI, Photos 1–4

Leaf hypostomatic. The epidermal cells on the *upper surface* of the leaflet are oblongs of sinuous sides, elongate in the direction of the leaflet axis, joining rounded ends much more often than truncated end walls. The ends of most cells are wedged in between the ends of the next two cells. A somewhat denser pattern is observed above the veins. The size range of the cells is 80 to 120 μ in length and 12 to 18 μ in width. The cell walls are usually of uniform thickness, with the wide lumen invariably following the outline of the cell. The walls are relatively thin (1 to 3 μ). Some cells contain numerous chloroplastids.

On the *undersurface* of the leaflet, the stomata occur in bands of 400 to 450 μ width with 35 to 45 of them to the sq. mm. There are 4 to 6 rows of stomata in most bands. The epidermal cells contained in the interbands of 150 to 200 μ width are much longer (150 to 200 μ) and somewhat narrower than those on the upper surface of the leaflet. In the bands, however, the epidermal cells are much shorter (30 to 110 μ), sometimes quite squat, and of a greater variety of forms. The size of the gaseous-interchange apparatus including the accessory cells is 70 to 80 by 45 to 50 μ. The usual number of accessory cells is 3 or 4: their walls facing the stomatal pit are somewhat thickened. The polar cells do not usually reach beyond the perimeter of the accessory cells. The guard cells, situated beneath the pits, are 20 to 25 μ long and 10 to 12 μ wide. The pit is either circular or an ellipse whose long axis (20 to 22 μ) is perpendicular to the slit between the guard cells. Pit depth is 3 to 4 μ.

Zamia silicea Britton (1916)

Plate CII, Drawing 61; Plate CLXXXII, Photos 1–4

Leaf hypostomatic. On the *upper surface* of the leaflet, the cells are parallel to the leaflet axis and meet either with obliquely cut, tapering ends or short transverse walls. Their usual range is 100 to 250 μ in length and 15 to 20 μ in width. Shapes are rather monotonous, elongate oblongs with sinuous sides and rounded ends being the most common. Some cells are wedged in halfway between the two adjoining ones. There are thick-walled (6 to 8 μ) and thin-walled (1·5 to 2 μ) cells. The lumina of the thick-walled cells exhibit irregular constrictions and expansions, whereas those of the thin-walled ones follow the outlines of the cells. The thin-walled cells usually contain chloroplastids; their walls bear several simple pits. The distribution of the thin-walled and thick-walled cells is far from being uniform.

On the *undersurface* of the leaflet, the stomata occur in bands of 300 to 400 μ width separated by interbands 100 to 150 μ wide. There are 60 to 70 stomata per sq. mm. Size, shape and arrangement of the epidermal cells are much the same in the interbands as on the upper surface of the leaflet. On the other hand, the epidermal cells between the stomata are much shorter (20 to 100 μ) and exhibit a much greater variety of shapes (see Photo 4). These features are due to the presence of the stomata.

The slits of the stomata are not invariably parallel to the leaflet axis. The stomata are usually surrounded by 3 or 6 accessory cells, most frequently of triangular, trapezoidal or crescent shape. Their walls facing the stomatal pit are somewhat thicker than their side walls, which are invariably thinner than the walls of the rest of the epidermal cells. The accessory cells contain chloroplastids.

The length of the stomata is 65 to 70 μ: their width is about the same. The size of the accessory cells is 40 to 42 μ by 32 to 35 μ. The slit between the two guard cells is longer than the diameter of the stomatal pit. Pit depth is 6 μ. The epidermal cells have walls as thick as on the upper surface of the leaflet and communicate through small pits.

(h) BOWENIA

Bowenia serrulata (W. Bull.) Chamberlain (1912)

Plate XCV, Drawing 1; Plate CLXXXIII, Photos 1–4; Figs 25 and 26

Leaf amphistomatic. Stomata are scarce on the upper surface (1 or 2 to the sq. mm), being much more numerous on the undersurface (50 to 62 to the sq. mm). Their distribution is rather random on the upper surface, whereas on the undersurface they are restricted to bands parallel to the venation of the leaflet.

On the *upper surface* of the leaflet, the epidermal cells are arranged parallel to the leaflet axis. Sizes are varied, the smallest being about 100 μ long and 10 to 20 μ wide, the longest attaining 330 μ. Their walls are medium thick (3 to 4 μ); the diameter of the lumen is 10 to 20 μ. The cells are spindle-shaped, elongate, arranged end to end with obliquely truncated end walls, although transverse walls are also fairly common. Both the side and end walls exhibit a fine pitting; the thickness of the walls is uniform, so that the lumen follows the outline of the cell. Constrictions of the lumen are fairly rare. Twin epidermal cells also occur sometimes. The elongate epidermal cells locally exhibit a variety of shapes. Some cells are in contact with 5 or 6 other cells and with randomly scattered lone stomata.

The length of the stomata is 50 to 70 μ, their width is 40 to 45 μ; the length of the slit is 20 to 30 μ, its width 3·5 μ. The usual number of the more or less isodiametric accessory cells is 4; the two polar cells are substantially elongated. The surface of the guard cells bears a fine tuberculate pattern. This structure much resembles the stomata of Devonian *Psilophyton*. On the *undersurface* of the leaflet, the stomata are arranged in longitudinal bands; their apertures are likewise invariably parallel to the venation. There are about 50 to 57 stomata per sq. mm. Each band includes 6 to 8 slightly sinuous rows of stomata. The bands are separated by stomaless interbands whose epidermal cells fully agree in size and shape with those on the upper surface of the leaflet, whereas the space between the stomata in the bands is filled with somewhat smaller epidermal cells. The shapes of these cells roughly resemble those of the upper surface cells.

The stomata are surrounded by 6, exceptionally by 8 cells. The two polar cells are invariably more elongate and narrower than the lateral cells. The end walls facing the stomatal pit of the accessory cells are not raised above the epidermal surface and do not consequently constitute a crater. The slit between the guard cells nowhere reaches the accessory cells. The radial side walls of the accessory cells are thinner than the walls of the other epidermal cells; their surface bears a fine tuberculate pattern which distinguishes them fairly well from the surrounding epidermal cells. The side walls of the accessory cells exhibit an exceedingly fine pitting. Locally pairs of stomata may occur side by side or end to end which makes them look like stomata. This feature is suggestive of the stomata of Devonian *Psilophyton princeps*, so that the assumption of a relationship between the two is not unfounded. The length of the guard cells is 25 to 30 μ, their width is 10 to 12 μ.

Bowenia spectabilis Chamberlain (1912)

Plate XCV, Drawing 2; Plate CLXXXIV, Photos 1–4; Figs 27a,b, 28

A few scattered stomata on the upper surface of the leaflet reveal this to be an amphistomatic leaf.

On the *upper surface* of the leaflet, the epidermal cells are elongate parallel to the venation. Their length is 70 to 150 μ, their width 15 to 20 μ. The cells exhibit a variety of shapes, most of them with tapering ends. The cells usually join the adjacent cells with half or one-third of their length. There are thick-walled (2·5 μ) and thin-walled (1·5 to 2 μ) cells. Most thin-walled cells contain numerous chloroplastids. Their walls are smooth and bear no pitting. Stomata are rather scarce: the length including the accessory cells of the gaseous-interchange apparatus is 120 to 130 μ, its width is 65 to 70 μ. One of the typical features of the accessory cells is that their walls are perforated, as it were, by numerous small simple pits. The length of the guard cells is 30 to 40 μ; their width is 15 to 17 μ. The length of the slit is 20 μ. The walls of the guard cells are 10 μ thick. The end walls of the guard cells meet at an angle of about 40°.

On the *undersurface* of the leaflet, the stomata occur in bands of 1000 to 1100 μ width separated by interbands of 150 to 200 μ width. Each band includes 8 to 10 longitudinal rows of stomata. The distribution of the stomata within the rows is fairly irregular; the rows are somewhat vague, too. There are 30 to 35 stomata per sq. mm. Size, shape and arrangement of the epidermal cells in the interbands fully agree with those on the upper surface of the leaflet. The epidermal cells between the stomata are somewhat shorter (50 to 90 μ) than on the upper surface of the leaflet; their width is 15 to 25 μ. The spacing between the stomata is in general equal to the length of 2, 3 or 4 stomata. The length of the gaseous-interchange apparatus including the guard cells is 80 to 90 μ, their width 65 to 70 μ. The length of the guard cells is 35 to 40 μ, their width is 14 to 15 μ. The accessory cell are pitted in the same way as on the upper surface of the leaflet; this perforation is not, however, present in all cells. 4 to 6 accessory cells (4 is the most frequent number) constitute a low crater around the stoma. The guard cells are slightly countersunk; crater depth is 3 to 4 μ. The epidermal structure of the leaflets renders it fairly easy to distinguish *Bowenia spectabilis* from *B. serrulata*.

RELATIONSHIPS OF THE CYCADS ON THE BASIS OF THEIR EPIDERMOLOGY

Plate CLXXXV

On the basis of their studies into the leaf epidermis of extinct *Cycadofilices* and living Cycads, Andrews, Arnold, Florin, Cookson and several eminent paleontologists in a number of books and papers have voiced the opinion that there is a

marked resemblance, indeed, a full agreement between the leaf epidermis of extinct ferus and seed ferus and the living Cycads. Thus the epidermal structure of the leaf of fossil *Lepidozamia hopeites*, described by Cookson from the Australia Tertiary is almost fully identical with that of living *Macrozamia hopei*. It is fairly hard to distinguish them, although the latest studies by Cookson do not permit them to be identified without reserve. The studies in question were based on the knowledge of the leaf epidermis of living *Macrozamia hopei* and *M. peroffskyana*. This single but significant case is in itself sufficient to prove the importance for paleontology of a thorough knowledge of the epidermal structure of living Cycads. To prove this statement, let us enumerate a few more cases which could be amplified at will by numerous other convincing ones.

Photo 1, on Plate CLXXXV, shows living *Zamia muricata*; the adjacent photo of identical magnification shows *Lyginodendron oldhamium* from the Lower Westphalian. The similarity of the stomata as well as of the size and shape of the accessory cells is convincing enough to support the hypothesis of some kind of relationship between the extinct genus *Lyginodendron* and the living genus *Zamia*.

The same holds for *Macrozamia miquelii*, whose epidermal structure strikingly resembles that of *Elatocladus amblus* from the Jurassic, which suggests a similar relationship, if not full identity, between the two genera.

The resemblance between the epidermis of *Dioon edule* and of *Elatocladus punctatus* from the Jurassic of Britain is even more remarkable. The typical feature of *Dioon edule* is the shape of its guard cells. No other living Cycad species exhibits similar ones (Florin 1933, p. 68). The apposed photo of *Elatocladus punctatus* shows the shape of the accessory cells and the size of the hexagonal aperture to be almost the same as in *Dioon edule*. This high degree of similarity – indeed, identity – likewise justifies the assumption of some kind of relationship.

A similar case can be made for the leaf epidermis of *Encephalartos lehmannii* and *Callipteris martensii*. The stomata as well as the size and shape of the accessory cells around them are markedly similar, which gives rise to the assumption of a further relationship.

The most intriguing case is, however, that of *Stangeria paradoxa* and of its resemblance to the genus *Ctenis* from the Rhaetian. The undulous outline of the epidermal cells of *Stangeria paradoxa*, the hairlock-like pattern of cuticular lamellae on their surface is so typical as to distinguish this species from all other living Cycads. On the other hand, the cuticular lamellae in particular of extinct *Ctenis nathorstii*, *C. wilsoni*, *C. minuta* and *C. latepinnata* resemble so much these features of living *Stangeria*, that it would be easy to confuse the photos of the two.

Even these few examples selected at random suffice to prove convincingly that paleontologists can indeed make very good use of a knowledge of the epidermal structure of living Cycads. Lacking this knowledge and a suitable comparative material of living forms, the determination of extinct Pteridosperms and Cycads is, if not impossible, still a highly uncertain business.

LITERATURE ON THE EPIDERMAL STRUCTURE OF THE CYCADS

Knowledge of the epidermal structure of the Cycads is important not only from the purely morphological viewpoint but also because of the light it sheds upon certain aspects of evolution and paleontology. Although this subject has been studied in detail for more than 100 years, no comprehensive treatment of it has been given so far.

In 1856, Bornemann published a short comparative study on the epidermal structure of living Cycads, to serve as a basis for the determination of leaf fragments of fossil Cycads. Bornemann's assumption was that the leaf remains of Mesozoic Cycads stand fairly close to some living genera and that this similarity is a useful guidance in determining the finds. Now, a century later, this principle is still accepted as valid. The leaf epidermis structure of the living Cycads suggests a very close relationship between the ancient Cycads and their near relations, the *Cycadofilices* (*Pteridospermae*) on the one hand and the living forms, on the other. Let us recall e.g. the great similarity between *Macrozamia hopeites* Cookson and living *Macrozamia hopei*. An ever increasing number of pertinent results proves today the importance of leaf-epidermis studies, complementary to xylotomy and pollen analysis, for the determination of fossil finds.

After the pioneering work of Bornemann, a treatise by Porsch (1905) should be mentioned in the first place. Not only did it elucidate the morphology of the stomata; it dealt in detail also with their phylogeny and, on these grounds, established phylogenic relationships. Illustrated with about 70 drawings including text-figures and four Table, the treatise points out similarities in the stoma structure e.g. of Ginkgo and some Cycads which suggest in their turn a certain degree of relationship.

Thomas (1911) compared the stoma of Carboniferous Calamites with those of living Equisetum and established a relationship between the two.

Of the papers on the epidermal structure of the Cycads, particular importance attaches to that of H. Thomas and N. Bancroft (1913).

M. Lamb (1923) published a paper describing the morphology of the leaflets and giving also a key. It is to be regretted that she gave no drawings or photographs of the different leaflet types.

Florin (1931) described the leaf epidermis of living *Coniferae*; in another important paper he (Florin 1933) examined the epidermal structures of *Psilophyton*, *Baiera*, *Pseudocycas*, *Callipteris*, *Ctenopteris*, *Dyctiozamites* and *Protozamites*, giving very convincing photographs of their resemblance to living forms. Florin discussed also several *Ctenis* species whose epidermal structure agrees with that of living *Stangeria paradoxa*. The striking similarity between the two suggests a close relationship, all the more so since among the living Cycads it is only the epidermal cells of monotypical *Stangeria paradoxa* that bear the same kind of radial cuticular lamellae as one observes in Mesozoic *Ctenis*. Consequently,

ancient *Ctenis* and living *Stangeria* can be considered, in the present author's opinion, as related species, on the strength of their peculiar and identical epidermal structure.

Unfortunately, Florin, who discussed in detail the epidermal and stomatal structure of the Cycads gave very few drawings and photographs.

In his treatise C.A. Arnold (1953) attributed considerable importance to stomatal structure in establishing relationships between Cycads and illustrated this statement with several examples of epidermal structures. T. Harris (1956) attaches a similar importance to the knowledge of cuticular structure.

Greguss (1957) published photographs of one type of each of the 8 Cycads genera but did not at that time carry out comparative examinations.

In his thesis, M. Kedves (1958) described the epidermal structure of the species of *Equisetum* and established the uniformity of their epidermal and stomatal structures.

The thesis of I. Maróti (1959) discussed the epidermal structure of the characteristic forms of the *Filicinae*, more particularly of the *Marattiaceae*, and compared it with the epidermal structures of other genera.

The thesis of S. Gulyás (1961) dealt with the stomatal structure of the *Lycopsida*, stating that in some Lycopsids, shape and structure of the stomata are greatly suggestive of the epidermal and/or stomatic structure of the *Musci*, as had already been suggested by Porsch (1905).

Recently it was Kräusel and Weyland (1959) who emphasized the importance of epidermal structure in the determination of fossil leaves.

In his study Greguss (1961b) dealt with the leaf epidermis of *Lepidozamia hopei* and *Microcycas calocoma*.

Recently A.E. Bobrov (1962) discussed in some detail the epidermal and stomatal structure of 33 species or varieties of Cycads, giving comprehensive tables of the species of the more populous families (*Macrozamia*, *Cycas*) and a taxonomic key in an attempt to distinguish the *Cycas* genera on the basis of their epidermal structure. The tables and the key constitute a brief survey of the epidermal structure of the living Cycads from which Bobrov (1962) tried to deduce also some genetical conclusions.

Pant and Nautiyal (1963), in their excellent paper described rather fully the epidermal structure of living Cycads. They also gave several accurate drawings and excellent photographs of several genera and presented the characteristic features in the form of tables. Although quite modern, this work is unfortunately incomplete. No comprehensive work dealing with the xylotomy of the living Cycads has in our knowledge appeared even in recent times.

In 1963 was published A. B. Graf's (1963) paper with many beautiful habitat photographs of Cycad species.

In 1965, R. A. Dyer published two important papers. In the first (Dyer 1965a) he described two new *Encephalartos* species of South Africa.

His second work (Dyer 1965b) is more important as it gives a short review and a

key for 26 living *Encephalartos* species of South Africa. He published also habitat pictures of these species, most of them in natural milieu. For the *Encephalartos* species this is a fundamental work.

In spite of these studies on the leaf-epidermis structure of the Cycads, no comprehensive treatise appeared as yet on the subject. The present author intends to fill this gap by annexing to the above description of xylotomical properties a survey of the leaf epidermis of living Cycads, going into details as far as possible. The fine anatomy and internal structure of the leaves are not dealt with in this book, since it has been thought that paleontologists comparing the living and fossil materials require in the first place a knowledge of superficial structure.

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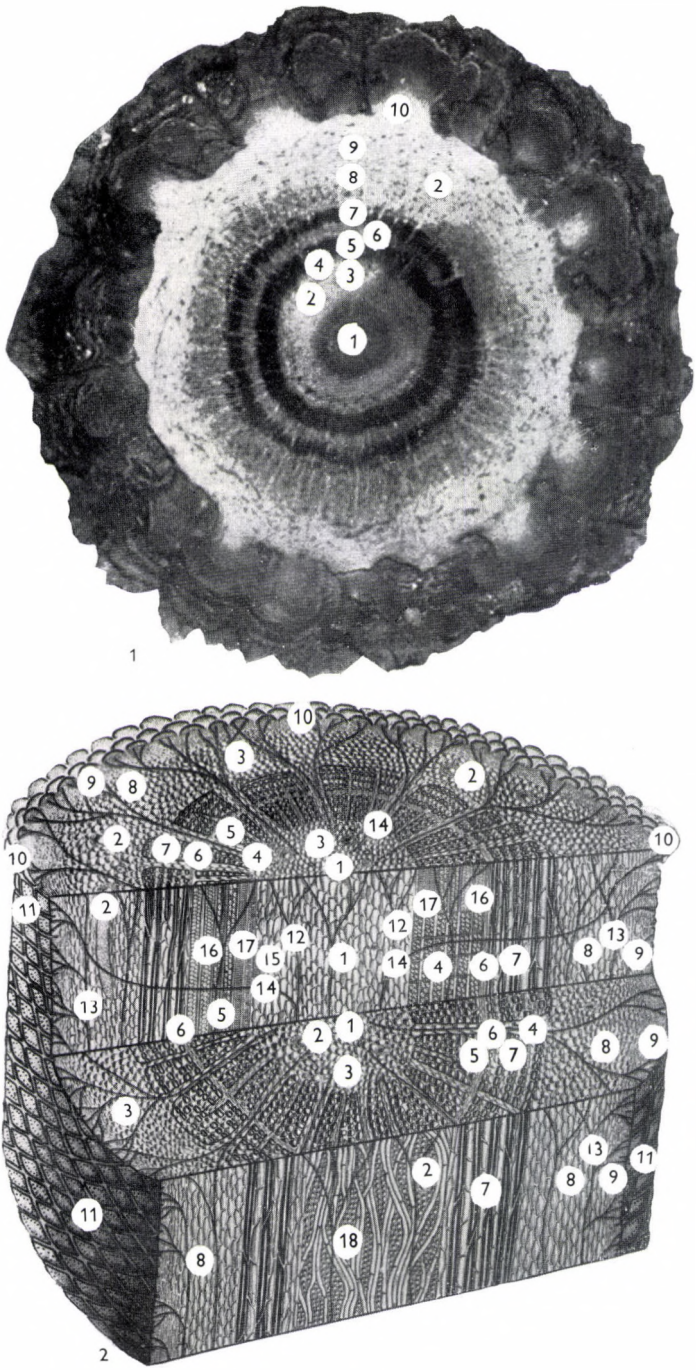
PLATES

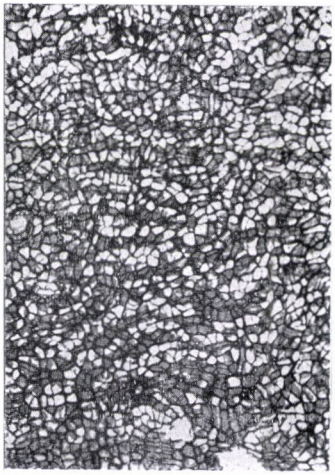
ABBREVIATIONS USED IN THE PLATES

a = pith, b = transfusion cells, c = xylem portion, d = phloem portion, e = cortex, f = periderm, g = mucilage canals, h = pith rays, i = calcium oxalate crystals



I. 1. Surface view of the cross section of the *Cycas revoluta*.
2. Schematic drawing of a *Cycas* stem in various planes of section.

1. Pith. 2. Mucilage canals. 3. Calcium oxalate druses. 4. Primary ray. 5. Xylem part. 6. Cambium. 7. Phloem part. 8. Cortex. 9. Periderm. 10. Vestiges of leaf bases. 11. Leaf scars. 12. Pith bundles. 13. The bundles in the cortex leaning out in the leaf bases. 14. The common bundles leaning out from the pith through the primary rays into the leaves. 15. Transfusion cells. 16. Tracheids with araucarioid pitting. 17. Tracheids with scalariform thickening. 18. Multiseriate rays. (Drawing by Z. Havas and P. Greguss)



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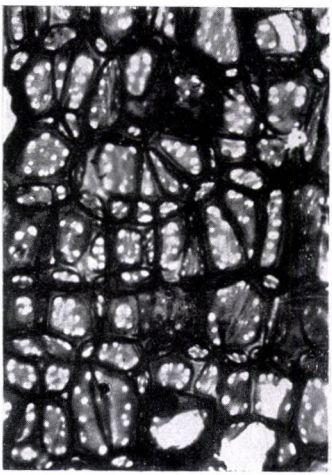

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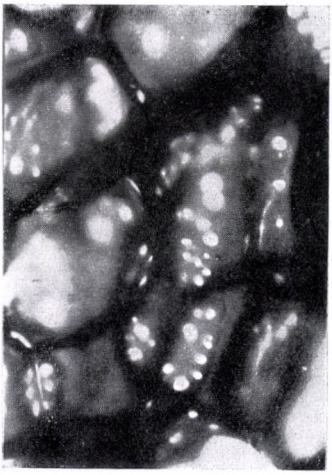

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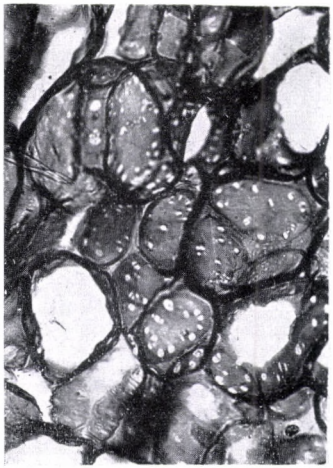

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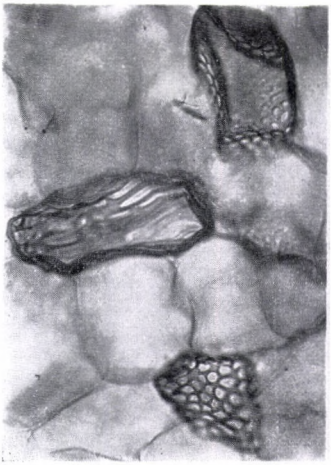

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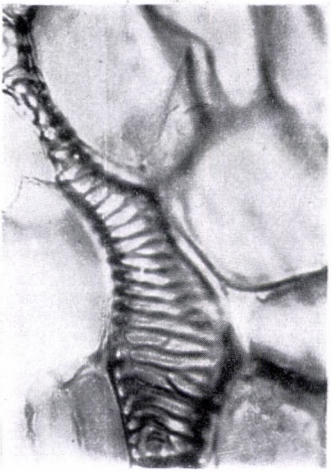

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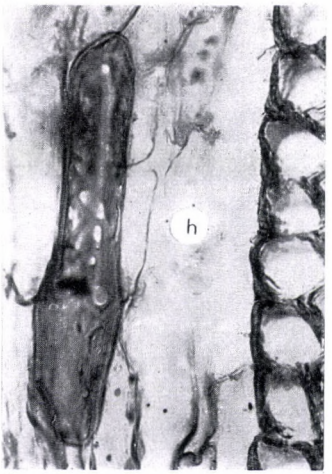
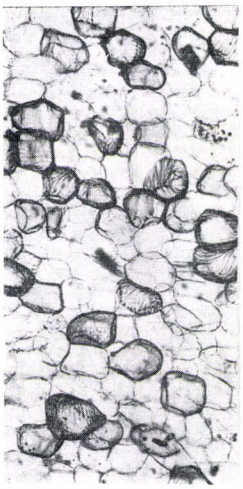


9

II. Thin- and thick-walled parenchyma cells in the tissue of the pith (Photos 1—8) and in the ray (Photo 9)



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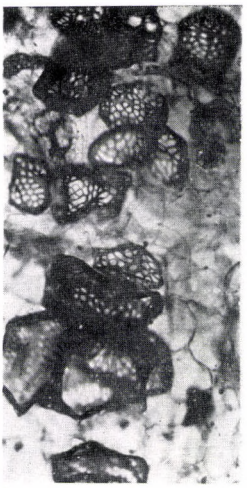

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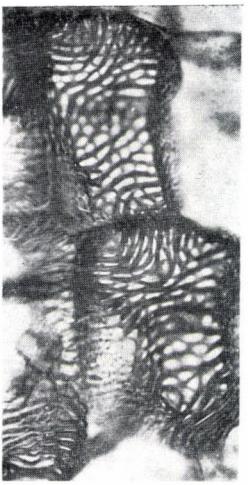

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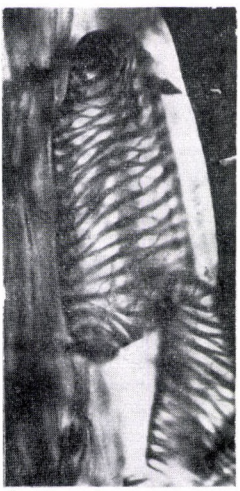

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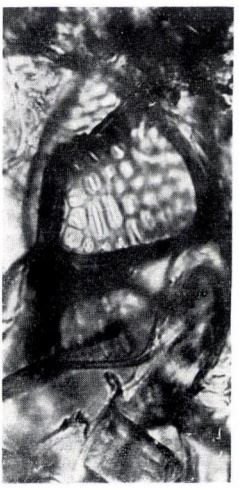

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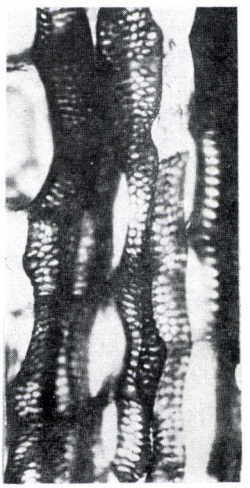

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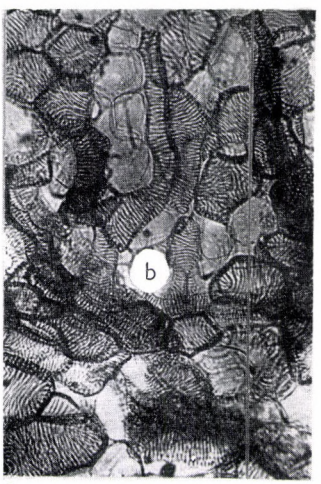

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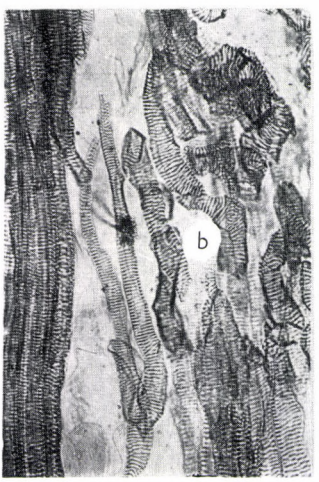

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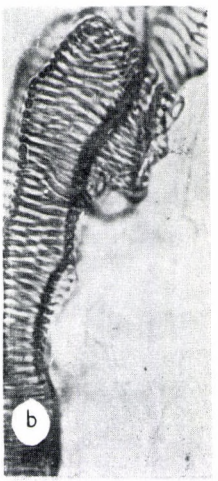

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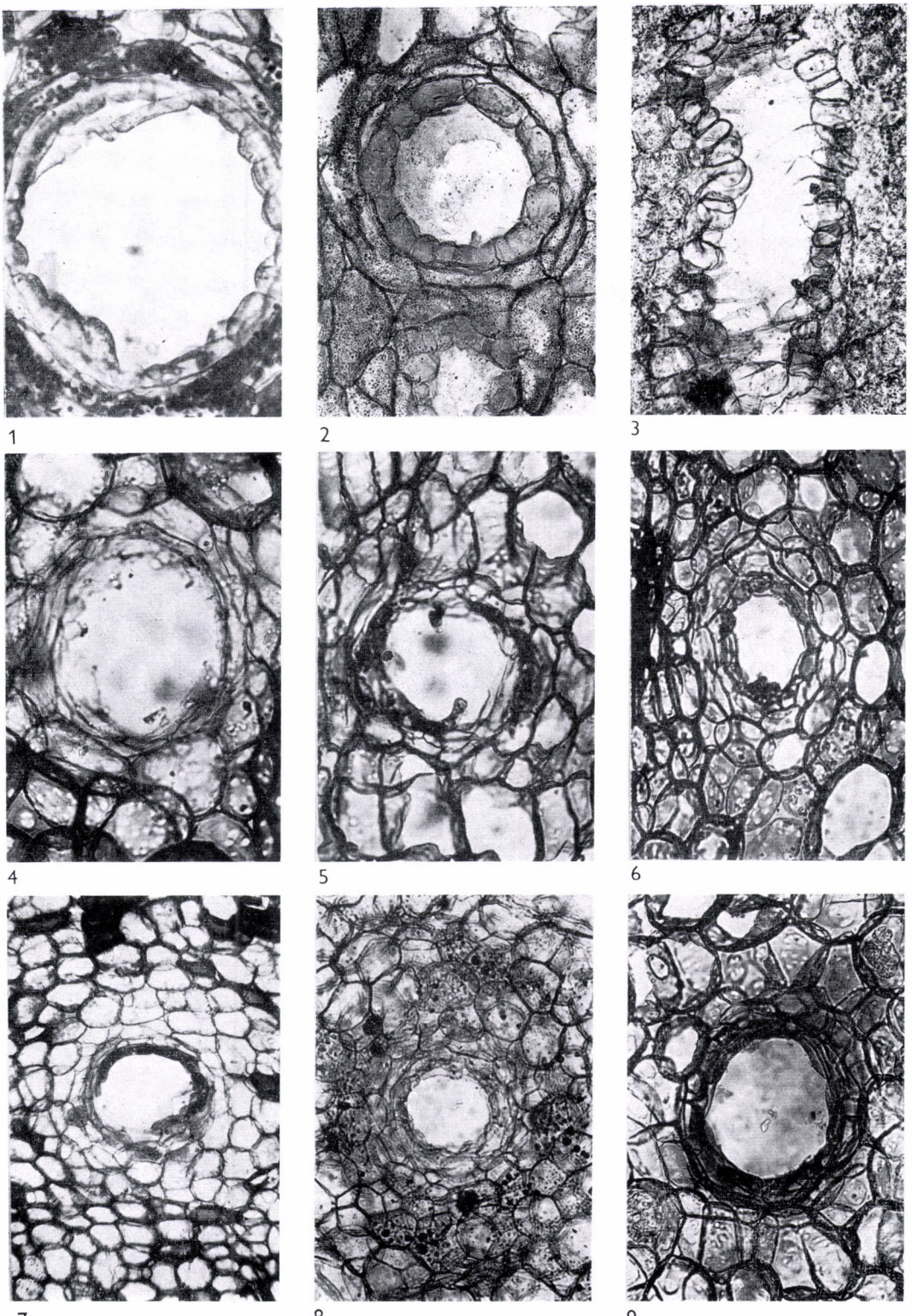
III. Transfusion cells in the Cycads (Photos 1—12)



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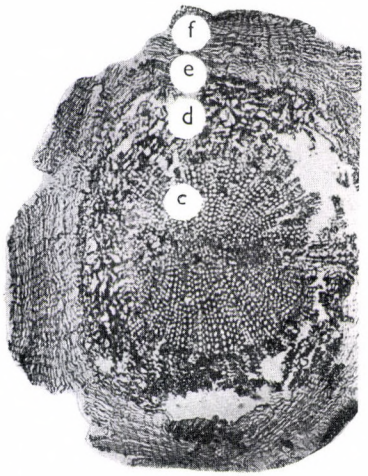
IV. Mucilage canals in the Cycads (Photos 1—9)



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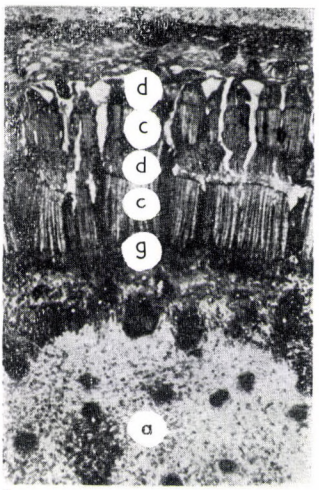

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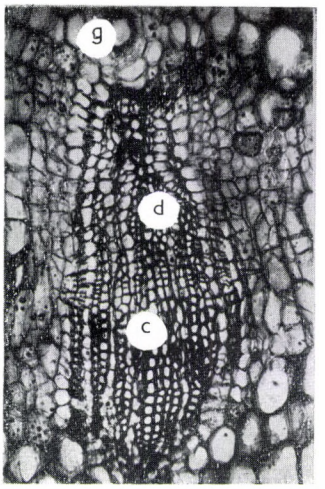

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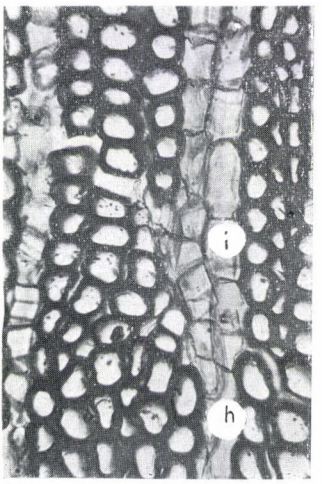

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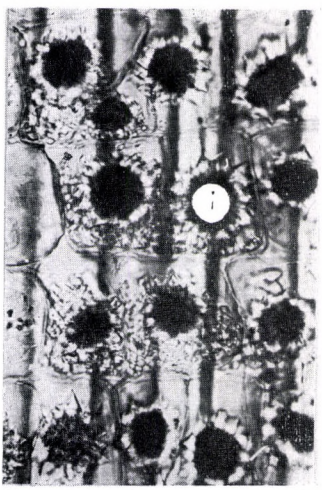

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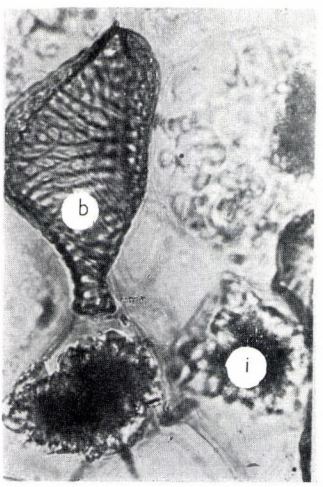

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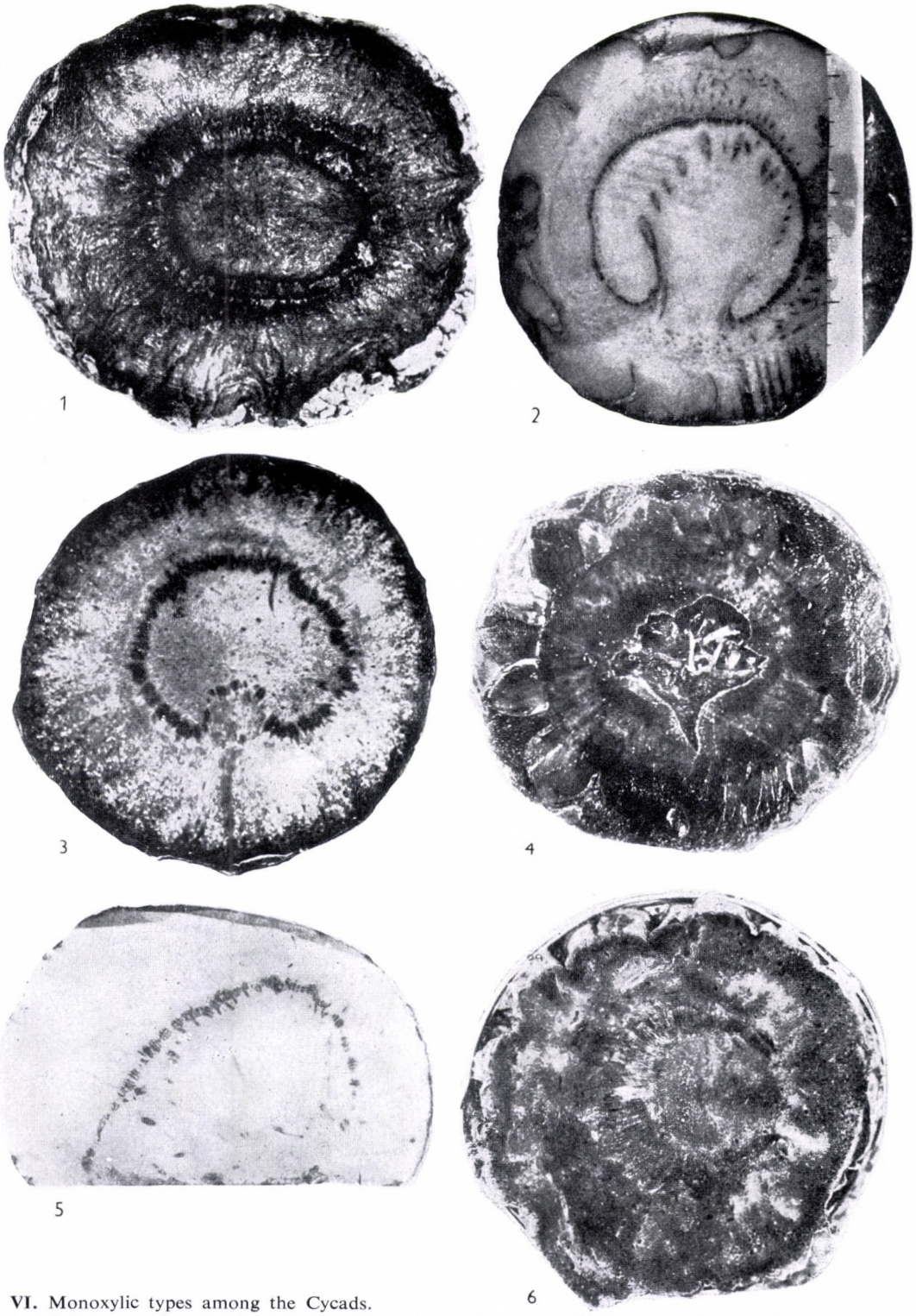
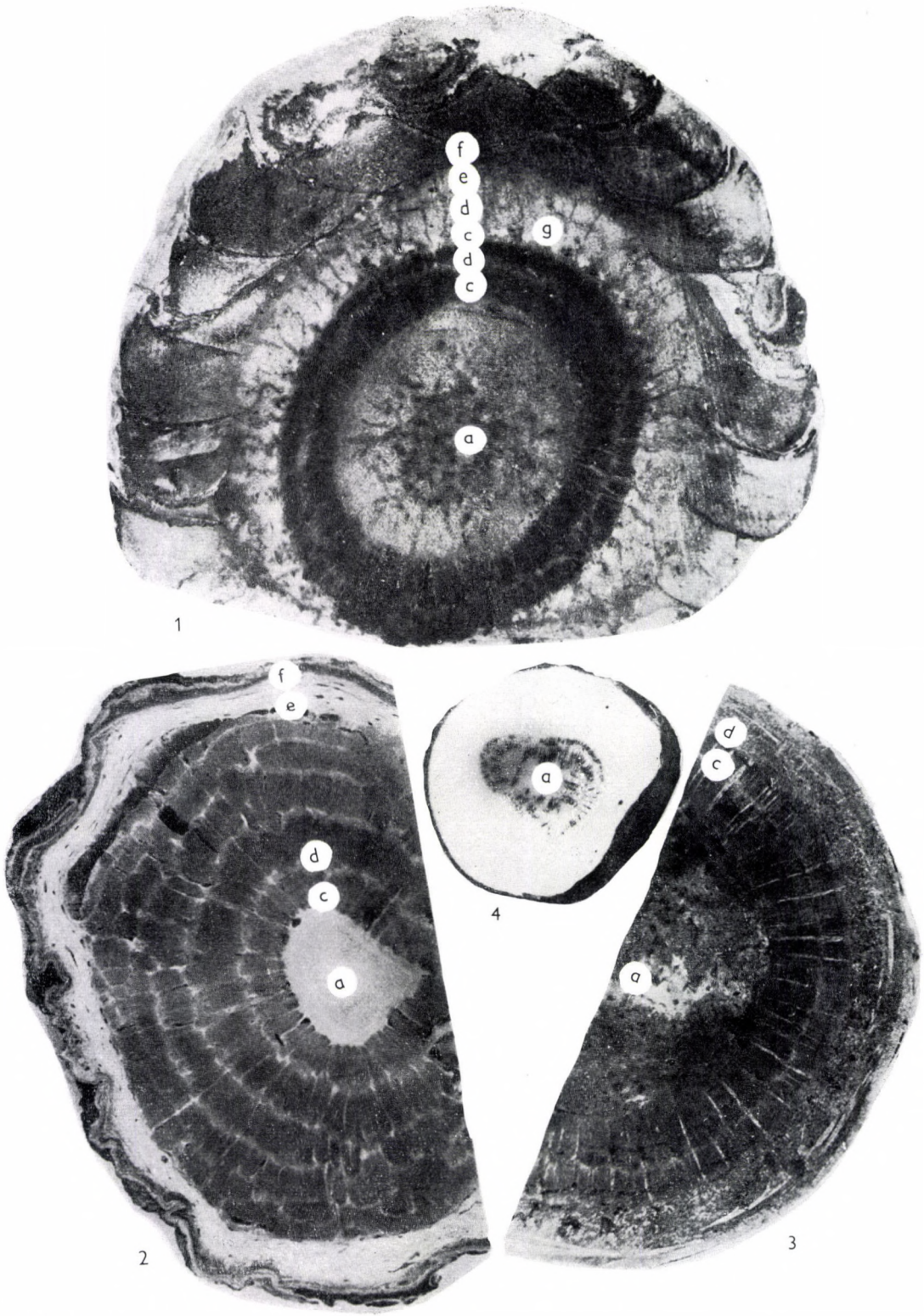
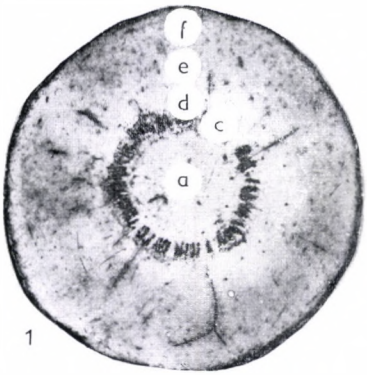
V. Xylem details in the bundles (Photos 1—6). Calcium oxalate crystals in the Cycads (Photos 7—9)



VI. Monoxylic types among the Cycads.
1. *Microcycas calocoma*. 2. *Ceratozamia mexicana*. 3. *Zamia floridana*. 4. *Dioon edule*.
5. *Stangeria eriopus*. 6. *Bowenia serrulata*



VII. Polyxylic types among the Cycads.
1. *Encephalartos lehmannii*. 2. *Cycas rumphii*. 3. *Macrozamia hopei*. 4. *Macrozamia miquelii*



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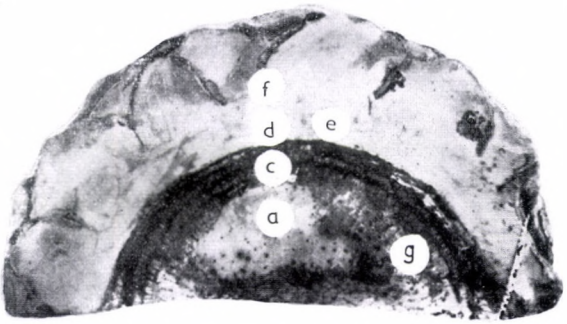

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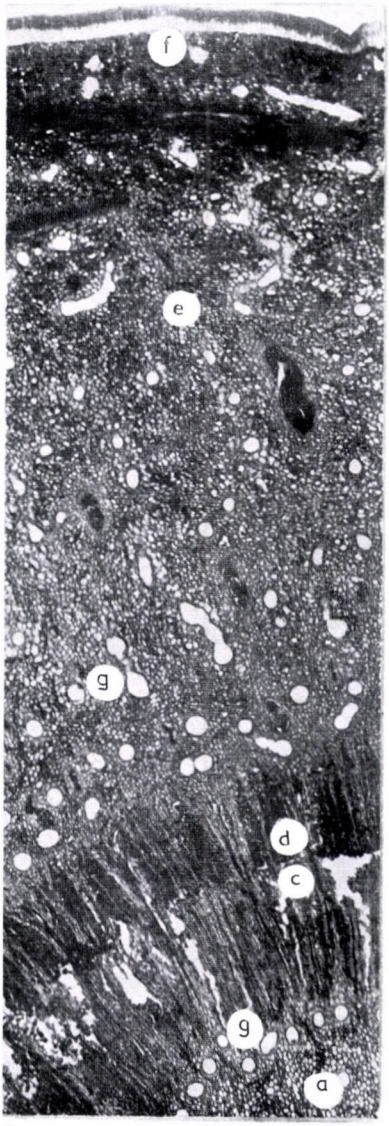

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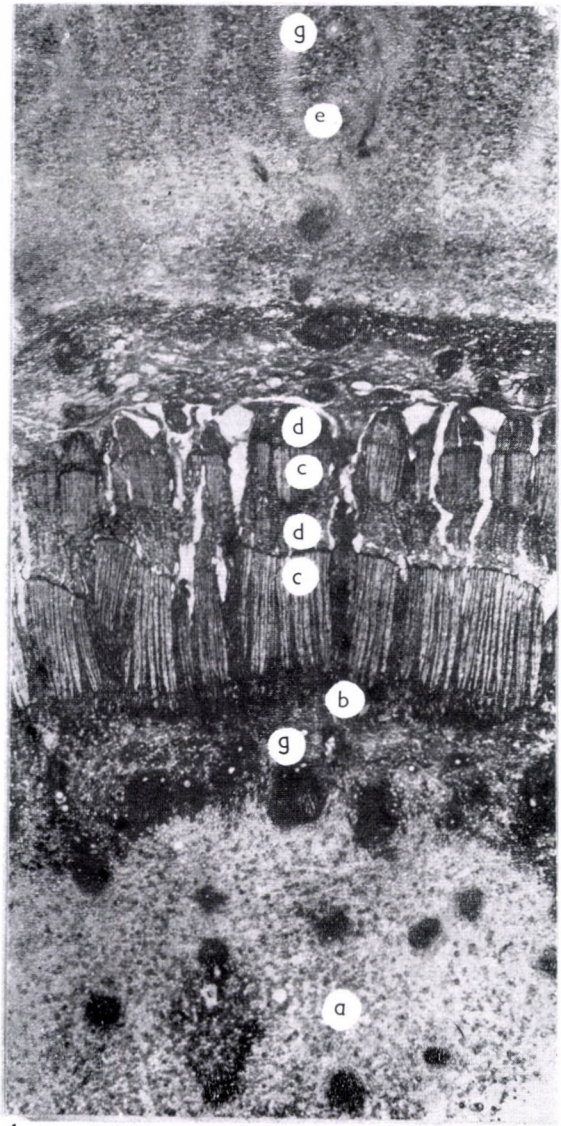

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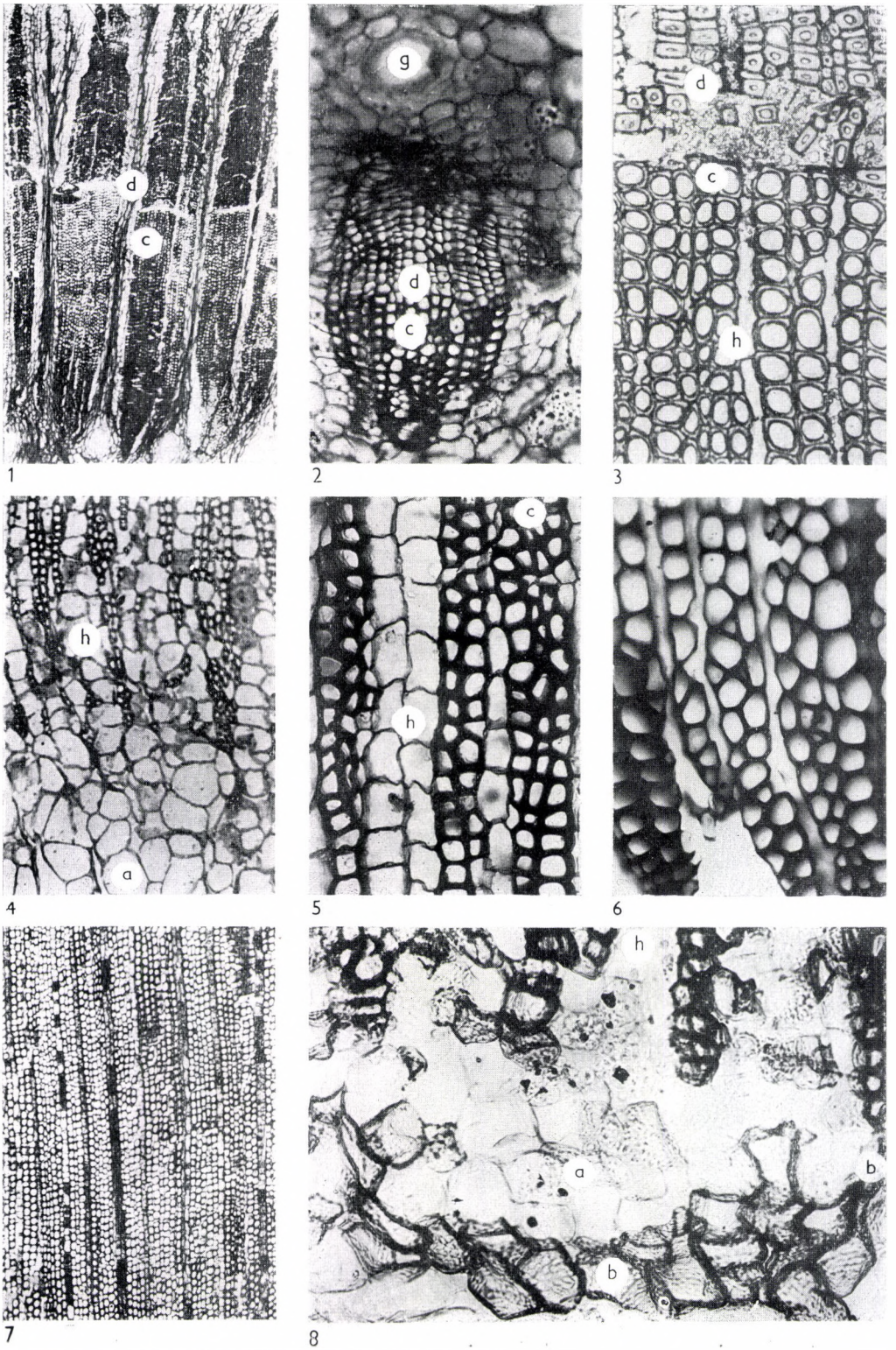
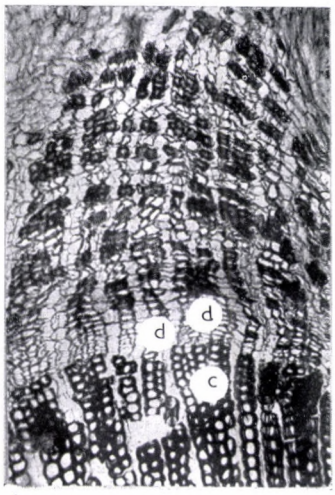
VIII. The finer details in monoxylic and polyxylic stems of Cycads, (Photos 1—2) *Zamia skinneri*, (Photos 3—4) *Encephalartos altensteinii*



IX. Finer structures of the xylem bundles (Photos 1—8)



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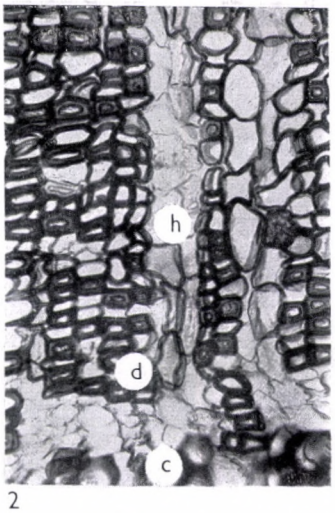

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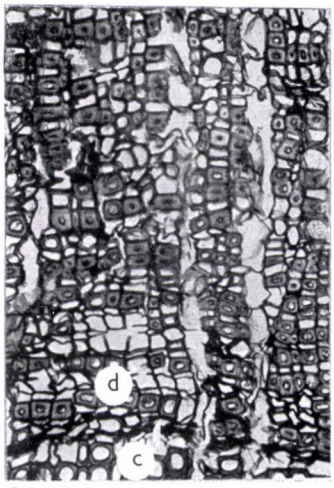

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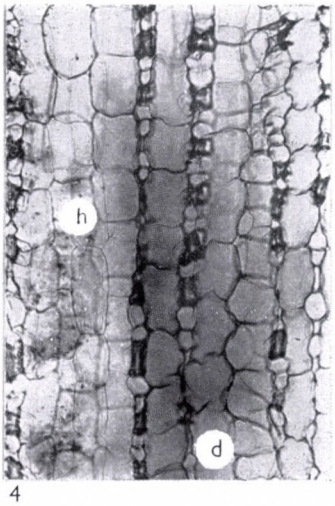

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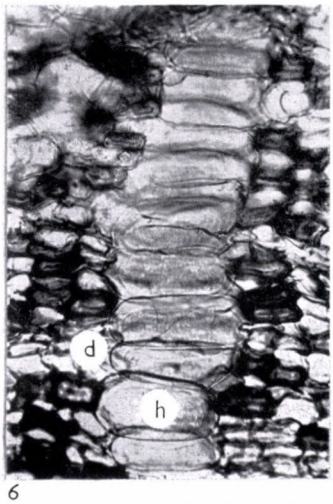

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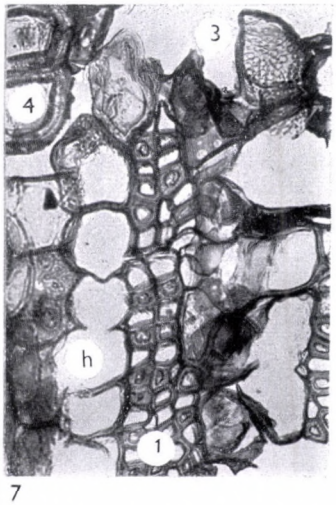

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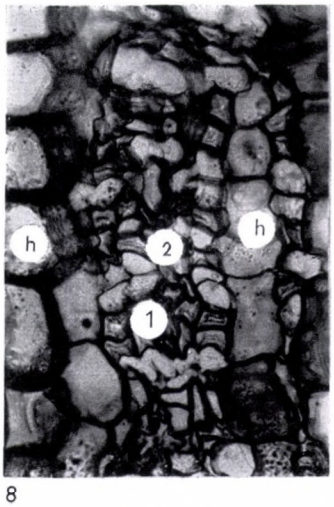

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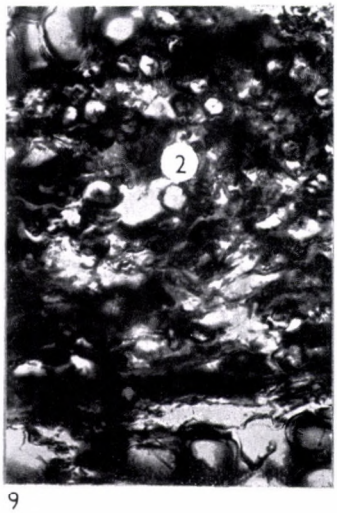

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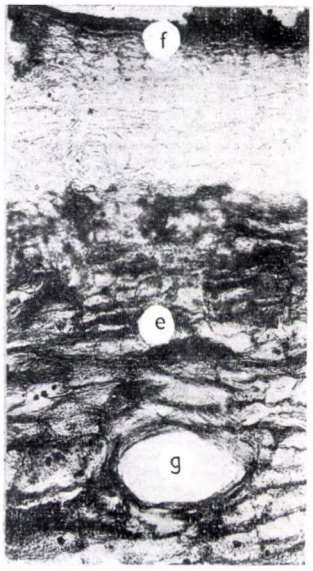
X. Finer structures of the phloem bundles (Photos 1–9)



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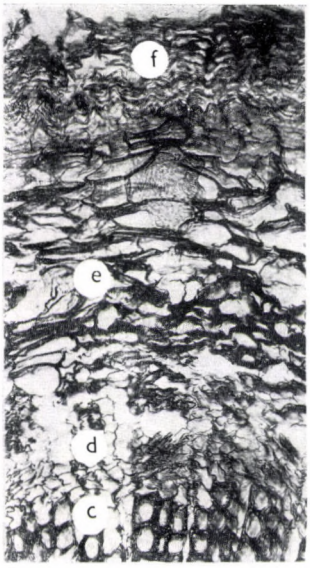

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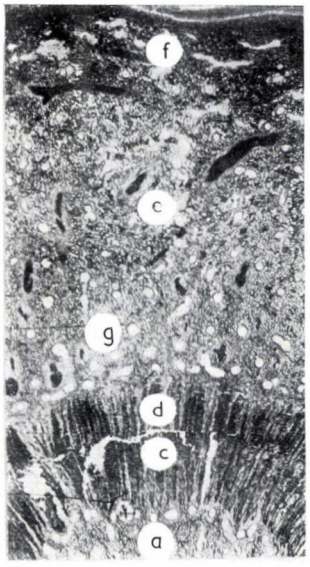

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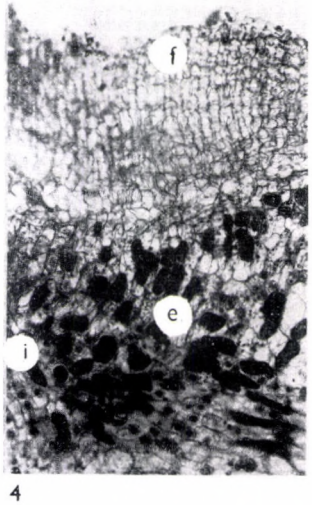

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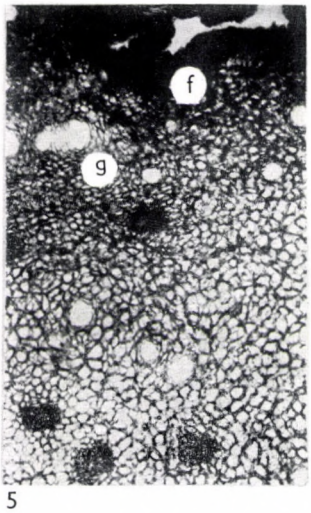

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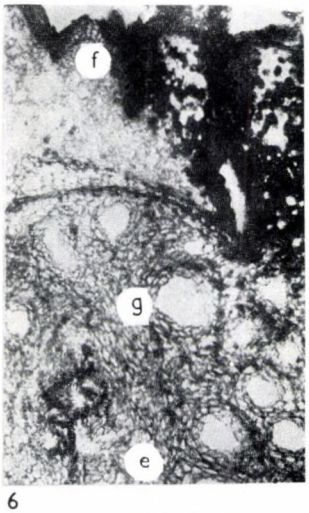

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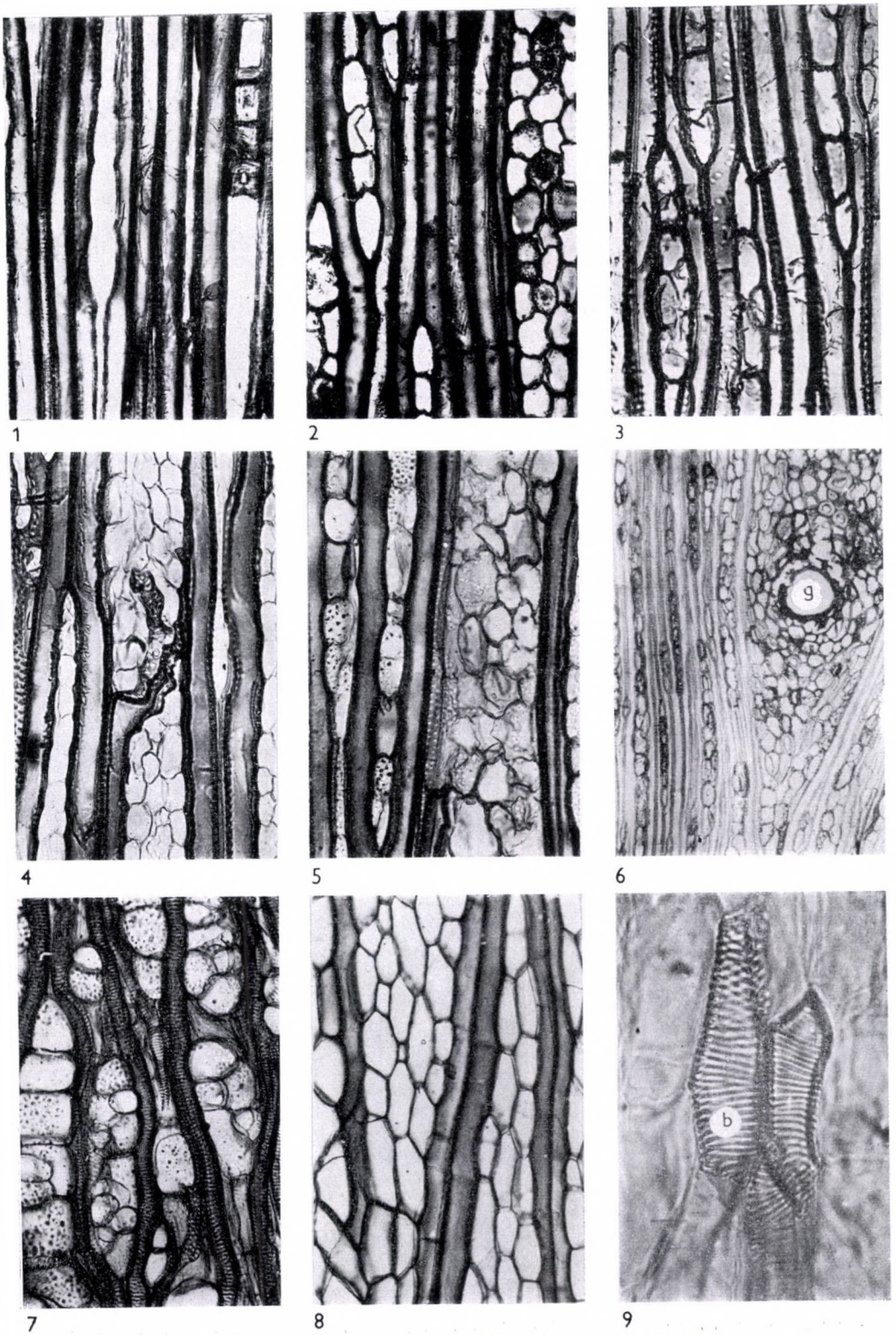
9

XI. Cortex and periderm in the stems (Photos 1–6). Leaf basis and leaf scars of stems (Photos 7–9)



XII. Tangential structures of the rays (Photos 1—8). Transfusion cells (Photo 9)



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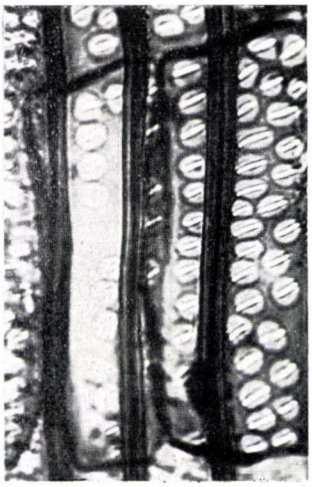

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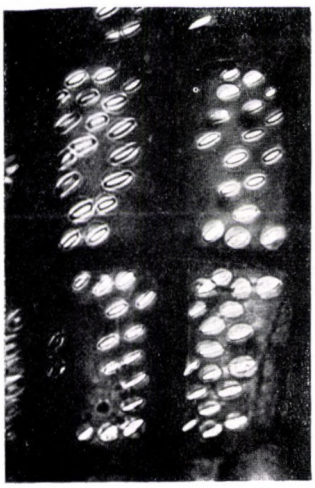

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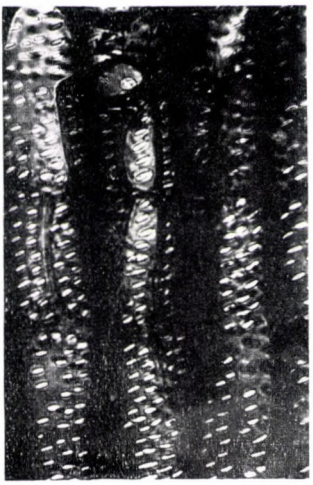

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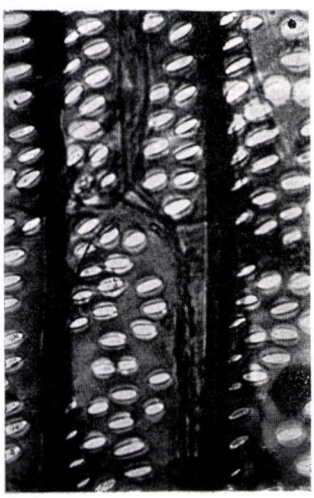

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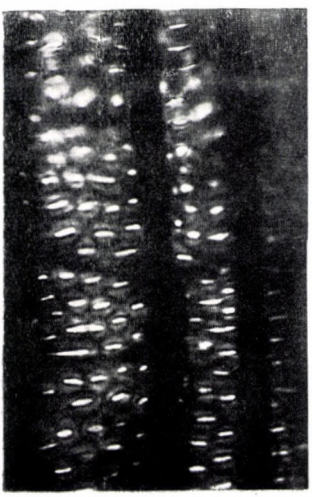

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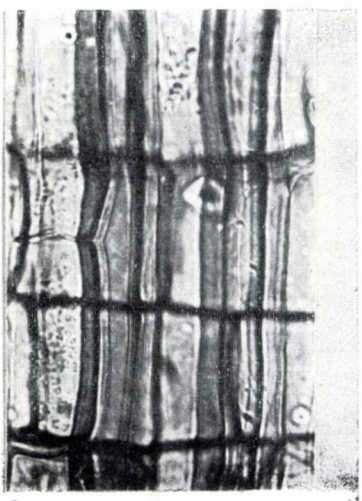

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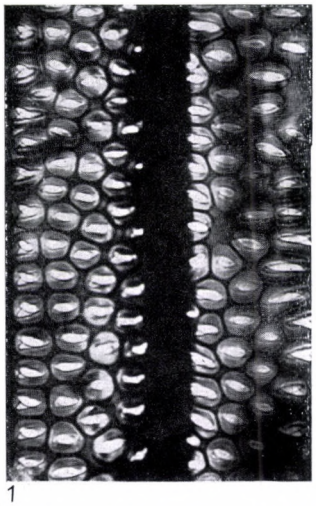
XIII. Radial structures in the stems (Photos 1—8)



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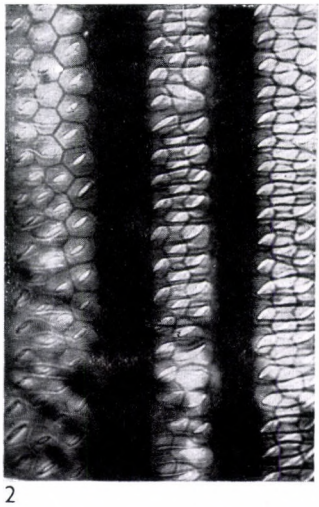

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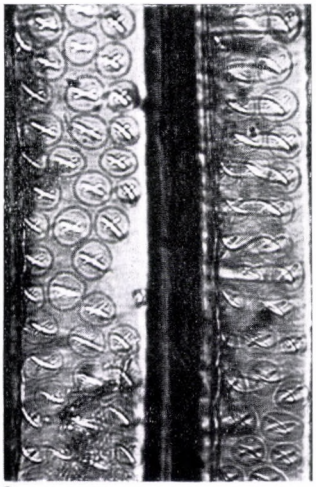

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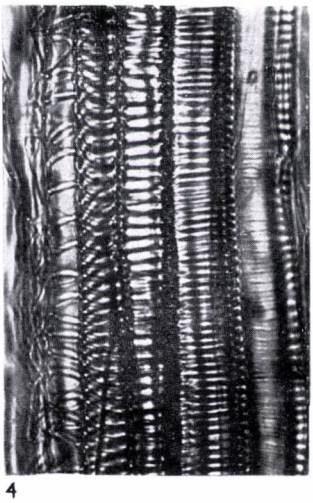

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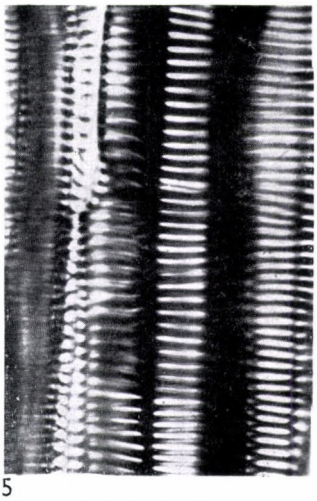

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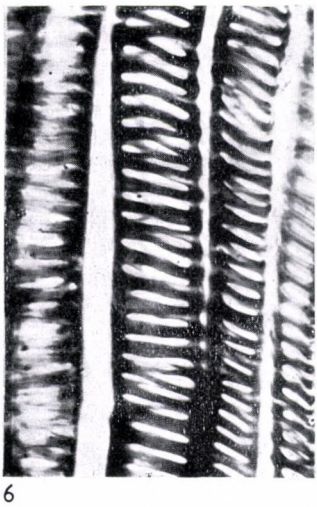

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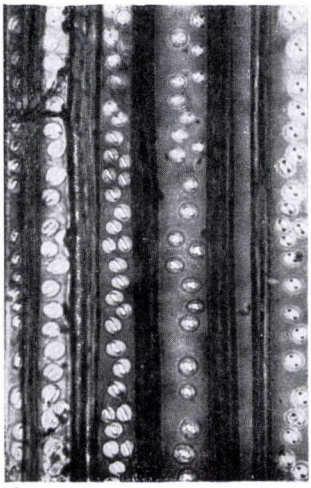

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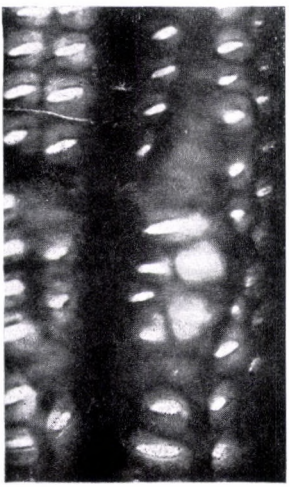

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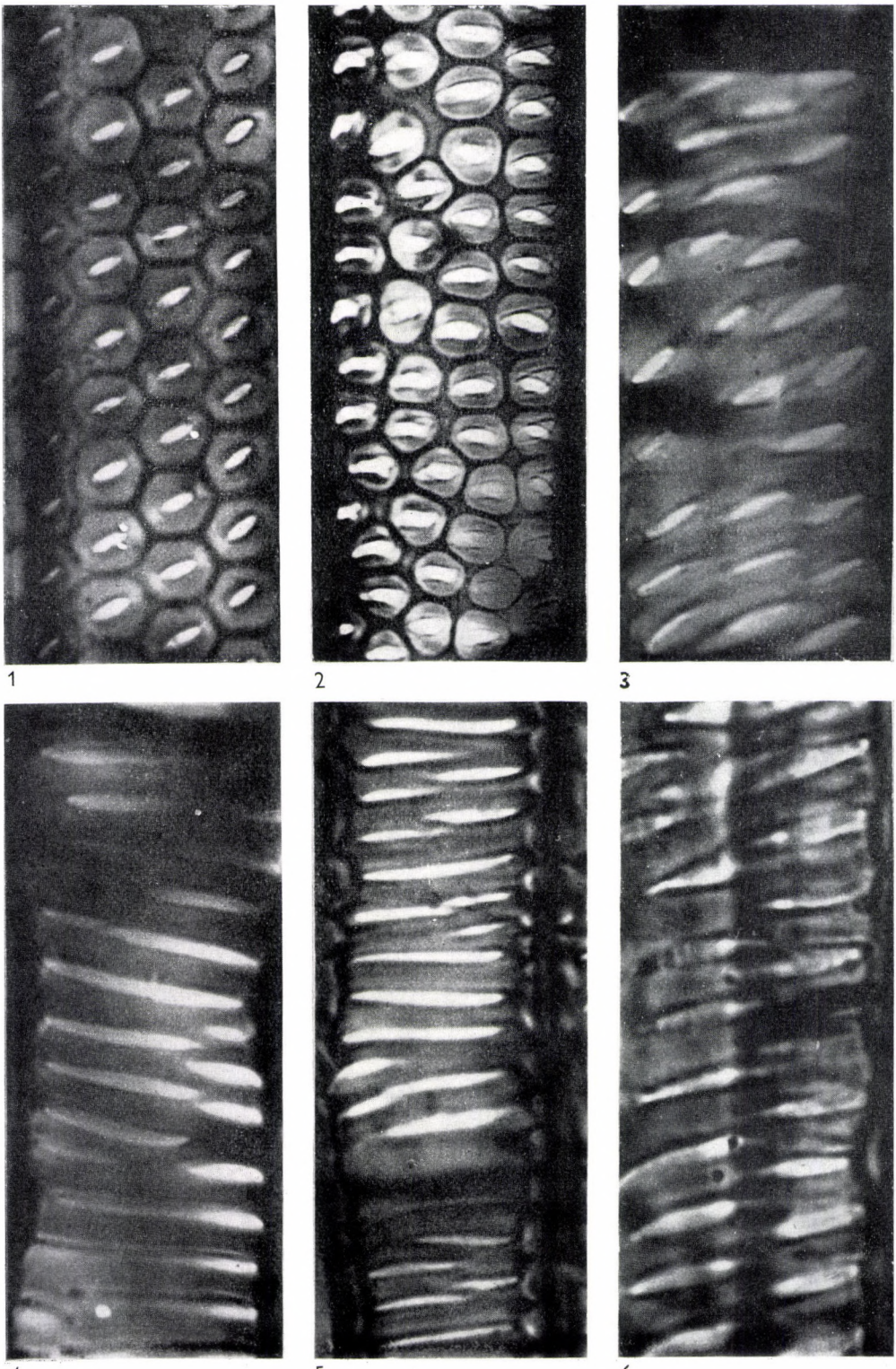
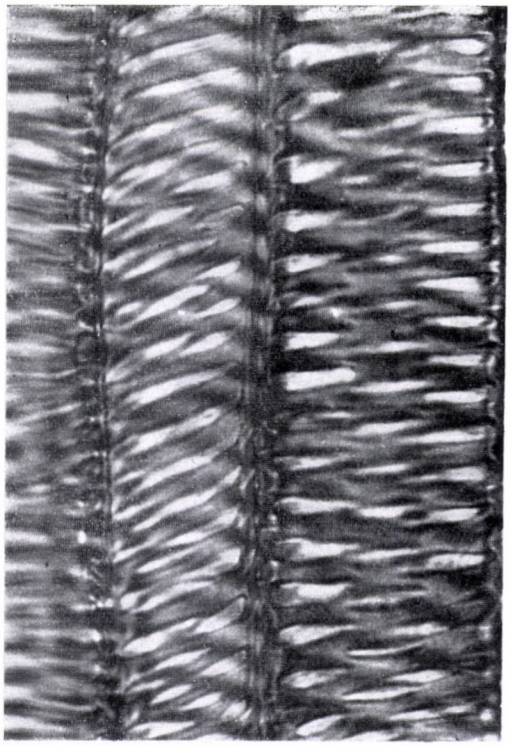
XIV. Different thickenings of tracheids in the stems (Photos 1—7)
Development of perforation in the tracheids (Photos 8–10)



XV. Different thickenings of the tracheids in the stems (Photos 1—6)



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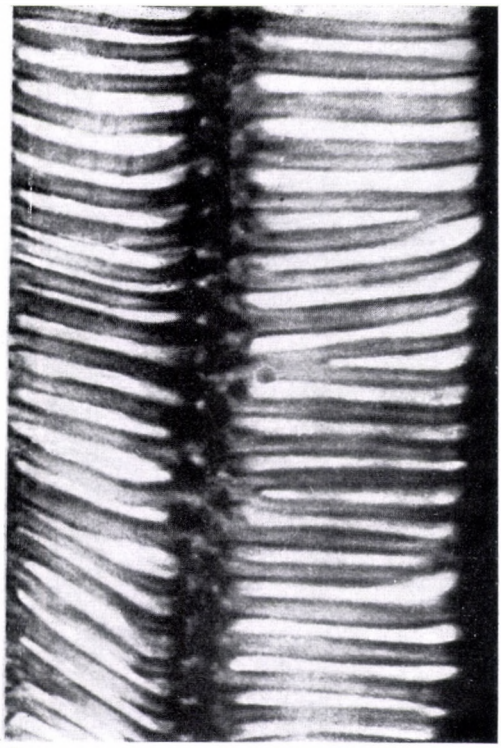

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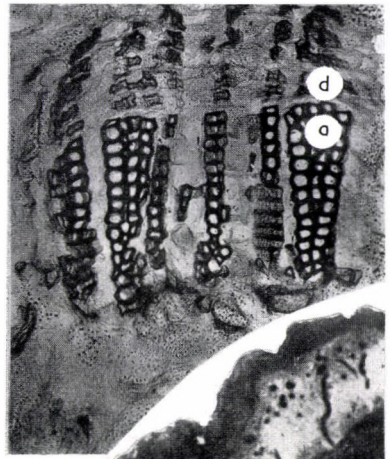
3

XVI. Different scalariform thickenings of tracheids in the stems (Photos 1—3)



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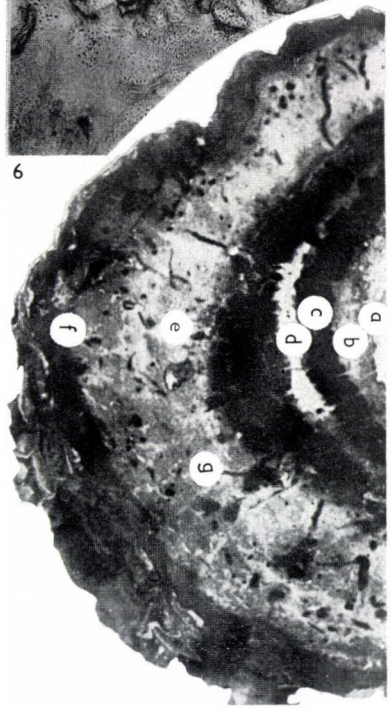

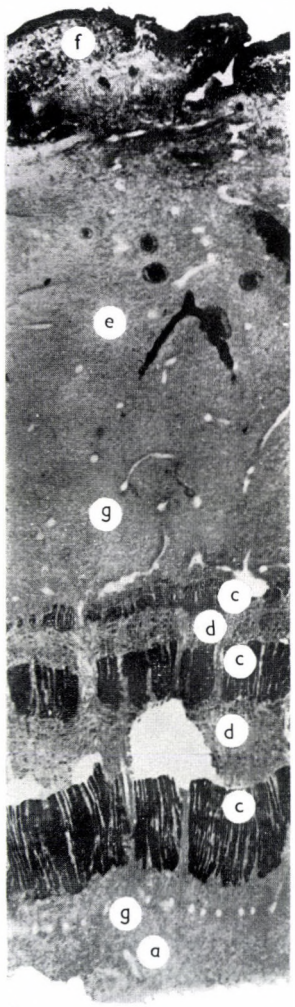

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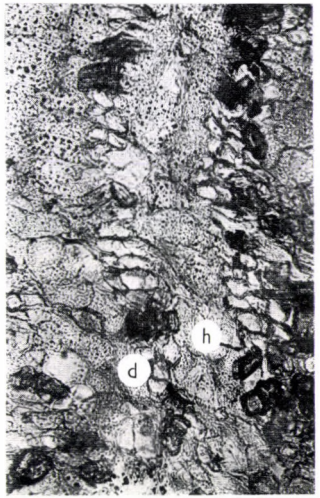

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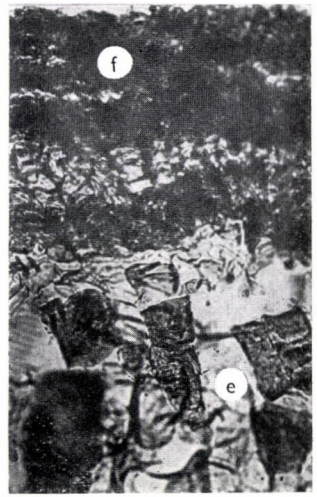

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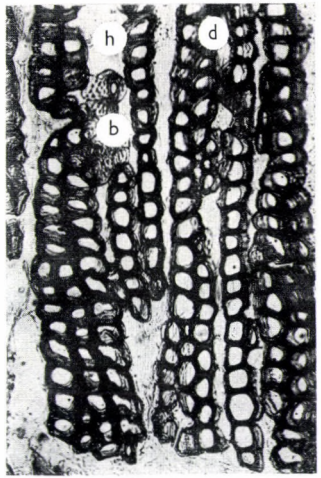

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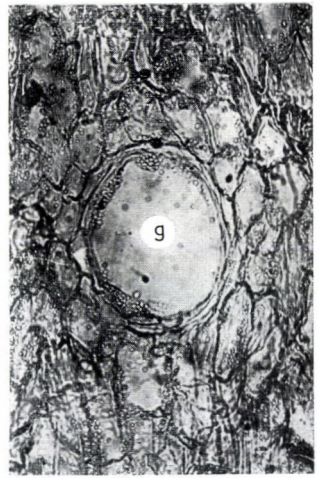

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XVII. *Cycas beddomei* Dyer



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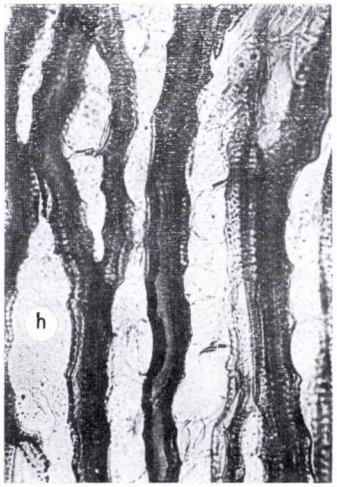

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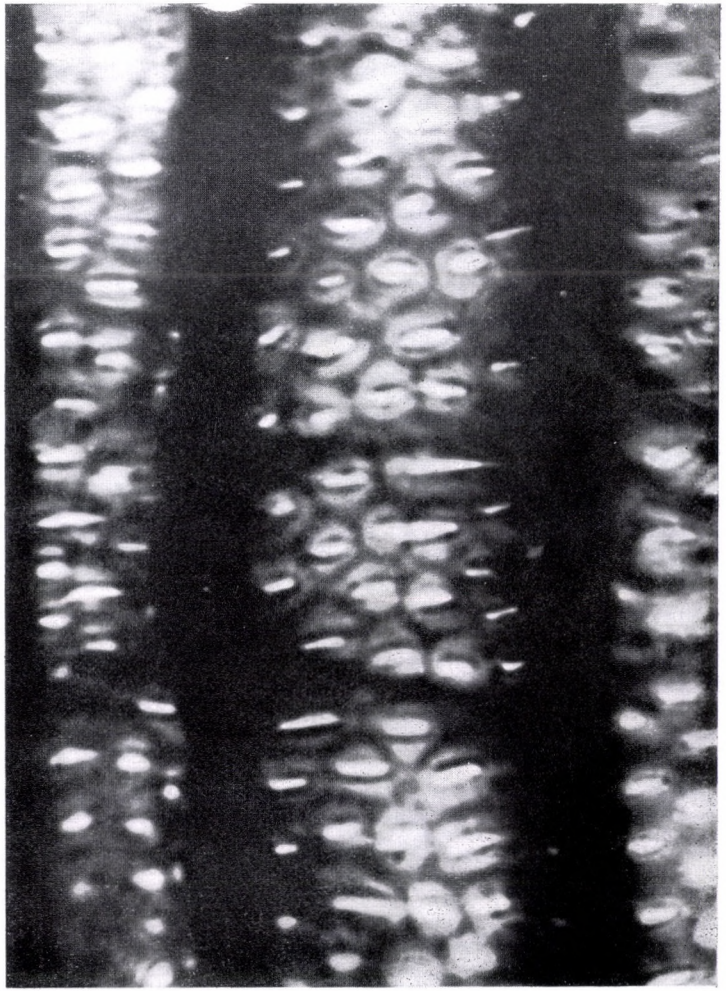

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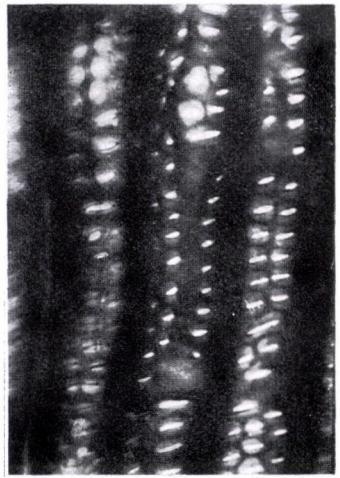

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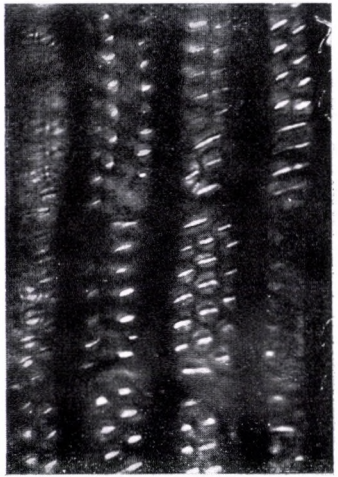

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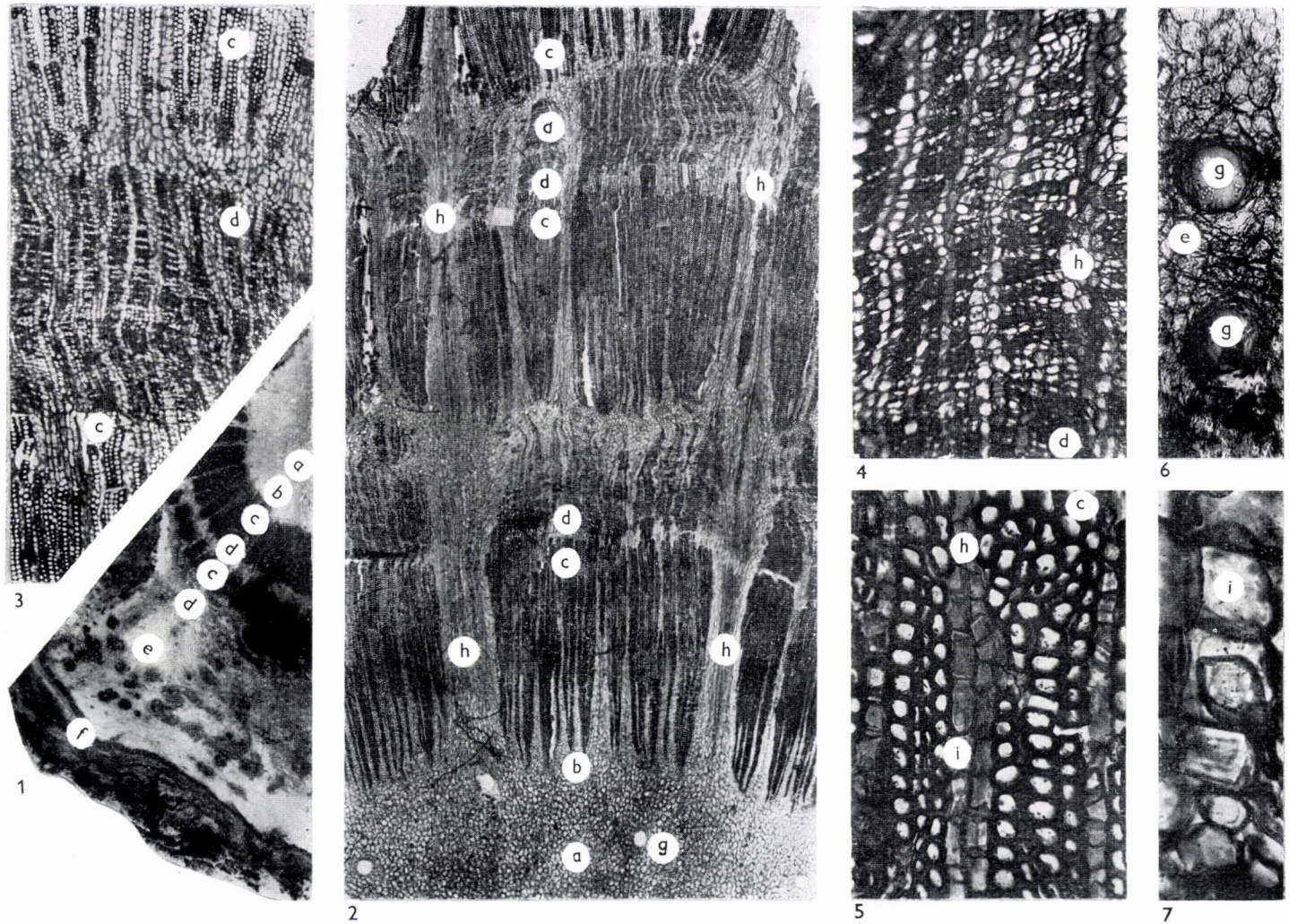
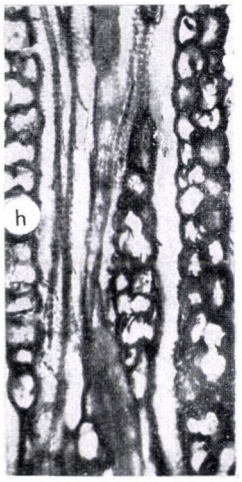
XVIII. *Cycas beddomei* Dyer



XIX. *Cycas circinalis* L.



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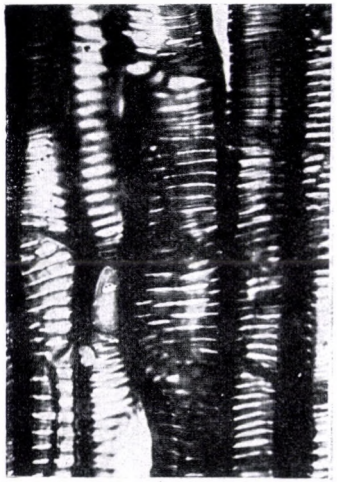

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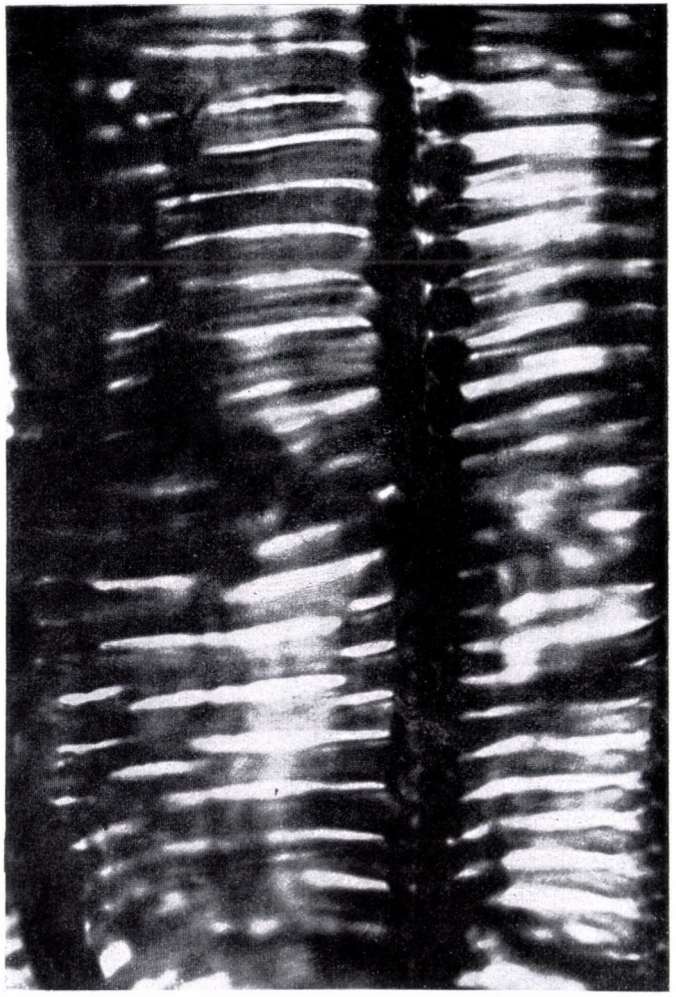

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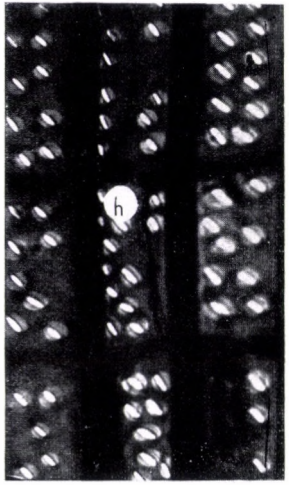

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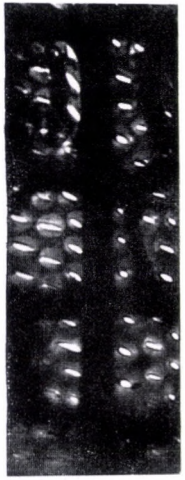

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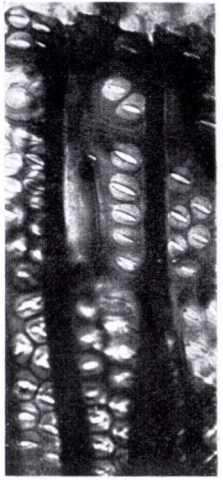

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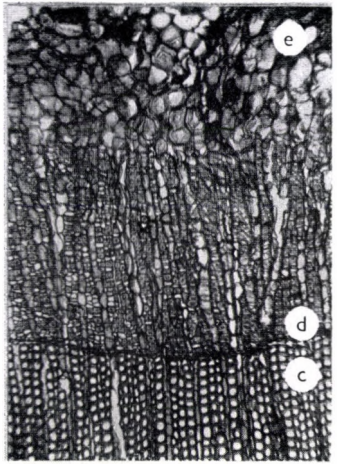
XX. *Cycas circinalis* L.



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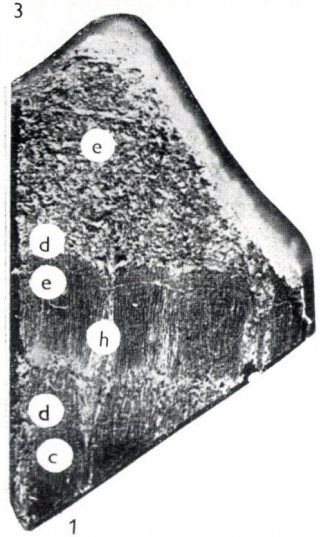

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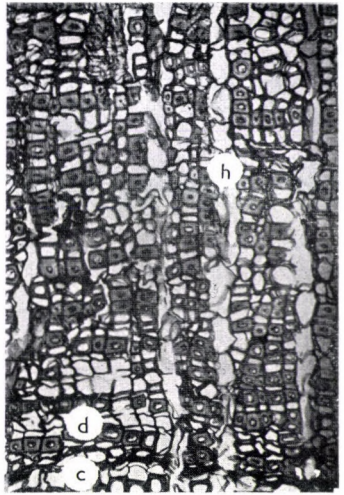

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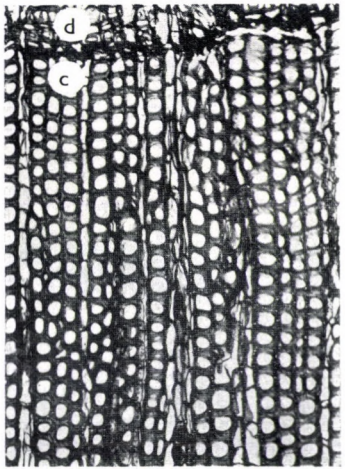

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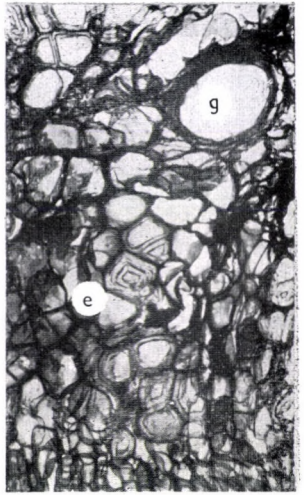

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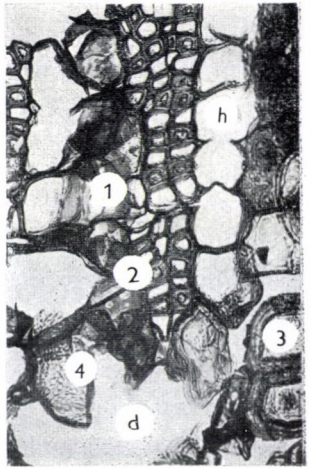

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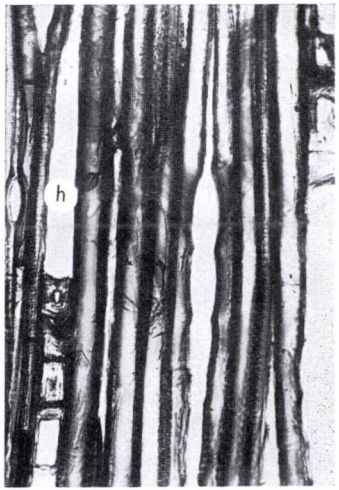
XXI. *Cycas media* R. Br.



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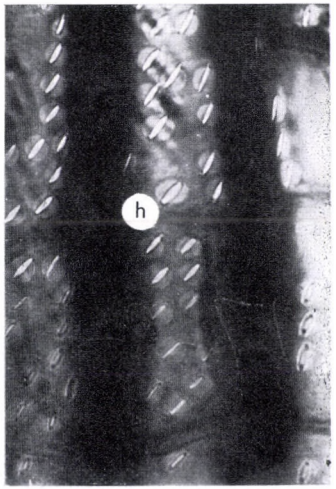

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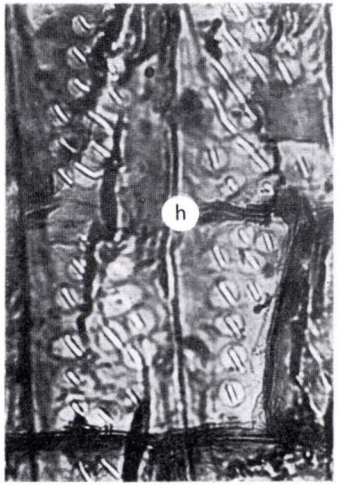

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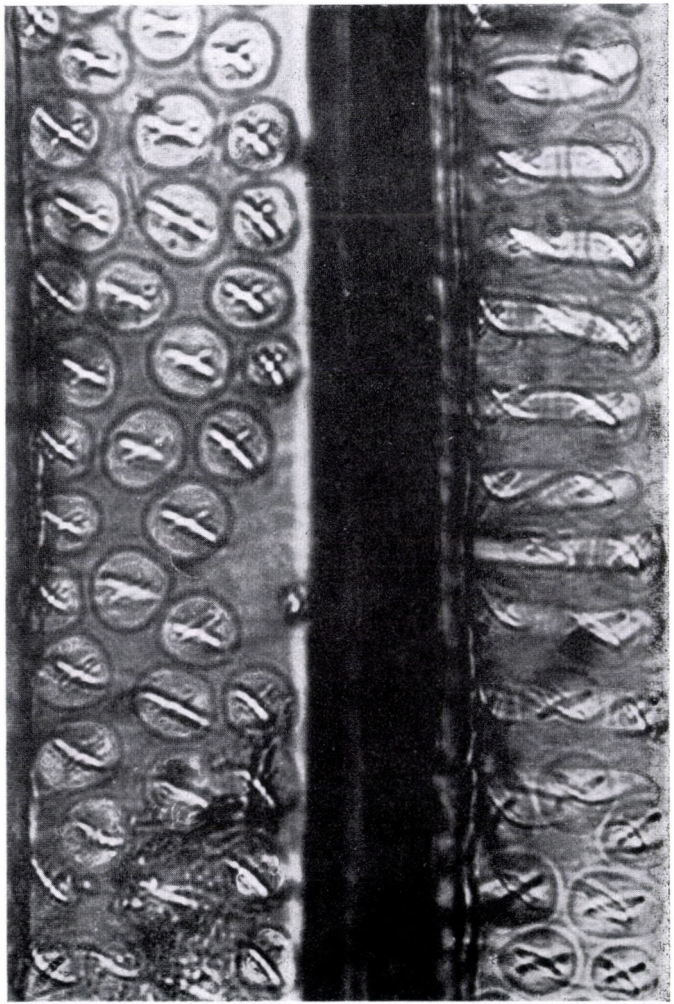

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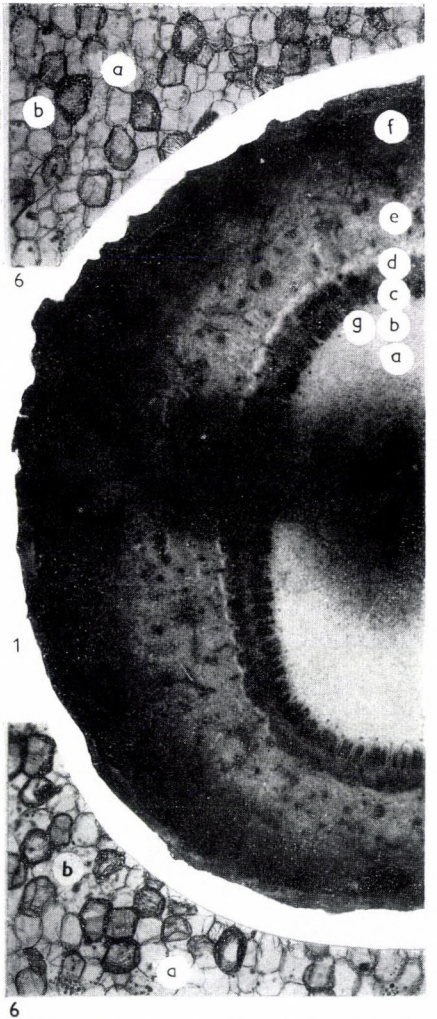
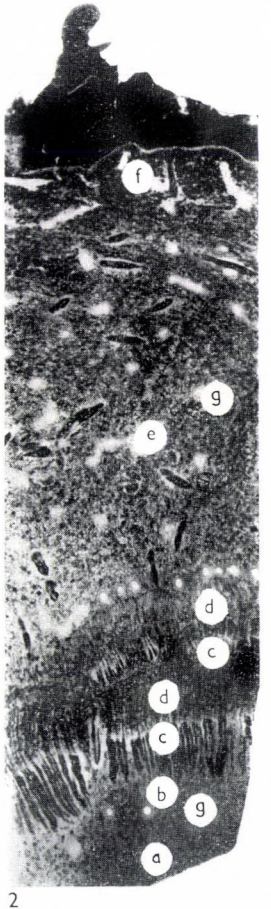
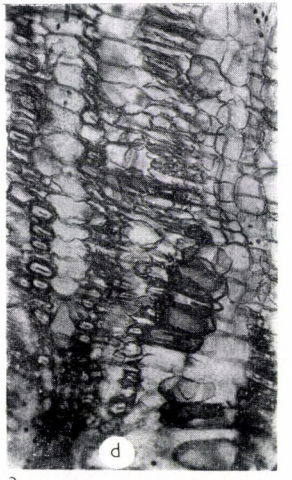
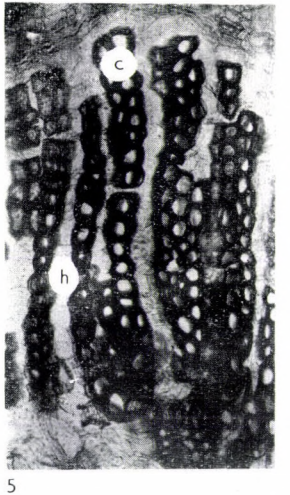
XXII. *Cycas media* R. Br.





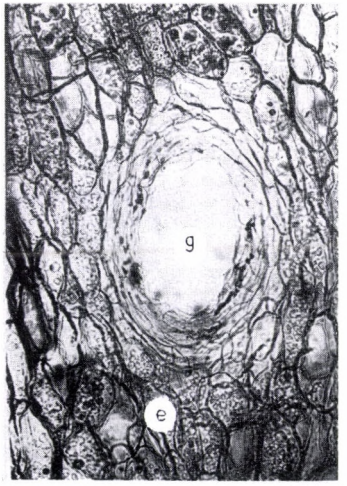








XXIII. *Cycas neocaledonica* Linden



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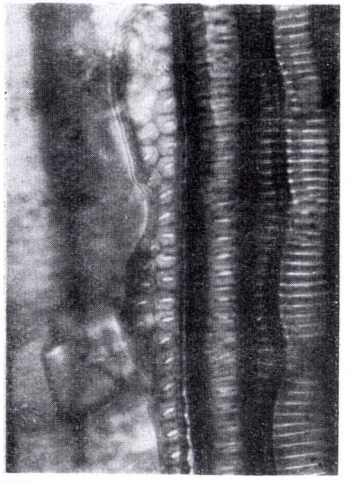

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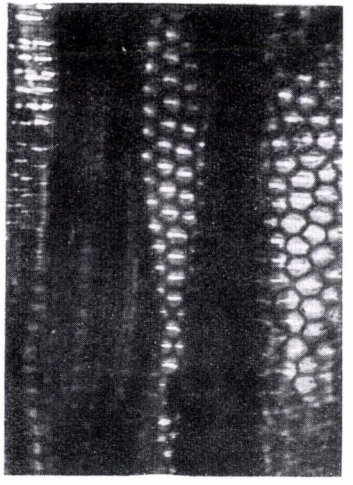

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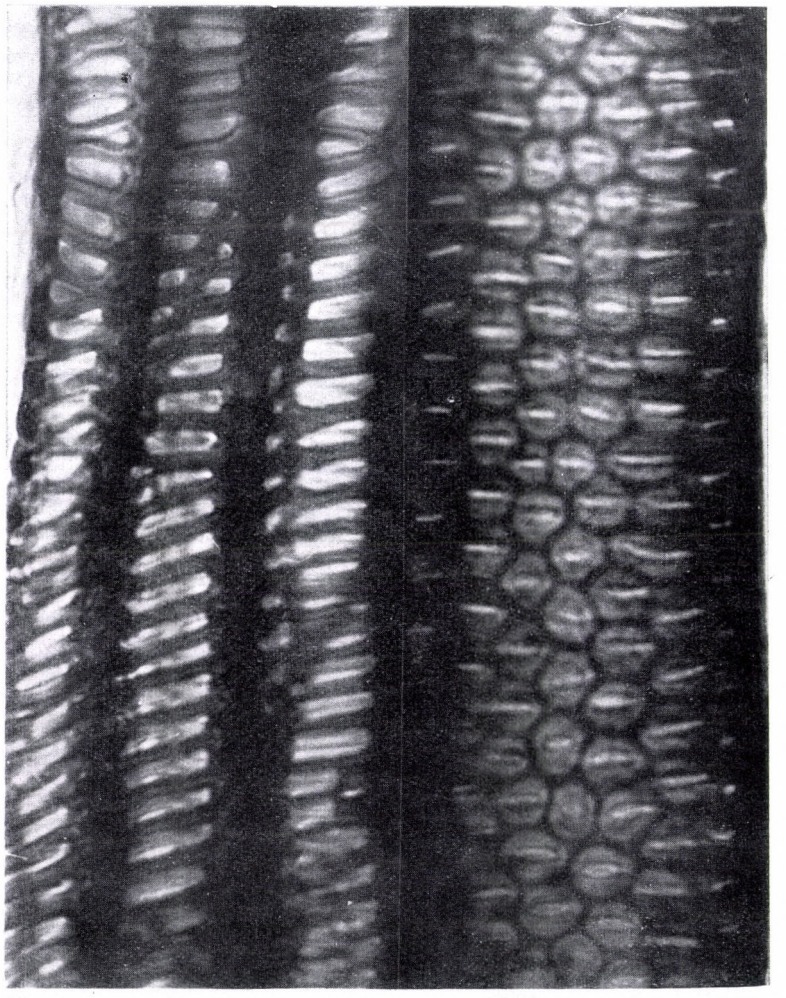

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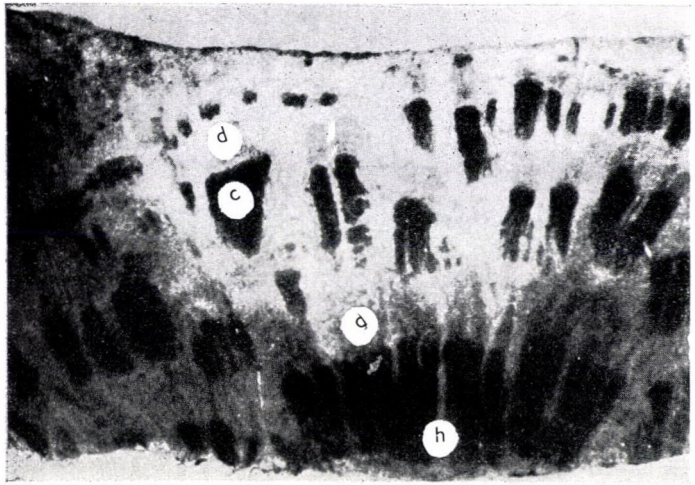
XXIV. *Cycas neocaledonica* Linden



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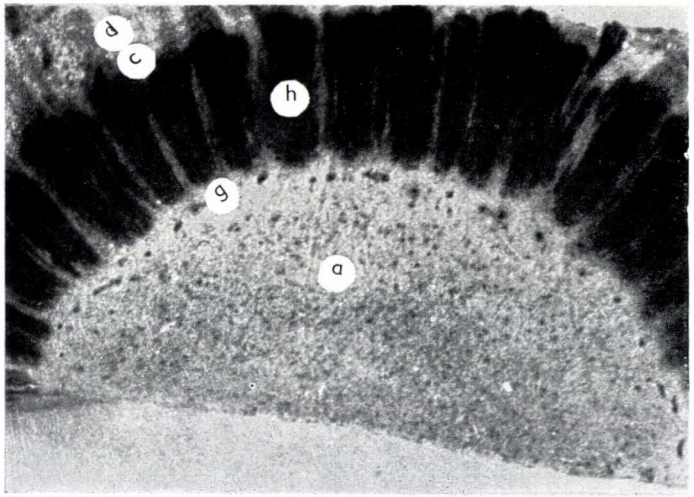

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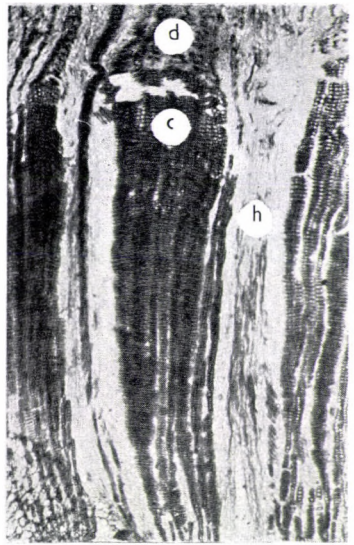

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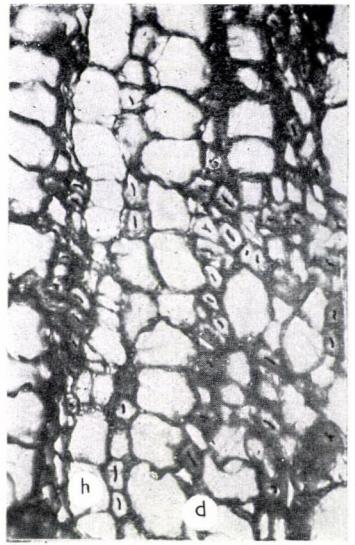

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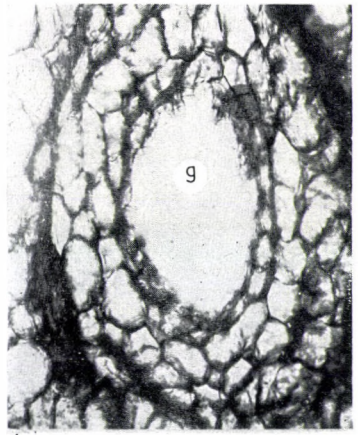

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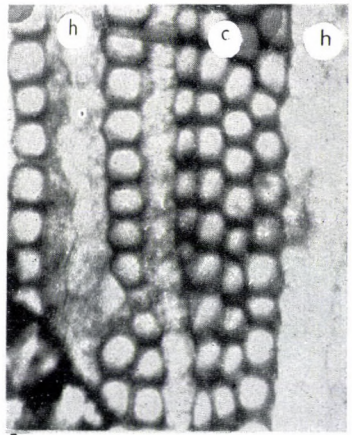

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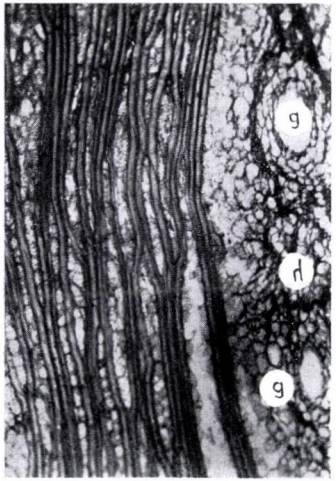
XXV. *Cycas normanbyana* F. Muell.



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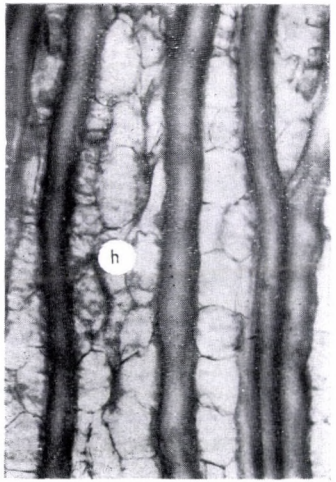

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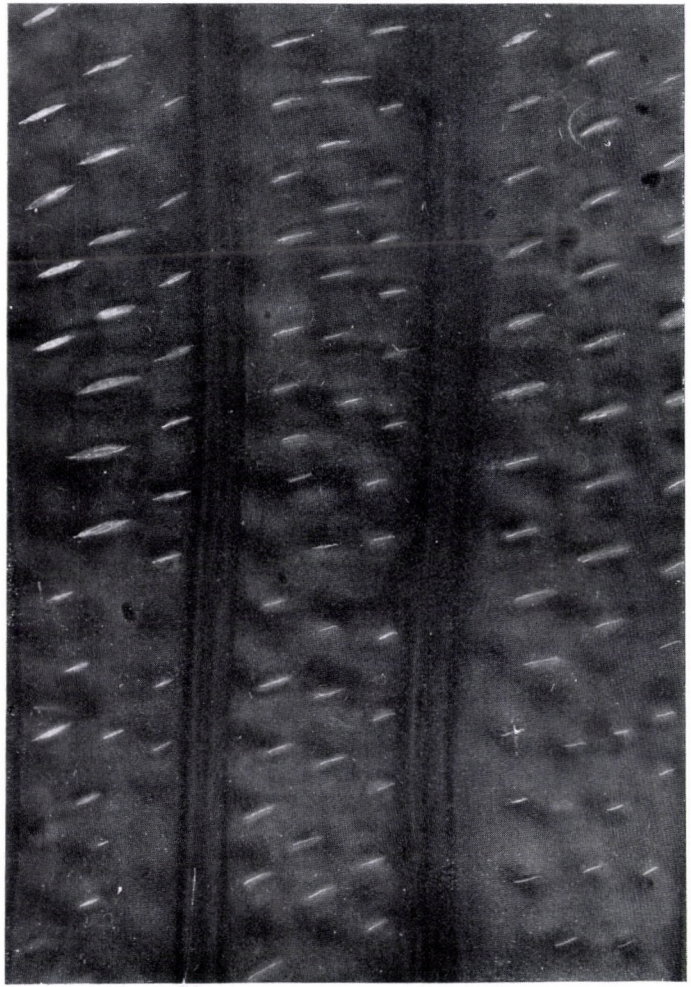

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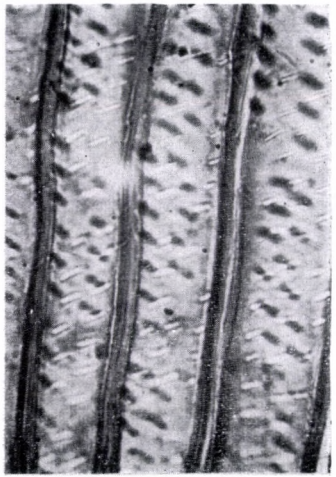

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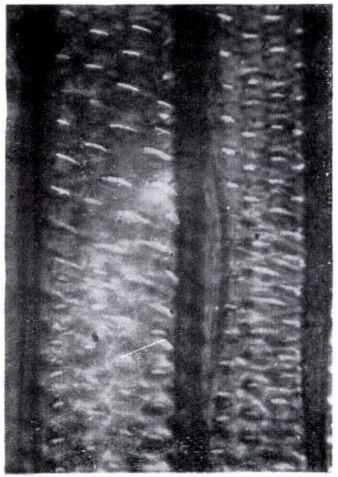

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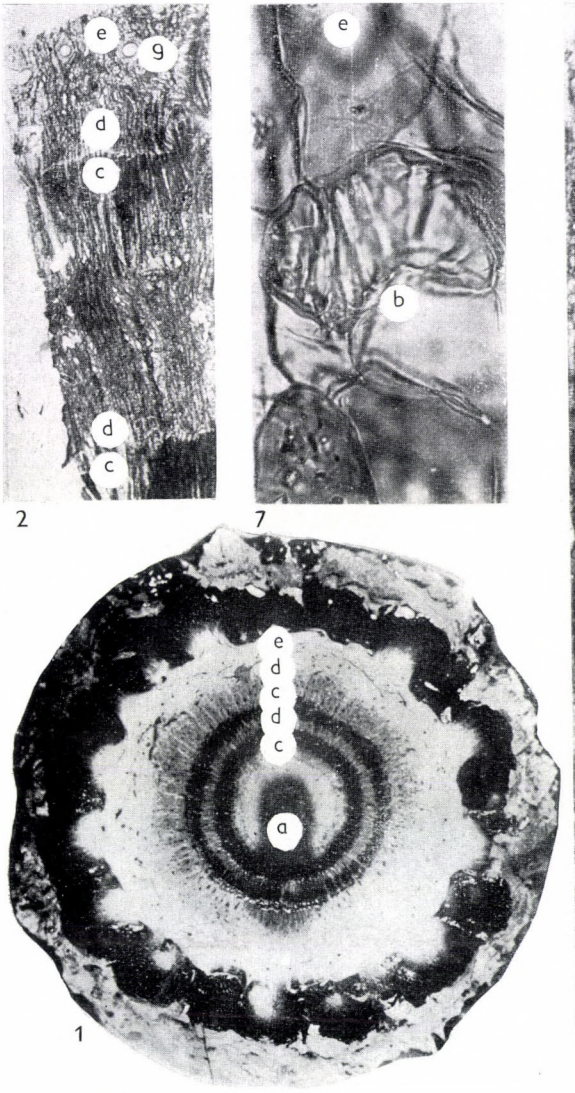
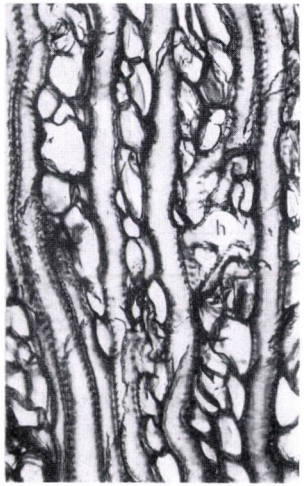
XXVI. *Cycas normanbyana* F. Muell.



XXVII. *Cycas revoluta* Thunb.



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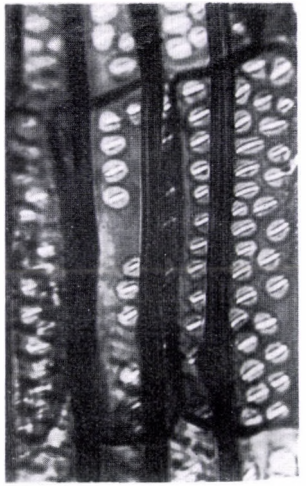

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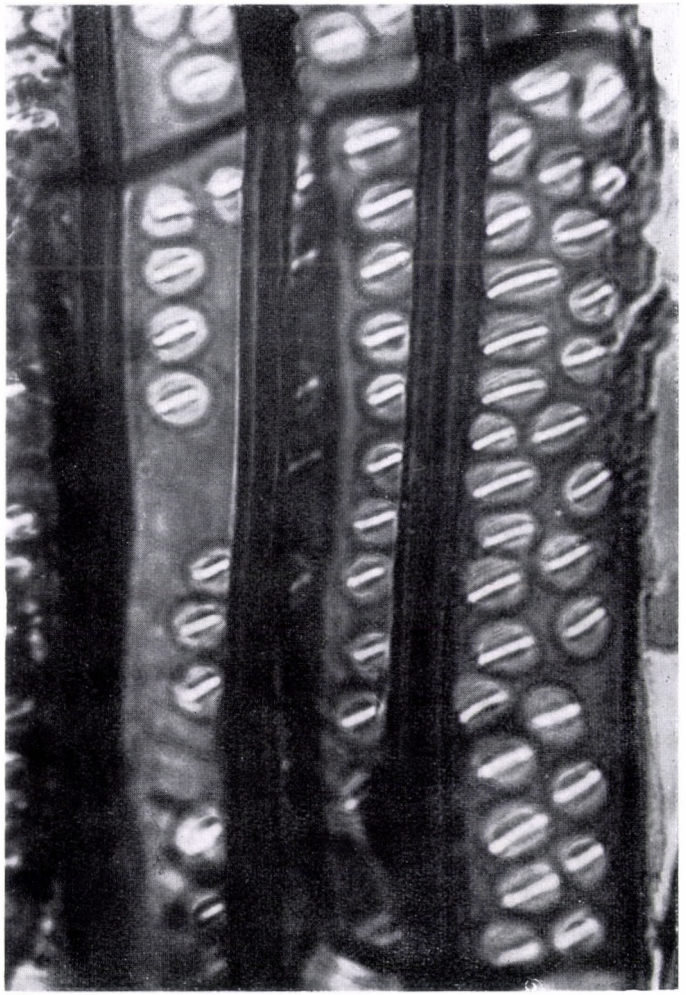

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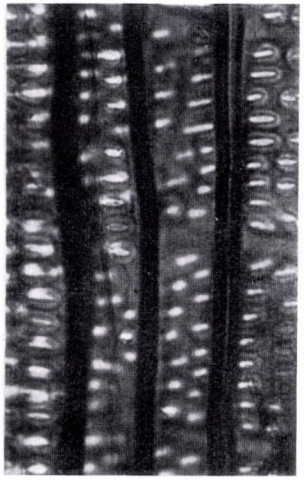

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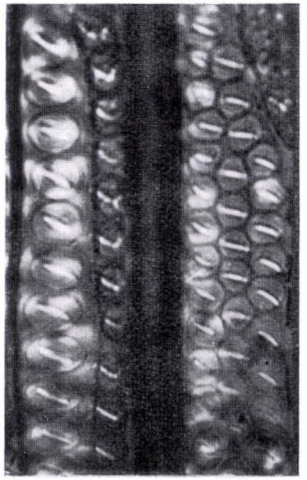

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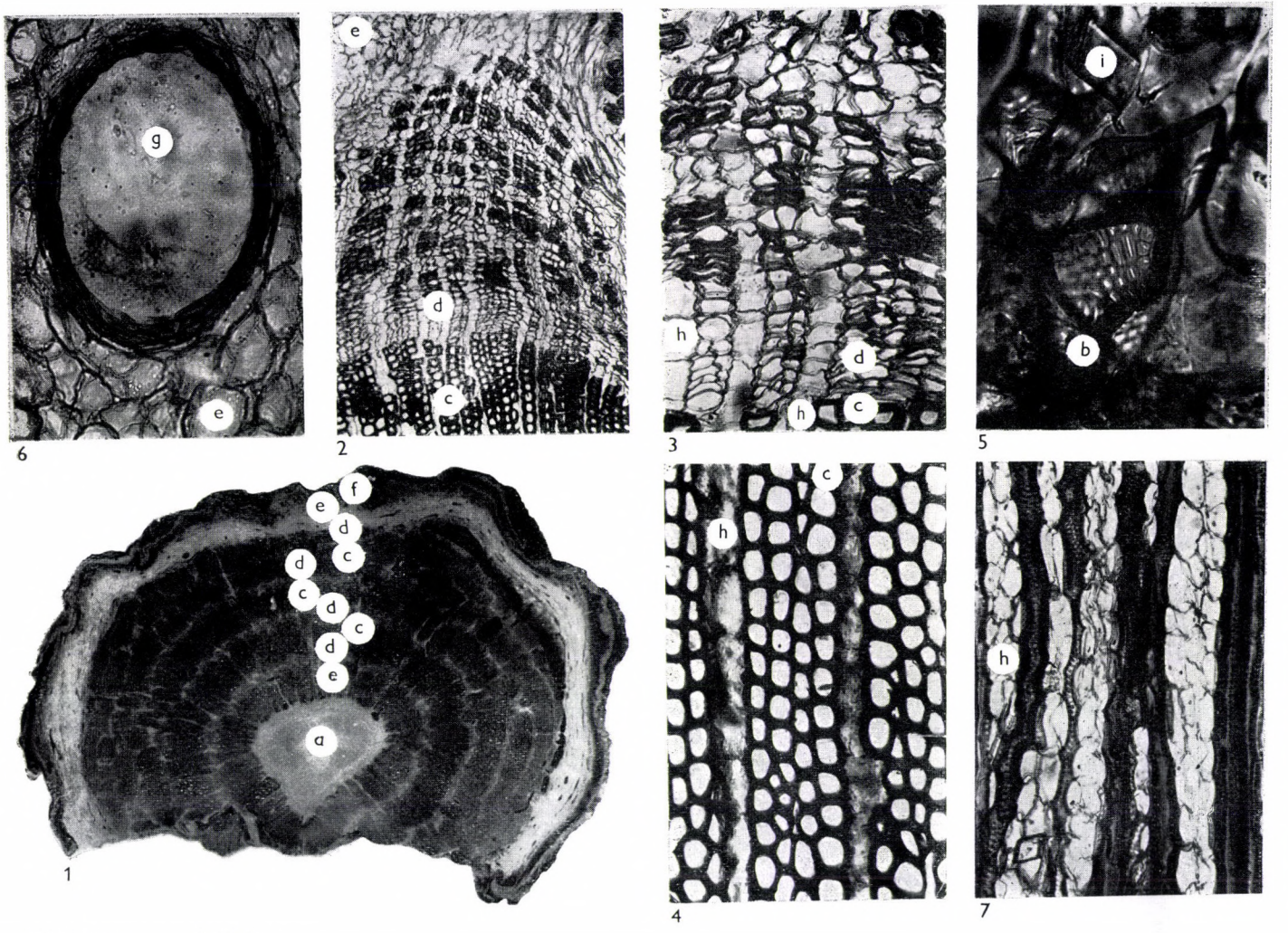
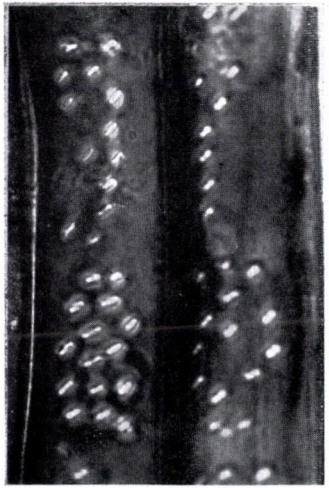
XXVIII. *Cycas revoluta* Thunb.



XXIX. *Cycas rumphii* Miq.



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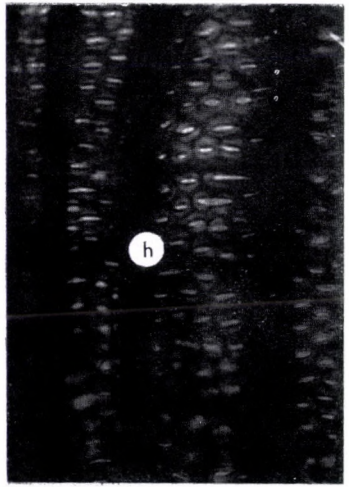

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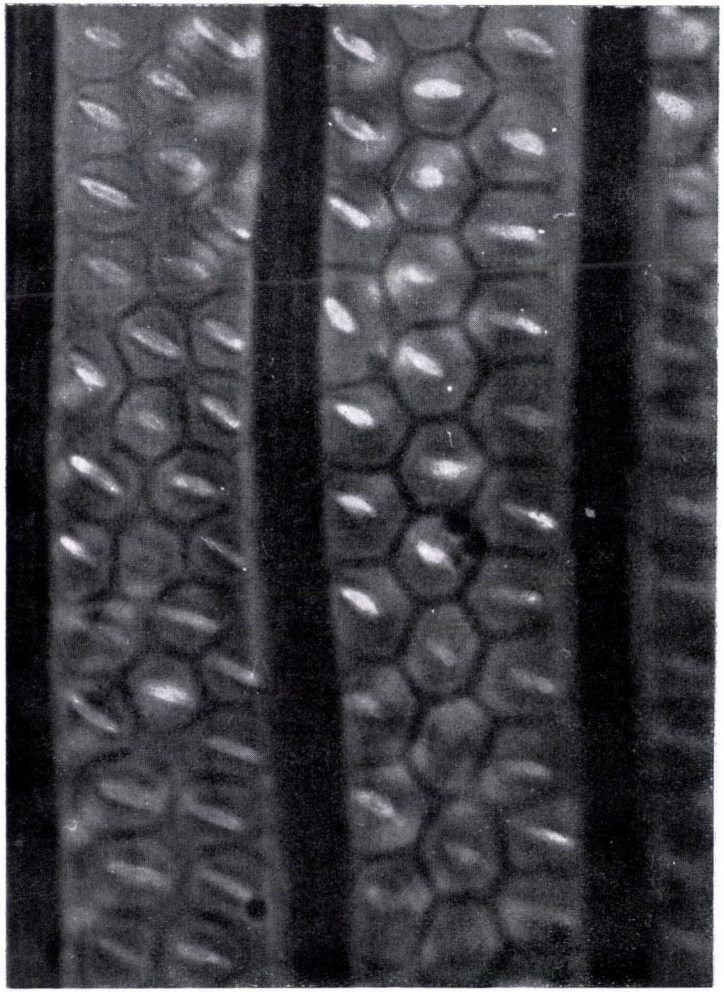

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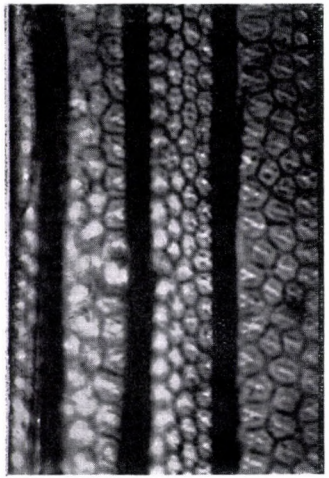

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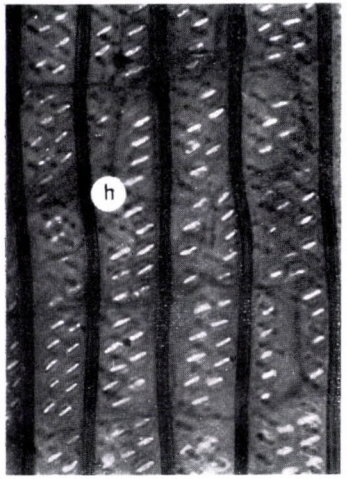

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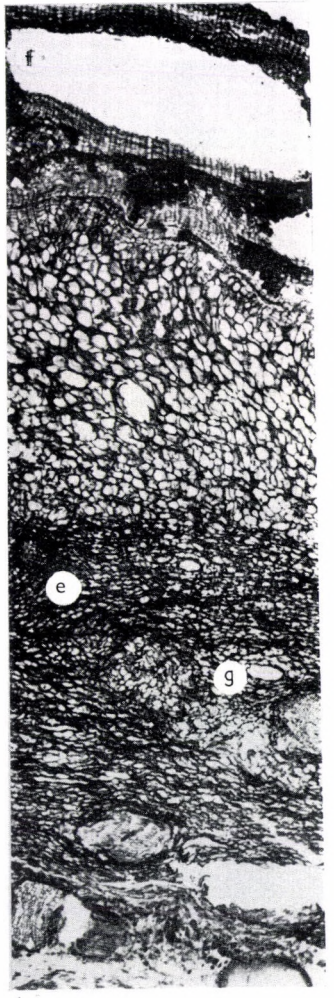
XXX. *Cycas rumphii* Miq.



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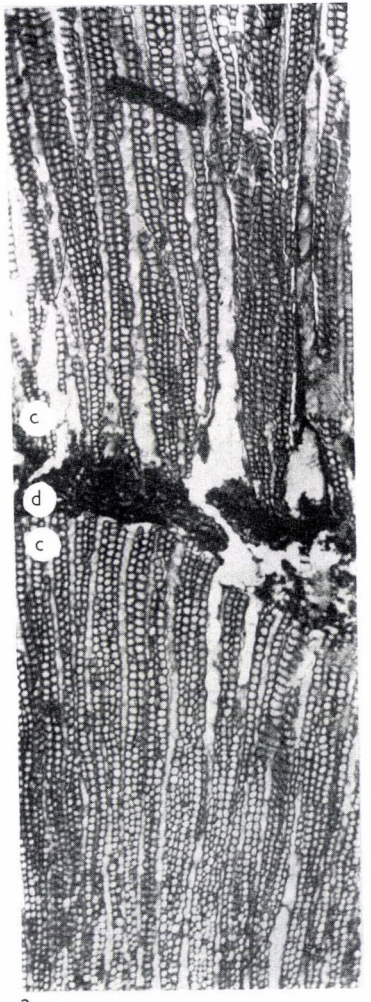

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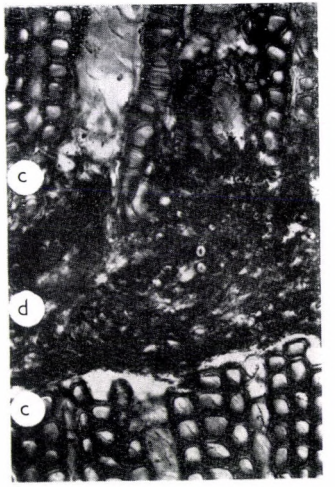

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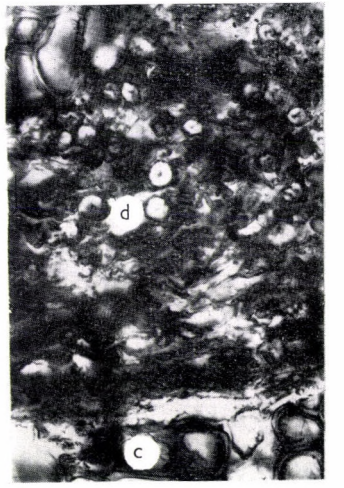

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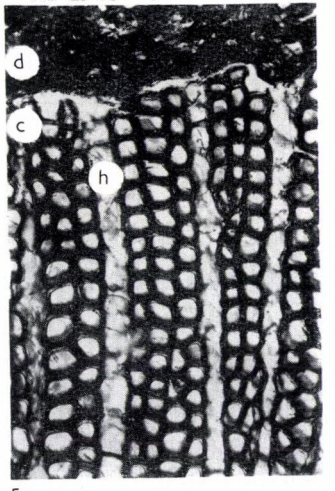

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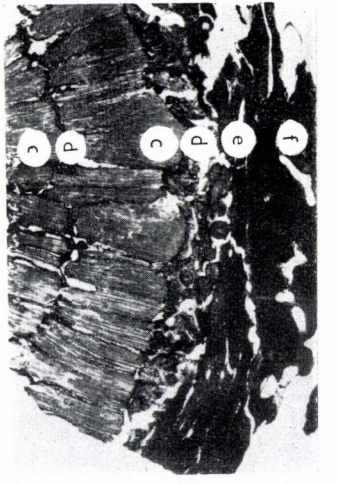

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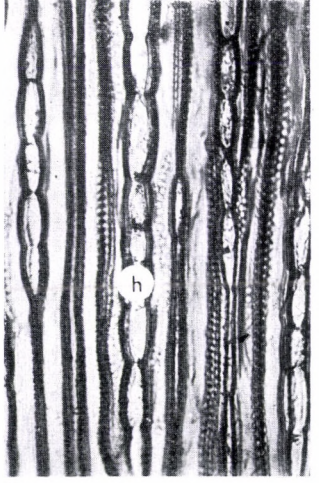

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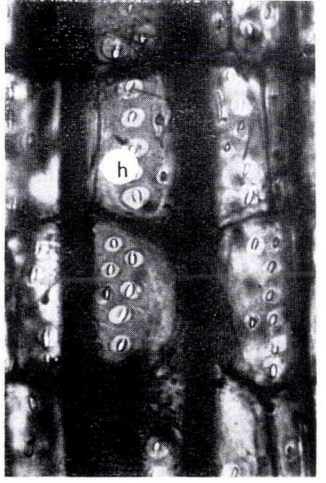

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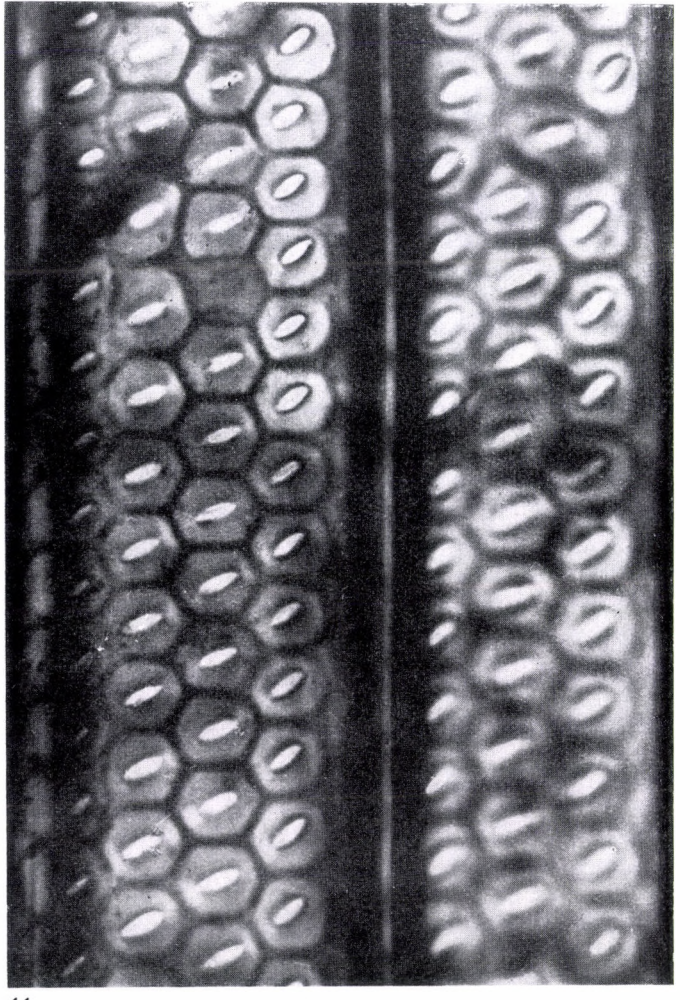

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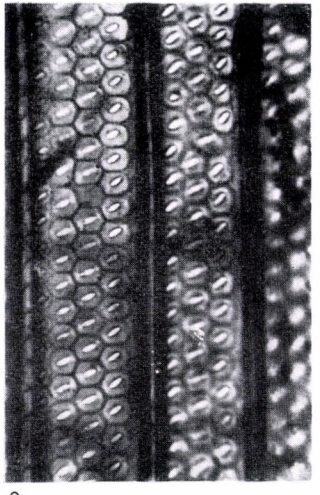

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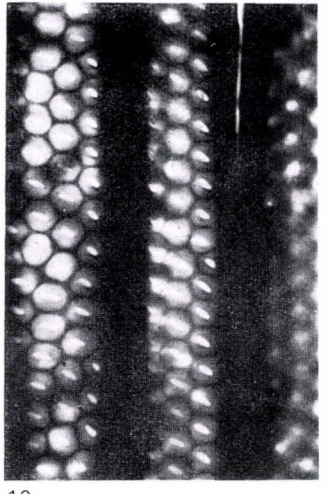

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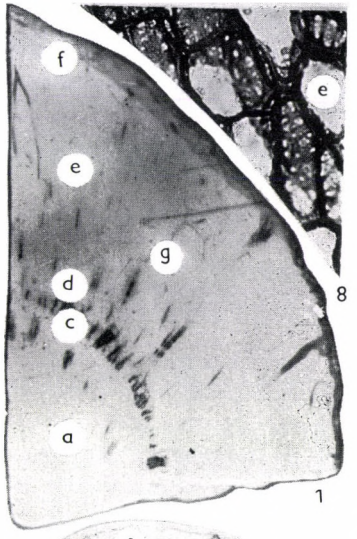

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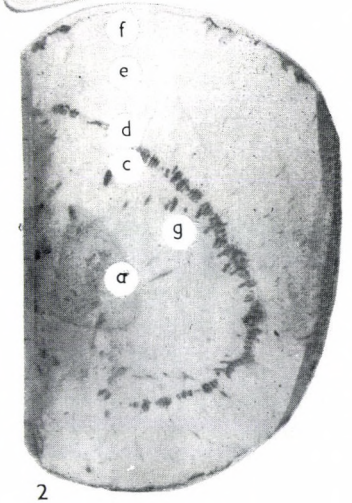

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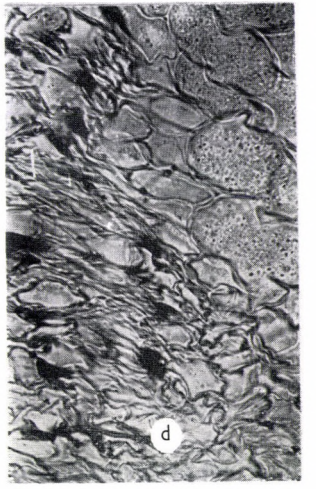

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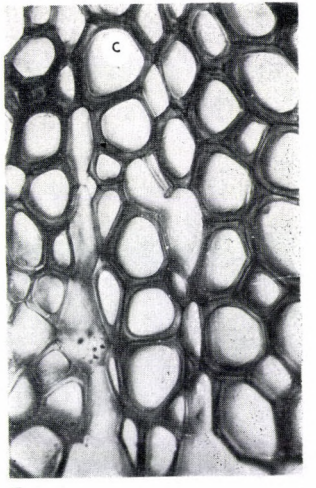

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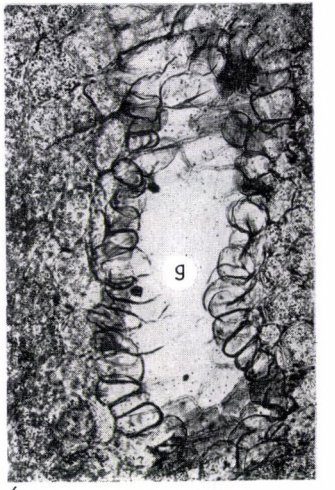

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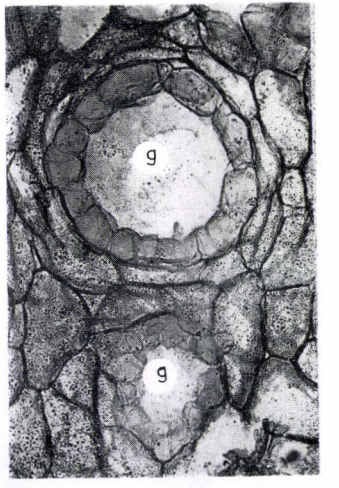

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XXXIII. *Stangeria paradoxa* Th. Moore



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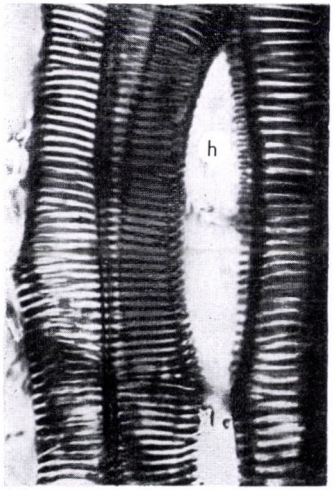

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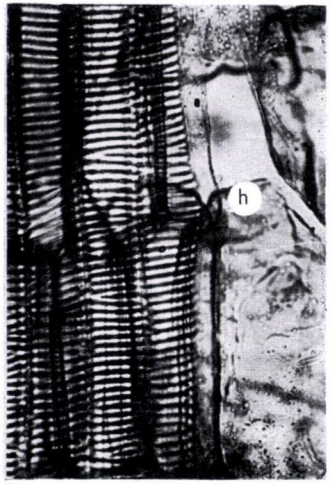

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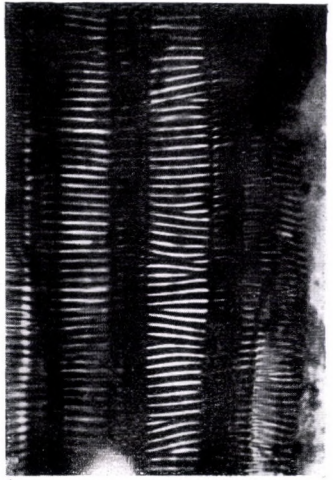

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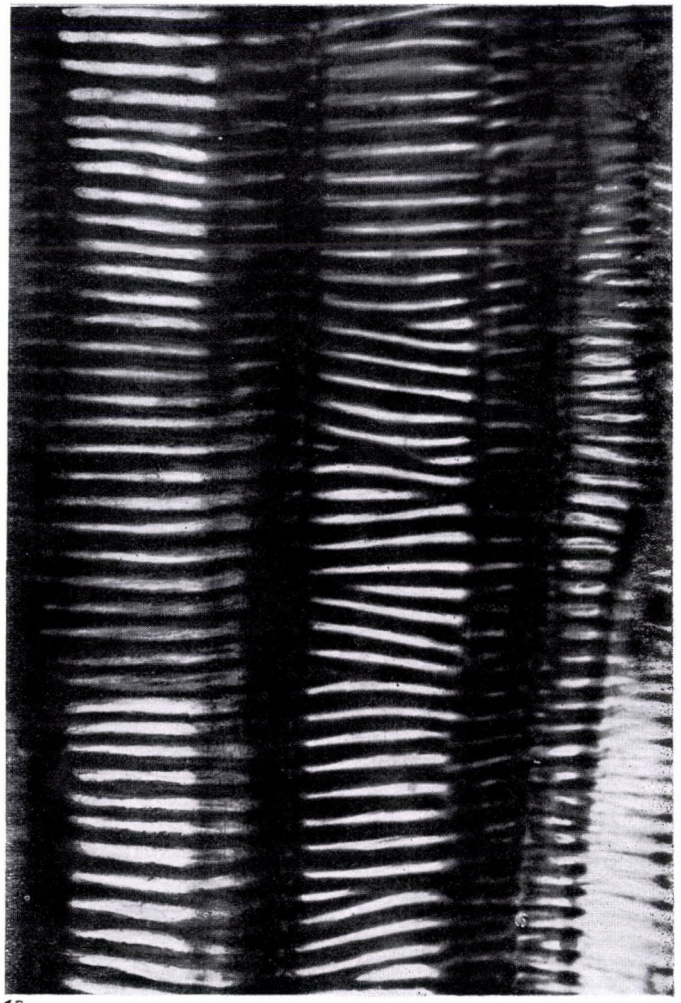

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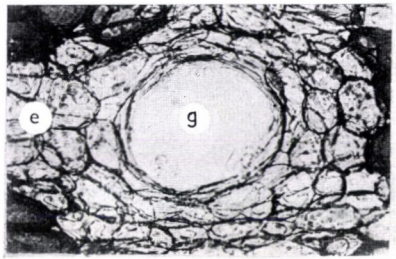
XXXIV. *Stangeria paradoxa* Th. Moore



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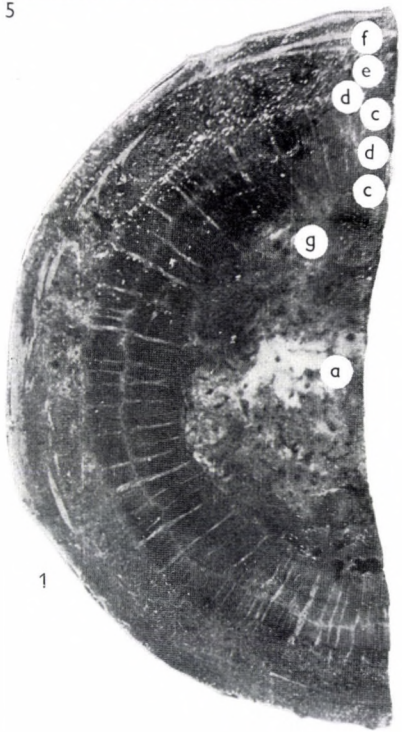

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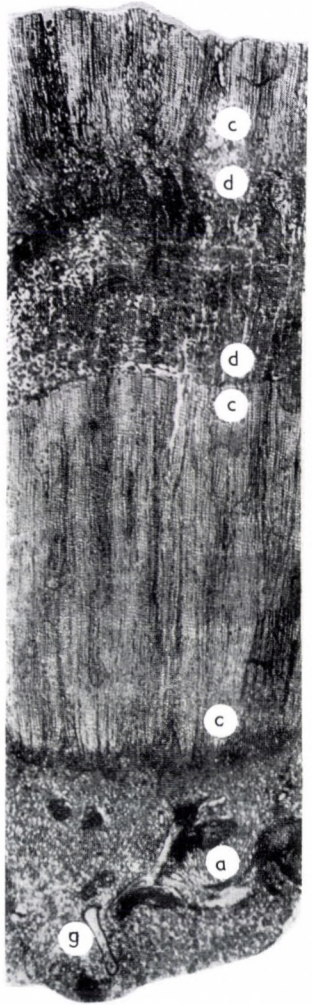

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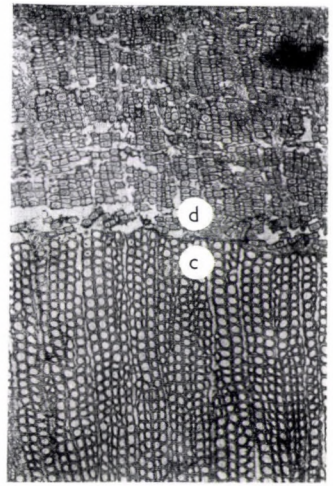

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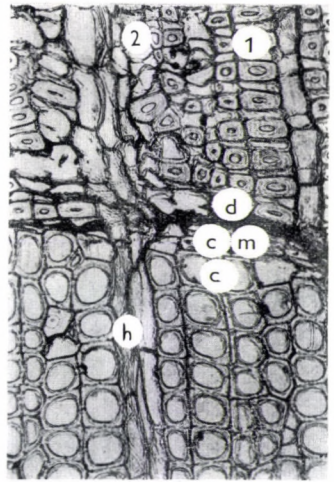

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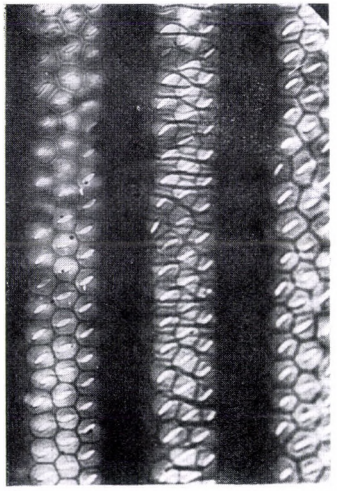
XXXV. *Lepidozamia hopei* Regel



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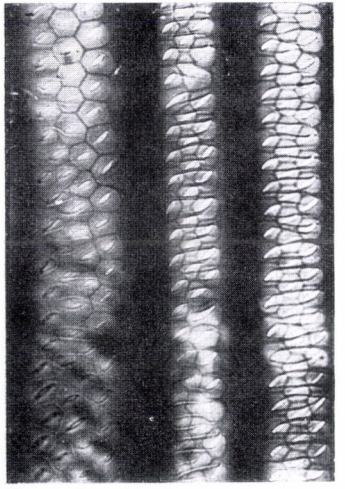

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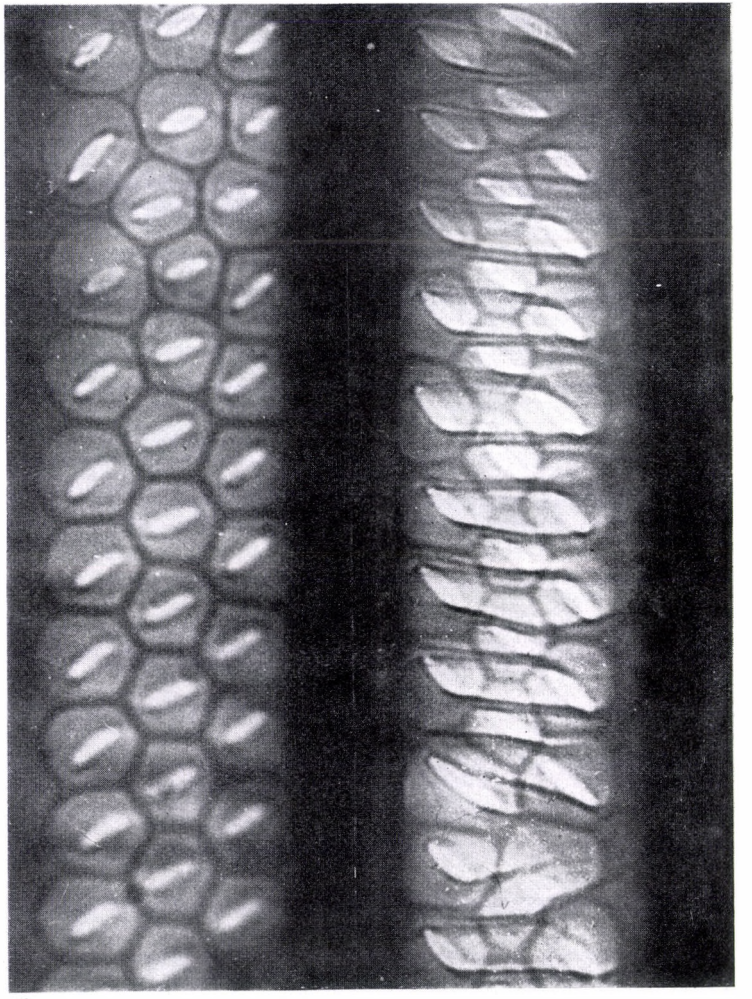

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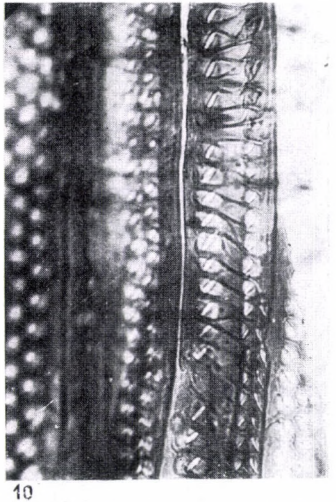

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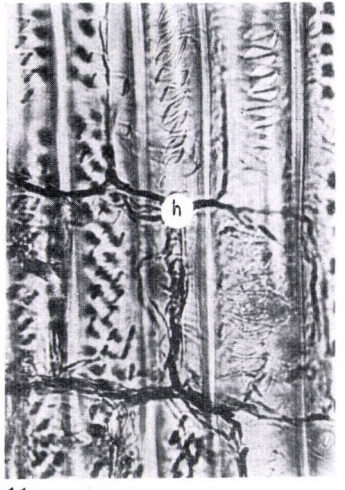

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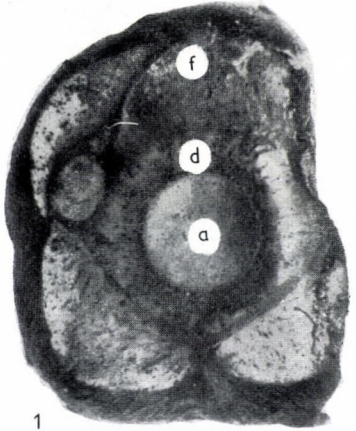
XXXVI. *Lepidozamia hopei* Regel



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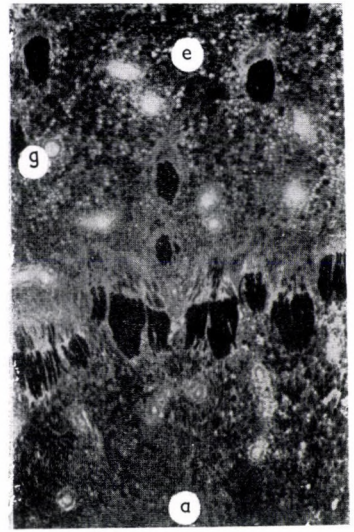

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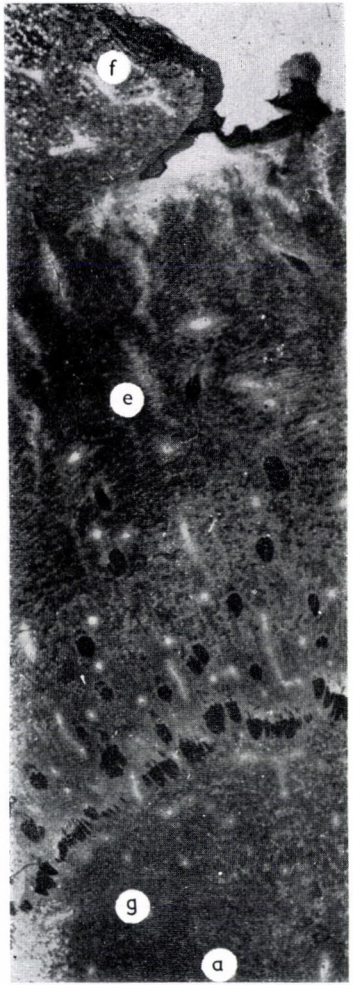

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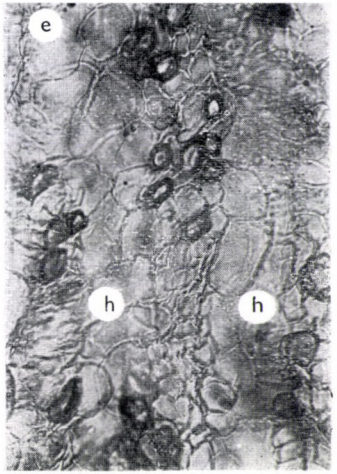

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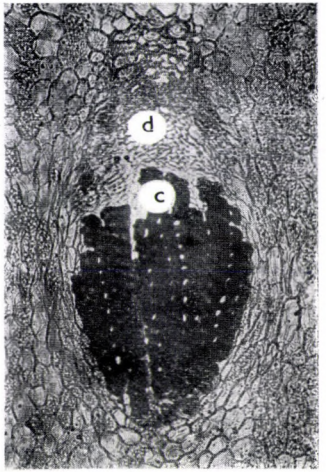

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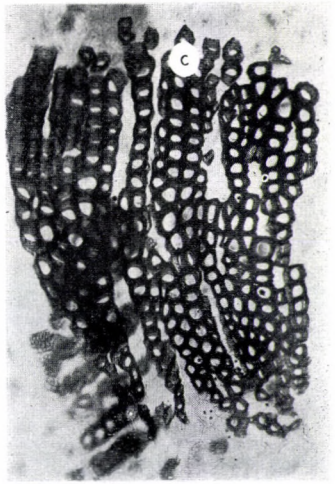

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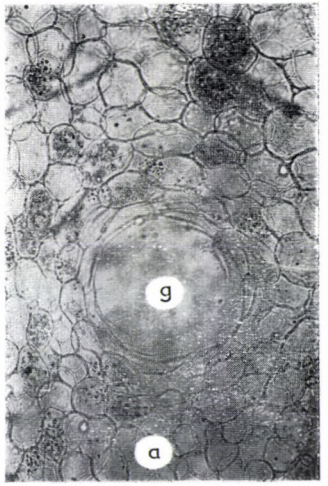

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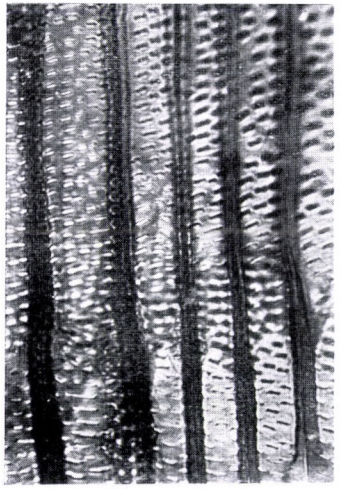
XXXVII. *Macrozamia communis* L. Johnson



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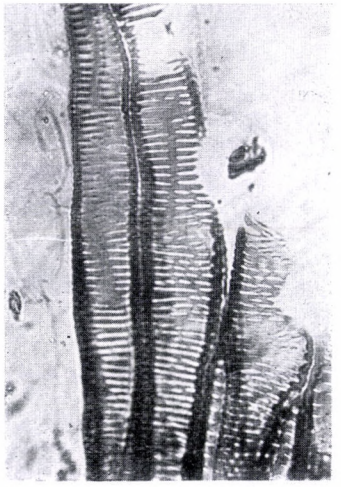

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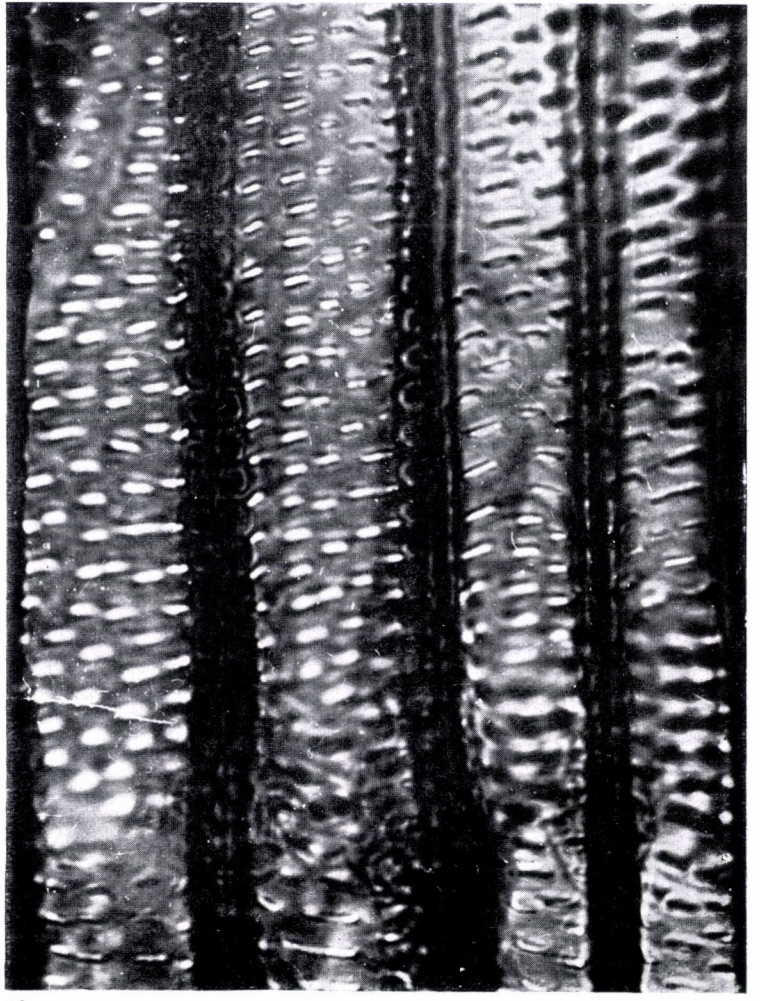

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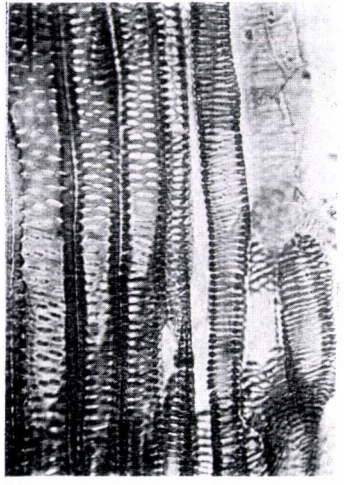

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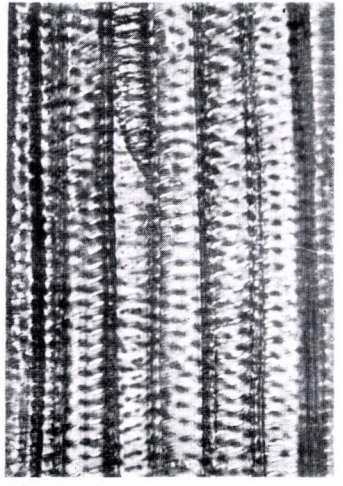

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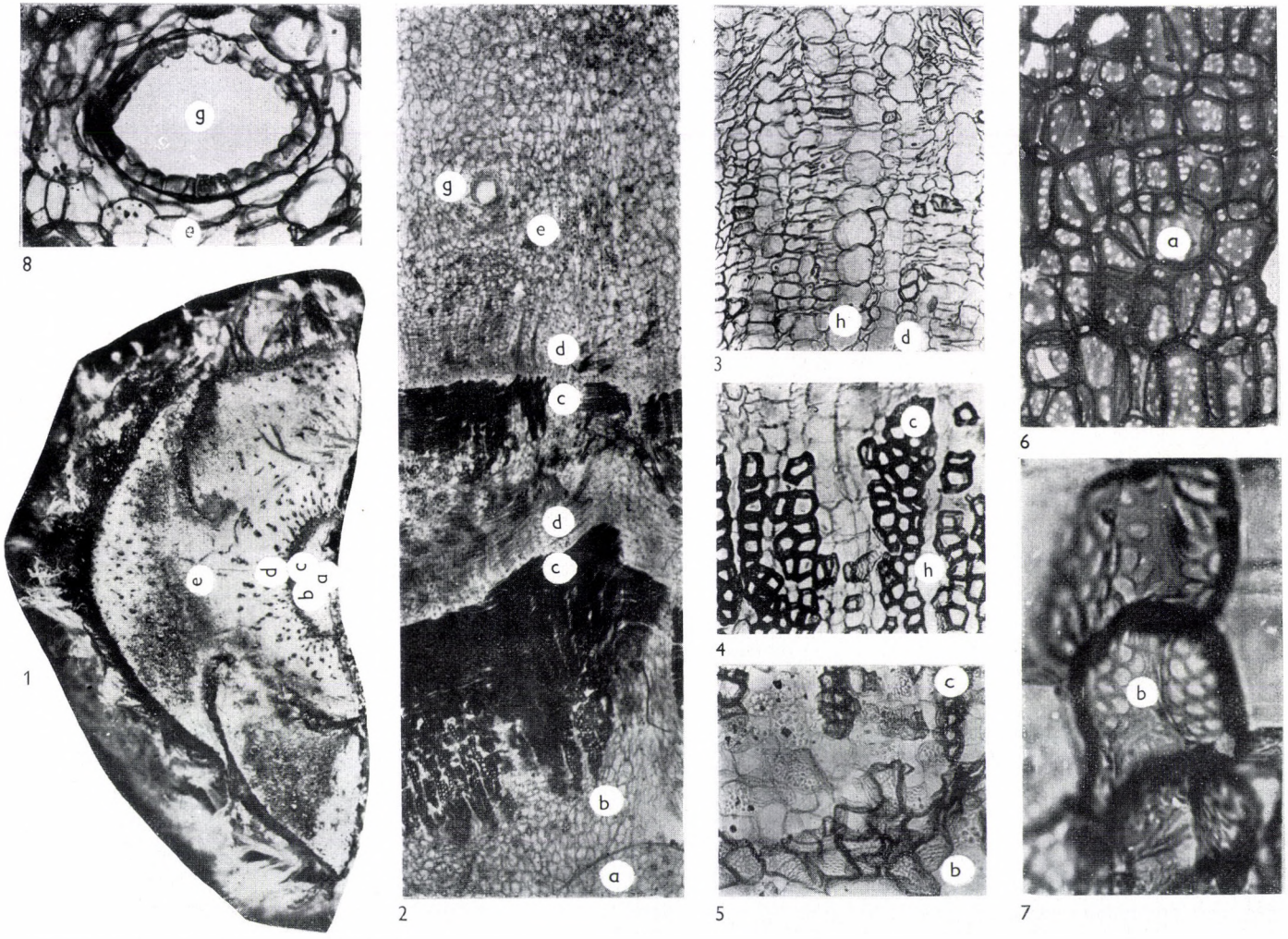
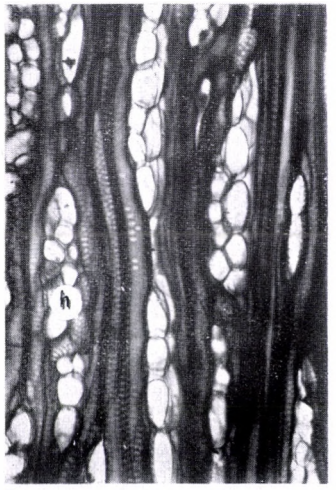
XXXVIII. *Macrozamia communis* L. Johnson



XXXIX. *Macrozamia douglasii* W. Hill



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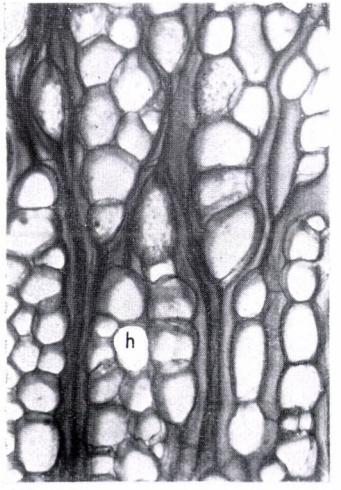

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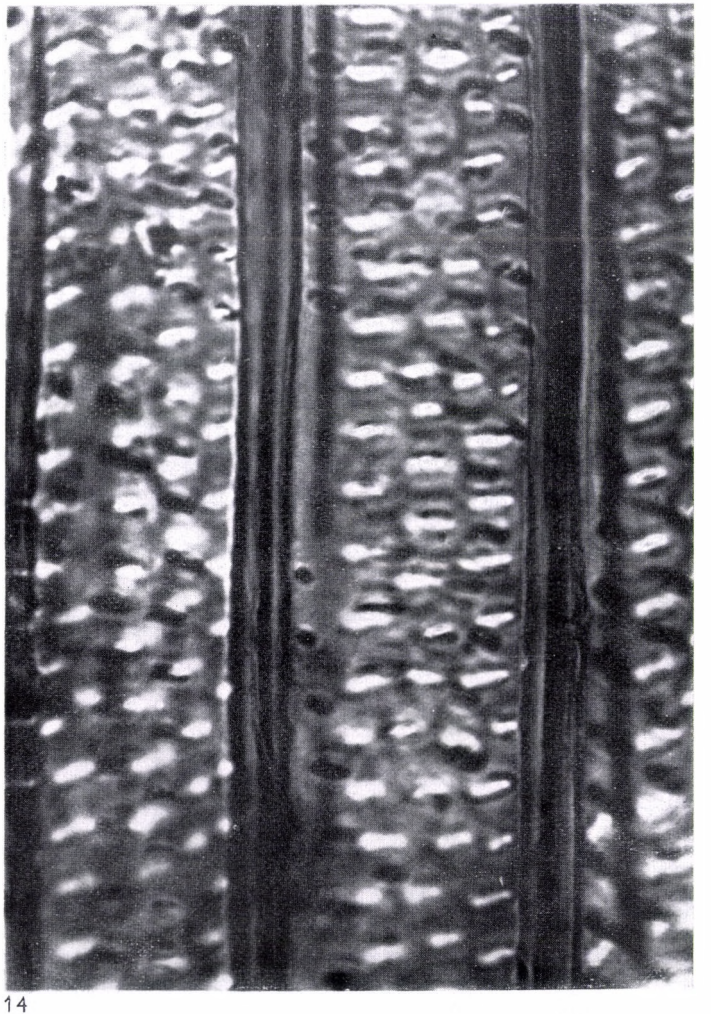

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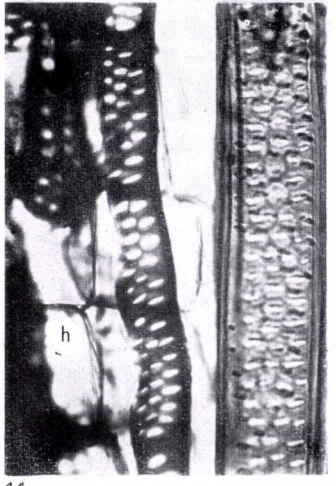

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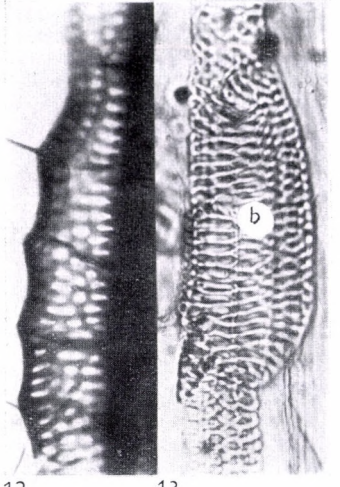

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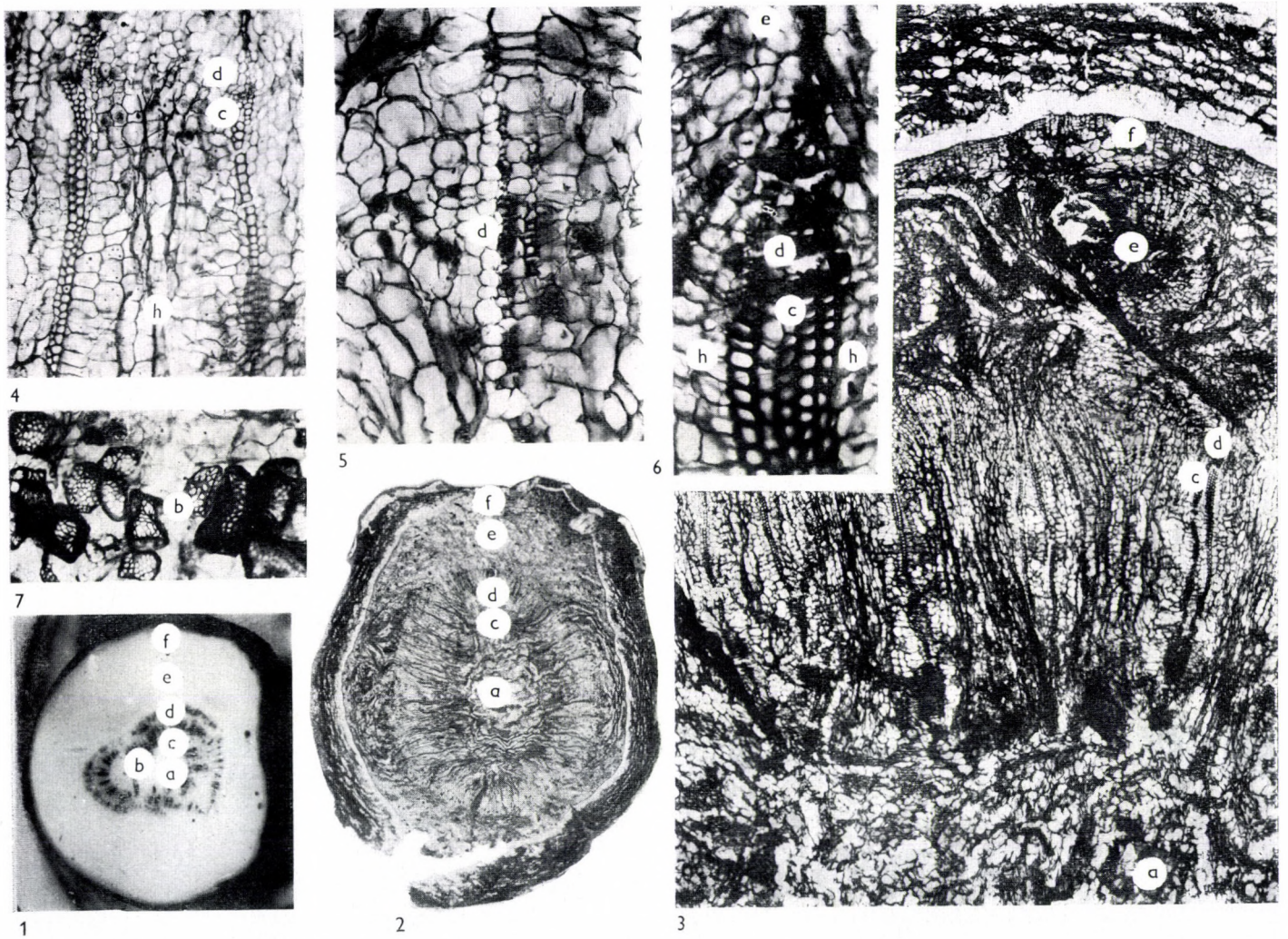
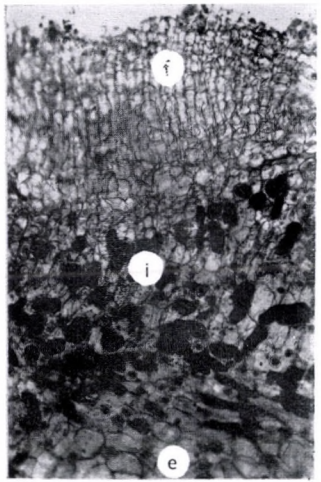
XL. *Macrozamia douglasii* W. Hill



XLI. *Macrozamia macdonnelli* (F. Muell.) A.DC.



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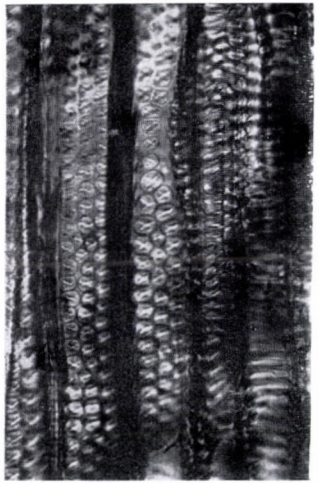

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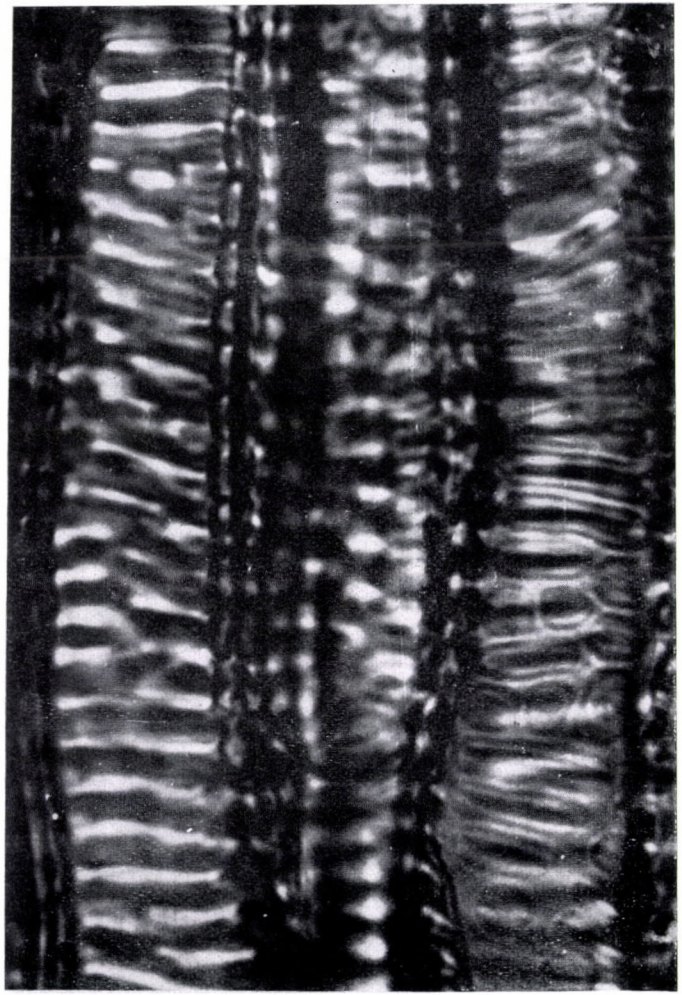

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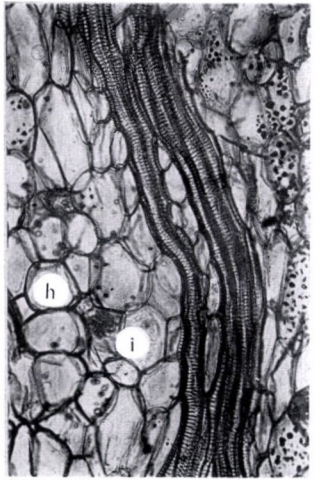

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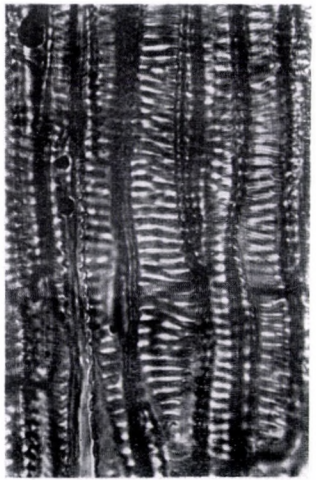

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XLII. *Macrozamia macdonnelli* (F. Muell.) A.DC.



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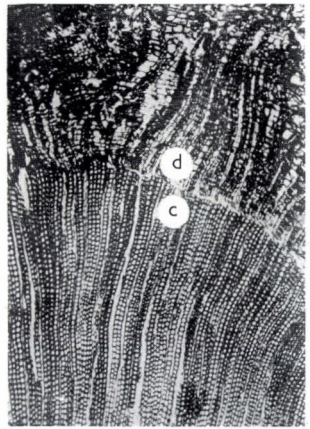

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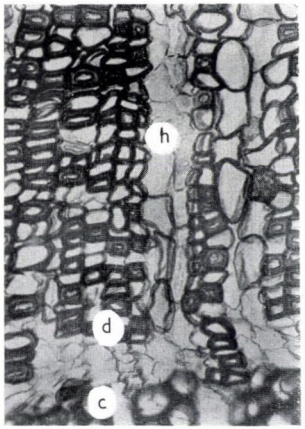

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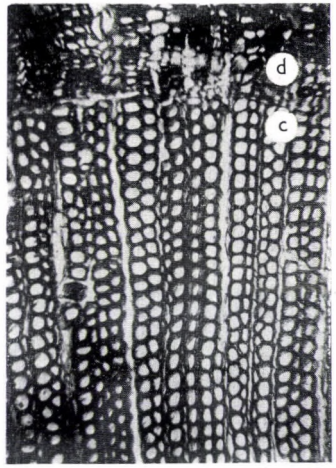

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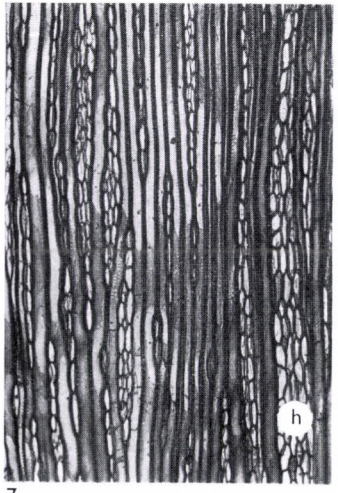
XLIII. *Macrozamia miquelii* (F. Muell.) A.DC.



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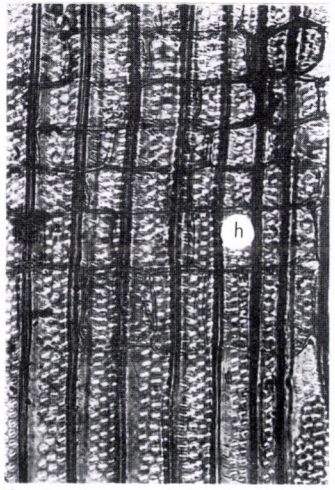

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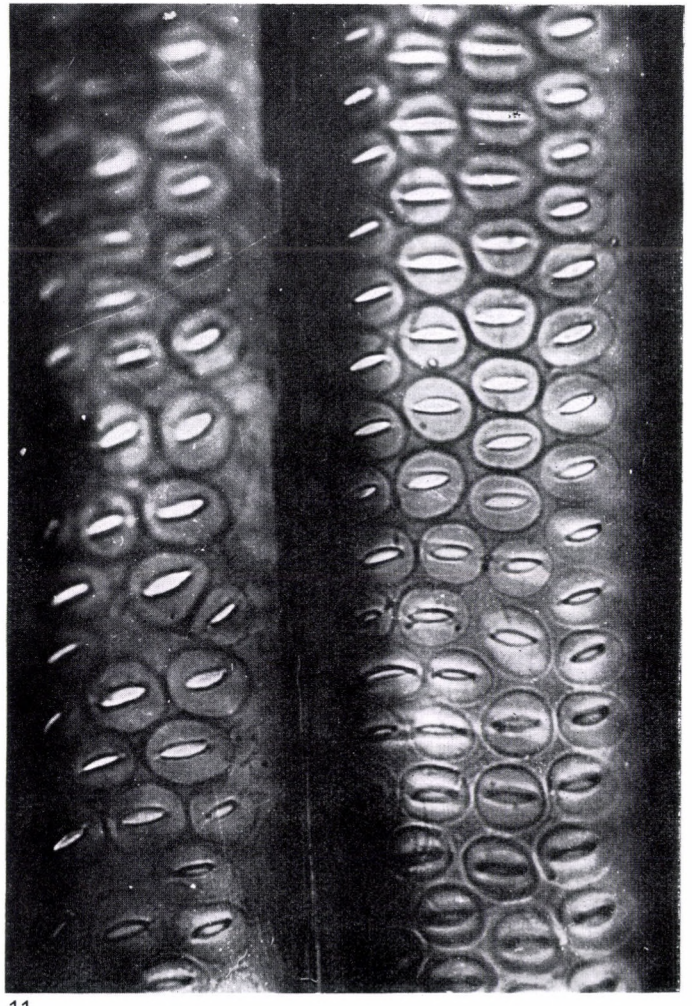

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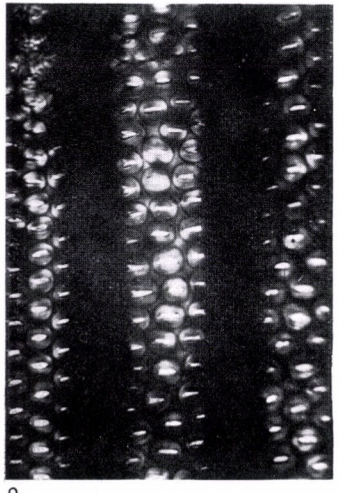

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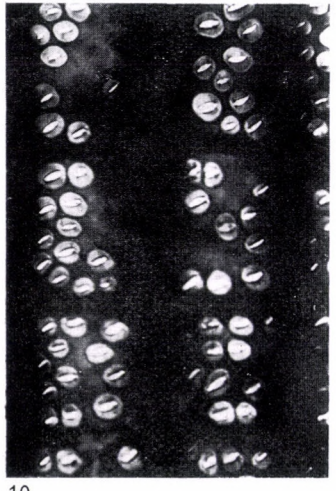

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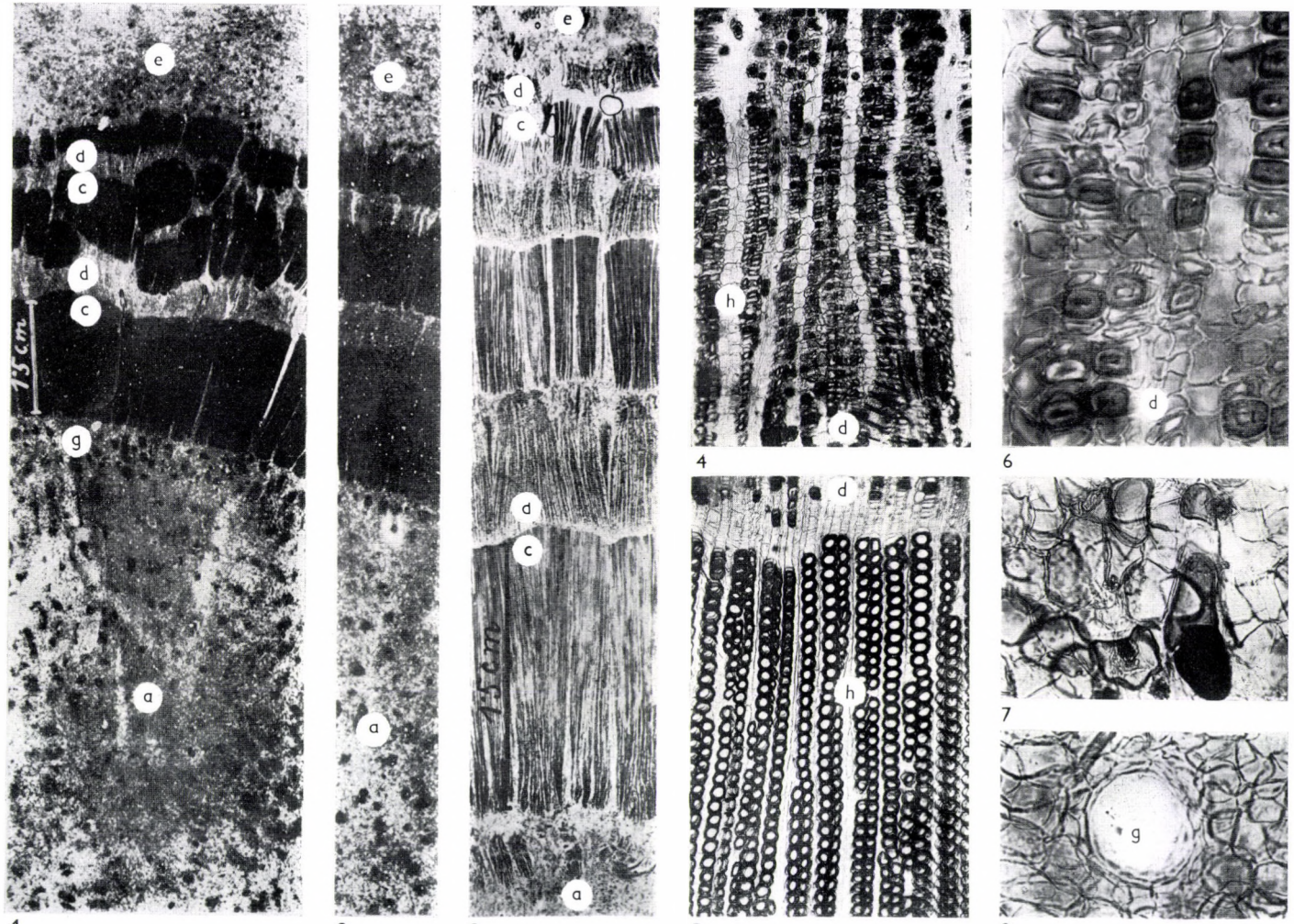
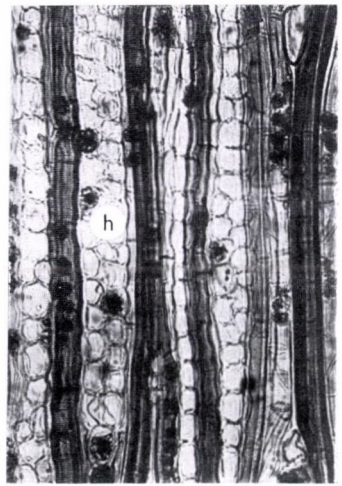


XLV. *Macrozamia moorei* F. Muell.



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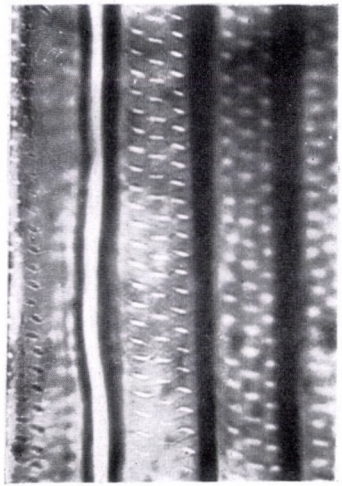

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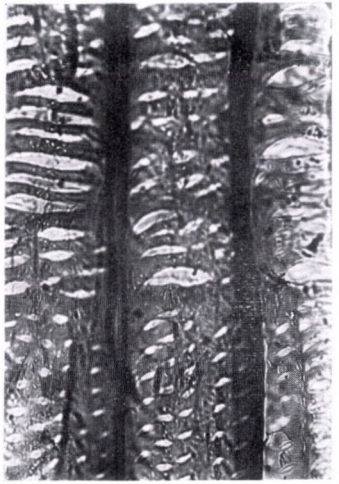

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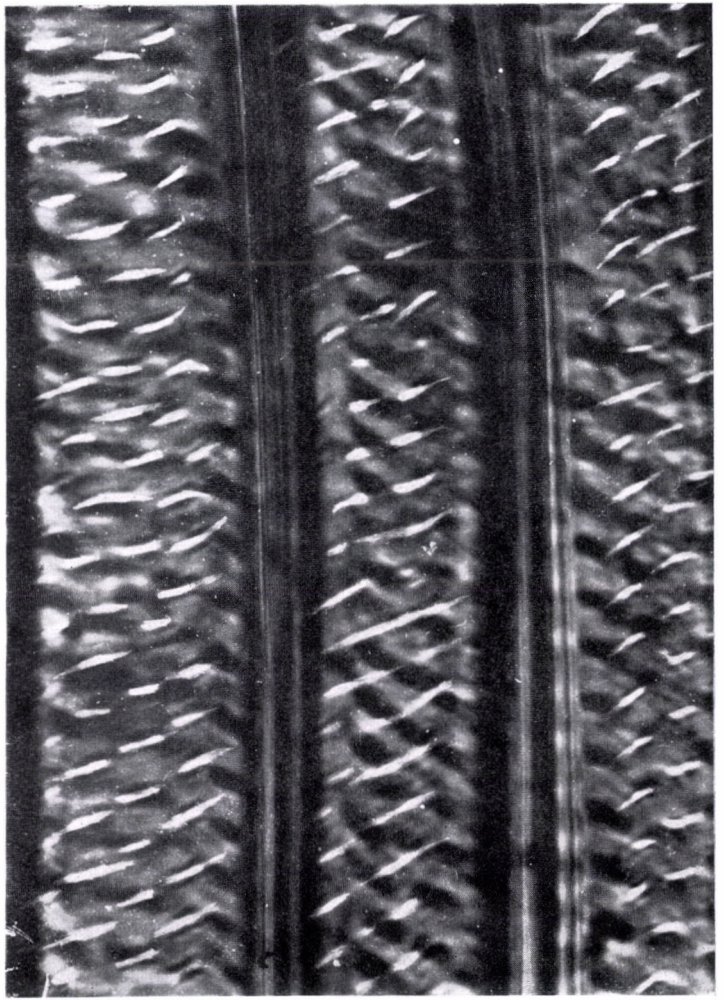

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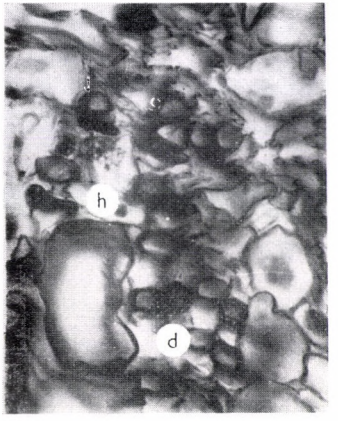
XLVI. *Macrozamia moorei* F. Muell.



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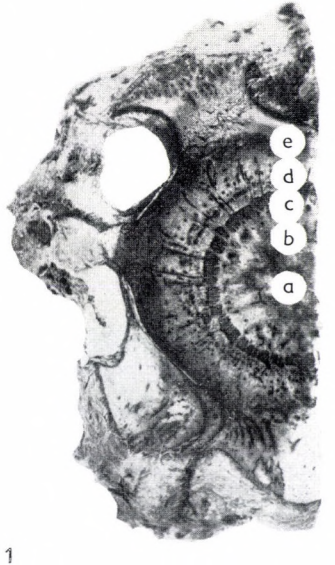

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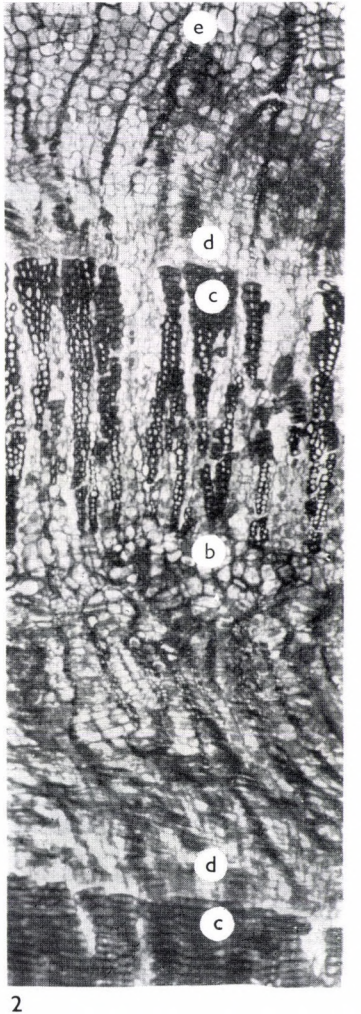

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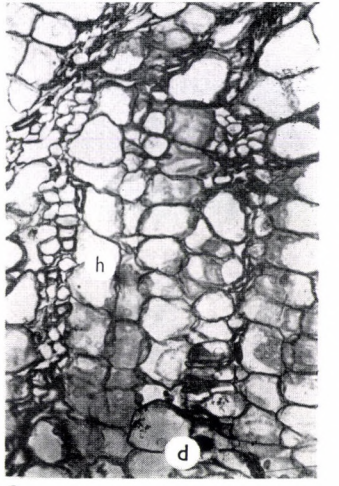

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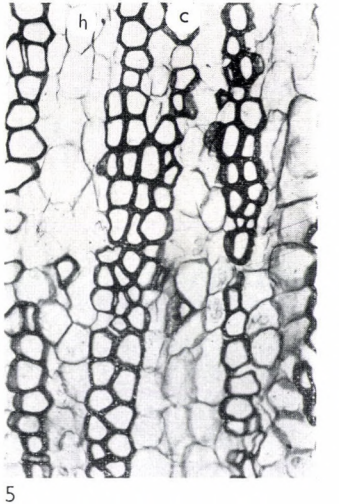

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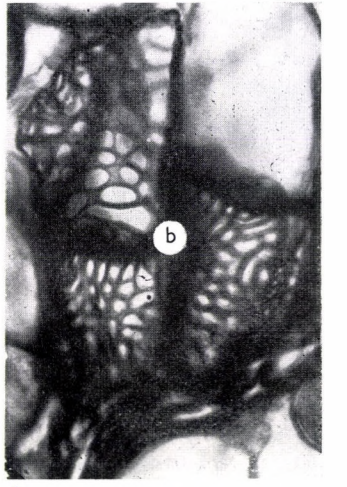

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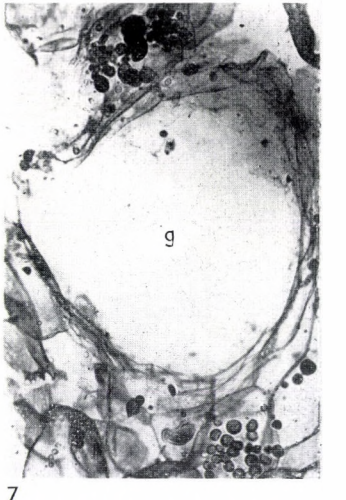

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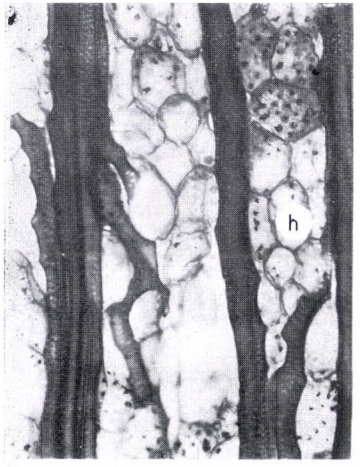
XLVII. *Macrozamia pauli-guilielmi* W. Hill et F. Muell.



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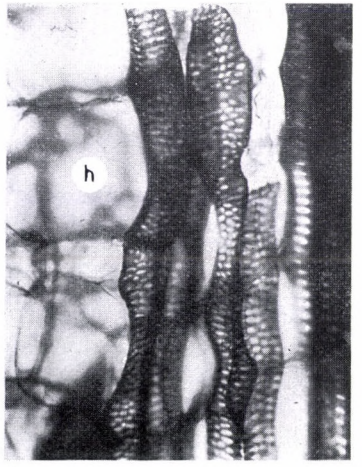

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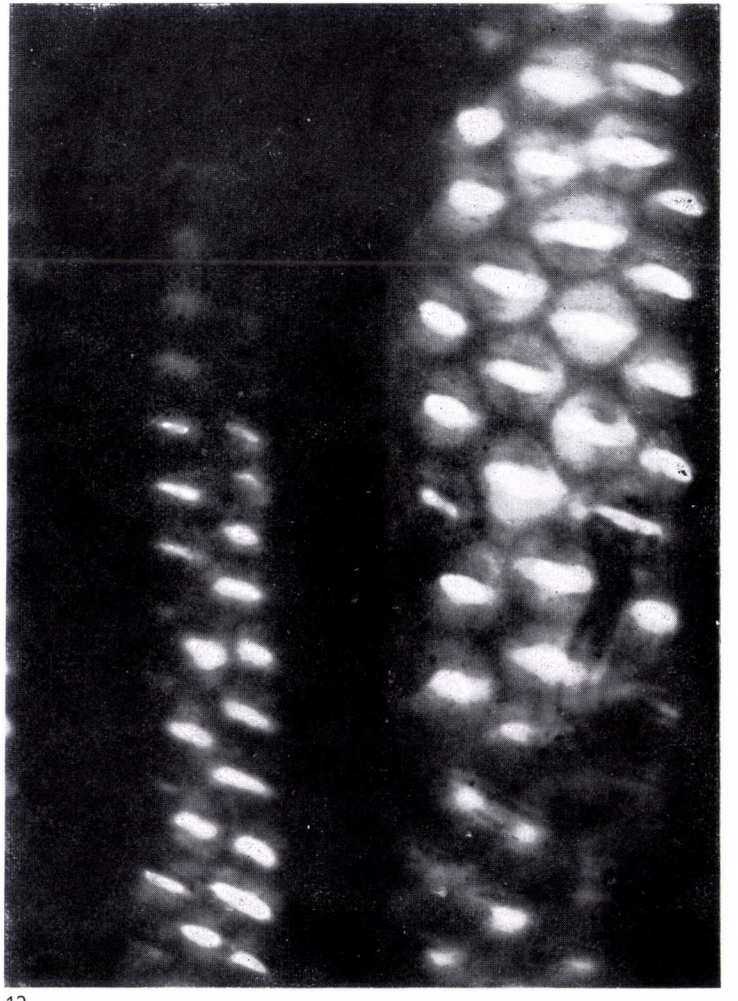

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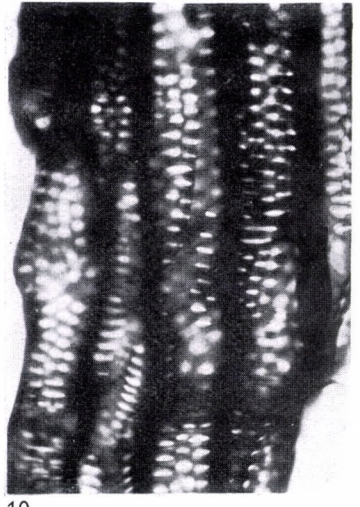

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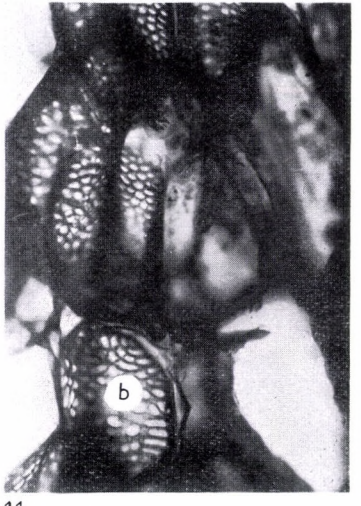

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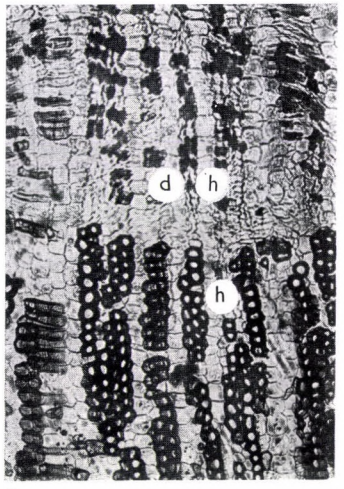

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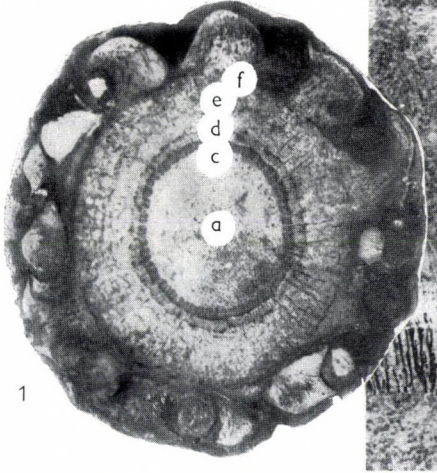

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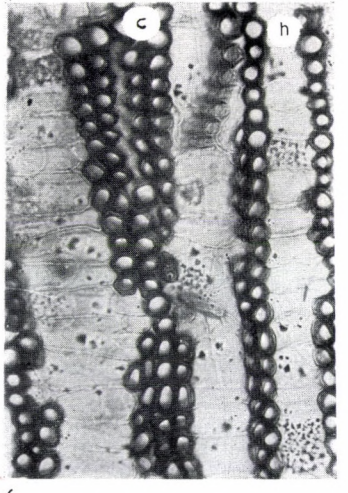

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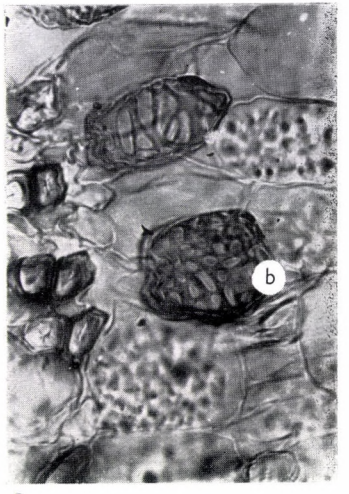

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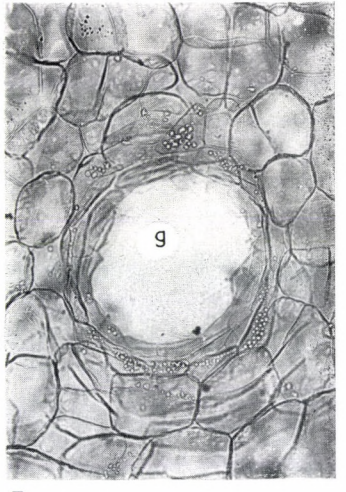

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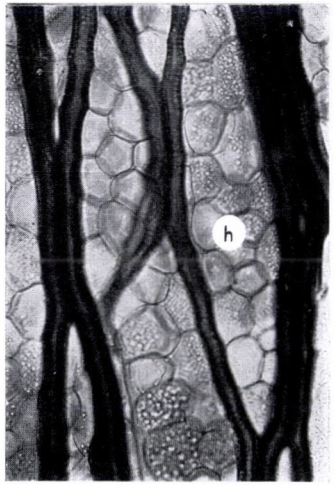
XLIX. *Macrozamia secunda* C. Moore



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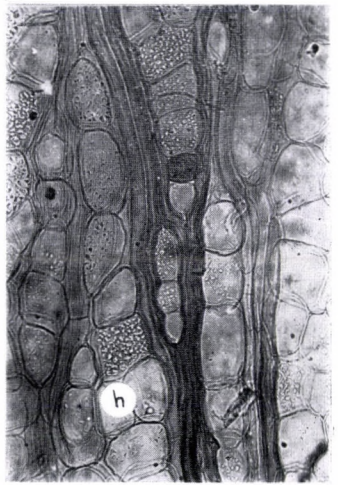

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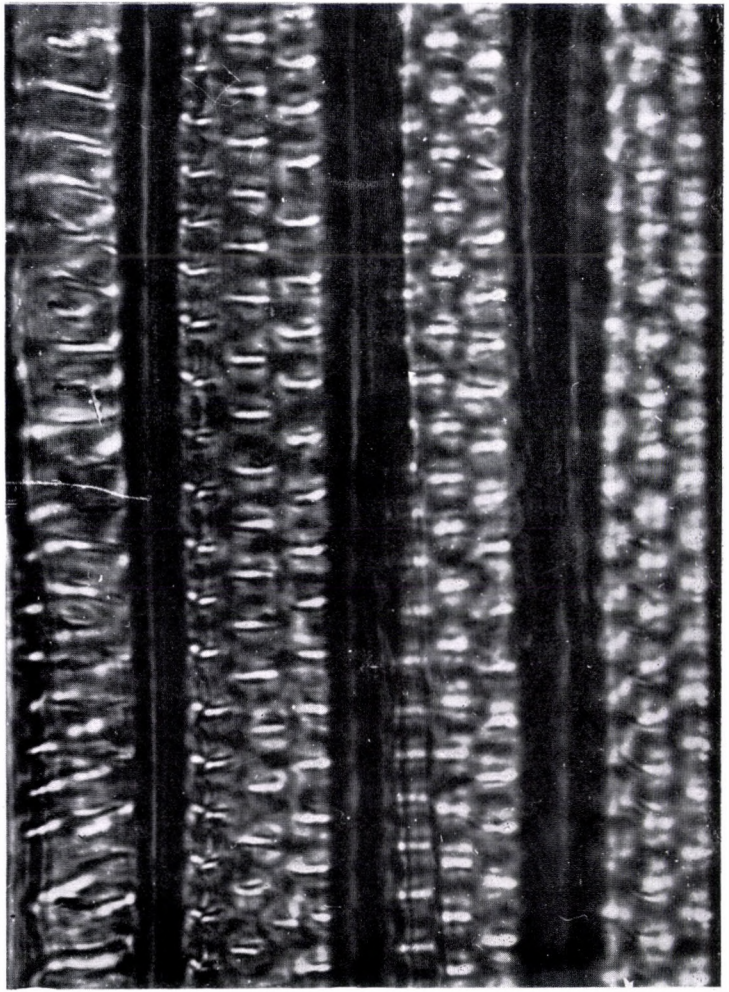

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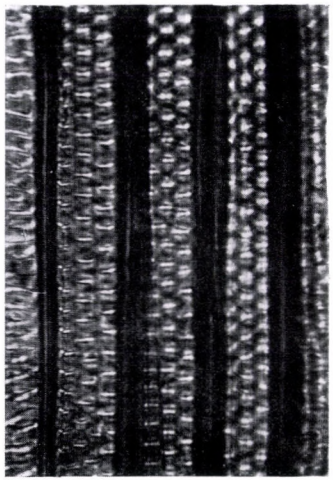

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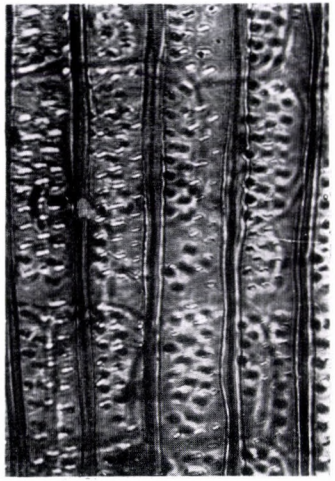

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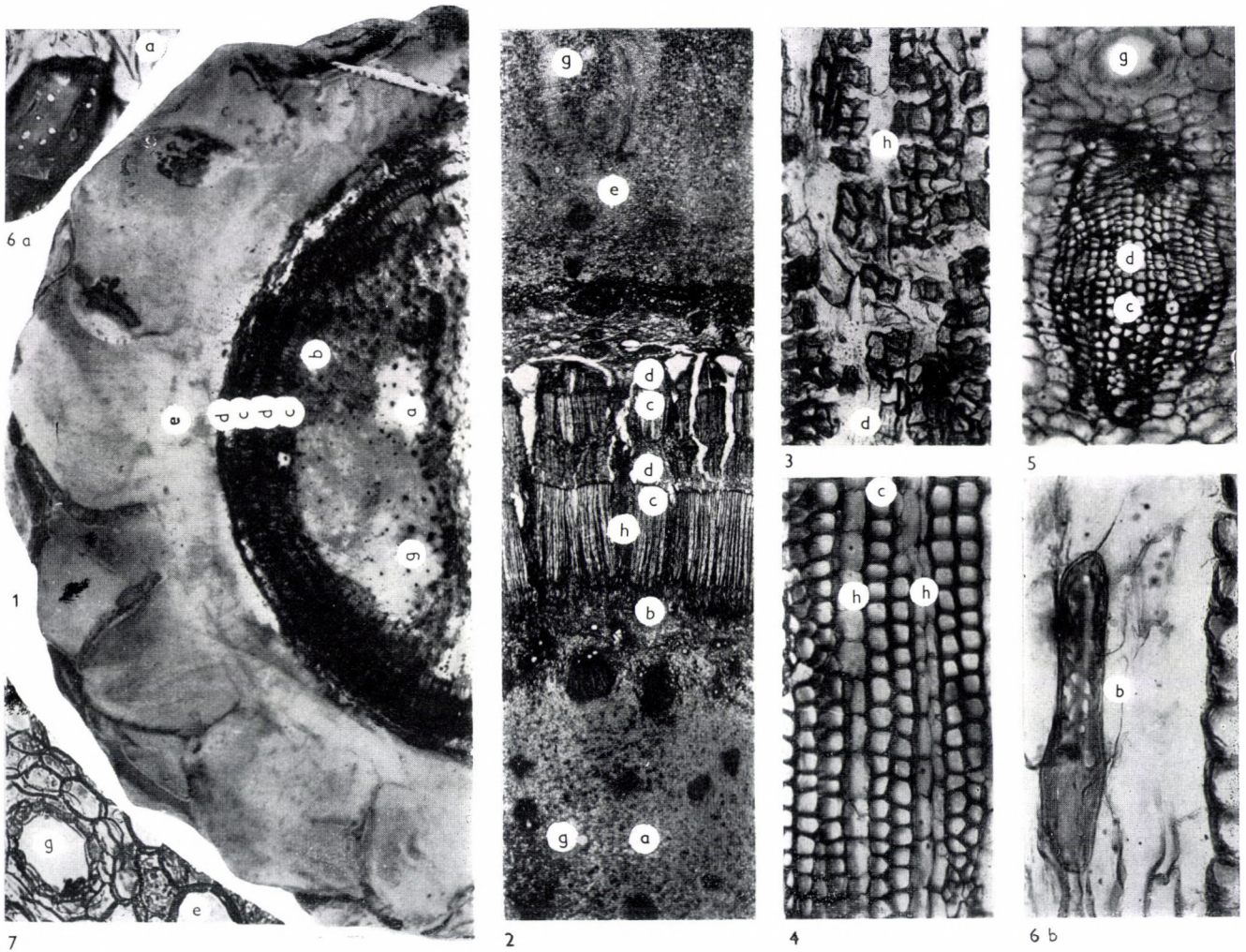
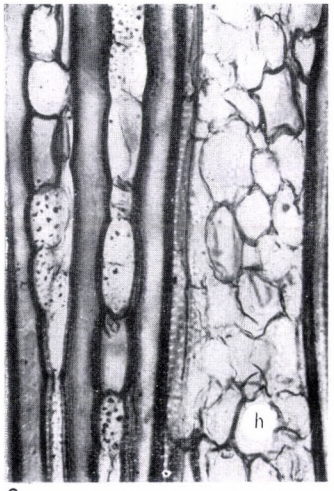
L. *Macrozamia secunda* C. Moore



LI. *Encephalartos altensteinii* Lehm.



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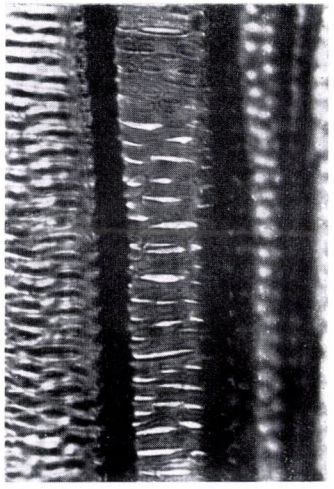

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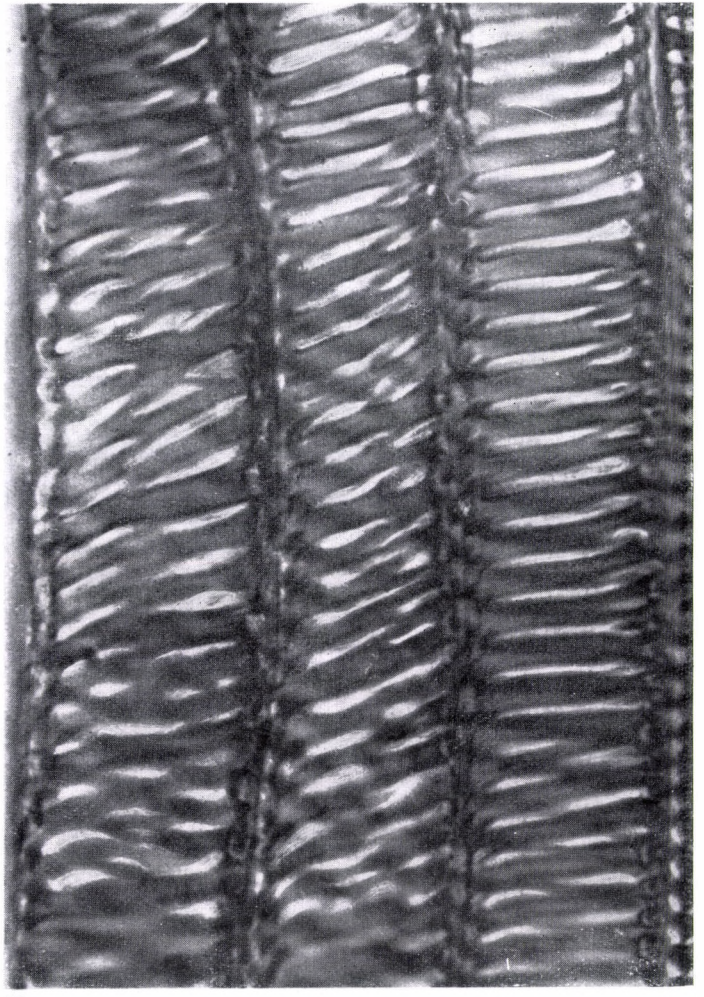

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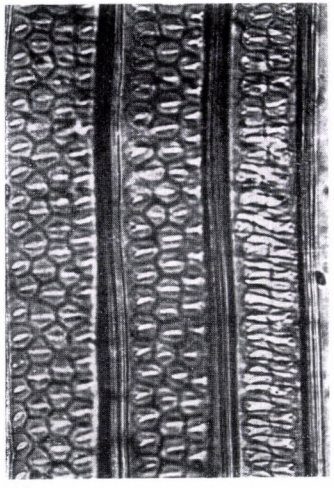

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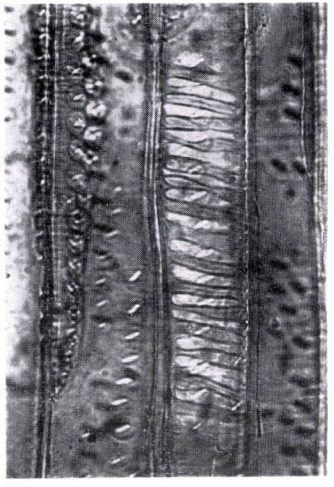

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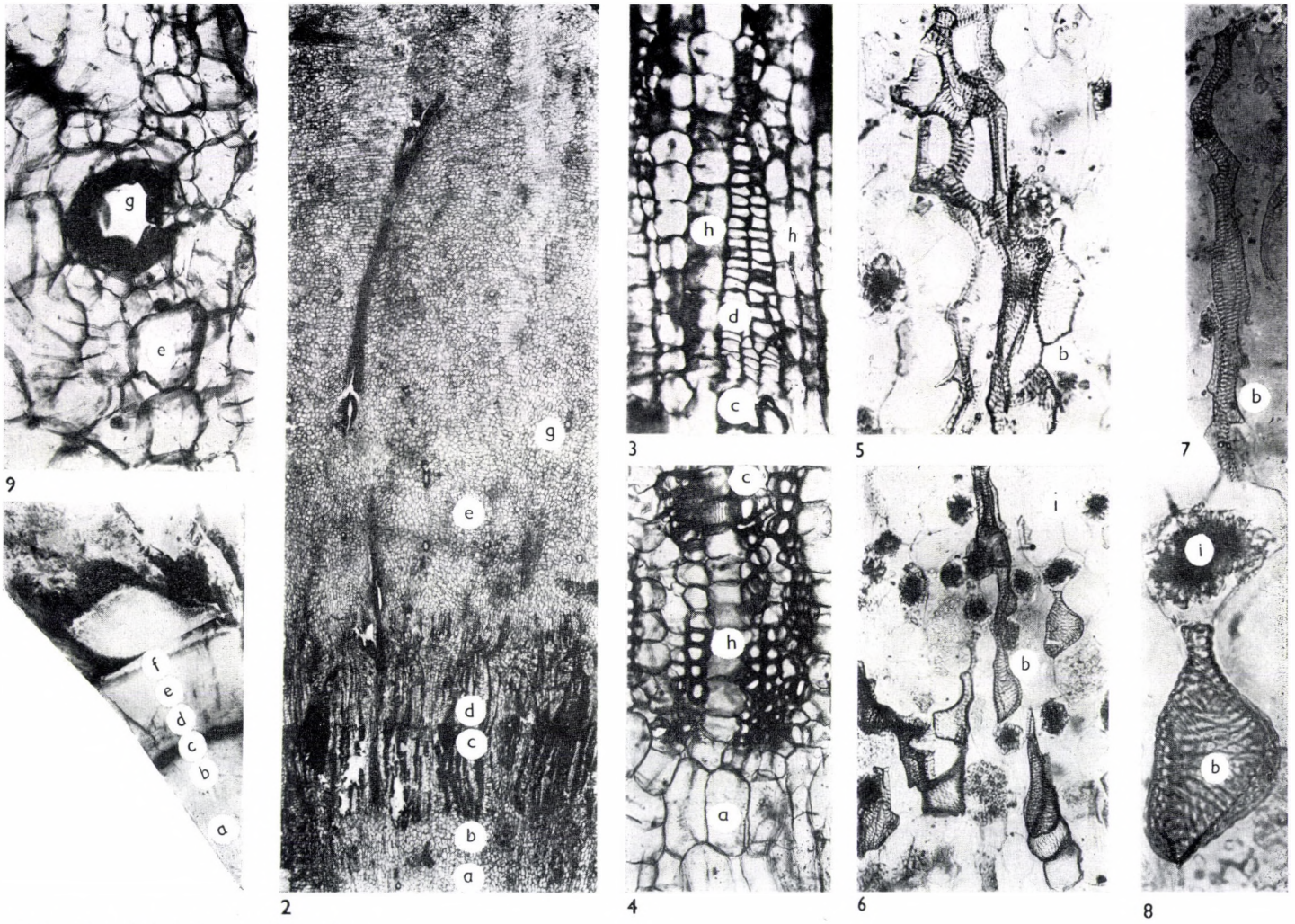
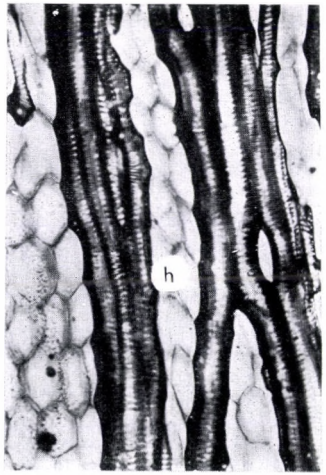
LII. *Encephalartos altensteinii* Lehm.



LIII. *Encephalartos barteri* Carruthers



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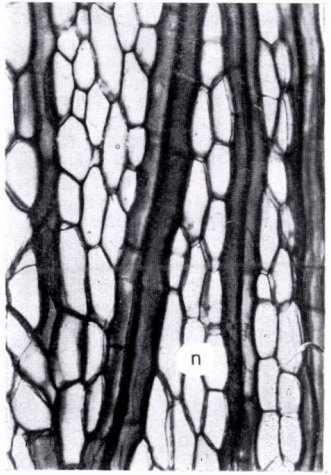

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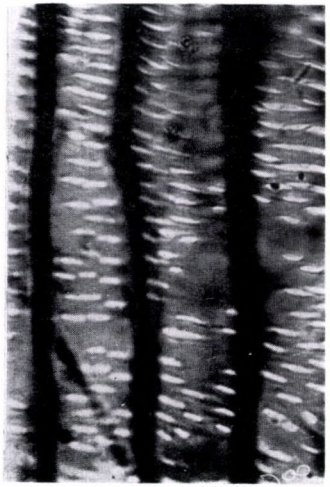

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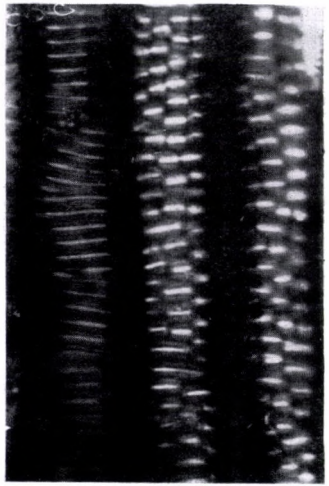

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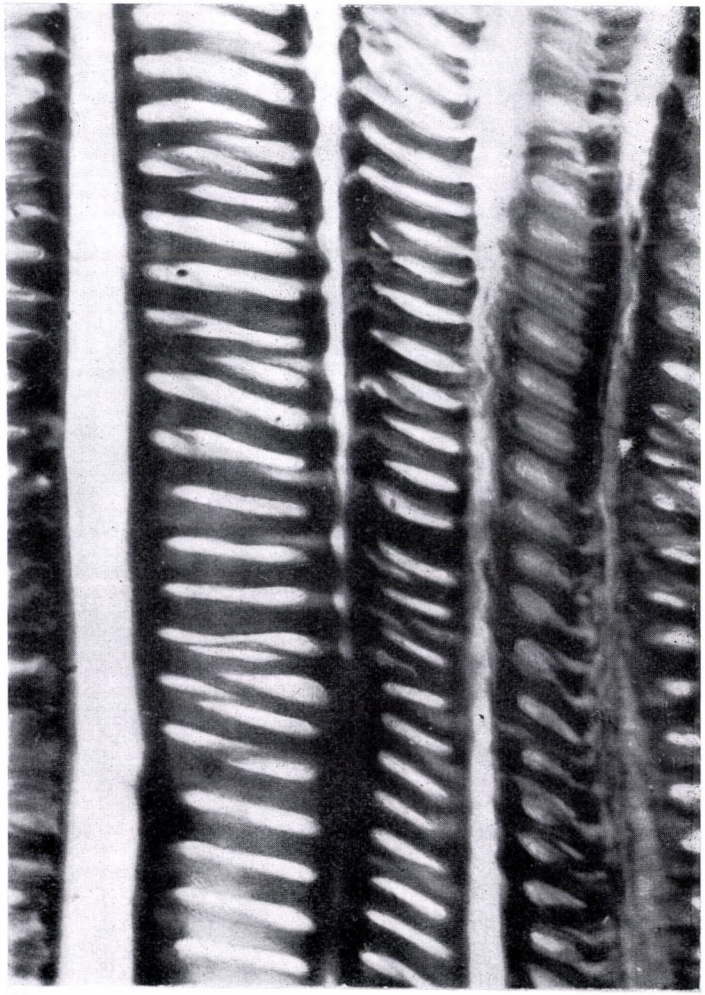

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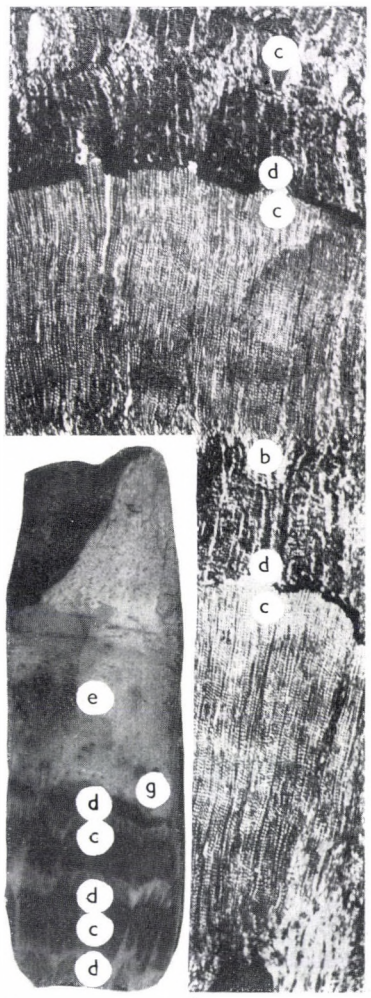
LIV. *Encephalartos barteri* Carruthers



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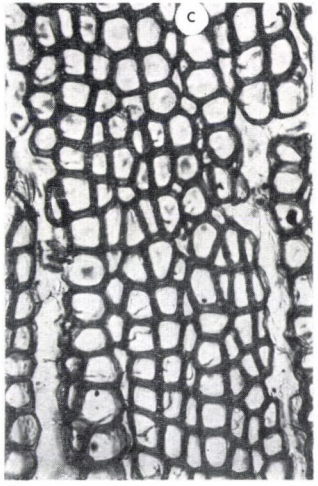

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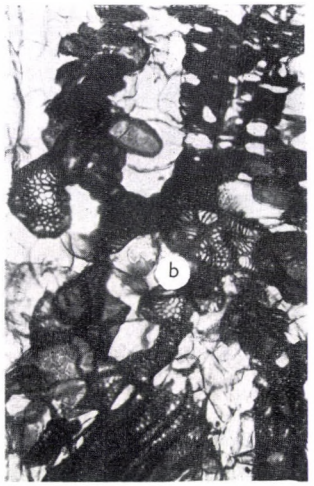

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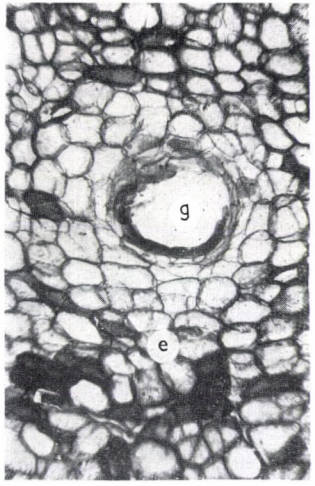

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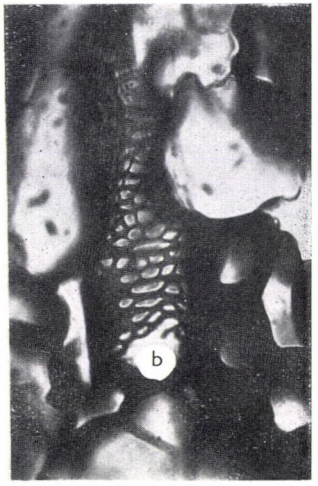

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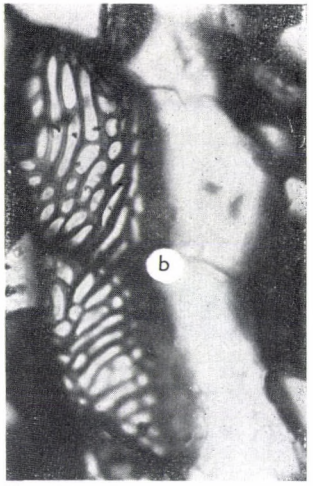

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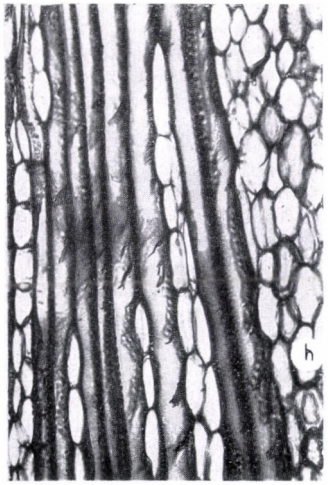
LV. *Encephalartos gratus* Prain



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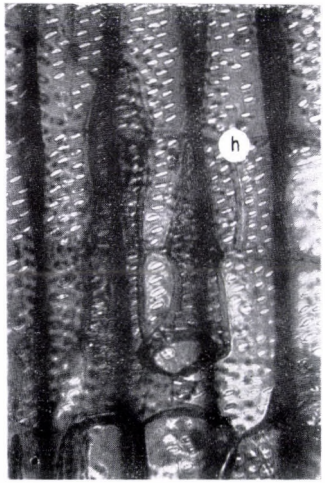

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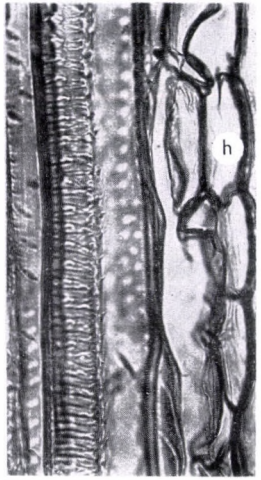

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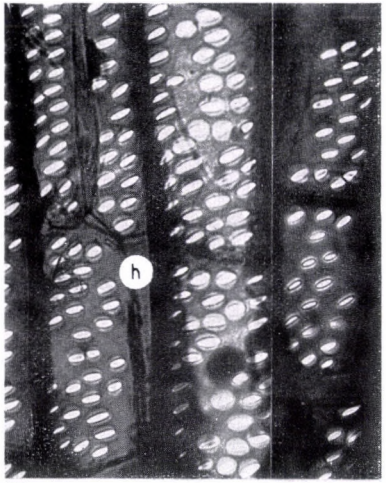

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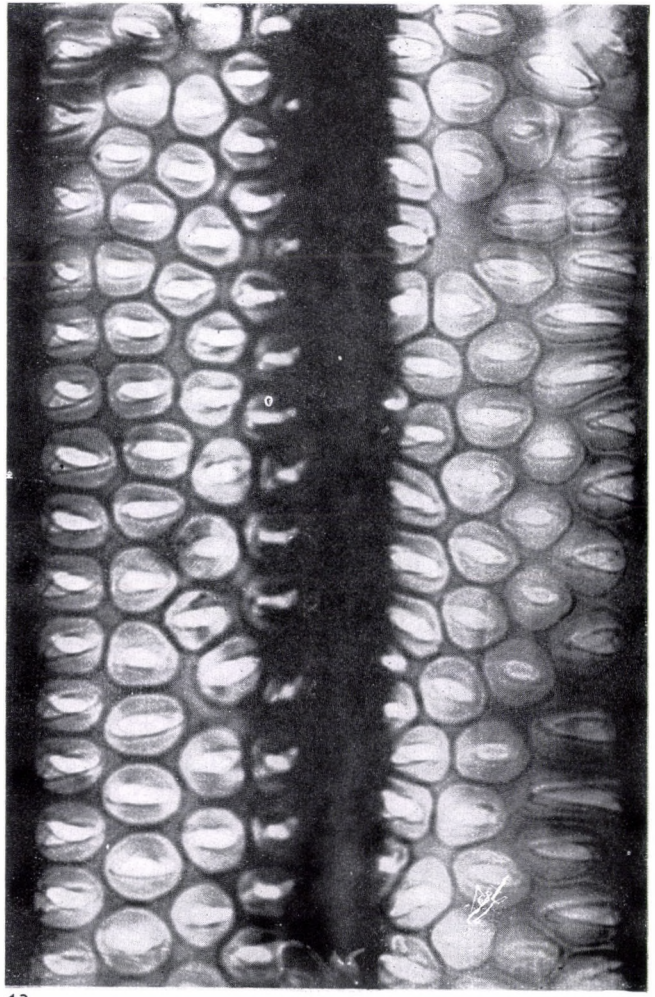

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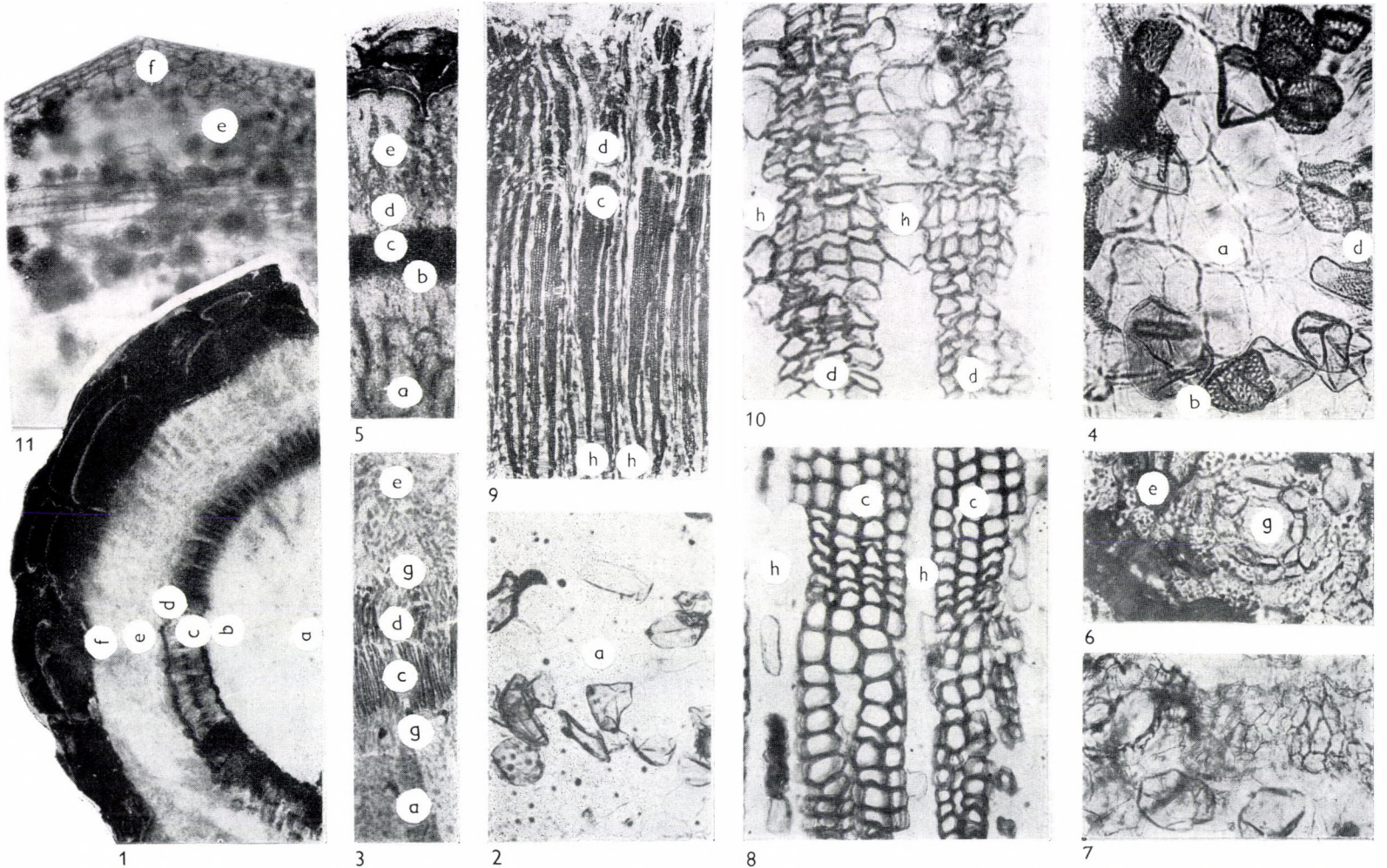
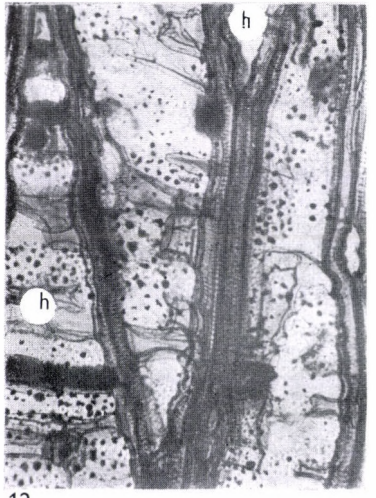
LVI. *Encephalartos gratus* Prain



LVII. *Encephalartos inopinus* Dyer



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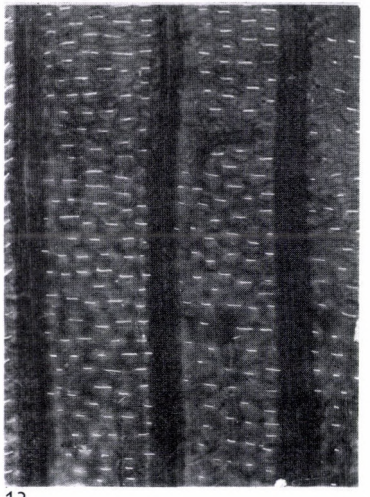

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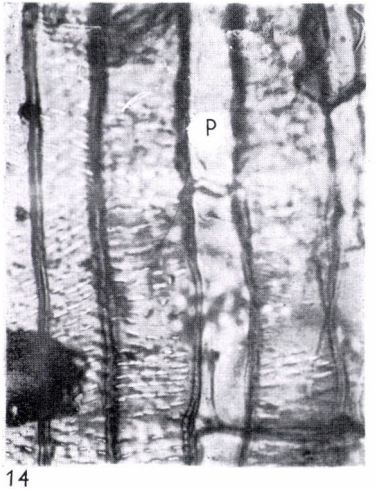

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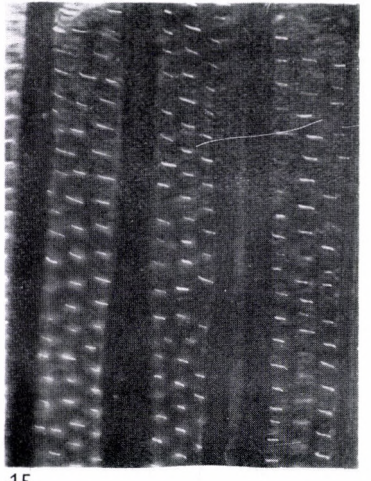

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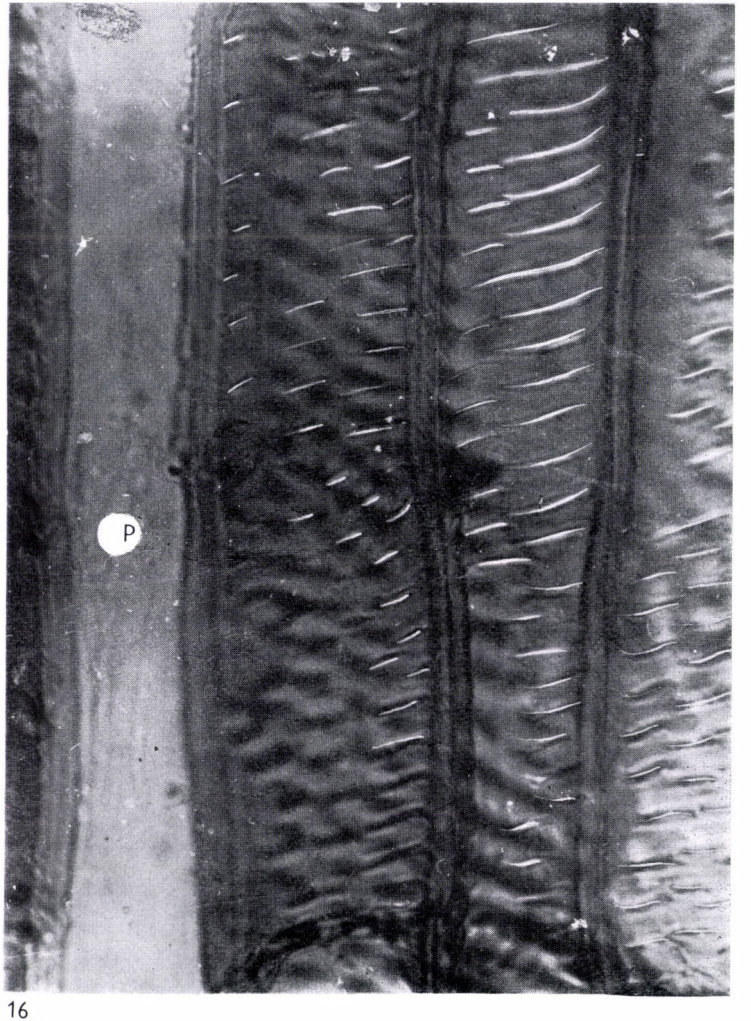

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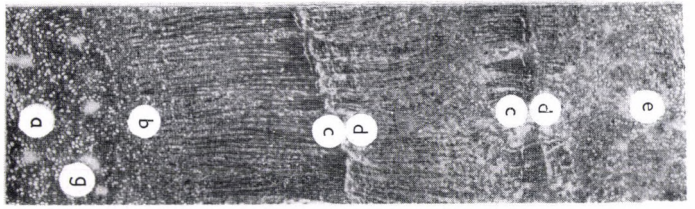
LVIII. *Encephalartos inopinus* Dyer



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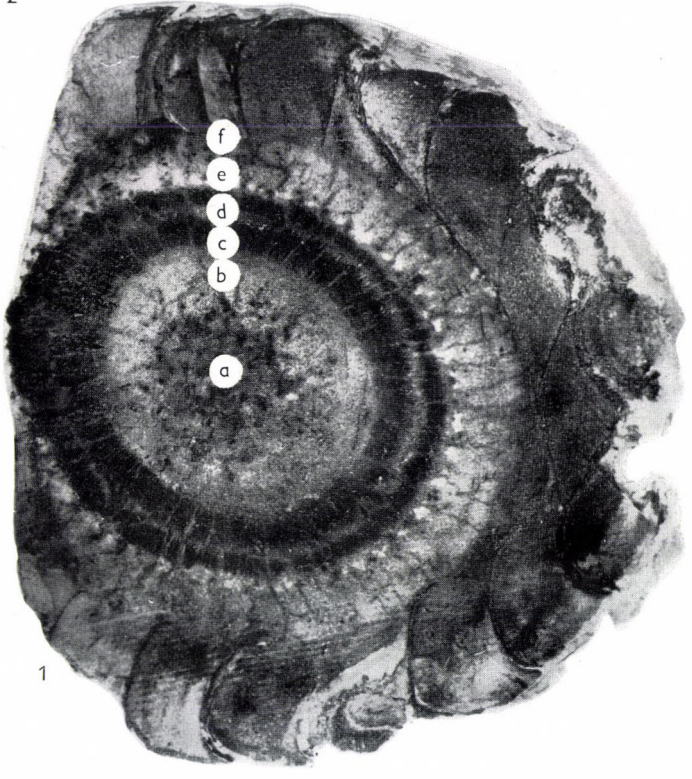

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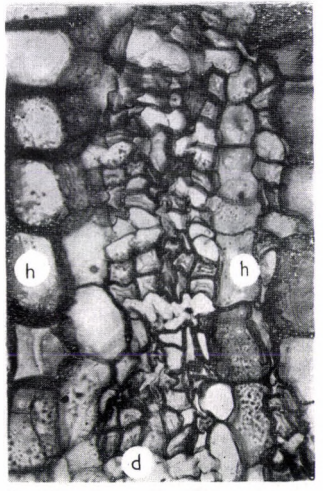

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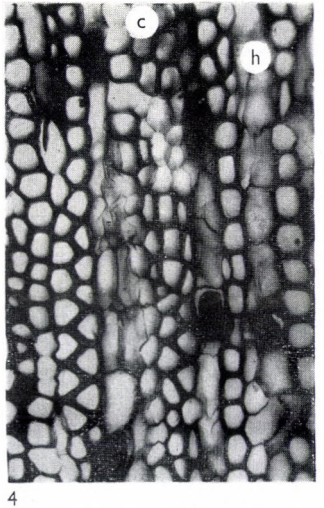

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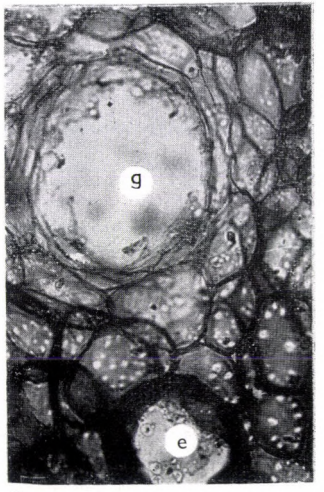

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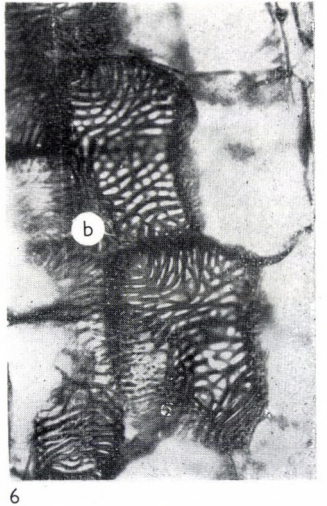

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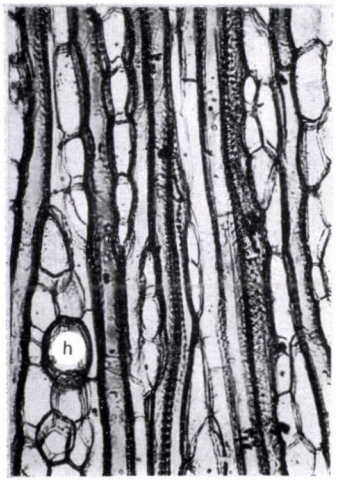
LIX. *Encephalartos lehmannii* Ecklon



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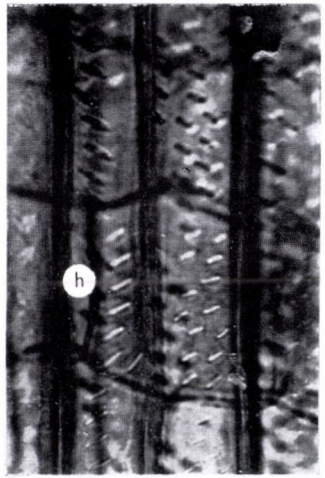

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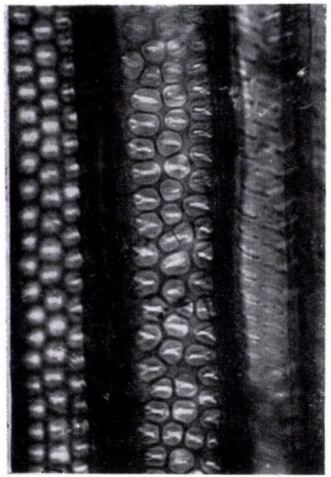

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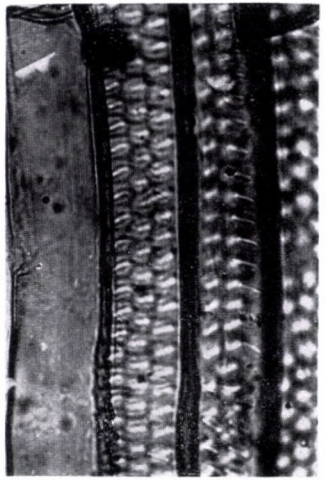

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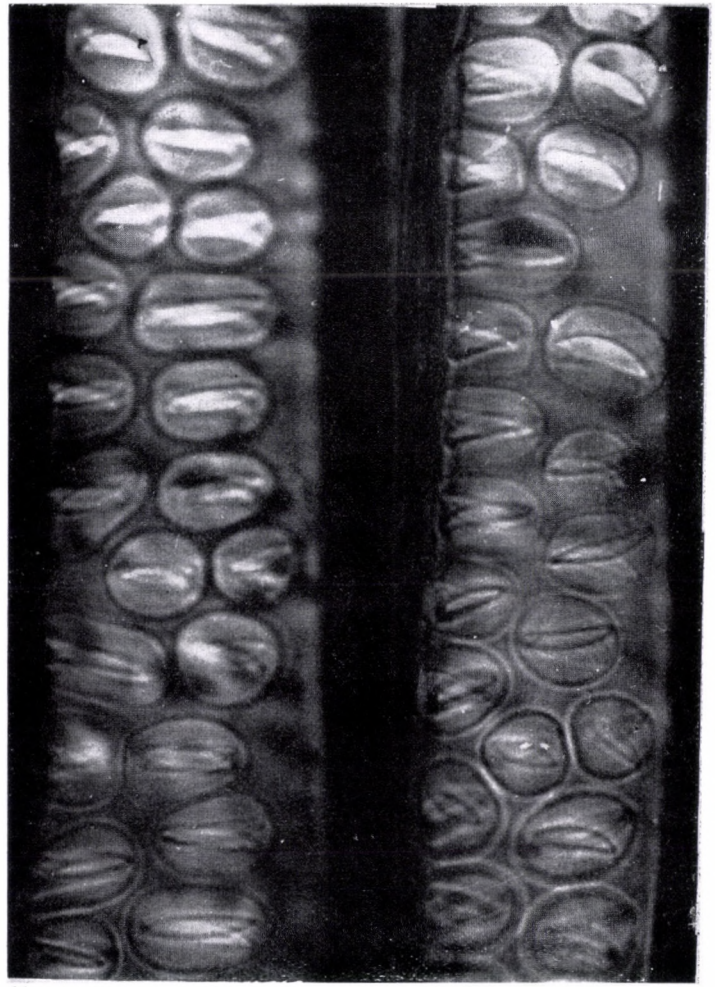

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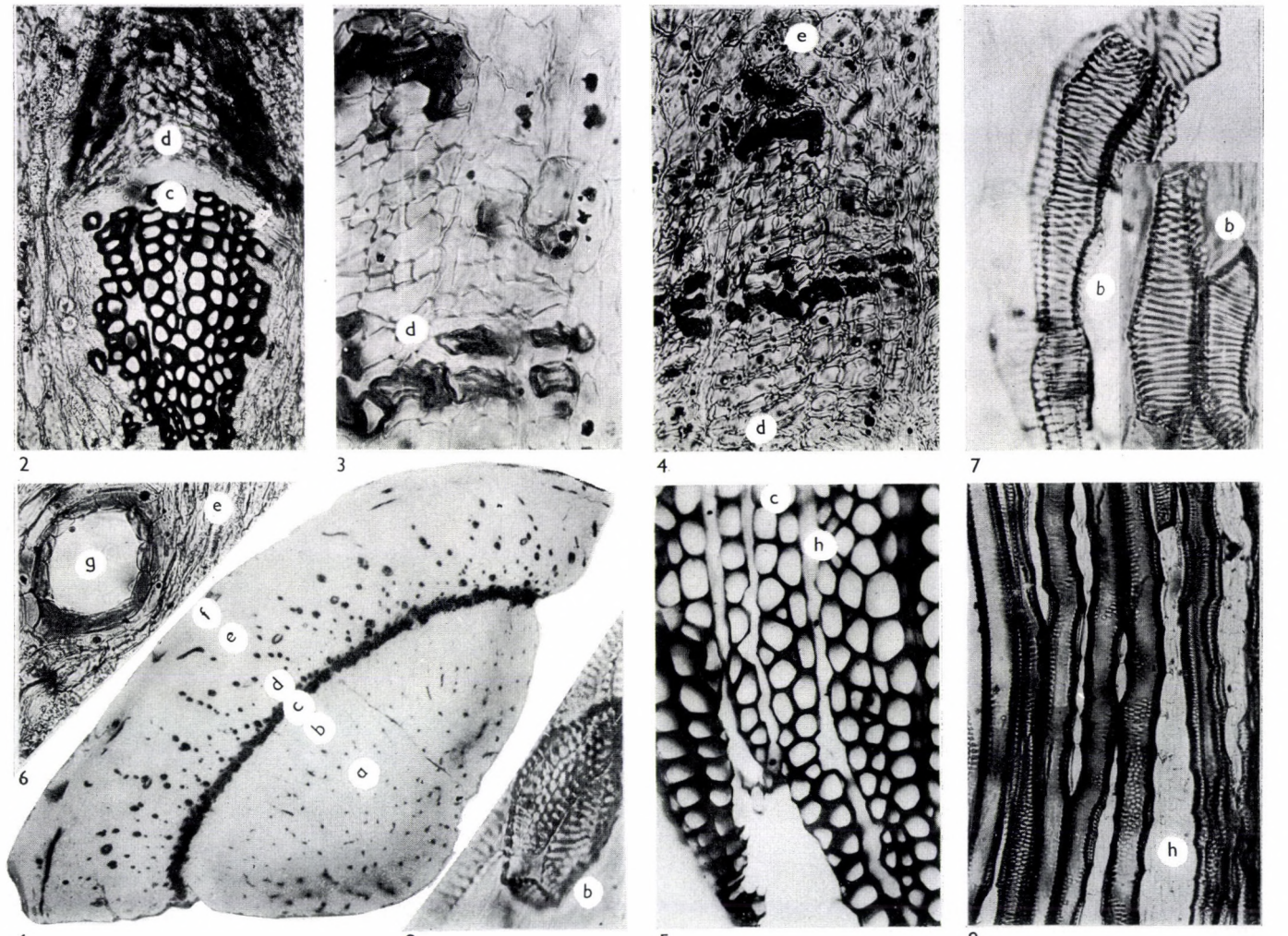
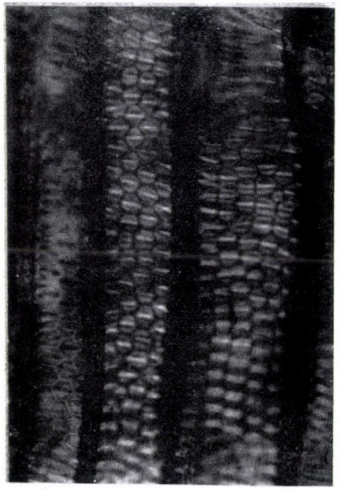
LX. *Encephalartos lehmannii* Ecklon



LXI. *Encephalartos septentrionalis* Schweinf.



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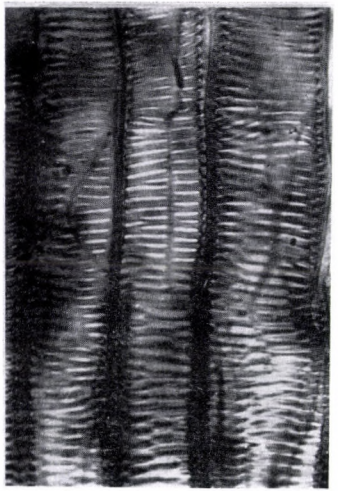

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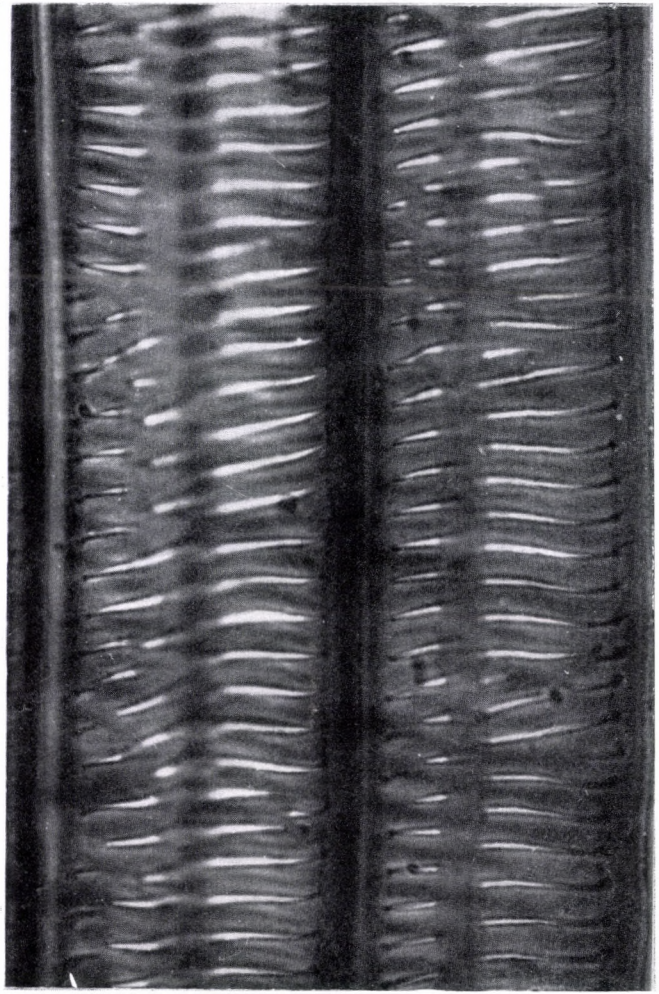

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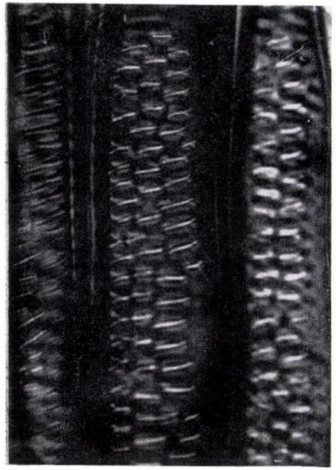

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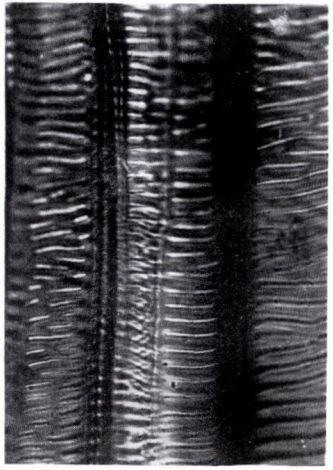

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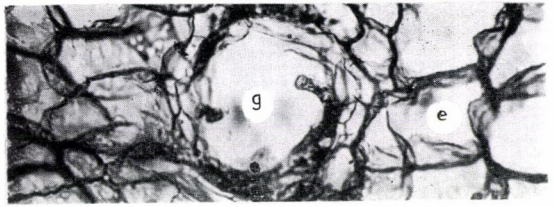
LXII. *Encephalartos septentrionalis* Schweinf.



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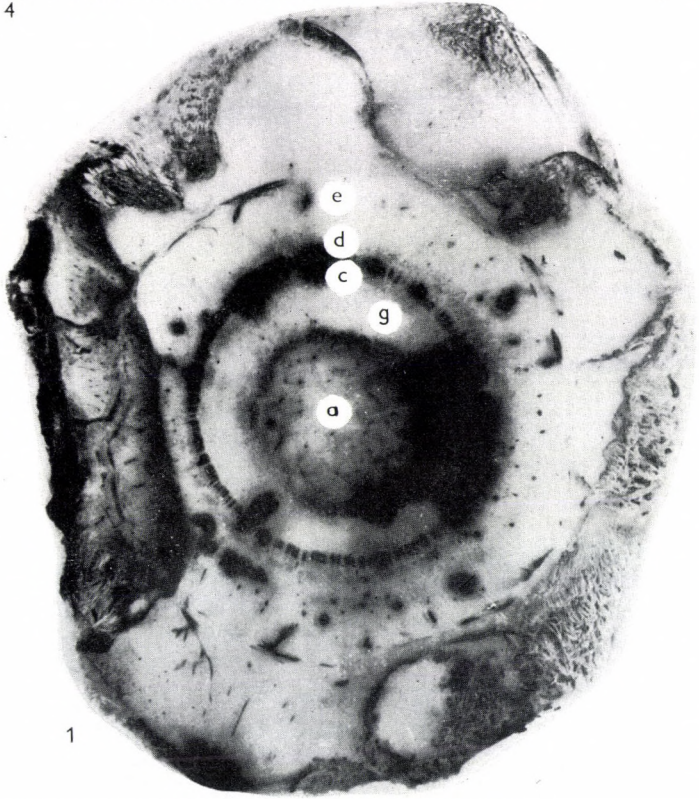

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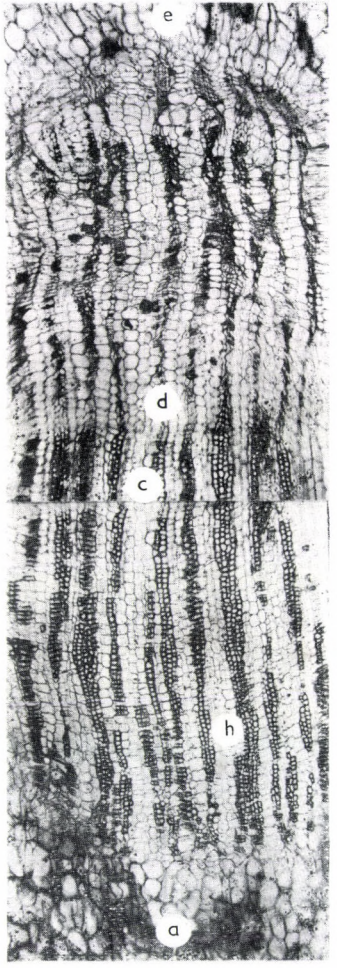

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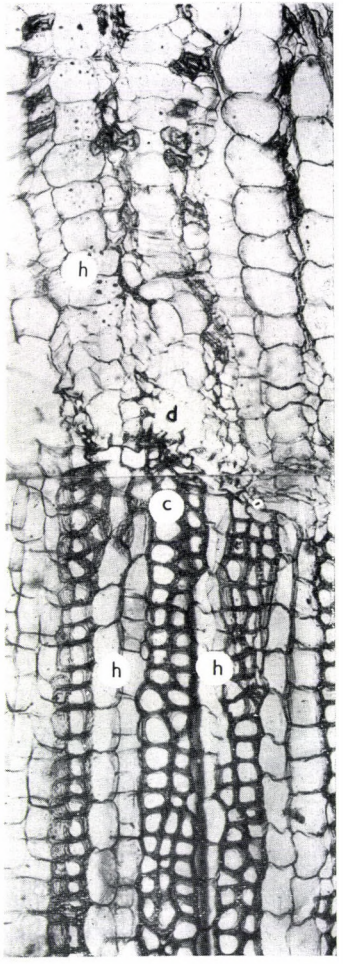

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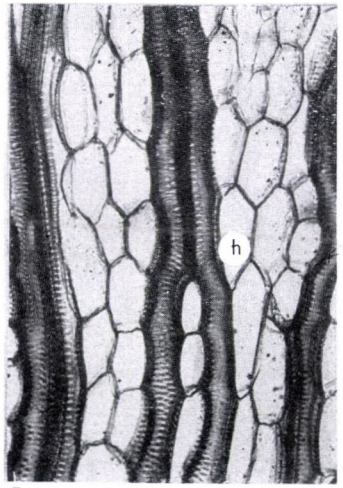
LXIII. *Encephalartos villosus* (Gaertn.) Lemaire



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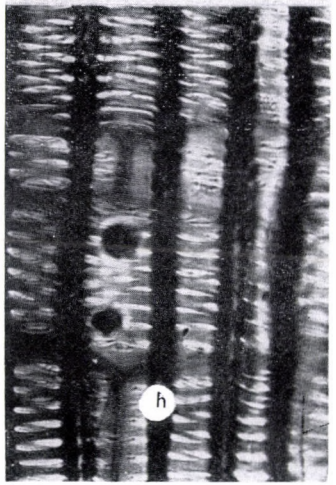

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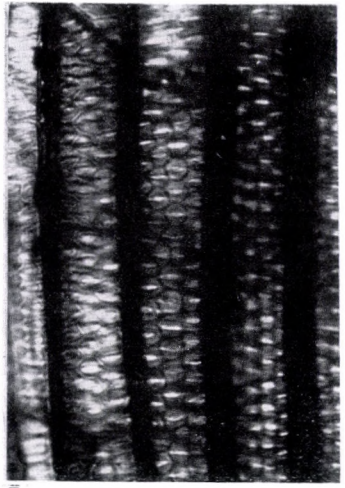

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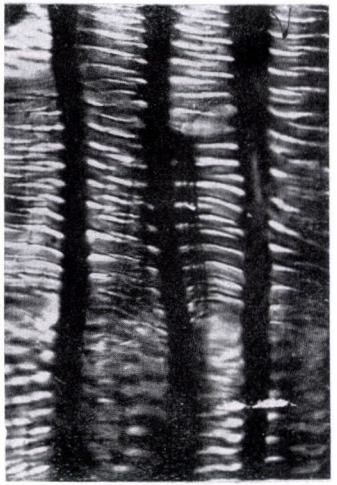

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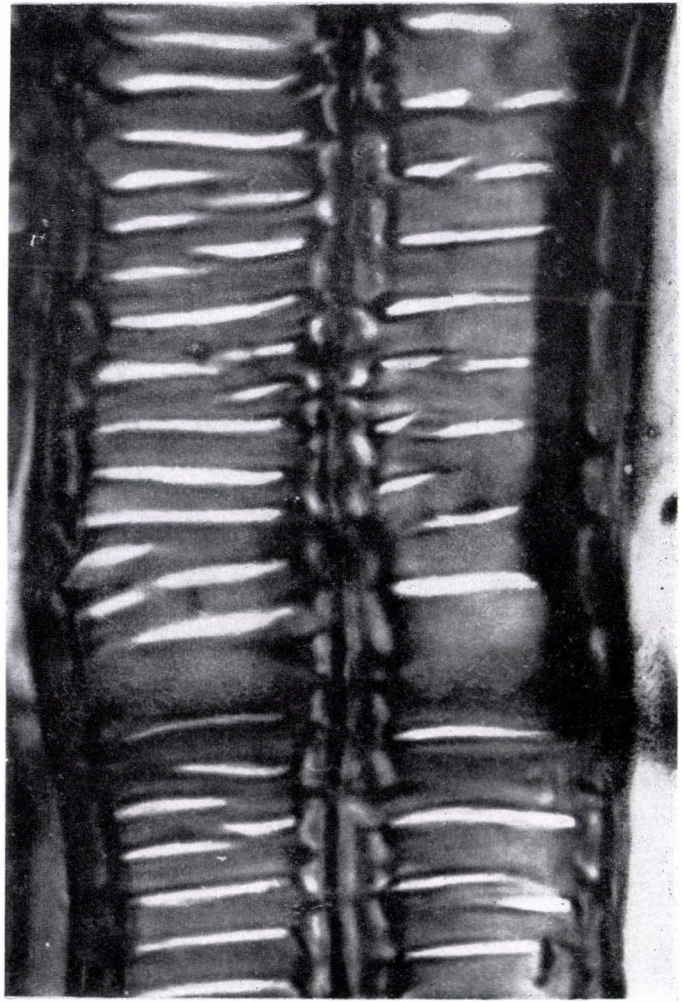

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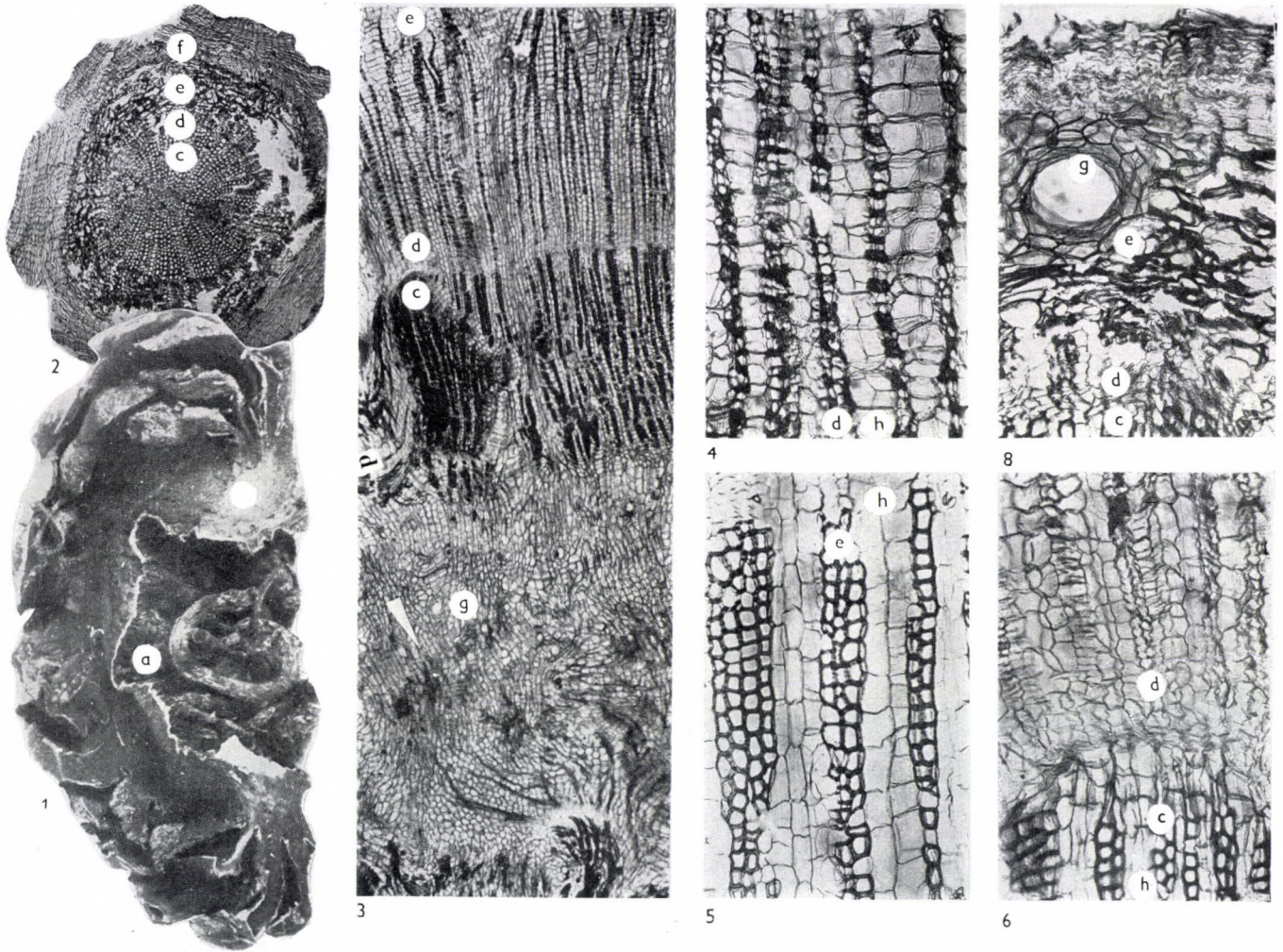
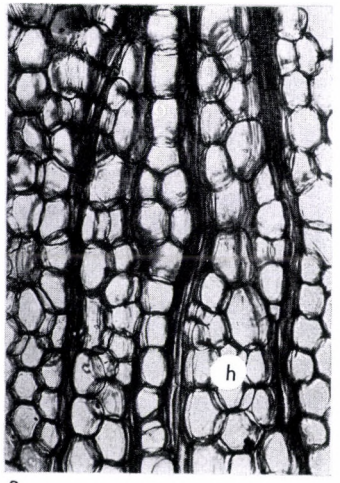
LXIV. *Encephalartos villosus* (Gaertn.) Lemaire



LXV. *Dioon edule* Lindl.



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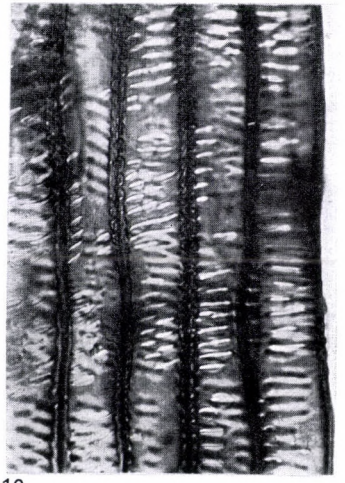

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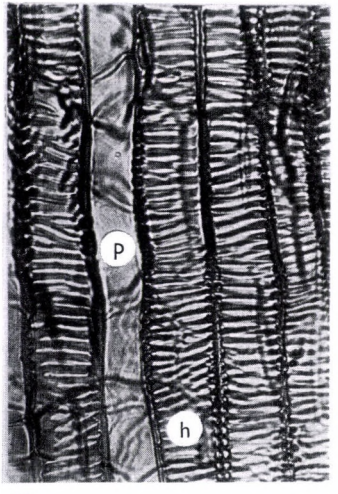

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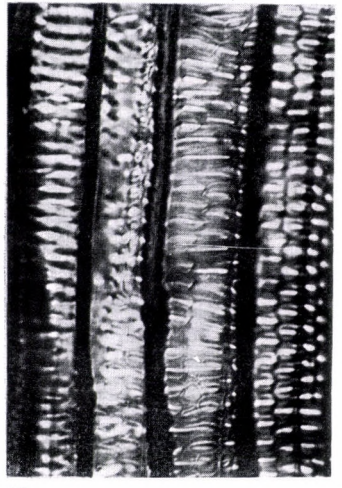

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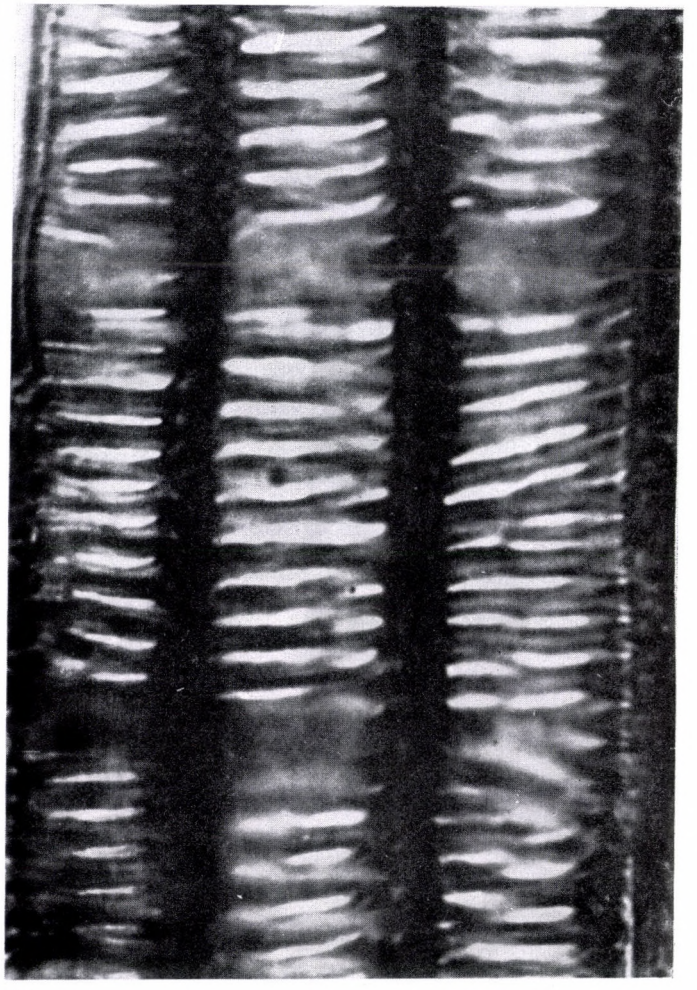

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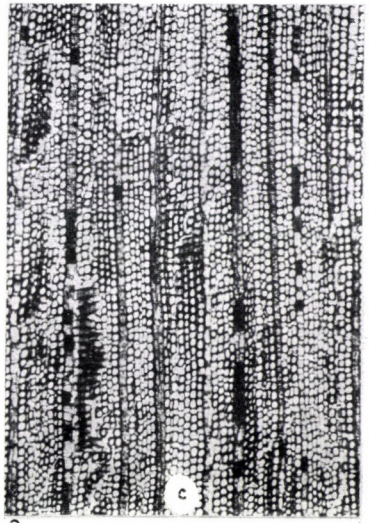
LXVI. *Dioon edule* Lindl.



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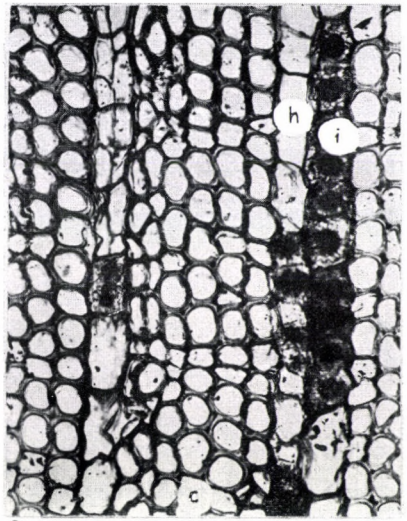

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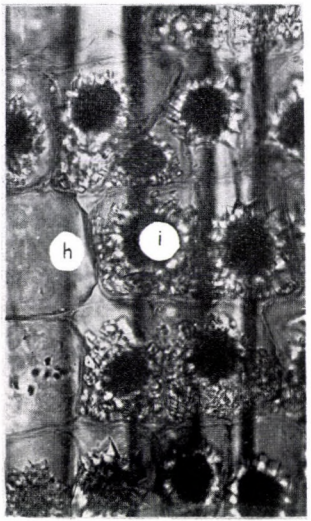

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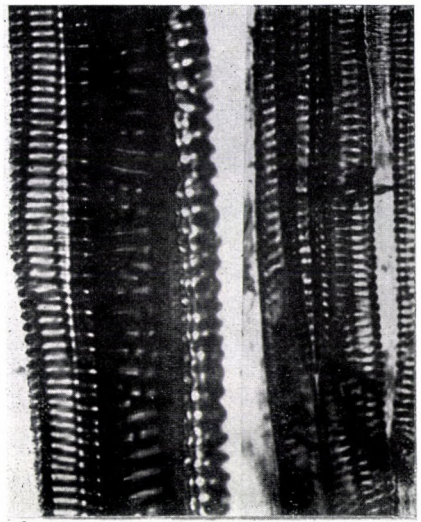

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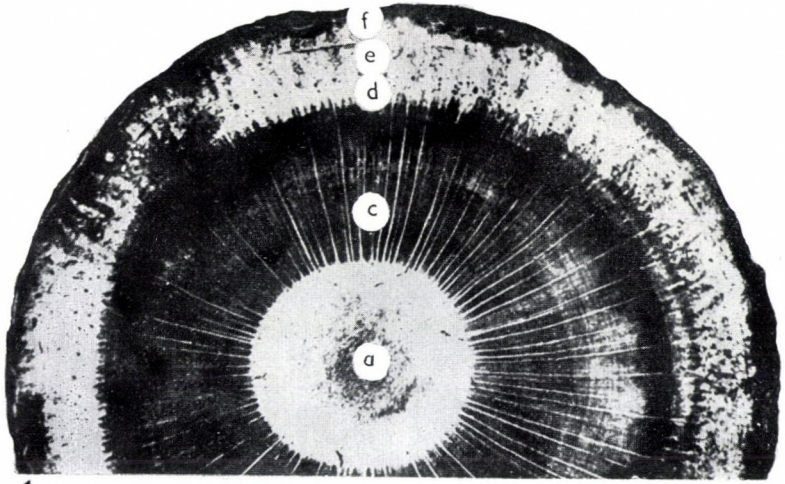

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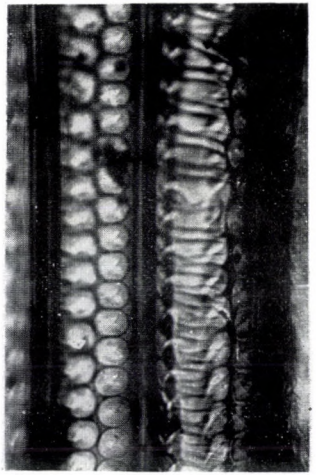

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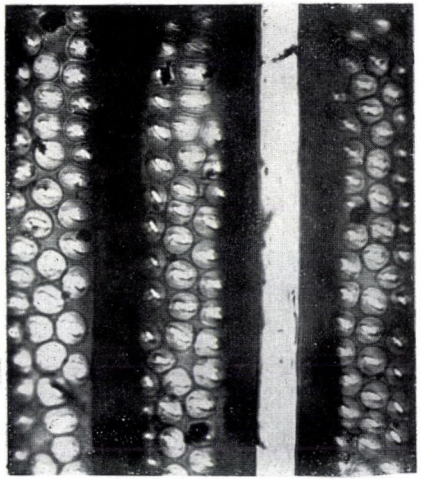

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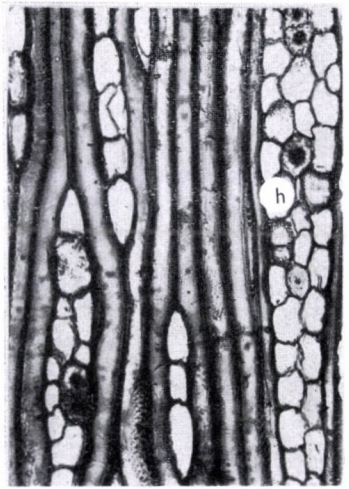
LXVII. *Dioon spinulosum* Dyer



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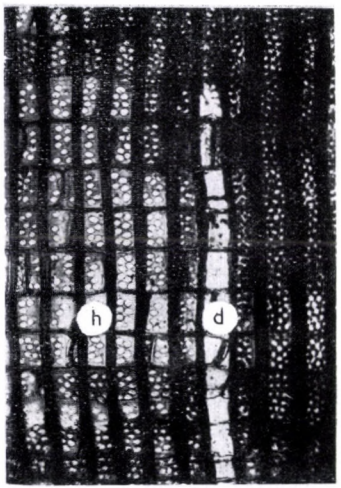

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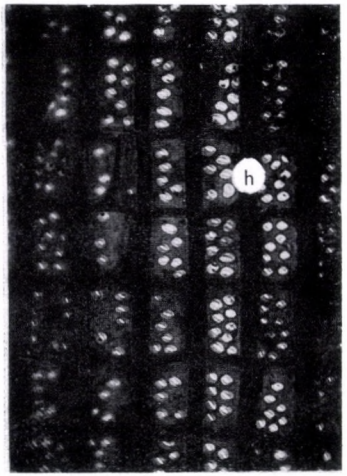

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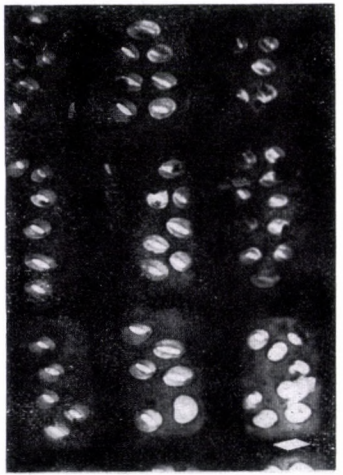

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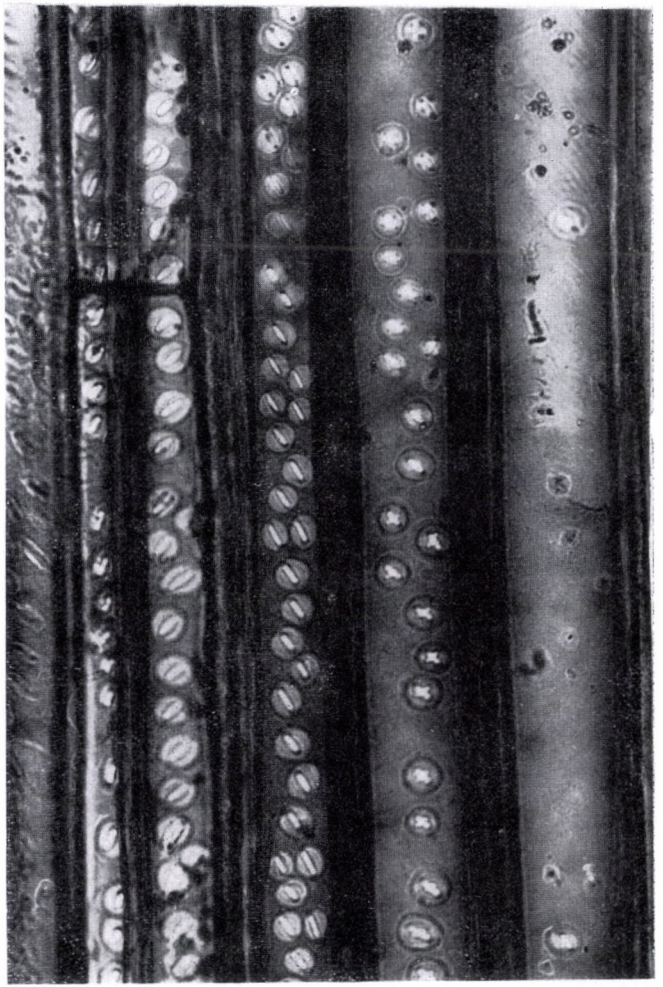

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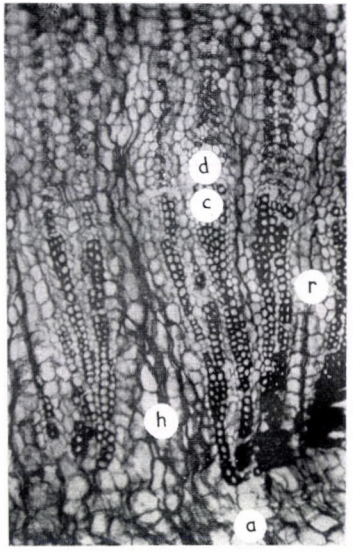
LXVIII. *Dioon spinulosum* Dyer



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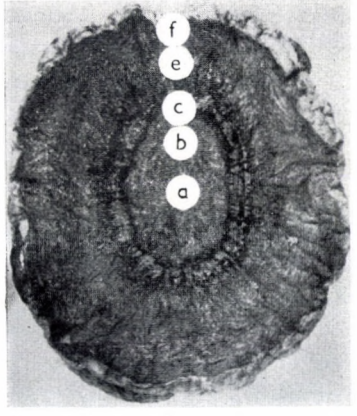

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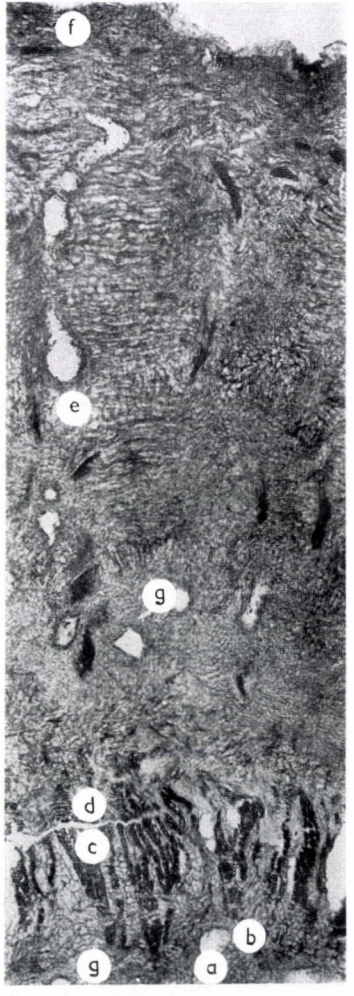

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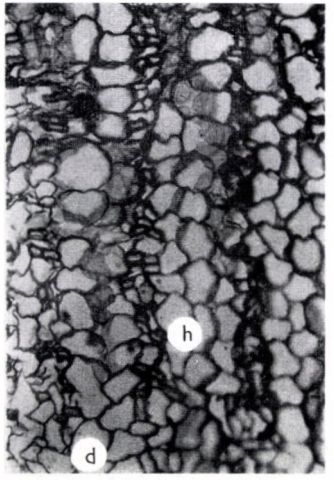

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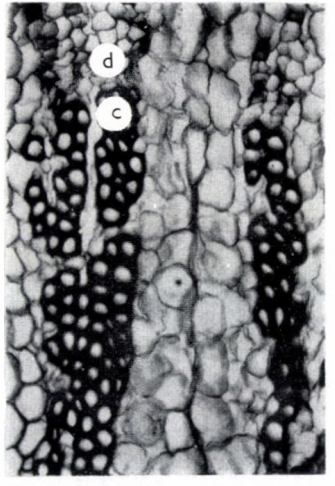

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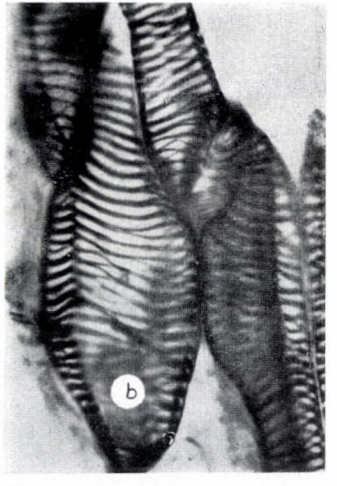

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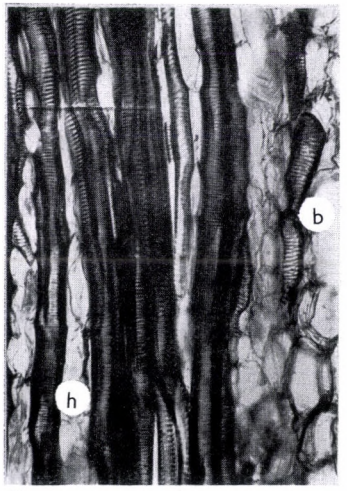
LXIX. *Microcycas calocoma* (Miq.) A.DC.



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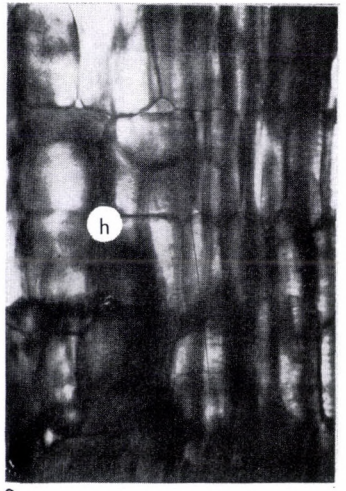

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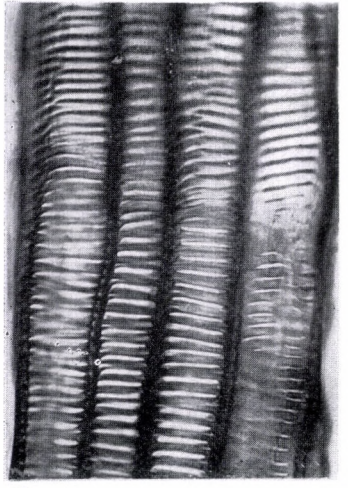

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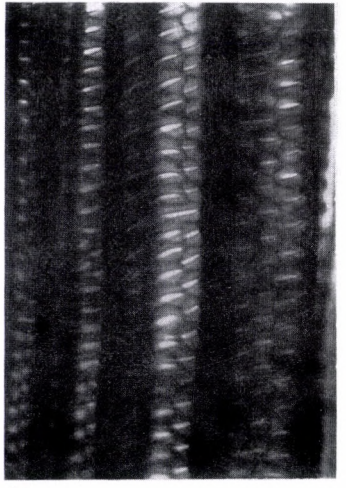

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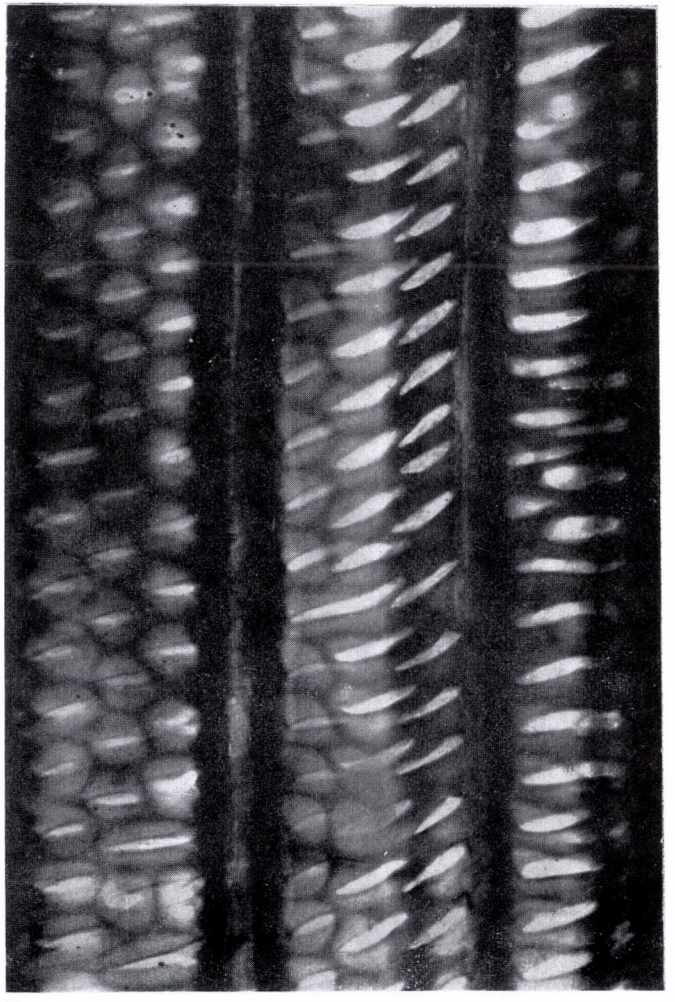

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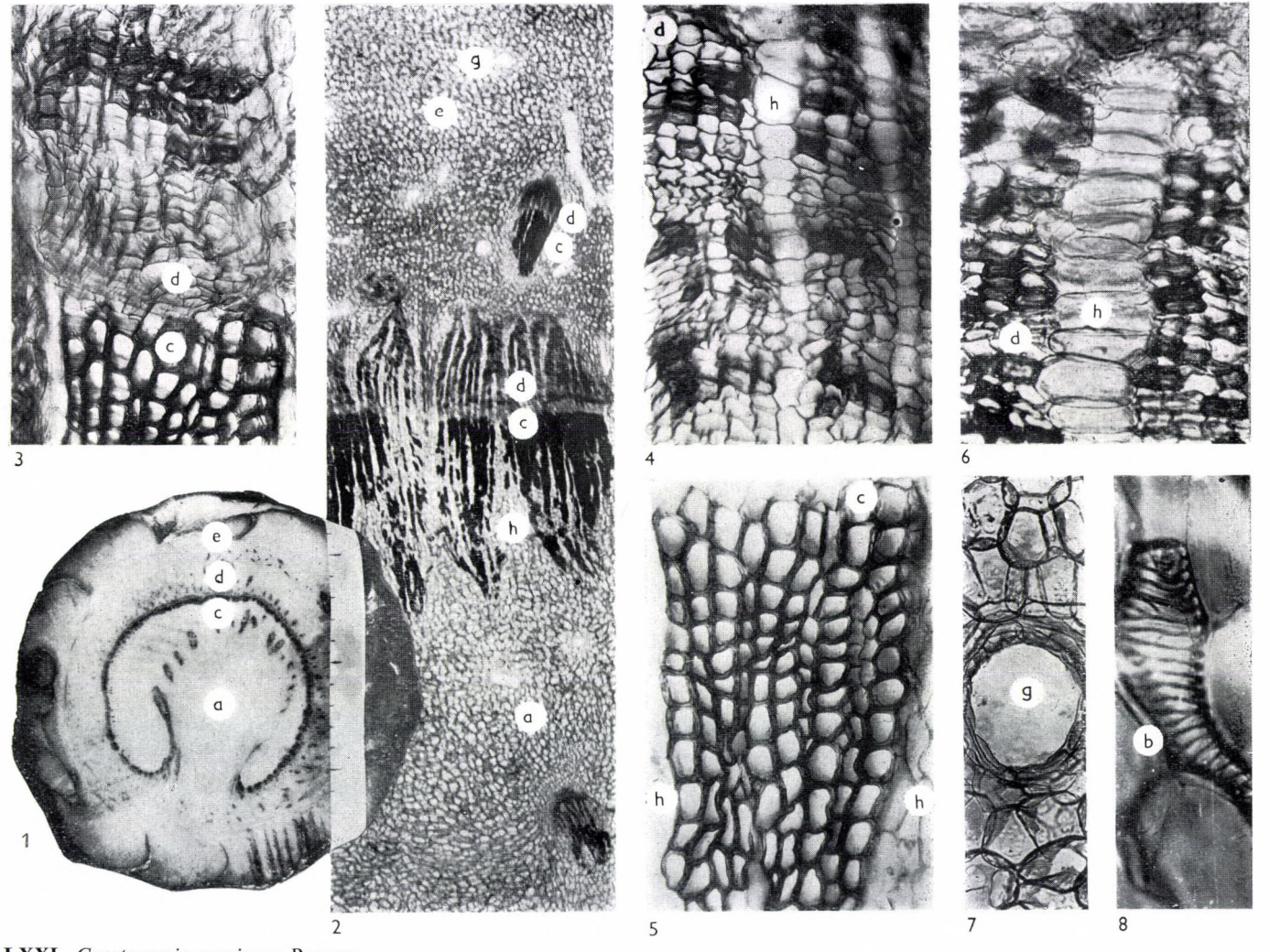
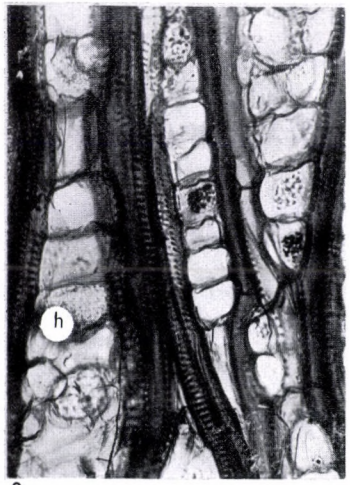
LXX. *Microcycas calocoma* (Miq.) A.DC.



LXXI. *Ceratozamia mexicana* Brongn.



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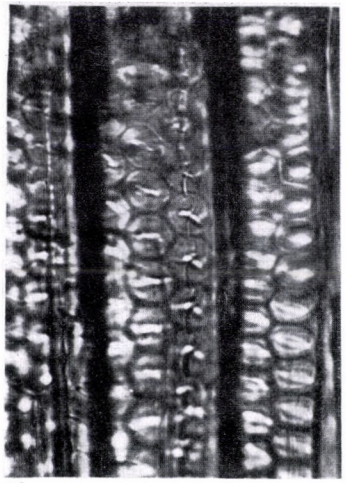

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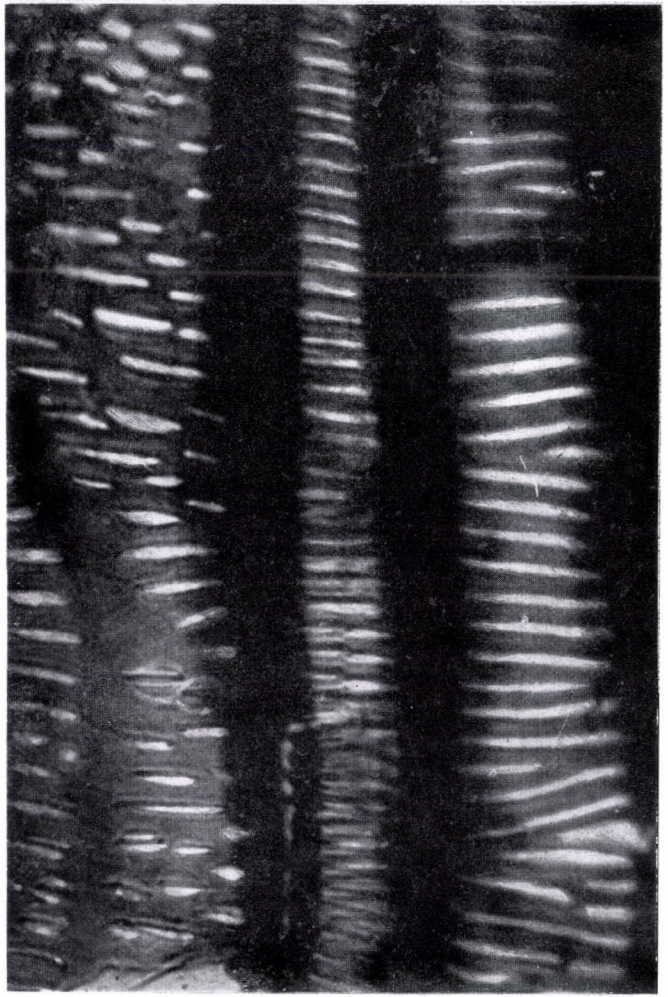

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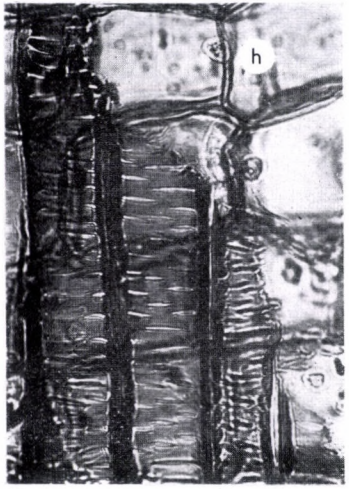

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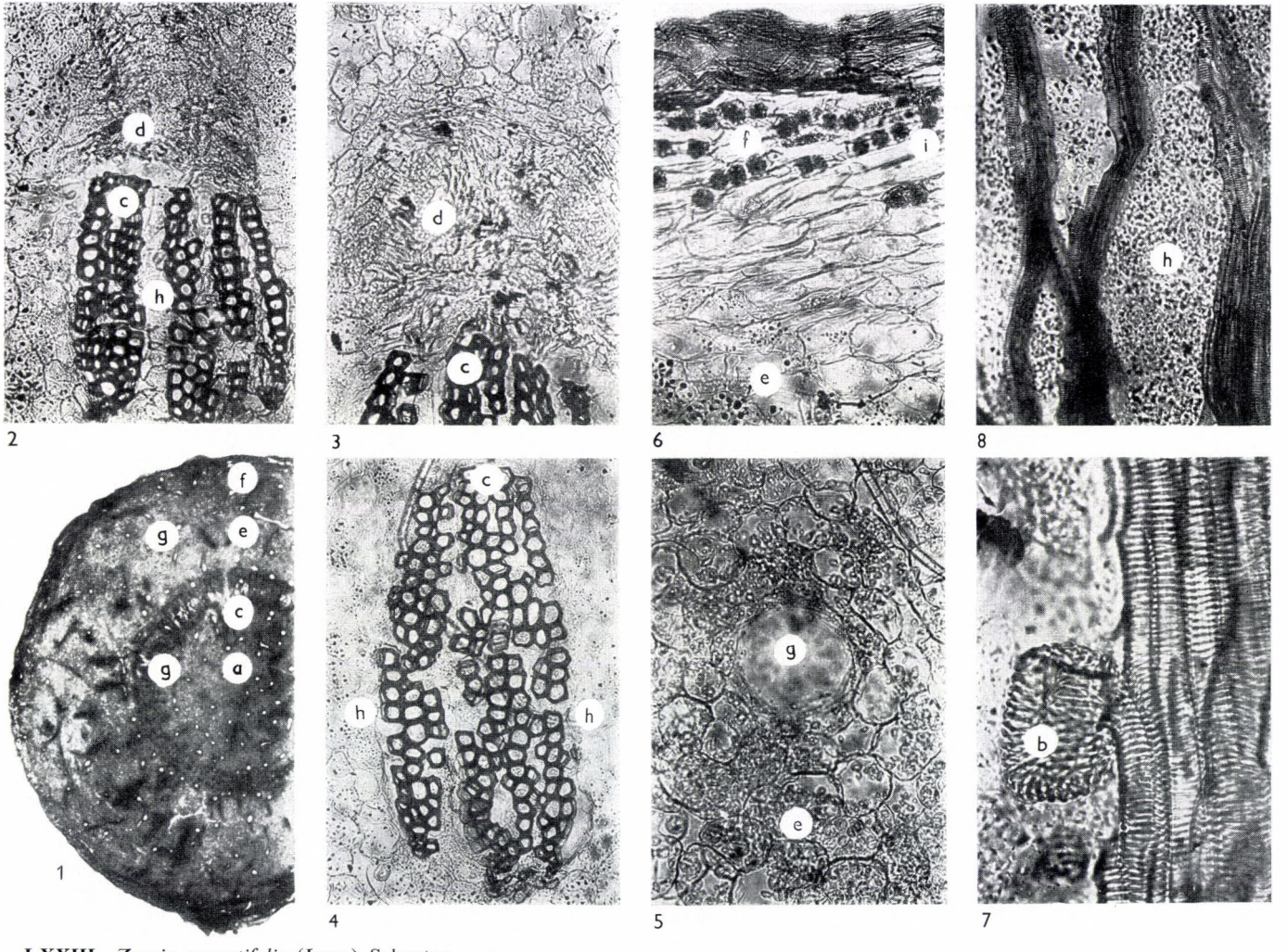
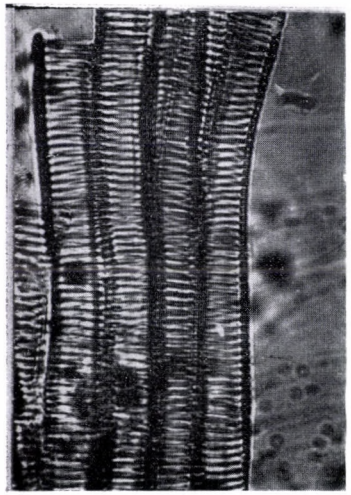
LXXII. *Ceratozamia mexicana* Brongn.



LXXIII. *Zamia angustifolia* (Jacq.) Schuster



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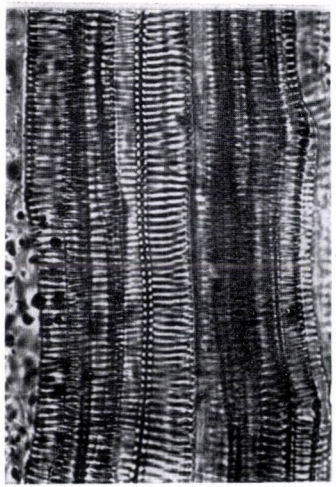

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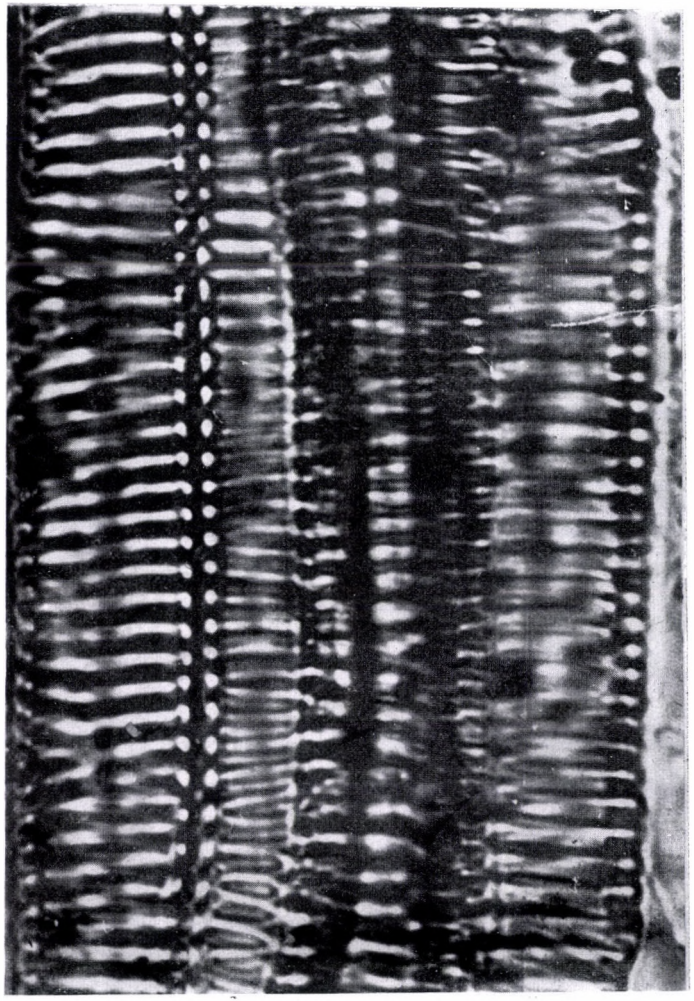

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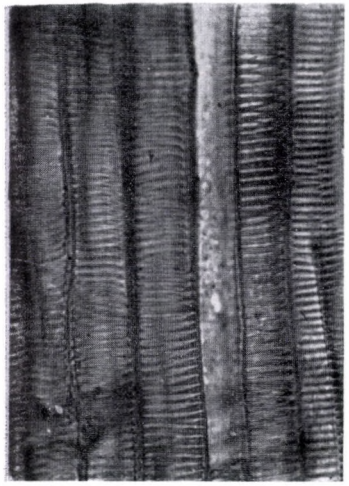

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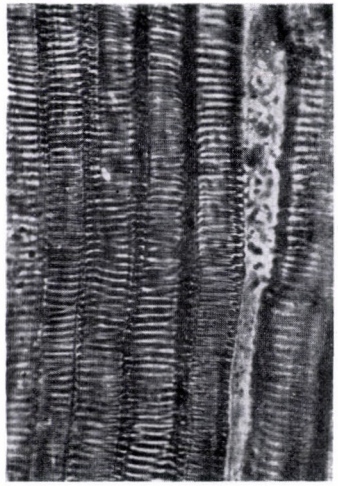

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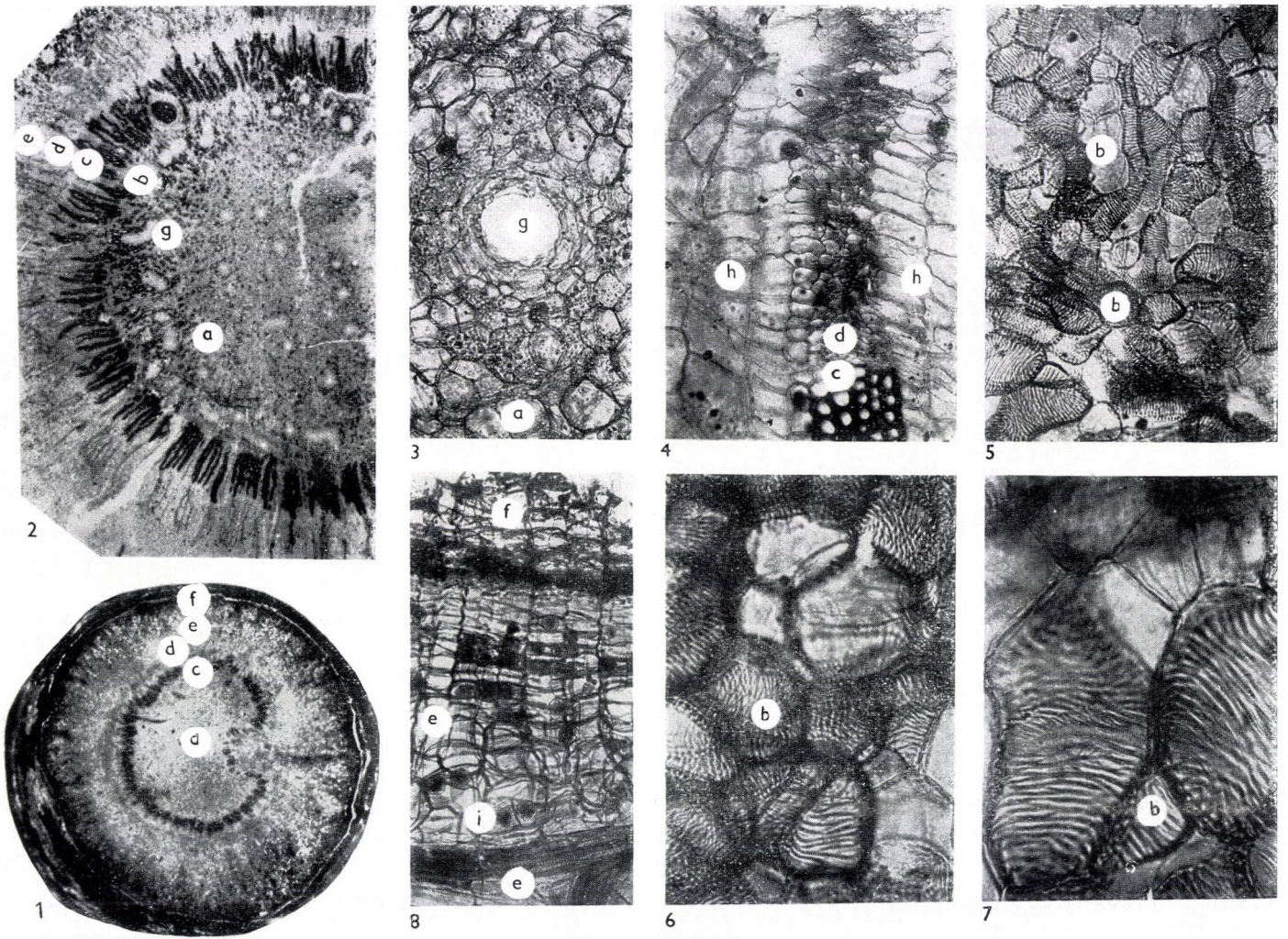
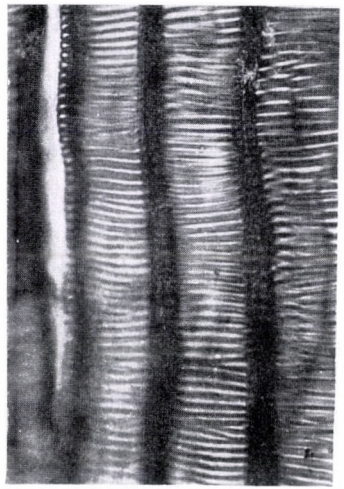
LXXIV. *Zamia angustifolia* (Jacq.) Schuster



LXXV. *Zamia floridana* A.DC.



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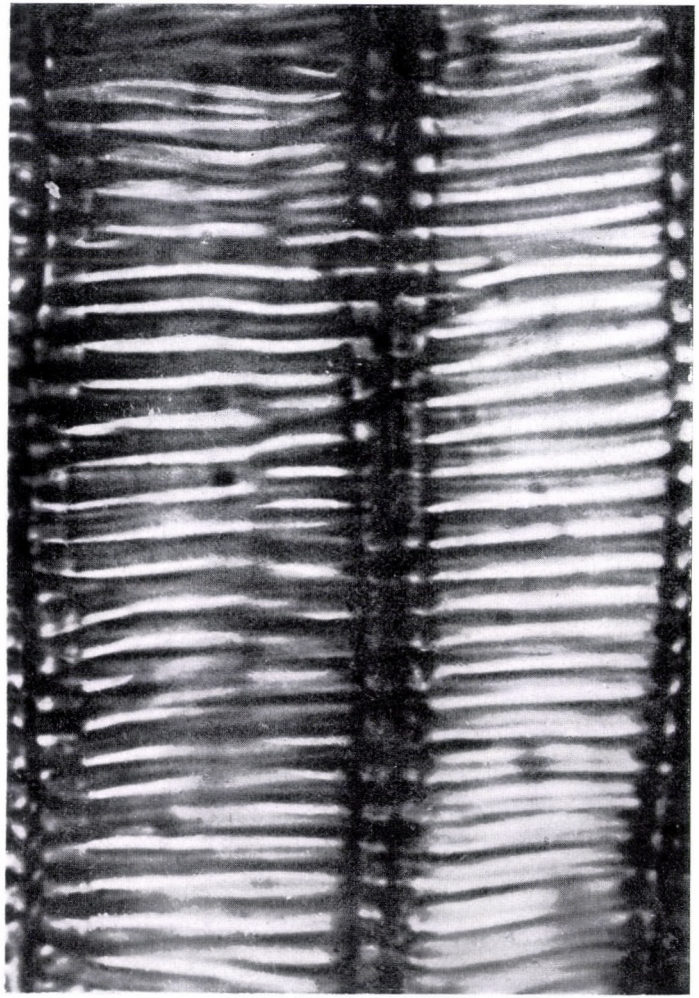

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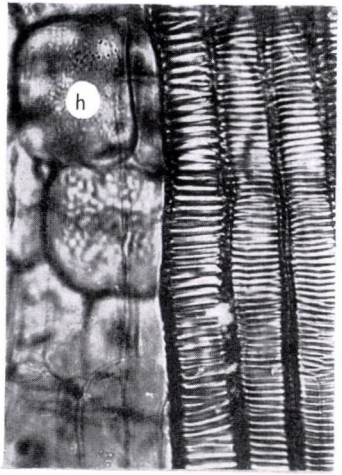

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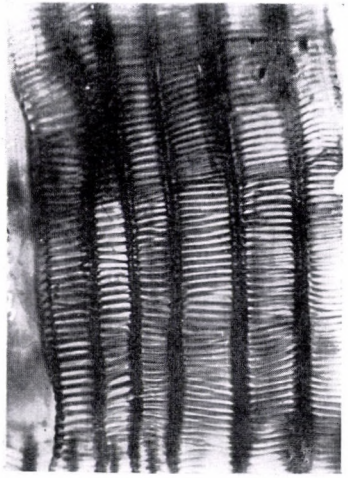

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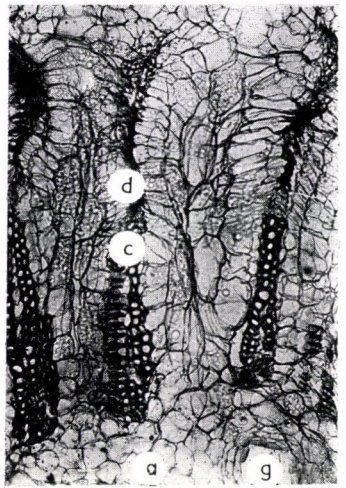
LXXVI. *Zamia floridana* A.DC.



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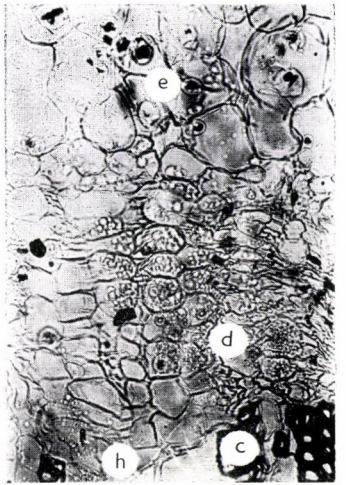

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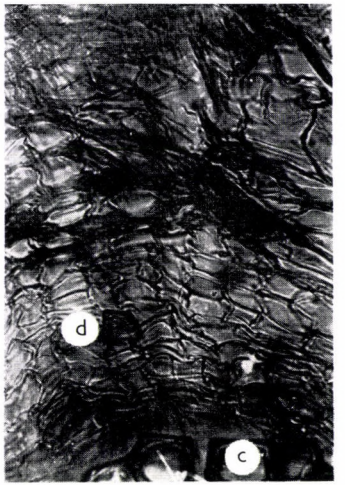

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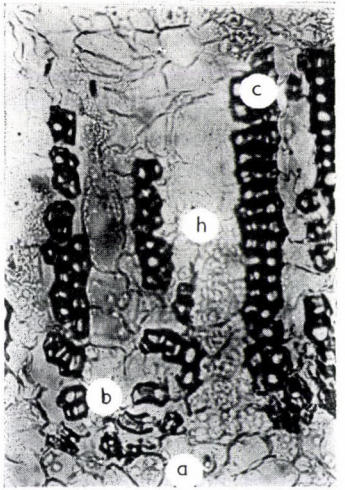

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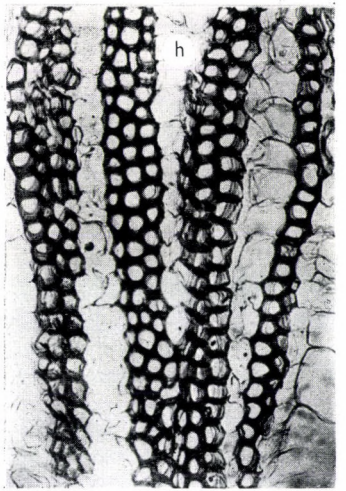

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LXXVII. *Zamia gutierrezi* Sauvalle



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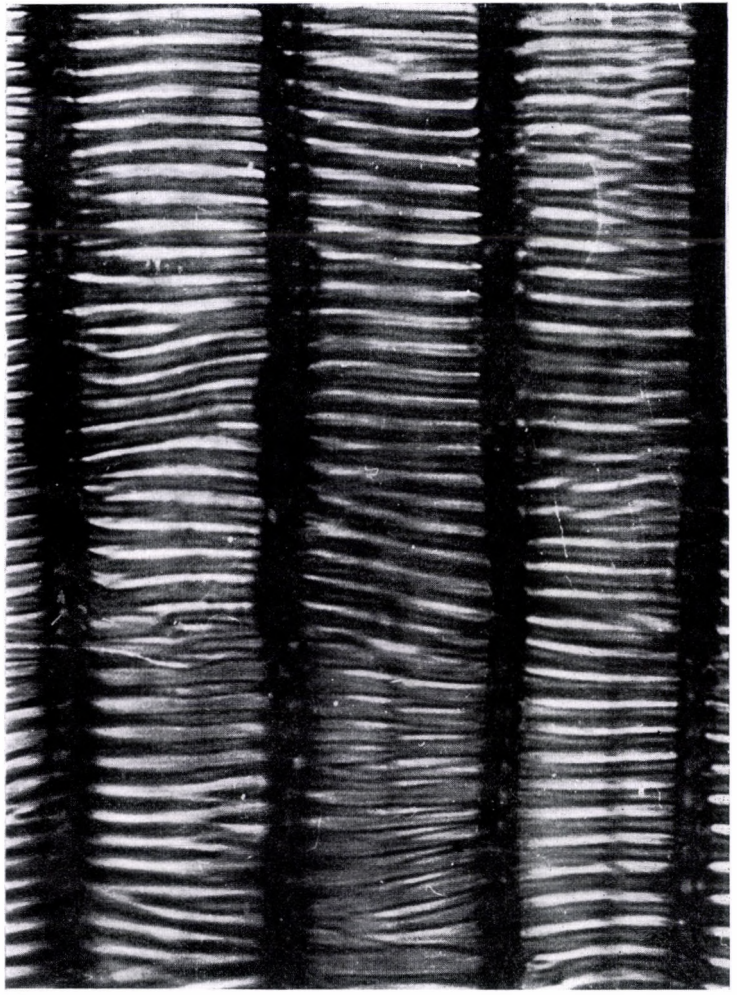

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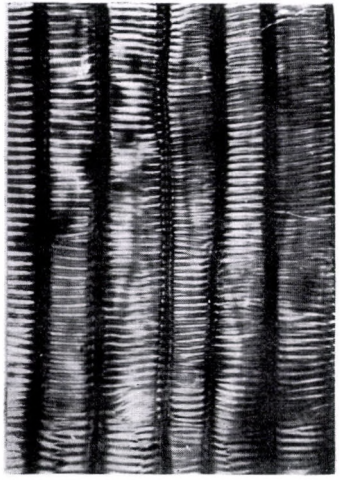

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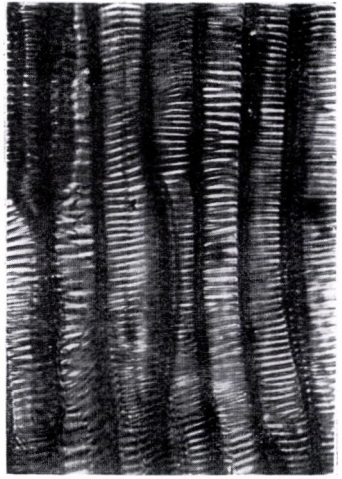

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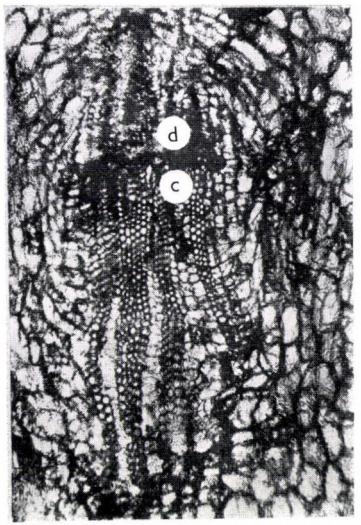
LXXVIII. *Zamia gutierrezi* Sauvalle



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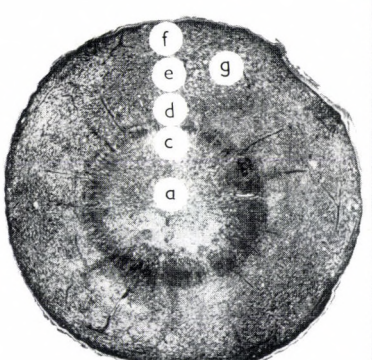

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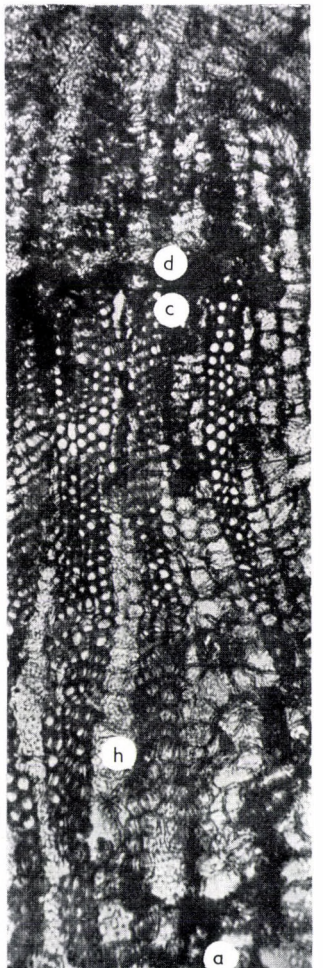

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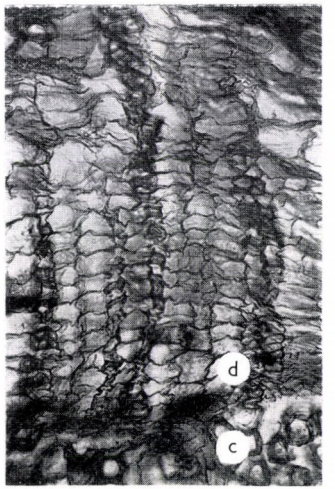

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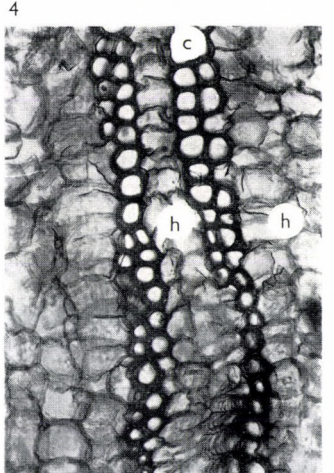

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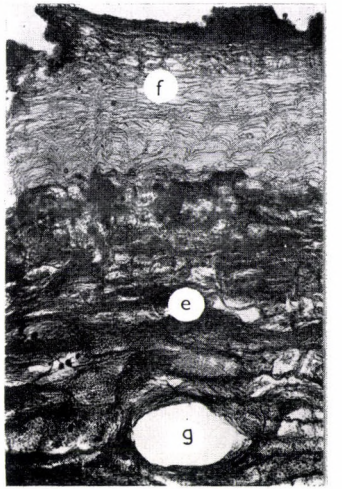

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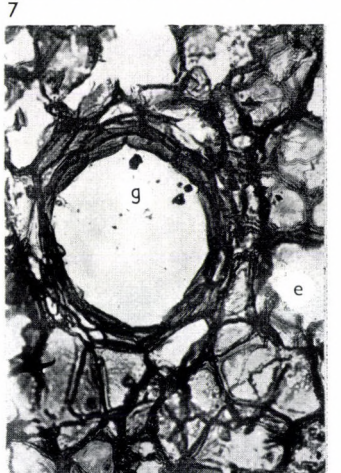

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LXXIX. *Zamia muricata* Willd.



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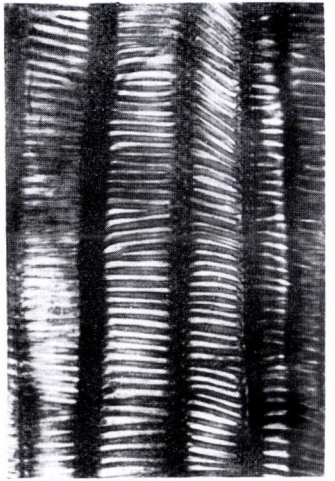

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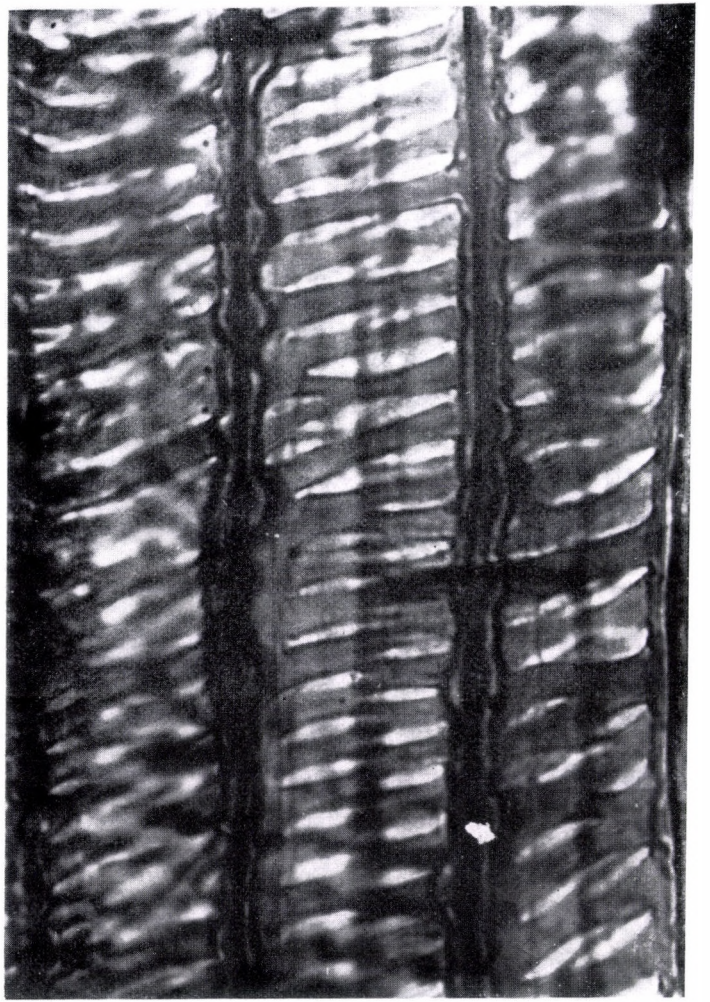

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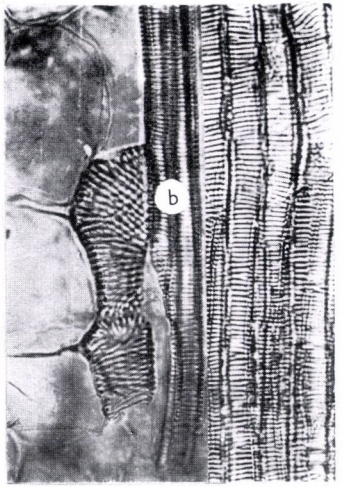

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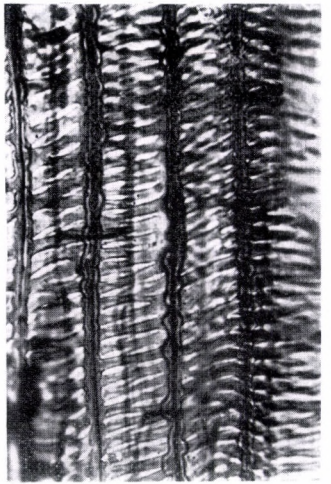

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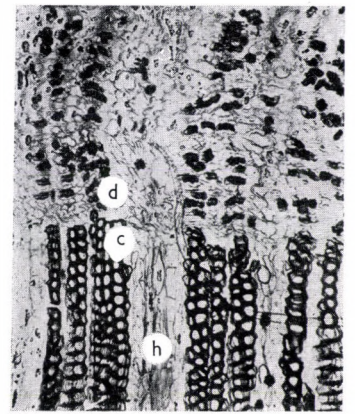
LXXX. *Zamia muricata* Willd.



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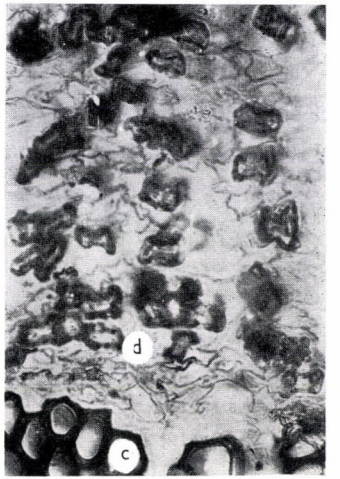

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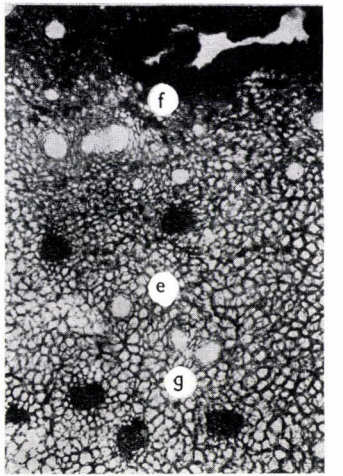

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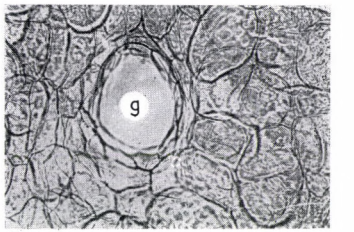

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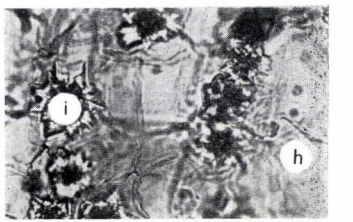

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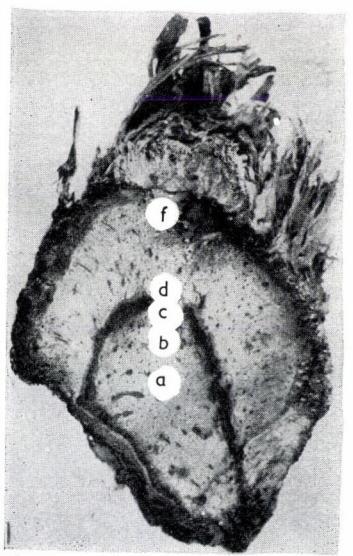

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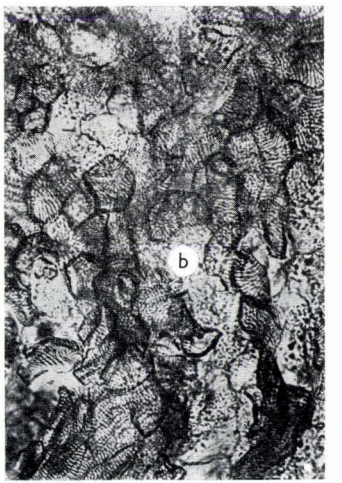

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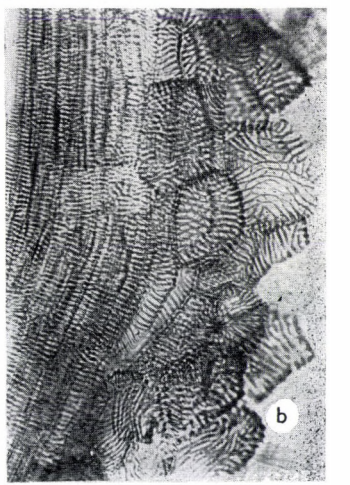

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LXXXI. *Zamia obidensis* Ducke



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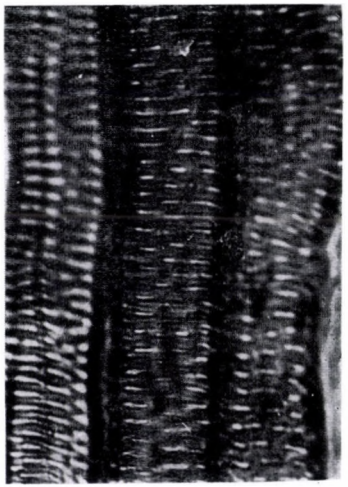

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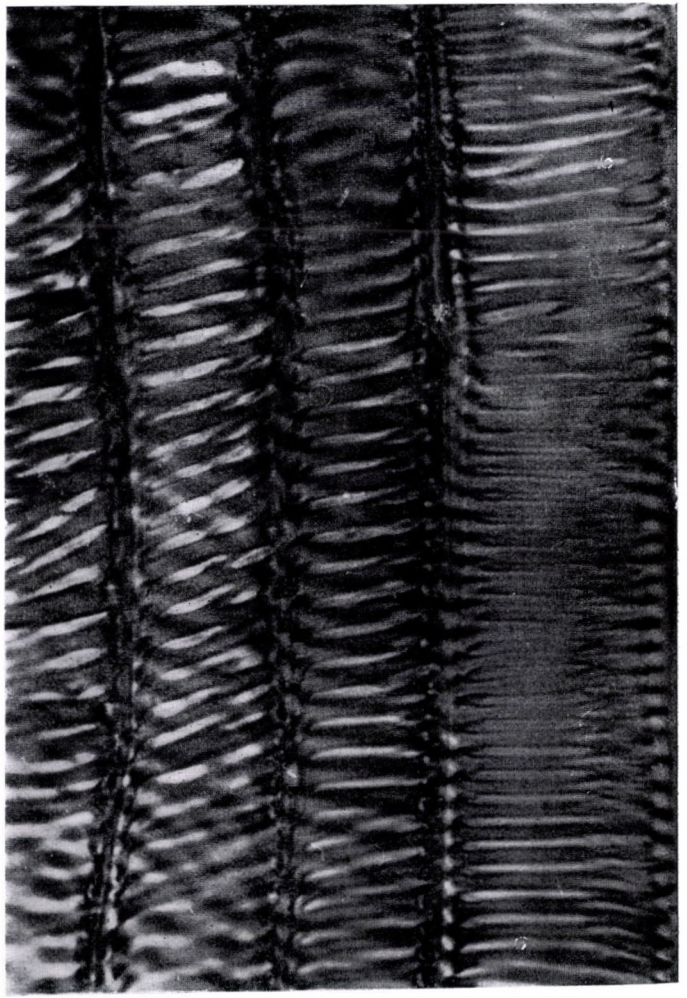

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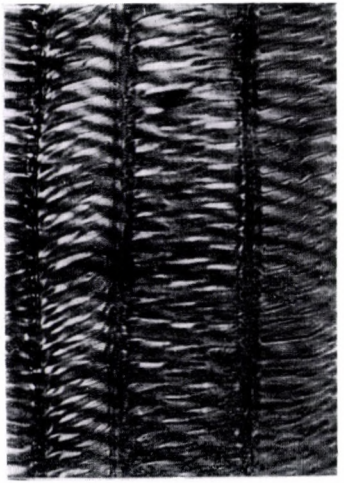

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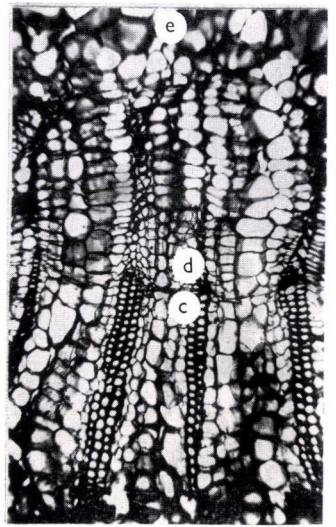
LXXXII. *Zamia obidensis* Ducke



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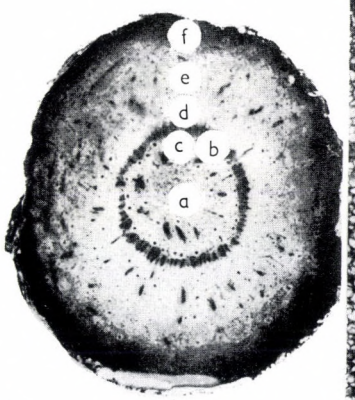

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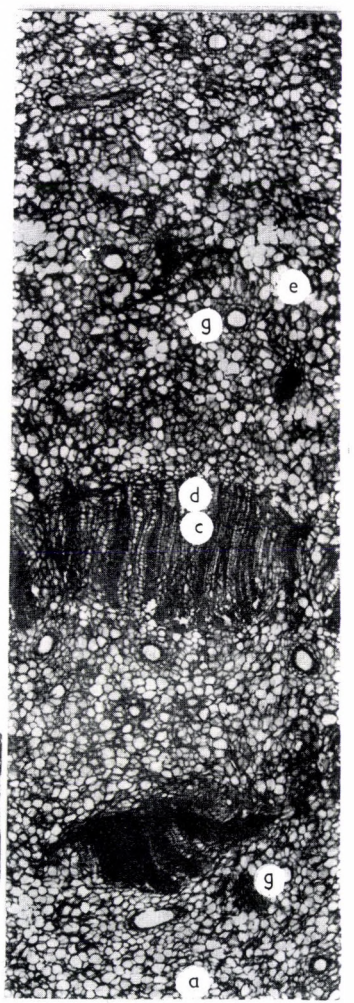

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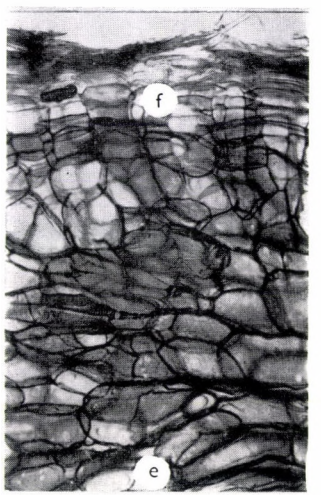

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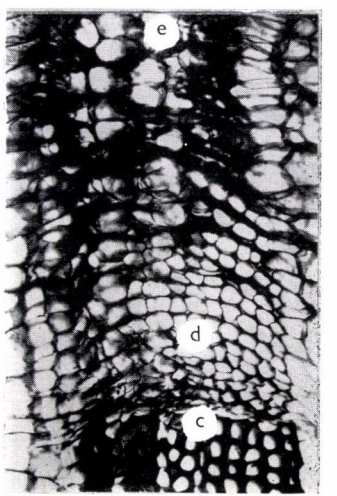

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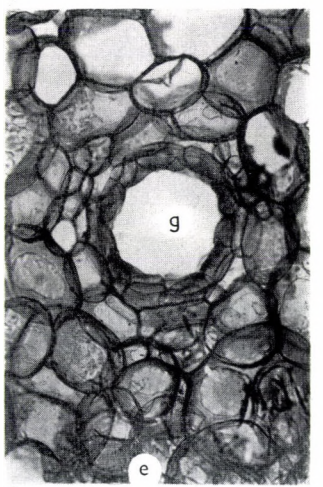

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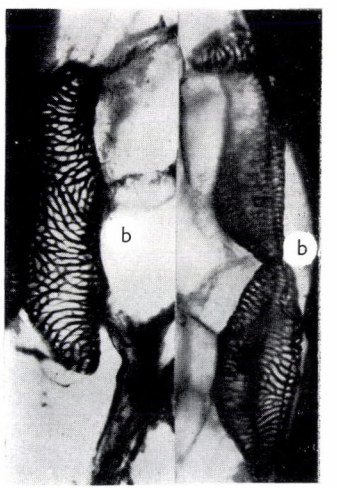

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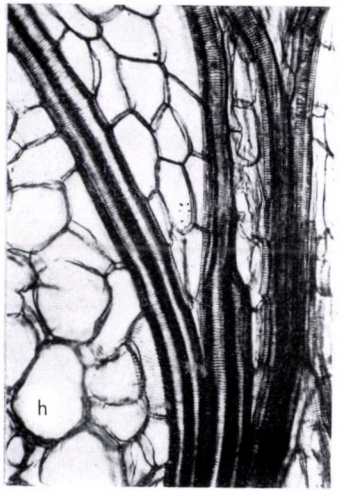
LXXXIII. *Zamia portoricensis* Urban



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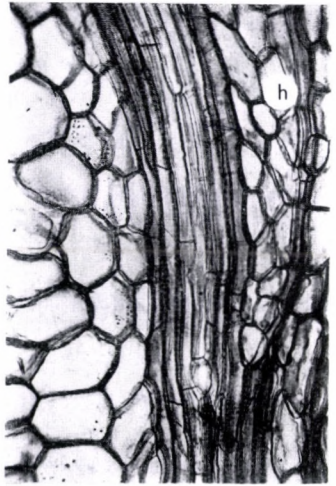

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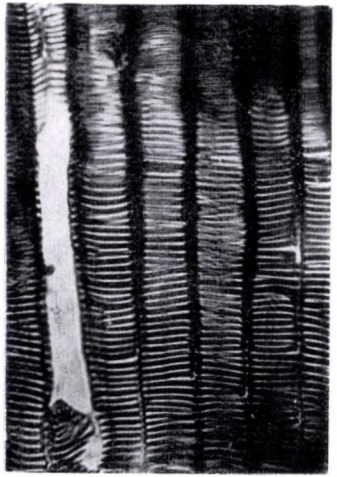

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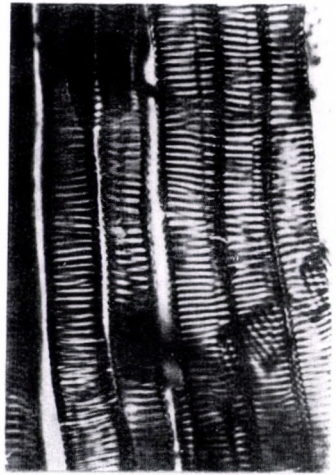

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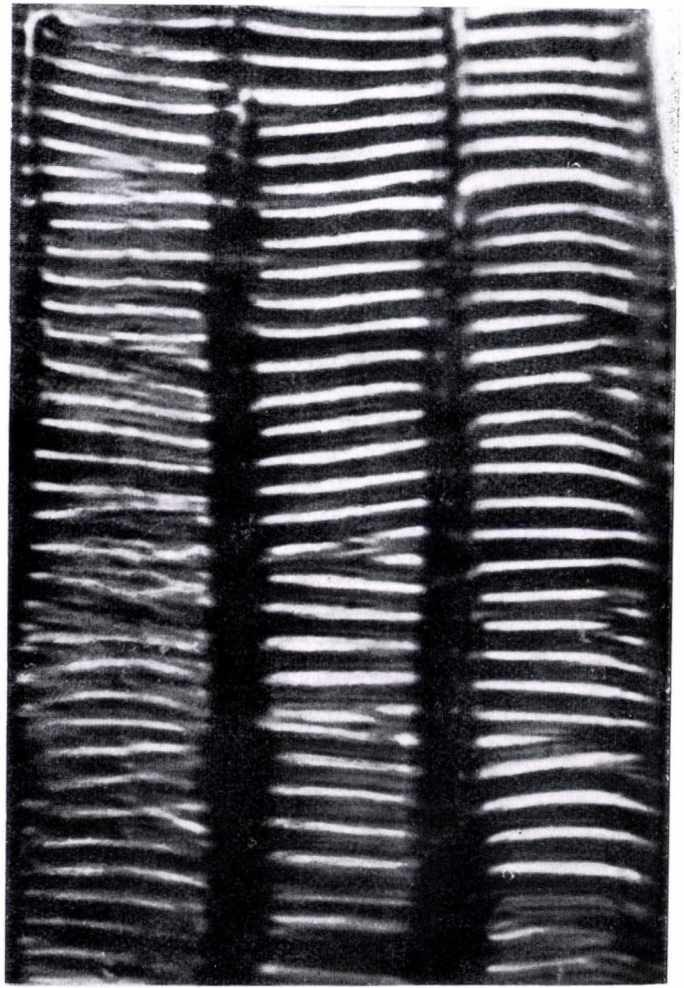

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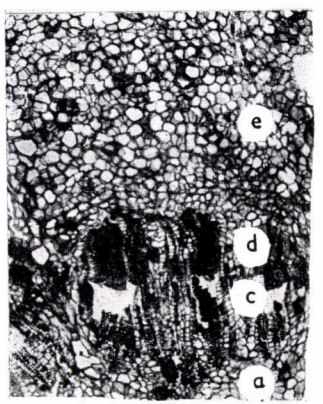
LXXXIV. *Zamia portoricensis* Urban



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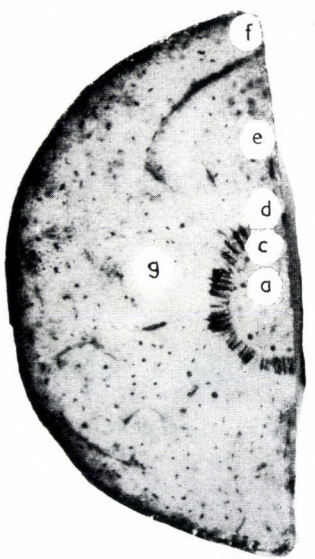

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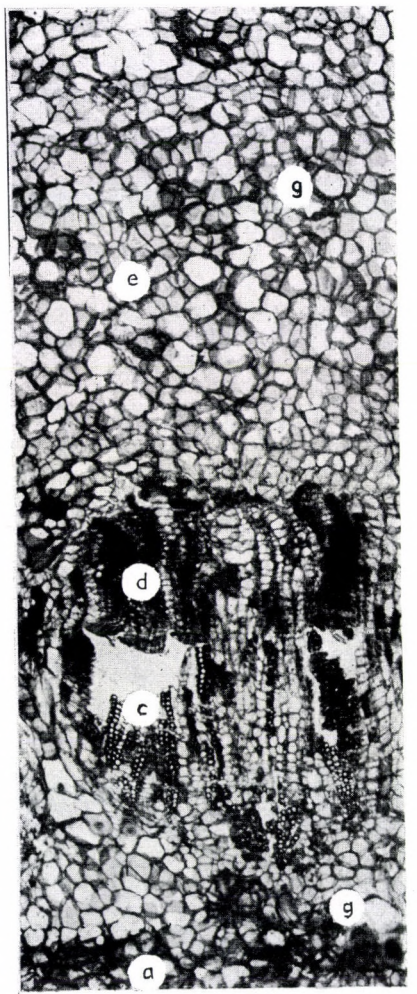

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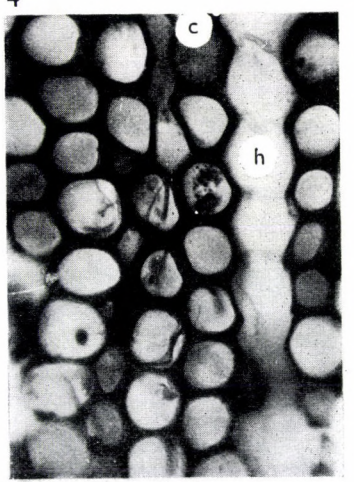

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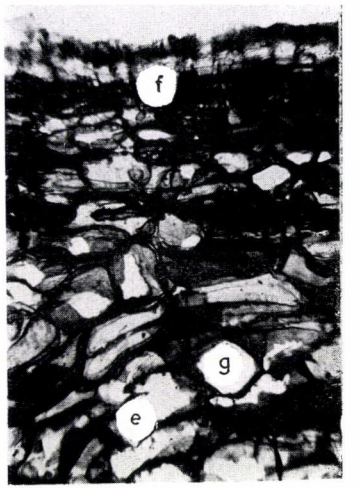

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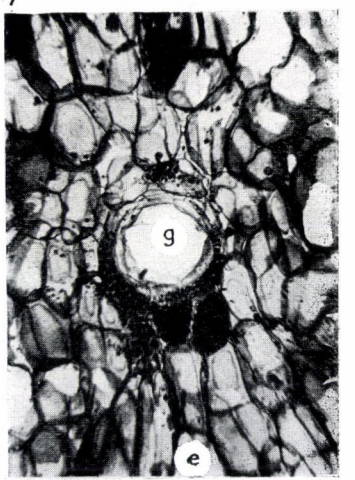

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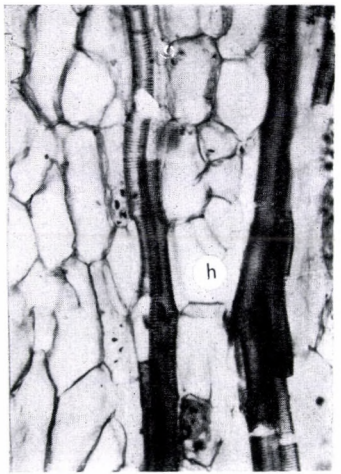
LXXXV. *Zamia pumila* L.



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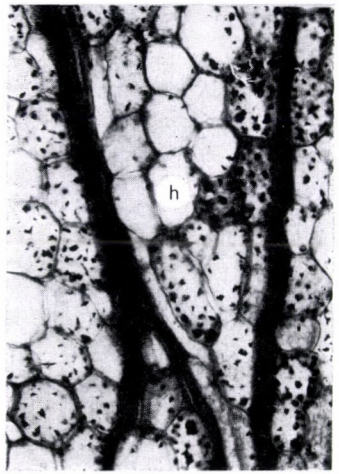

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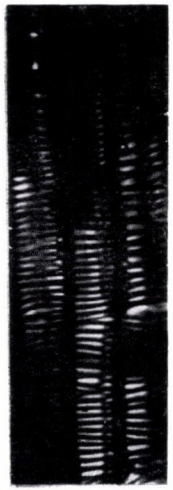

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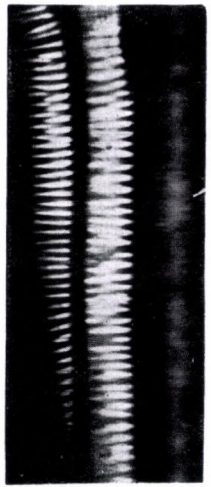

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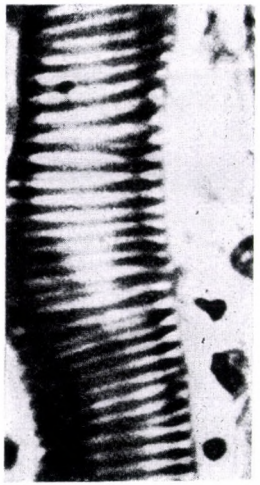

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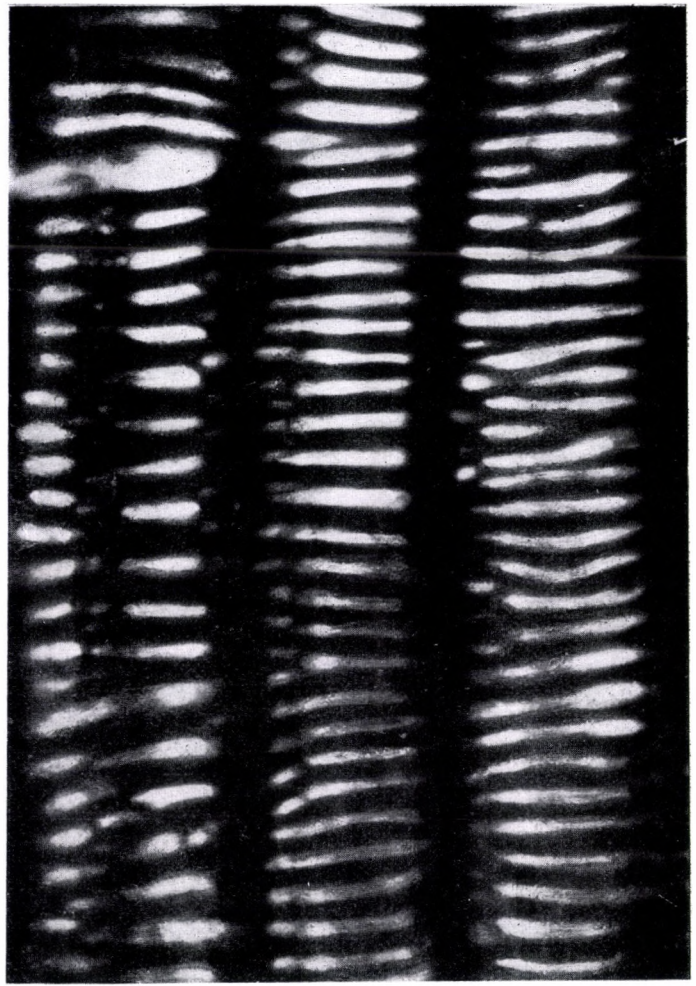

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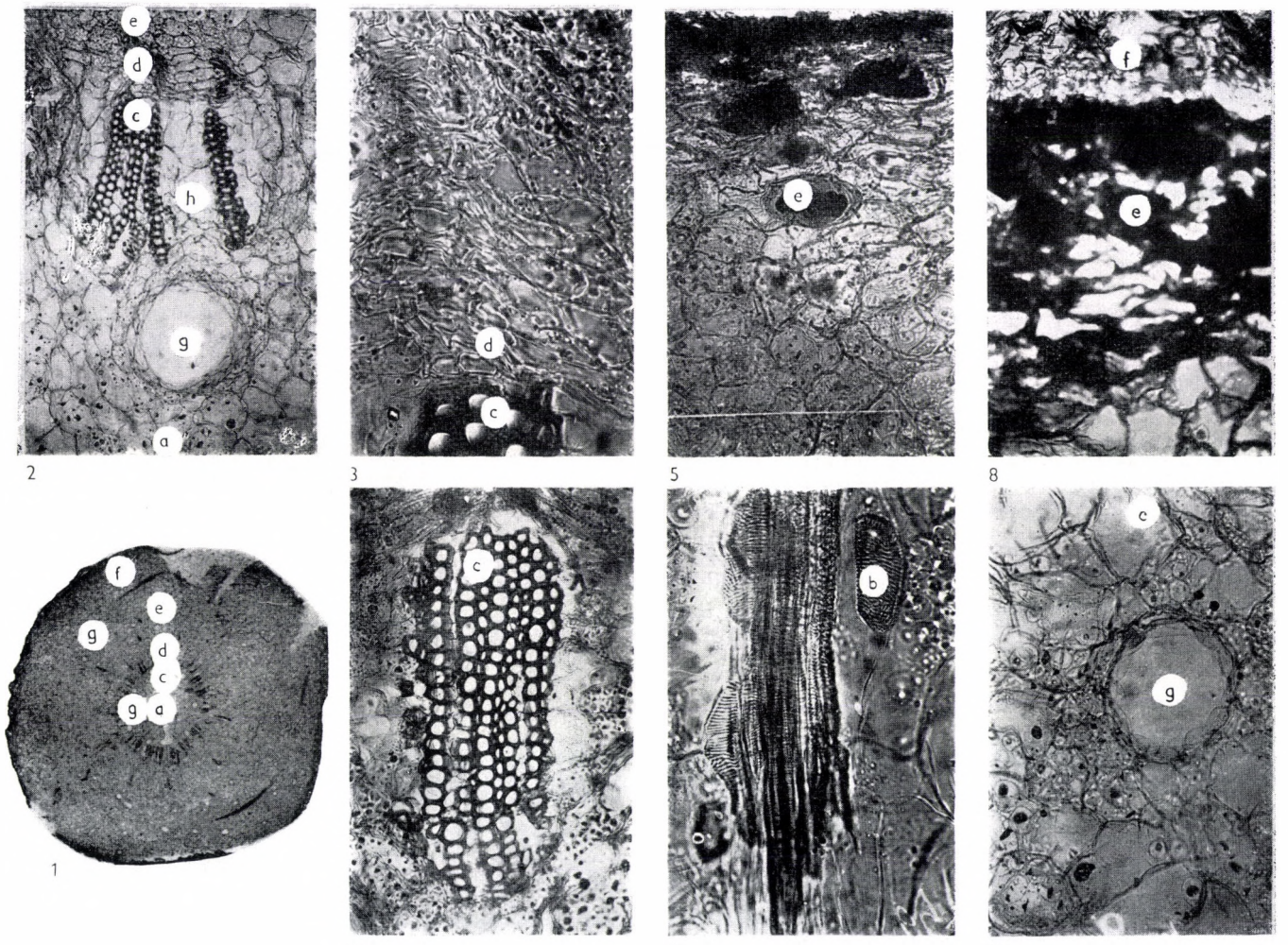
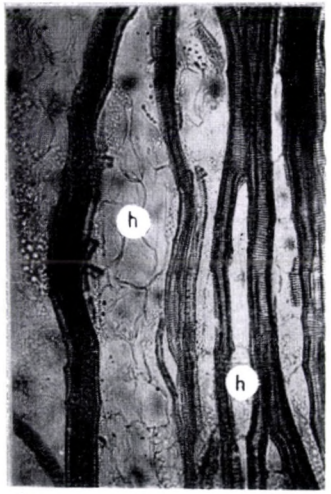
LXXXVI. *Zamia pumila* L.



LXXXVII. *Zamia silicea* Britton



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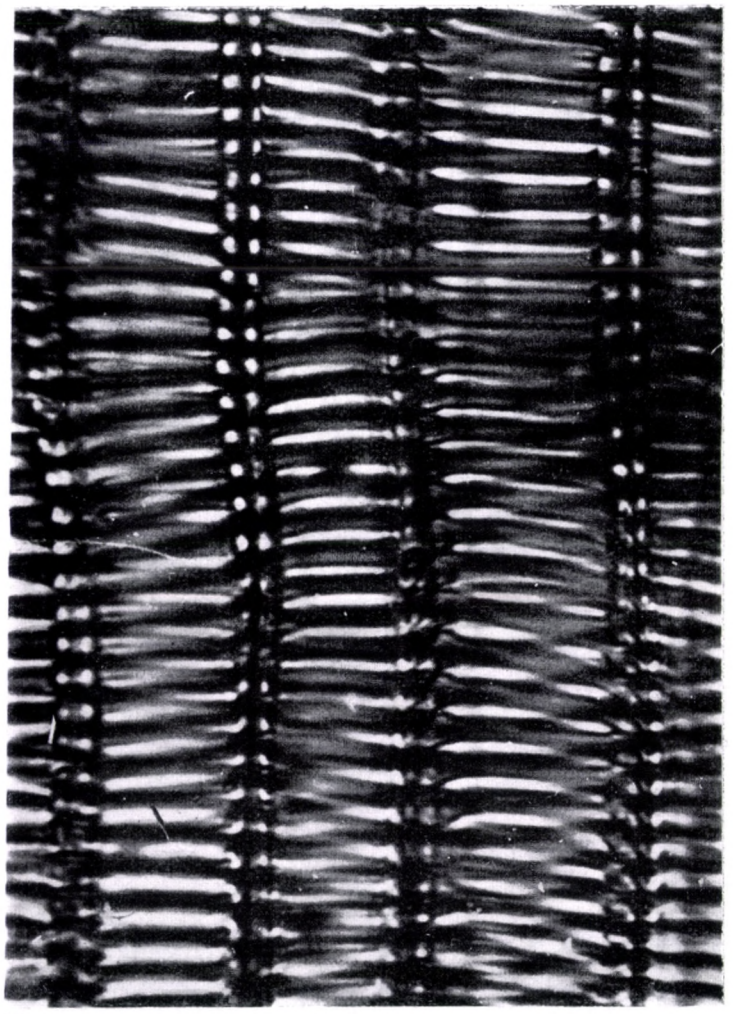

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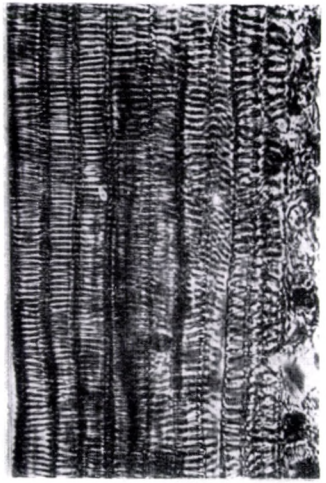

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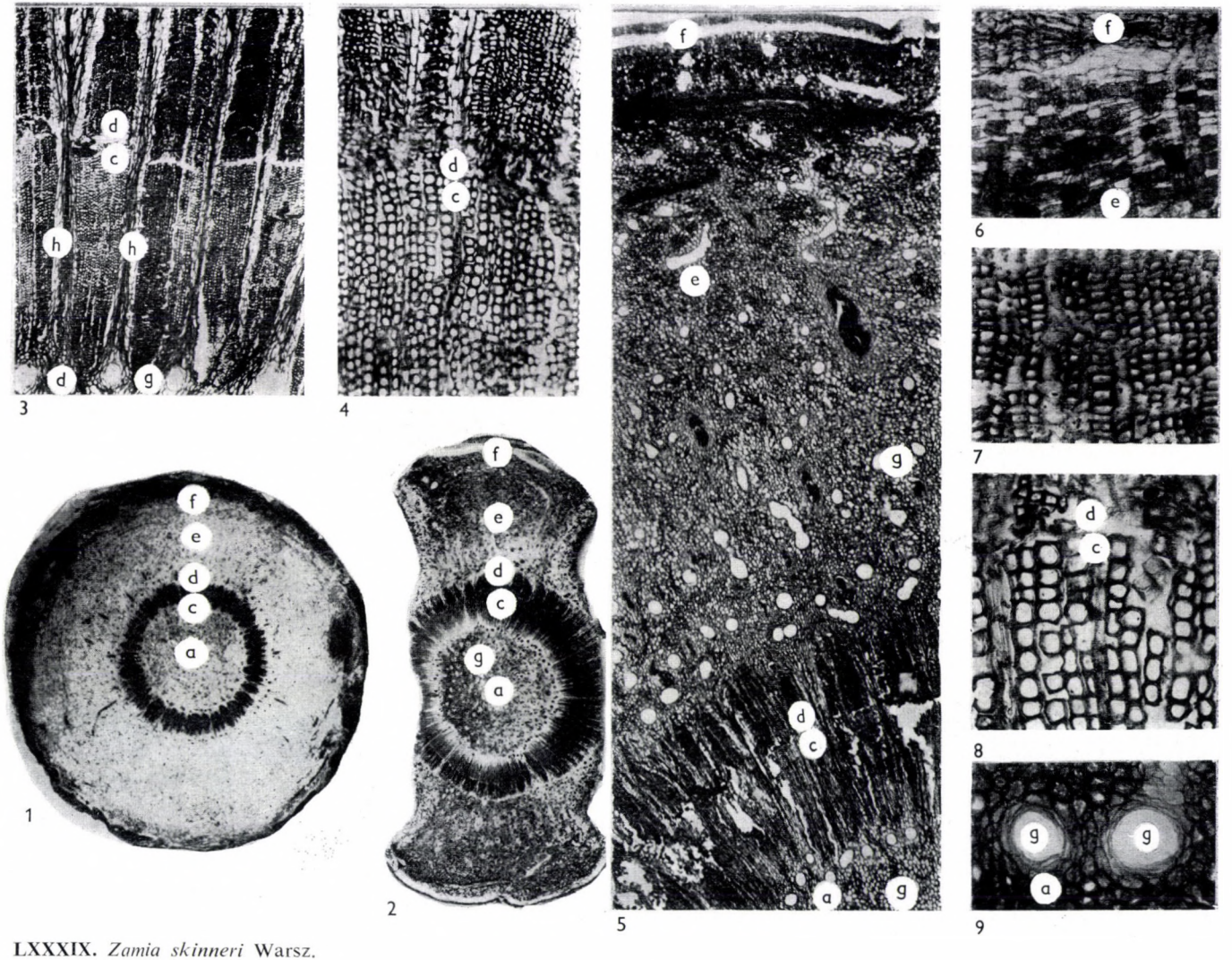
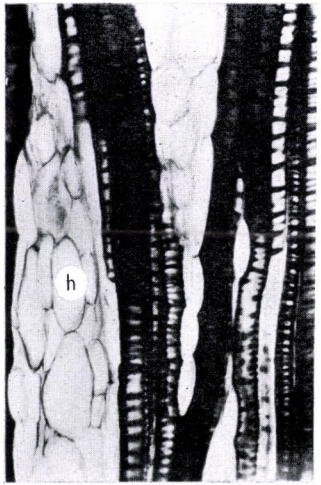
LXXXVIII. *Zamia silicea* Britton



LXXXIX. *Zamia skinneri* Warsz.



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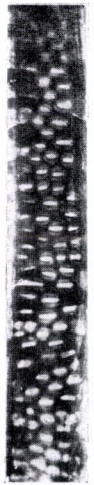

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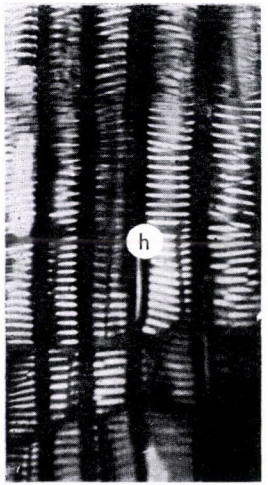

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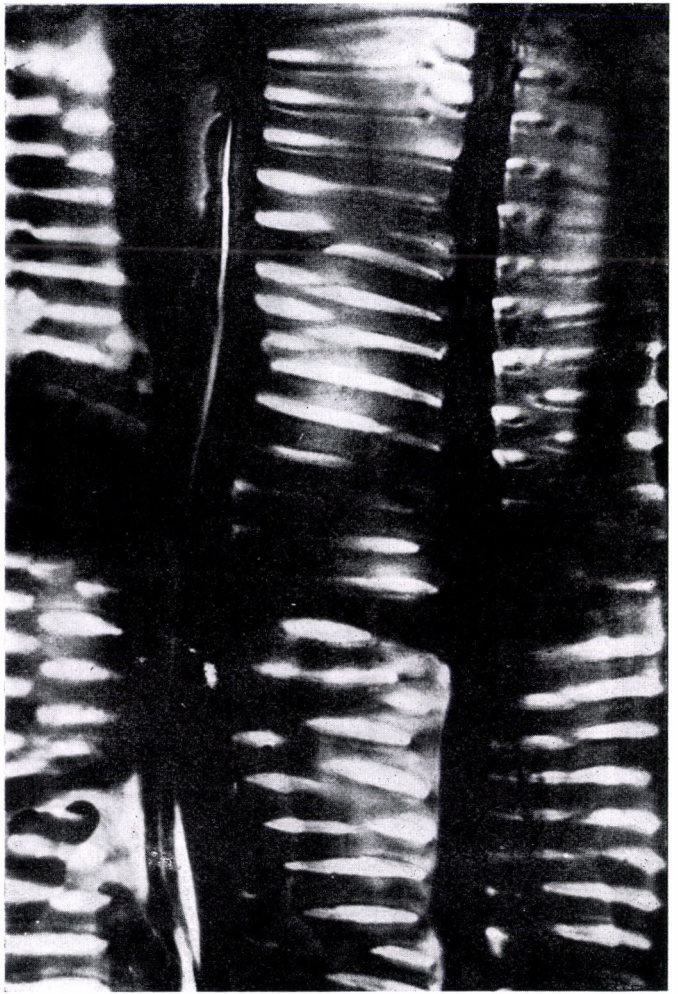

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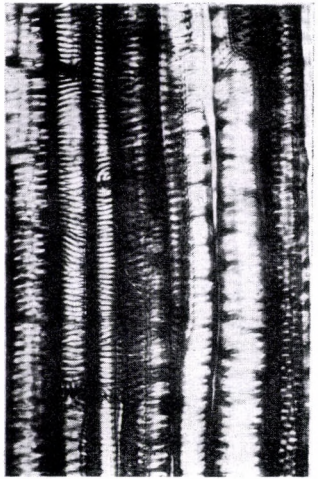

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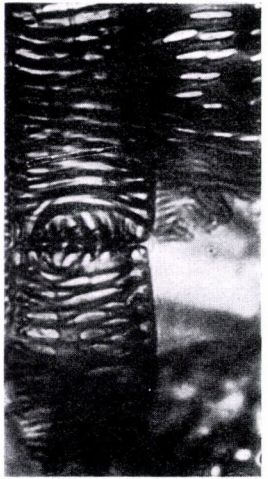

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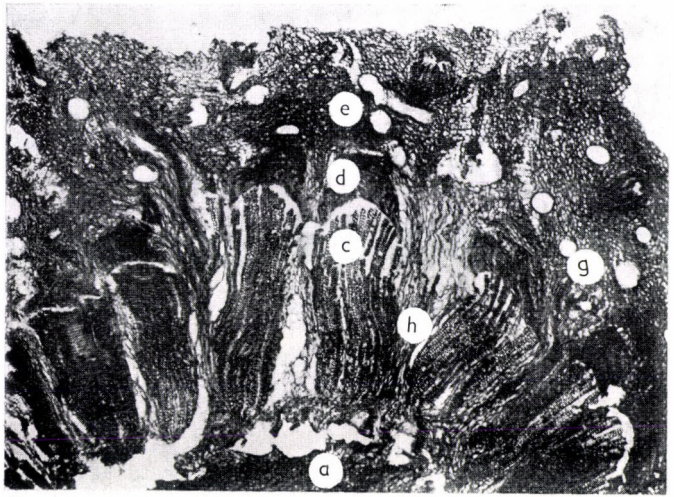
XC. *Zamia skinneri* Warsz.



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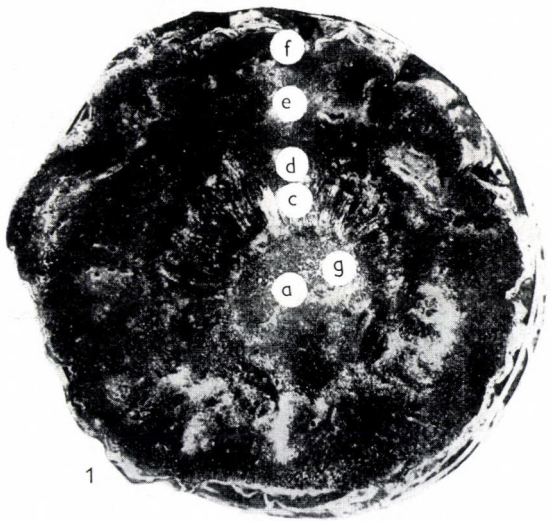

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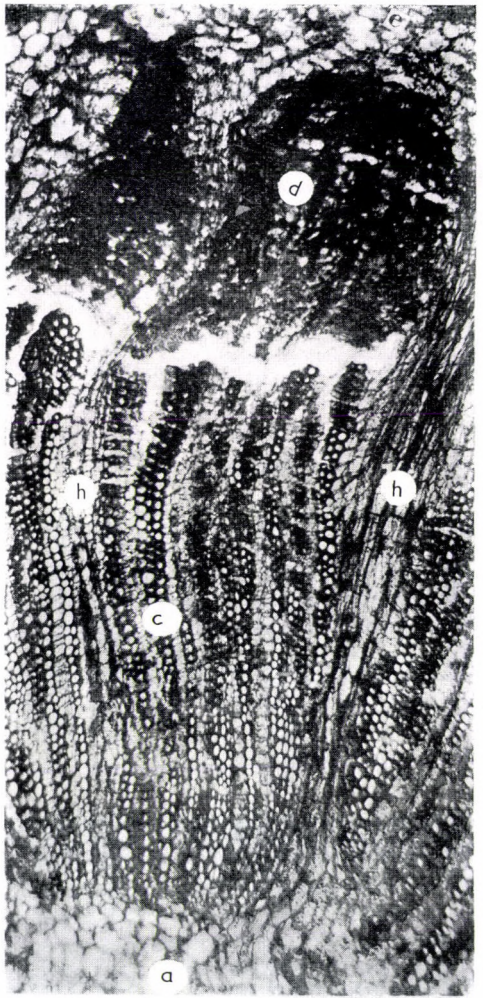

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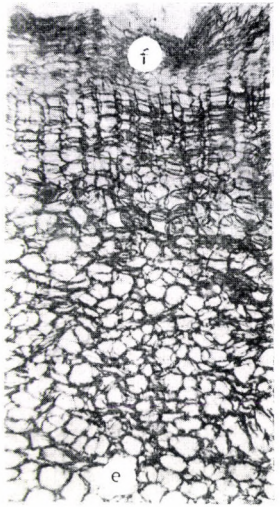

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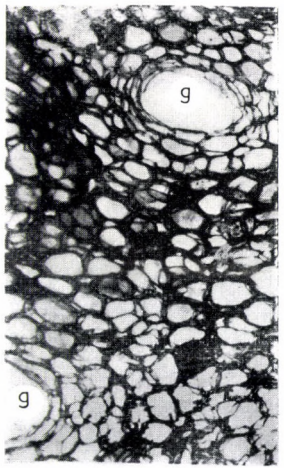

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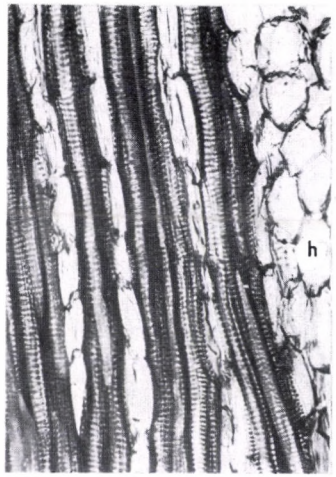
XCI. *Bowenia serrulata* (W. Bull) Chamberlain



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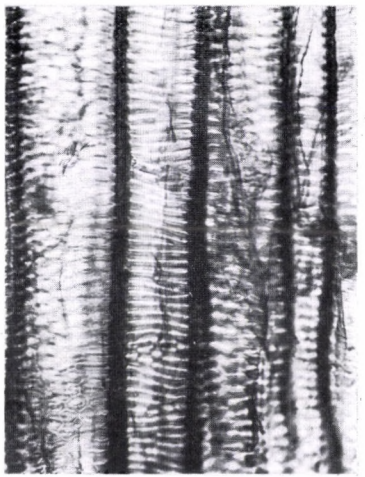

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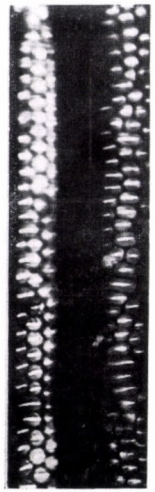

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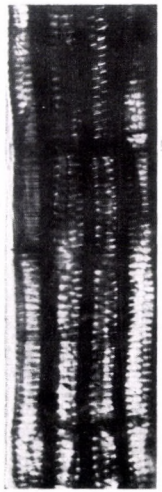

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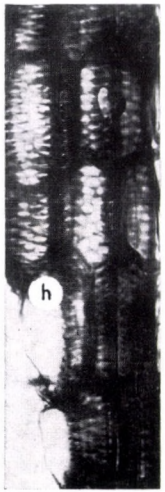

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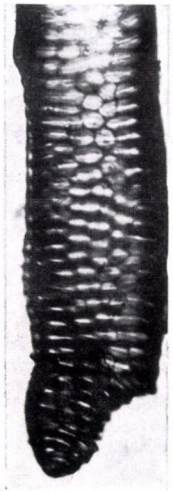

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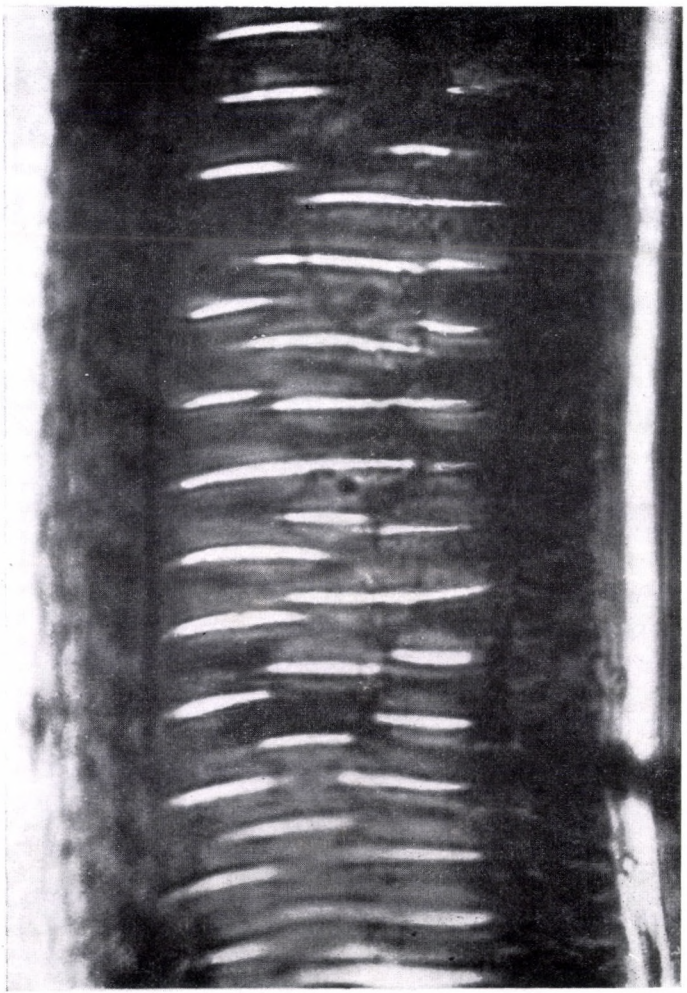

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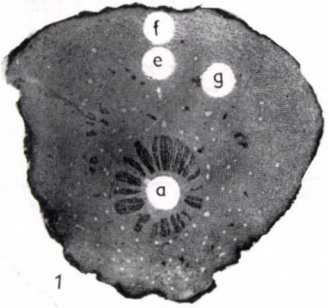
XCII. *Bowenia serrulata* (W. Bull) Chamberlain



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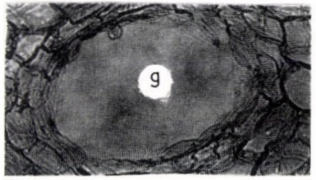

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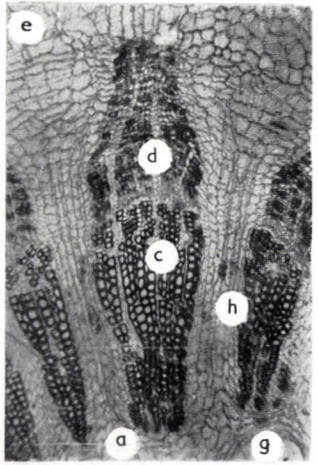

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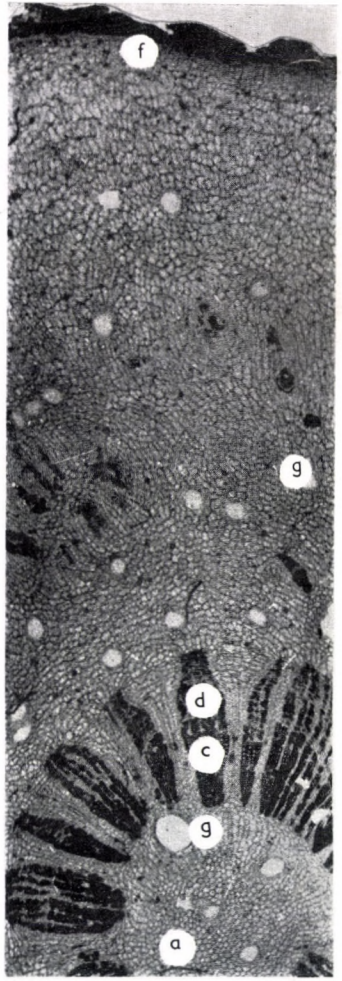

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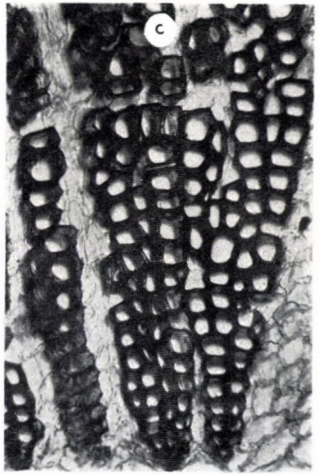

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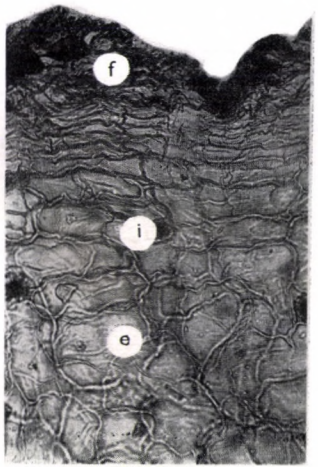

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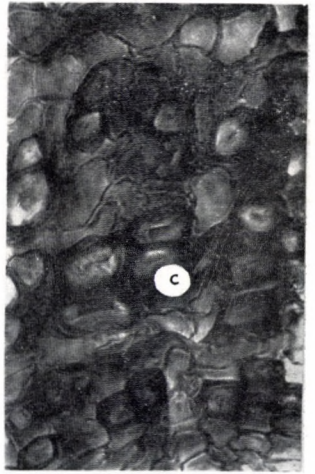

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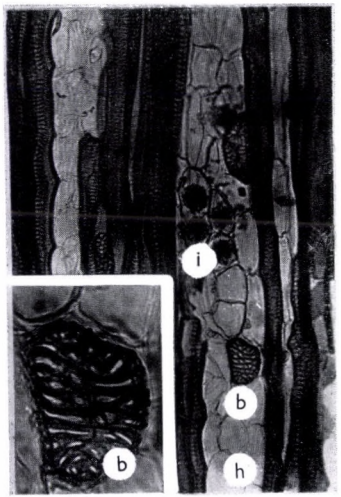
XCIII. *Bowenia spectabilis* Hook



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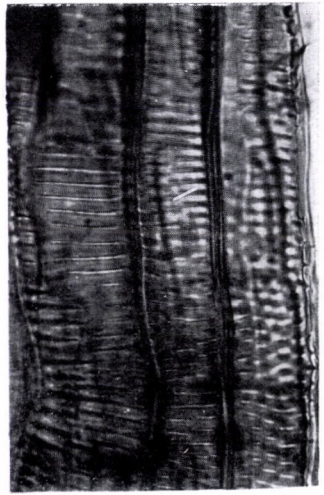

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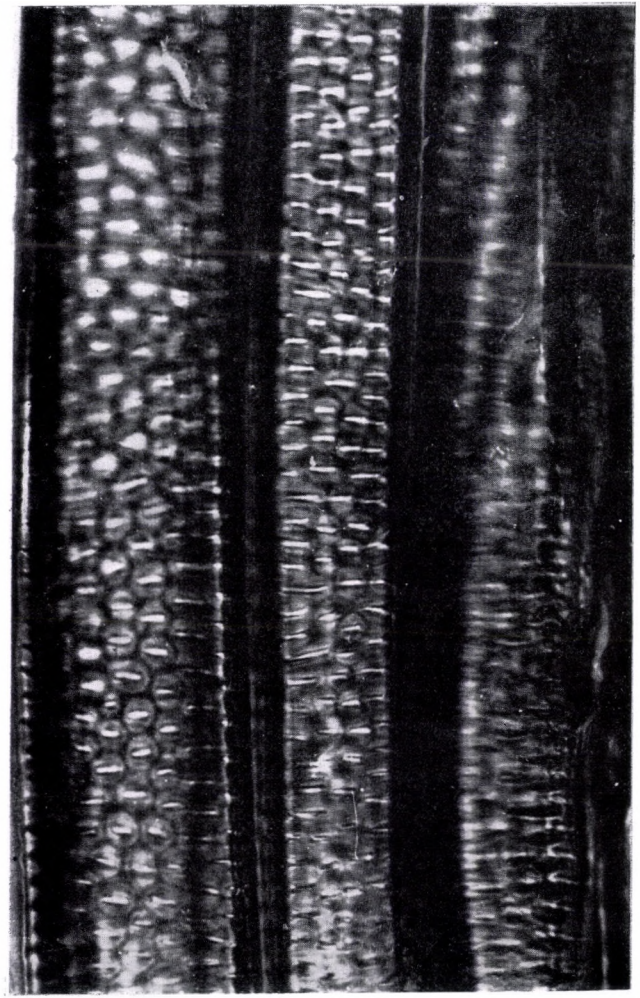

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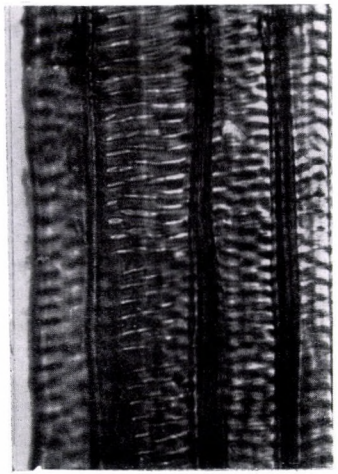

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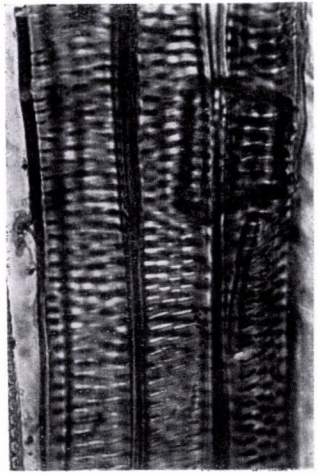


12

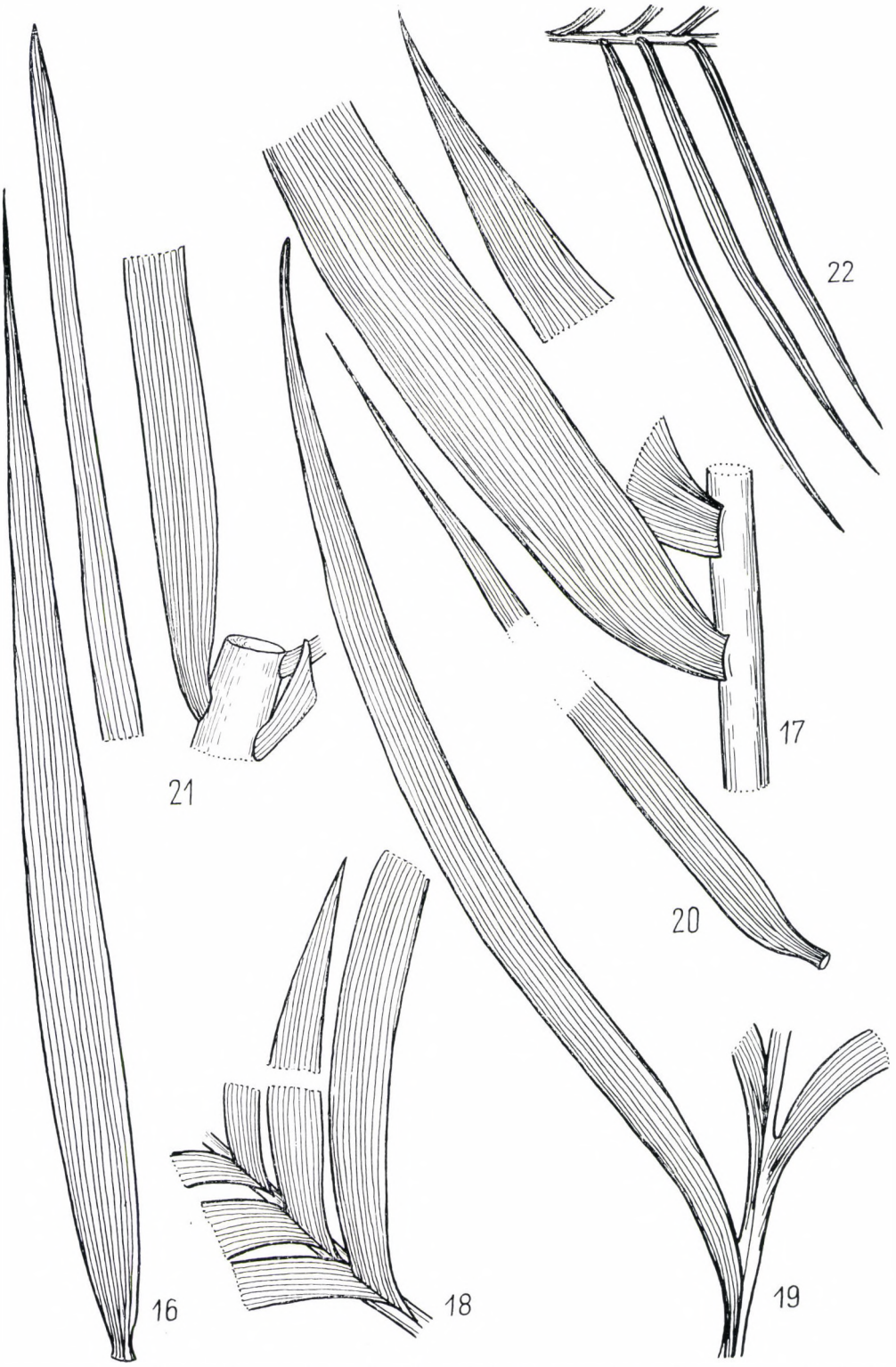
XCIV. *Bowenia spectabilis* Hook



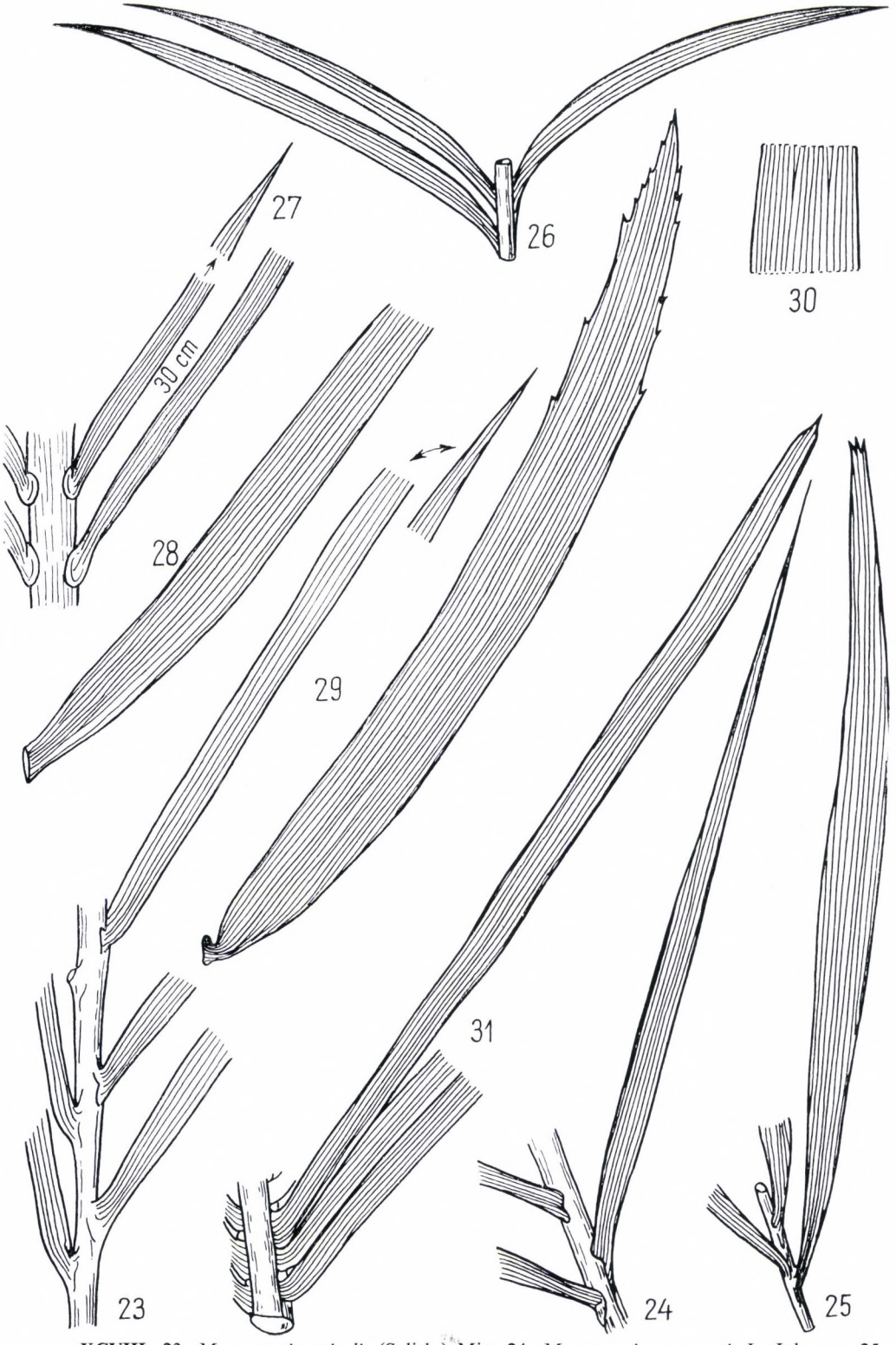
XCV. 1. *Bowenia serrulata* (W. Bull) Chamberlain. 2. *Bowenia spectabilis* Hook. 3. *Stangeria eriopus* Nash. 4. *Microcycas calocoma* (Miq.) A.DC. 5. *Dioon pectinatum* H. Wendl. 6. *Dioon edule* Lindl. 6a. *Dioon spinulosum* Dyer



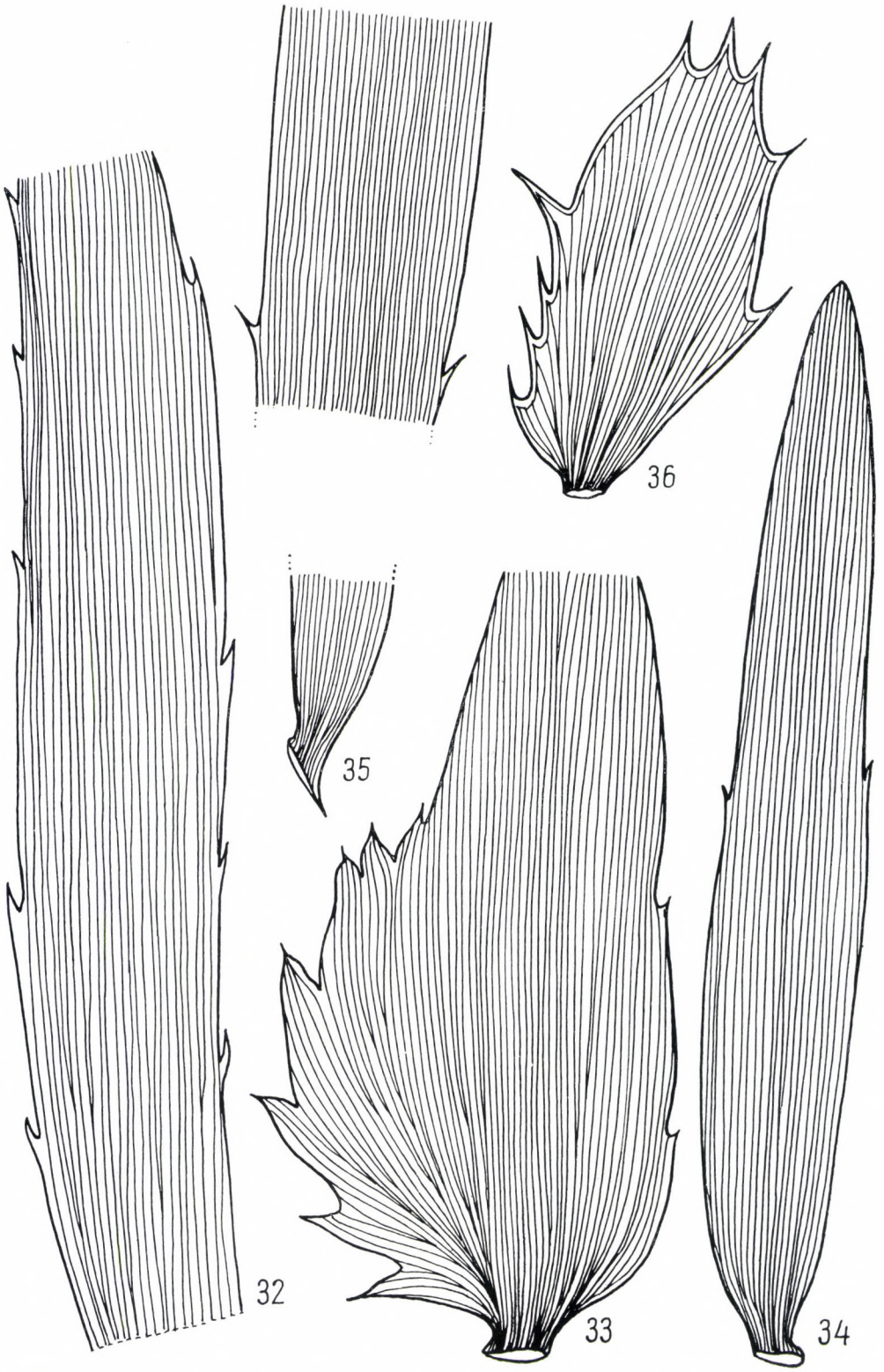
XCVI. 7. *Cycas revoluta* Thunb. 8. *C. taiwaniana* Carruthers. 9. *C. circinalis* L. 10. *C. seemannii* (A. Braun) Schuster. 11. *C. rumphii* Miq. 12. *C. thouarsii* R. Brown. 13. *C. celebica* Miq. 14. *C. siamensis* Miq. 15a. *C. media* R. Br. 15b. *C. neocaledonica* Linden



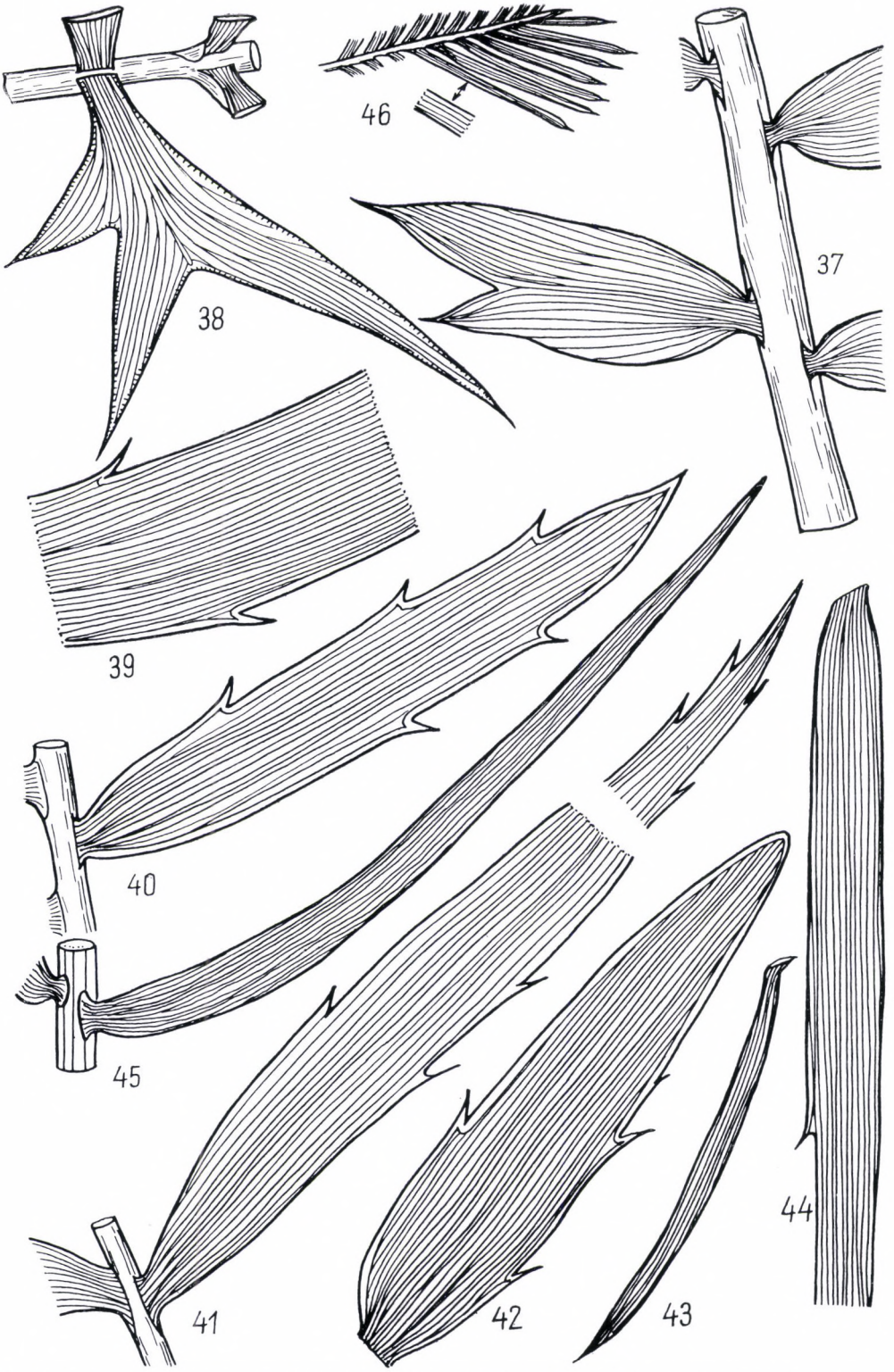
XCVII. 16. *Ceratozamia kuesteriana* Regel. 17. *Ceratozamia mexicana* Brongn. 18. *Lepidozamia peroffskyana* Regel. 19. *Lepidozamia hopei* Regel. 20. *Macrozamia macdonneli* (F. Muell.) A.DC. 21. *Macrozamia moorei* F. Muell. 22. *Macrozamia miquelii* (F. Muell.) A.DC.



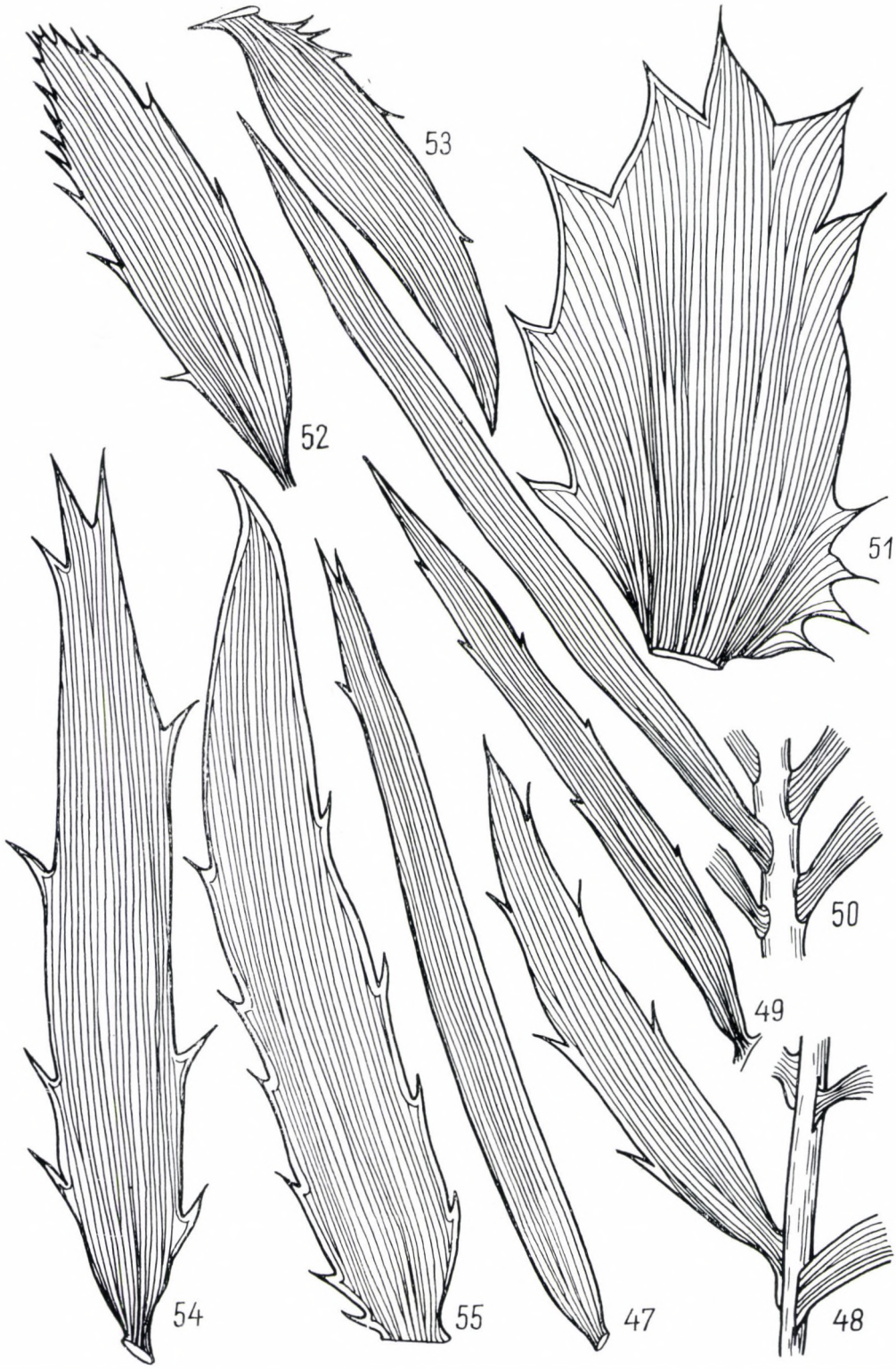
XCVIII. 23. *Macrozamia spiralis* (Salisb.) Miq. 24. *Macrozamia communis* L. Johnson. 25. *Macrozamia fawcettii* C. Moore. 26. *Macrozamia secunda* C. Moore. 27. *Macrozamia pauli-guilielmi* W. Hill et F. Muell. 28. *Encephalartos caffer* Miq. 29. *Zamia loddigesii* Miq. 30. *Ceratozamia robusta* Miq. 31. *Encephalartos cycadifolius* Lehm.



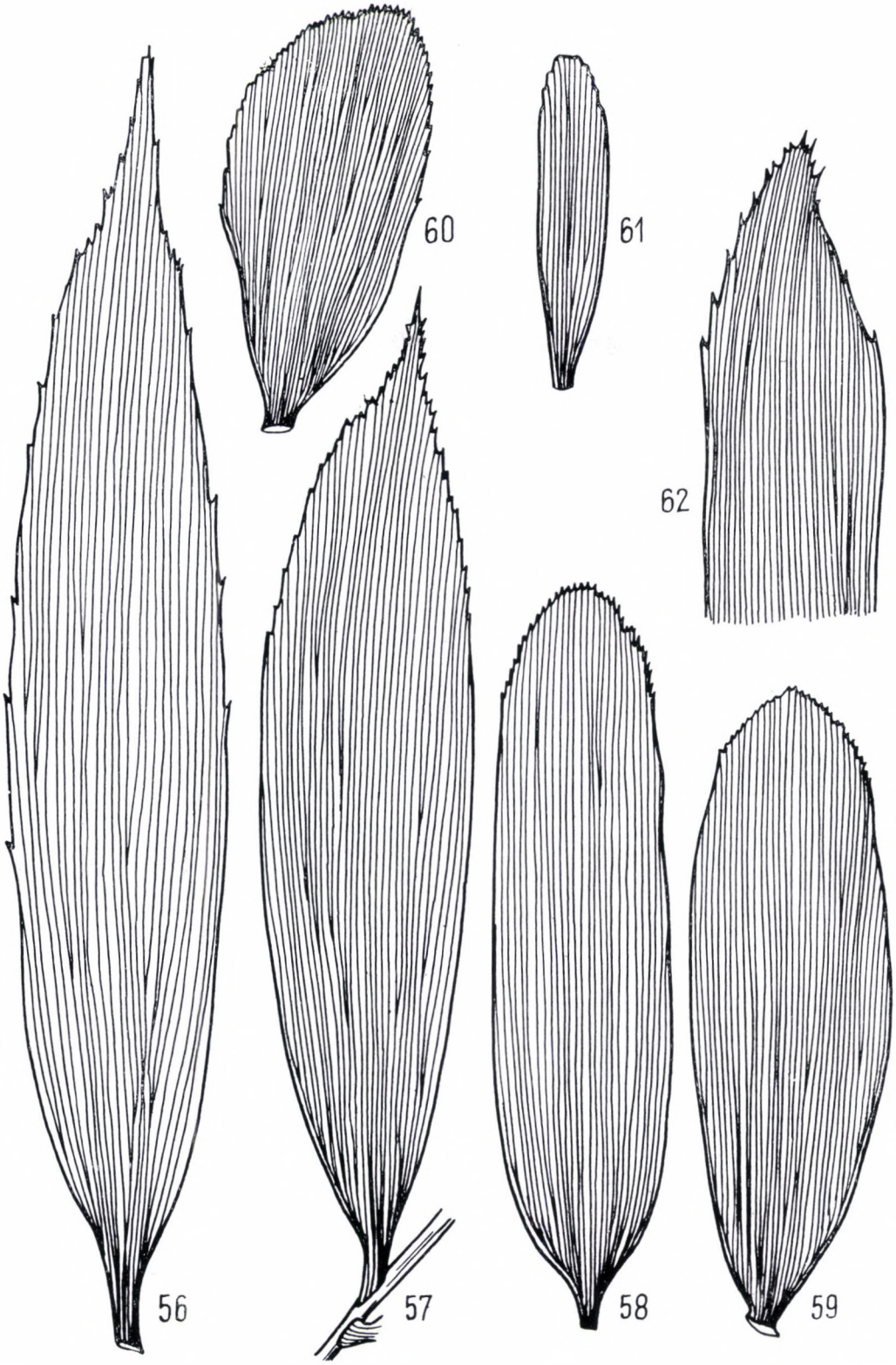
XCIX. 32. *Encephalartos laurentianus* De Wilden. 33. *E. woodii* Prain. 34. *E. longifolius* (Jacq.) Lehm. 35. *E. tegulanus* Melville. 36. *E. ferox* Bertol



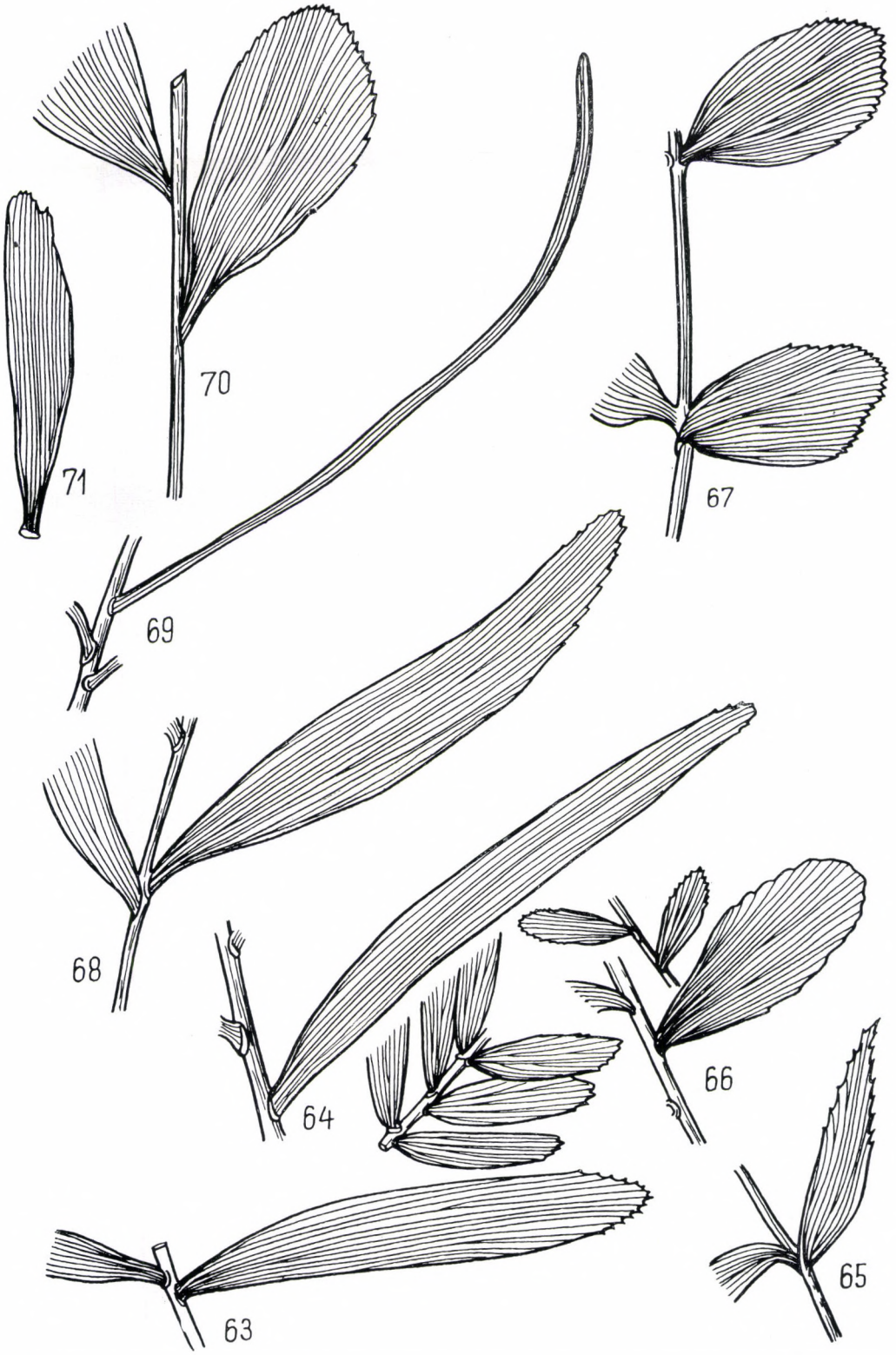
C. 37. *Encephalartos arenarius* R.A. Dyer. 38. *E. horridus* (Jacq.) Lehm. 39. *E. natalensis* Dyer et Verdoorn. 40. *E. altensteinii* Lehm. 41. *E. villosus* (Gaertn.) Lemaire. 42. *E. transvenosus* Stapf et Davy. 43. *E. humilis* Verdoorn. 44. *E. poggei* Aschers. 45. *E. inopinus* Dyer. 46. *E. eximius* Verdoorn



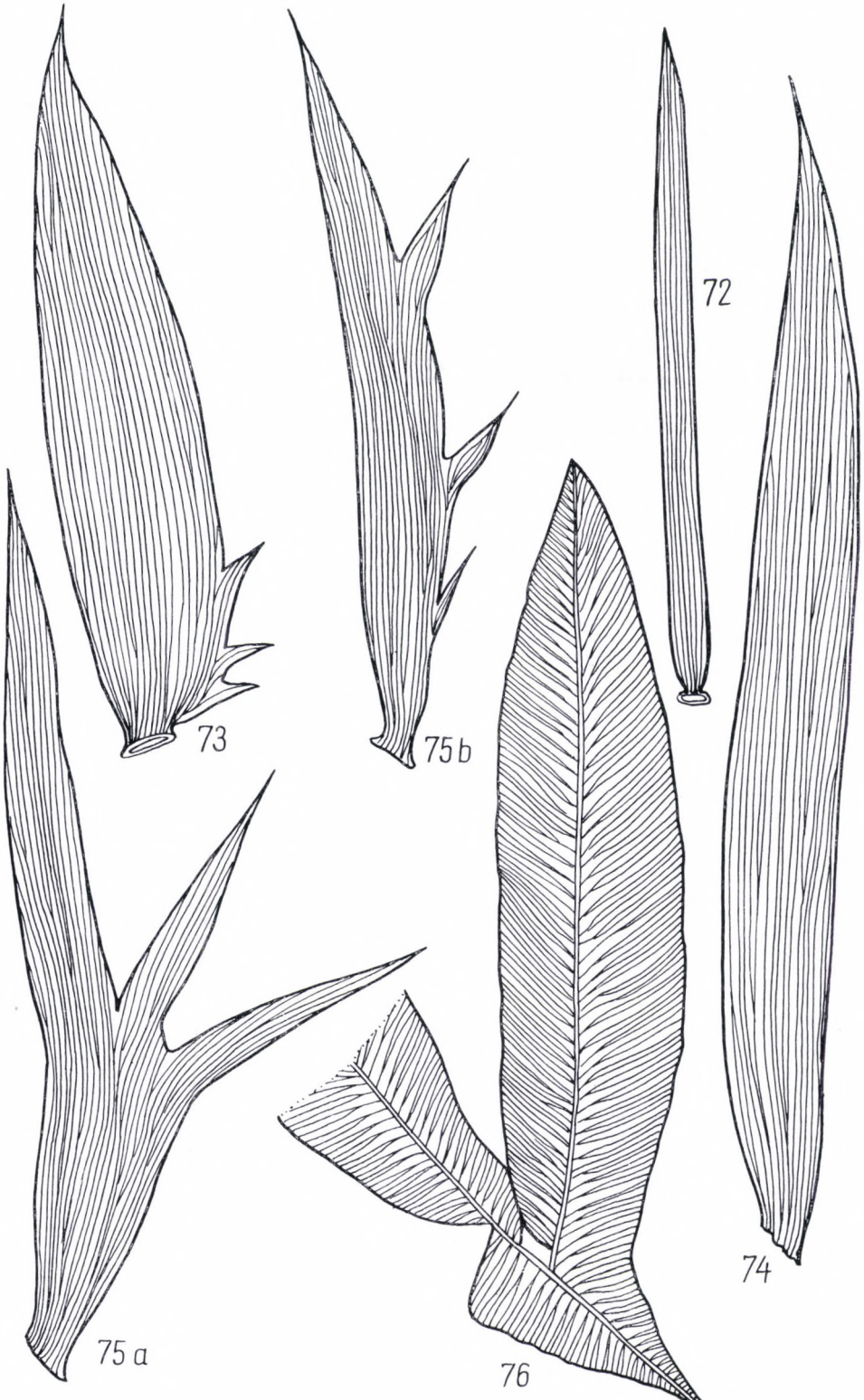
CI. 47. *Encephalartos umbeluziensis* R.A. Dyer. 48. *E. lebomboensis* Verdoorn. 49. *E. barteri* Carruthers. 50. *E. lehmannii* Ecklon. 51. *E. latifrons* Lehm. 52. *E. gratus* Prain. 53. *E. bubalinus* Melville. 54. *E. hildebrandtii* A. Braun et Bouché. 55. *E. septentrionalis* Schweinf.



CII. 56. *Zamia gutierrezi* Sauvalle. 57. *Z. muricata* Wild. 58. *Z. latifolia* Lodd. 59. *Z. furfuracea* L. fil. 60. *Z. ottonis* Miq. 61. *Z. silicea* Britton. 62. *Z. lindenii* Regel



CIII. 63. *Zamia pumila* L. 64. *Z. pumila* L. 65. *Z. fischeri* Miq. 66. *Z. pygmaea* Sims. 67. *Z. kickxii* Miq. 68. *Z. media* Jacq. 69. *Z. angustifolia* (Jacq.) Schuster. 70. *Z. latifoliata* Prenleloup. 71. *Z. floridana* A.DC.



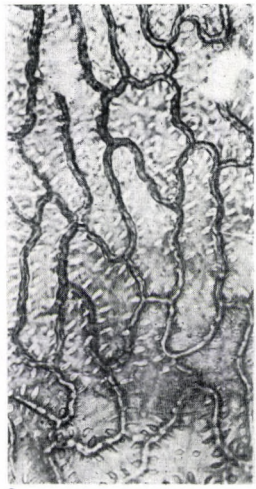
CIV. 72. *Encephalartos friderici-guilielmi* Lehm. 73. *Encephalartos manikensis* Gilligand. 74. *Encephalartos princeps* R.A. Dyer. 75a, b. *Encephalartos trispinosus* (Hook) R.A. Dyer. 76. *Stangeria paradoxa* Th. Moore



1



1a



2



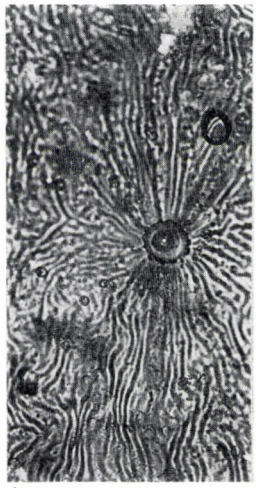
2a



3



3a



4



4a



5



5a



6



6a

CV. 1,1a. *Cycas revoluta* Thunb. 2,2a. *Cycas rumphii* Miq. 3,3a. *Microcycas calocoma* (Miq.) A.DC. 4,4a. *Stangeria paradoxa* Th. Moore. 5,5a. *Bowenia serrulata* (W. Bull) Chamberlain. 6,6a. *Dioon edule* Lindl.



7



7 a



8



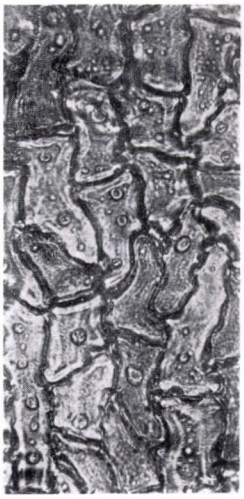
8 a



9



9 a



10



10 a



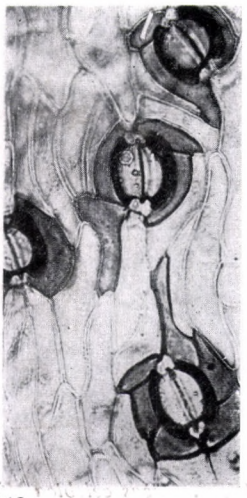
11



11 a

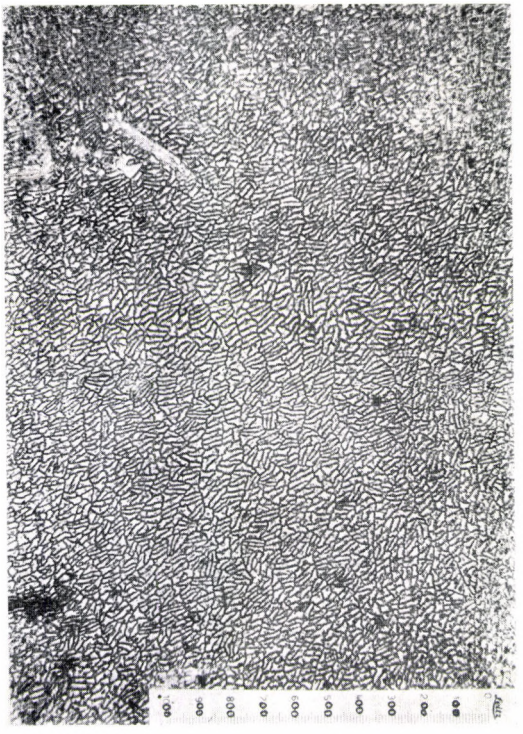


12



12 a

CVI. 7,7a. *Encephalartos tegulanus* Melville. 8,8a. *Encephalartos septentrionalis* Schweinf. 9,9a. *Ceratozamia mexicana* Brongn. 10,10a. *Macrozamia communis* L. Johnson. 11,11a. *Lepidozamia peroffskyana* Regel. 12,12a. *Zamia muricatà* Willd.



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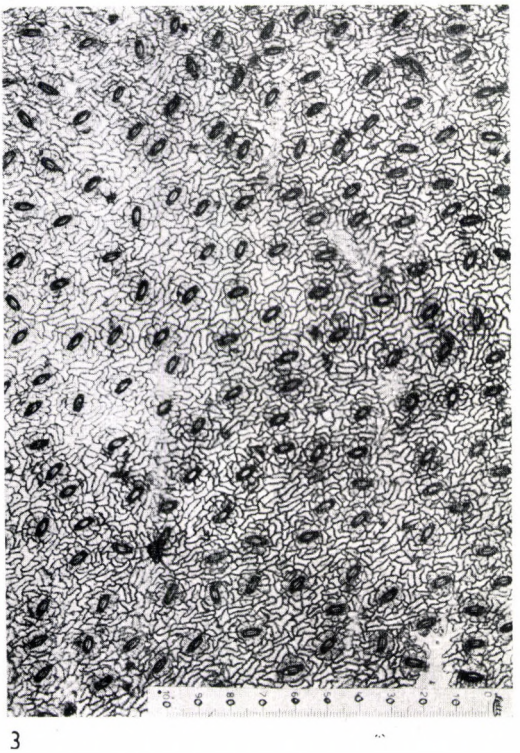

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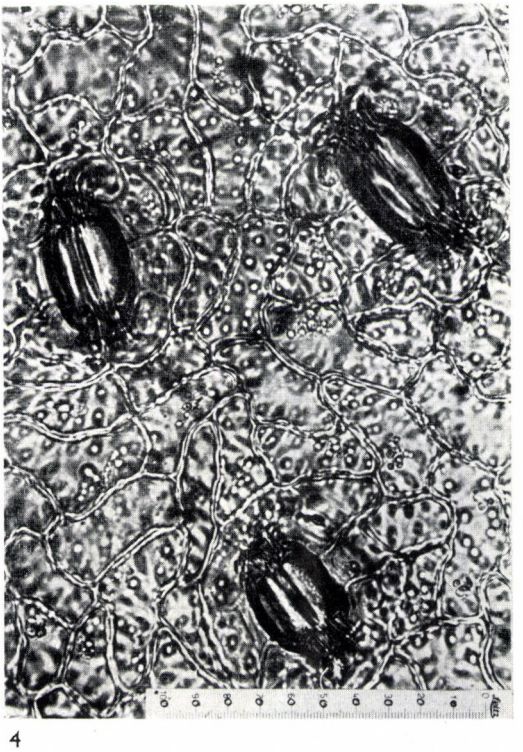
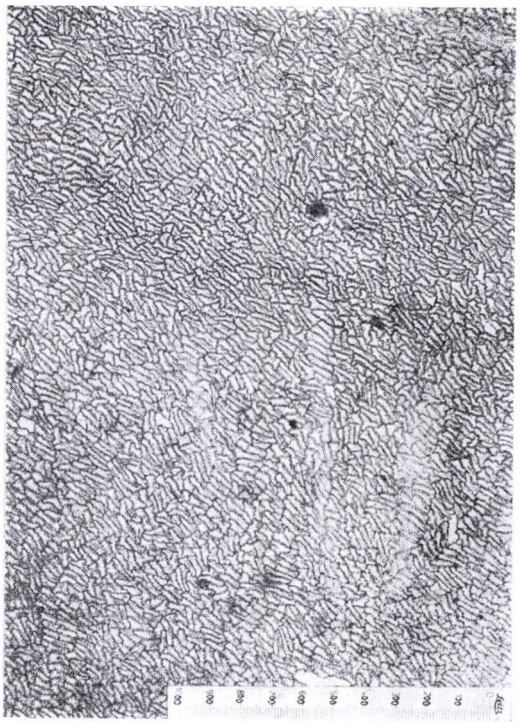


4

CVII. *Cycas celebica* Miq.
1. upper surface [x40]. 2. upper surface [x400]. 3. undersurface [x40]. 4. undersurface [x400]



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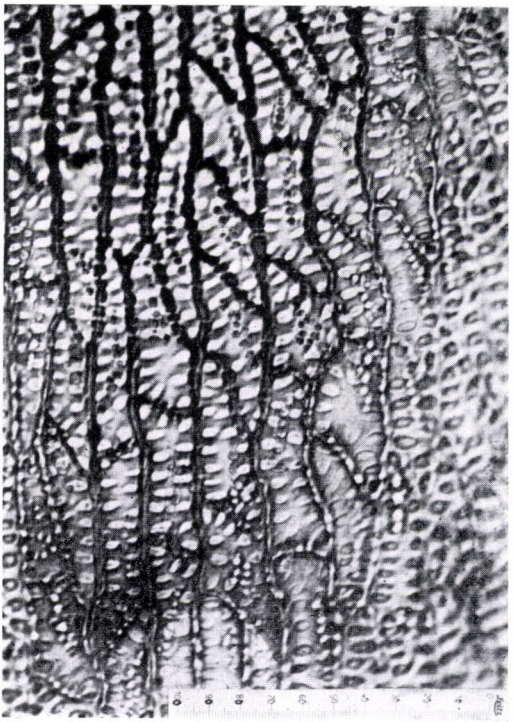

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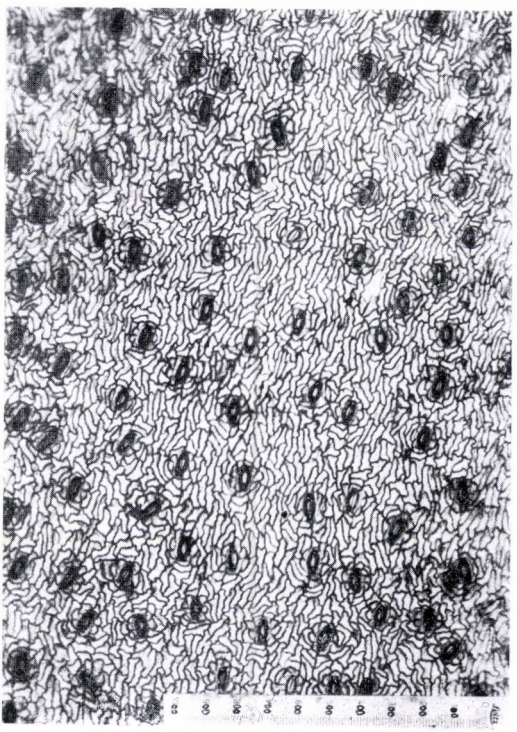

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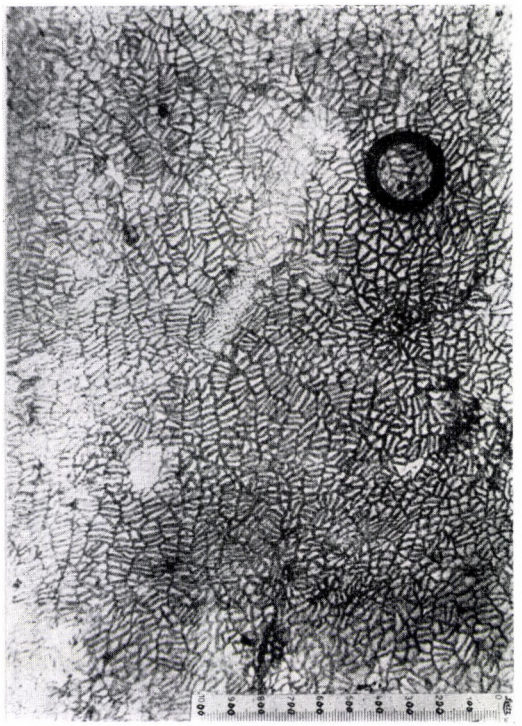
4

CVIII. *Cycas circinalis* L.



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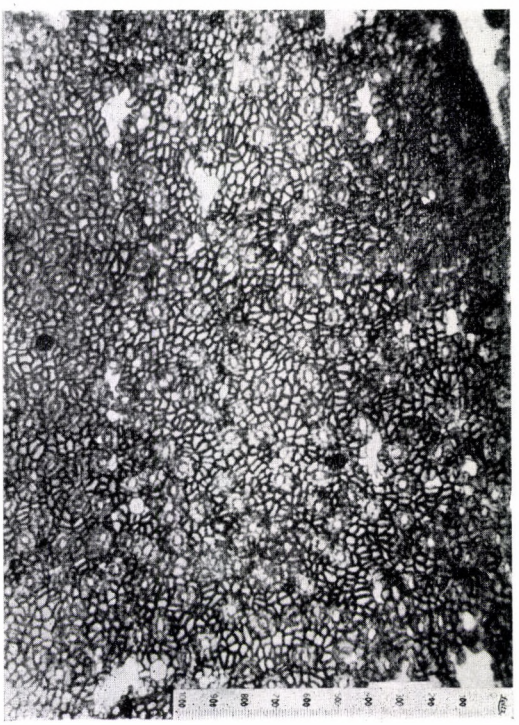

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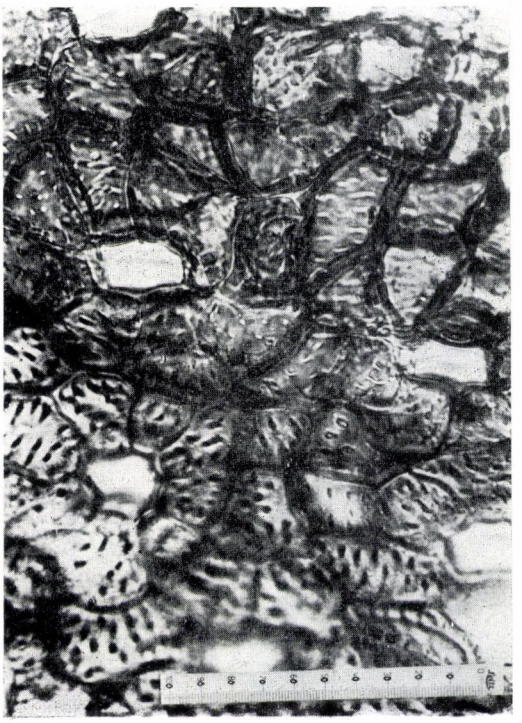
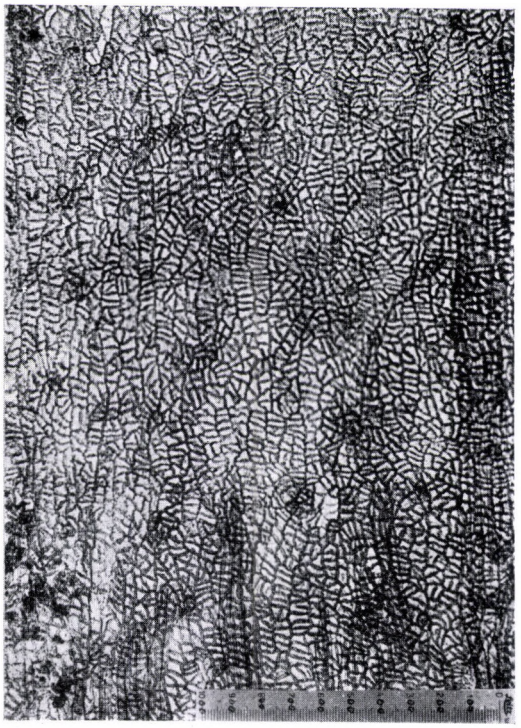


4

CIX. *Cycas media* R.Br.



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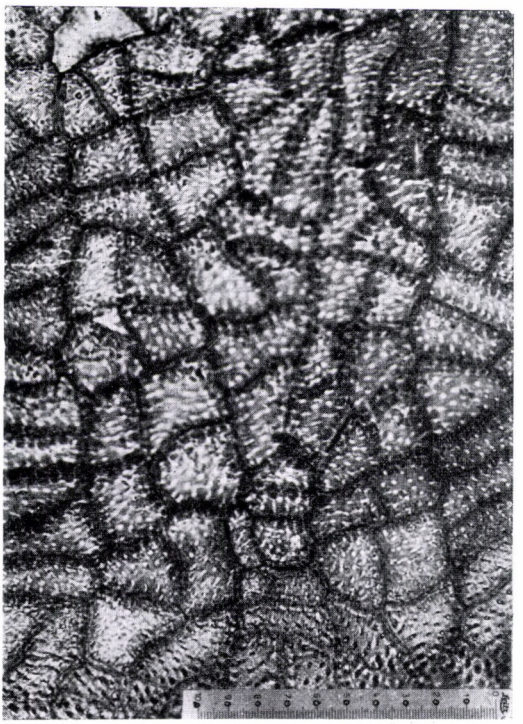

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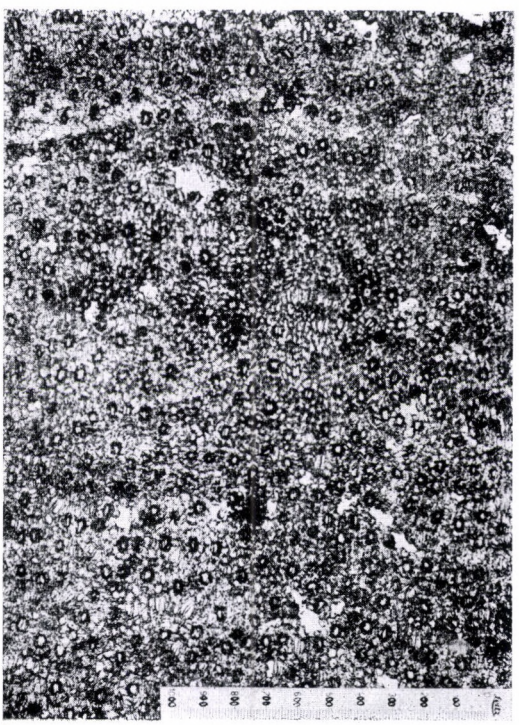

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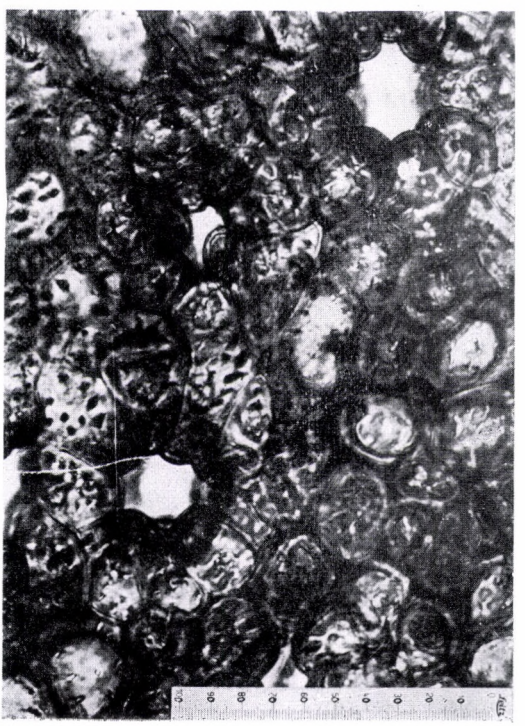
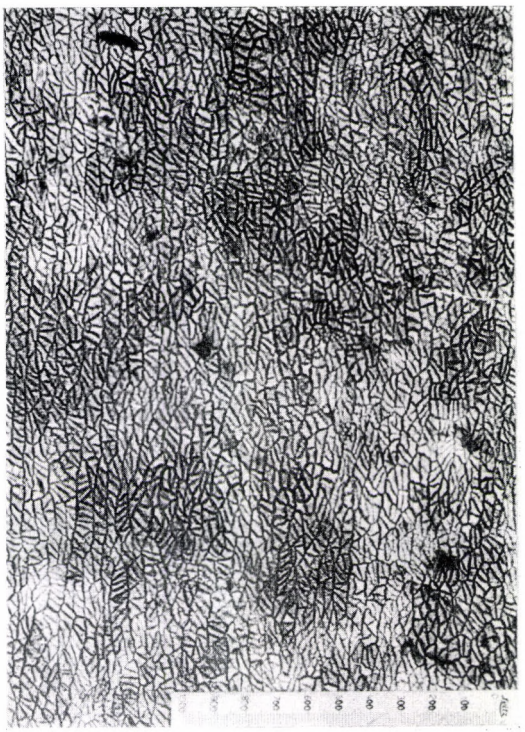


4

CX. *Cycas neocaledonica* Linden



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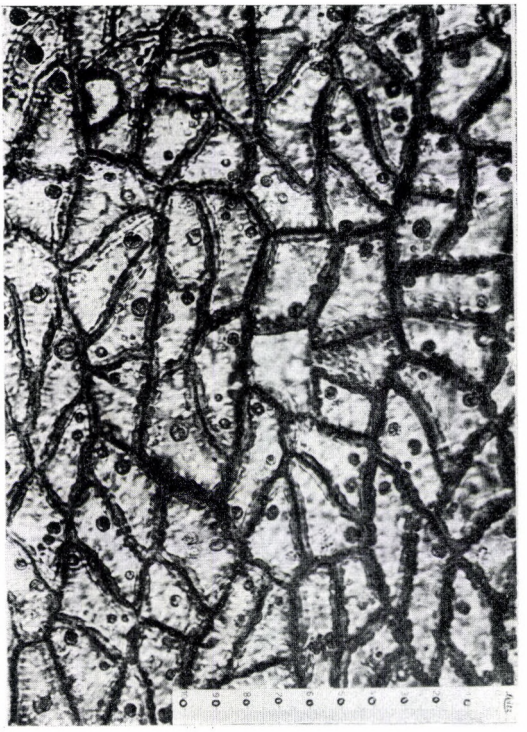

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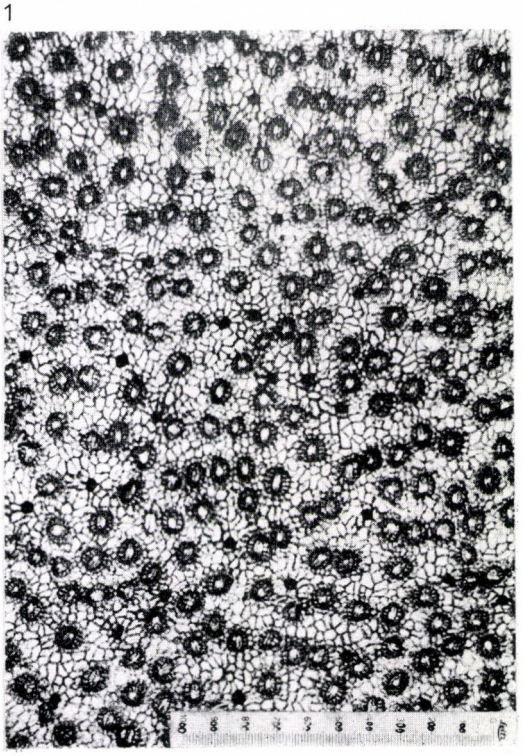

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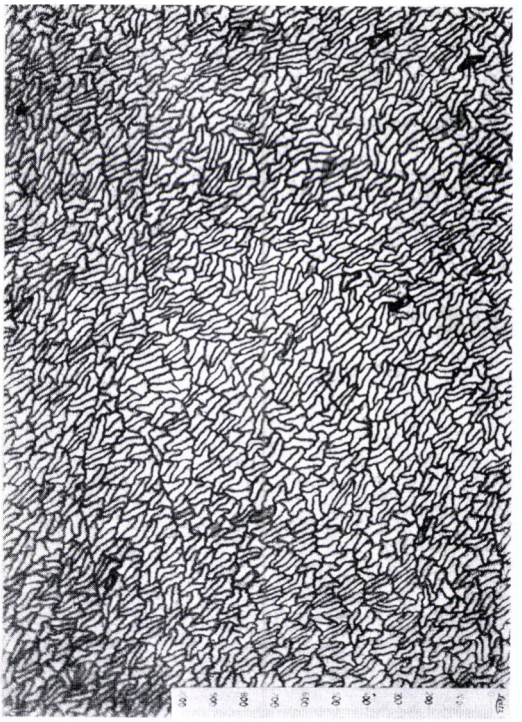
4

CXI. *Cycas revoluta* Thunb.



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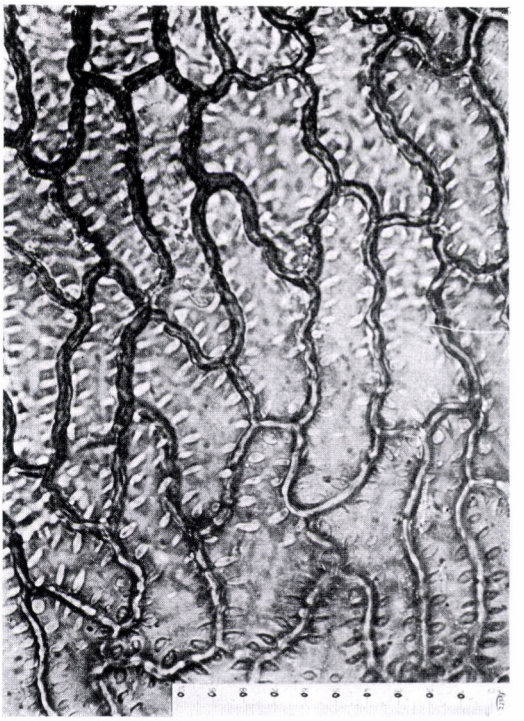

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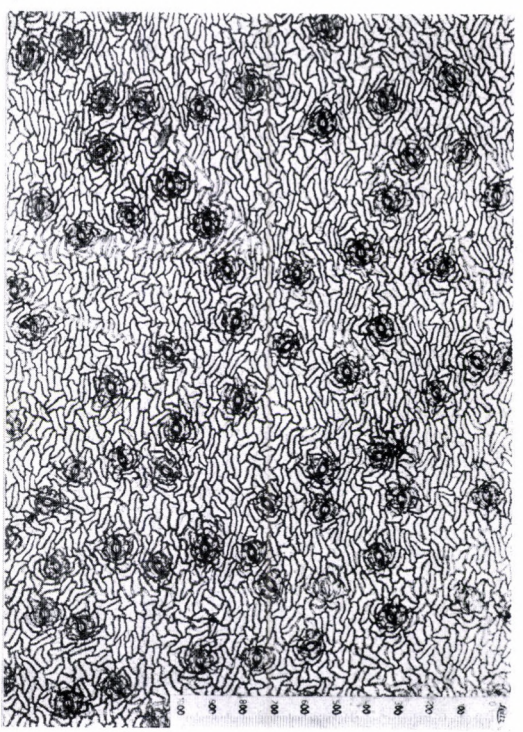

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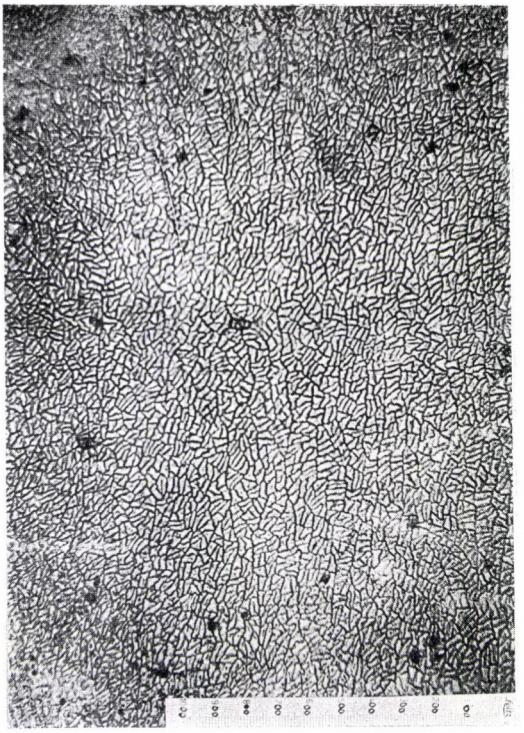
4

CXII. *Cycas rumphii* Miq.



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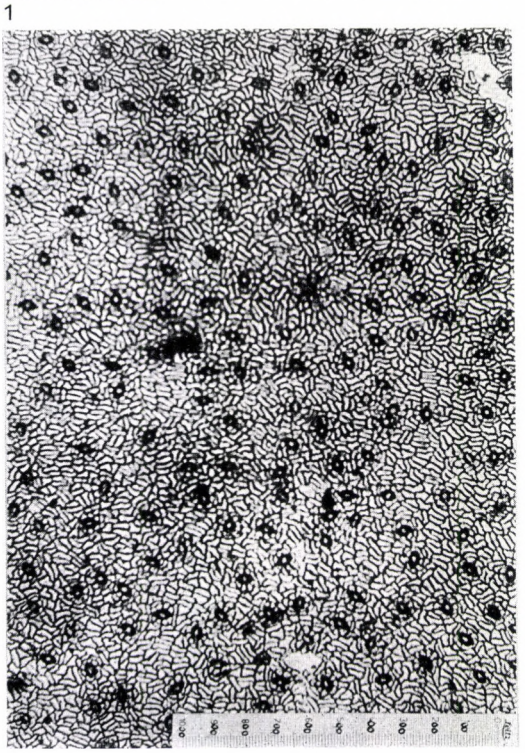

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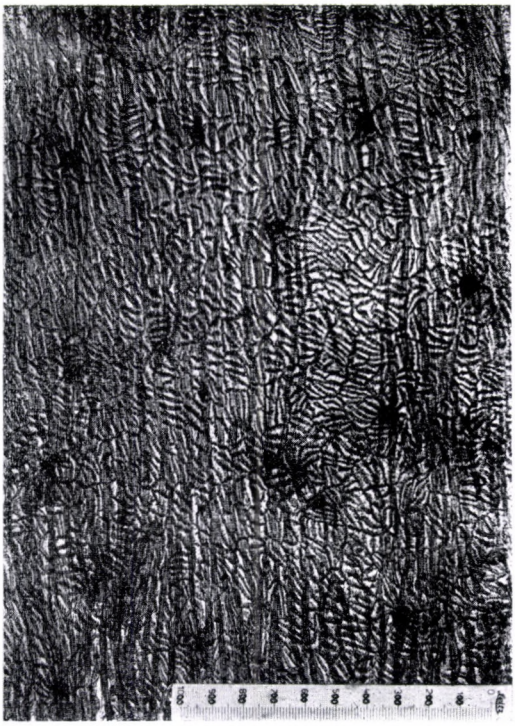
4

CXIII. *Cycas seemannii* A. Braun



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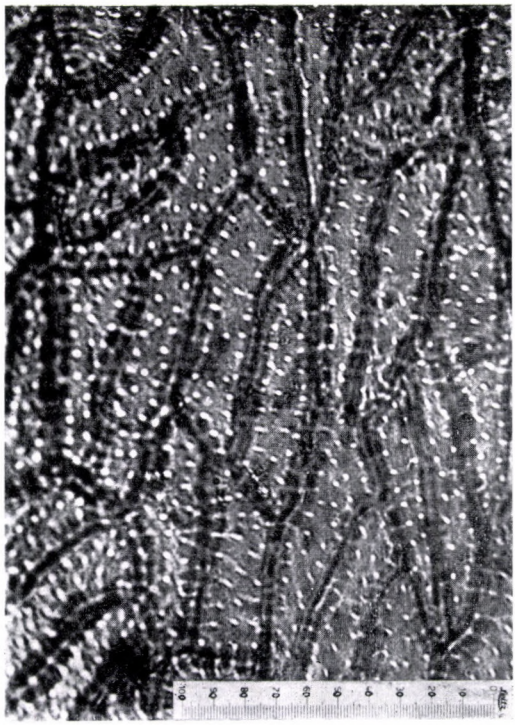

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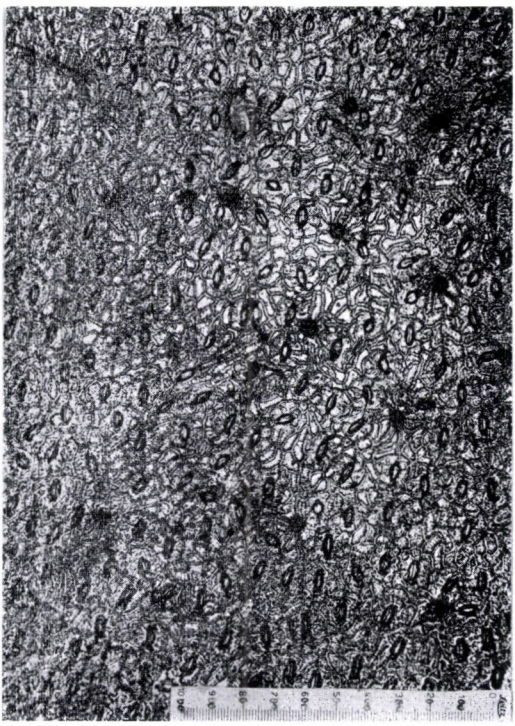

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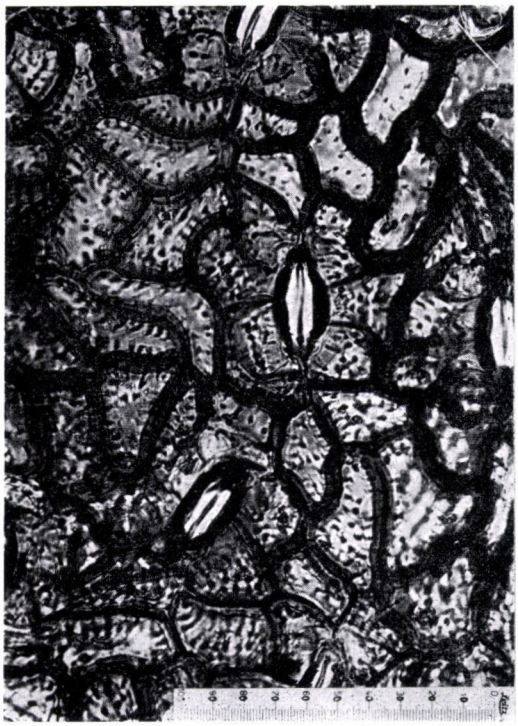

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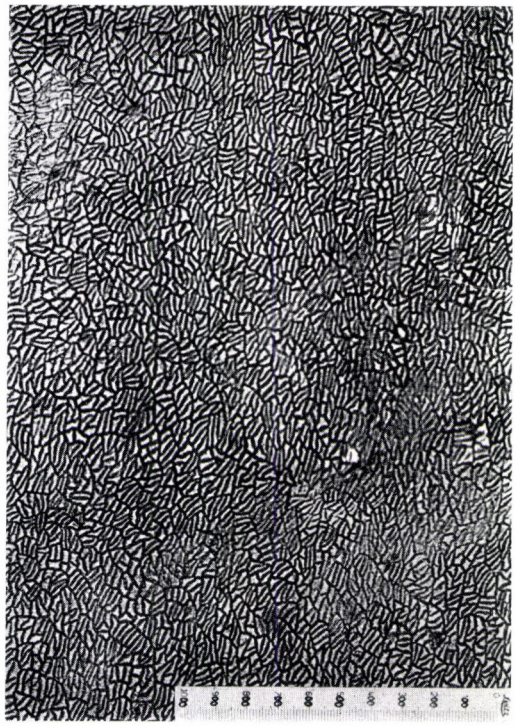
CXIV. *Cycas siamensis* Miq.



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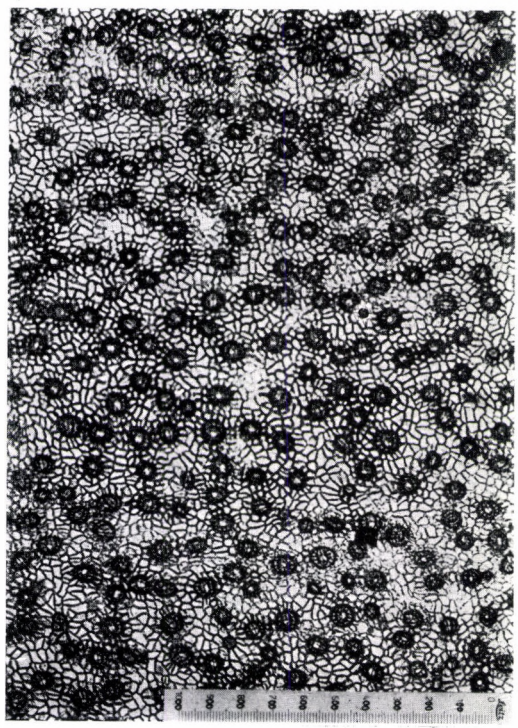

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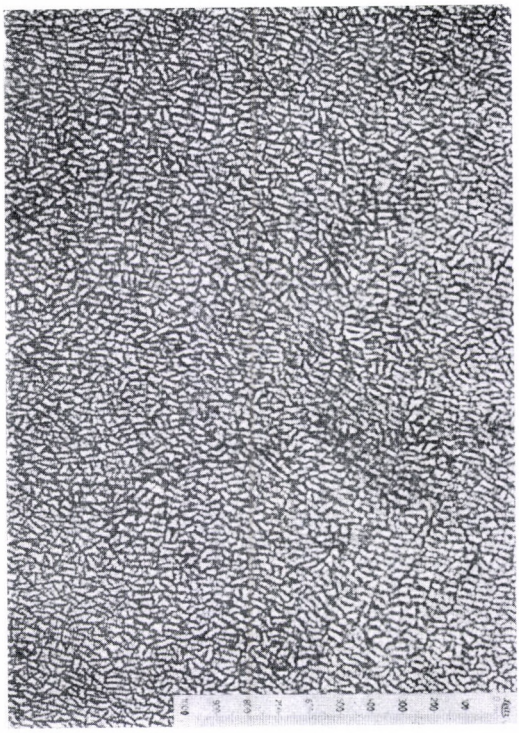
4

CXV. *Cycas taiwaniana* Carruth.



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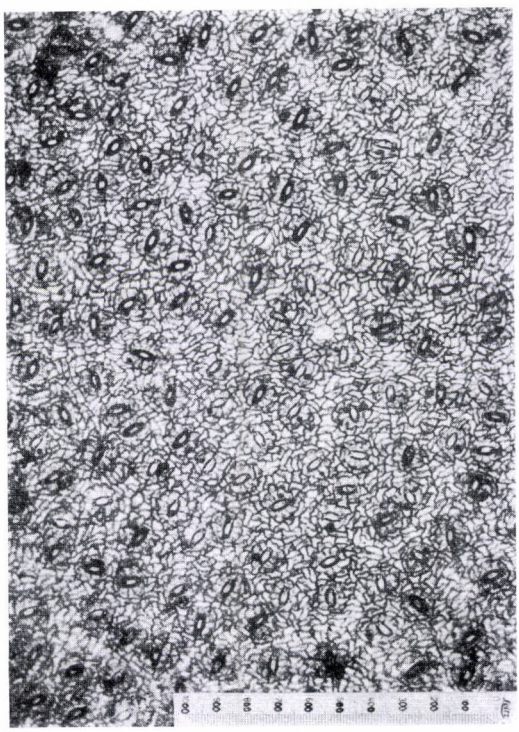
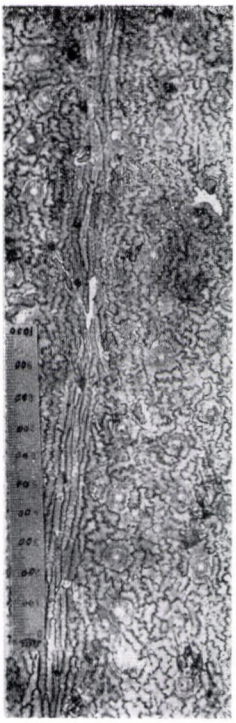


3



4

CXVI. *Cycas thouarsii* R. Brown



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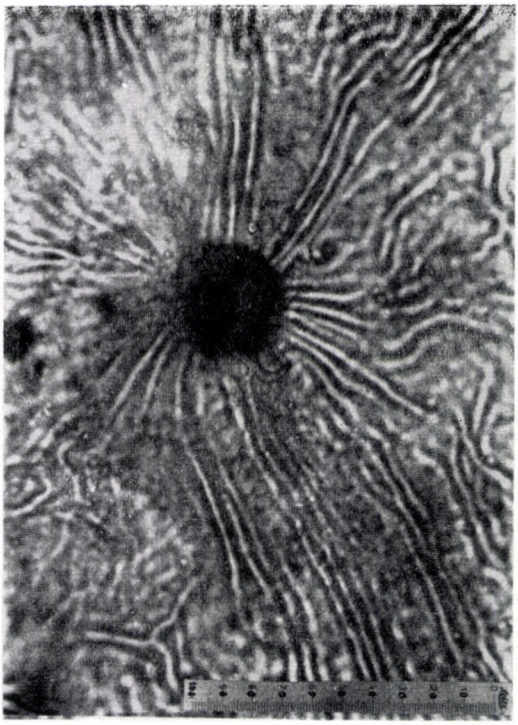

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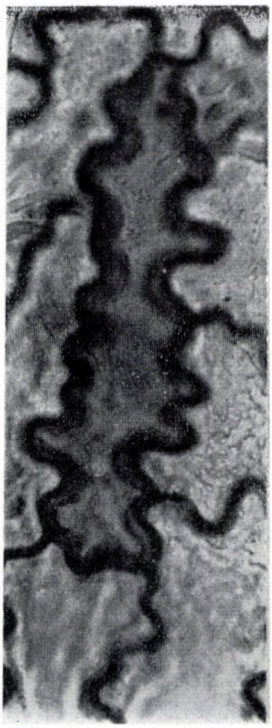

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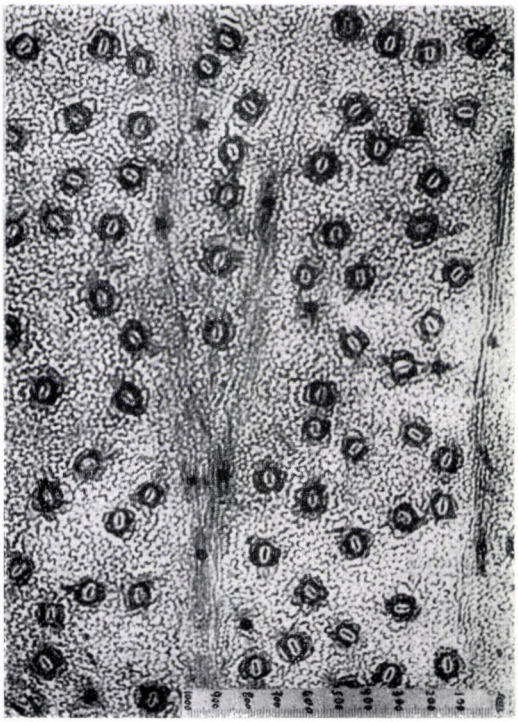

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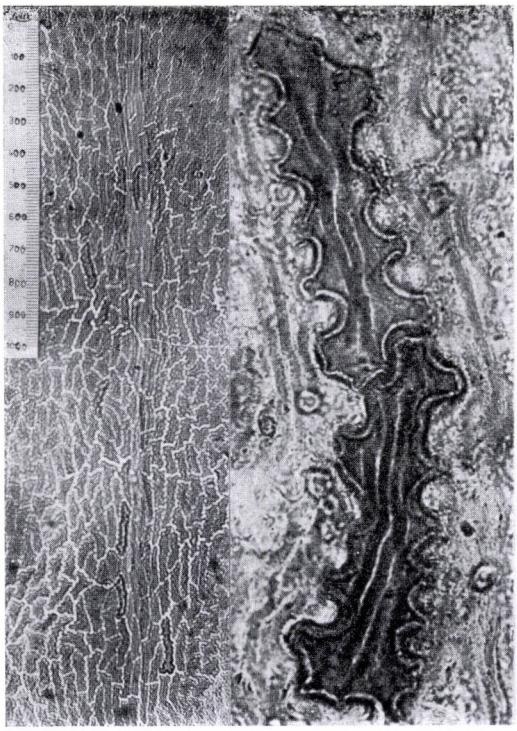
CXVII. *Stangeria eriopus* Nash



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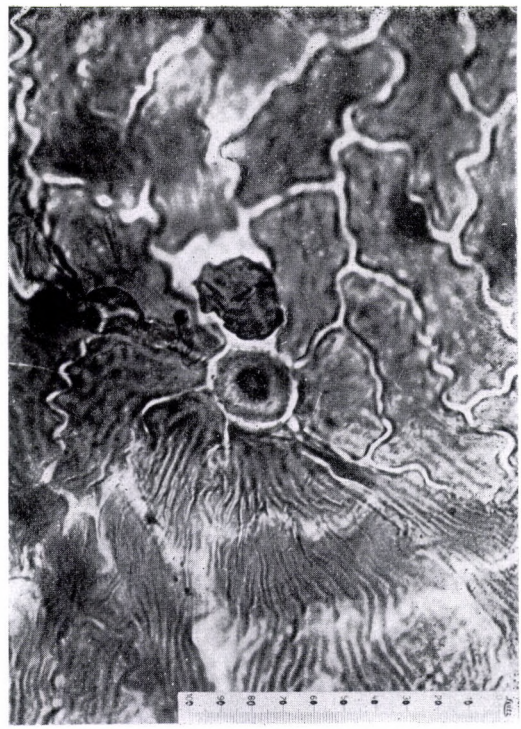

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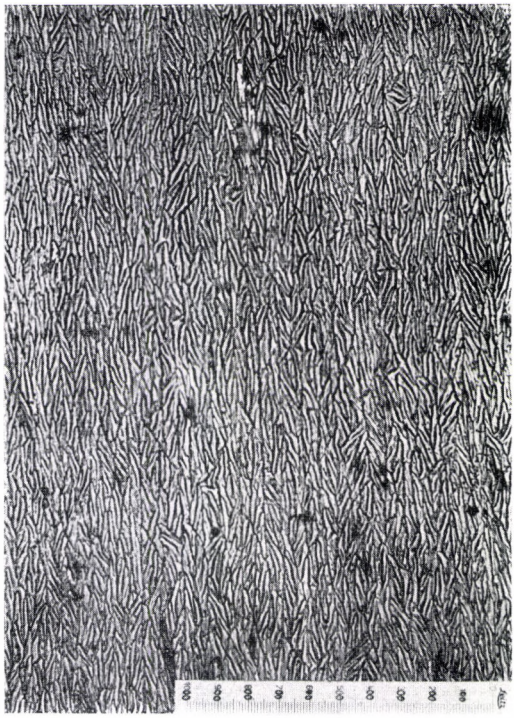
CXVIII. *Stangeria paradoxa* Th. Moore



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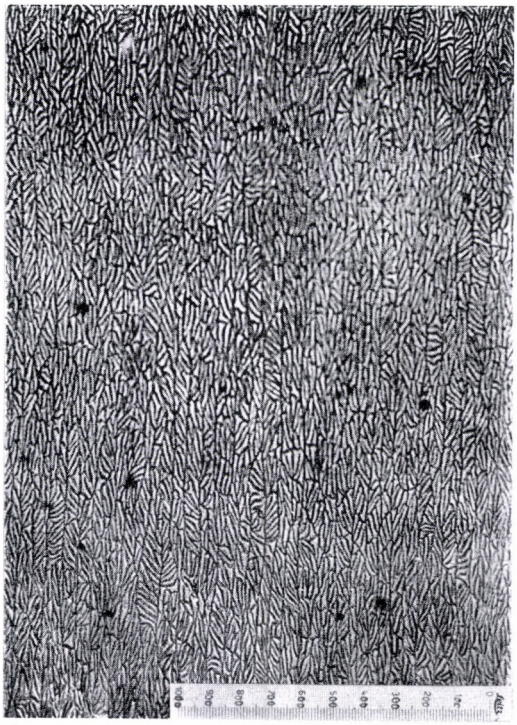
CXIX. *Lepidozamia hopei* Regel



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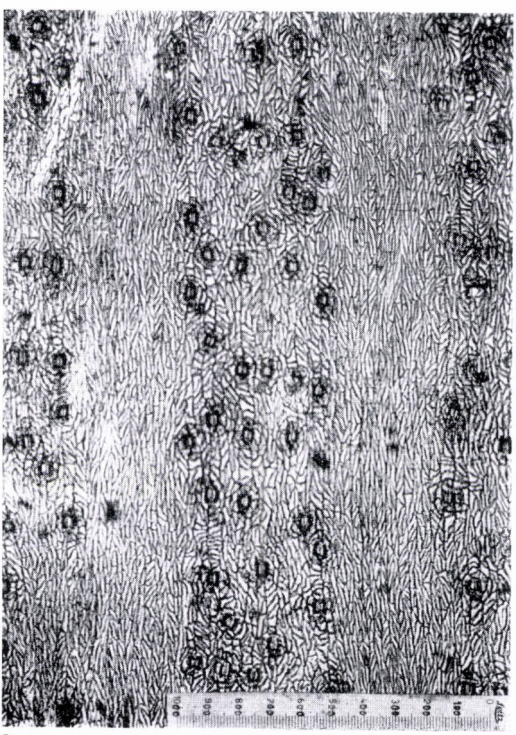

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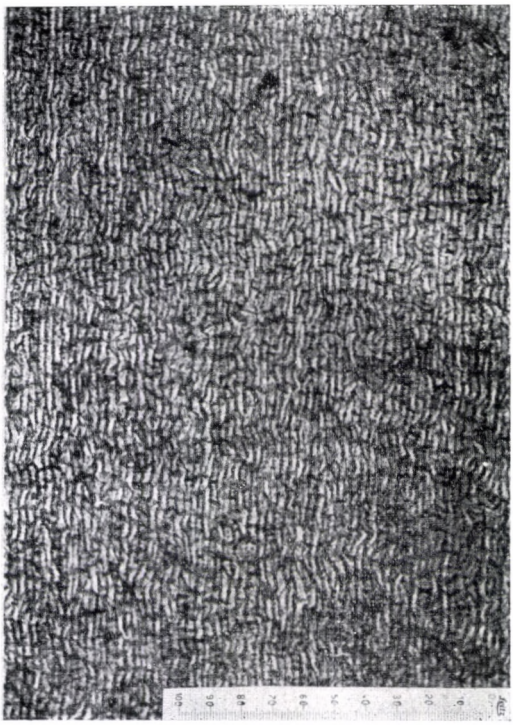
CXX. *Lepidozamia peroffskyana* Regel



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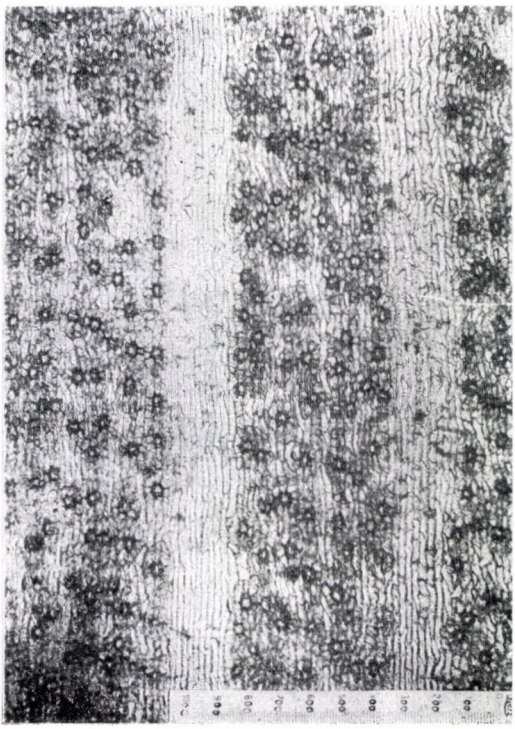

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CXXI. *Macrozamia communis* L. Johnson



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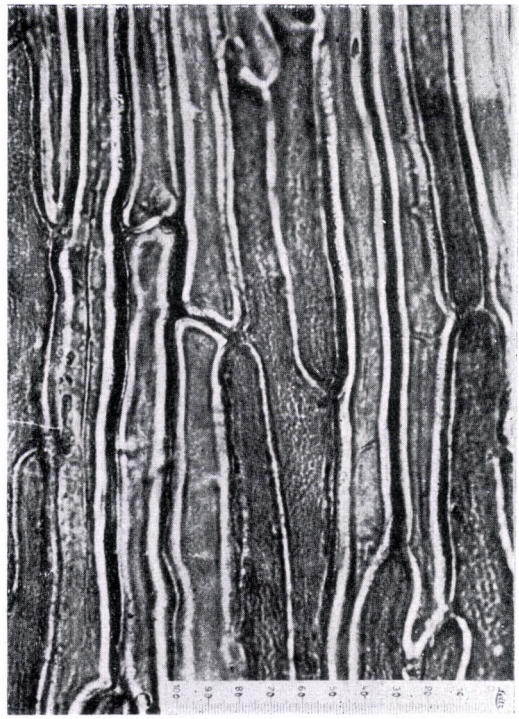

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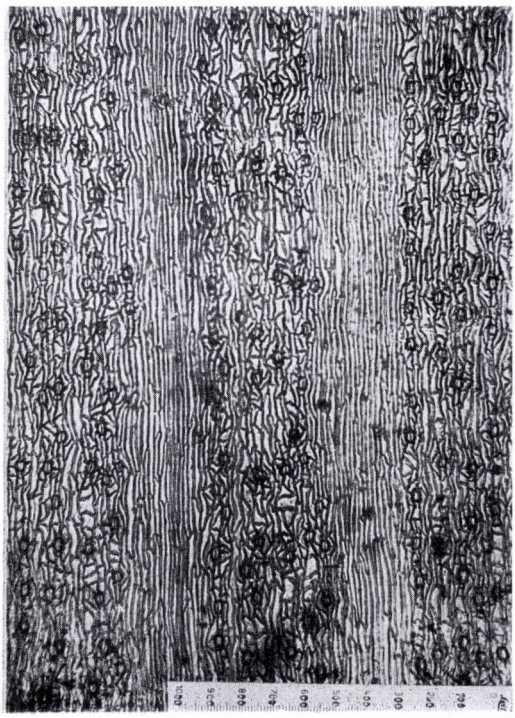

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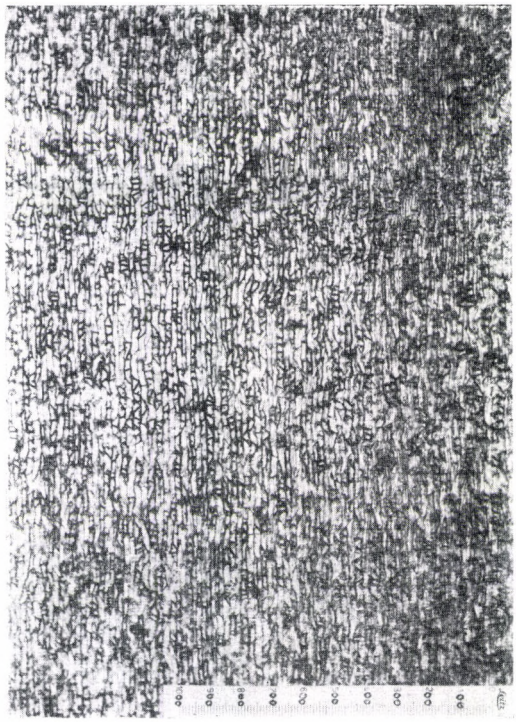
CXXII. *Macrozamia fawcettii* C. Moore



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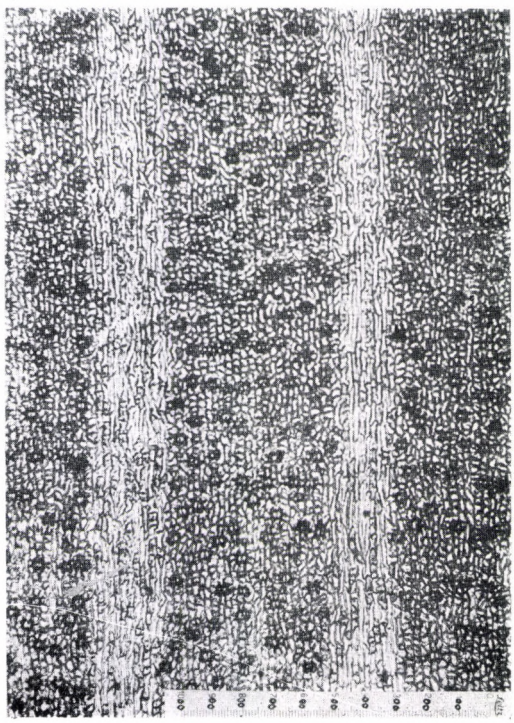

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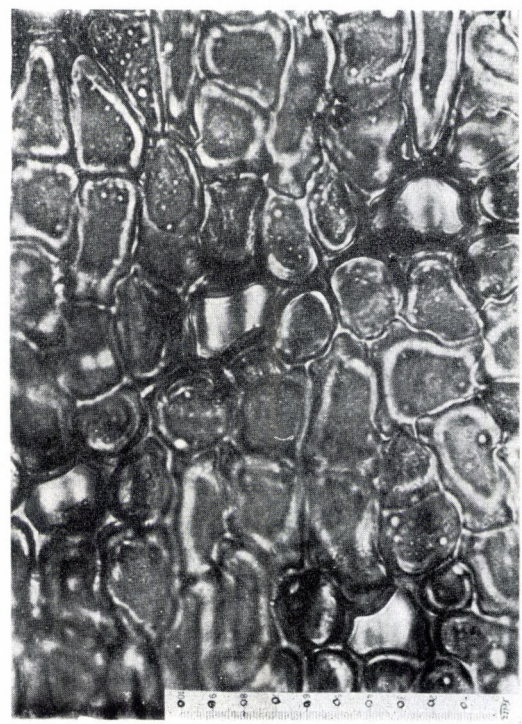

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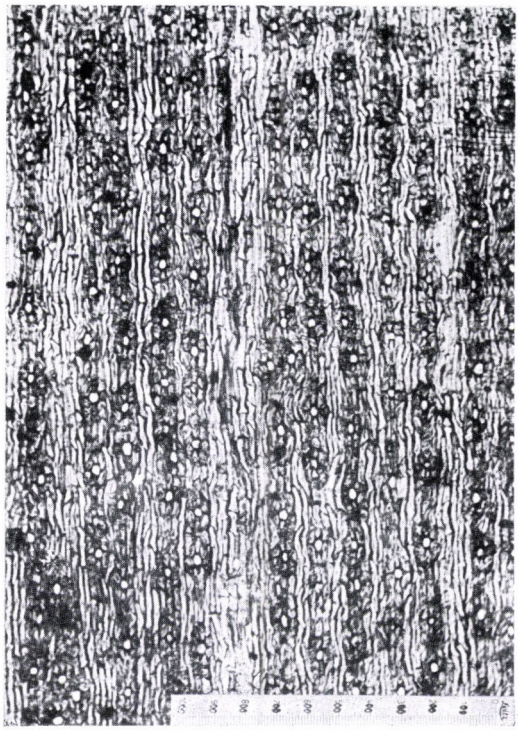
CXXIII. *Macrozamia macdonnelli* (F. Muell.) A. DC.



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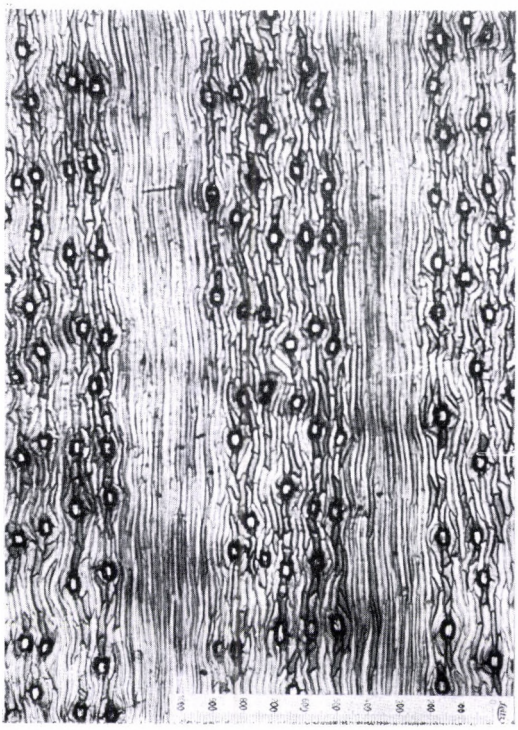

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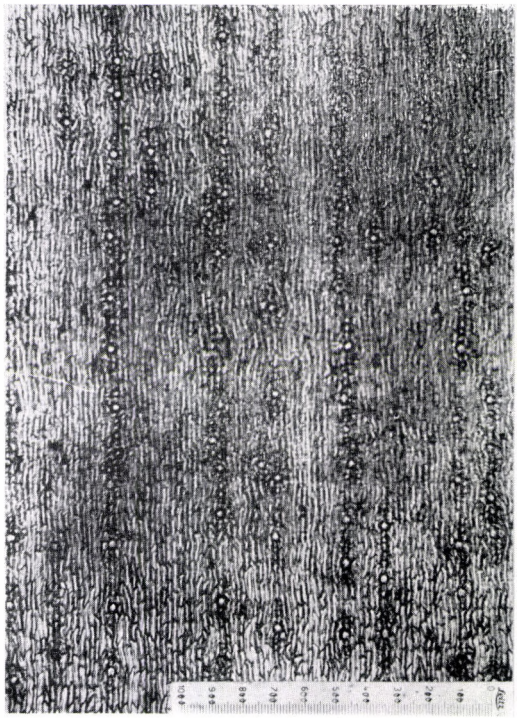
CXXIV. *Macrozamia miquelii* (F. Muell.) A.DC.



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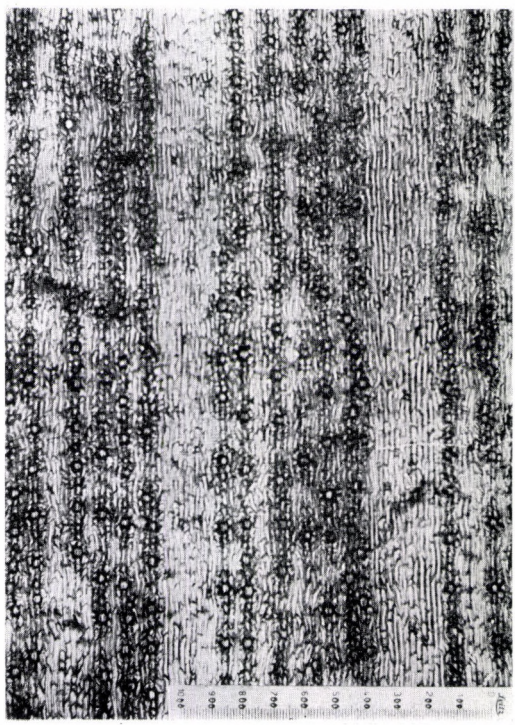

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CXXV. *Macrozamia moorei* F. Muell.



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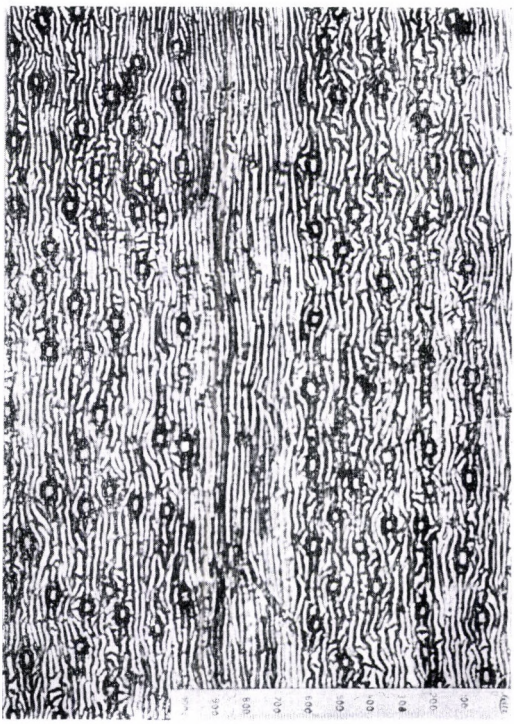
2



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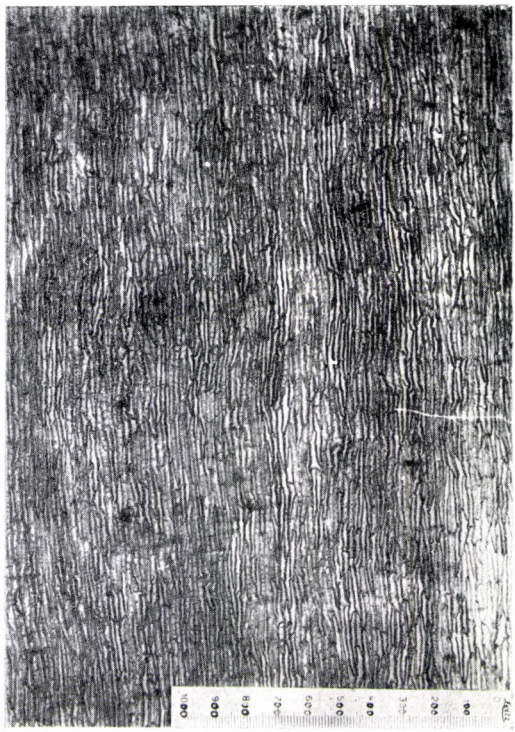
CXXVI. *Macrozamia pauli-guilielmi* W. Hill et F. Muell.



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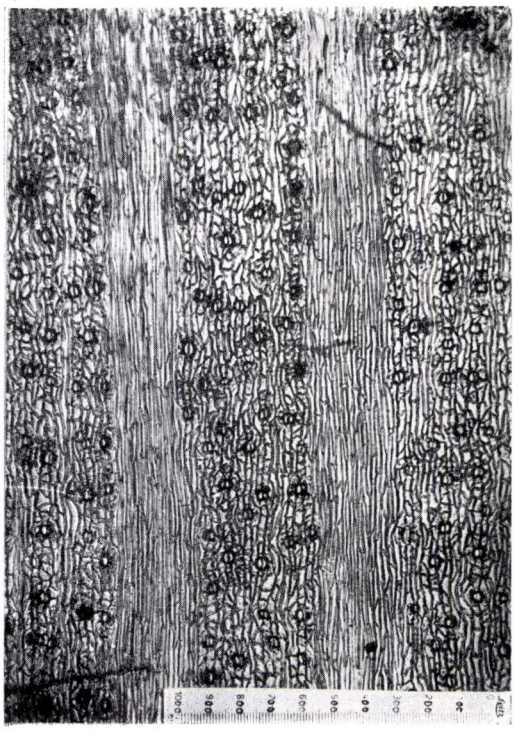

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CXXVII. *Macrozamia secunda* C. Moore



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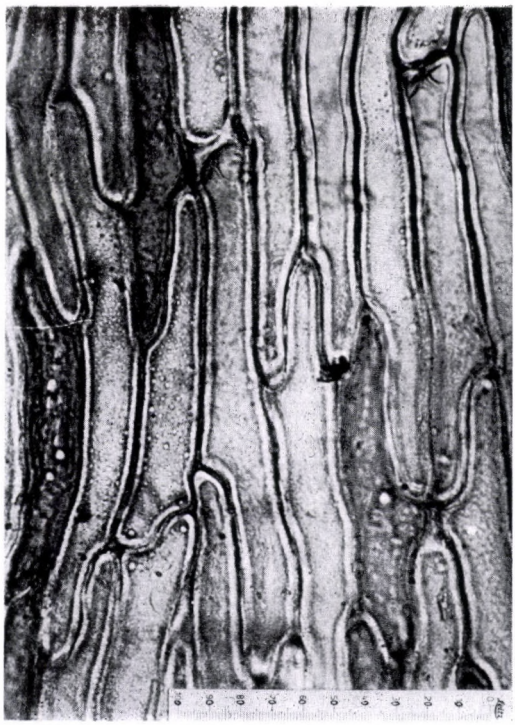

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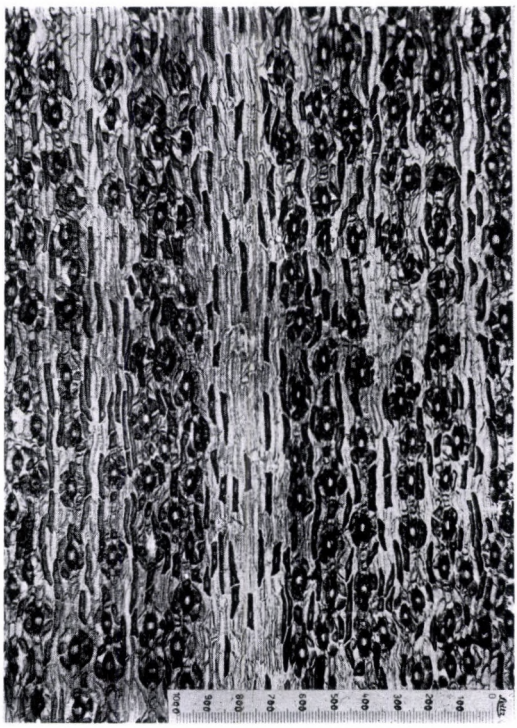

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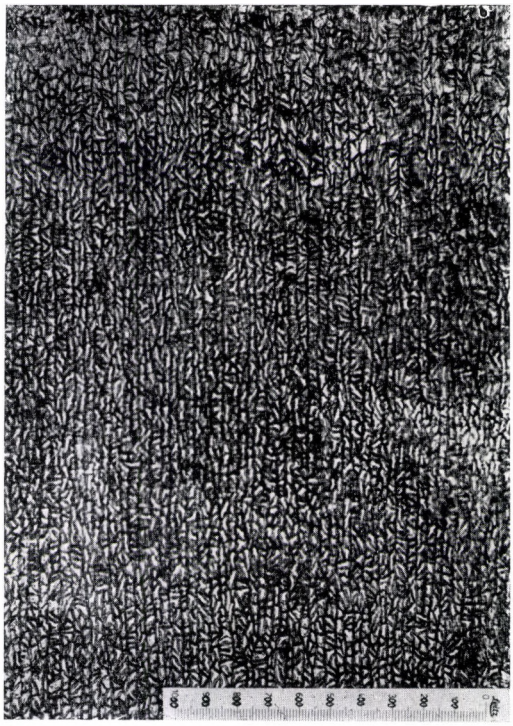
CXXVIII. *Macrozamia spiralis* (Salisb.) Miq.



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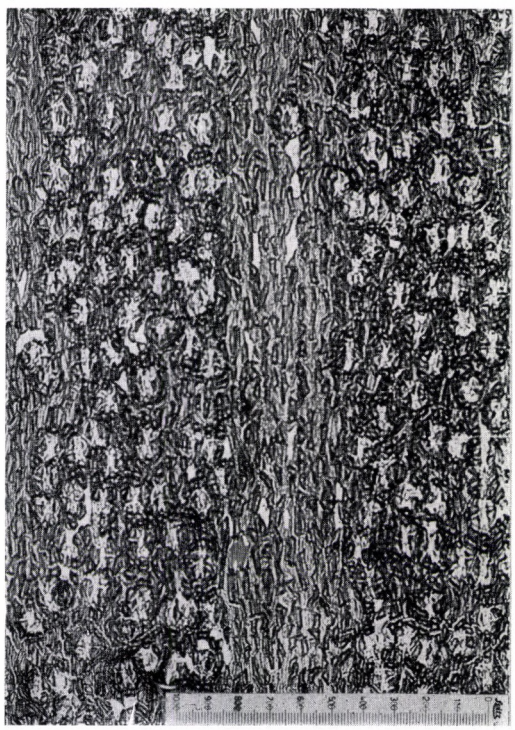

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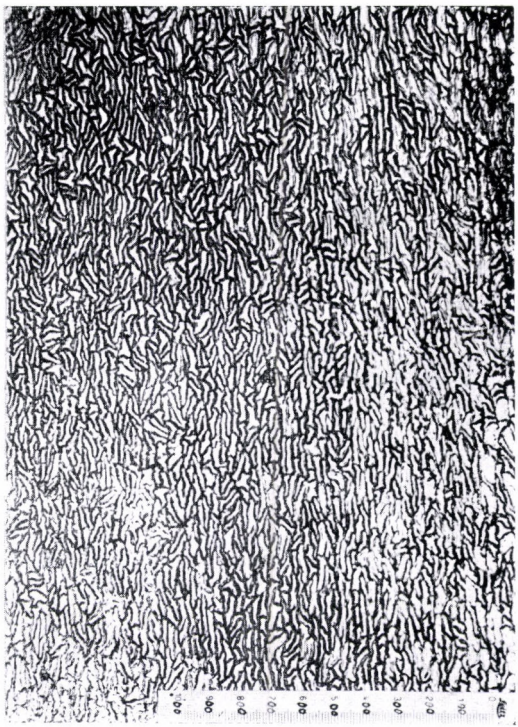
CXXIX. *Encephalartos altensteinii* Lehm.



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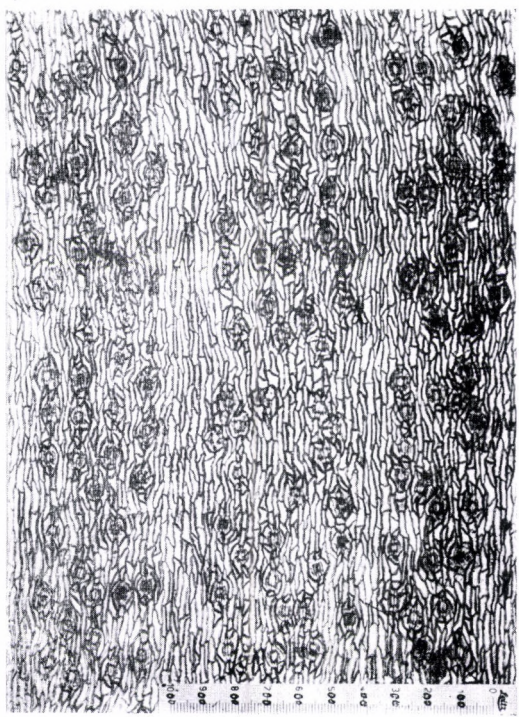

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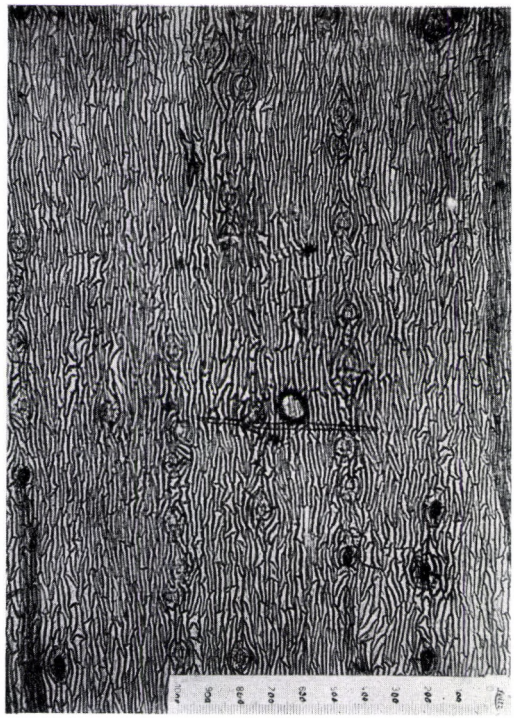
CXXX. *Encephalartos arenarius* R.A. Dyer



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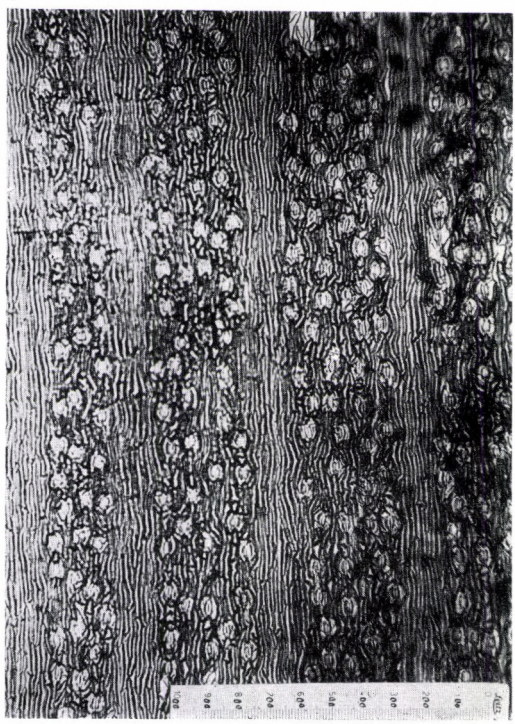

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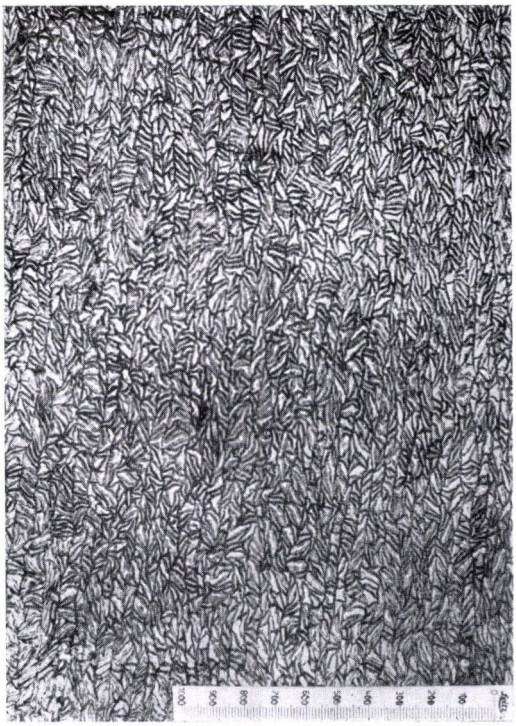
CXXXI. *Encephalartos barteri* Carruthers



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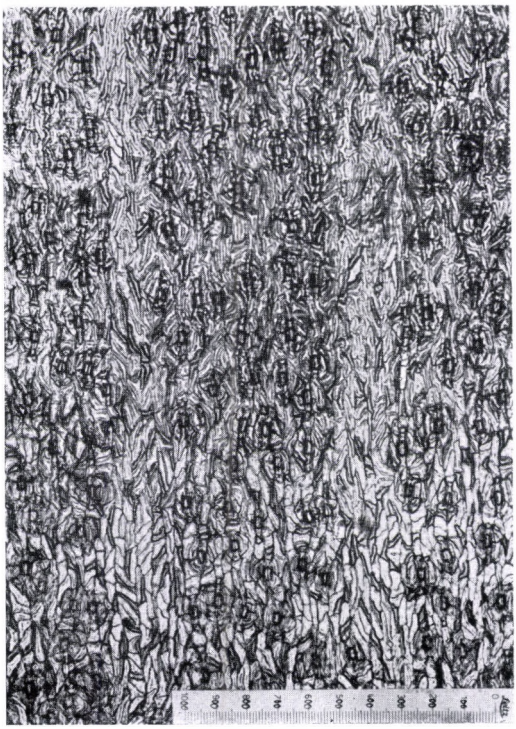

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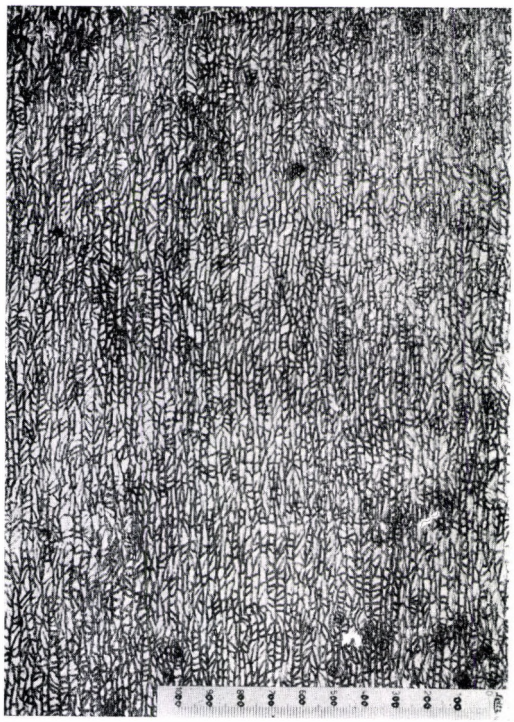
CXXXII. *Encephalartos bubalinus* Melville



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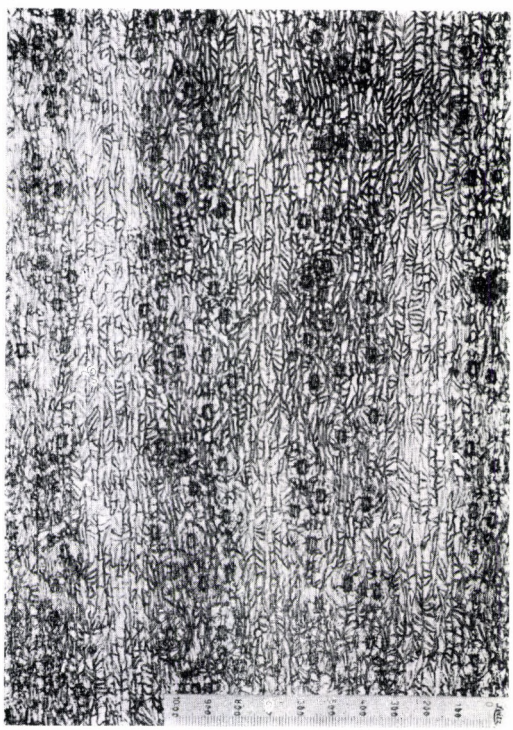

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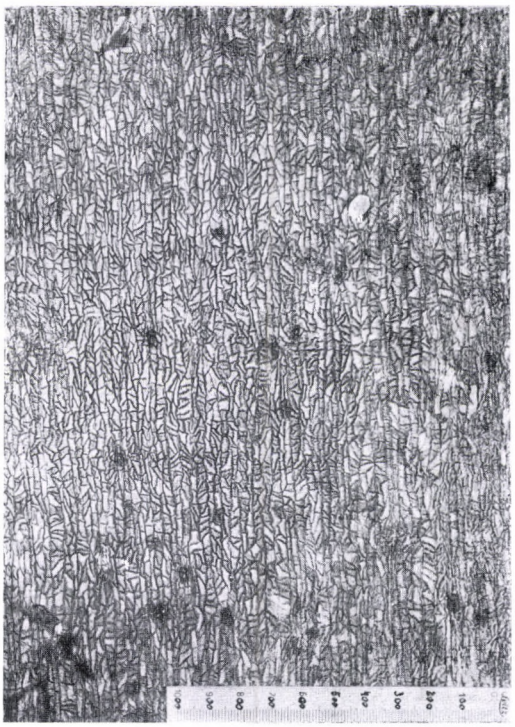
CXXXIII. *Encephalartos caffer* (Thunb.) Miq.



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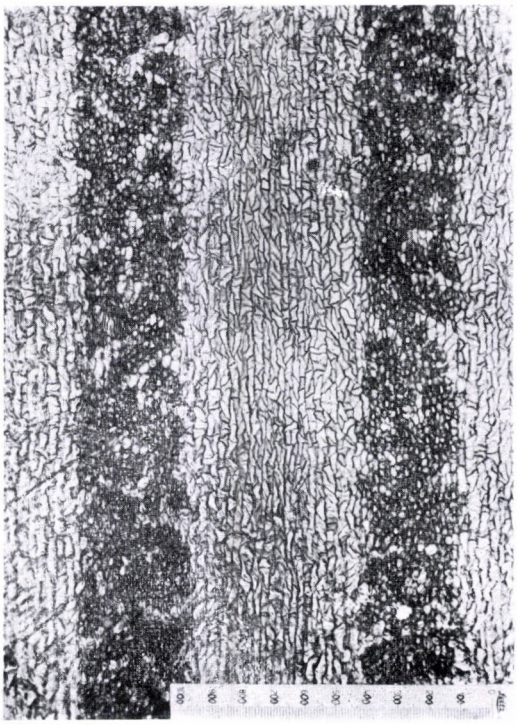

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CXXXIV. *Encephalartos cycadifolius* (Jacq.) Lehm.



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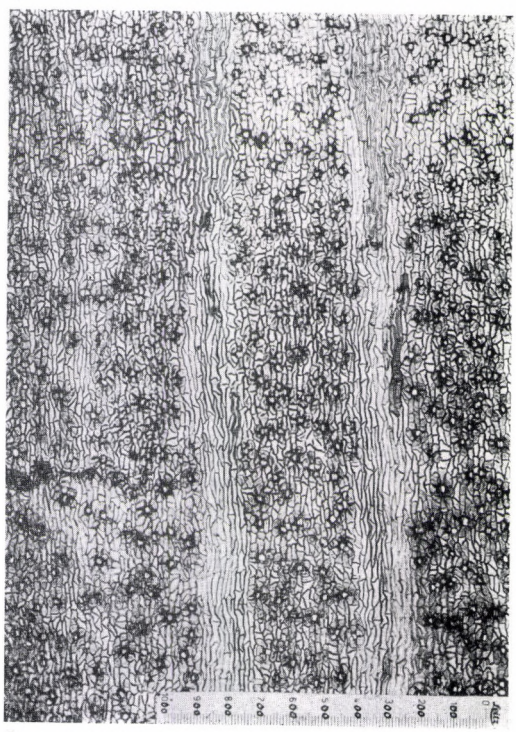

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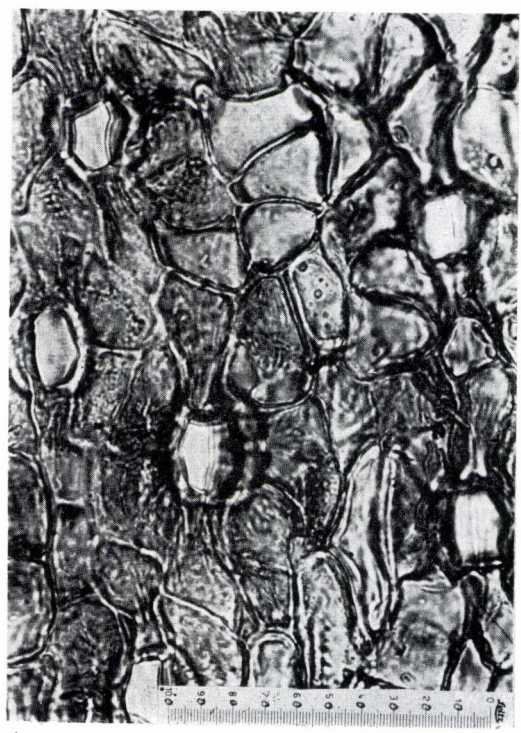

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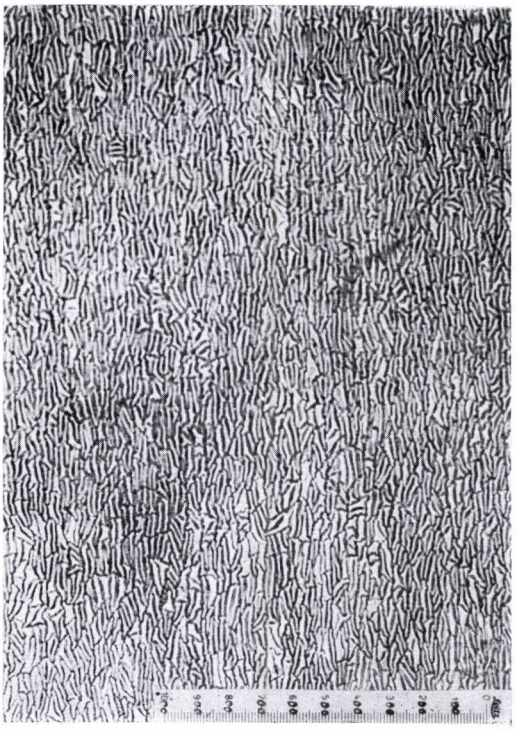
CXXXV. *Encephalartos eximius* Verdoorn



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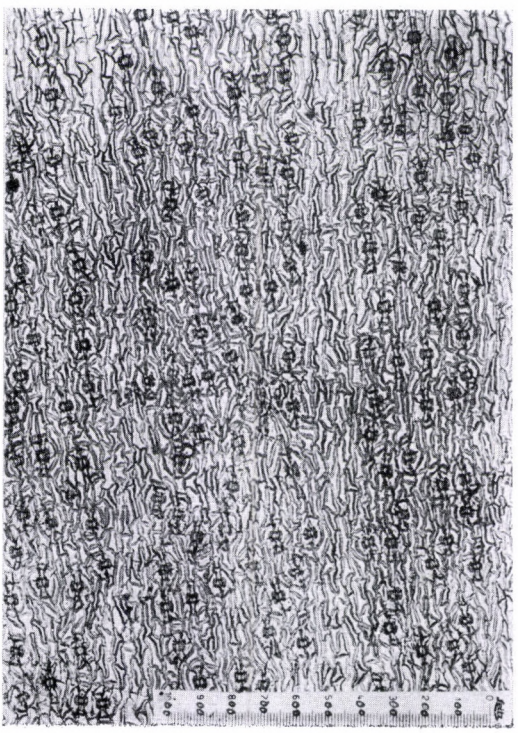

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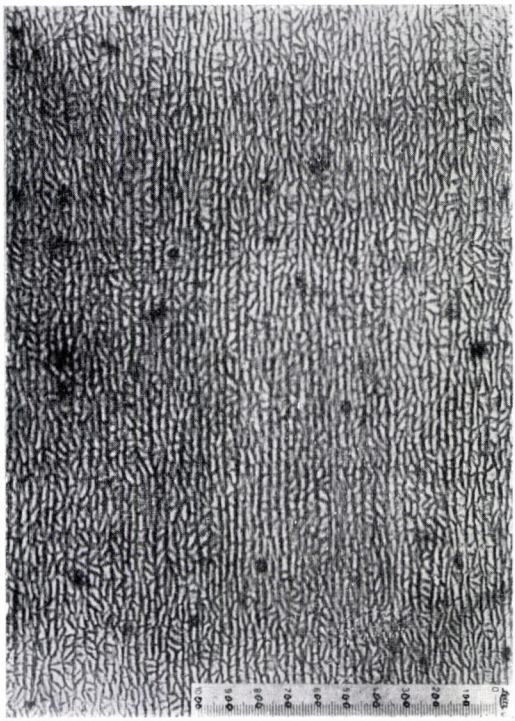
CXXXVI. *Encephalartos ferox* Bertol.



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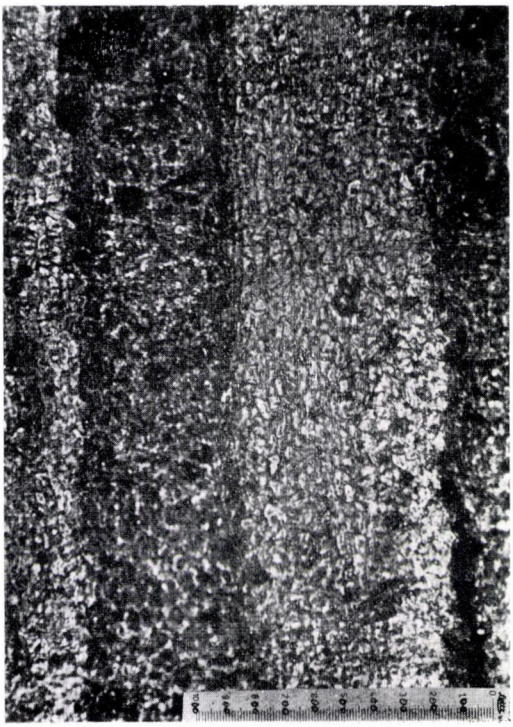

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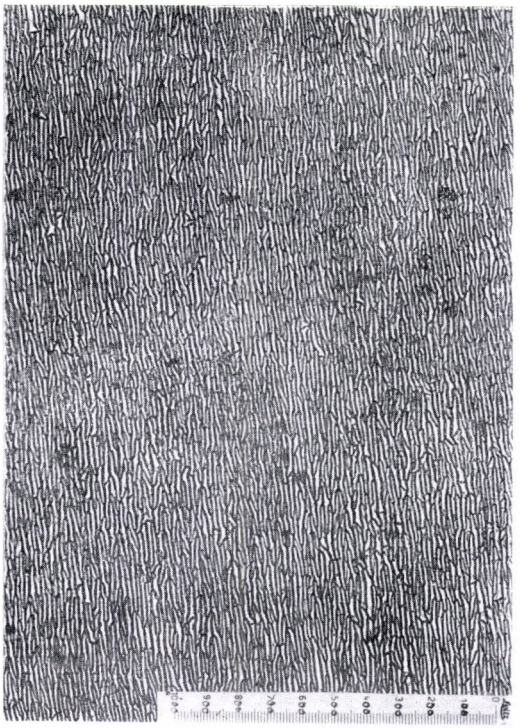
CXXXVII. *Encephalartos friderici-guilielmi* Lehm.



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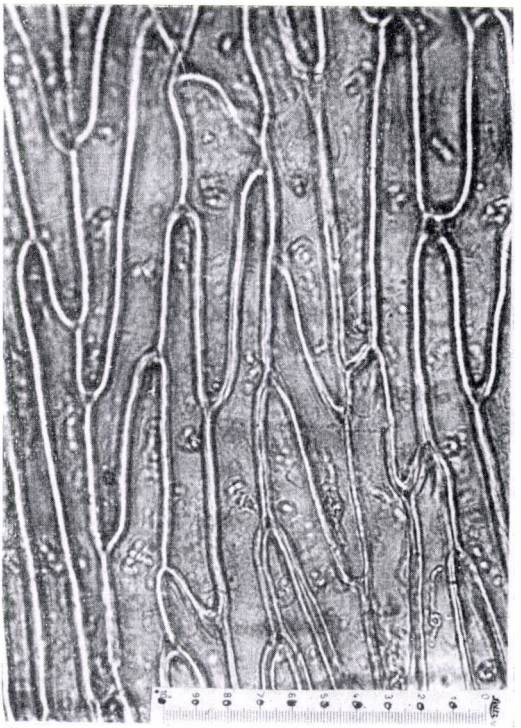

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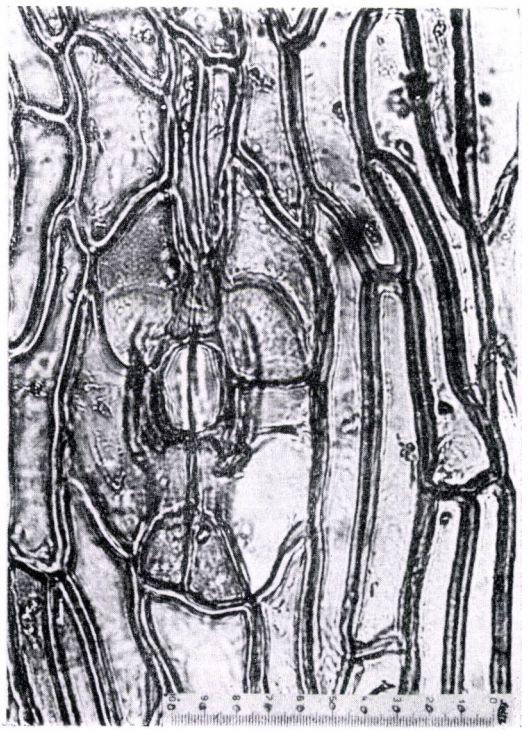

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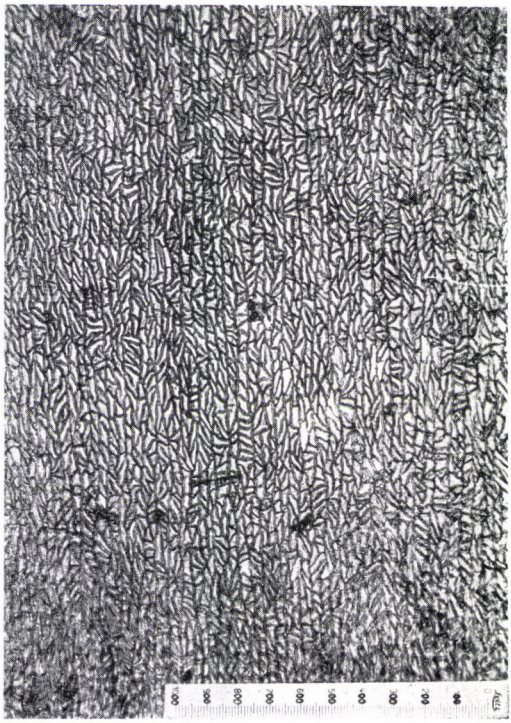
CXXXVIII. *Encephalartos gratus* Prain.



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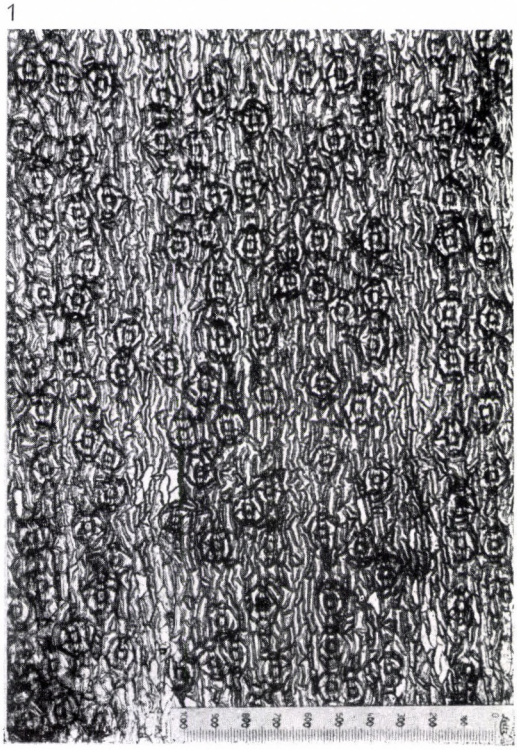

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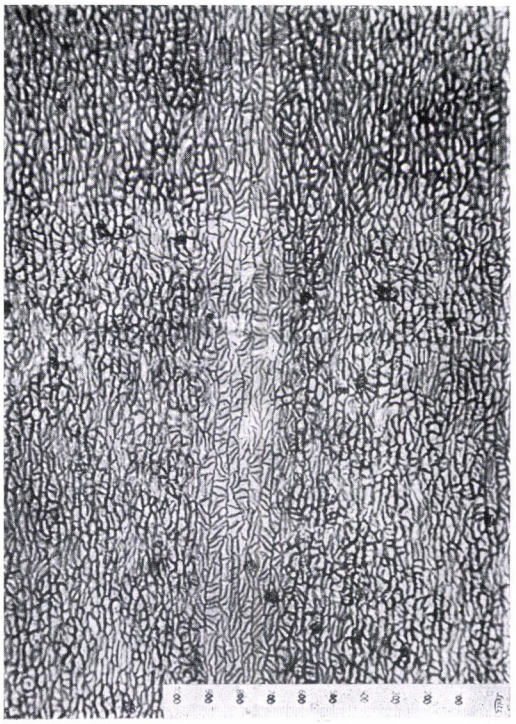
CXXXIX. *Encephalartos hildebrandtii* A. Braun et Bouché



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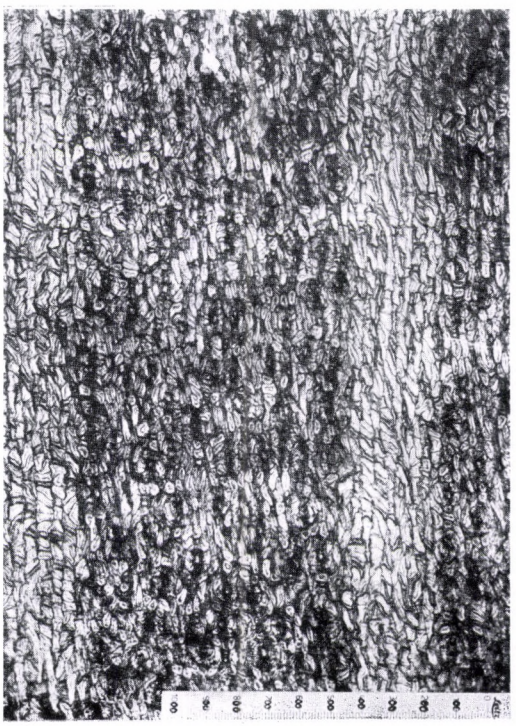

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CXL. *Encephalartos horridus* Lehm.



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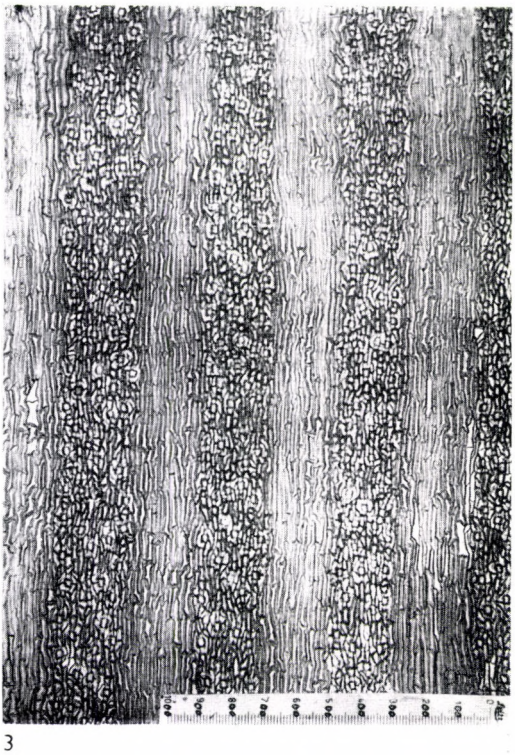

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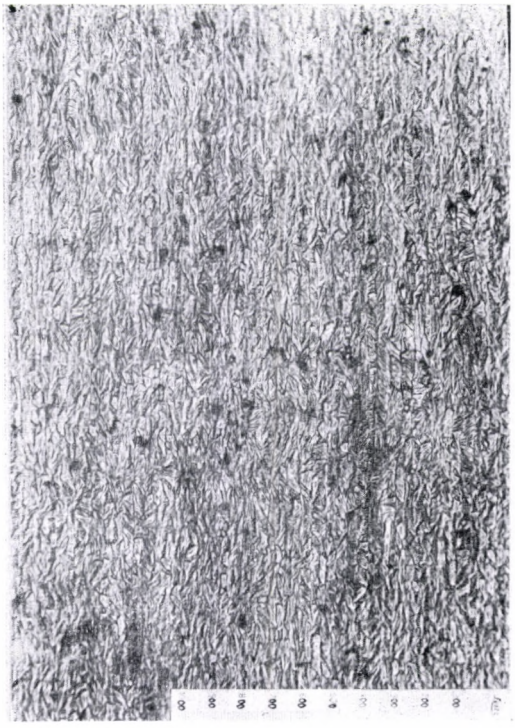
CXLI. *Encephalartos humilis* Verdoorn



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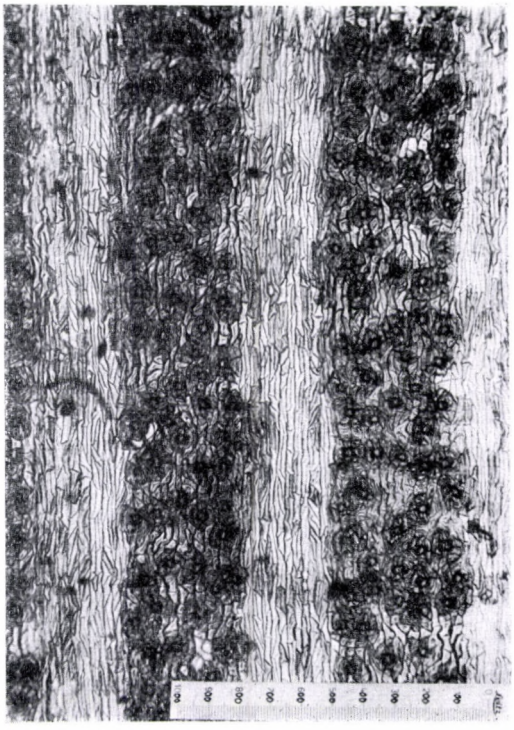

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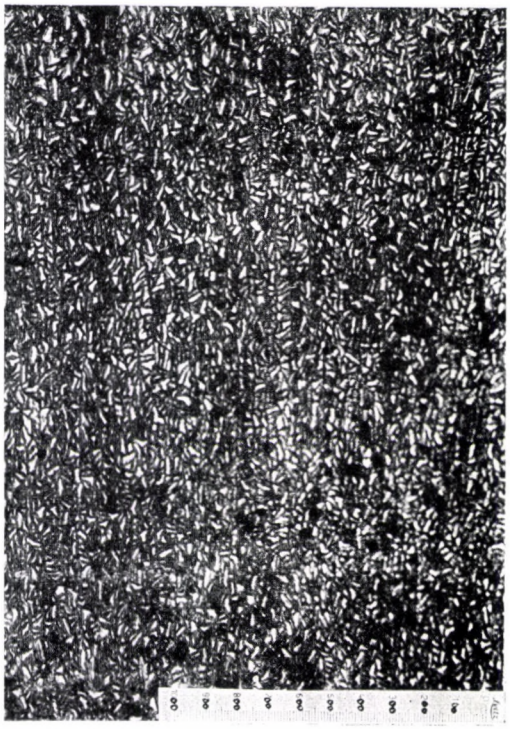
4

CXLII. *Encephalartos inopinus* R.A. Dyer



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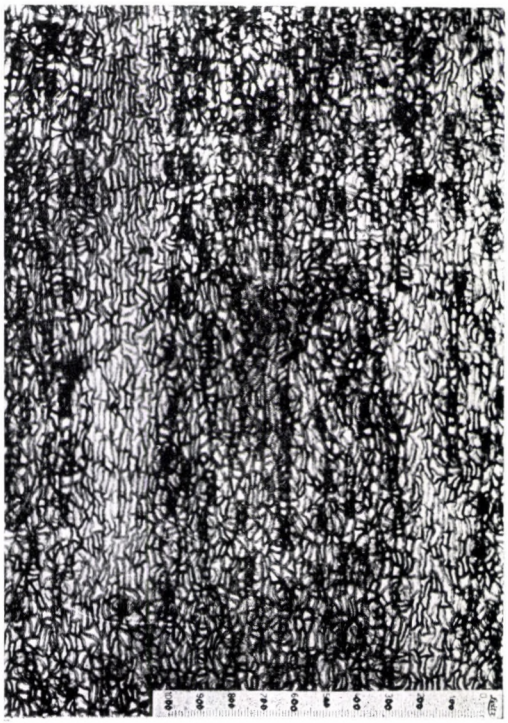

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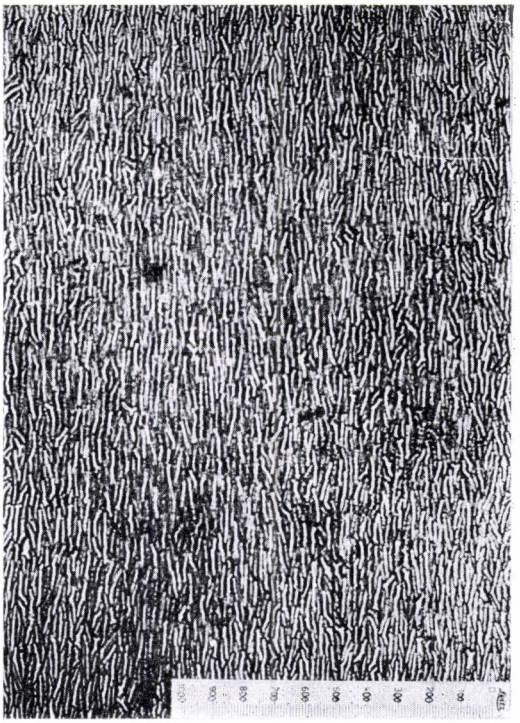
CXLIII. *Encephalartos latifrons* Lehm.



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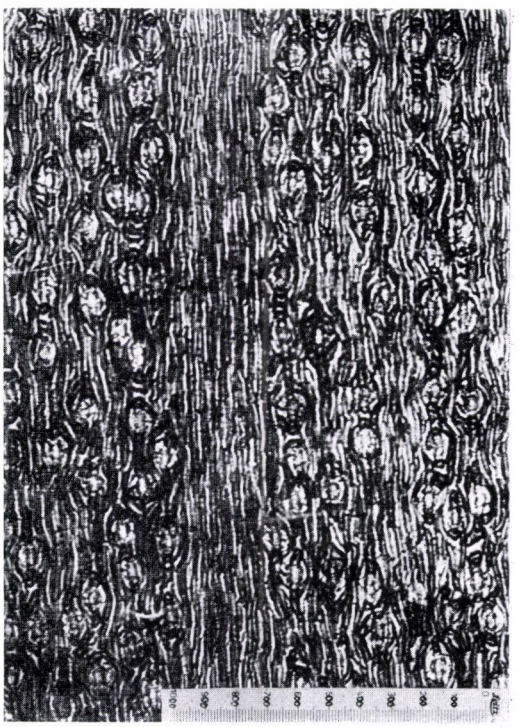

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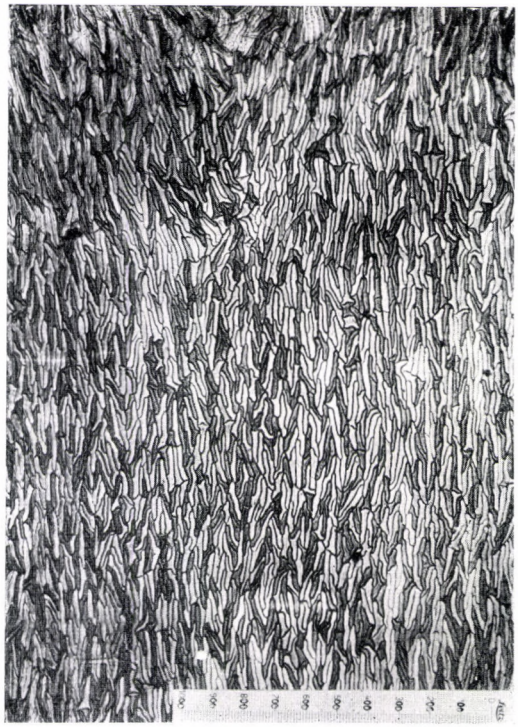
CXLIV. *Encephalartos laurentianus* De Wild



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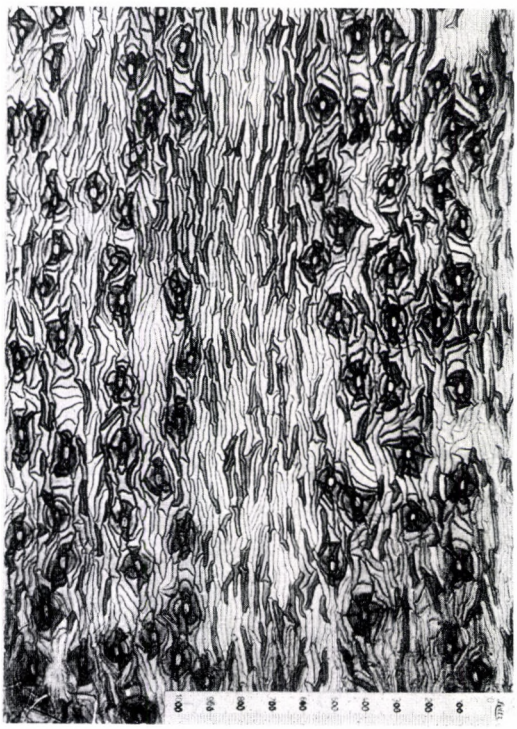

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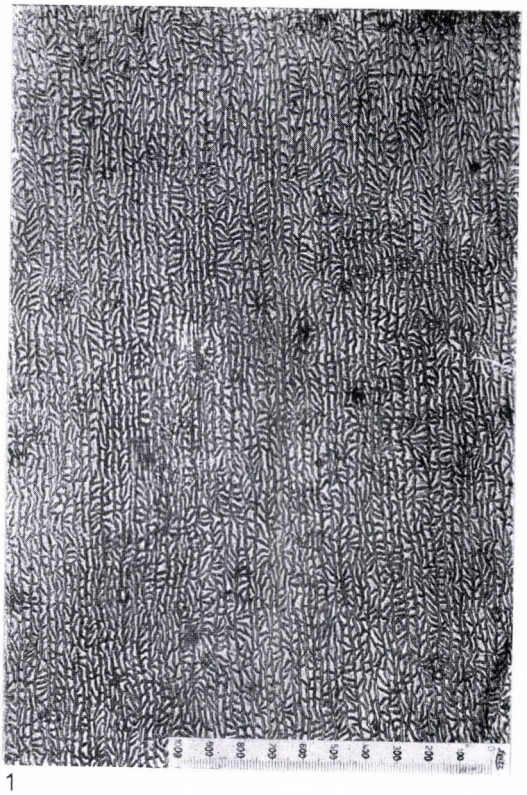
CXLV. *Encephalartos lebomboensis* Verdoorn



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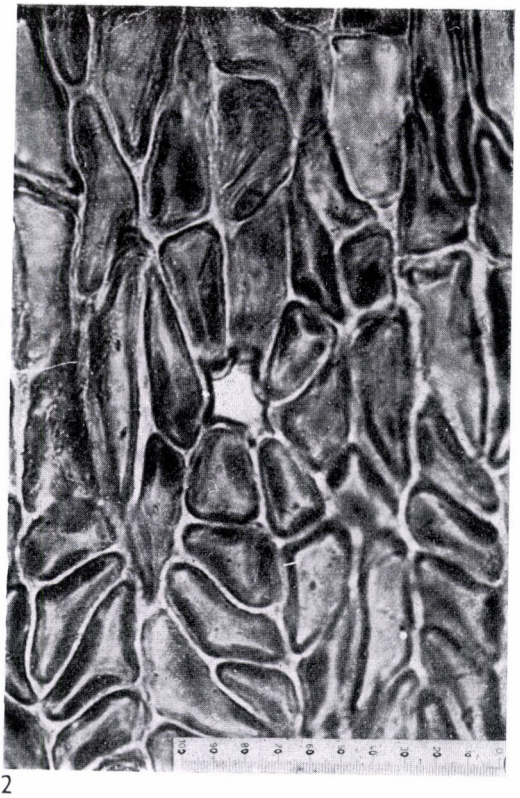

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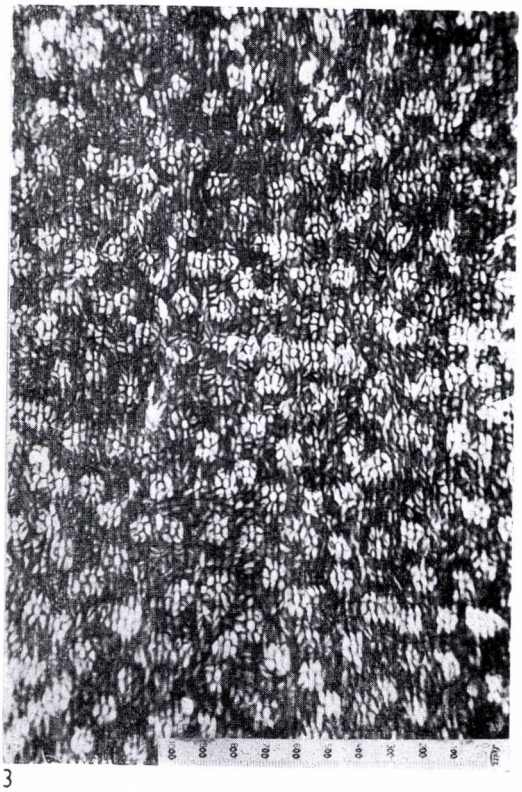

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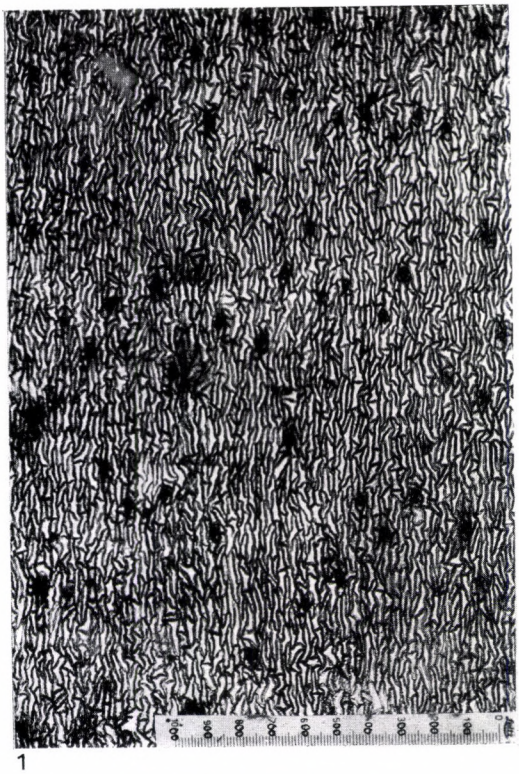
CXLVI. *Encephalartos lehmannii* Ecklon



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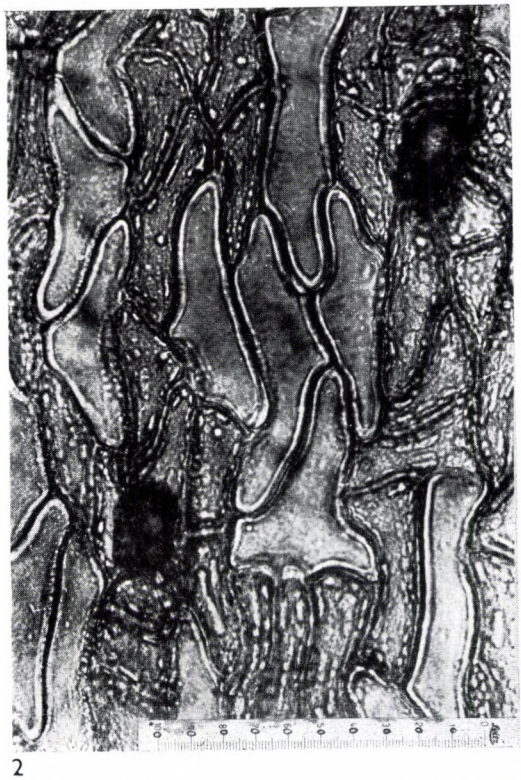

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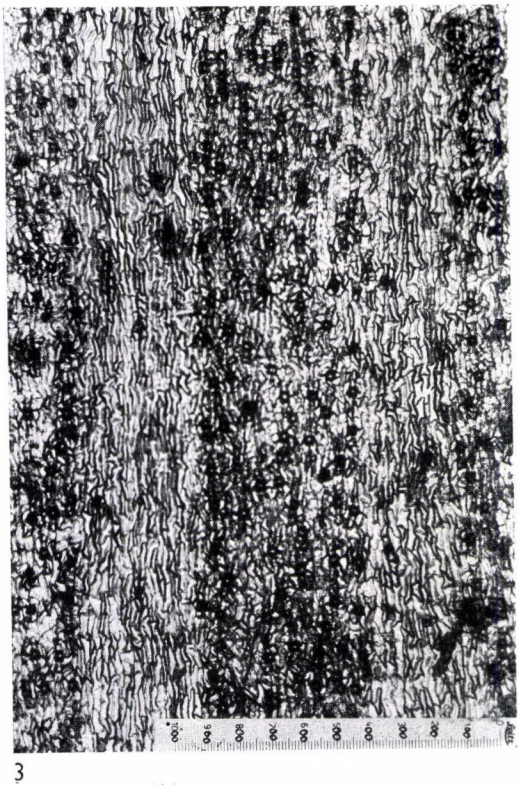

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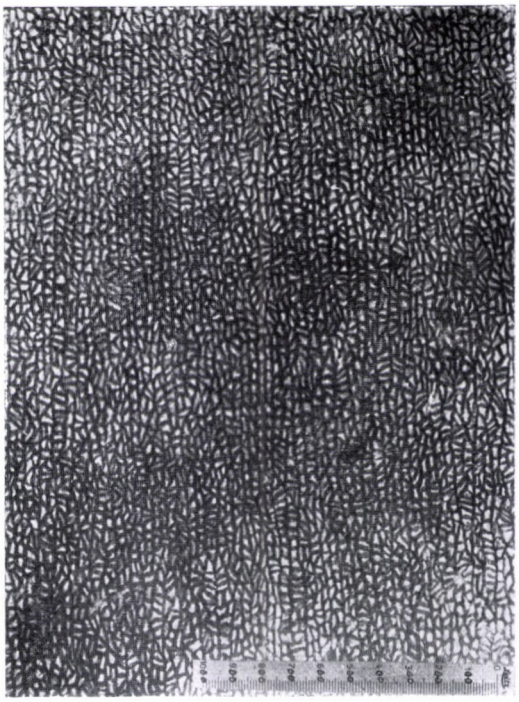
CXLVII. *Encephalartos longifolius* (Jacq.) Lehm.



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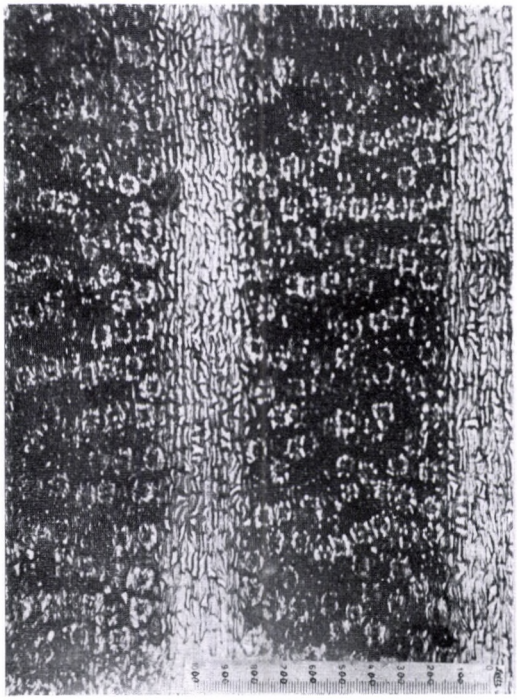

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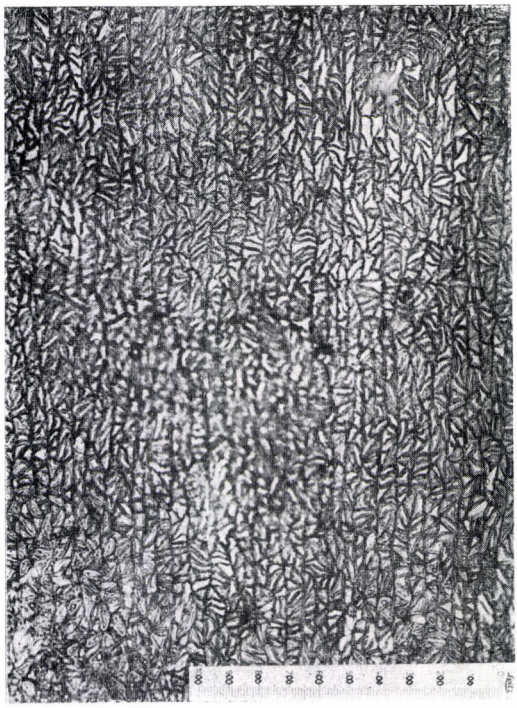
CXLVIII. *Encephalartos manikensis* Dyer



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CXLIX. *Encephalartos natalensis* Dyer et Verdoorn



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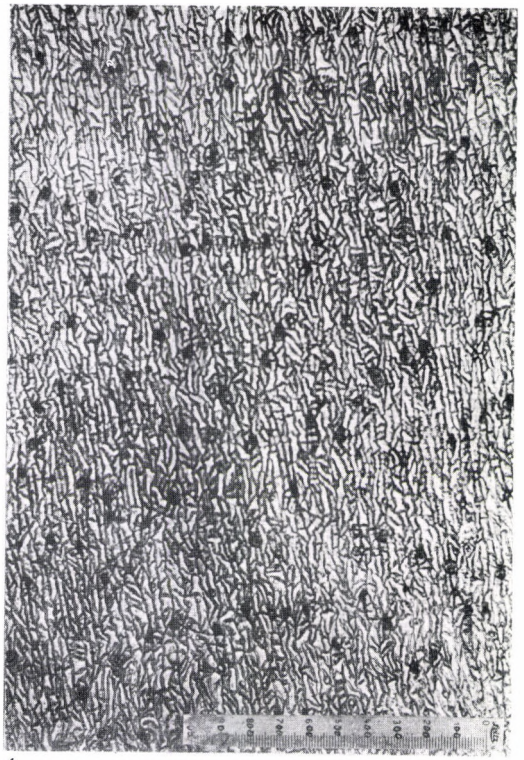
CL. *Encephalartos poggei* Aschers



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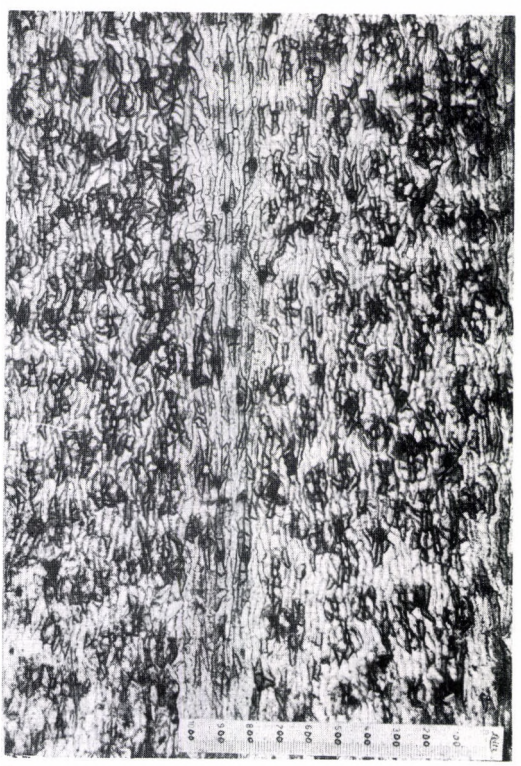

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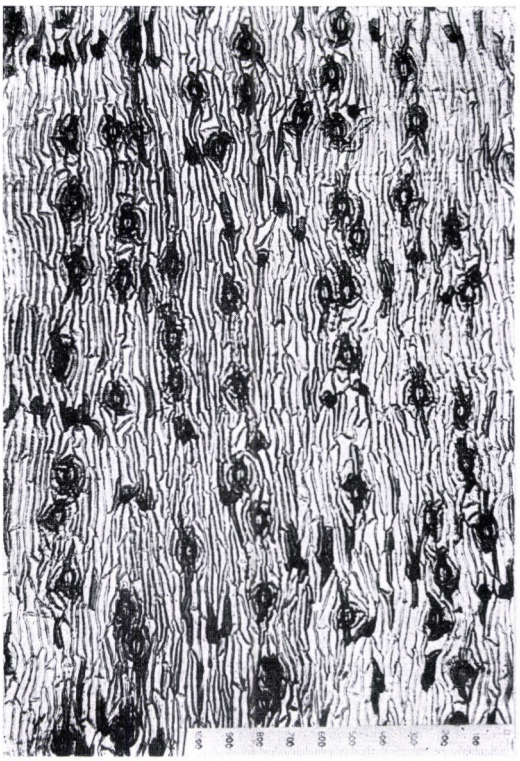
4

CLI. *Encephalartos princeps* R.A. Dyer



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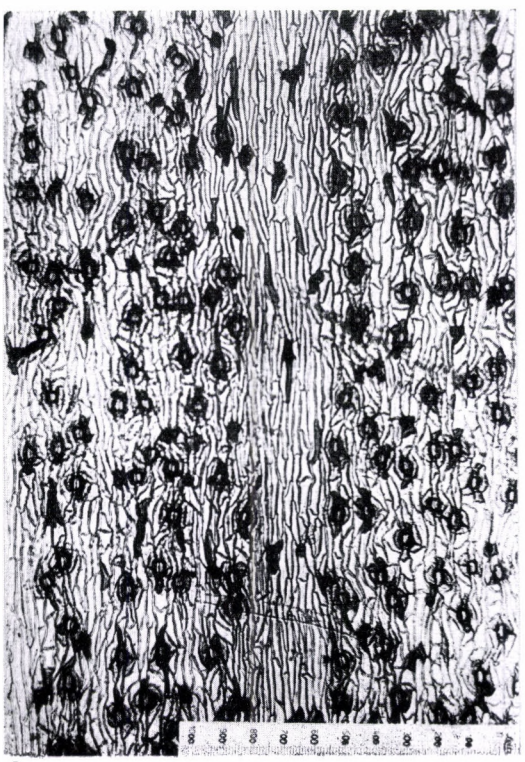

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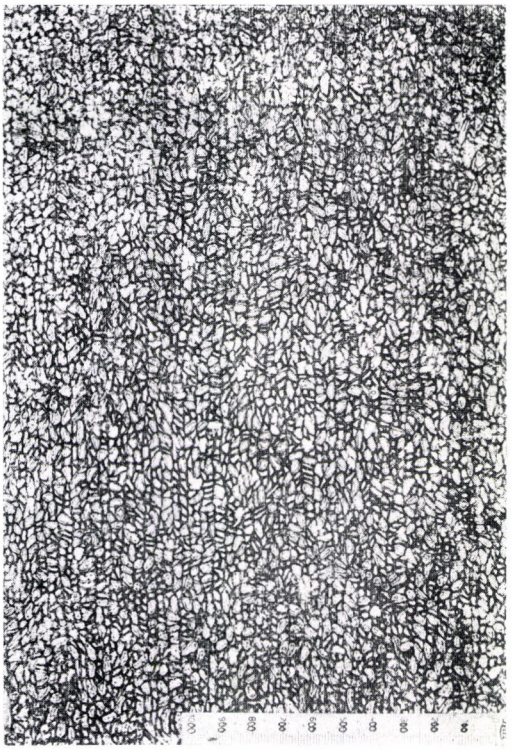
CLII. *Encephalartos septentrionalis* Schweinf.



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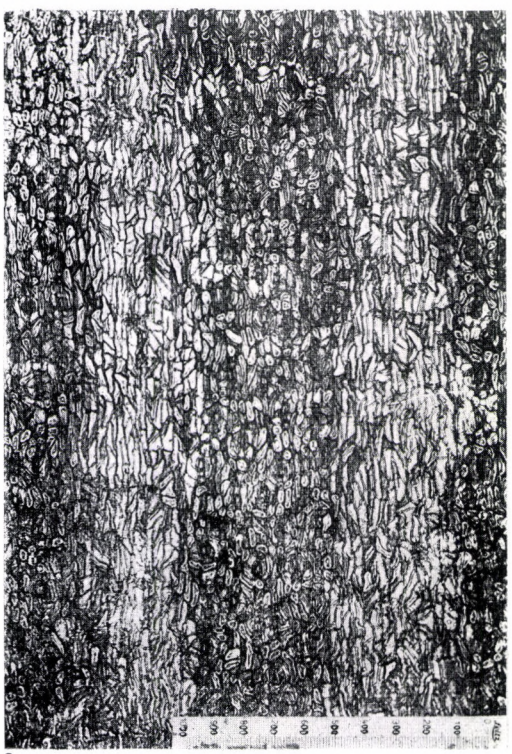

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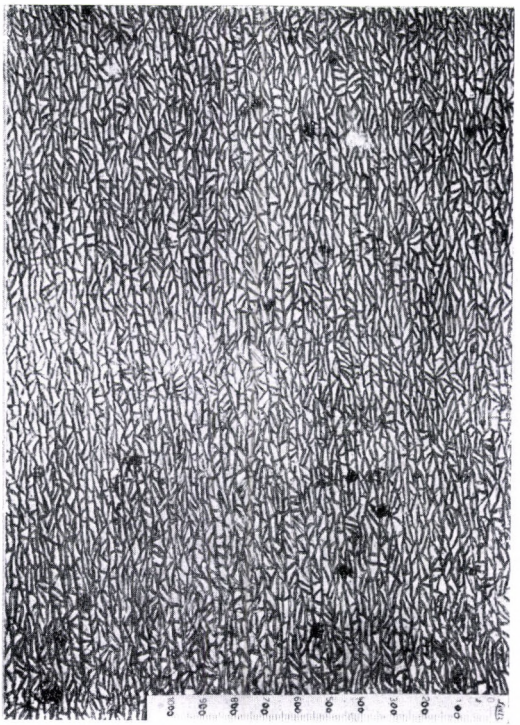
CLIII. *Encephalartos tegulanus* Melville



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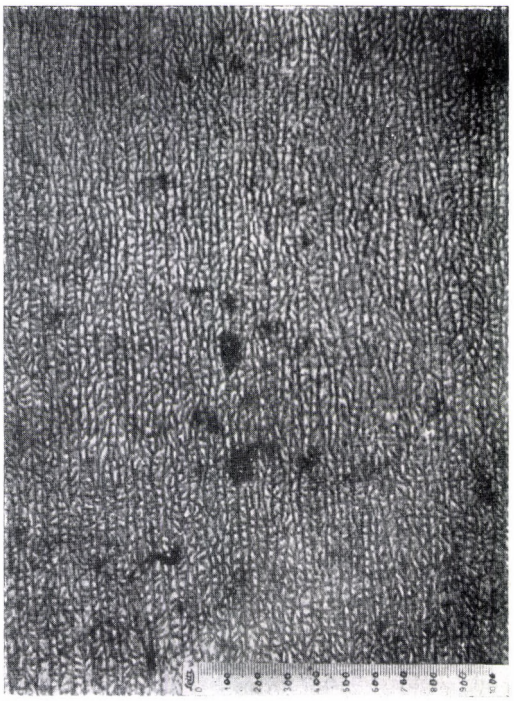
CLIV. *Encephalartos transvenosus* Stanpf. et Davy



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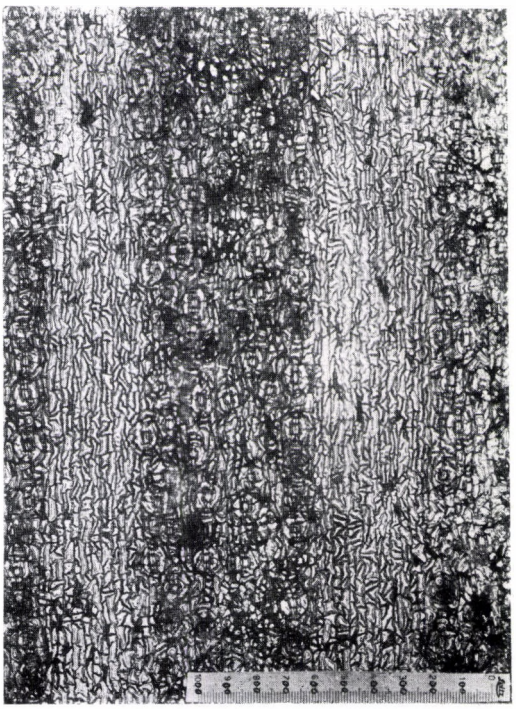

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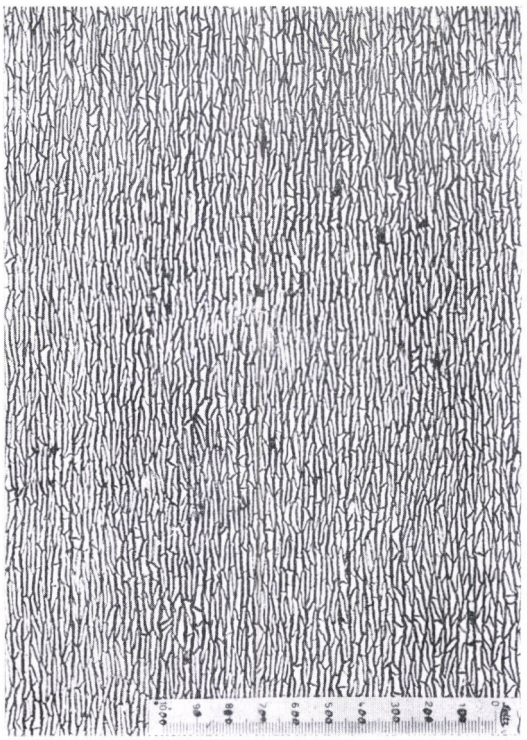
CLV. *Encephalartos trispinosus* (Hook) R.A. Dyer



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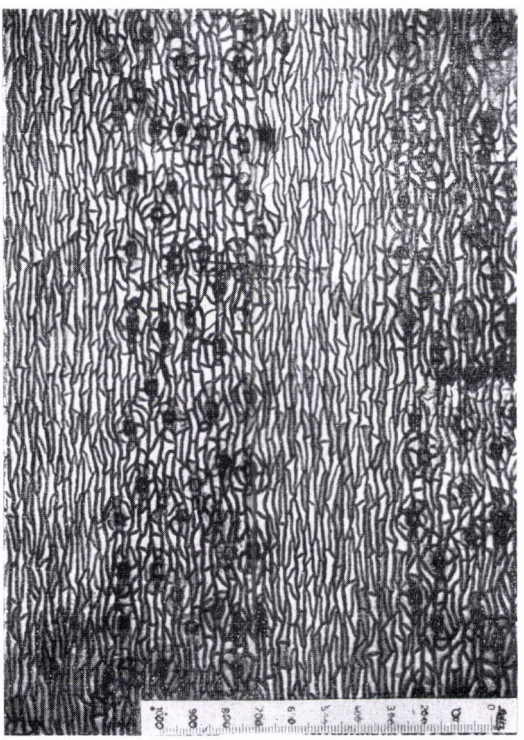

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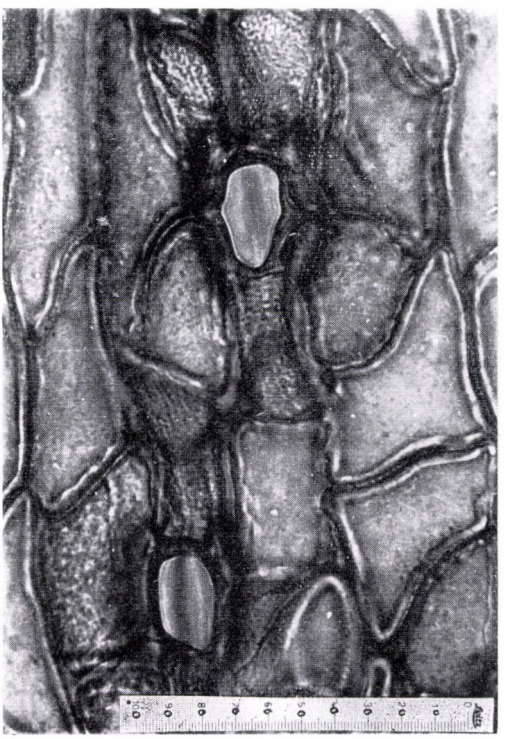

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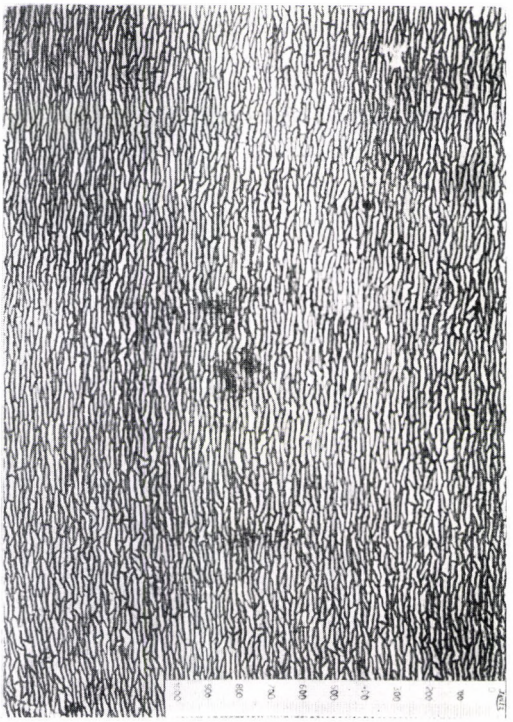
CLVI. *Encephalartos umbeluziensis* R.A. Dyer



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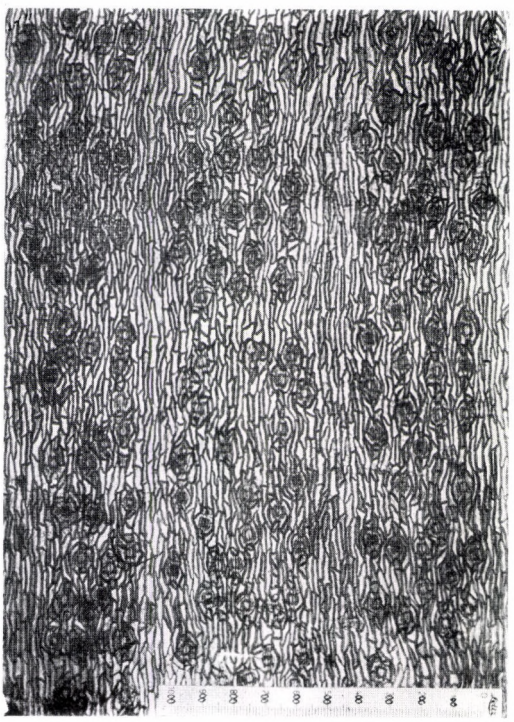

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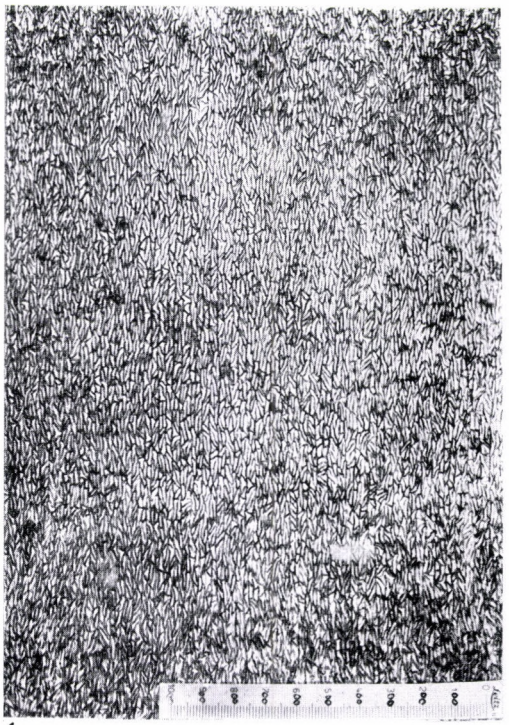
CLVII. *Encephalartos villosus* (Gaertn.) Lemaire



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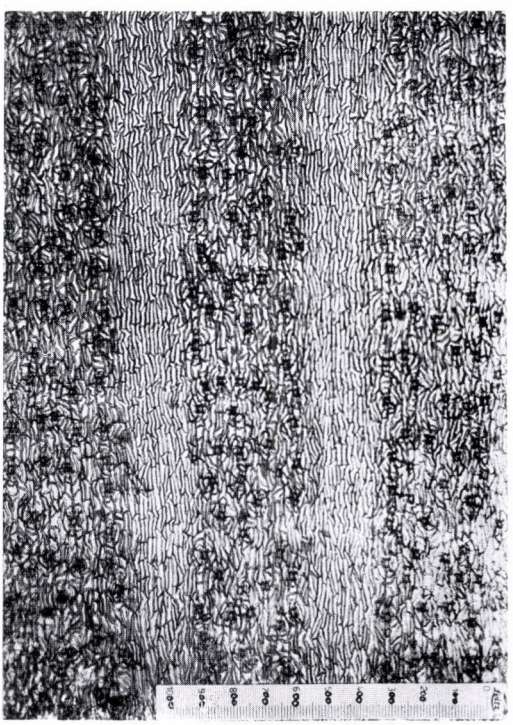

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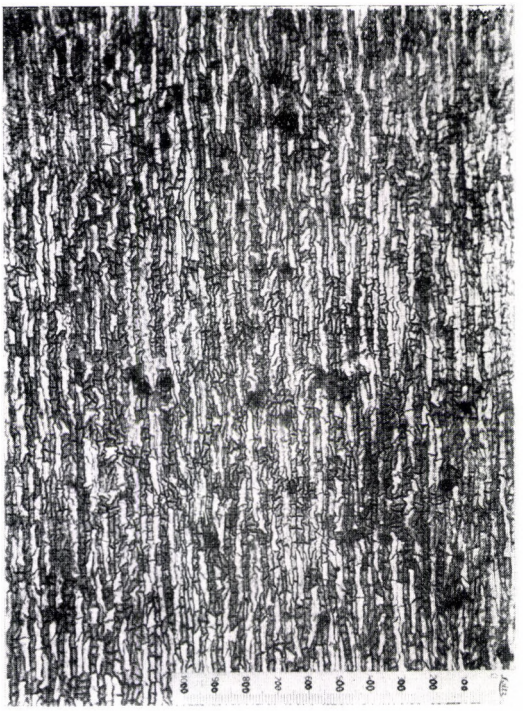
4

CLVIII. *Encephalartos woodii* Prain



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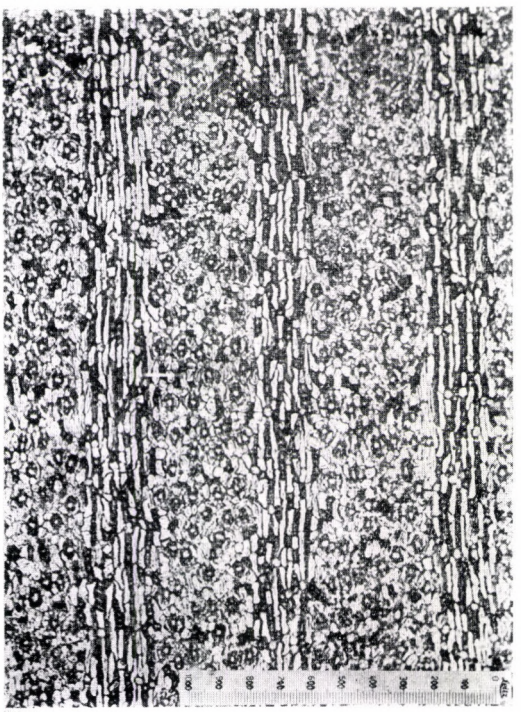

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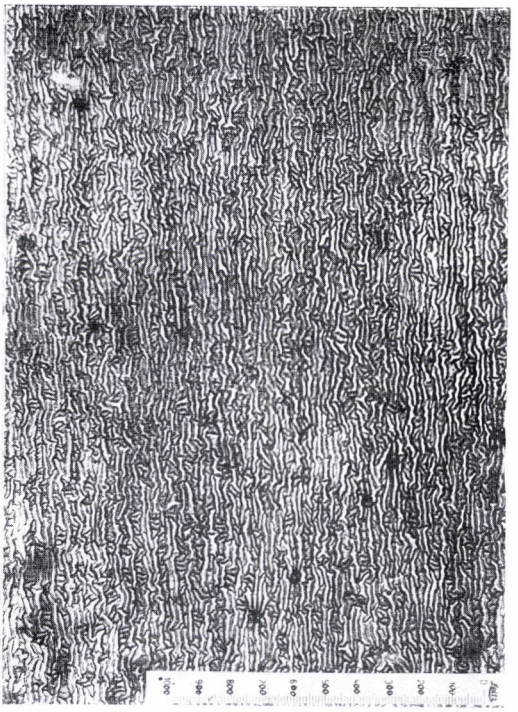
4

CLIX. *Dioon edule* Lindl.



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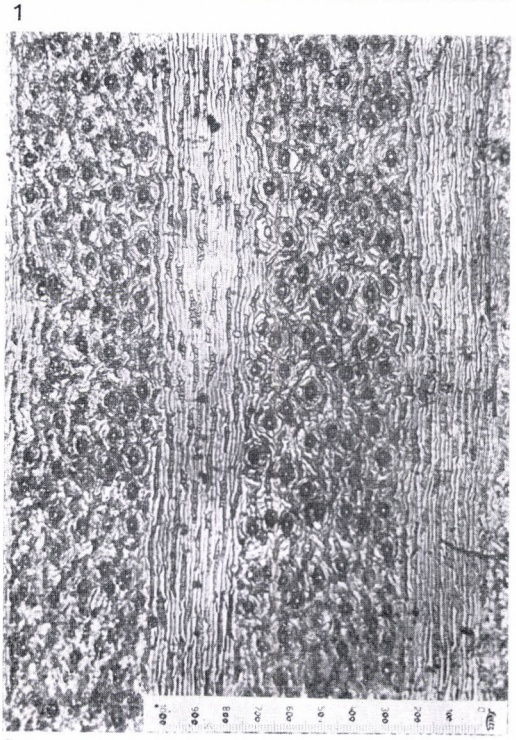

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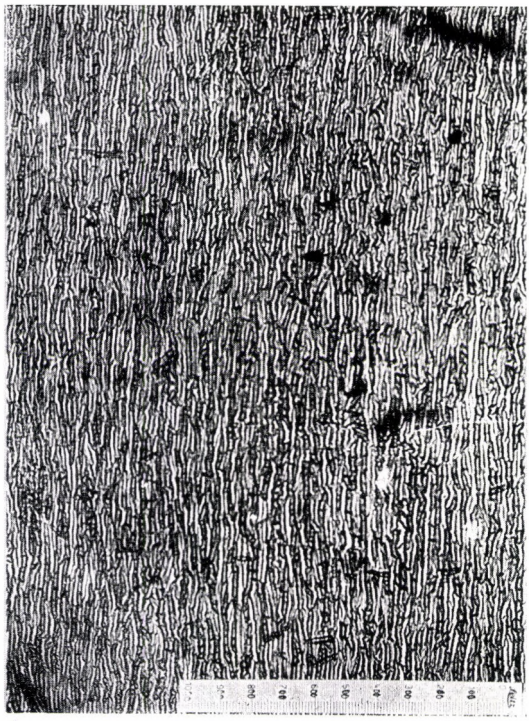
CLX. *Dioon pectinatum* H. Wendl



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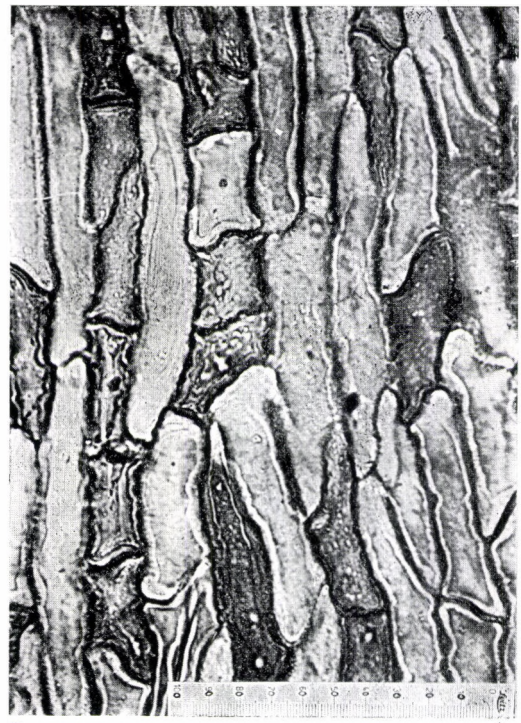

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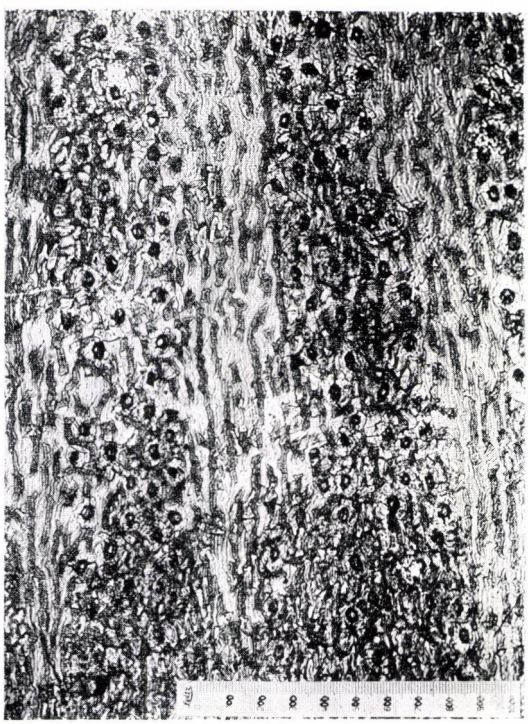

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4

CLXI. *Dioon spinulosum* Dyer



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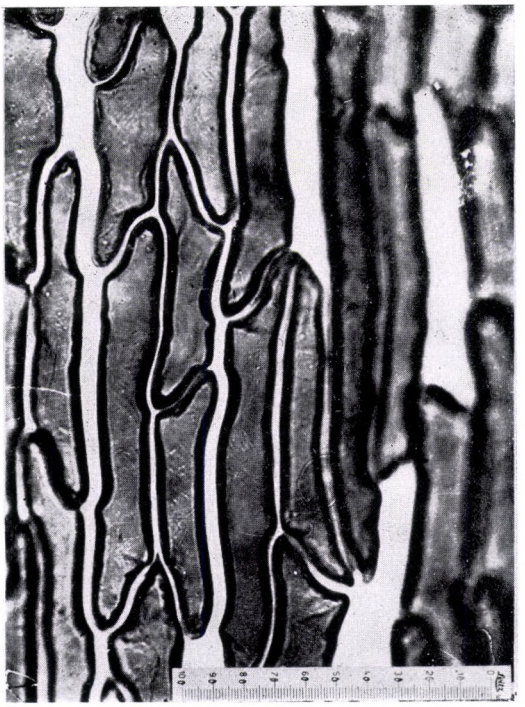

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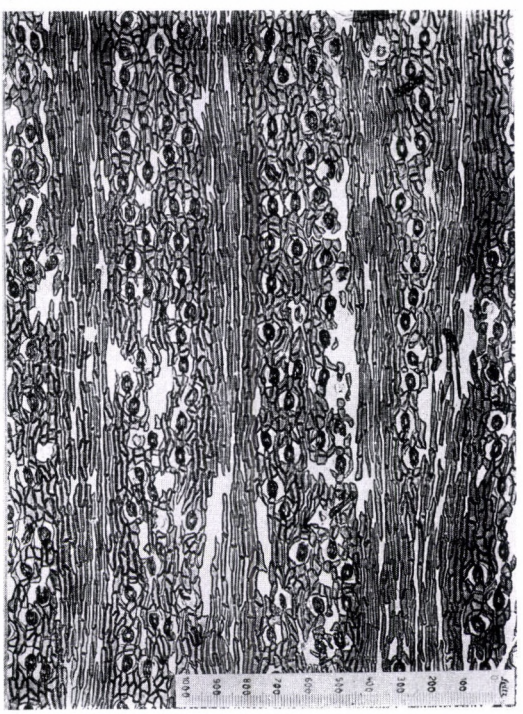

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CLXII. *Microcycas calocoma* (Miq.) A.DC.



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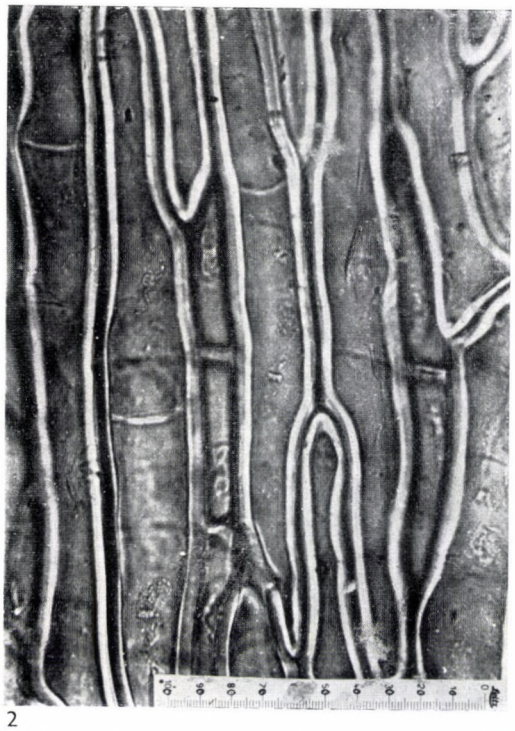

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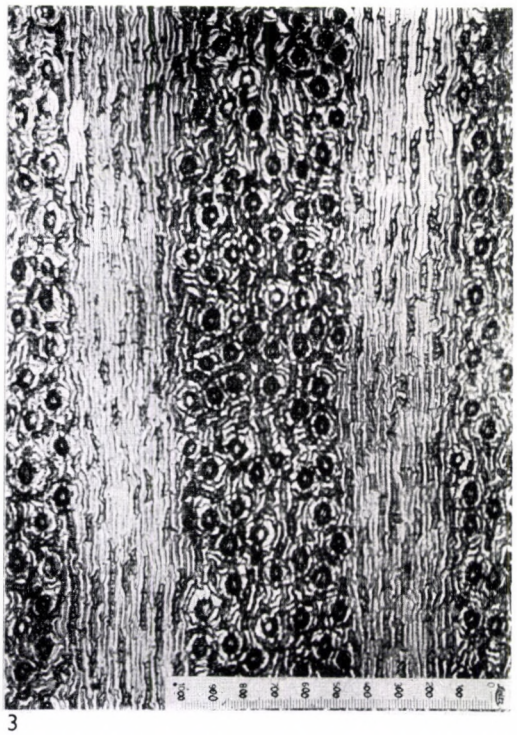

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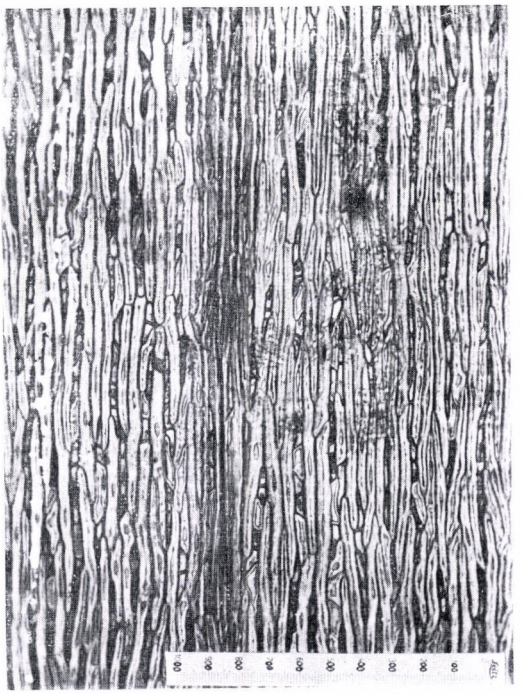
CLXIII. *Ceratozamia kuesteriana* Regel



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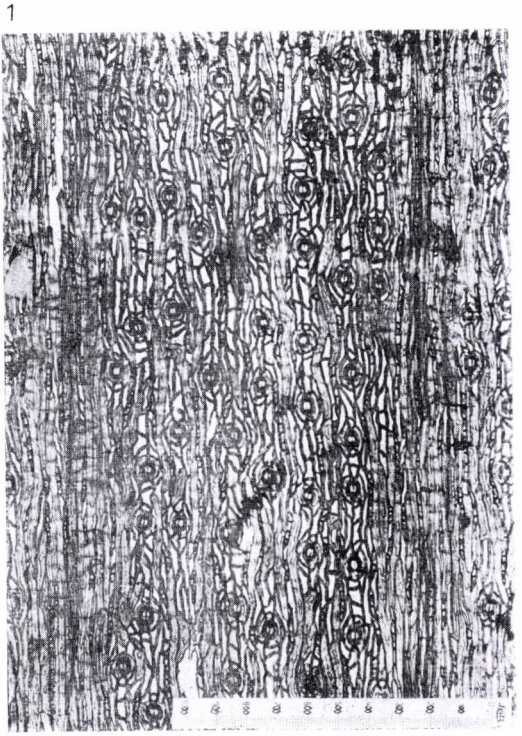

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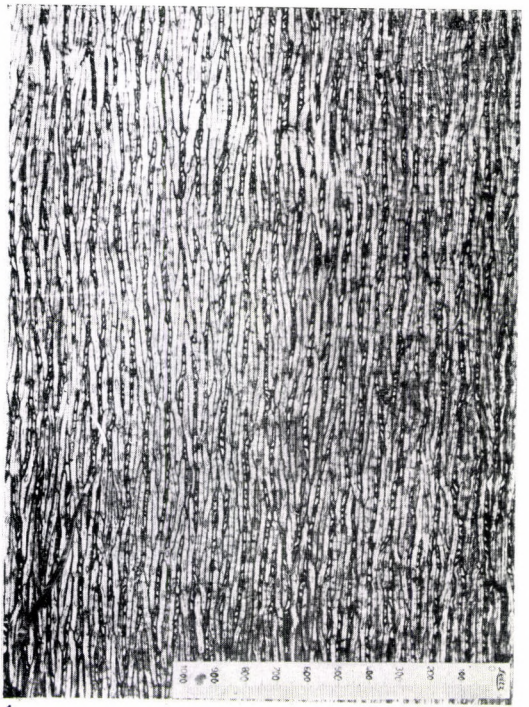
CLXIV. *Ceratozamia mexicana* Brongn.



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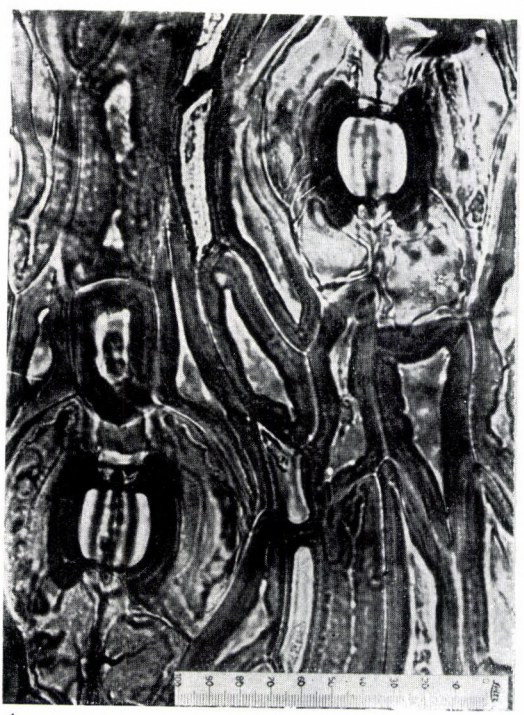

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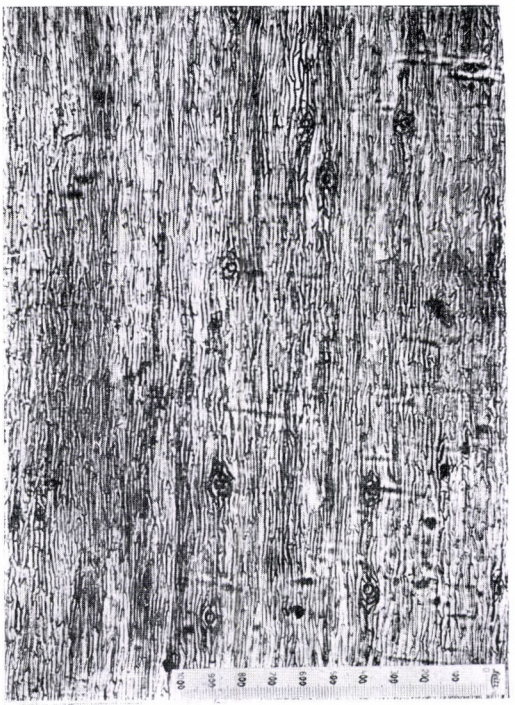
CLXV. *Ceratozamia robusta* Miq.



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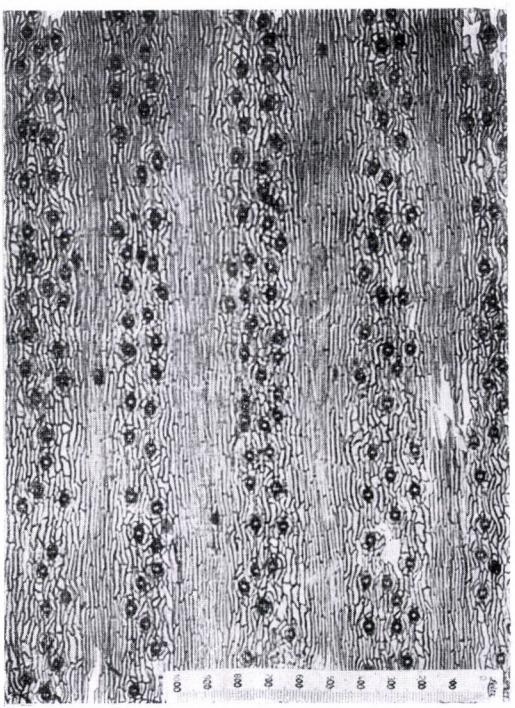

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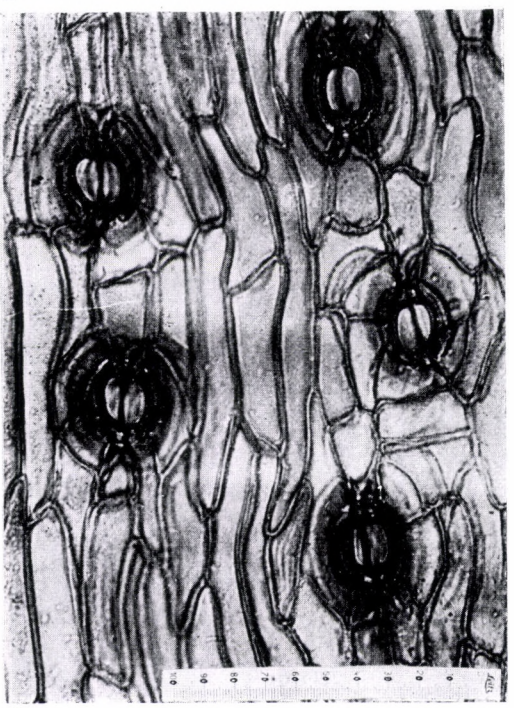

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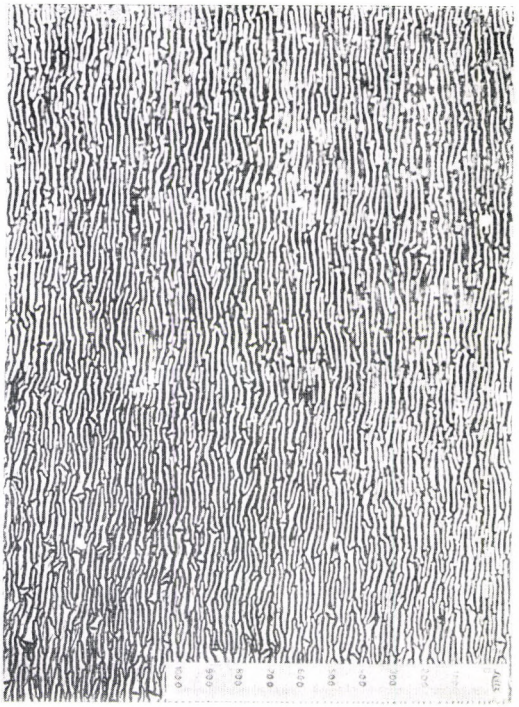
CLXVI. *Zamia angustifolia* (Jacq.) Schuster



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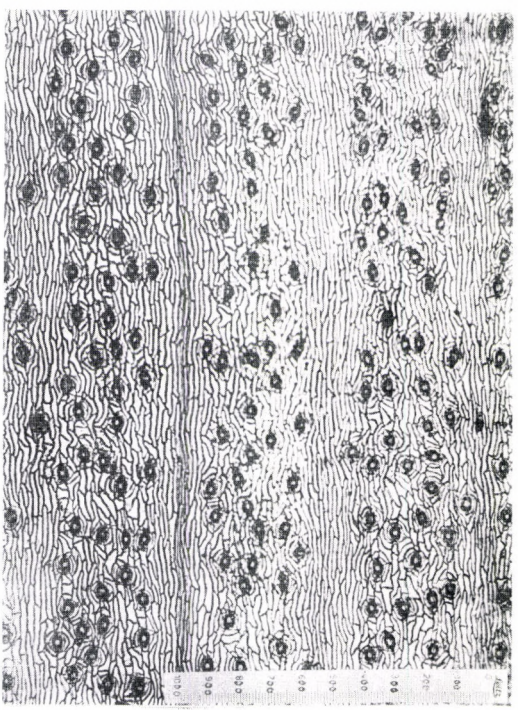

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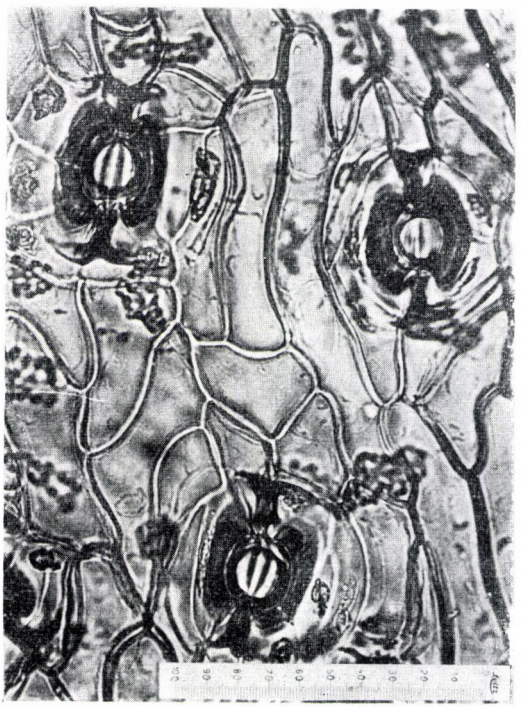

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CLXVII. *Zamia fischeri* Miq.



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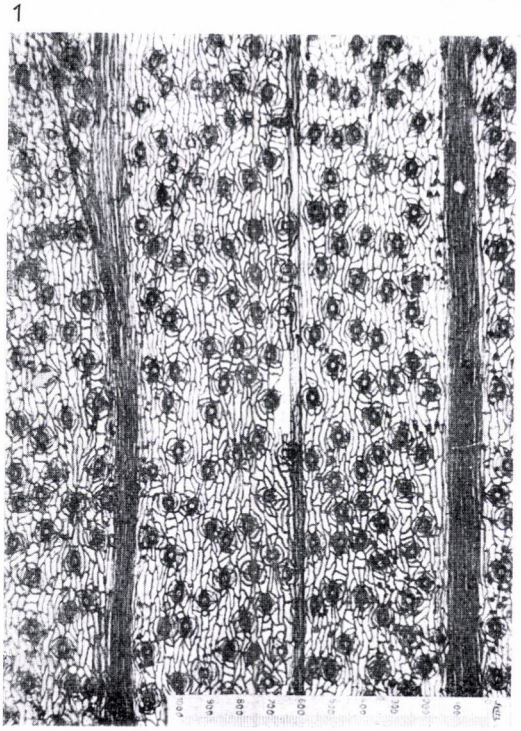

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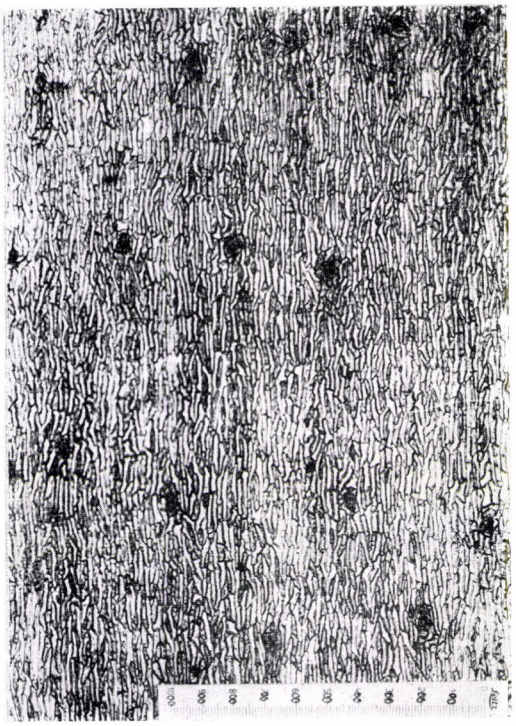
4

CLXVIII. *Zamia floridana* A.DC.



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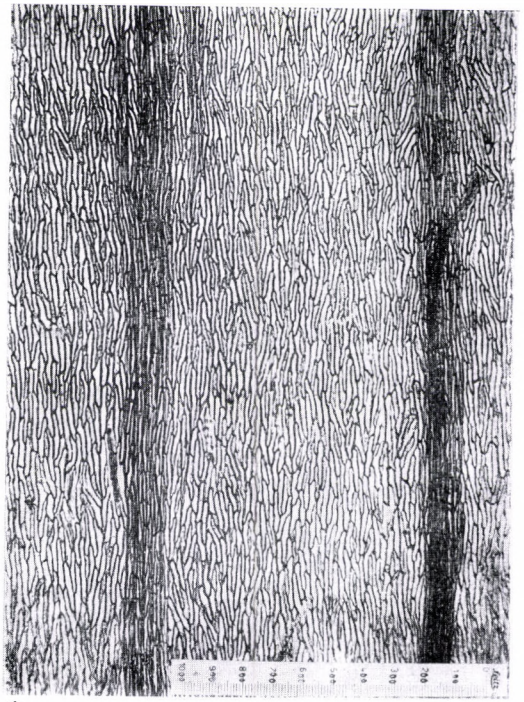
CLXIX. *Zamia furfuracea* L. fil.



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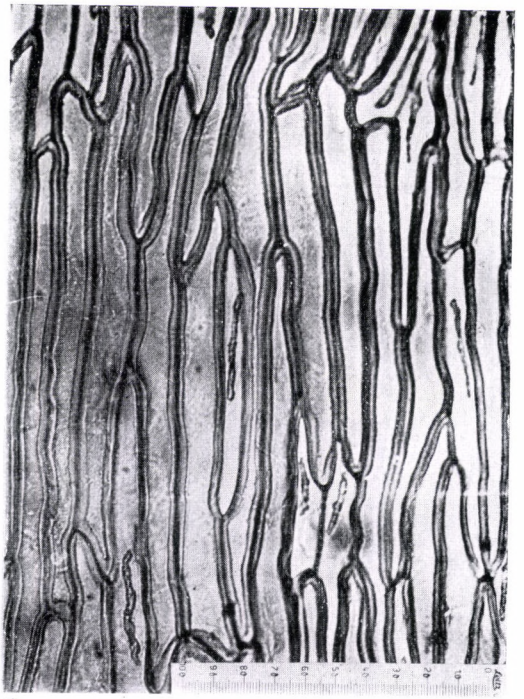

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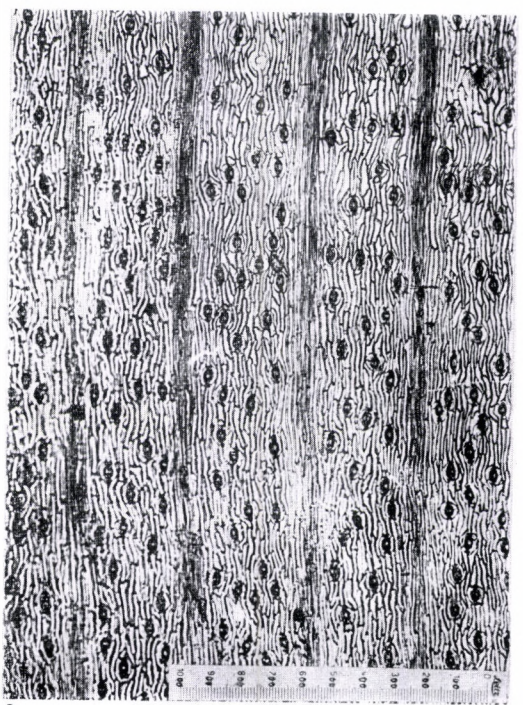

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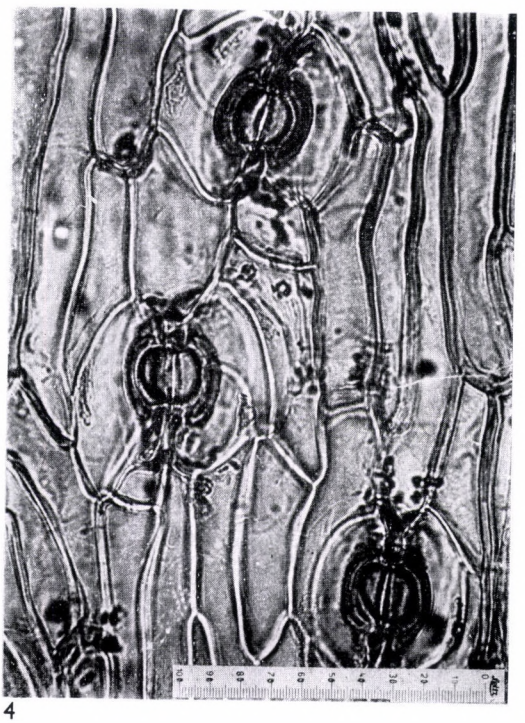

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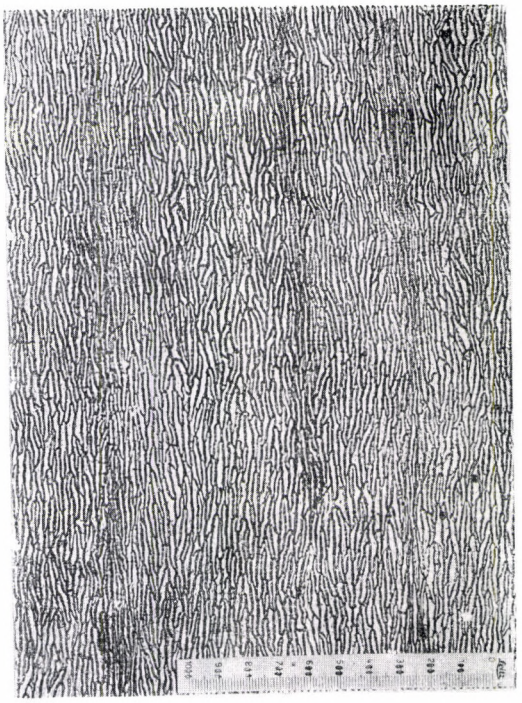
CLXX. *Zamia gutierrezi* Sauvalle



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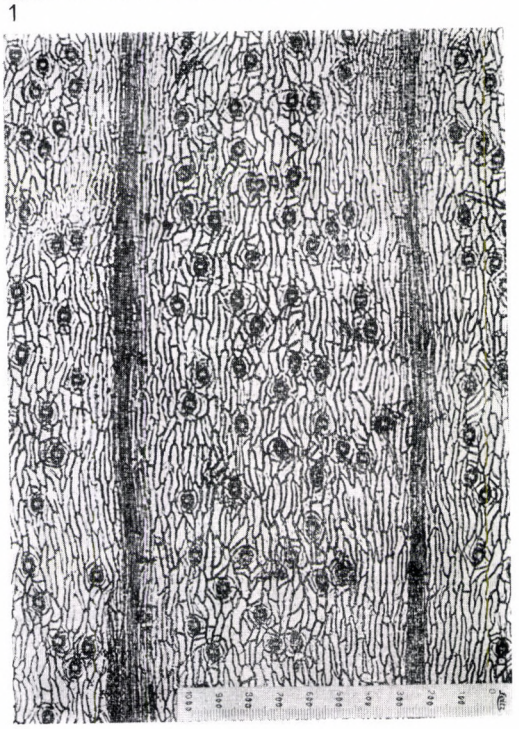

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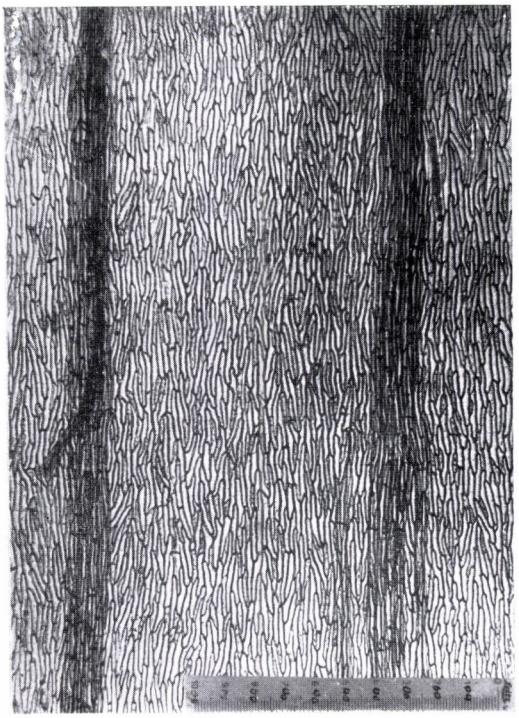
CLXXI. *Zamia kickxii* Miq.



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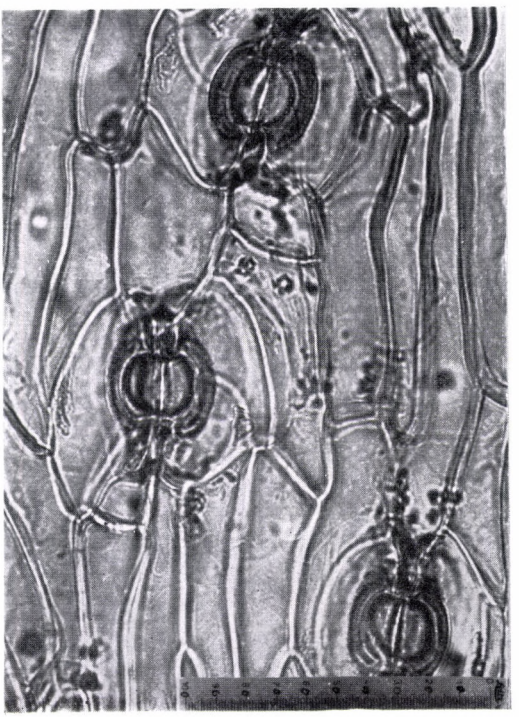

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CLXXII. *Zamia latifolia* Lodd.



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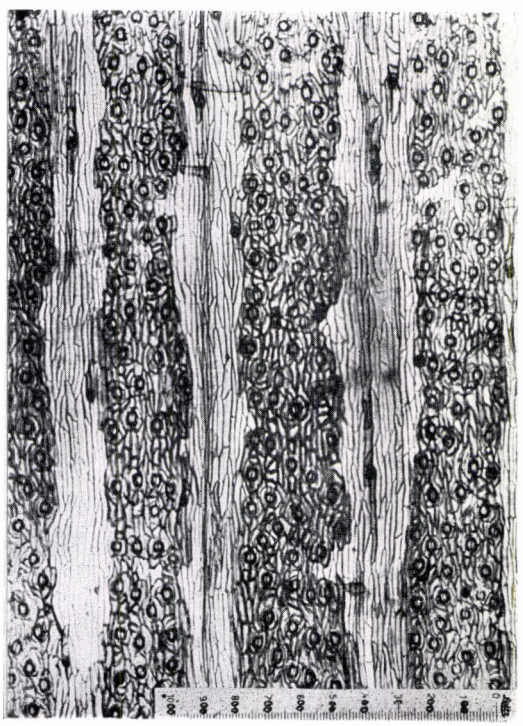

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CLXXIII. *Zamia latifoliata* Prenleloup



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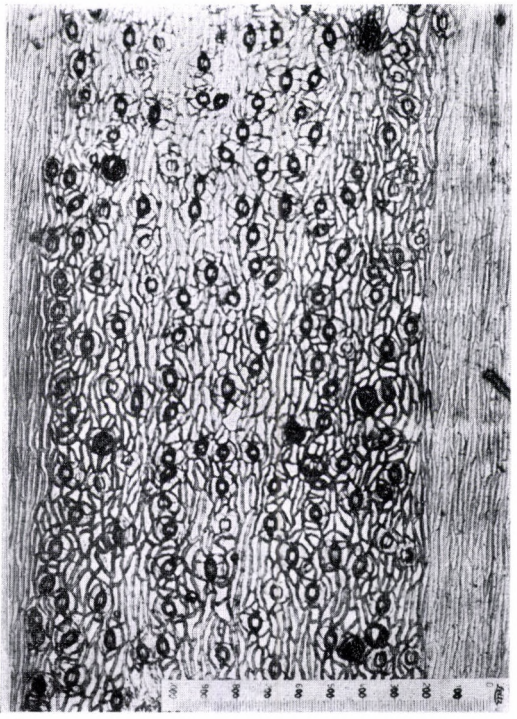

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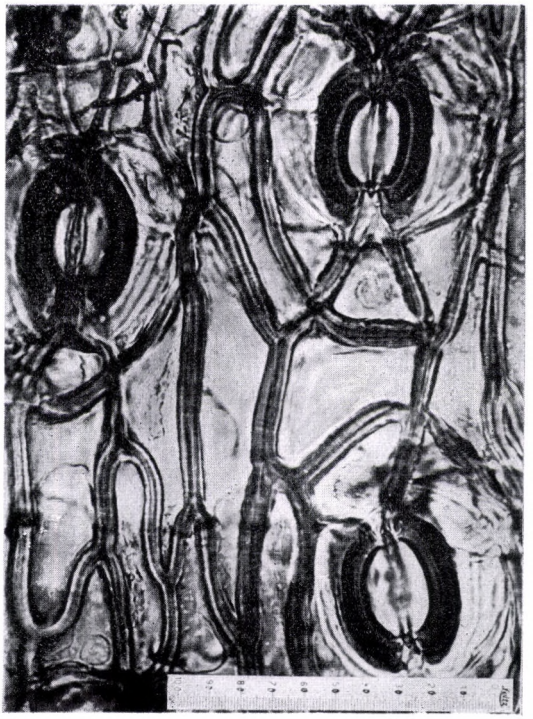

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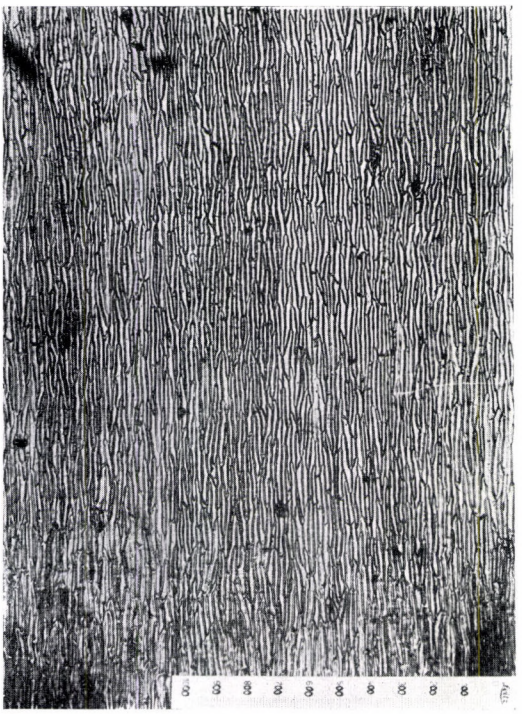
CLXXIV. *Zamia lindenii* Regel



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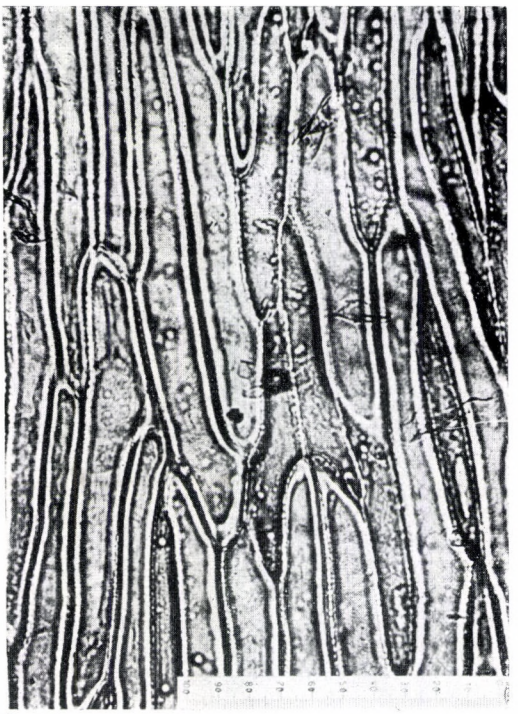

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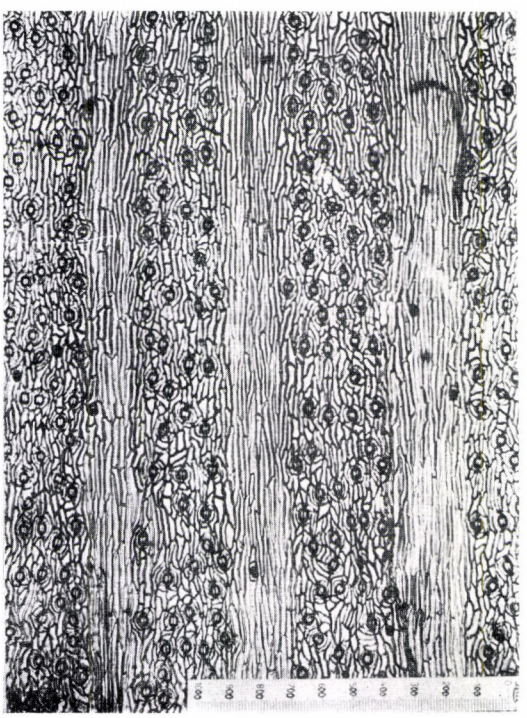

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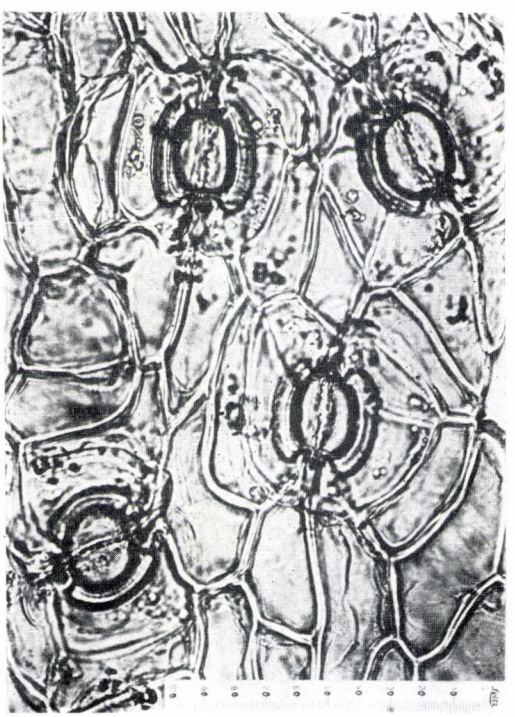

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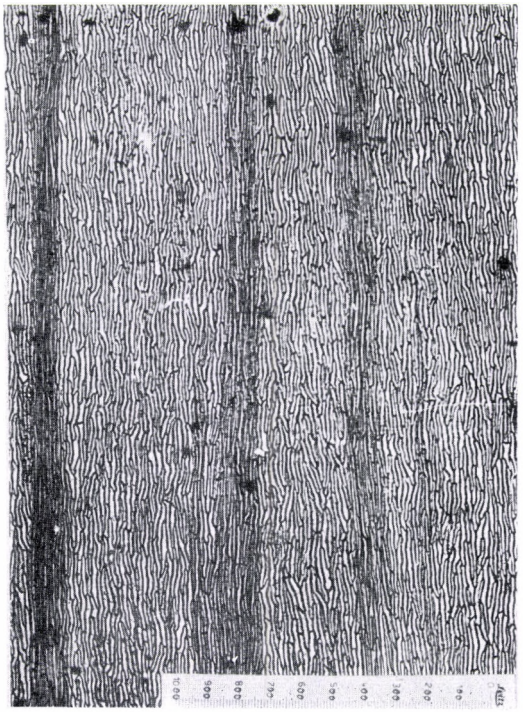
CLXXV. *Zamia loddigesii* Miq.



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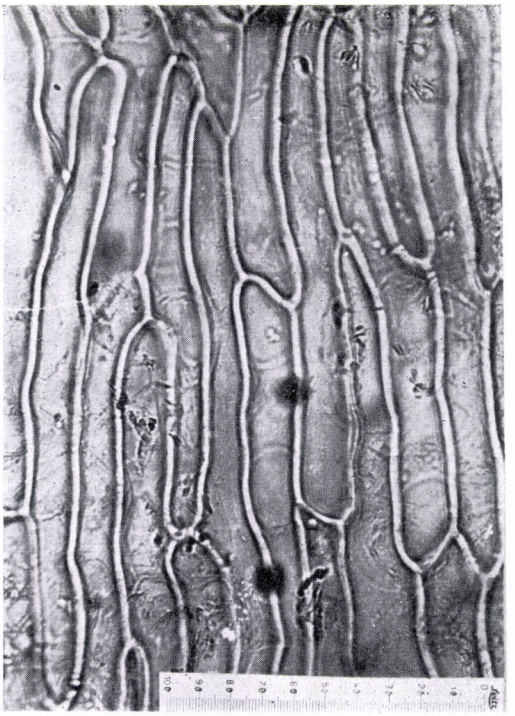

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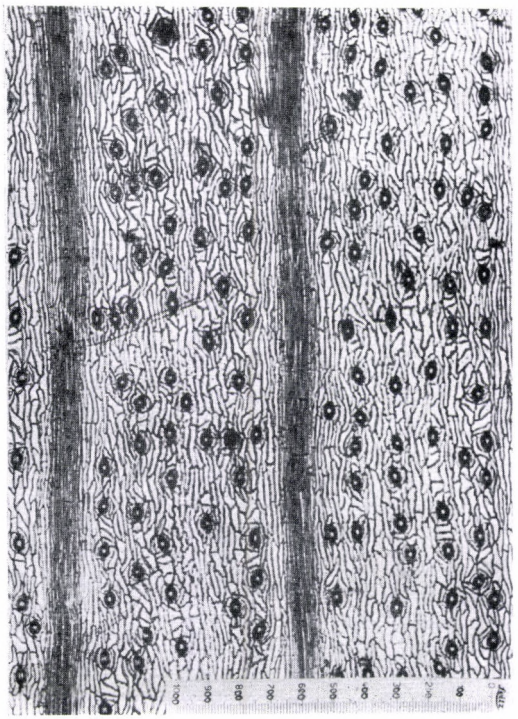

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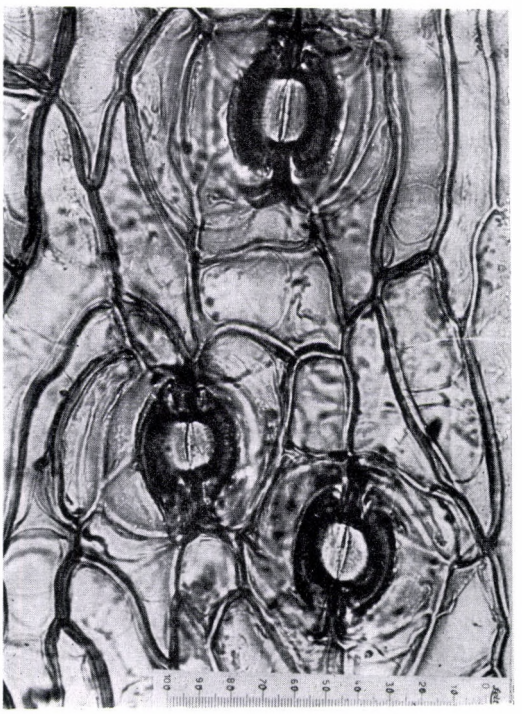

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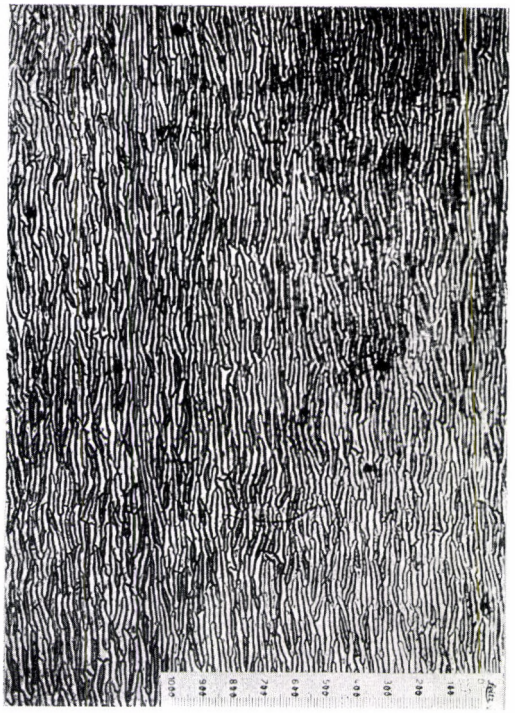
CLXXVI. *Zamia media* Jacq.



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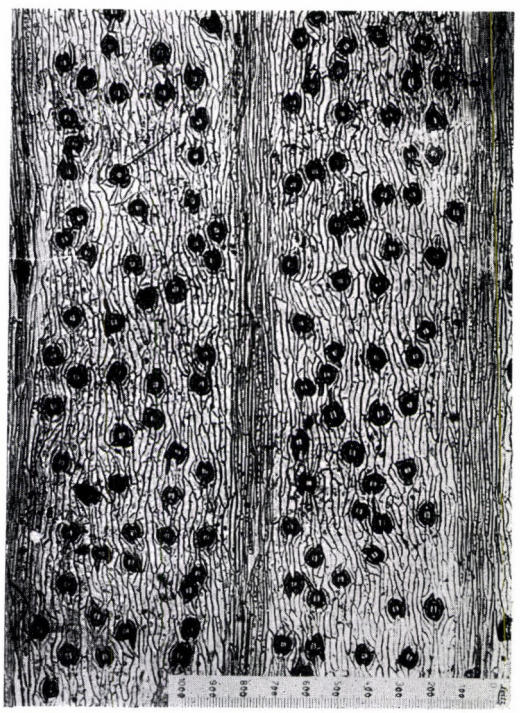

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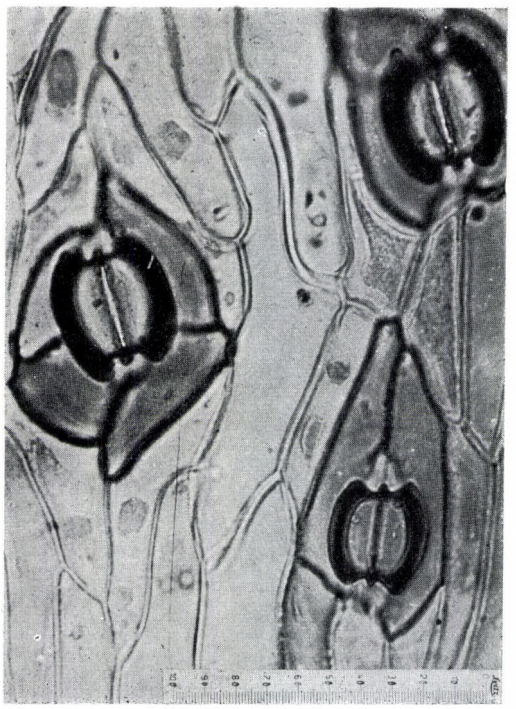

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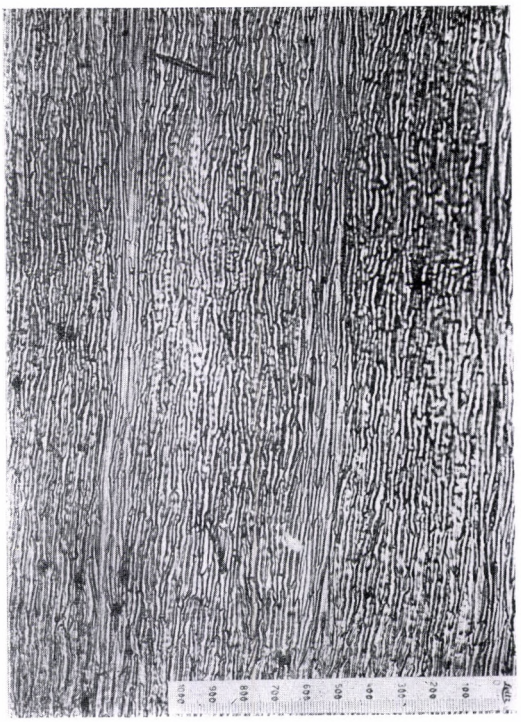
CLXXVII. *Zamia muricata* Willd.



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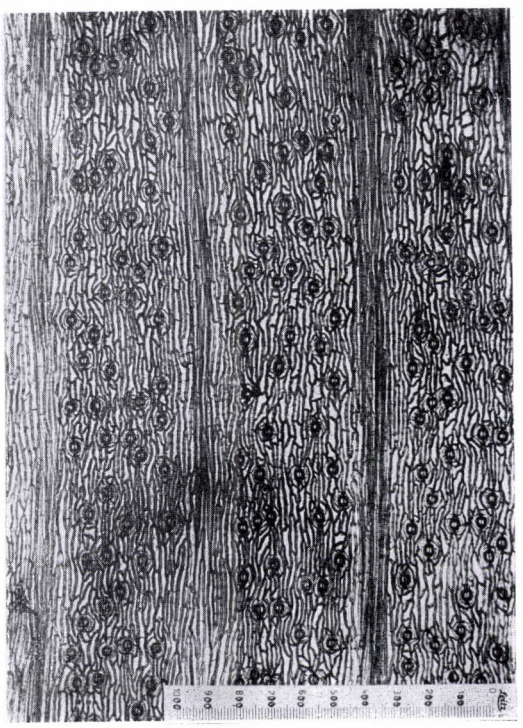

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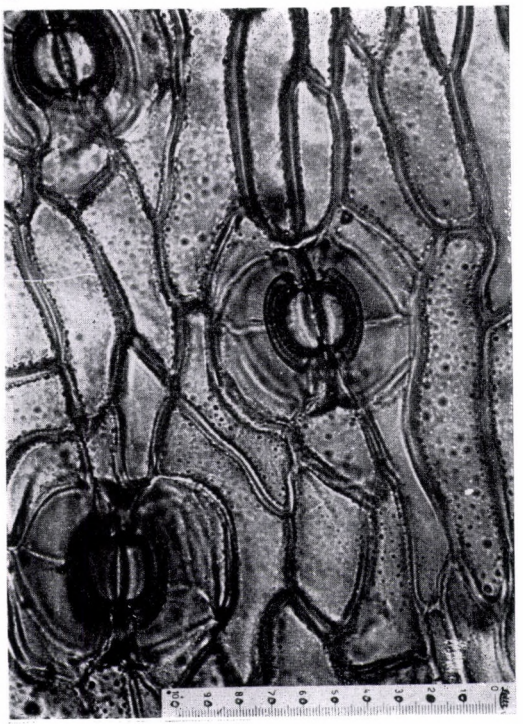

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CLXXVIII. *Zamia ottonis* Miq.



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CLXXIX. *Zamia portoricensis* Urban



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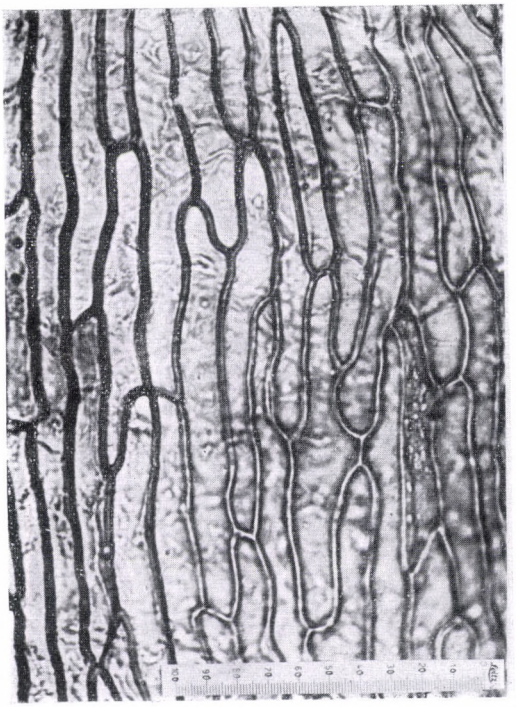

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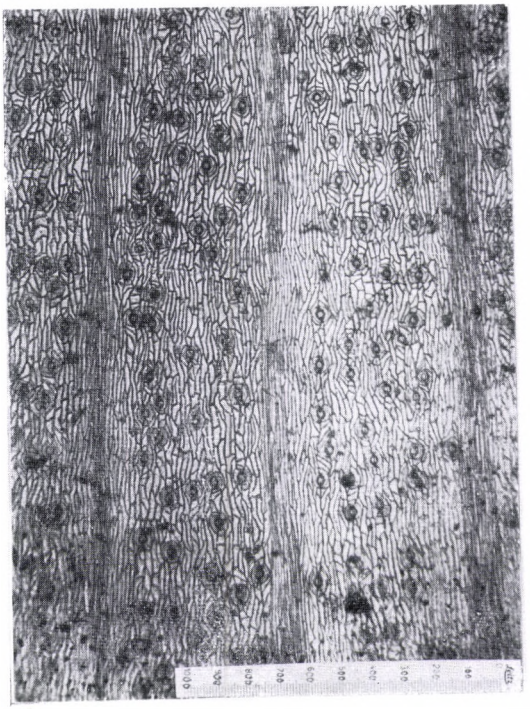

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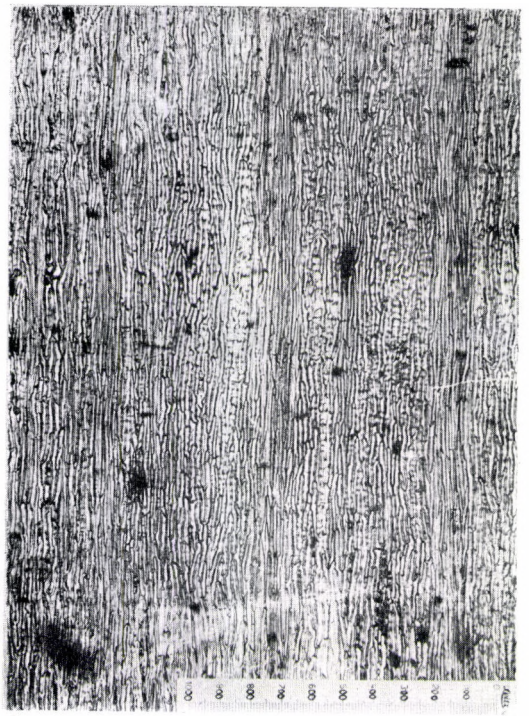
CLXXX. *Zamia pumila* L.



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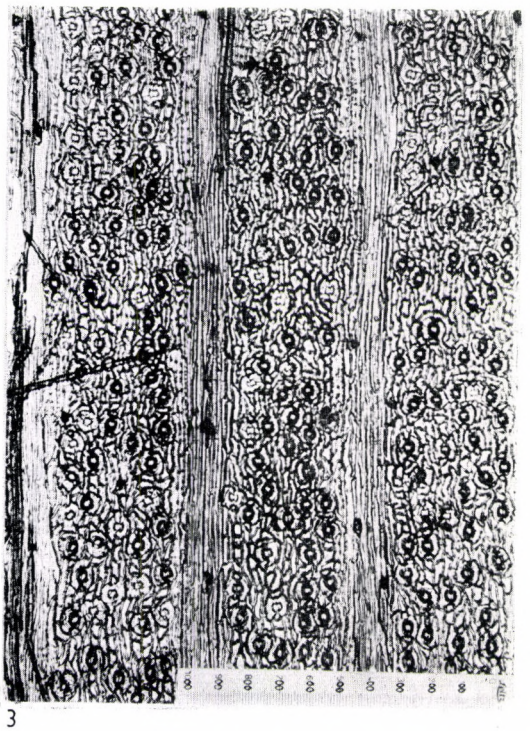

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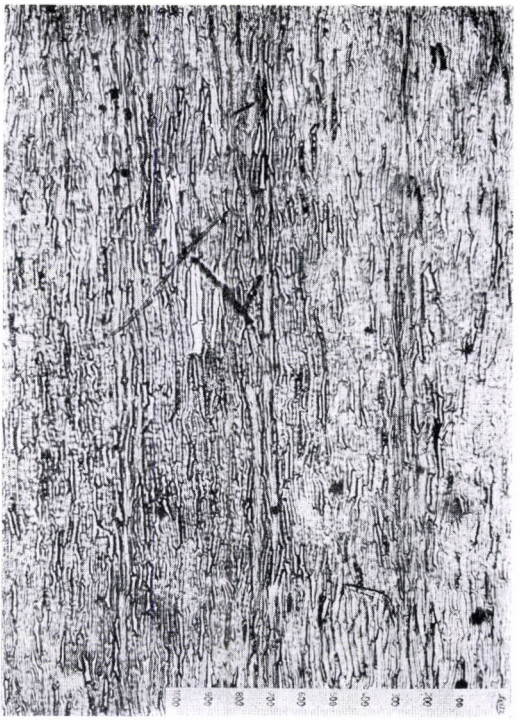
4

CLXXXI. *Zamia pygmaea* Sims.



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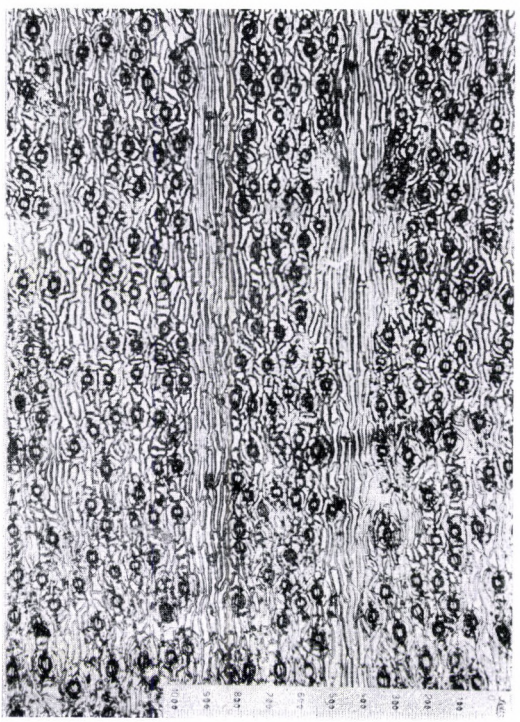

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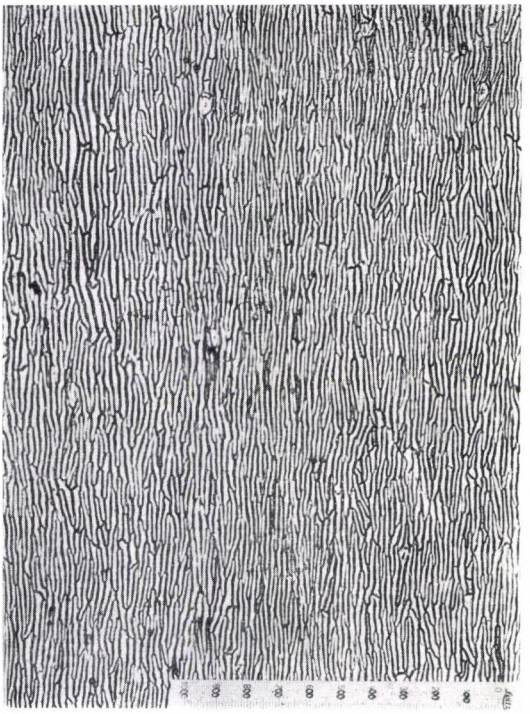
CLXXXII. *Zamia silicea* Britton



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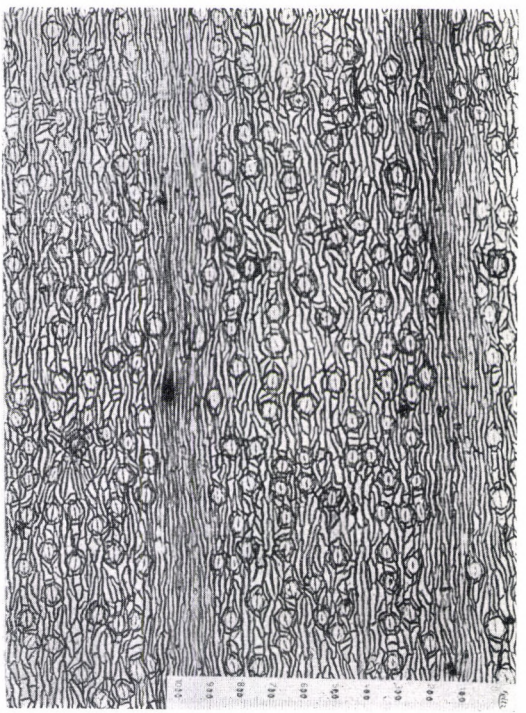

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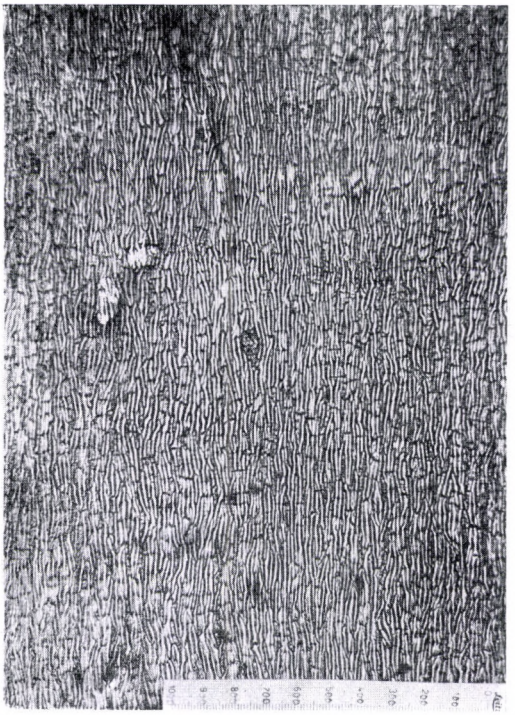
4

CLXXXIII. *Bowenia serrulata* (W. Bull.) Chamberlain



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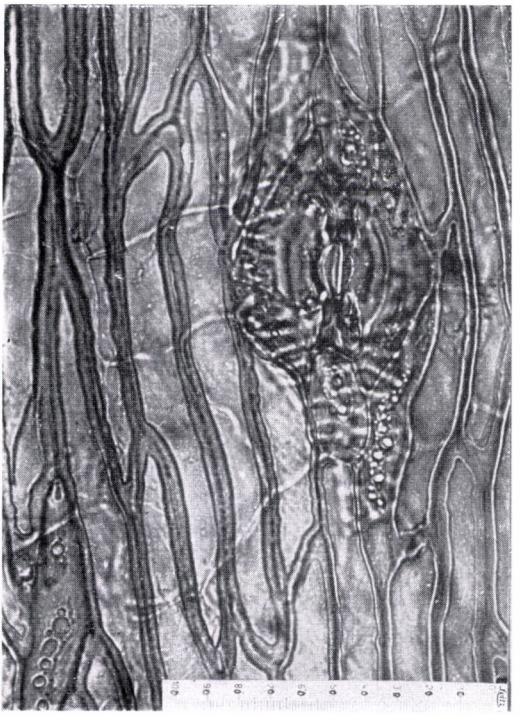

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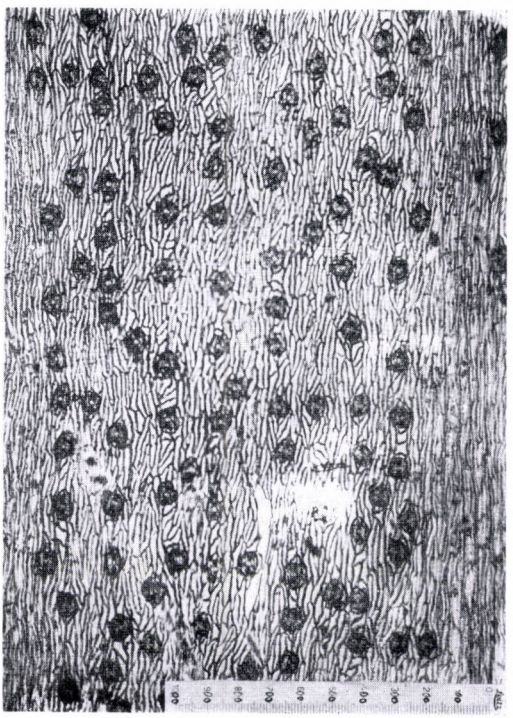

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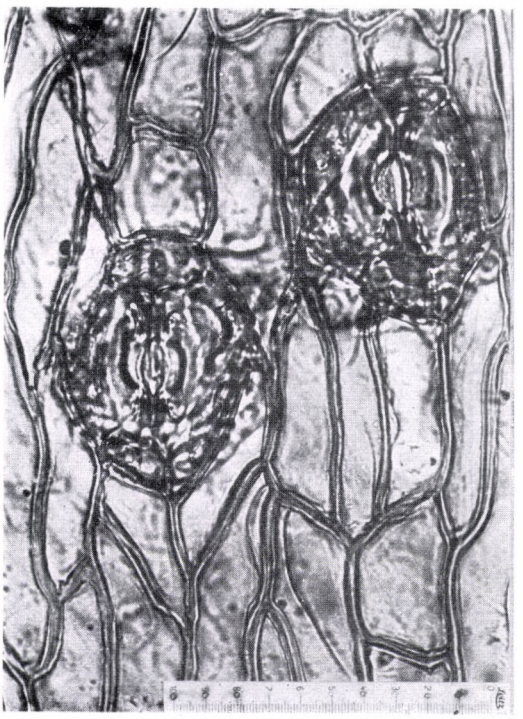

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CLXXXIV. *Bowenia spectabilis* Chamberlain



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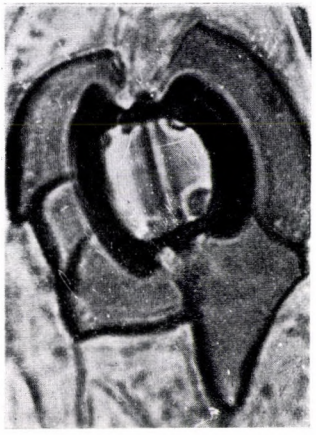

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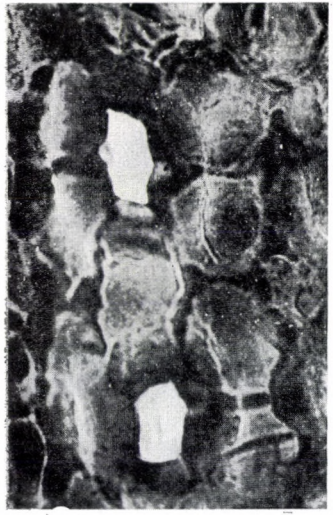

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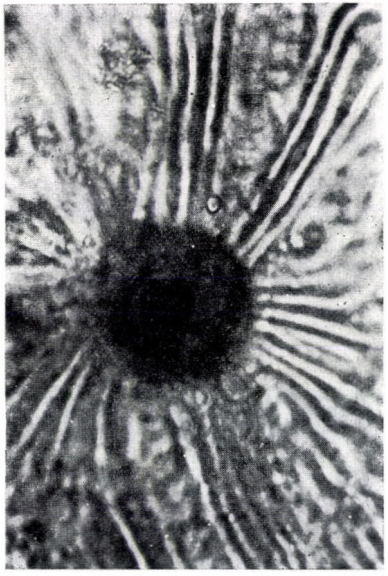

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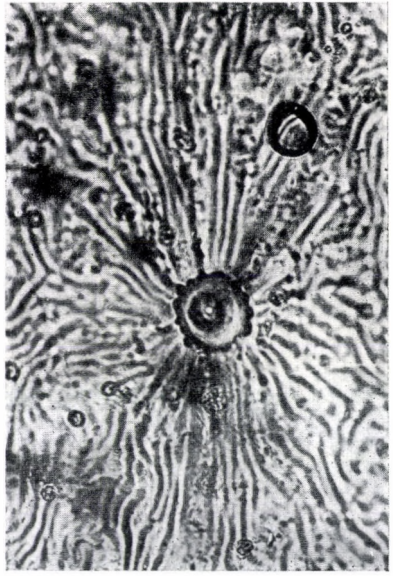

8

CLXXXV. The similar structure of the stomata in the extinct and recent *Cycadales*.
1. From the recent *Zamia muricata*. 2. From *Lyginodendron oldhamium*, originating from the Lower Westphalian (Florin). 3. ***Dioon edule***. 4. Similar structure of *Elatocladus punctatus* (Jurassic, Florin). 5. From the recent *Macrozamia miquelii*. 6. From *Elatocladus amblus* (Jurissac, Florin). 7. Epidermis cell-wall thickening from the recent *Stangeria paradoxa*. 8. Cuticular lath thickenings from *Ctenis minuta* (Jurassic). (All photos of 250-fold magnification)

Responsible for publication: Gy. Bernát
director of the Publishing House of the
Hungarian Academy of Sciences and of the
Academy Press

Responsible editor: I. Gombos
Technical editor: M. Mezneric
Jacket design by: T. Piros
Set in 10/11 point New Times Roman

Published by the same author

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