

THE FAMILIES OF CYCADS AND THE ZAMIACEAE OF AUSTRALIA.

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(Four Text-figures.)

[Read 25th March, 1959.]

Synopsis.

The general classification of the Cycadales is reviewed and grounds are put forward for the recognition of three families: Cycadaceae (*Cycas*), Stangeriaceae, fam. nov. (*Stangeria*) and Zamiaceae (remaining genera). A taxonomic revision of the Australian members of the Zamiaceae is provided. Three genera, all endemic, are recognized: *Lepidozamia* Regel (2 spp.), *Macrozamia* Miq. (14 spp.: 6 in sect. *Macrozamia*, 8 in sect. *Parazamia*), and *Bowenia* Hook. ex Hook. f. (2 spp.). New taxa are described and new combinations made as follows: *Lepidozamia hopeites* (Cookson) L. Johnson (fossil species), *Macrozamia communis*, *M. diplomera* (F. Muell.) L. Johnson, *M. lucida*, *M. stenomera*, *M. pauli-guilielmi* W. Hill and F. Muell. sspp. *plurinervia* and *flexuosa* (C. Moore) L. Johnson. The name *M. spiralis* (Salisb.) Miq. is shown to be correctly applied to the species known as *M. corallipes* Hook. f. The species known as *M. spiralis* in Queensland and New South Wales are the n. spp. *M. lucida* and *M. communis* respectively. Keys and discussions are provided for all taxa and the very confused synonymy is reviewed and clarified.

INTRODUCTORY.

This study has arisen out of the necessary revision of the New South Wales species of *Macrozamia* for the forthcoming *Flora of New South Wales*, part 1 (in press). It was clear from the outset that the specific limits needed clarification and that the nomenclature was in a state of chaos. Moreover, it soon became evident that generic as well as specific concepts were at issue and this in turn led to a consideration of the general taxonomy of the cycads.

PART I. THE FAMILIES OF CYCADS.

General.

It has been customary to refer all the true living cycads (universally accepted as the order Cycadales) to a single family, Cycadaceae, variously divided by different authors into subfamilies, tribes and subtribes. Schuster (1932, p. 63) gives a synopsis of these arrangements. Amongst these categories, however, all authors have recognized a suprageneric taxon including *Cycas* alone. In recent times only Wettstein (1923) has placed *Cycas* in a family (Cycadaceae *sensu stricto*) by itself, grouping the remaining genera as Zamiaceae. The latter family had, however, been established much earlier by Reichenbach (1837), though several cycad genera were then unknown.

Taxonomists have a tendency to recognize very inclusive families in the more unfamiliar groups of plants. The cycads are rather few, they are all very different from other living plants and they are clearly related to each other; consequently most botanists, impressed by this apartness, are content to lump them together and to minimize the differences within the group. Now all taxonomic classification, at least above the specific level, is to a considerable degree subjective as regards the status of admittedly related taxa. To take familiar examples from the flowering plants, the dismembering of the Leguminosae *s. lat.* into the three families Mimosaceae, Caesalpiniaceae and Papilionaceae must be more subjectively based than the exclusion of Paeoniaceae from Ranunculaceae. In the former case few will deny that the segregate groups have a closer phylogenetic relationship among themselves than any one of them has to other living families; the claim for family status rests on the

rather indefinable (though not unreal) degree of difference between, and coherence within, the groups. In the latter case morphological, anatomical and cytological grounds exist (Eames, 1953; Cronquist, 1957) for believing that *Paeonia* is in fact closely allied to certain families (the Dilleniales line) quite different from Ranunculaceae, and that it has been placed in the latter family on the basis of superficial resemblance; this is an objectively based segregation, provided that the general system of families in the dicotyledons is accepted as a frame of reference.

The small, self-contained group of the cycads lacks any such established frame of reference and the case for segregate families is thus scarcely a *provable* one. It is nevertheless a reasonable one. We can show that certain genera have many characters in common and could easily be derived from a common ancestral population which (at this stage) would still be quite different from the conceivable ancestors of other living genera. There are, furthermore, no links or breakdowns between these groups. Thus the groups are natural and their distinctions indicate evolutionary divergence at an early stage in the history of the Order. To justify family status we can apply to no fixed criterion, but can say that the differences are of such a nature that common ancestry for the whole assemblage must be very remote and that each of the family groups must be the result of considerable evolution since the divergence, the present members doubtless being relict forms with many lost relatives. Unfortunately, the fossil record of the true cycads is scanty (see, for instance, Cookson, 1953) in contrast to those of their distant relatives the Mesozoic Bennettitales and the broad, more or less ancestral, chiefly late Palaeozoic group of the Pteridosperms, and it is not at present likely to throw much light on evolution within the Cycadales.

On the principles outlined above, the Cycadales may be classified in three families: Cycadaceae *s. str.*, Stangeriaceae and Zamiaceae, the last of which may be subdivided (with less assurance) into tribes. The genera as commonly recognized are entirely natural with the exception of *Macrozamia*, from which *Lepidozamia* must be excluded (see below, p. 83).

There is little point in detailing the history of the many previous classifications, but of the more recent systems three may be mentioned. Hutchinson (1924) recognized two tribes, Cycadeae (*Cycas*) and Encephalarteae, the latter comprising the following subtribes: Encephalartinae* (*Dioon*, *Macrozamia*, *Encephalartos*), Stangeriinae* (*Stangeria*), Zamiinae* (*Bowenia*, *Ceratozamia*, *Microcycas*, *Zamia*); this is a reasonable arrangement and comes close to that adopted here apart from differences in status and Hutchinson's curious placing of the distinctive Stangeriinae between his other two more similar subtribes. I have used Hutchinson's key to some extent in devising the one hereunder. Pilger (1926) recognized five subfamilies, of which the first four were monotypic, containing *Cycas*, *Stangeria*, *Bowenia* and *Dioon* respectively; the fifth subfamily (Zamioideae) included the remaining genera without subdivision. The only merit of this is the recognition of *Stangeria* as rather distinctive. The subfamilial segregation of *Bowenia* and *Dioon*, while retaining such genera as *Zamia* and *Macrozamia* in a single equivalent taxon, is a characteristically unrealistic consequence of the analytical "key-character" used as a basis of classification. Schuster (1932), the latest monographer of the Cycadales, has two subfamilies, Cycadoideae (*Cycas*) and Zamioideae, the latter comprising eight tribes, each containing but a single genus! He does not say what purpose this is meant to serve.

The present system, unlike those of Pilger and Schuster, is derived not by the use of key-characters, but synthetically by marshalling like genera together using the whole complex of their characters, and analytically by the recognition of fundamental and irreconcilable differences. Parallelism and convergence are pitfalls, as usual, and grouping within the Zamiaceae is difficult. As to characters, the three very different systems of leaflet venation are surely of greater evolutionary significance and more difficult to derive from each other than are some of the different conditions in

* Given here in the correct forms under the present International Code of Botanical Nomenclature (Lanjouw, 1956); Hutchinson wrote "Encephalartineae", "Stangerineae" and "Zamineae".

reproductive characters traditionally considered of more importance. When critically examined, these latter, with the exception of those distinguishing *Cycas*, are seen to be nothing more than modifications of the shape and regularity of arrangement of the essentially similar sporophylls.

The chromosome numbers (from Darlington and Wylie, 1955) are not particularly enlightening in the cycads. They support the distinction of *Cycas* ($x = 11, 12?$), but in the Zamiaceae, while $x = 9$ is found in five genera and $x = 8$ in two (*Zamia* has both numbers), one genus (*Microcycas*) has $x = 13$. *Microcycas* agrees morphologically with the other Zamiaceae, but its chromosome number at least suggests a long history as an independent genus. The female gametophyte of *Microcycas* is remarkable for the very large number of archegonia and the male for the large number of spermatozoids produced (Chamberlain, 1919). The genus has no resemblance to *Cycas*, and certainly does not seem to be generally primitive in the Zamiaceae. Its chromosome number presents an intriguing problem, assuming, of course, that the count is correct. Finally, *Stangeria* has $x = 8$ but is very different from the two Zamiaceae (*Zamia* and *Ceratozamia*) with this number. The course of caryotype evolution is obscure.

The characters of the Cycadales as a whole may be found in any of the standard works (e.g. Schuster, 1932); *The Living Cycads* (Chamberlain, 1919), though semi-popular in style, still provides an excellent extended account and comparative discussion.

*Key to the Families and Genera.**

CYCADALES.

1. Pinnae with a single thick midrib and no lateral veins, circinately involute in bud. Female sporophylls not forming a determinate cone but spirally arranged in a terminal mass, and falling separately at maturity, the central axis eventually continuing vegetative growth (male sporophylls in definite cones). Female sporophylls with a pinnatifid, pectinate or toothed "lamina", ovules 2-several, marginally inserted proximal to the lamina, obliquely directed outwards ("ascending"). Trunk clothed with old frond-bases. $x = 11, 12?$ Old World tropics I. CYCADACEAE.
1. *Cycas*.
- 1.* Pinnae (or pinnules) with many lateral or longitudinal nerves, usually straight in bud (frond circinate as a whole in *Ceratozamia*). Sporophylls of both sexes in determinate cones, the female sporophylls scale-like, more or less peltate with a thickened and laterally expanded end on the axis-facing margins of which the 2 (sometimes 3 in *Lepidozamia* and rarely 3 or more in other genera) inward-facing ("inverted") ovules are inserted. Caudex various.
2. Pinnae penniveined, with a definite midrib and numerous transverse parallel dichotomously-branched lateral veins, convolute in bud. Sporophylls imbricate but in almost vertical rows. Caudex subterranean, naked (frond-bases deciduous). Superficially fern-like plants. $x = 8$. E. and S.E. Africa II. STANGERIACEAE.
2. *Stangeria*.
- 2.* Pinnae (or pinnules) lacking a midrib, with numerous more or less parallel longitudinal nerves (dichotomously-branched near the base), imbricate but not convolute in bud. Sporophylls and caudex various. $x = 8, 9, 13$ III. ZAMIACEAE.
3. Sporophylls imbricate, not in vertical rows. Caudex clothed with persistent frond- and cataphyll-bases. Pinnae not obviously articulate, though somewhat deciduous when old in a few species.
4. Cones axillary (sometimes erect and appearing falsely terminal, but not terminating main axis). Ovules sessile on the sporophyll. Female sporophylls greatly thickened towards the ends and tightly imbricate, glabrous or tomentose but scarcely woolly. $x = 9$. Australia and Africa a. Tribe *Encephalarteae*.
5. Sporophyll-ends acutely or bluntly pointed or with a terminal spine (sometimes reduced to a narrow transverse wing, but never a facet). Cones sessile or stalked. Australia.
6. Cones sessile or subsessile; sporophyll-ends tomentose, produced into a spreading obtuse to acute but not spinescent wing, curved upward or downward. Successive crowns of fronds markedly separated by broad series of cataphylls. Pinnae inserted on the adaxial midline of the rhachis. Frond-bases shortly tomentose. E. Australia 3. *Lepidozamia*.

* The terminology is the same as that used in Part II (see p. 77). Hutchinson's (1924) key and the excellent vegetative key of Regel (1876) have been used freely in constructing this one which, however, is based as far as possible on actual material. The key does not, of course, give all the distinguishing characteristics of the taxa. Each genus has a characteristic facies due to the form and arrangement of the fronds and their segments.

- 6.* Cones stalked ("pedunculate"); sporophyll-ends glabrate, often glaucous, at least the females subterminally compressed to form a more or less vertical surface, on which (in both sexes) the margins form a transverse ridge terminating in a rigid more or less erect spine. Successive crowns of fronds little separated by a few cataphylls. Pinnæ inserted near the edges of the rhachis. Frond-bases silky or woolly with long hairs. $x = 9$. Australia 4. *Macrozamia*.
- 5.* Sporophyll-ends truncate, more or less prismoidal, with a 4- or 6-sided terminal facet, somewhat decurved. Cones sessile. $x = 9$. Africa 5. *Encephalartos*.
- 4.* Cones (sessile or shortly stalked) terminating growth of the main stem, which continues vegetative growth sympodially from the base of the cone (the subterminal "cone-dome" ultimately engulfed by the new growth so that the trunk appears continuous). Ovules usually borne on a short stalk-like outgrowth (false funicle) of the sporophyll. Female sporophylls somewhat thickened but loosely imbricate at least at the ends (which are reduced in *D. spinulosum*), the woolly ends flattened and erect. $x = 9$. Central America b. Tribe *Diöeeae*.
6. *Dioon*.
- 3.* Sporophylls apparently valvate, arranged in vertical rows, their ends (at least in the females) hexagonal or rhomboid. Caudex various, often naked. Cones terminal (always?) in origin, on the main stem or short branches, though often pushed aside by new stem growth. Pinnæ definitely articulate at the base or, if not, then fronds decompound c. Tribe *Zamiæae*.
7. Sporophylls either shortly woolly or 2-horned at the end. Trunk robust, clothed with leaf-bases and cataphylls or at length naked. Fronds simply pinnate, pinnæ articulate.
8. Sporophyll-ends obtuse or truncate, not horned, tomentose with short, crisped hairs. Frond-bases and cataphylls said to be at length deciduous. $x = 13$. Cuba 7. *Microcycas*.
- 8.* Sporophyll-ends 2-horned, not tomentose. Frond-bases and cataphylls persistent. $x = 8$. Mexico 8. *Ceratozamia*.
- 7.* Sporophylls truncate, not woolly or horned. Caudex naked, usually slender or short, sometimes subterranean. Fronds either decompound or, if simply pinnate, then the pinnæ articulate.
9. Fronds simply pinnate, pinnæ articulate at the base. $x = 8, 9$. Tropical N. and S. America 9. *Zamia*.
- 9.* Fronds decompound, pinnæ and pinnules not articulate at the base. $x = 9$. N.E. Australia 10. *Bowenia*.

Enumeration and Discussion.

In this paper I can neither list the detailed synonymy nor deal at length with the extra-Australian taxa, other than those newly established herein. Those interested may consult the monograph of Schuster (1932) for generic descriptions and bibliography, but will be wise not to rely on it, especially at the specific level. Probably all the larger genera need thorough revision, on modern lines, by workers familiar with most of their species in the field.

I. Family CYCADACEAE L. C. Rich.* in Pers., *Enchir.*, 2 (1807), 630.

As here restricted this includes only the genus *Cycas*. This is the most distinct of all the genera of cycads and in many respects preserves the most primitive characters, especially in the frond-like megasporophylls and their loose undifferentiated arrangement. However, *Cycas* cannot be considered to represent a form ancestral to the other living genera, since its single-veined pinnæ could hardly have given rise to either the Stangeriaceae or the Zamieae condition.

The circinate vernation of the pinnæ (not the whole frond) is an apparently primitive feature. The much greater specialization of the male as compared with the female structures is the most remarkable feature of the family. This indicates that determinate male and female cycad "cones" may not be homologous as complete structures, but only in so far as they are aggregations (attained at different stages) of sporangium-bearing reduced determinate branch-systems (sporophylls) more or less

* As "Cycadeae" but in family rank.

equivalent to the fronds which (phylogenetically speaking) are somewhat less reduced, similar but sterile branch-systems.

1. *Cycas* L. Type species: *C. circinalis* L.

Perhaps 20 species, extending to Madagascar and East Africa but chiefly in South-East Asia, tropical Australia and the western Pacific. Chromosome numbers: $x = 11, 12?$ ($2n = 22$, but 24 in one count).

Schuster (1932) recognizes only eight species but his treatment would appear to be no sounder than that of *Macrozamia* (see below, p. 72). *Cycas* is much in need of satisfactory revision but this would certainly require a wide knowledge of the species in the field and extensive living and herbarium collections from the whole of its wide range. Much herbarium material is practically useless. For these reasons I have not attempted to deal with the Australian species. The synonymy also is most complex and confused, as in *Macrozamia*. A difficult and protracted task awaits any responsible monographer of the genus.

II. Family STANGERIACEAE! L. Johnson, fam. nov.

I can trace no previous publication of this taxon in family rank.

Familia inter Cycadalibus frondium pinnis unicostatis arcte penninerviis (venis dichotomis rectiusculis) vernatione rectis sed convolutis* distincta. Sporophylla utriusque sexus conos determinatos formantia, squamiformia peltataque, mascula sporangiis multis infra instructa, feminea ovulas duas versus axem coni directas in marginibus gerentia. Chromosomata ut $x = 8$ numerata.

Genus typicum (unicum): *Stangeria* T. Moore.

Stangeria has not usually been considered as distinct as *Cycas* from the other cycad genera, and indeed there is no apparent character in the reproductive structures inconsistent with its inclusion in the Zamiaceae. However, the view that "good" taxa above the rank of species (or even species in some opinions) must always differ in reproductive characters is surely an example of archaic formalism lacking any firm evolutionary basis. "Good taxonomic characters" have no absolute significance and can be evaluated only in relation to the whole complex of circumstances in particular cases. A "conservative" character in one series of organisms may be quite radically modified in a closely related series or even in individual species within the same series. Evolutionary processes are no respecters of "characters", and useful as generalizations about characters may be when discussing trends, to apply them dogmatically in classification is to reduce taxonomy to a formal game rather than a branch of biology. This is in contrast to the view of Davis (1952, p. 149).

It is clear that the strongly-developed midrib and the many crowded, spreading, lateral veins of *Stangeria* pinnae must develop by organogenetic growth processes considerably different from those which produce the longitudinally-nerved midribless frond segments of the Zamiaceae. Neither condition is easily derivable from the other.† This implies an early separate development along two lines from some ancestral group with a more generalized vascularization of the fronds.

Anyone familiar with living plants of all or most of the cycad genera must be struck by the divergent appearance of *Stangeria*. Its fern-like, rather Marattiaceous, aspect is quite unlike that of any of the Zamiaceae or of *Cycas*. The resemblance to a *Marattia* or an *Angiopteris* is, of course, due to convergent, or perhaps more properly to parallel, evolution of a similar frond pattern from the more primitive forms of megaphyllous leaf (major determinate branch system) found in the very early

* The vernation of the pinnae is usually described (e.g. by Schuster, 1932) as plicate; in the living material which I have examined the young pinnae are strongly convolute and certainly not plicate, except perhaps at the tips.

† It is conceivable that the simply pinnate frond of *Stangeria* is equivalent to a bipinnate type of Zamiacean frond (cf. *Bowenia*) in which individual pinnules have undergone "phylogenetic fusion". However, this seems very doubtful and *Stangeria* could still not be derived from anything like the known Zamiacean genera — certainly not from *Bowenia*.

Pteropsida. There is no particular relationship between the groups, which differ profoundly in reproductive structures and internal anatomy. On the other hand, the difference between *Stangeria* and the Zamiaceae is certainly not superficial, and suggests that some of their reproductive resemblances may be due to parallel development from early proto-cycadalean ancestors. With little doubt the naked tuberous stem and the geophytic habit are secondary and do not imply any relationship between *Stangeria* on the one hand and *Bowenia* or *Zamia* on the other.

Such internal schisms notwithstanding, the unity of the Cycadales as a whole seems clear. The correspondence of all three families in structure and organization is too close to be the result of convergence from unlike ancestors, though parallel development of different lines from a common ancestral group seems probable. For a comparative discussion of homology, parallelism and convergence, and their significance in classification, see Simpson (1945, pp. 8-12). In the present paper I have attempted to apply principles of evolution-reflecting classification developed from considerations similar to those so admirably expressed by Simpson in this remarkable *tour de force*.

2. STANGERIA T. Moore. Type species: *S. eriopus* (Kunze) Nash (*S. paradoxa* T. Moore).

A single variable species (as usually treated) in south-east Africa. Chromosome number: $x = 8$ ($2n = 16$).

III. Family ZAMIACEAE Reichenb., *Handb.* (1837), 139.

Eight genera and perhaps 80 species in the tropical to warm-temperate regions of Africa, Australia and North and South America.

The Zamiaceae appear to be a natural group. All the genera certainly agree in many fundamentals of structure despite considerable diversity of detail and size. The characteristic longitudinal dichotomous venation has already been stressed when discussing the other two families. The basic chromosome number $x = 9$ predominates, with $x = 8$ (a reduction? Not found in the apparently more primitive genera) in two genera and the anomalous-seeming $x = 13$ in *Microcycas*. Chamberlain (1919) indicates various reduction and specialization series from genus to genus, but these are by no means always concurrent in different organs and it is obvious that, although some of them have a greater number of advanced features than others, the living genera do not represent an evolutionary series but rather the present end-points of a number of different lines, doubtless cognate with others now extinct. To judge from the phylogenetic series which many authors put forward even today for Recent organisms of all kinds, it is still necessary to state this evolutionary platitude.

With some diffidence I have attempted to arrange the genera into three tribes. These are perhaps not entirely natural (especially Zamieae, which includes the rather non-conforming *Microcycas*), but they do bring together similar genera, some of which are undoubtedly not too distantly related.

Phytogeographers should beware of basing any far-reaching arguments upon the distributions of these rather tentatively defined tribes.

a. Tribe ENCEPHALARTEAE (Miq.) L. Johnson, comb. nov.*

Three genera, in Australia and Africa.

These genera have relatively few advanced features, though certain specializations are found. Although each genus is very distinct, a true relationship seems likely. F. Mueller at various times united them under *Encephalartos* and indeed suggested sinking this under *Zamia*; he did not believe in evolution (see below, p.—), but in the individual creation of species and the consequent artificiality of genera. Affinity, apart from mystical connotations, meant merely resemblance in certain chosen characters.

* Cycadaceae ("Cycadeae") tribe Encephalarteae Miq., *Prodr. Syst. Cycad.* (1861), 5. Schuster (1932, p. 64) attributes this to himself, in spite of his citation on p. 63 of its use by Miquel and other authors.

3. LEPIDUZAMIA Regel. Type species: *L. peroffskyana* Regel.

Two species in tropical and subtropical eastern Australia. Chromosome number unknown.

Discussed in detail in Part II (p. 83).

4. MACROZAMIA Miq. Type species: *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn. (see p. 87).

Fourteen species in subtropical and warm-temperate Australia. Chromosome number: $x = 9$ ($2n = 18$).

Discussed in detail in Part II (p. 87).

5. ENCEPHALARTOS Lehm. Type species to be selected by a monographer.

Fifteen–twenty species in Central and South Africa. Chromosome number: $x = 9$ ($2n = 18$).

The genus still needs some revision, but the tropical species have been fully treated by Melville (1957).

b. Tribe DIÖEAE (Schuster) L. Johnson, comb. nov.*

A single genus in Central America.

This tribe was rather meaningless as set up by Schuster, since all his tribes were unigeneric. However, *Dioon* does stand somewhat apart from the Encephalarteae, their common characters being chiefly merely the generally primitive ones of the family. It may be convenient to allot it a tribe to itself. The cones are terminal (according to Chamberlain's studies), as in the Zamieae, but *Dioon* differs considerably from that tribe in other characters.

6. DIOON Lindl. Type species: *D. edule* Lindl.

Three (or more?) species in Central America (chiefly Mexico). Chromosome number: $x = 9$ ($2n = 18$).

Dioon and *Lepidozamia* have the least modified megasporophylls in the Zamieaceae. They are otherwise not particularly alike.

c. Tribe ZAMIEAE.†

Four genera, in America and Australia.

As stated above, this tribe possibly includes the products of convergence rather than close affinity. The genera are grouped mainly on the regular arrangement of the sporophylls in the cone, in which definitely vertical orthostichies are apparent. The sporophylls are, of course, at the same time arranged in parastichies (spirals) as in the other tribes. Phyllotactic modification to the regular vertical arrangement could easily have taken place more than once. *Bowenia* is geographically isolated from the other genera and its resemblance to *Zamia* in sporophylls, cones and habit could be secondary, at least in part. *Microcycas* has 13 gametic chromosomes and some gametophytic peculiarities, and thus stands rather apart from the other genera. *Ceratozamia* shares the number $x = 8$ with some species of *Zamia*, but this probably does not indicate any special relationship. In habit, at least, *Ceratozamia* seems more primitive than *Zamia* and its sporophylls are distinctive. These American genera and *Bowenia* need

* Cycadaceae tribe Diöeae ("Diooneae") Schuster, Pflanzenr., IV, i (1932), 64. Schuster's spelling is to be corrected, as above. Since *Dioon* is from the Greek $\delta\iota$ and $\omega\nu\rho$, and the stem of the latter, transliterated, is "ö-" (cf. "oospore", "Oidium"), then the stem of the compound is surely "Dio-". Under the I.C.B.N. the tribal ending "-eae" must be added to the stem. Classical Latin authors, supposing them to have used such a word at all, would doubtless have latinized it to the less outlandish-looking "Dioveae". One may perhaps enter a protest against the too common pronunciation of *Dioon* to rhyme with "soon"; it rhymes with "so on". Lindley's original publication as "*Dion*" was a mere slip, later corrected.

† As the tribe containing the type, this requires no author citation. It was first established as Cycadaceae ("Cycadeae") tribe Zamieae Reichenb., *Consp. Regn. Veg.* (1828), 40. (Not seen; the reference is from Schuster (1932, p. 63). On p. 64 he cites his own name as author, though Zamieae had been used by many earlier workers.)

a comparative study, with taxonomic rather than purely morphological principles in mind. Whether the cones are in fact always terminal in origin, as stated by Chamberlain (1919), needs to be confirmed. The cones of *Ceratozamia*, at least, appear lateral to the external view.

7. *MICROCYNAS* (Miq.) A.DC. Type species: *M. calocoma* (Miq.) A.DC.

A single species in Cuba. Chromosome number $x = 13$ ($2n = 26$).

I have seen no living plants of this genus and little herbarium material. Regel (1876) states that the frond-bases and cataphylls ("perulae") are at length deciduous, leaving a naked stem. By contrast, Hutchinson (1924) keys out the genus on its "trunk . . . covered with persistent leaf-bases and prophylls". This is a character of some importance in other genera. As stated above, the position of *Microcynas* is in some doubt. It does, however, show a number of resemblances to *Zamia*.

8. *CERATZAMIA* Brongn. Type species: *C. mexicana* Brongn.

About four species in Mexico. Chromosome number: $x = 8$ ($2n = 16$).

A distinctive genus. Its relationship is not certain, but appears to be rather distantly with *Zamia*. The fronds are more or less circinate in veneration.

9. *ZAMIA* L. Type species: *Z. floridana* L. (lectotype, Hutchinson, 1924).

About 30-40 species in the tropics of the New World. Chromosome number: $x = 8$, 9 ($2n = 16, 18$).

Like *Cycas*, *Zamia* needs a modern monographic treatment, in this case by an American worker. Regel's genus *Aulacophyllum* (Regel, 1876) is worthy of reconsideration. Regel was a discerning worker and his treatment of cycad genera was sound. *Aulacophyllum* may be as good a genus as the equally neglected *Lepidozamia*.

10. *BOWENIA* Hook. ex Hook. f. Type species: *B. spectabilis* Hook. ex Hook f.

Two species in north-eastern Australia. Chromosome number: $x = 9$ ($2n = 18$).

This is the only living cycad with truly decompound fronds, though *Stangeria* and *Macrozamia* may have forked pinnae. Discussed in detail in Part II (p. 109).

PART II. THE ZAMIACEAE OF AUSTRALIA.

Historical.

Early authors.

Since Salisbury described *Zamia spiralis* (now *Macrozamia spiralis* (Salisb.) Miq.) in 1796, many authors have contributed to the systematics of the Australian Zamiaceae. No useful purpose would be served by a detailed account of their treatments and the progress, and at times regression, in the classification over the last century and a half. All the relevant references and an index of names may be found hereunder, in the formal systematic treatment. The more important landmarks and workers, however, may be briefly mentioned.

Miquel established the genus *Macrozamia* in 1842, the three known species (under a single name) having previously been referred at first to *Zamia* and later to *Encephalartos*. This Dutch botanist studied the cycads in general for some thirty years and published numerous short and long papers on the group. Although many confusions are inevitably found in this early work, his studies are marked by a steady progress in understanding at both generic and specific levels, and his general discussions and contributions to cycad morphology are as praiseworthy as his taxonomic contributions. Unquestionably Miquel remains pre-eminent among taxonomic cycadologists and (the period taken into account) is overshadowed only by Chamberlain in the morphological field. Several of these studies (Miquel, 1861, 1863, 1868, 1869) are of particular importance. The first is a concise general review of the cycads of the world, while the second is a revision of the Australian members in which he reduced *Macrozamia* and the recently described *Lepidozamia* Regel to sections of *Encephalartos* and set up also the section *Parazamia*. The 1868 and 1869 papers are French and Dutch versions respectively of part of a series of morphological and taxonomic papers, of which the most important to us deals with the "Cycadëen van extratropisch Nieuw-

Holland", namely *Macrozamia* (restored here to generic rank, and embracing *Lepidozamia* as a section) and *Bowenia*.

F. Mueller (latterly F. von Mueller) published numerous notes and brief commentaries between 1858 and 1889 (see references in formal section). On the credit side he made known a number of newly-discovered species, stimulated collection and increased the knowledge of distribution; unfortunately this was counterbalanced by serious confusion of quite dissimilar species (most notably *M. miquelii* with *M. fawcettii*) and thirty years of vacillation between recognition of *Macrozamia* and its inclusion in *Encephalartos*. Each change of opinion was accompanied by a new combination or two. Mueller had little field knowledge of these plants, despite his residence in Australia.

A notable cycadologist whose work is largely overlooked was Regel, who gathered a large collection of living plants at the then St. Petersburg Botanic Garden and paid particular attention to the most useful and significant vegetative characters of the genera. Among his many papers, two (Regel, 1857, 1876) are of special importance, dealing respectively with the new genus *Lepidozamia* (the distinctive characters of which subsequent authors have not properly appreciated) and with a general revision of all the Cycads. This little-known work is essentially more sound than later reviews of greater pretensions.

J. D. Hooker (1863, 1872) described the distinctive genus *Bowenia*. A. De Candolle (1868) produced a useful monograph largely following Miquel. In the *Flora Australiensis*, Bentham (1873), working in England from inadequate herbarium material, provided a better treatment than did Mueller on the spot, but, as he was himself aware, it is not very satisfactory. Successful cycad studies require years of familiarity with the plants.

In a modest paper, Charles Moore (1884) gave the most realistic account yet published of the eastern species of *Macrozamia* (including *Lepidozamia*). Unlike other authors, Moore had the advantage of an extensive and critical field knowledge of most of the species. He also studied them side by side in the garden and laid the foundations of the present cycad collection in the Sydney Botanic Gardens. Apart from understandable partial confusion of the species now defined as *Macrozamia diplomera*, *M. heteromera* and *M. stenomera* (see p. 105) and neglecting minor matters of nomenclature with which he did not concern himself, the only flaws in his account arose from following Mueller with undue respect. Virtually the same arrangement was used in condensed form by Moore and Betcher (1893).

At various times, but especially in the *Queensland Flora*, F. M. Bailey (1902) reviewed the Queensland species. As with Moore, some field experience put Bailey in touch with reality, though not all of his species can now be maintained.

From this encouraging position Maiden and Betcher (1916) reverted to confusion by reducing all but one of the true *Macrozamia* species of New South Wales to their inflated concept of *M. spiralis*, claiming that they were all connected by intergradation. This is not so.

Schuster's monograph.

As a greater anticlimax, Schuster (1932) produced his monograph in *Das Pflanzenreich*. In his treatment of *Macrozamia*, despite its comprehensive scope and superficial aspect of detailed finality, Schuster so profusely introduces new and profound confusions in taxonomic concepts of every rank and in nomenclature, so blatantly contravenes the rules of priority, and so unreliably cites both synonymy and specimens that the work is quite egregious even for a compendium of such unequal quality as *Das Pflanzenreich*. Despite several years of unfortunately necessary detailed study of this work, I can form no idea of the principles, if any, which Schuster followed in arriving at his conclusions. Virtually identical plants, even the same specimens, are referred to entirely different species. Most diverse species are treated as subspecies, varieties or forms under a single (misapplied!) name, often appearing more than once in quite

different branches of this elaborate false hierarchy, while species closely allied to some of these are given full specific rank. For instance, Schuster places materials of *M. heteromera* as (i) (the typical variety of) an independent species, but there confused with two other species; (ii) a form of a variety (the type form of which is a different species) of this same species; (iii) a form of a variety of a subspecies of "*M. tridentata*", this form being a mixed concept of two species, the variety a mixed concept of four other species, and so on through the higher categories. With one or two partial exceptions, his arrangement and circumscription of all taxa from sections down to forms bear almost no relation to the real affinities and the distinctions between the species in nature. The result is a jumble which almost defies disentanglement. It is hard to see why Schuster did not follow the earlier treatments which, though imperfect, should have been a useful guide.

In most branches of science worthless work may be forgotten and need not hinder progress; taxonomy is bedevilled by the requirement that no validly published name may be ignored. Thus taxonomists spend much of their time in unprofitable antiquarianism rather than scientific study. So that future students of Australian Zamiaceae need not repeat much of this labour, and perhaps to help those in charge of overseas cycad collections who have naturally had recourse to Schuster's monograph in naming their plants, I have provided a table (Table 1) interpreting his usage.

Further details may be found in the synonymy of the various species in the formal section, below. In using this tabulation one should bear in mind that in any subdivided taxon Schuster's method was to describe and list first all material which he treated as typical and to follow this by his first named subsidiary category; (supposedly) typical subdivisions were not named in the lower rank. For example, his "*Macrozamia tridentata*" has two named and numbered subspecies, but these are preceded by a description and citations applying only to what one must consider as the "typical" subspecies (though the term has little meaning here; how Schuster regarded it one can only guess). Similarly his first subspecies includes three named varieties exclusive of the "typical" variety and so on. In Table 1 the total ambit of his inclusions ("concept" is hardly the word) under any one taxon must be obtained from the sum of the interpretations of its subdivisions.

In order to achieve finality in this tedious matter the identity of these "synonyms" and specimens has been checked with great care, and the reductions, as amplified in the formal section, may be accepted as authoritative according to the concepts of the present treatment. All cases of residual doubt or ambiguity are clearly indicated. Column 2 of the table gives the present correct position of the type(s) of the basionyms (and absolute nomenclatural synonyms) of Schuster's names, not the actual basionym itself. The latter may be determined from the synonymy in the formal section. Similarly, column 4 lists the correct positions of the types of the various alleged synonyms cited by Schuster, excluding the absolute synonyms.

Schuster's descriptions are frequently largely copied or translated from those of other authors and do not necessarily apply to the specimens or synonyms cited with them.

Present Study.

Scope.

This paper aims to present a fully-documented and definitive taxonomic revision of, and commentary on, all species of the three Australian genera of Zamiaceae. Amongst these the New South Wales species have received most attention, and indeed have most needed it.

No new cytological or anatomical investigations have been made, but the results of such studies are taken into account in forming taxonomic judgments. General ecological observations have been made and their taxonomic significance assessed. Economic and horticultural aspects lie outside the scope of this paper, but have been borne in mind in the course of the work. Evolutionary and theoretical questions are discussed when relevant.

TABLE 1.

Name Used by Schuster (1932) (spellings corrected).	Correct Name in the Present Revision. [<i>Macrozamia</i> spp. belonging to sect. <i>Parazamia</i> marked (P), others belong to sect. <i>Macrozamia</i> .]		
	Basionym (present correct position).	Specimens Cited.	"Synonyms" Cited (excl. Invalid Names and Absolute Synonyms) (present correct position).
<i>M. tridentata</i> (Used in contravention of priority, since Schuster's circumscription included the types of several earlier names, viz. <i>Z. spiralis</i> Salisb., <i>Z. pallida</i> Salisb., <i>Z. pungens</i> Ait.)	<i>Macrozamia</i> or <i>En- cephalartos</i> sp., un- identifiable (juv.) (= <i>Z. tridentata</i> Willd.)	<i>M. miquelii</i> . <i>M. communis</i> . (and perhaps <i>M. lucida</i> (P) by in- ference).	<i>M. miquelii</i> . <i>M. communis</i> . <i>M. spiralis</i> (P). <i>Zamia</i> , <i>Encephalartos</i> or <i>Macrozamia</i> sp.? (<i>Z. pallida</i> Salisb.).
ssp. <i>mountperriensis</i> ("mountperryensis")	<i>M. miquelii</i> .	<i>M. miquelii</i> .	
var. <i>miquelii</i> (nom. illegit.) ..	<i>M. miquelii</i> (lectotype) and <i>M. fawcettii</i> (P).	<i>M. miquelii</i> .	<i>M. miquelii</i> . <i>M. fawcettii</i> (P).
f. <i>milkaui</i> (nom. illegit.) ..		<i>M. miquelii</i> (juv.). <i>M.</i> or <i>Enceph.</i> sp. (juv.) (= <i>Z. tridentata</i> Willd.)	<i>M.</i> or <i>Enceph.</i> sp. (= <i>Z. tridentata</i> Willd.).
f. <i>oblongifolia</i>	<i>M. miquelii</i> .	<i>M. communis</i> (juv.).	
var. <i>mackenzii</i>	<i>M. miquelii</i> .	<i>M. miquelii</i> .	
var. <i>douglasii</i>	<i>M. miquelii</i> .	<i>M. miquelii</i> .	
ssp. <i>cylindrica</i>	<i>M. miquelii</i> .	<i>M. miquelii</i> . <i>M. communis</i> . <i>M. moorei</i> .	
var. <i>secunda</i>	<i>M. secunda</i> (P).	<i>M. secunda</i> (P). <i>M. pauli-guilielmi</i> ssp. <i>plurinervia</i> (P).	
var. <i>corallipes</i>	<i>M. spiralis</i> (P).	<i>M. spiralis</i> (P).	<i>M. spiralis</i> (P).
f. <i>wallsendensis</i>		<i>M. communis</i> (semi- juv.).	
f. <i>dielsii</i>		<i>M. spiralis</i> (P).	
f. <i>vavilovii</i>		<i>M. communis</i> ? or <i>M. miquelii</i> ?	
var. <i>pungens</i>	<i>Encephalartos</i> sp.? (obscure, not Aus- tralian).	<i>M. communis</i> . <i>M. miquelii</i> . <i>M. moorei</i> <i>M. lucida</i> (P).	<i>Zamia</i> , <i>Enceph.</i> or <i>Macroz.</i> sp.? (<i>Z. pallida</i> Salisb.).
f. <i>hillii</i>		<i>M. miquelii</i> or <i>M. communis</i> ? (or even <i>M. riedlei</i> ?).	<i>M. miquelii</i> or <i>M. communis</i> ? (or even <i>M. riedlei</i> ?).
f. <i>diplomera</i>	<i>M. diplomera</i> (lecto- type) and <i>M. heteromera</i> (P).	<i>M. diplomera</i> . <i>M. heteromera</i> (P).	

TABLE 1.—Continued.

Name Used by Schuster (1932) (spellings corrected).	Correct Name in the Present Revision. [<i>Macrozamia</i> spp. belonging to sect. <i>Parazamia</i> marked (P), others belong to sect. <i>Macrozamia</i> .]		
	Basionym (present correct position).	Specimens Cited.	"Synonyms" Cited (excl. Invalid Names and Absolute Synonyms) (present correct position).
<i>M. moorei</i>	<i>M. moorei</i> .	<i>M. moorei</i> .	
<i>M. flexuosa</i>	<i>M. pauli-guilielmi</i> ssp. <i>flexuosa</i> (P).	<i>M. pauli-guilielmi</i> ssp. <i>flexuosa</i> (P). <i>M. p.-g.</i> ssp. <i>pluri-</i> <i>nervia</i> (P).	
<i>M. heteromera</i>	<i>M. heteromera</i> (P) (lectotype) and <i>M. diplomera</i> .	<i>M. heteromera</i> (P). <i>M. stenomera</i> (P). <i>M. diplomera</i> .	
var. <i>dicranophylloides</i>		<i>M. stenomera</i> (P).	
var. <i>tenuifolia</i> (nom. illegit., later homonym).		<i>M. stenomera</i> (P).	
f. <i>harmsii</i>		<i>M. heteromera</i> (P).	
<i>M. pauli-guilielmi</i> ("pauli-guilelmi") ..	<i>M. pauli-guilielmi</i> ssp. <i>pauli-guilielmi</i> (P).	<i>M. pauli-guilielmi</i> ssp. <i>pauli-guilielmi</i> (P). <i>M. p.-g.</i> ssp. <i>flexuosa</i> (P.) <i>M. p.-g.</i> ssp. <i>pluri-</i> <i>nervia</i> (P).	<i>M. pauli-guilielmi</i> ssp. <i>pauli-guilielmi</i> (P).
<i>M. fauccettii</i>	<i>M. fauccettii</i> (P).	<i>M. fauccettii</i> (P). <i>M. pauli-guilielmi</i> ssp. <i>flexuosa</i> (P). <i>M. p.-g.</i> ssp. <i>pluri-</i> <i>nervia</i> (P).	
<i>M. platyrachis</i> ("platyrhachis")	<i>M. platyrachis</i> (P).	<i>M. platyrachis</i> (P).	
<i>M. denisonii</i> (Used in contravention of priority.)	<i>Lepidozamia</i> <i>peroffskyana</i> .	<i>L. peroffskyana</i> . <i>L. hopei</i> .	<i>L. peroffskyana</i> .
var. <i>hopei</i>	<i>L. hopei</i> .	<i>L. hopei</i> .	
<i>M. preissii</i> (Used in contravention of priority.)	<i>M. riedlei</i> .	<i>M. riedlei</i> . <i>M. macdonnellii</i> .	<i>M. riedlei</i> . <i>M. macdonnellii</i> .
ssp. <i>dyeri</i>	<i>M. riedlei</i> .	<i>M. riedlei</i> .	
<i>M. Sect. Polyorientales</i> (nom. illegit.) ..	As to type sp. <i>M. §Macrozamia</i> .	<i>M. §Macrozamia</i> (part). <i>M. §Parazamia</i> (part).	
Subsect. <i>Attenuatae</i> (nom. illegit.) ..	<i>M. §Macrozamia</i> .	<i>M. §Macrozamia</i> (part). <i>M. §Parazamia</i> (part).	
Subsect. <i>Acutae</i>	<i>M. §Parazamia</i> .	<i>M. §Parazamia</i> (part).	
Subsect. <i>Curvatae</i>	<i>M. §Parazamia</i> .	<i>M. §Parazamia</i> (part).	
<i>M. Sect. Monoorientales</i> (nom. illegit.) ..	<i>Lepidozamia</i> (Genus).	<i>Lepidozamia</i> (Genus).	
<i>M. Sect. Monooccidentales</i> (nom. illegit.)	<i>M. §Macrozamia</i> .	<i>M. §Macrozamia</i> (part).	

TABLE 1.—*Continued.*

Name Used by Schuster (1932) (spellings corrected).	Correct Name in the Present Revision. [<i>Macrozamia</i> spp. belonging to sect. <i>Parazamia</i> marked (P), others belong to sect. <i>Macrozamia</i> .]		
	Basionym (present correct position).	Specimens Cited.	"Synonyms" Cited (excl. Invalid Names and Absolute Synonyms) (present correct position).
<i>Bowenia spectabilis</i>	<i>B. spectabilis</i> .	<i>B. spectabilis</i> .	
var. <i>serrulata</i>	<i>B. serrulata</i> .	<i>B. serrulata</i> . <i>B. spectabilis</i> (?).	<i>B. serrulata</i> .

Basis.

The materials used are: (1) The herbarium and museum collections of the New South Wales National Herbarium (NSW), together with certain material from the Botanic Museum and Herbarium, Brisbane (BRI), the National Herbarium, Melbourne (MEL), the Museum of Applied Arts and Sciences, Sydney (TECH), and the Botany Department, University of Sydney (SYD). Since the outstanding problems were centred in New South Wales, only selected specimens from the other State herbaria were examined. Their full collections will, of course, fill in details of distribution, but are not likely to affect the conclusions, at least without concurrent field study. (2) The living cycad collections in the Royal Botanic Gardens, Sydney. (3) Natural populations of the following species: *Lepidozamia peroffskyana*, *Macrozamia moorei*, *M. macdonnellii*, *M. communis*, *M. diplomera* (limited observation), *M. lucida*, *M. spiralis*, *M. secunda*, *M. heteromera*, *M. stenomera* and *M. pauli-guilielmi* (especially ssp. *plurinervia*). The only species not examined either in the field or the garden are *L. hopei*, *M. platyrachis* and *M. riedlei*. The last certainly needs some field study. (4) Published and unpublished illustrations and descriptions. Information solely derived from such descriptions, except when they are very clearly fully reliable, is specified as such in the text.

Outlook.

Since systematists are notoriously individualistic, it is always helpful to appreciate a particular worker's standpoint and philosophical approach to the subject. Underlying the present treatment is the conviction that taxonomic classification, in one way or another, should reflect, if not express, the results of evolution. When little palaeontological evidence is available one can do this only by inference, using the accumulated knowledge of what is known to have happened in other and especially related groups of organisms, and evidence of every possible kind must be evaluated and taken into account. Bearing in mind genetic, evolutionary and ontogenetic principles, one must try to determine the most probable relative phylogenetic relationships and divergences of the various individuals, populations and groups of populations, and decide their taxonomic status accordingly. The success of this method depends greatly on the student's knowledge and insight, but on a balance of probabilities it leads to more satisfactory conclusions than those obtained by the static or formalistic approach, which rejects evolutionary speculation and depends solely on morphological differences and resemblances in their own right. It is well known that similar conclusions may often be reached from these really quite fundamentally different starting points. That they quite often lead to different conclusions is frequently forgotten.

I have, of course, used the customary, chiefly macroscopic and external, morphological characters in the keys and descriptions. However, characters as such were not regarded as the basis of taxonomic decisions, but rather as indices of the natural populations or groups of populations between which, on grounds of evolutionary

probability, if not direct evidence, we can infer relationship. It is often held that the best taxonomic characters are those which are selectively neutral. The existence of truly selectively neutral characters is dubious; practically every characteristic of a line of organisms is in some sense adaptive, within the range of genetic possibilities open to the particular group. Though selection may operate chiefly on some genetically and developmentally correlated characters rather than those we observe as taxonomic differences, any deleterious effects will tend to be minimized by adaptive compensation (Stebbins, 1950, pp. 121-123). There are, of course, many genetic and physiological balances and counterbalances, multiple genetic effects, and time-lags, and some characters do appear fixed because they are adapted not to the external environment, but rather to the complex of balanced organization within the organism itself in such a way that any uncoordinated change is disadvantageous.

Such characteristics are indeed of great taxonomic value and phylogenetic significance, but they are not confined to any particular set of organs, and one cannot uphold the often expressed view that, in the vascular plants, leaf and stem characters have less taxonomic value than reproductive characters. Variations in over-all shape and size, whether due to genic or direct environmental differences, cause little upset in the complex processes of the plant; such variations are indeed most common in vegetative organs, but may be found in the reproductive system as well. For instance, cone and sporophyll size varies considerably, both according to conditions and (apparently) genetically, within single species of *Macrozamia*.

In short, my attitude to taxonomic theory in relation to evolution is in general similar to that of Simpson (1945, 1953), with the difference that my emphasis is on the *classification* of the present-day plants in the light, where possible, of the *evolution* of their ancestors. To fit arrays of organisms widely separated in geologic time into a single classificatory system is often impossible. Organisms are related both to their contemporaries and to their forebears, but the relationships are not comparable.

Concepts.

The *genera* of cycads are too clearly distinct and too coherent in themselves to cause much argument as to status. This applies as well to *Lepidozamia* as to the currently-accepted genera. Botanists (except Regel) have simply neglected to look at it or think critically about it. The characters by which genera differ may be anything at all, according to the particular case.

A *species*, in this normal sexual group, is taken to be a population or group of similar populations effectively isolated in nature *by any means* which prevents a degree of interbreeding sufficient to cause large-scale merging in characters with related but genotypically and phenotypically consistently different populations. This is a crude but practical definition. The category cannot be precisely defined, and populations may occur which could reasonably be called either species or subspecies.

A *subspecies* I take to be a geographically or ecogeographically characterized population (or group of populations) consistently and recognizably different in several respects from, but intergrading to a considerable degree with neighbouring populations. A subspecies must be coherent as a population, that is, there must be much more breeding within the subspecies than between them. A variation of the definition is that if subspecies A and B merge, but a third very similar group C is isolated, C may be regarded as another subspecies rather than a distinct species.

The category of *variety* is not used for reasons given below (p. 108).

Morphological terminology.

Much confusion and false argument could be saved by a precise rationalized terminology for comparative morphology, to be clearly distinguished where necessary from non-committal, purely descriptive terms. In the present case one must bear in mind that most structures of cycads are not homologous with those bearing similar names in the Cordaite-*Ginkgo-Ephedra* (Eames, 1952)-Taxad-Conifer (Florin, 1948, 1954)

group* with which they are commonly grouped as "Gymnosperms". (It is high time that this term and "Pteridophyta" were relegated to the history of botany. Their continued use misleads not only students but learned botanists into the belief that they apply to natural groups.) The cycads, of course, belong to the Pteropsida, in company with the true fern groups both ancient and modern, Pteridosperms, the *Glossopteris* (*Scutum*) group (Plumstead, 1956), Bennettitales, Caytoniales, *Welwitschia*, *Gnetum* (Eames, 1952, p. 96) and, with little doubt, the Angiosperms. It does not follow that every organ called by the same name in these groups is homologous, though many are so, at least in a broad sense.

In general I have used terms which either (a) are well known to be descriptive and without comparative morphological significance, or (b) have a definite morphological sense which applies correctly to the cycads. However, a few terms fall between these categories and need comment.

Frond is used rather than "leaf", to indicate that these organs are generally comparable to the fronds of a fern, that is to say, they clearly show their derivation from the branch-systems of early Pteropsida, but have become two-dimensional and of quite determinate and predominantly intercalary growth. The leaves of Angiosperms may be homologous, but are certainly rather dissimilar structures. The "leaves" of non-pteropsids are either not at all or only in a very broad sense homologous.

Petiole is used as a descriptive term, without morphological significance, for the frond-stalk proximal to the first pinnae. *Stipe(s)*, used for the equivalent of the petiole in ferns, is traditionally used for the stalk of the megasporophyll in the cycads.

Rhachis is used for the frond-axis from the lowest pinnae onwards.

Pinna is used for the primary frond-segments. *Pinnule* is used only for the ultimate segments of *Bowenia*, whether these are borne on a secondary rhachis or on the end of the primary rhachis. The term is not applied to the segments of the bifurcating pinnae of some species of *Macrozamia*. "Leaflet", like "leaf", is not used.

Cataphyll, rather than "scale-leaf", which is scarcely apt here, is used for "reduced" leaves.

Cone (in Latin descriptions *conus* rather than *strobilus*) is used in a non-committal descriptive sense. The cycad cone is not at all equivalent to the female cone of conifers (a compound strobilus), nor is it really equivalent to the male cone of the same group, since the sporophylls are not homologous. Both terms "cone" and "strobilus" are used for a number of non-homologous structures; for comparative purposes they need replacement by special terms of obvious significance. I suggest *stroboid* for the cycad "cone", *strobe* for the male (or single unit of a female) conifer cone, *synstrobe* for the female conifer cone, *anthoid* for the Bennettitalean bisexual structure, but I shall pursue this matter elsewhere. Further simple, euphonious terms of obvious meaning are necessary for "cones" of Lycopods, Lepidodendrids, and the Sphenopsida. Such a terminology would add to precision, while retaining a degree of simplicity of language.

Cone-stalk† (*axis coniger*) is preferable to the usual "peduncle" (which it is not, since it bears the approximate equivalent of a single flower) or "pedicel" which suggests a more slender structure.

Sporophyll is used in preference to "cone-scale". The structure is quite different from the complex female cone-scale of the conifers. Admittedly it is not really homologous with the sporophyll of the male conifer strobilus and certainly not with the "sporophyll" of the Lycopods. Again the term is used in the non-committal sense of a simple (or

* For this great branch of the vascular plants the terms *Pityopsida* or *Pityophyta* (according to rank) are suggested as etymologically preferable to *Coniferopsida* and *Coniferophyta* (cf. Arnold, 1948), which are Latin-Greek mongrel terms. *Pityis* is Greek for a pine and is also the name of a genus of Palaeozoic near-conifers. Since the I.C.B.N. fortunately does not enjoin respect of priority in naming higher groups, we may surely choose to use euphonious, well-formed and meaningful names.

† Peduncle is used in my forthcoming account in the *Flora of New South Wales*, due to its use in the earlier ms. of that work.

apparently so) sporangium-bearing organ more or less equivalent to a "leaf" of the same plant.

Melville (1957) has introduced an elaborate special terminology to describe the various angles and faces of the sporophylls of *Encephalartos*. These terms certainly facilitate description of the very geometrical sporophyll-ends in that genus, where, moreover, these details are of taxonomic importance. In the Australian genera, however, they are not necessary and frequently not applicable. I have simply referred to the *sporophyll-end*, its *wing* and its *spine*. The last two (in *Macrozamia*) are actually continuations of the margins and the end of the lamina of the sporophyll. The sporophyll-end is the swollen portion distal to the stipe, and the descriptions apply especially to its outer surface on the cone, which really includes both adaxial and abaxial faces.

Male and *female* (rather than "microsporangiate", etc.) are applied freely to the cones and sporophylls (and plants). The sexual differentiation, which is finally expressed in the gametes, is carried back into the sporophyte, and I see no more objection to the use of sexual terms for a plant sporophyte than for an animal diplont, such as a man. *Megasporophyll* is, however, used at times (not in the descriptions).

Ovule is used for the megasporangium with its integument. The term is a descriptive one not implying complete homology in different groups. The same applies to *seed*.

All such terms as "flower", "stamen", "staminate", and "anther", though they have been widely used, especially on the continent of Europe, in cycad and conifer descriptions, are better confined to the angiosperms.

Taxonomic criteria.

Certain characters have proved useful for the recognition and formal definition of the taxa, though these are not necessarily more essential than others less useful. The keys and descriptions herein merely differentiate, circumscribe and partially describe the natural populations in terms of the readily observed external morphology. No character, as such, is essential to any one taxon. The correct identification of an individual is the determination of the natural population of which it is part, not the key-characters which it possesses. The latter are merely a generalization, as accurate as possible. For example, plants of *Macrozamia communis* may rarely be found with spirally twisted fronds, contrary to the key and descriptions. These aberrant plants are still constituents of the population defined as *M. communis* and the key (as a 99+ per cent. generalization) is not wrong. The dimensions given, in particular, are not to be considered absolute; cycads are especially variable in this respect. Nevertheless, the dimensions used in the keys apply to all the specimens actually examined, and there should not be many departures from them.

The characters which have been found useful will be evident from the keys and the discussions under the genera and sections. They need not be detailed here. In all the Australian Zamiaceae, many vegetative characters are quite as consistent as those of the cones, and these are given prominence in the keys. They will be especially useful in *Macrozamia* section *Parazamia*, in which cones are irregularly produced and frequently only vegetative individuals may be found; the cones are much the same throughout this group.

Juvenile and semi-juvenile plants are usually indeterminable unless their geographic origin is known. Only adult plants (old enough to bear cones) are described herein (see below, p. 89). The shapes of rhachis and petiole change somewhat on drying, as the parenchymatous tissue shrinks and the sclerenchyma is externally revealed as ridges. As far as possible both living and dried material is described.

Morphological and anatomical studies.

The detailed morphology, anatomy and life-history of the cycads have attracted a great deal of attention, especially from Chamberlain and his students. This work, of great importance in the comparative morphology of the vascular plants generally,

cannot be discussed here, and it is assumed that any serious student of cycads is familiar with its chief conclusions. The most notable Australian study is that of Brough and Taylor (1940) on *Macrozamia communis* ("*M. spiralis*" in their usage). The bibliography of their paper will provide an entry to the morphological literature.

Chromosome numbers.

All the Australian species cytologically examined have the chromosome number $2n = 18$, except for an early count ($n = 12$) on *M. riedlei* (q.v.), which needs confirmation. The numbers are cited after the descriptions of the genera and species. No chromosome count has yet been made in *Lepidozamia*.

Distribution.

The detailed distribution is indicated under each species and the present distribution patterns, which show much vicariism, are discussed under the genera.* Not a great deal can be said about past distribution (but see the discussion under *Lepidozamia hopei*, p. 86). *Macrozamia* section *Macrozamia* must have extended across the southern half of the continent during the Tertiary, though not necessarily continuously at any one time. Section *Parazamia* and the other two genera are confined to eastern Australia. The nearest relationships of *Lepidozamia* and *Macrozamia* appear to be with the African *Encephalartos*, but since the cycads in general are a relict group with scattered surviving genera, not too much weight can be placed on this. *Bowenia* is very different from the other Australian Zamiaceae, and is probably closer to some of the American genera. Again, the phytogeographic significance of this is hard to evaluate in an ancient and fragmented group.

Table 2 gives the distribution by States. No Zamiaceae occur in Victoria, Tasmania or South Australia. It must be kept in mind that this table excludes *Cycas* (Cycadaceae s. str.) which has species in the tropical parts of Western Australia, the Northern Territory and Queensland. Distribution maps are given under the respective genera and sections, below.

Speciation.

While little can be said about details of the evolution of the genera and sections, the distribution patterns suggest that the more recent speciation in the Australian Zamiaceae has been dependent on geographic isolation of segments of formerly continuous populations, associated with differentiation in response to environmental changes. This classical ecogeographic speciation is perhaps not quite complete in some cases especially in *Macrozamia* section *Parazamia* (see p. 100).

There is no evidence of recent polyploidy in any of the living cycads. The universal dioecism would make successful polyploidy unlikely, though not impossible. Outbreeding is, of course, complete. Some local ecotypic differentiation is found in the more widespread species (see discussions under the individual sections and species of *Macrozamia*).

Hybridism.

As would be expected in anemophilous, dioecious plants, all (so far as known) with the same number of chromosomes, some natural hybridism is found in *Macrozamia* where the species come into contact. Some introgressive hybridization is possible in the case of *M. diplomera* (q.v.), but in general the hybrids do not appear to be of much importance. A few spontaneous hybrids have arisen in the *Macrozamia* collections in the Sydney Botanic Gardens.

Particular cases are discussed under the respective parental species (below, or in Johnson, in press), but the following apparent hybrids have been found in the field or in herbarium collections: *M. diplomera* \times *M. heteromera*, *M. lucida* \times *M. moorei*, *M. heteromera* \times *M. secunda*, *M. heteromera* \times *M. stenomera*, *M. pauli-guilielmi* ssp.

* The subdivisions of New South Wales are defined as in the *Flora of New South Wales* (Anderson, in press).

plurinervia \times *M. stenomera* (or perhaps *M. heteromera*). Others may be expected. All of these have been recognized by obviously intermediate frond characters and their occurrence as single or infrequent individuals in mixed communities of the apparent parents. Cones have not been available and no progenies could therefore be raised.

Ecology.

The particular ecology is discussed under each taxon. Most species grow in *Eucalyptus* (sclerophyll) forest, but *Lepidozamia hopei* (and to some extent *L. peroffskyana*) and *Bowenia spectabilis* may be found in certain sites within or near

TABLE 2.

	Qld.	N.S.W.	N.T.	W.A.
Number of genera	3	2	1	1
Number of species	9 (2 : 5 : 2)	12 (1 : 11 : 0)	1	1
<i>Lepidozamia</i>				
<i>hopei</i>	+			
<i>peroffskyana</i>	+	+		
<i>Macrozamia</i>				
(Sect. <i>Macrozamia</i>)				
<i>moorei</i>	+	+		
<i>riedlei</i>				+
<i>macdonnellii</i>			+	
<i>miquelii</i>	+	+		
<i>communis</i>		+		
<i>diplomera</i>		+		
(Sect. <i>Parazamia</i>)				
<i>platyrachis</i>	+			
<i>lucida</i>	+	+		
<i>spiralis</i>		+		
<i>secunda</i>		+		
<i>heteromera</i>		+		
<i>stenomera</i>		+		
<i>pauli-guilielmi</i>	+	+		
ssp. <i>p.-g.</i>	(+)	(+)*		
ssp. <i>plurinervia</i>	(+)*	(+)		
ssp. <i>flexuosa</i>		(+)		
<i>fawcettii</i>		+		
<i>Bowenia</i>				
<i>spectabilis</i>	+			
<i>serrulata</i>	+			

* Intergrades only.

rainforest. Only one species, *M. macdonnellii*, occurs under really arid conditions, and even this is confined to the refugium of the Central Australian range system where conditions are somewhat better than elsewhere in the interior. The species of *Macrozamia*, in contrast to the other two genera, are usually associated with other sclerophyllous species of the "Australian" floristic element. The plants are rather slow-growing, but by no means as excessively so as sometimes stated (see *Lepidozamia peroffskyana*, p. 86). Apogeotropic roots regularly form coralloid end-systems containing Cyanophyta (Nostocaceae: *Anabaena* and perhaps *Nostoc*) (Fritsch, 1945, pp. 872-4). These blue-green algae may be in a symbiotic relationship with the cycad plant. Nitrogen-fixing bacteria (e.g. *Azotobacter*) also occur in these nodules in a number of cycads (refs. in Thieret, 1958).

Economics.

Like other cycads, the Australian Zamiaceae contain toxic substances (Hurst, 1942; Webb, 1948; Gardner and Bennetts, 1956) which are at times responsible for poisoning

of stock, especially cattle. For this reason they have been killed out in certain areas. In view of their great botanical interest and the low pastoral quality of much of the land on which they occur, their destruction is particularly unfortunate. Nevertheless, in the past some botanists, especially in Queensland and Western Australia, have joined the agriculturists in issuing publications recommending methods of poisoning the plants.

The starchy endosperm of the seeds, and sometimes the pith of the caudex, served the aborigines as food, as *Cycas* still does in Arnhem Land (Specht, 1958), after washing and roasting to remove the poison. Various cycads are used similarly in other continents. Thieret (1958) gives a comprehensive review of the literature on the economics of cycads, but much of the cited information is out of date.

In horticulture, various species are to be seen in home and occasionally public gardens in Australia, but many species have been cultivated under glass in European collections, especially during the nineteenth century. The description of such plants (usually from vegetative and often semi-juvenile material) has been responsible for much of the extraordinary confusion of the nomenclature.

Taxonomic Revision.

Note.

This paper will be followed very shortly by the publication of the first parts of the *Flora of New South Wales* (ed. Anderson, in press). My treatment of the Zamiaceae forms Part 1 of this work. For reasons of space, descriptions (except Latin descriptions of new taxa), detailed synonymy and lists of specimens of the New South Wales species are not given in the present paper, but will be found in the *Flora*. Reference to the latter is made where necessary in the text hereunder. A complete index of synonyms, however, is given below (p. 113).

For most purposes the keys herein will be sufficient for identification, especially if the geographical origin of the material is known, but for critical investigation this revision and the *Flora* must be used in conjunction. I regret this necessity.

Family ZAMIACEAE Reichenb.

Sporophylls of both sexes in definite simple cones, of determinate growth. Cones dioecious, rather large, axillary or terminal, with numerous scale-like sporophylls arranged spirally or apparently in vertical rows; male sporophylls (microsporophylls) with many small, globose sporangia more or less clustered in groups (sori) in two collateral sometimes confluent areas on the undersurface, sporangia dehiscent by slits; female sporophylls (megasporophylls, macrosporophylls) simple, consisting of a barren stipes and an expanded and thickened end, the latter bearing two (rarely three in *Lepidozamia*) sessile ovules on its axis-facing margins ("inner surface"). Pollen wind-borne; fertilization by naked multiflagellate spermatozoids. Seeds large, from subglobose to subcylindrical or variously angled, with a broad chalazal area and more or less apiculate micropylar end, seed-coat with a fleshy outer layer and a woody inner layer; (haploid) endosperm present, cotyledons two, germination hypogeal.

Somewhat palm-like plants; stem subterranean to tall, not or little branched, with a crown of spirally arranged pinnate or bipinnate leaves (fronds) and interspersed rudimentary leaves (cataphylls), leaf-bases persistent and clothing the stem, or deciduous. Fronds usually straight and folded in bud (circinate in *Ceratozamia* of Mexico); leaf-segments without a midrib, with few to many longitudinal nerves, straight, not circinate, in bud.

A family of eight genera and about 80 species, with a scattered distribution in tropical to warm-temperate parts of N. and S. America, Australia and Africa.

For a key to the tribes and genera see Part I, p. 66.

Australian members: Tribe Encephalarteae: I. *Lepidozamia*; II. *Macrozamia*. Tribe Zamieae: III. *Bowenia*.

I. LEPIDOZAMIA Regel.

Regel in *Bull. Soc. Imp. Nat. Mosc.* (1857), n. 1, 182, and in *Gartenfl.* 6 (1857*), 11, *ibid.* (1870), 227, (1875), 42 and (1876), 4, also in *Acta Hort. Petrop.*, 4 (1876), 294; Miq., *Prodr. Syst. Cycad.* (1861), 10; A.DC., *Prodr.*, 16, pt. 2 (1868), 547 (as "Genus dubium").

Typification: *L. peroffskyana* Regel. TYPE SPECIES (the sole original species).

Synonymy:

Catakidozamia W. Hill in *Gard. Chron.* (Nov., 1865), 1107 (type sp.: *C. hopei* W. Hill). [This is to be regarded as a combined "generico-specific" description, since only one valid species was included, though "*C. macleayi*" was mentioned as a *nomen nudum*. Schuster (1932, p. 86), who seems to have cited many publications without seeing them, has followed *Index Kewensis* in giving the author as T. Hill. The generic name evidently circulated amongst European gardeners (e.g. Haage and Schmidt) as "*Katakidozamia*", and is thus cited, in synonymy, by Regel (1876, both papers), but without reference to Hill. Schuster mis-cites it as "*Katikidozamia*".]

Encephalartos Lehm. sect. *Lepidozamia* (Regel) Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 371.

Macrozamia Miq. sect. *Lepidozamia* (Regel) Miq., in *Arch. Néerl.*, 3 (1868), 253, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 56.

Macrozamia sect. *Monoorientales* Schuster, *Pflanzenr.*, IV, i (1932), 88, nom. illegit. (exactly equivalent to the above).

Palm-like plants with a usually unbranched trunk clothed by the persistent leaf-bases, often tall, all parts shortly pubescent to tomentose when young, but some glabrescent with age. Fronds numerous, large, simply pinnate, not twisted. Cataphylls abundant, fleshy, linear-subulate, shortly tomentose, mostly in series alternating with the successive crowns of fronds. Base of petiole swollen, shortly tomentose. Pinnae numerous, spreading, inserted more or less alternately along the adaxial midline of the rhachis, falcate, slightly narrowed but not callous at the base, stomata confined to lower surface. Cones of both sexes almost or quite sessile, large, axillary among the cataphylls of the crown, the spirally-arranged sporophylls tomentose at the ends, not spiniferous. Male sporophylls with a linear-spathulate fertile region and a more or less triangular-rhomboid, laterally expanded end, deflexed in spiral series at sporangial dehiscence. Female sporophylls with an elongated, terete to subangular stipes and a dorsiventrally biconvex, laterally expanded, somewhat deflexed, shortly tomentose end bearing two or sometimes three ovules on the inward-facing margins (inner surface), tapered into the flattened, more or less acute, at first deflexed, but on drying more or less upturned, ultimate tips. Outer seed-coat fleshy, red or yellowish, inner coat hard.

Endemic in the eastern coast region of Australia, with two species, one in tropical Queensland, the other in subtropical Queensland and the north coast of New South Wales, in wet sclerophyll forest and around rainforest (Text-figure 1).

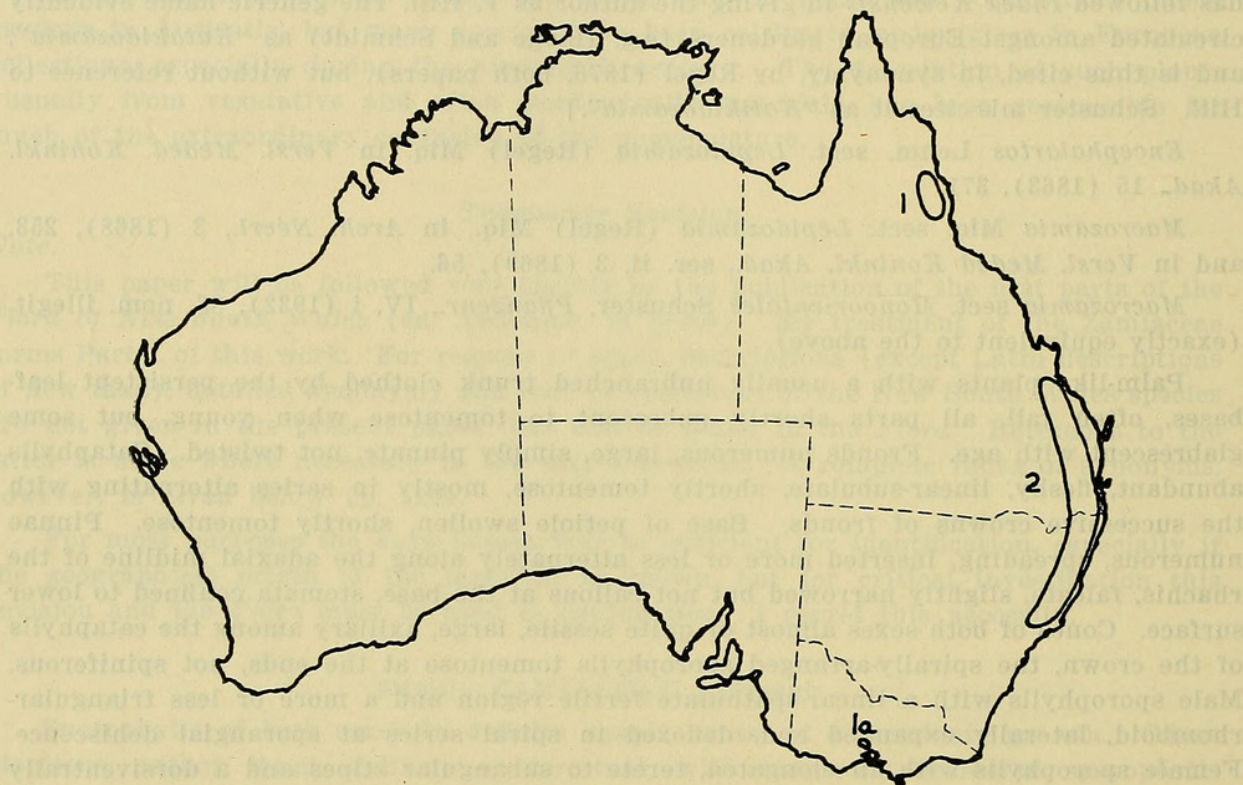
Except by Regel himself, *Lepidozamia* has been generally placed under *Macrozamia* ever since its Australian origin was known (the type species was described from a garden plant in the then St. Petersburg, of unknown origin, and was at one time thought to be from Mexico). However, it is quite as distinct as any other genus of *Zamiaceae*, and I can see no especially close affinity with *Macrozamia*.

Encephalartos, *Macrozamia* and *Lepidozamia* would all appear about equally similar—and dissimilar—and if they appear to stand together apart from other *Zamiaceae*, this is perhaps due to the absence of certain advanced or specialized characteristics, rather than to any very positive features in common. They can, of course, be made to stand together in a key, but keys are an unsafe guide to relationships.

Lepidozamia is readily distinguished from *Macrozamia* by the almost or quite sessile cones, the quite differently-shaped sporophyll-ends which lack the characteristic

* Later than the first-cited reference. I have not seen the four *Gartenflora* references, which are quoted from Regel's second 1876 paper.

spinescent modification of *Macrozamia* and moreover are closely tomentose-pubescent with short hairs, the short swollen rather than laterally expanded and shortly rather than silky-woolly tomentose petiole-bases, the fleshy subulate shortly-tomentose cataphylls, the structurally more involute rhachis with median insertion of the falcate pinnae which lack callous bases, the straight torque-free vernation of the fronds and the more open crown with frond-series markedly interrupted by wide cataphyll-series. Furthermore, as Thomas and Bancroft (1913) and, in a more exhaustive study, Cookson (1953) have found, the epidermal anatomy of the species referred to *Lepidozamia* differs strikingly from that of *Macrozamia* proper. In *Lepidozamia* the long axes of the epidermal cells are oblique or transverse to the long axis of the pinna, in contrast to the longitudinal orientation in *Macrozamia*.



Text-fig. 1.—Distribution of *Lepidozamia*: 1: *L. hopei*; 1a: site of *L. hopeites* fossils; 2: *L. peroffskyana*.

A remarkable feature is the presence in some cones of a number of megasporophylls with three ovules. I have not been able to obtain sufficient fresh material of such sporophylls to determine the original position of the third ovule. It appears to be inserted above and between the other two, though rather to one side, but is probably lateral in ontogeny as in the Cycadales generally. The pluriovulate condition would appear to be a primitive feature, and indeed the unspecialized sporophylls suggest that *Lepidozamia* is relatively primitive in the Zamiaceae. Chamberlain (1909, p. 410) has recorded up to five or six abortive ovules in a cone of *Dioon spinulosum* and, as a rarity, as many as four ovules in *Zamia* and *Ceratozamia*. In *Lepidozamia*, however, the condition is more common and all three ovules may develop into seeds.

In very young seedlings the pinnae arise from the margins of the upper surface of the rhachis, as in *Macrozamia*. In successive fronds these margins are found to be closer together (relative to the increasing diameter of the rhachis) until the apparently median insertion of the adult stage is attained. This, of course, appears to be a specialization. The fronds superficially somewhat resemble those of *Ceratozamia*, but the sporophylls are very different.

Regel established his genus on vegetative material alone, and maintained it later (1876) when he had knowledge of the cones. In this he showed greater discernment than other cycadologists, though Miquel was aware that it was a rather distinctive

group and, of course, Hill recognized it as *Catakidozamia*. The name *Lepidozamia* refers to the scale-like frond-bases clothing the stem.

Schuster (1932) inexplicably (unless his arrangement was based, as the meanings of his Greek-Latin hybrid names suggest, not on morphology but on geography) placed his section *Monoorientales* (= *Lepidozamia*) between his other two sections of *Macrozamia*, although the latter contain extremely closely allied species.

Key to the Species.

1. Broadest pinnae 17-30 mm. broad, 20-40 cm. long, 17-30-nerved. N. Queensland 1. *L. hopei*.
- 1.* Broadest pinnae 7-14 mm. broad, 10-32 cm. long, 7-14-nerved S. Queensland and N.S.W. 2. *L. peroffskyana*.

1. *L. HOPEI* Regel* in *Gartenfl.* (1876), 6, and in *Acta Hort. Petrop.*, 4 (1876), 296.

Typification: Based on a living plant cultivated by Haage and Schmidt, doubtless originally from Hill. The brief description unmistakably refers to this species.

Synonymy:

Catakidozamia hopei W. Hill in *Gard. Chron.* (Nov., 1865), 1107 ("from tropical Eastern Australia").

Macrozamia hopei W. Hill ex F. M. Bail., *Syn. Queensl. Fl.*, Suppt. 1 (1886), 52 (from "Daintree and Johnstone Rivers". To be considered as a new publication; Bailey did not cite Hill's earlier binomial or description, though he attributed his new binomial to Hill), and *Queensl. Fl.*, 5 (1902), 1506; also W. Hill ex C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 116, nomen nudum.

M. denisonii C. Moore & F. Muell. var. *hopei* (W. Hill) Schuster, *Pflanzenr.*, IV, i (1932), 101 [this may be taken as truly based on Hill's name of 1865, which is the earliest cited].

Trunk 2-20 m. tall. Fronds numerous, at first suberect, later spreading, 2-3 m. long on adult plants, more or less puberulous, especially the rhachis, but glabrescent with age; petiole 30-60 cm. long (the short, much swollen, shortly tomentose base ca. 3-4 cm. long), rounded to angular beneath, angled or (when dry) keeled and broadly two-furrowed above, or sometimes very slender and laterally compressed (when dry); rhachis more or less rounded when living but when dry angular beneath, more or less laterally compressed, angled to the median pinna-bearing keel above. Pinnae 160-200 or more, spreading but recurved-drooping towards the ends, entire, shining above, recurved-falcate, broadly strap-shaped, 20-40 cm. long (lower somewhat shorter than the median ones, but never very short and spinescent), 15-30 mm. broad, with 15-30 scarcely raised nerves beneath, tapered to the acute apex, slightly contracted at the base, with stomata on the undersurface only. Cones subsessile, usually solitary, axillary but often appearing quasi-terminal, surrounded at the base by several rows of fleshy, velvety-tomentose, subulate-tipped cataphylls. Male cones not seen, doubtless similar to those of *L. peroffskyana*. Female cones ovoid, sometimes somewhat contracted at the base, 40-60 (or more?) cm. long, 20-25 (-30?) cm. diam.; sporophylls ca. 5-8 cm. long, 3.5-6.5 cm. broad, the shortly tomentose end deflexed, but the extreme tip often again upturned. Seeds 4-5.5 (-6?) cm. long, 2.5-3.5 cm. thick, outer coat fleshy, bright red when ripe.

Distribution: North-east Queensland from the Daintree River (or further north?) to the Rockingham Bay region in hilly country near or within rainforest.

Specimens examined: Babinda Creek, P. R. Messmer, 12.viii.1954 (NSW.30536); Bellenden Ker, C. T. White 1295, iii.1922 (NSW.40971); Cardwell, H. L. White, vii.1911 (NSW, cone material only).

* This is not nomenclaturally based on *Catakidozamia hopei* W. Hill, the publication of which appears to have been unknown to Regel. Regel cited "*Katakidozamia Hopei* h. Haage et Schm.", a garden name of no validity, though, of course, derived ultimately through horticultural channels from Hill. Regel's *Gartenflora* reference is the earlier of the two; it was cited in the other 1876 paper.

L. hopei, one of the tallest of all cycads, is reputed to reach a height of up to 20 m. It is very similar to *L. peroffskyana* in most respects, but is readily distinguished by its broad pinnae. Cookson (1953) describes clear differences in details of epidermal anatomy between the two species. I have not seen sufficient cone material to determine whether there are significant differences in these organs. If so, they are certainly not very great, and Bailey's (1902) key is not reliable. In Bentham's treatment (1873, pp. 253-4) the species is not distinguished from "*M. perowskianä*", but since Bailey's time it has been generally recognized as specifically distinct, except by Schuster.

Although *L. hopei* is at present confined to the wet tropics and is replaced further south by *L. peroffskyana*, a plant very similar to the former grew in Victoria during the early Tertiary. This is the following:

LEPIDOZAMIA HOPEITES (Cookson) L. Johnson, comb. nov. (sp. foss.).

Basionym: *Macrozamia hopeites* Cookson in *Phytomorphology*, 3 (1953), 307, f. 1-5.

Typification: "collected from a sandy bed exposed during 1947 and 1948 on top of the early Tertiary brown coal at the Lucifer Mine, Bacchus Marsh, Victoria". Fragments of pinnae. Nat. Mus. Vic. P15781 is the HOLOTYPE.

Cookson's description and beautifully clear photographs of the epidermal anatomy of these pieces show the unmistakable resemblance to *L. hopei*. The epidermis of *L. peroffskyana* differs from these in detail, and that of *Macrozamia* is very different in orientation and shape of the cells. Dr. Cookson described the species as a *Macrozamia* pending completion of the present revision (Cookson, *l.c.*, p. 311), but was aware at the time of the considerable differences between *Lepidozamia* and *Macrozamia*, which her studies have indeed established more firmly.

The former occurrence of this plant, rather than one resembling *L. peroffskyana*, in Victoria illustrates the risk involved in deducing past history from present distribution. It may be, of course, that whereas little change has taken place in the tropical segment of a former single population, the more southern segment has changed considerably, giving rise to *L. peroffskyana*. On the other hand, the ancestors of the latter may have been already differentiated in the early Tertiary, but somewhere else.

2. *L. PEROFFSKYANA* Regel in *Bull. Soc. Imp. Nat. Mosc.* (1857), n.1, 184, t.IV, f.20, 21, and in *Gartenfl.*, 6 (1857*), 11, t.186, f.23, 31, *ibid.* (1870), 227, t.660, (1875), 42 and (1876), 4, also in *Acta Hort. Petrop.*, 4 (1876), 295; Miq., *Prodr. Syst. Cycad.* (1861), 10, 22; A.DC., *Prodr.*, 16, pt. 2 (1868), 547 (under *Genus dubium*).

Typification: The HOLOTYPE was a living plant cultivated in the Botanic Garden, St. Petersburg. From the description and figures there is no doubt of its identity.

Synonymy:

Macrozamia denisonii C. Moore & F. Muell. in F. Muell., *Fragm. Phytogr. Austral.*, 1 (1858), 41 [of the three syntypes the following may be taken as LECTOTYPE: "In vicinia fluminis Manning. Stephenson." NSW.40975, an old collection from Moore's time, but labelled only "Manning River", is almost certainly part of this. Moore (1884, p. 119) gives 1855 as the date of this collection].

Further synonymy is given by Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Description and Specimens: See Johnson in Anderson, *l.c.*

Distribution: Subtropical eastern Queensland and North Coast of New South Wales to the Manning River district, usually in hilly country in wet sclerophyll forest sometimes bordering on rainforest.

L. peroffskyana† has been most generally known, especially in Queensland, as *Macrozamia denisonii*, but Regel's name has clear priority and undoubtedly belongs to

* Later than the first-cited reference. I have not seen the four *Gartenflora* references. They are quoted from Regel's second 1876 paper.

† The epithet has been spelt in various ways. Regel named it in honour of Count Perofsky, an Imperial Russian Minister and benefactor of the St. Petersburg Botanic Garden.

the species. The distribution is scattered, small communities being found here and there in forested hilly country of the subtropical east coast. The plants are handsome and striking, but not as large as those of *L. hopei*; their maximum height appears to be about 7 m. Absurdly exaggerated claims of great individual age (to 10,000 years or more) for these plants have been made at tourist centres and in the popular Press. These estimates are usually attributed to C. J. Chamberlain, but I have found no such claim in any of Chamberlain's publications. His estimates of the ages of other cycad species, though perhaps a little high, are certainly not of this order. Plants of *L. peroffskyana* in the Sydney Botanic Gardens have attained a trunk height of 2 m. in less than a century. Since the plants grow only by apical increase of a single stem, and produce about the same number of fronds in each new crown, even the tallest individuals on this reckoning would be less than 500 years old.

Bentham (1873) included *L. hopei* in his concept of this species. Bailey (1902) distinguished the two, but used unreal differences in his key. He records *L. peroffskyana* only from south of Brisbane, but localities as far north as the Tropic of Capricorn are cited by Moore and Mueller, Miquel and other authors, though I have not seen this material. Schuster (1932) used the name *M. denisonii*, though citing the earlier *L. peroffskyana* in synonymy, and included *L. hopei* as a variety. The distinction between the two species of *Lepidozamia* seems quite clear (see above, p. 86).

II. MACROZAMIA Miq.

Miq., *Monogr. Cycad.* (1842), 35, also *Prodr. Syst. Cycad.* (1861), 8, 18, and in *Arch. Néerl.*, 3 (1868), 247, and *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 50 (excl. sect. *Lepidozamia*); A.DC., *Prodr.*, 16, pt. 2 (1868), 535 (excl. *M. denisonii*); Benth., *Fl. Austral.*, 6 (1873), 250 (excl. *M. "perowskiana"*); Regel in *Acta Hort. Petrop.*, 4 (1876), 317; Schuster, *Pflanzenr.*, IV, i (1932), 86 (excl. sect. *Monoorientales* = *Lepidozamia*).*

Typification: Miquel originally accepted two supposed species in his new genus, which he named *M. spiralis* and *M. fraseri*. *M. fraseri* Miq. was very briefly described from imperfect material and cannot, as such, be the generic type. It is now known to be a synonym of the Western Australian species, *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn. The generic character was taken from material illustrated in drawings of Ferdinand Bauer, which was the whole basis of Miquel's description under *M. spiralis*. This material is now known also to belong to *M. riedlei*. However, the name *M. spiralis* (Salisb.) Miq. is nomenclaturally based on *Zamia spiralis* Salisb., cited by Miquel. The typification of this is discussed below (p. 103) under *M. spiralis*; it is a very different plant from *M. riedlei*. Miquel (1842, p. 37) was aware that Salisbury's plant may not have been the same as those he described, but saw no specimens. Under *M. spiralis* he also cited, but did not see, plants from Port Jackson previously described by R. Brown under "*Zamia spiralis* Salisb.", but which in fact belong to *M. communis* L. Johnson. Later, in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368, Miquel pointed out that Bauer's figures and hence his own description of *M. spiralis* pertained in fact to the same species as his *M. fraseri*. He then used "*M. spiralis*" for *M. communis* (with some confusion with plants later described under *M. miquelii* (F. Muell.) A.DC.). Later authors used "*M. spiralis*" chiefly for either *M. communis* or *M. lucida* L. Johnson, but the name is herein (p. 103) restored to Salisbury's original species.

Hutchinson, in *Kew Bull.* (1924), 51, named "*M. spiralis*" (without author) as type species of *Macrozamia* Miq., but was unaware of the complicated circumstances and had made no detailed study of the genus. His selection is not binding. The International Code of Botanical Nomenclature (Lanjouw, 1956) lays down that the type of a generic name is a *species* (not a specimen nor, one may add, a specific name). Now a species consists of living organisms, past, present or future. Its nature must be elucidated by biological enquiry, and the circumscription of our concept of it is determined by taxonomic, not nomenclatural, considerations. Although the specific name *Macrozamia spiralis* (Salisb.) Miq. must be applied to a group of organisms including the plant

* Only important treatments purporting to cover the whole genus are cited.

described by Salisbury, this plant was certainly only in the vaguest way part of the concept in Miquel's mind when he described his new genus. On the contrary, he drew his description almost wholly from the plants represented in Bauer's plates.

Consequently I consider that the TYPE SPECIES of *Macrozamia* Miq. is the species to which Bauer's plants belong, whatever its name is held to be; in my treatment this is *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn.

By this typification we may preserve Miquel's sectional treatment, as far as it is applicable. True *M. spiralis* (Salisb.) Miq. belongs to section *Parazamia* (Miq.) A.DC. (based on *Encephalartos* sect. *Parazamia* Miq., typified by *M. pauli-guilielmi* W. Hill and F. Muell.), while *M. riedlei* belongs to the section regarded by Miquel as typical: section *Macrozamia* of my treatment (*Encephalartos* sect. *Macrozamia* Miq., *Macrozamia* sect. *Genuinae* Miq.). If *M. spiralis* as fixed by Salisbury's type were taken as type species, Miquel's "typical" section would require a new name and his *Parazamia* would become *Macrozamia*.

It is regrettable that nomenclatural procedure demands so detailed an argument to settle permanently (one may hope) a matter of plain common sense.

Synonymy: There are no actual generic synonyms of *Macrozamia* when *Lepidozamia* Regel is excluded. Infrageneric names are listed below, under the two sections. The genus was included in *Encephalartos* by F. Mueller intermittently over many years (see refs. under the species), also briefly by Miquel, in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368. Before 1842, individual species were referred to *Zamia* or *Encephalartos*, and Mueller, *Fragm. Phytogr. Austral.*, 5 (1866), 172, stated: (translation) "I have reduced all the species of *Encephalartos* in the collections of the Melbourne museum subgenerically to *Zamia*." Despite this remark, he had continued to use *Encephalartos* (incl. *Macrozamia*) on the same page, and certainly did not formally establish *Encephalartos* in subgeneric rank under *Zamia*, as Schuster's (1932, p. 86) citation seems to indicate. In 1881 in his paper on *M. moorei* (q.v.) Mueller again expressed his view that *Macrozamia* was a "sub-generic group" of *Encephalartos*, if indeed both were not to be placed under *Zamia*, adding that "all genera are mere artificial groups to facilitate classification, and aid memory, while species in their true sense are originally created beings, which when perished . . . would require the godly might as much for their restoration as they did for their origination". This philosophy should be borne in mind when interpreting any pronouncement of Mueller's on classification or nomenclature.

More or less palm-like plants with a usually unbranched stem forming a subterranean caudex or a rather massive aerial trunk, clothed by the persistent leaf-bases, all parts more or less pubescent when very young, but glabrous (except petiole-bases) at maturity. Fronds few to numerous, simply pinnate (but the pinnae sometimes dichotomously divided), rhachis straight or twisted. Cataphylls present, angular-subulate, at first silky or woolly, finally often glabrescent. Base of petiole expanded, in most species silky or woolly-tomentose. Pinnae numerous in mature plants, spreading or secund, inserted near the edges of the rhachis towards the adaxial side, simple or once to thrice forked, straight or falcate, contracted and sometimes callously thickened at the base, stomata on lower or both surfaces. Cones of both sexes stalked, axillary among the fronds (with several cataphylls below and sometimes on the stalk), the spirally-arranged sporophylls glabrate (often glaucous) and spiniferous at the ends (spines sometimes almost obsolete on lower sporophylls). Male sporophylls with a broadly cuneate fertile region bearing the sporangia beneath in two separate to more or less confluent areas, and an upturned end terminated by an erect or spreading-erect spine, the latter sometimes very short on the lower sporophylls. Female sporophylls appearing peltate, with an angular-rounded stipes and a laterally expanded more or less terminally compressed end, the latter with a narrow transverse wing (continuation of the margins) terminated by a more or less erect short to long spine; the two ovules borne on the inward-facing margins ("inner surface") of the sporophyll-end; the sporophylls falling with the seeds attached by the outer fleshy red or yellow seed-coat, the inner seed-coat hard.

Chromosome number: $x = 9$. The number $2n = 18$ has been found in *M. miquelii*, *M. moorei* and material named "*M. tridentata*" (refs. in Darlington and Wylie, 1955), and also in *M. communis* (Brough and Taylor, 1940, as "*M. spiralis*"). Light (1924) records $n = 12$ for *M. riedlei* (as *M. fraseri*), but this early count is doubtful; if correct it suggests triploidy.

Endemic in Australia, with 14 species in the warm-temperate and subtropical regions, barely reaching the Tropic: 12 of them in eastern Australia (New South Wales 11, Queensland 5), 1 in Central Australia, 1 in south-western Australia. This excludes the quite distinct *Lepidozamia* (see above, p. 83), which most authors have included in the genus. The species grow mostly on nutritionally poor, frequently siliceous, soils in sclerophyll communities, in association with members of the old "Australian" floristic element. Most parts of the plants contain a toxic substance, *macrozamin* (Hurst, 1942; Webb, 1948; Gardner and Bennetts, 1956), and various species are held responsible for a form of stock poisoning known as "wobbles" (or miscalled "rickets"), especially common in cattle which can eat the tough fronds. The aborigines ate the starchy endosperm of the seeds after roasting and prolonged washing to remove the poison (Bailey, 1902; and various notes in herb. NSW). Several species have been cultivated as ornamentals.

As indicated above (p. 72), the taxonomy and especially the nomenclature of the genus have been quite extraordinarily confused and unstable.

Key to the Sections and Species.

Note: Juvenile plants of *Macrozamia* may differ considerably from the adult forms in details of the fronds; in particular the pinnae are usually toothed at the ends and the petioles are long and slender. The stomata of juvenile plants are confined to the lower pinna-surface. Only adult organs are described in the key and descriptions given here. Similarly, cone dimensions apply to mature cones (males at sporangial dehiscence, females at ripening of the seeds). *Petiole lengths do not include the woolly expanded base* and may be taken as the distance from the end of the tomentose portion to the lowest pinnae. The stomata are readily seen at a magnification of $\times 15-20$ diameters, or with practice at $\times 10$ diameters, especially in fresh material. To determine their presence or absence the upper pinna-surface should be compared with the lower, which, of course, always bears stomata.

1. Large plants with 15-150 fronds in the crown, aerial trunk present or absent, caudex 15-100 cm. diam. Fronds 50-300 cm. long; rhachis not strongly twisted, usually angled beneath (at least in petiolar portion) when dry, flat to angled and laterally 2-channelled (when dry) above, 6-30 mm. broad at lowest pinnae. Pinnae straight for most of their length, spreading, *nerves visible but narrow and not or scarcely raised on the lower surface when dry*; bases markedly callous on the anterior margin (\pm rugose when dry); the lowest pinnae usually progressively reduced and sometimes spine-like (not always so in *M. miquelii*). Mucilage canals present in the pinnae. ♀ cones 15-90 cm. long, 8-27 cm. diam., longest sporophyll spines 1-10 cm. long; seeds 2.5-8 cm. long. ♂ cones 15-50 (-60?) cm. long, longest sporophyll spines 1.5-5 cm. long i. Section *Macrozamia*.
2. Reduced spine-like pinnae extending almost to the base of the frond (spine-free petiole, excluding swollen base, 0-10 cm. long). Plants with massive trunks to 2-5 m. tall, 60-80 cm. diam. Fronds 150-300 cm. long with 150-250 pinnae. Rhachis 12-30 mm. broad at lowest pinnae. Stomata on both surfaces of pinnae. ♀ cones 40-90 cm. long, ♂ cones 30-45 cm. long. C. Queensland and N.S.W. Far N. Coast 1. *M. moorei*.
- 2.* Reduced pinnae not extending to near base of frond (petiole 12-60 cm.). Aerial trunk present or absent. Fronds 50-220 (-250?) cm. long, with 60-170 pinnae. Stomata on both surfaces of pinnae or on lower surface only. Cones various.
3. Stomata on both upper and lower surfaces of pinnae. Pinnae simple. West and Central Australian species.
4. Fronds not or scarcely glaucous. Seeds 3-5 (-6?) cm. long, 2-3.5 cm. thick. Spines of uppermost ♀ sporophylls 1.5-6 (or more?) cm. long, lower sporophylls usually with short broad spines. S.W. Australia 2. *M. riedlei*.
- 4.* Fronds markedly glaucous. Seeds 6-8 cm. long, 4-5.5 cm. thick. Spines of uppermost ♀ sporophylls ca. 1-2 cm. long, lower sporophylls almost spineless. Central Australia 3. *M. macdonnellii*.
- 3.* Either stomata on lower surface of pinnae only and pinnae simple or stomata on both surfaces and most pinnae forked. Eastern species.
5. Pinnae simple, stomata on lower surface only.
6. Pinnae thin and rather lax, easily bent, shining above, often rather crowded along the rhachis. Most sporophylls of ♀ and ♂ cones short-spined; longest spines (♀)

- 2-3½ cm., (♂) 1-2 (2½) cm. Most of the ♀ sporophyll-ends less than twice as broad as high; spines of ♂ sporophylls slender, 2-5 mm. broad at the base. Seeds 2.5-3.5 cm. long. Eastern parts of C. and S. Queensland and Far N. Coast (Richmond R.) of N.S.W. 4. *M. miquelii*.
- 6.* Pinnae thicker and more rigid, rather dull, often rather widely separated along the rhachis. Many sporophylls of ♀ and ♂ cones long-spined; longest spines (♀) 4-10 cm., (♂) 2-5 cm. Most of the ♀ sporophyll-ends at least twice as broad as high (excl. spine); spines of ♂ sporophylls 5-12 mm. broad at the base. Seeds 3-4.5 cm. long. Macleay River to Bega, also Goulburn River Valley, eastern N.S.W. ... 5. *M. communis*.
- 5.* Most pinnae dichotomously once-divided. Stomata on both surfaces. Coonabarabran and country north of Liverpool Range, N.S.W. 6. *M. diplomera*.
- 1.* Rather small plants with 2-12 (rarely up to ca. 40 in *M. lucida*?) fronds in the crown, caudex almost or wholly subterranean, 5-30 cm. diam. (more in *M. platyrachis*?). Fronds 30-120 cm. long; rhachis straight or twisted, rounded or angular beneath, rounded to flat or concave above (sometimes with two lateral grooves), 3-18 mm. broad at lowest pinnae. Pinnae straight or falcate, spreading or erect, *nerves thick and prominent on the lower surface (especially when dry)*; bases not or only slightly callous on the anterior margin (not rugose when dry); the lowest pinnae usually not much reduced (sometimes somewhat so in spp. with secund pinnae or twisted rhachis). Mucilage canals absent from the pinnae. ♀ cones (10-)15-25 cm. long, 6-10 cm. diam., longest sporophyll-spines 0.5-4 (-5?) cm. long; seeds 2-3.5 cm. long. ♂ cones 10-25 cm. long, longest sporophyll-spines 0.2-1.5 cm. long ii. Section *Parazamia*.
7. Rhachis not or moderately spirally twisted (0-180°, rarely to 360° but if so petiole 20-40 cm. long or pinnae divided) though sometimes recurved near the end. Pinnae simple or divided.
8. Pinnae simple. Stomata on lower surface only.
9. Broadest pinnae 15-20 mm. broad, 15-18-nerved. Rhachis flat, 13-18 mm. broad at lowest pinnae. C. Queensland 7. *M. platyrachis*.
- 9.* Broadest pinnae 3-12 mm. broad, 5-11-nerved. Rhachis rounded or ± flat or concave above, 3-9 mm. broad at lowest pinnae.
10. Pinnae spreading in the living state. Rhachis scarcely to moderately (0-180°, rarely 360°) twisted; petiole rounded or flat above, 15-50 cm. long. Broadest pinnae 6-12 mm. broad, 12-35 cm. long, not or scarcely glaucous.
11. Pinnae glossy, ± falcate, *whitish at the base* when living, the longest ones 15-35 cm. long, 7-12 mm. broad. Petiole rounded, (20)25-50 cm. long. S. Queensland, N.S.W. (Far N. Coast) 8. *M. lucida*.
- 11.* Pinnae rather dull, straight to ± falcate, *pinkish to red or orange at the base* when living, the longest ones 12-25 cm. long, 5-10 mm. broad. Petiole rounded or subangular, (15)20-40 cm. long. N.S.W. (C. Coast to Goulburn R. Valley and Dunedoo) 9. *M. spiralis*.
- 10.* Pinnae secund, rising ± vertically from rhachis in living state. Rhachis not or slightly twisted, but recurved near the end; petiole concave above, 5-22 cm. long. broadest pinnae 3-8 mm. broad (8-20 cm. long), often ± glaucous. N.S.W. (C.W. Slopes) 10. *M. secunda*.
- 8.* Pinnae once to thrice dichotomously divided. Stomata on lower or both surfaces. N.W. Slopes of N.S.W.
12. Stomata present on both surfaces of pinnae. Pinnae once or twice divided, rather stiff, dull above, often ± glaucous beneath. Rhachis little if at all twisted (0°-90°-180°). N.S.W. (Warrumbungles, Pilliga Scrub and Warialda-Howell, on sandy soil) 11. *M. heteromera*.
- 12.* Stomata confined to lower surface of pinnae. Longest pinnae usually 2-3 times divided (if only once divided segments nevertheless very narrow), rather lax, dark green above, not glaucous. Rhachis usually twisted near the end (90°-180°-360°). N.S.W. (Nandewars and surrounding district, on stony hillsides) 12. *M. stenomera*.
- 7.* Rhachis strongly twisted (360° or much more, rarely less in depauperate short fronds of *M. pauli-guilielmi* ssp. *plurinervia* but if so then the petiole 5-15 cm. long). Pinnae simple (but sometimes toothed).
13. Broadest pinnae 3-7 mm. broad, 3-10-nerved, adult ones entire or closely 2-toothed at the apex. S. Queensland and N.S.W. (N. Tablelands, N.W. Slopes and Manning R.-Lake Macquarie) 13. *M. pauli-guilielmi*.
- 13.* Broadest pinnae 9-17 mm. broad, 10-13-nerved, adult ones 2-7-toothed at the apex. N.S.W. (N. Coast: Richmond R.-Macleay R.) 14. *M. fawcettii*.

i. Section MACROZAMIA.

Typification: As for the genus, the species now known as *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn.

Synonymy (infrageneric):

Encephalartos Lehm. sect. *Macrozamia* Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368 (this included only species of the section as here understood, exclusive of sect. *Parazamia* and of *Lepidozamia*. Type as for the genus *Macrozamia*).

Macrozamia Miq. sect. *Genuinae* Miq. in *Arch. Néerl.*, 3 (1868), 247, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 50 (absolutely equivalent to the above).

Macrozamia sect. *Polyorientales* Schuster, *Pflanzenr.*, IV, i (1932), 87 (in part, excluding several species. Nomenclaturally illegitimate since it includes the type of the earlier section *Parazamia* Miq., though not based on this. I select *M. moorei* F. Muell. as LECTOTYPE, since the other names included by Schuster are confused. Even should *M. moorei* be sectionally separated, Schuster's name remains rejected).

Macrozamia sect. *Polyorientales* Schuster subsect. *Attenuatae* Schuster, *l.c.* (for the greater part. I select *M. moorei* F. Muell. as LECTOTYPE).

Macrozamia sect. *Monooccidentales* Schuster, *l.c.* (this comprises only *M. riedlei* and *M. macdonnellii*, considered conspecific by Schuster, and distinguished sectionally by no tangible character from his sect. *Polyorientales*. It is nomenclaturally illegitimate since it is based on the type of the genus—see above, p. 87. Schuster nowhere refers to Miquel's earlier sectional names).

Pinnae predominantly straight and spreading, nerves visible but narrow and not or scarcely prominent on the lower surface when dry, apices always entire in adult fronds, bases markedly callous and (when dry) rugose on the anterior margin, mucilage canals present in the pinnae, the lowest pinnae usually progressively reduced.

Usually large plants with many large fronds, aerial trunk sometimes present and robust. Rhachis never strongly twisted (except in rare aberrant individuals), usually flattened above and angled beneath when dry. Cones usually large (females 15–90 cm. long, 8–30 cm. diam.; males 15–45 cm. long), sporophyll-spines short to long, always erect.

This is the more widespread section, having one species each in the south-west and the centre of the continent, as well as four in the east. The species show less evidence of reduction than those of sect. *Parazamia*, which suggests that sect. *Macrozamia* is the more primitive, or more conservative, of the two. Individuals of the various species, unlike those of section *Parazamia*, usually occur plentifully in fairly dense communities and may form quite an important and conspicuous part of the vegetation. Regeneration is vigorous in most places. In distribution the species show a replacement pattern without overlap, except in the case of *M. moorei* and *M. miquelii*, where the former is found both north-west and south of the latter's area, but not within it. Naturally-occurring hybrids are consequently unknown within the section. On the other hand the distribution of species of sect. *Macrozamia* frequently overlaps that of species of sect. *Parazamia*, and mixed stands occur in places. A few hybrids may be found, but the specific limits do not break down.

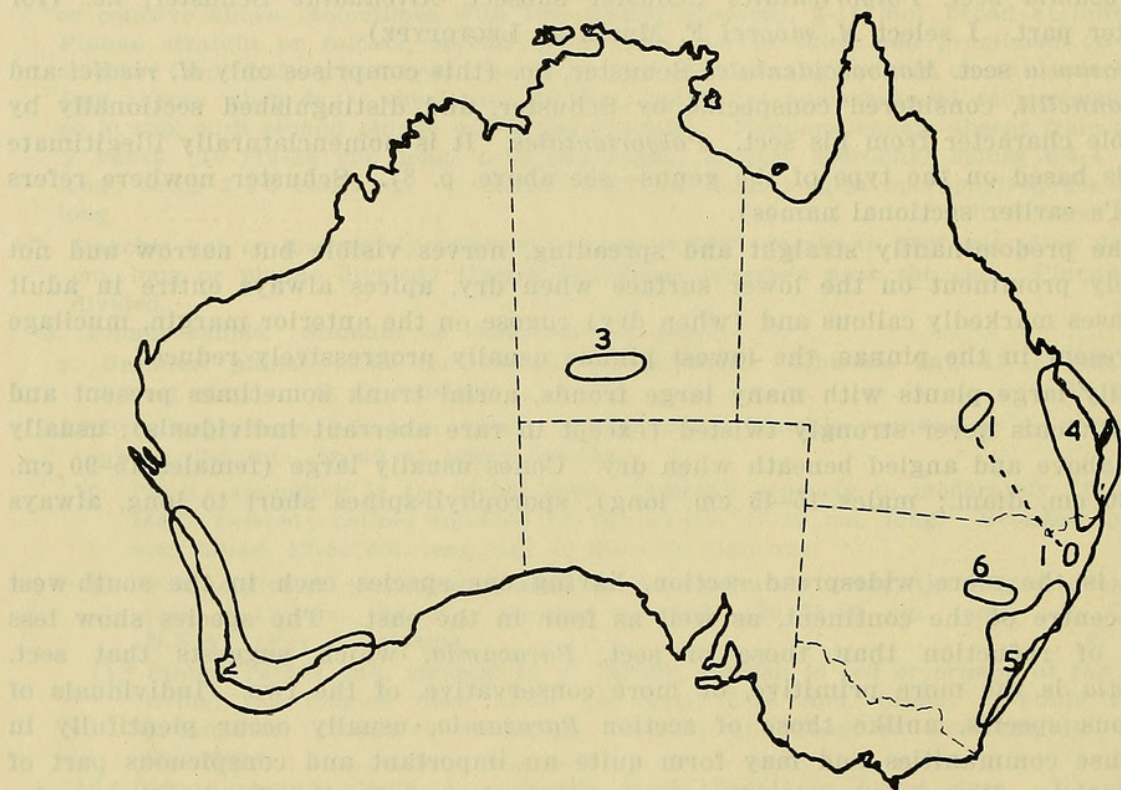
The six species of this section fall naturally into the following three groups: (a) the remarkable *M. moorei* alone, (b) the two vicarious western and central species *M. riedlei* and *M. macdonnellii*, (c) the three vicarious eastern species *M. miquelii*, *M. communis* and *M. diplomera*. Groups (b) and (c) may themselves be considered as a pair of vicarious "superspecies" (Text-figure 2).

1. *M. MOOREI* F. Muell. in *Chemist and Druggist, Australas. Suppt.*, 4 (March, 1881), 84.

Typification: "With certainty known from the mountainous regions of Queensland at the verge of the tropics", with a reference to its cultivation by Charles Moore in the Sydney Botanic Gardens, is the only information in the original publication, but in August, 1881 (see below) Mueller cited "In collibus praesertim altioribus lapidosis ad originem fluminis Nogo-River imprimis circum urbem [sic!] Springsure satis frequens; J. G. Macdonald; P. A. O'Shanesy". (I have not seen these SYNTYPES and therefore cannot name a lectotype, but the identity of the species is unmistakable from the description and locality.)

Synonymy:

Encephalartos moorei (F. Muell.) F. Muell., *Fragm. Phytogr. Austral.*, 11 (August, 1881), 125. In the preamble to his original publication of March, 1881, Mueller vacillated, as he had done for many years in various publications, regarding the generic recognition of *Macrozamia* as distinct from *Encephalartos*. The title of his paper referred to a "species of *Encephalartos*", and in his discussion he appeared to imply that *Macrozamia* was to be regarded as a subgenus of *Encephalartos*, if indeed both of these were not to be included in *Zamia*! However, although the preamble was equivocal, in the formal treatment the species was described under the binomial *Macrozamia moorei*, and in his later publication in August of the same year, when placing 'he species definitely under *Encephalartos*, Mueller cited *Macrozamia moorei* as a synonym,



Text-fig. 2.—Distribution of *Macrozamia* section *Macrozamia*: 1: *M. moorei*; 2: *M. riedlei*; 3: *M. macdonnellii*; 4: *M. miquelii*; 5: *M. communis*; 6: *M. diplomera*.

with full reference to its earlier publication. Clearly, Mueller did not really know whether or not he himself *accepted* his binomial *Macrozamia moorei* at the time of publication, and its validity under the I.C.B.N. depends on this. Since the case may be argued either way, I consider that *M. moorei* F. Muell. should be accepted as validly and legitimately published in March, 1881, thus preserving the established nomenclature and citation. The alternative is to reject *M. moorei* F. Muell., March, 1881, as invalid; the first valid publication would then be as *Encephalartos moorei* F. Muell., August, 1881, and the first valid publication under *Macrozamia* would be as *M. moorei* F. Muell. ex F. M. Bail., *Syn. Queensl. Flora* (1883), 501, which is not based on a reference to *Encephalartos moorei* F. Muell., but is to be treated as a new publication. A much more detailed nomenclatural discussion of this matter is possible, but, being devoid of biological significance, would be unprofitable. For further citations and misapplications see Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Description, specimens and further discussion: See Johnson in Anderson, *l.c.*

Chromosome number: $2n = 18$.

Distribution: Queensland and New South Wales: Two disjunct areas, in Central Queensland (Springsure-Carnarvon Range districts) and the Clarence River (Dalmorton) district of the North Coast of N. S. Wales, in dry sclerophyll forest or

in the ecotone between semi-wet sclerophyll forest and rainforest, on rather shallow, rocky or stony soils.

Apparently an old species now fragmented into two widely disjunct groups of populations, but within these still vigorous, *M. moorei* stands somewhat apart from the other species of the section, particularly in the long series of reduced pinnae extending almost to the frond-base, and in the large numbers of cones (especially males). Chamberlain (1913) was so impressed by the numerous lateral cones that he devoted a whole paper to this species and suggested a close relationship with the Mesozoic Bennettitales. However, the nature of the "strobilus" and its parts differs so greatly in Cycadales and Bennettitales that the relationship is now held to be rather a distant one. Certainly *Macrozamia* cannot be derived from anything like the Bennettitales.

The plants are massive and spectacular and of fairly rapid growth; individuals with trunks 2 m. tall and 60–70 cm. thick in the Sydney Botanic Gardens are less than 100 years old. Some apparent natural hybrids between *M. moorei* and *M. lucida* (of section *Parazamia*) are discussed in the forthcoming *Flora of N.S.W.*, part 1.

2. *M. RIEDLEI** (Fisch. ex Gaudich.) C. A. Gardn., *Enum. Pl. Austral. Occid.* (1930), 3; C. A. Gardn. in Gardn. and Bennetts, *Toxic Pl. W. Austral.* (1956), 6 (s. ampl.).

Basionym: *Cycas riedlei** Fisch. ex Gaudich. in Freycinet, *Voy. autour du Monde, Bot.* (1826), 434.

Typification: "In Novae Hollandiae orâ occidentali (Port du Roi George)." This is in herb. Paris. I have not seen it, but it was seen by Miquel, and from the locality there is no doubt of its identity.

Synonymy:

Macrozamia fraseri Miq., *Monogr. Cycad.* (1842), 37 [Schuster (1932) states that this is "sine descr.", but Miquel's description, brief as it is, is sufficient to validate the name]; Miq., *Prodr. Syst. Cycad.* (1861), 8, also in *Arch. Néerl.*, 3 (1868), 247, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 50; Benth., *Fl. Austral.*, 6 (1873), 252. Not *M. spiralis* (Salisb.) Miq. [var.] δ *fraseri* Regel in *Acta Hort. Petrop.*, 4 (1876), 318.

M. preissii Lehm., *Pugill.*, 8 (1844), 31, descr. (not seen) and in *Cat. Hort. Hamb.* (1842), nomen? (not seen); Heinzel in *Nov. Act. Acad.*, 21, i (1844), 203, t. 10–13 (not seen); Lehm., *Pl. Preiss.*, 1 (1845), 645; F. Muell., *Fragm. Phytogr. Austral.*, 1 (1858), 41, and various later references; A.D.C., *Prodr.*, 16, pt. 2 (1868), 525; Regel in *Acta Hort. Petrop.*, 4 (1876), 318; Schuster, *Pflanzenr.*, IV, i (1932), 101 (in part, excl. syn. *M. macdonnellii* and Central Australian citations).

Encephalartos preissii (Lehm.) F. Muell. in *Quart. Journ. Pharm. Soc. Vict.*, 2 (1859), 90 [this is validly published, but in the further reference given by Schuster (1932) to Miquel (1863) the name is mentioned only in synonymy of *E. fraseri*].

E. fraseri (Miq.) Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368.

E. oldfieldii Miq., *l.c.*, 370.

Macrozamia oldfieldii (Miq.) A.D.C., *Prodr.*, 16, pt. 2 (1868), 535; Miq. in *Arch. Néerl.*, 3 (1868), 250 [cited by Schuster from the separate as "Nouv. Matér. (1868) 58"]; Miq. in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 53. [Schuster (1932) gives this the first citation, as "Nieuw. Bijdr. Cycad. (1868) 53", but the paper thus entitled was published in the above-cited journal, the title-page of which is dated 1869; I can find no indication in it of an earlier date of publication of the paper, though this is possible. It matters little.]

* In publishing the combination, and consistently since, Gardner, who apparently did not consult the original, writes "*reidlei*" (all epithets here quoted with lower case initials though originally capitalized). Miquel (1868, 1869) and Schuster (1932) both cited "*riedleyi*"; and Regel (1876) gave "*riedeli*". The species was named for the French gardener Riedlé, and was correctly spelt "*riedlei*" by Gaudichaud. Though he used Fischer's herbarium name, Gaudichaud suspected that the plant's affinity was with *Zamia* rather than *Cycas*. The description is brief but sufficient.

*Encephalartos dyeri** F. Muell. in *Chemist and Druggist, Australas. Suppt.*, 8 (1885), 12.

*Macrozamia dyeri** (F. Muell.) C. A. Gardn., *Enum. Pl. Austral. Occid.* (1930), 3.

M. preissii Lehm. ssp. *dyeri*† (F. Muell.) Schuster, *Pflanzenr.*, IV, i (1932), 102.

Caudex sometimes mostly subterranean, but frequently forming a trunk 1–5 m. tall or said to be sometimes procumbent, 60–120 cm. diam. Fronds numerous (usually 50–100 or more?), at first erect, later spreading or drooping, up to 150–200 cm. long on mature plants; spine-free petiole (excluding the silky-woolly swollen base) 12–30 (or more?) cm. long, rhachis not markedly twisted, more or less flattened, 10–20 mm. broad at the lowest pinnae, flat to somewhat concave or convex above, often somewhat keeled distally, with two narrow lateral grooves (more marked when dry) decurrent from the bases of the pinnae, convex and usually subangular to angular beneath. Pinnae 100–150 (or more?), spreading, but the two ranks often inclined to each other, forwardly directed at an acute angle (the lowest least so), mostly rather crowded, but the lowest ones more distant, decidedly rigid, entire, straight, linear, the longest 20–35 cm. long, several of the lowest progressively reduced and spine-like, 6–11 (–15 in *dyeri* forms) mm. broad with 8–15 (–18 in *dyeri*) scarcely raised nerves beneath, gradually tapered to the pungent apex, contracted to the pale or somewhat reddish and anteriorly callous and (when dry) rugose base, green but not shining, with numerous stomata on both upper and lower surfaces. Cones stalked, in either sex 1–several(?) per plant, axillary among the fronds,* the base of the stalk surrounded by several spine-like, angular-subulate to strap-shaped cataphylls (pubescent or tomentose when young), sometimes with a few shorter decurrent cataphylls on the stalk itself. Male cones cylindrical, often somewhat curved when old, 20–40 (–60 in *dyeri*) cm. long, ca. 10 cm. diam. (sometimes more?); sporophylls cuneate to obovate-lanceolate, 3–5 (–6 acc. to Schuster) cm. long, ca. 1.5–2.5 cm. broad, the triangular to elongate upturned spines from almost obsolete to 1.5–5.5 cm. long (the longest near the apex of the cone). Female cones ovoid-cylindrical, 25–45 (or more?) cm. long, 15(?)–25 cm. diam., stalk ca. 12–20 (or more?) cm. long, to 3–4 (–5?) cm. thick; sporophylls ca. 5–8 (–10 acc. to Schuster) cm. long (stipes ca. 3–6 cm.), the expanded ends glaucous, 4.5–9 cm. wide, ca. 3–5 cm. high, the flattened erect spines increasing in length towards the apex of the cone, the lowest from almost obsolete to ca. 0.8 cm. and often lacerate, the uppermost from 1.5–6 (–10 acc. to Schuster, but doubtful) cm. long, broad-based; inner parts of the cone salmon-pink when fresh. Seeds 3–5 (–6?) cm. long, 2.5–3.5 cm. thick, outer coat bright red when ripe.

Chromosome number: $n = 12$, according to Light (1924), but this may well be a miscount, since it does not agree with related species ($n = 9$).

Distribution: Western Australia: South-western and southern coast region, from the Murchison River to east of Esperance, in dry and wet sclerophyll forest (or scrub) on sandy and lateritic soils.

Specimens examined: WESTERN AUSTRALIA: Bullsbrook area, 27 miles N.N.E. of Perth, Kennington, 31.v.1957 (NSW.42034); Armadale, J. M. Griffiths, viii.1900 (NSW.40660); Big Brook, M. Koch 1419, vi.19— (NSW.40662); Bow River, S. W. Jackson, xii.1912 (NSW.40661); Western Australia, J. B. Cleland, 1907 (NSW.40663); Western Australia, E. Brown, 1898 (NSW.40656).

M. riedlei exhibits considerable variation in size and habit, but if Gardner (in Gardner and Bennetts, 1956) is correct, all the Western Australian populations are to be regarded as conspecific. The only authentic material of *M. dyeri* which I have seen is a pair of collodion cuticular pulls from dorsal and ventral surfaces of a pinna of an apparent isotype ("Esperance Bay, W.A.") in herb. Kew, made available by the

* Included in the synonymy on the testimony of Gardner (1956). See discussion below.

† Gardner (1956) states that "the female has a solitary terminal central cone". Doubtless this is based on superficial observation; whatever the species, the cone (in individuals bearing but one) may appear terminal but on careful inspection is seen to be lateral. Again, it would be surprising if *M. riedlei* never bore more than a single cone, unlike its congeners.

kindness of Dr. R. Melville. These show stomata on both surfaces. The descriptions of *M. dyeri*, however, indicate that the pinnae are considerably broader than any which I have seen in available specimens of *M. riedlei*. Miss A. Baird (pers. comm.) indicates that *M. riedlei* varies greatly in stature in various parts of Western Australia and, as in *M. communis* in New South Wales, the development of the trunk above ground level tends to be greatest on shallow soils, in which the caudex cannot be pulled far below ground by the contractile roots. Gardner (*l.c.*) states that the largest forms occur towards the northern and eastern limits of its distribution.

While lacking personal field experience and sufficient herbarium materials of the Western Australian populations, I must follow Gardner in recognizing only a single species, though with reservations.

Both R. Brown (1810) and Miquel (1842) included material of this species under the names *Zamia spiralis*/*Macrozamia spiralis*. Bauer's figures reproduced by Miquel (*l.c.*, Pl. 4-5) actually represent *M. riedlei*, as Miquel himself (1863) later pointed out. This is discussed above under the typification of the genus, and below under *M. spiralis*. Schuster (1932) included *M. macdonnellii* under his "typical" *M. preissii* (= *M. riedlei*), though he gave *M. dyeri* subspecific rank. Bentham (1873) likewise included *M. macdonnellii* under *M. fraseri* (= *M. riedlei*). However, *M. macdonnellii* seems reasonably distinct and is certainly isolated.

Fronds of *M. riedlei* often appear very similar to those of *M. communis*, but the pinnae are generally even more rigid and may be distinguished by the presence of stomata on the upper surface.

3. *M. MACDONNELLII** (F. Muell. ex Miq.) A.DC., *Prodr.*, 16, pt. 2 (1868), 537; Miq. in *Arch. Néerl.*, 3 (1868), 249, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 53; F. Muell., *Fragm. Phytogr. Austral.*, 9 (1875), 124 (and *ibid.*, 2 (1861), 179, nomen); Ewart and Davies, *Fl. Northern Territory* (1917), 19.

Basionym: *Encephalartos macdonnellii** F. Muell. ex Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 376.

Typification: "Nova Hollandia centralis, ad flumen Neales in Macdonnell-range, unde reportavit cel. peregrinator J. M. Stuart" (not seen, but of certain identity from the general locality and description. The present Neales River is a rarely-flowing stream in South Australia, debouching into Lake Eyre. There are certainly no *Macrozamia* species in this most arid region. Either there was some confusion as to the precise locality, or it was merely meant that the plant was collected at some time on the Neales River—Macdonnell Range stage in Stuart's epic expedition. The plant could not be missed in the Macdonnells).

Trunk usually developed above ground (the plants grow on shallow soils), 1-2 (-3) m. tall, but often more or less procumbent, 60-80 (or more?) cm. diam. Fronds numerous (50-100 or more), at first erect, later spreading or drooping, 150-220 cm. long on mature plants; spine-free petiole (excluding the silky-woolly expanded base) 12-25 (or more) cm. long; rhachis not markedly twisted, more or less flattened, 15-25 mm. broad at the lowest pinnae, flat to somewhat concave but usually more or less keeled above, with two narrow lateral grooves (more marked when dry) decurrent from the bases of the pinnae, convex and subangular to angular (when dry) beneath. Pinnae 120-170, spreading but the two ranks usually inclined to each other, forwardly directed at an acute angle, mostly rather crowded but the lowest usually 4-5 cm. apart, decidedly rigid, entire, straight, linear, the longest 20-30 cm. long, *ca.* 8-20 of the lowest progressively reduced and spine-like, 7-11 mm. broad with 8-15 scarcely-raised nerves

* By Miquel (1863, 1868, 1869), but not by Mueller or De Candolle, spelt "*macdonelli*" but the single "n" is to be regarded as an unintentional error. Miquel correctly spelt "*Macdonnell-range*". F. Mueller (1875) is usually cited as the author of the valid combination under *Macrozamia*, but De Candolle definitely made it in 1868, though as a *species incerta*. De Candolle's treatment was published in mid-July, 1868, according to Stearn (1941); Miquel's paper in *Archives Néerlandaises* (1868) was probably published late in that year, although no month is indicated on the cover or title page of the part.

beneath, gradually tapered to the pungent apex, contracted to the pale anteriorly callous and (when dry) often somewhat rugose base, dull and (rhachis also) decidedly glaucous on both surfaces (especially when living), with numerous stomata on both upper and lower surfaces. Cones stalked, in either sex 1-several per plant, axillary among the fronds, the base of the stalk surrounded by several spine-like cataphylls, usually with a few shorter decurrent cataphylls on the stalk itself. Male cones cylindrical, often somewhat curved when old, 25-40 cm. long, *ca.* 8-10 cm. diam.; sporophylls cuneate-obovate, 3-4 cm. long, *ca.* 1.5-2 cm. broad, the expanded ends very glaucous and the triangular-acuminate to elongate upturned spines from obsolete on the lower sporophylls to 1.5-2.5 cm. long near the apex of the cone. Female cones ovoid-cylindrical, 40-50 cm. long, 20-27 cm. diam., stalk 12-20 (or more?) cm. long, to 4-5 cm. thick; sporophylls 7-10 cm. long (stipes *ca.* 5-7 cm.), the expanded ends glaucous, 8-12.5 cm. wide, *ca.* 4-6 cm. high, the spines almost or quite obsolete on the lower sporophylls, flattened and triangular to 1-2 cm. long near the apex of the cone. Seeds 6-8 cm. long, 4-5.3 cm. thick, outer coat bright orange-red when ripe.

Distribution: Northern Territory: Central Australia in the Macdonnell and associated parallel range systems, sometimes in sclerophyllous communities with *Eucalyptus* or rarely *Livistona*, but sometimes as scattered plants on almost bare rocky slopes with *Triodia* species.

Specimens examined: NORTHERN TERRITORY: Alice Springs, R. H. Pulleine, vii.1917 (NSW.40659); Standley Chasm, J. Garden and V. Lhuedé, vii.1954 (NSW.40657), photo; Standley Chasm, N. Forde 864, 23.v.1957, and 10.iii.1957 (NSW.41470); Standley Chasm, L. A. S. Johnson, x.1957 (NSW., male cone); Central Australia, R. Tate, 1894 (NSW.40658). Also living material examined, Standley Chasm, L. A. S. Johnson, x.1957.

M. macdonnellii is clearly a relict species, closely related to *M. riedlei* but isolated from it by arid country and with sufficient consistently different characteristics to be given specific rank.

Bentham (1873), with only a fragment before him, could not distinguish it from *M. fraseri* (= *M. riedlei*), while Schuster (1932) placed it in the synonymy of his "typical" *M. preissii* (= *M. riedlei* excluding *M. dyeri*) without comment. The species is characterized by the glaucous fronds, the massive female cones (to almost 20 kgm. in weight) with most of the sporophyll-spines obsolete, and the huge seeds.

Popularly, *M. macdonnellii* has been much confused with the very restricted relict palm species *Livistona mariae*, with which it is associated at Palm Valley, but the *Macrozamia* is a much more widely distributed plant in Central Australia, found at times in very forbidding habitats, though always in the Macdonnell Range complex. The extraordinarily large seeds of this species may have evolved as a selective adaptation to the uncertain rainfall of the interior. Their great food reserves must serve to give seedlings a good start in life. Glaucous bloom is likewise most strongly developed in this species, again suggesting adaptive significance.

4. *M. MIQUELII* (F. Muell.) A.DC., *Prodr.*, 16, pt. 2 (1868), 535 (in part, as to lectotype); Miq. in *Arch. Néerl.*, 3 (1868), 248, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 51 (in part).

Basionym: *Encephalartos miquelii* F. Muell., *Fragm. Phytogr. Austral.*, 3 (1862), 38 (in part, as to lectotype).

Typification: "Ad ostium fluminis Richmond River; C. Moore. Ad sinum Moreton Bay; W. Hill. Ad flumen Fitzroy River sub circulo capricornu; A. Thozet." Mueller's original concept was strangely mixed; Moore's specimen belonged to the species later described as *M. fawcettii* C. Moore (sect. *Parazamia*), whereas Hill's and Thozet's represented the present most dissimilar species. The description was derived in part from each of these species and the confused concept survived by copying in later publications by A. De Candolle, Miquel and Mueller himself (see refs. in *Fl. N.S.W.*, pt. 1, in press) both under the name of *Macrozamia/Encephalartos miquelii* and the misapplied name *M. tridentata* (Willd.) Regel. It was never explicitly resolved, but

in time the name *M. miquelii* came to be applied (e.g. by Bentham, *Fl. Austral.*, 6 (1873), 253, and F. M. Bailey, *Queensl. Fl.*, 5 (1902), 1504) to the present species alone, whilst the other species has been generally known as *M. fawcettii*. Schuster's (1932) treatment is wholly confused and irrelevant in this connection.

The type folder in herb. MEL contains three sheets, as follows: (1) Rockhampton, Thozet (with old male cone). (2) Moreton Bay, collector not indicated (this includes female cone fragments in a packet, probably a later addition; the cone at least is not part of the type series since Mueller had no female material). (3) Richmond River, C. Moore (with seeds in a packet labelled in Mueller's hand: "*M. miquelii*. This represents the genuine species according to locality"). Of these, 1 and 2 are the present species and 3 is *M. fawcettii* C. Moore. I have no doubt that 1 is the original Thozet syntype indicated by Mueller as "Ad flumen Fitzroy River . . ."; the frond of 2 may be the Hill syntype, but the cone is not; the frond of 3 may or may not be the Moore syntype (which from the description must have belonged to *M. fawcettii*), but the seeds at least are a later collection. Mueller's annotation on 3 does not mean that he deliberately selected this element as lectotype; his concept always remained quite confused. Since Mueller's description applies in equal parts to both elements and the only definitely authentic syntype extant is Thozet's, which moreover includes male cone material mentioned in the original description, and since this specimen represents the species currently known as *M. miquelii*, I choose it (Rockhampton, Thozet MEL) as LECTOTYPE.

Synonymy, description and further discussion; see Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press). The synonymy and nomenclatural history, quite apart from the original confusion discussed above, are bewilderingly complex.

Chromosome number: $2n = 18$.

Distribution: Queensland and New South Wales: Central and southern coast districts of Queensland from Rockhampton southwards, and far North Coast of N. S. Wales (Upper Richmond River), in sclerophyll forest on poor sandy or stony soils.

Specimens examined: QUEENSLAND: Rockhampton, Thozet (MEL, LECTOTYPE); Berserker Range, Rockhampton, J. L. Boorman (N.S.W., seeds only); Fraser Island, per Queensland Forest Service, xii.1922 (TECH); Mount Perry, J. L. Boorman, vii. 1912 (NSW.40624, 40625); Moreton Bay [W. Hill?] (MEL); Queensland (N.S.W., cone only, old collection labelled *M. douglasii*, prob. from F. M. Bailey). NEW SOUTH WALES: In low flat ground between the Upper Richmond and Clarence Rivers, C. Moore, 1861 (NSW.40610, HOLOTYPE of *M. cylindrica* C. Moore). Also studied from living and preserved cultivated material.

M. miquelii, as here defined, includes *M. douglasii* W. Hill ex F. M. Bail. from Fraser Island and *M. mountperriensis* F. M. Bail. from Mt. Perry, inland from Bundaberg. These have been regarded, especially in Queensland (see Johnson in Anderson, *l.c.*, for references), as distinct from *M. miquelii*, while *M. cylindrica* C. Moore has been regarded as distinct in New South Wales, though it is little known outside cultivation. However, I can find no real discontinuity nor any greater variation within this series of populations than exists in *M. communis* in New South Wales or *M. riedlei* in Western Australia. *M. douglasii* represents luxuriant plants from the deep sands and wet climate of Fraser Island, and *M. mountperriensis* the other extreme of small plants from the more continental climate of Mt. Perry, while *M. miquelii* and *M. cylindrica* (between which there seems to be no difference at all) represent the more average forms from scattered localities in the coast districts. The differences in stature and in number of reduced basal pinnae, however, must be to some extent genetically determined, since cultivated plants preserve them to some degree. The same applies to local ecotypes of *M. communis* and *M. heteromera* cultivated in Sydney. On the other hand there is a clear morphological as well as geographic discontinuity between the populations of *M. miquelii* and *M. communis*, though they show parallel variation. This is discussed further by Johnson in Anderson, *l.c.* I know of no hybrids of *M. miquelii*. The species has been cultivated in Australia and overseas, and has a plethora of names in every conceivable rank (see Johnson, in press).

5. *M. COMMUNIS* L. Johnson, sp. nov.

Typification: About three miles west of Mossy Point, near Mogo, New South Wales, J. W. Vickery, iv.1958 (NSW.43071), female. HOLOTYPE.

Caudex plerumque subterraneus (per contractionem radicum seppultus) sed in solo minime profundo usque ad 1–2 m. altus, 30–60 cm. diametro. Frondes in corona usque ad 50–100 sed saepe pauciores, 70–200 cm. longae, petiolo (basi lanata expansa exclusa) 12–40 cm. longo, rhachi non torta (stirpibus insanis exceptis) plus minusve applanata, ad pinnas infimas 8–20 mm. lata, supra vel concava vel convexa aliquando carinata, sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa, infra subangulato-convexa. Pinnae 70–130, patentes, angulo acuto prorsum directae, plurimae arctae sed infimae saepe distantes, quam illis *M. miquelii* crassiores rigidioresque, integrae, rectae, lineares, eae longissimae 16–35 cm. longae, 3–15 infimarum gradatim reductae spiniformesque, 4–12 mm. latae, infra vix prominule nervis 7–13 striatae, apicem pungentem versus sensim angustatae, basi pallida arcte contractae et in axillis callosae rugosaeque (in sicco), supra saturate virides haud vel vix nitentes, pagina inferiore sola stomatibus instructa. Coni feminei 1–6, masculi 1–10, axillares inter frondibus, basi axis conigeri cataphyllis spiniformibus (ad 18 cm. longis) instructa. Coni masculi cylindracei (vetustiores aliquanto curvati) 20–45 cm. longi, 8–12 cm. diametro (5–8 cm. in stirpibus depauperatis), sporophyllis cuneatis vel obovato-cuneatis 2–4 cm. longis, 1.5–2.5 cm. latis, spinis planis erectis 0.1–5 cm. longis (longissimis 2–5 cm. versus apicem coni) basi 5–12 mm. latis. Coni feminei cylindracei, 20–45 cm. longi, 10–20 cm. diametro, in axibus 8–30 cm. longis 2–3 (–4?) cm. crassis gesti, sporophyllis 4–7 cm. longis (stipite 3–4.5 cm. incluso) parte terminali expansa glauca maturitate plerumque latitudine (3–8.5 cm.) quam altitudine (1.5–4.3 cm.) saltem duplo majore, spinis planis erectis, ad basin coni brevissimis (1–2.5 cm. longis) versus apicem longissimis (4–8 cm.), basi 8–20 mm. latis. Semina 3–4.5 cm. longa, 2–3 cm. crassa, integumentum parte exteriori carnosa miniata. Chromosomata somatica $2n = 18$.

Description (English), *specimens* and full *discussion*: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Coast and ranges from Macleay River to Bega and westward to the head of the Goulburn River, in dry sclerophyll forest, on sandy or stony soils.

This is the plant, familiar to every botanist who has worked in the Sydney district, which has been wrongly known in New South Wales as "*M. spiralis*"; it is not the species which has been called "*M. spiralis*" in Queensland (see below, under *M. spiralis* and *M. lucida*). Despite frequent references to it in the literature under this and other misapplied names (see Johnson, in Anderson, *l.c.*), it has never been described as a new species, hence the present description. The specific epithet reflects the abundance of this species in many parts of the Coast districts of New South Wales. *M. communis* shows a good deal of individual and some local variation in size of organs, but is clearly discontinuous in nature from related species of section *Macrozamia*. The Type is characteristic of the most luxuriant forms from the South Coast. Despite its occurrence in places near stands of certain species of section *Parazamia*, I have not yet found any evident hybridism either in the wild or in cultivated collections. Nevertheless, to judge by the behaviour of other species (e.g. *M. moorei*), hybrids are to be expected. *M. communis* is cultivated in gardens in Australia and overseas. Its well-known vernacular name is usually spelt "Burrawang", but today pronounced "Burrawong". For a discussion of the past nomenclatural confusion surrounding this species see Johnson in Anderson, *l.c.*

6. *M. DIPLOMERA* (F. Muell.) L. Johnson, stat. nov.

Basionym: *Encephalartos spiralis* (Salisb.) Lehm. var. *diplomera* F. Muell., *Fragm. Phytogr. Austral.*, 5 (1866), 172 (in part, as to lectotype, see below).

Typification: "... ab amico Carolo Moore in montibus Wambungle Mountains ad flumen Castlereaghii detectam." In point of fact these collections were made by

Moore's collector W. Carron, but Moore sent duplicates to Mueller. The type sheet is in herb. MEL labelled: Castlereagh River at the Wambungle [sic] mountains [New South Wales], [W.] Carron [before 1866]. This is a mixed collection: the sheet bears three pieces of fronds, of which two belong to the species here defined as *M. diplomera* (these I choose as LECTOTYPE) and one belongs to the species here defined as *M. heteromera* C. Moore (which was of similar mixed typification, see below). Mueller's description and epithet ("two-parted") clearly fit the former species better. The actual locality, of course, is the Warrumbungle Mountains, in the eastern sandstone foothills of which this species is found.

Synonymy: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Since Mueller's original description in varietal rank is very brief and rather informal (though valid), I now provide a new Latin description (for English description, see Johnson in Anderson, *l.c.*):

Caudex plerumque subterraneus, 20(?)–40 cm. diametro. Frondes in corona usque ad 50 (?), sed saepe pauciores, 60–120 cm. longae, petiolo (basi lanata expansa exclusa) 10–20 cm. longo; rhachi non torta, plus minusve applanata, ad pinnae infimas 8–12 mm. lata, supra concaviuscula vel convexa (proxime saepe plus minusve carinata), sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa, infra subangulato-convexa. Pinnae 70–120, valde patentes, angulo acuto prorsum directae, plurimae arctae sed infimae 2–4 cm. distantes, rigidiusculae, omnes paucis apicalibus exceptis angulo acutissimo in segmentis duobus vix divergentibus dichotome divisae (plerumque versus basin pinnae sed in pinnis subapicalibus versus medium, rare segmento uno pinnarum nonnullarum infimarum ipso diviso vel sub apice unidentato), eae longissimae 15–20 (–25?) cm. longae, nonnullae infimarum gradatim abbreviatae spiniformesque, 5–10 mm. latae (segmentis 2.5–5 mm. latis), infra 6–13 nervis (in segmentis 3–7 nervis) vix prominule striatae, (pinnae segmentave) ad apicem pungentem sensim angustatae, basi pallida flavescentive constricta et in axillis callosae rugosaeque (in sicco), sinu furcae pinnarum etiam saepe calloso rugosiusculoque, supra virides non nitentes (in sicco saepe flavescentes), paginis utrisque stomatibus instructis. Coni non certe noti, probabiliter illis minoribus *M. communis* similes, axe conigero femineo fide auctorum ferrugineo-tomentoso [cataphylla juniora in speciebus plurimis tomentosa sunt. L.J.].

Distribution: New South Wales: Southern part of North-west Slopes, around Coonabarabran and the eastern foothills of the Warrumbungle Mountains and east to the Mooki River, in dry sclerophyll forest on sandy or stony siliceous soils.

Specimens and further discussion: See Johnson in Anderson, *l.c.*

This species, of which cones are unfortunately unknown, is noteworthy for its divided pinnae. This character and the amphistomatic fronds clearly distinguish it from *M. communis*, the smaller inland forms of which it otherwise resembles. It is remarkable that its range corresponds in part with that of *M. heteromera*, which also has divided and amphistomatic pinnae, but which is as clearly a member of section *Parazamia* as *M. diplomera* is of section *Macrozamia*. Hitherto, most collectors and systematists have failed to distinguish *M. diplomera* from *M. heteromera*, usually including also a third species, *M. stenomera* (sect. *Parazamia*), which has divided but hypostomatic pinnae and is found to the north-east of this area. These facts of distribution suggest causal correlation of some kind: probably plants with divided pinnae possess some selective advantage, or at least are certainly not at a disadvantage, in the regional environment, but it is further possible that there has been introgressive gene-flow between populations belonging to the two rather diverse sections. A detailed study of these populations and their genetics should be of interest. In the field I have only once seen *M. diplomera*, in passing, and have been able to study *M. heteromera* only in areas where *M. diplomera* is absent. An apparent hybrid between the two was once grown in the Sydney Botanic Gardens from seed from the Coonabarabran district. The various distinctions between *M. diplomera* and *M. heteromera* are discussed by Johnson in Anderson, *l.c.*

ii. Section PARAZAMIA (Miq.) Miq.

In *Arch. Néerl.*, 3 (1868), 250, and in *Versl. Meded. Koninkl. Akad.*, ii, 3 (1869), 541; amplified hereunder.

Basionym: *Encephalartos* Lehm. sect. *Parazamia* Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 374.

Typification: Miquel (1863) included only *Encephalartos pauli-guilielmi* (W. Hill & F. Muell.) F. Muell. in his new section. The type species of *Macrozamia* sect. *Parazamia* is thus *M. pauli-guilielmi* W. Hill & F. Muell. The section as I conceive it includes the species correctly called *M. spiralis* (Salisb.) Miq. Hutchinson (1924) gives this binomial as type-species of *Macrozamia*, but, as argued above (p. 87), *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn. should be the generic type. The sectional name *Parazamia* may be used in the present circumscription only on this interpretation.

Synonymy (infrageneric):

Macrozamia sect. *Polyorientales* Schuster (nom. illegit.) subsect. *Acutae* Schuster, *Pflanzenr.*, IV, i (1932), 87 (I choose *M. pauli-guilielmi* W. Hill & F. Muell. as LECTOTYPE. This permanently disposes of the name. Schuster nowhere mentions Miquel's earlier sectional names).

Macrozamia sect. *Polyorientales* subsect. *Curvatae* Schuster, *l.c.* (I select *M. fawcettii* C. Moore as LECTOTYPE).

Pinnae usually more or less curved, spreading to erect (secund), nerves prominent on the lower surface especially when dry, apices entire to 2-7-toothed in adult fronds, bases slightly callous but never rugose, mucilage canals absent from the pinnae (present as always in the larger organs of the plant), the lowest pinnae not or only slightly, or one or two irregularly, reduced.

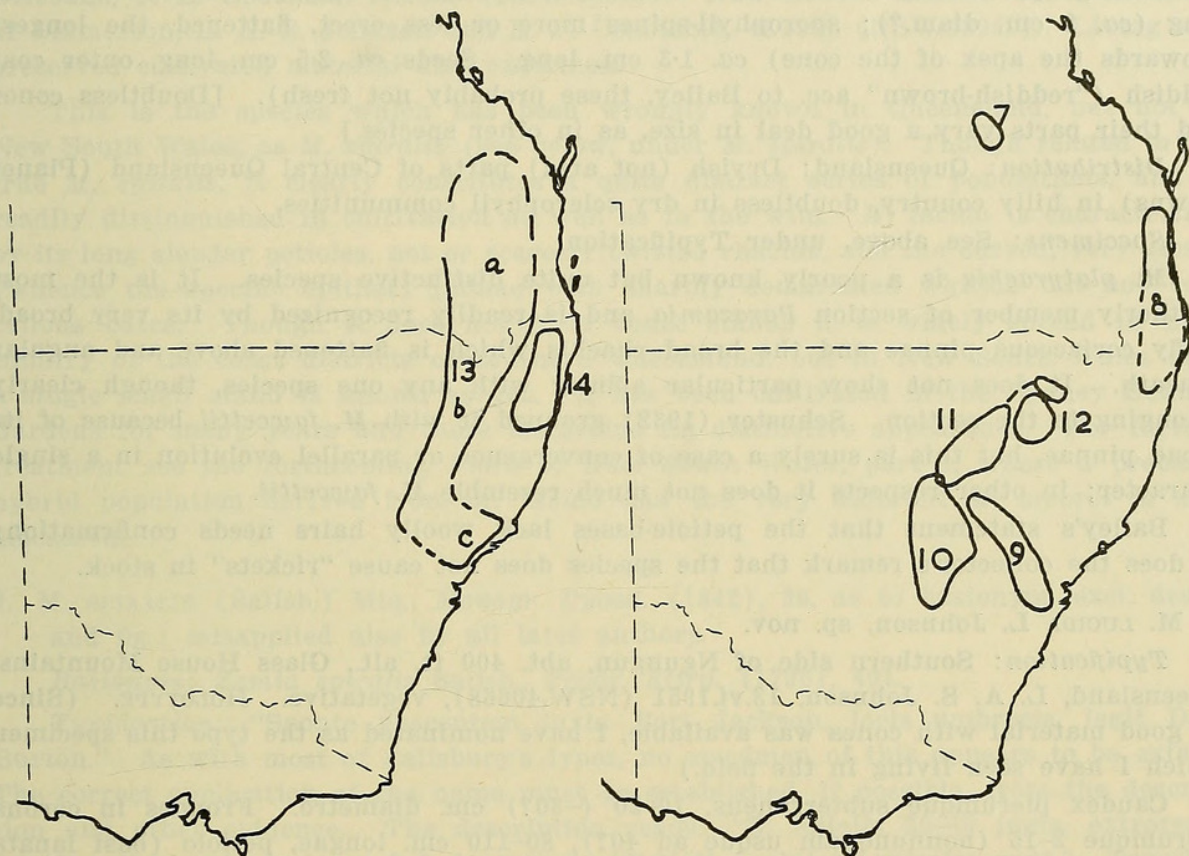
Small plants with few fronds, caudex wholly subterranean or only its crown protruding. Rhachis sometimes straight, but more often moderately to very strongly spirally twisted or strongly recurved or incurved near the tip, from rounded to flattened or even markedly concave above, rounded or less often somewhat angular beneath when dry. Cones small (females 10-25 cm. long, 6-10 cm. diam.; males 8-25 cm. long), sporophyll-spines short to medium (5 cm.), spreading to erect.

This very natural section is confined to eastern Australia, and its species show evidence of reduction and some degree of neoteny or carrying-over of semi-juvenile characteristics (prominent nerves, unreduced basal pinnae, toothed pinna-tips, lack of mucilage-canals in pinnae, rounded petioles, small caudices) into the adult state. Accordingly it is probably of relatively recent origin, that is to say, as an evolutionary line its adult character-complex has been evolved more recently than those characters preserved in and characteristic of sect. *Macrozamia*. Furthermore, speciation appears to be still in progress in sect. *Parazamia* (cf. the races of *M. pauli-guilielmi*) and some of the species are very closely allied. On the other hand the plants seem on the whole less successful than in sect. *Macrozamia*; the populations are diffuse, rarely forming close stands, though in such species as *M. heteromera* and *M. secunda* the total population is by no means small. Since the plants are scattered, small and relatively inconspicuous, and produce few cones at irregular intervals, they are frequently overlooked by collectors and good cone-material is lacking for some species. Since the cones seem to be very similar throughout the section, this is not such a taxonomic handicap as it may appear.

The species tend to show a replacement pattern (Text-figure 3), but this is not without overlap, though no two species of the section form mixed stands except marginally. Some marginal hybridism seems to occur between *M. secunda* and *M. heteromera*, *M. heteromera* and *M. stenomera*, *M. heteromera* and *M. pauli-guilielmi* ssp. *plurinervia*, and possibly between *M. secunda* and *M. spiralis*. In the case of the three subspecies of *M. pauli-guilielmi* there is a large-scale breakdown. Species of sect. *Parazamia* at times grow with or near species of sect. *Macrozamia* and hybrids may be found, as in the case of *M. lucida* and *M. moorei* at Dalmorton. Several apparent

chance inter-sectional hybrids have come up in the cycad beds in the Sydney Botanic Gardens. No chromosome numbers are recorded in this section.

One cannot arrange the eight species of the section neatly in subgroups, but certain of them do form rather close pairs or triplets; these are: (a) *M. lucida*-*M. spiralis*-*M. secunda* (the two end members differ markedly, but each is close to *M. spiralis*), (b) *M. heteromera*-*M. stenomera*, (c) *M. pauli-guilielmi*-*M. fawcettii*. Other cross-relationships are also evident, however, and *M. platyrachis* does not seem to fit in any one group better than another.



Text-fig. 3.—Distribution of *Macrozamia* section *Parazamia*: 7: *M. platyrachis*; 8: *M. lucida*; 9: *M. spiralis*; 10: *M. secunda*; 11: *M. heteromera*; 12: *M. stenomera*; 13: *M. pauli-guilielmi* (a: ssp. *pauli-guilielmi*, b: ssp. *plurinervia*, c: ssp. *flexuosa*); 14: *M. fawcettii*.

7. *M. PLATYRACHIS** F. M. Bail. in *Queensl. Agric. Journ.*, 3 (1898), 356, and in *Queensl. Flora*, 5 (1902), 1503 (as "*platyrhachis*"); Schuster, *Pflanzenr.*, IV, i (1932), 99 ("*platyrhachis*").

Typification: Range near Planet Downs, Queensland, H. C. Brock-Hollinshead, male, HOLOTYPE (a female cone was also sent). This is in herb. BRI. There is an ISOTYPE (vegetative) in NSW(40970).

Caudex mostly subterranean, to 60 cm. diam. according to Bailey, probably often less. Fronds few (to ca. 12?) in the crown, to ca. 100 cm. long, petiole ca. 15–25 cm. long excluding the expanded base (which Bailey describes as with "no woolly substance"); rhachis not or only moderately twisted (to ca. 180°?), 13–18 mm. broad at the lowest pinnae, flattened above with the two lateral furrows very shallow and obscure even when dry, convex and angular (at least when dry) beneath. Pinnae ca. 50 (sometimes more?), somewhat spreading to spreading-erect, more or less forwardly directed and twisted at the base, the upper ones fairly crowded but the lowest 2–3 cm. apart, rather stiff and very coriaceous, entire, from somewhat recurved-falcate to fairly

* The original spelling *platyrachis* should, I think, be retained. In 1902 and subsequently Bailey used *platyrhachis* but did not indicate this as a deliberate correction of an unintentional error. Neither form is particularly good Greek ("rrh-" would be best), but "-rachis" is acceptable latinized Greek.

straight, broad-linear, the longest 30–40 cm. long and the lowest ones not reduced, 12–20 mm. broad with *ca.* 15–18 rather prominent nerves beneath, somewhat tapered, but finally rather abruptly rounded to the mucronate apex, contracted to the somewhat paler, rather decurrent but not or scarcely callous base, green and somewhat glossy above, with stomata confined to the lower surface. Cones not examined; the following is from Bailey's data: Cones stalked, 1–several (at least in the males) per plant (presumably axillary amongst the fronds). Male cones cylindrical (probably immature ones measured), 7.5–10 cm. long, *ca.* 2.5 cm. diam., sporophyll-spines erect, slender, to 1 cm. long (prob. longer at times). Female cone more or less cylindrical, *ca.* 16 cm. long (*ca.* 8 cm. diam.?); sporophyll-spines more or less erect, flattened, the longest (towards the apex of the cone) *ca.* 1.3 cm. long. Seeds *ca.* 2.5 cm. long, outer coat reddish ("reddish-brown" acc. to Bailey, these probably not fresh). [Doubtless cones and their parts vary a good deal in size, as in other species.]

Distribution: Queensland: Dryish (not arid) parts of Central Queensland (Planet Downs) in hilly country, doubtless in dry sclerophyll communities.

Specimens: See above, under Typification.

M. platyrachis is a poorly known but quite distinctive species. It is the most northerly member of section *Parazamia* and is readily recognized by its very broad, stiffly coriaceous pinnae and the broad rhachis which is flattened above and angular beneath. It does not show particular affinity with any one species, though clearly belonging to the section. Schuster (1932) grouped it with *M. fawcettii* because of its broad pinnae, but this is surely a case of convergence or parallel evolution in a single character; in other respects it does not much resemble *M. fawcettii*.

Bailey's statement that the petiole-bases lack woolly hairs needs confirmation; so does the collector's remark that the species does not cause "rickets" in stock.

8. *M. LUCIDA* L. Johnson, sp. nov.

Typification: Southern side of Ngungun, abt. 400 ft. alt., Glass House Mountains, Queensland, L. A. S. Johnson, 13.vi.1951 (NSW.40668), vegetative. HOLOTYPE. (Since no good material with cones was available, I have nominated as the type this specimen which I have seen living in the field.)

Caudex plerumque subterraneus, 10–20 (–30?) cm. diametro. Frondes in corona plerumque 2–15 (nonnunquam usque ad 40?), 80–110 cm. longae, petiolo (basi lanata expansa exclusa) 25–50 cm. longo; rhachis non torta, teretiuscula, ad pinnas infimas 3–7 mm. lata, supra saepissime rotundato-convexa (sed nonnunquam applanata vel proxime plus minusve medio subsulcata), sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa (in sicco), infra semper rotundato-convexa (haud angulata). Pinnae 50–100, patentes (seriebus duabus tamen non in eodem plano) et presertim versus apices suos decurvatae, plurimae angulo acuto prorsum directae sed infimae cum rhachi angulum rectum saepe formantes, basi tortae, plurimae arctae sed infimae saepe 1.5–3 cm. distantes, integrae, pleraeque plus minusve recurvato-falcatae (sed versus apices suos aliquando prorsum curvatae), lineares, eae longissimae 15–35 cm. longae, infimae haud vel vix abbreviatae, 7–11 mm. latae, infra nervis prominentibus 5–11 striatae, apicem pungentem versus sensim angustatae, basi conspicue pallida callosiuscula sed non rugosa constrictae, supra nitentes virides, pagina inferiore sola stomatibus instructa. Coni maturi non visi, probabiliter illis *M. spiralis* similes; sporophyllis masculis usque ad 4 cm. longis, spinis brevibus. Conos ad *M. lucidam* probabiliter pertinentes, F. M. Bailey (1902) sequens nunc describo: Axis coniger usque ad 30 cm. longus. Coni masculi cylindricei, 15 cm. longi (vel longiores), *ca.* 4 cm. diametro, [immaturi? L.J.] spinis sporophyllorum infimorum obsolescentibus eis sporophyllorum apicalium usque ad 1.2 cm. longis. Coni feminei 15–20 cm. longi, 7.5–9 cm. diametro, sporophyllorum parte terminali ad 4 cm. lata et 2 cm. alta, spinis 0.6–5 cm. longis longissimis versus apicem coni dispositis. Semina *ca.* 2.5 cm. longa, *ca.* 2 cm. crassa, integumentum parte exteriori rubella.

Description (English) and *discussion* of misapplied names: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: Queensland and New South Wales: Southern Coast region of Queensland from Wide Bay to Moreton District, and Clarence River (N. Coast of N.S.W.).

Specimens examined: QUEENSLAND: Southern side of Ngungun, abt. 400 ft. alt., Glass House Mountains, L. A. S. Johnson, 13.vi.1951 (NSW.40668); Mt. Coonowrin, Glass House Mountains, ca. 300 ft., C. E. Hubbard 4112, 21.ix.1930 (BRI); Taylor's Range, near Brisbane, C. T. White, i.1912 (BRI); Palmwoods, C. T. White, 6.v.1907 (BRI); Enoggera Creek, F. M. Bailey, 7.i.1875 (BRI); Enoggera, C. T. White, vi.1919 (NSW.40699); Cedar Creek, near Brisbane, C. T. White 1961, 6.v.1923 (NSW.40671); Brisbane, J. L. Boorman, iv.1899 (NSW.40670). NEW SOUTH WALES: Three miles E. of Dalmorton, L. A. S. Johnson and E. F. Constable, vi.1957 (NSW.43069). Living and preserved cultivated material also examined.

This is the species which has been wrongly known in Queensland, but not in New South Wales, as *M. spiralis* (see below, under *M. spiralis*). Though related to the true *M. spiralis*, it clearly constitutes a quite distinct series of populations, and is readily distinguished in cultivation as well as in the wild. *M. lucida* is characterized by its long slender petioles, not or scarcely twisted rhachis, and the curved, very glossy (whence the specific epithet) pinnae with sharply demarcated whitish but not very callous bases. Though it does not form dense stands it is widely spread in hilly country of the coast districts of southern Queensland, but in New South Wales only a single small stand is known as yet. It has been cultivated in the Sydney Botanic Gardens for many years and there maintains its distinctive appearance. For further treatment see the forthcoming *Flora of New South Wales*, part 1, where a probable hybrid population derived from *M. lucida* and the very different *M. moorei* is also discussed.

9. *M. SPIRALIS* (Salisb.) Miq., *Monogr. Cycad.* (1842), 36, as to basionym, excl. descr. and fig.; misapplied also by all later authors.

Basionym: *Zamia spiralis* Salisb., *Prodr. Stirp.* (1796), 401.

Typification: "Sponte nascentem juxta Port Jackson, locis umbrosis, legit Dav. Burton." As with most of Salisbury's types, no specimen of this appears to be extant. The correct application of the name must be established, if possible, from the description and other evidence. The description reads: "*Z. foliolis* 30-40 jugis, extrorsum falciformibus apice spinose 3-5 dentatis." "*Petioli paululum spirales sunt.*" Together with the information on locality, habitat and collector quoted above, which was interpolated by Salisbury between the first and second descriptive sentences, this is the whole of the original information. The first author to do more than repeat Salisbury's description was R. Brown, *Prodr.* (1810), 348, who applied the name *Z. spiralis* to a mixture of the species now treated as *M. communis* L. Johnson and *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn., but expressed doubt whether these were conspecific. Miquel (1842), in making the new combination under *Macrozamia*, described only plants of *M. riedlei* (from figures of F. Bauer), but quoted R. Brown for the Port Jackson locality (representing *M. communis*), and, of course, his combination is nomenclaturally based on Salisbury's name, of which he had not seen the type. However, he remarked that Brown's description and Bauer's figures did not agree with Salisbury's description of dentate-tipped leaflets, and added "Quam ob rem credere posset, speciem ab his auctoribus recensitam a vera *Zamia spirali* Salisb. differre", with further remarks illustrating this doubt and also the confusion with the garden plants known as *Encephalartos tridentatus* and *E. pungens* (these were based, as *Zamia tridentata* Willd. and *Z. pungens* Ait., on young cultivated plants of supposed South African origin and of quite uncertain identity. Juvenile plants of *Macrozamia* and *Encephalartos* cannot be determined to the species).

Later, in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368-370, Miquel made it clear that Bauer's plates (from which his earlier description of *M. spiralis* had been taken) in fact depicted his *Encephalartos fraseri* (= *Macrozamia riedlei*) and went on to treat as "*Encephalartos spiralis* [Salisb.] Lehm." a mixture of *M. communis* and *M. miquelii*.

In a similar treatment, but under *Macrozamia* (Miquel, 1868, p. 249; 1869, p. 52), he again expressed doubt regarding Salisbury's plant.

Other authors have applied the name *M./E. spiralis* in various ways, but most generally to *M. communis* (e.g. Mueller, *passim*, Bentham, and such N. S. Wales authors as C. Moore, Maiden and Betcher, Brough and Taylor. Full refs. in *Fl. N.S.W.*, Part 1, in press), though they often included one or more other species in their concept. Queensland botanists, following F. M. Bailey (esp. in *Queensl. Fl.*, 5 (1902), 1504), have used *M. spiralis* for the quite different species *M. lucida* L. Johnson.

Schuster, *Pflanzenr.*, IV, i (1932), 88, ignored priority and synonymized *M. spiralis** and *Z. spiralis** under his extraordinarily inclusive and confused concept of "*M. tridentata* (Willd.) Regel", based, of course, on the unidentifiable *Z. tridentata* Willd. (1806).

No one apart from Miquel (1842, 1869) seriously considered the original application of Salisbury's name. This we must now do.

Two species grow sufficiently close to Port Jackson to have been collected by David Burton before 1796. These are *M. communis* L. Johnson ("*M. spiralis*" of N.S.W. botanists) and the species hitherto known as *M. corallipes* Hook. f. While it would be convenient to retain the usage traditional in N. S. Wales (though not in Queensland), an honest application of the International Code of Botanical Nomenclature will not allow this.† In the absence of a material type, a name's application must be determined from the author's words and associated facts. Only when a reasonable degree of certainty is impossible does the Code permit a name to be dropped.

Juvenile fronds of all species have toothed pinnae, but Salisbury's description cannot apply to a wholly juvenile plant, since he mentions 30–40 pairs of pinnae. As in section *Macrozamia* generally, plants of *M. communis* old enough to have 60–80 pinnae in their fronds never have falciform pinnae spinosely 3–5-toothed at the apex, nor is the petiole (or rhachis) spiral (even "paululum"). On the other hand this description applies perfectly to many submature individuals of *M. corallipes* (sect. *Parazamia*). Consequently I have no doubt that Salisbury's plant was the latter species, for which the name *Macrozamia spiralis* (Salisb.) Miq., being nomenclaturally based on *Zamia spiralis* Salisb., must henceforth be used. The implications of this in the typification of the genus *Macrozamia* Miq. are discussed above (p. 87).

Synonymy, description and specimens: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press). The synonymy and history of misapplication are complex.

Distribution: New South Wales: North-east part of Central-western Slopes to Central Coast, from Dunedoo and the Goulburn River Valley to the lower Blue Mountains, Sydney and Waterfall districts, in dry or rarely semi-wet sclerophyll forest on poor, sandy or gravelly soils.

M. spiralis, as here defined, includes only those populations which would have been referred in the past to *M. corallipes* Hook. f. The plants are usually scattered and inconspicuous, with few fronds. The semi-juvenile fronds often seen, especially after fires, may be spirally twisted through 180° or more, and often have relatively few, widely-spaced pinnae with 2–several small teeth near their tips. Fronds of fully adult form, however, are little twisted and have more crowded pinnae usually simply mucronate at the tips. Occasionally *M. spiralis* grows close to stands of *M. communis*, but no hybrids are known. It overlaps *M. pauli-guilielmi* ssp. *plurinervia* in the Goulburn

* He cited both of these as "ex parte", which is meaningless for *Z. spiralis* Salisb., described from a single specimen. He nowhere indicated what he imagined the other part of this to be.

† Every responsible taxonomist, to say nothing of other botanists, must be disturbed by the number of such irritating corrections of ancient mistakes which the present rules of nomenclature make necessary, but the remedy cannot lie in individual botanists' refusal to obey the Code. In any case the nomenclature of *Macrozamia* has been so confused that a new point of departure should be welcome. I hope the present revision will satisfactorily supply this.

River Valley, but I have found no actual contact of populations. *M. spiralis* is replaced to the west by the closely allied *M. secunda*, and one or two inadequate specimens suggest that some interbreeding may occur, though I have seen no living intergrading plants.

It is important to remember that morphological studies (e.g. by Brough and Taylor, 1940) and chromosome counts under the name of *M. spiralis* apply in fact to *M. communis*.

10. *M. SECUNDA* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 120; Moore & Betche, *Handb. Fl. N.S.W.* (1893), 379, excl. var.?

Typification:* "Near Reedy Creek, east of Mudgee, where it was first found in 1858, but without fruit. Again found with only one old fruiting cone not far from Dubbo, by Rev. J. Milne Curran, in 1883. . . ." Only the former collection is extant, in herb. MEL, labelled: Reedy Creek, C. Moore, 1858. I therefore select it as LECTOTYPE.

Synonymy, description, specimens and discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Central-western Slopes and lower parts of Central Tablelands, from near Gilgandra to Grenfell and east to the Main Divide from Mudgee to Capertee, in dry sclerophyll forest on sandy or stony country.

M. secunda and *M. spiralis* may be regarded as a pair of vicarious species. The distinction seems sharp enough to justify specific rank. The concave petiole and stiff, usually narrow, second pinnae with very crowded nerves are characteristic. As in other species found in dry localities, the pinnae have much sclerenchymatous tissue and some glaucous bloom. Some hybridism with *M. heteromera* is evident where the species meet, as discussed by Johnson in Anderson, *l.c.* The name *M. secunda* var. *dichotoma* C. Moore & Betche, *Handb. Fl. N.S.W.* (1893), 379, probably applies to such a hybrid, but the type has been lost.

11. *M. HETEROMERA* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 122 (in part, as to lectotype and excl. var. *tenuifolia*); Moore & Betche, *Handb. Fl. N.S.W.* (1893), 380, in part.

Typification: "Among the Warrenbungle ranges and on the Castlereagh River country. Discovered in 1858; since collected near Rocky Glen, between Coonabarabran and Gunnedah." An old sheet dating from Moore's time, labelled "Warrumbungle Ranges", without collector's name, but probably collected by W. Carron or by Moore, is in NSW (40720). No specimen from Rocky Glen is extant. No original cone material has been preserved. I consider that NSW.40720 is the type sheet, but it bears a mixture, consisting of two pieces of frond belonging respectively to *M. heteromera* as here defined, and *M. diplomera* (F. Muell.) L. Johnson. Moore's description and comments covered both species, but specimens and cultivated plants later named by him chiefly belong to the former. Consequently I select as LECTOTYPE that part of NSW.40720 representing *M. heteromera* as herein defined. Both *M. diplomera* (see above, page 98) and *M. heteromera* are thus based on a mixture of the same two species, probably from duplicates from the same original collection, but selection of lectotypes in accordance with the emphasis of original descriptions or later usage allows both names to be used. The respective epithets ("two-parted", and "different-" or "variably-parted") are particularly appropriate in their present application. Moore's total concept was extended by two varieties (see below).

Synonymy:

M. heteromera var. *glauc*a C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 122.

M. spiralis (Salisb.) Miq. var. *heteromera* (C. Moore) Maid. & Betche, *Census* (1916), 9, in part.

* Moore made no reference to *M. spiralis* (Salisb.) Miq. var. ? *secunda* Benth., *Fl. Austral.*, 6 (1873), 252, which is therefore not the basionym but an earlier synonym in a different rank. Maiden and Betche, *Census* (1916) 9, later made the homonymous varietal combination based on *M. secunda* C. Moore.

M. heteromera var. *tenuifolia* Schuster* forma *harmsii* Schuster, *Pflanzenr.*, IV, i (1932), 96.

Description, specimens and further discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1, in press. A specimen from Warialda, per Glenfield Veterinary Research Station, ix.1958 (NSW.46090) was collected too late for citation in the Flora.

Distribution: New South Wales: North-western Slopes, in the eastern and southern Pilliga Scrub from Narrabri to Coonabarabran and the foothills of the Warrumbungle Mountains, with an apparent outlier to the north-east near Warialda and Howell, in dry sclerophyll forest on siliceous soils.

M. heteromera resembles *M. stenomera* in its dichotomously divided pinnae, but these differ in the consistent presence of stomata on the upper surface. The degree of division varies considerably, both individually and locally, but is on the average less than that in *M. stenomera*. In cultivation, Moore's var. *glauca* preserves its characters of rather broad, once-divided, glaucous pinnae, but plants can be found showing every gradation in these characters and the *glauca* forms do not seem to show sufficient geographic or ecological cohesion to be treated as a subspecies. Var. *tenuifolia* C. Moore is *M. stenomera* (q.v.). The distinction from and possible hybridism with *M. diplomera* are dealt with above (p. 99). Some apparent hybrids with the adjacent *M. secunda* and *M. stenomera* are discussed by Johnson in Anderson (*l.c.*). Probable hybrids with *M. pauli-guilielmi* ssp. *plurinervia* also occur, near Warialda.

Note added 11th June, 1959.—A recent collection, from 19 miles east of Coonabarabran on Gunnedah road, W. Morris, v. 1959 (NSW.47164), has the pinnae quite undivided, and in general appearance resembles *M. spiralis*, but has the amphistomatic pinnae and short petiole (11 cm.) of *M. heteromera*. The locality is within the range of the latter species and about fifty miles north of the nearest known *M. spiralis*. The intervening areas may possibly reveal some intergradation between the two species.

12. *M. STENOMERA* L. Johnson, sp. nov.

Typification: Above Coryah Gap at 4500 ft., Nandewar Mountains, New South Wales, L. A. S. Johnson and E. F. Constable, xi.1954 (NSW.32204), vegetative. HOLOTYPE.

Synonymy:†

M. heteromera C. Moore var. *tenuifolia* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 122 (not *M. tenuifolia* Hort. ex Miq. in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 55, in synon., nom. invalidum).

M. heteromera var. *tenuifolia* Schuster, *Pflanzenr.*, IV, i (1932), 96, nom. illegit., in part, excl. forma *harmsii* Schuster (this var. is described as new, not taken from C. Moore).

M. heteromera var. *dicranophylloides* Schuster, *l.c.*

Caudex plerumque subterraneus, ca. 8–15 cm. diametro. Frondes in corona paucae (ca. 2–10), 40–80 cm. longae, petiolo (basi lanata expansa exclusa) 7–15 cm. longo; rhachi plerumque praesertim apicem versus plus minusve torta (per 90°–360°) etiam plus minusve recurvata vel sinuosa, ad pinnas infimas (4–)5–9 mm. lata, supra proxime plana vel concaviuscula vel nonnunquam aliquantulum carinata sed versus apicem rotundato-convexa, sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa (in sicco), infra plerumque rotundato-convexa. Pinnae 70–120, patentes (seriebus duabus tamen non in eodem plano) vel suberectae, plus minusve prorsum directae, basi tortae, plurimae arctae sed infimae 1.3–4 cm. distantes, quam illis *M.*

* See under *M. stenomera*, below.

† Since the synonyms are all in varietal rank and of confused past application, and since they were based on a specimen rather than a population-concept, I prefer (as the I.C.B.N. permits) to use a new epithet and a new type in describing the taxon in specific rank. This epithet may be legitimately retained in the rank of subspecies, should further knowledge show this to be more appropriate.

heteromerae laxiores, omnes (apicalibus aliquando exceptis) plerumque versus bases suas in segmentis angusto-linearibus plus minusve divergentibus 1-4-plo (plerumque 2-3-plo) dichotome divisae, longissimae 10-20 cm. longae, infimae haud vel vix abbreviatae nunquam spiniformes; segmentis primariis 2-4 mm. latis (secundariis tertiariisque 1-3 mm.) infra nervis prominentibus 4-6 (2-5 in segmentis secundariis tertiariisque) striatis, (segmentis ultimis) in apicem mucronatum vel aliquando bidentatum augustatis vel ultime abruptiuscule rotundatis, (pinnae) basi flavescenti aurantiacave callosiuscula sed non rugosa constrictae (callo in sinu furcarum pinnarum vel obsoleto vel parvo), supra virides vix nitentes (sed quam illis *M. heteromerae* viridiores), infra non glaucae, pagina inferiore sola stomatibus instructa. Coni non certe noti, probabiliter illis *M. heteromerae* specierumque aliarum sectionis *Parazamia* similes.

Description (English), *specimens* and further *discussion*: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: North-western Slopes and Northern Tablelands outlier in and around the Nandewar Mountains, in dry sclerophyll forest, on stony but not highly siliceous soils.

In the past these plants have not been distinguished from *M. heteromera*, but they appear to constitute a reasonably distinct group of populations which I have accordingly treated as a distinct species. Definitely matched cones are unfortunately lacking, but within section *Parazamia* these organs differ little from species to species and, though their collection is much needed, they probably have little bearing on the independent status of *M. stenomera*. The specific epithet refers to the characteristically narrow segments of the pinnae which, together with their usually higher degree of division, lack of glaucousness and especially lack of stomata on the upper surface, distinguish the species from *M. heteromera*. Spiral twisting of the fronds is also generally more pronounced in *M. stenomera*. The species grows on less siliceous soils than *M. heteromera*.

Specimens of apparent hybrids of *M. stenomera* with the adjacent *M. heteromera* are discussed by Johnson in Anderson, *l.c.*

13. *M. PAULI-GUILIELMI** W. Hill & F. Muell. in F. Muell., *Fragm. Phytogr. Austral.*, 1 (1859), 86.

Typification: "In vicinia sinus Moreton Bay rara. W. Hill" (MEL, not seen but unmistakable from the description).

As here defined this species comprises three geographic races, the extreme forms of which differ from each other quite as much as do several other population-groups treated in this revision as full species. However, in the latter cases the populations are effectively discontinuous (though some limited local interbreeding may occur), whereas the contiguous races of *M. pauli-guilielmi* show no such discontinuity but rather a clinal transition. Each of the three races, however, has decided characteristics of its own (preserved in cultivation under identical conditions) and occupies an area of distinct ecological character. Furthermore, the geographically intermediate race is by no means simply intermediate morphologically between the two terminal races, but is more extreme in certain features than either of them. We may reasonably infer either (a) that three populations have been effectively isolated in the past (later Tertiary and/or Pleistocene?), during which time they became genotypically and phenotypically differentiated, but that subsequent breakdown of isolation has led to extensive gene interchange in broad transitional contact zones, or (b) that differentiation has taken place under strong (ecological) selection pressure within a widespread, at least originally more or less panmictic population of high potential genetic

* Unlike such epithets as "*fawcettii*", here corrected according to the I.C.B.N. to "*fawcettii*", the epithet *pauli-guilielmi* is a direct Latin genitive (from "Paulus Guilielmus", i.e. Paul Wilhelm, Prince of Wurtemberg) and the terminal "i" should not be doubled. The clumsy epithet has been spelt in several ways (see *Fl. N.S.W.*, pt. 1) but the original orthography "*Pauli Guilielmi*" is not to be altered except by decapitalization and hyphenation, as authorized by the I.C.B.N.

variability, but without development of a fully effective breeding-barrier (genetic or spatial) between the population segments. (There is no evidence of effective introgression from any other species, another theoretically possible cause of intergrading geographic races.) In either case the three segments at the present time cannot be regarded as specifically distinct in nature, but each of them has sufficient cohesion and ecological and morphological distinctness to be treated as a subspecies.*

Full descriptions, synonymy and discussions of *M. pauli-guilielmi* and its three subspecies, and citation of New South Wales collections, will be found in the forthcoming *Flora of N.S.W.*, part 1. Only the following key, enumeration and necessary Latin diagnosis are given here.

1. Petiole much flattened, 5-15 cm. long. Pinnae lax, numerous (140-200), pale at base. Broadest pinnae 2-4 (-5) mm. broad, 3-5-nerved (odd ones rarely to 7). S. Queensland a. ssp. *pauli-guilielmi*.
- 1.* Petiole flattened to rounded, 5-30 cm. long, if flattened and less than 15 cm. long then broadest pinnae 4-7 mm. broad and 6-10-nerved and usually pinkish at the base.
 2. Petiole 5-20 (-25) cm. long, 5-11 mm. broad at lowest pinnae. Pinnae concave to convex, the broadest 4-7 mm. broad (10-30 cm. long), 6-10-nerved, often rather stiff, pinkish at the base when living. Extreme S. Queensland and N. Tablelands, N.W. Slopes and Upper Hunter Valley (N.S.W.) b. ssp. *plurinervia*.
 - 2.* Petiole 20-30 cm. long, 4-8 mm. broad at lowest pinnae. Pinnae concave, the broadest 3-5 mm. broad (17-30 cm. long), 5-6 (-7)-nerved, lax, pale at the base. Manning River-Lake Macquarie (N.S.W.) c. ssp. *flexuosa*.

a. ssp. PAULI-GUILIELMI.

Typification: As for the species.

Synonymy, description and further discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: Queensland: Southern areas, somewhat away from the coast, in the Districts of Burnett, Darling Downs and western portion of Moreton.

In the southernmost part of this range the subspecies shows clinal intergradation with ssp. *plurinervia*, and such intergrades extend into the far north of New South Wales, for instance near Acacia Creek. Plants of this subspecies have been cultivated a good deal, both in Australia and abroad.

b. ssp. PLURINERVIA L. Johnson, subsp. nov.

Typification: "Reedy Creek" Station, near Bonshaw, New South Wales, J. Leader, iv.1956 (NSW.40958), male. HOLOTYPE. (Female cone pieces are also associated with this sheet.)

Frondes (30-)40-90 cm. longae, petiolo (5-20, rare 25 cm. longo, basi expansa exclusa) cum rhachi supra applanato vel plus minusve rotundato vel aliquanto sulcato, infra angulato rotundato, ad pinnas infimas 5-11 mm. lato, rhachi valde torta per revolutionibus una vel pluribus (vel in frondibus per brevibus plantarum depauperatarum per ca. 180°). Pinnae 50-150, arctae vel sparsiusculae, 10-30 cm. longae, rigidae vel laxiusculae, 4-7 mm. latae, 6-10-nerviae, aliquando plus minusve glaucae, basibus plerumque aurantiacis rubellisve, supra concavae vel planae etiam convexiusculae. Coni plerumque glauci, feminei saepissime ovoidei spinis plerisque sporophyllorum patentorectis.

Description (English), *specimens* and *further discussion*: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

* The category of *variety*, which many taxonomists still use to cover variations of diverse nature and of very unequal and frequently undefined biological and evolutionary significance (often not populations at all), usually conveys no more than that an author has chosen to name individuals differing in certain ways from the nomenclatural type, itself an object of no biological significance. *Subspecies*, on the contrary, though used by few taxonomic botanists in this country, has come in recent years to have a fairly definite meaning, at least to those whose interest is in evolutionary processes. This concept of an ecogeographic segment of a species has nothing in common with Schuster's (1932) virtually meaningless "subspecies" in *Macrozamia*.

Distribution: Queensland and New South Wales: Extreme south of Darling Downs District (Queensland) and lower parts of N. Tablelands, North-western Slopes and Upper Hunter Valley (New South Wales), in dry sclerophyll forest or woodland on stony slopes.

Intergrading forms to ssp. *pauli-guilielmi* are found in the extreme north of this region (see above). Hunter Valley populations show a clinal approach to ssp. *flexuosa*. Plants of the ssp. *plurinervia* series of populations have usually been referred to *M. flexuosa* or *M. pauli-guilielmi*. A full discussion is given in *Flora of N.S.W.*, part 1.

c. ssp. FLEXUOSA (C. Moore) L. Johnson, comb. et stat. nov.

Basionym: *Macrozamia flexuosa* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 121.

Typification: Moore says only “. . . grows plentifully between Raymond Terrace and Stroud”. There is only the following collection from Moore's time and this district in herb. NSW, and I consider it to be the HOLOTYPE: Limeburner's Creek, New South Wales, E. Betche, i.1883 (NSW.40951), vegetative, associated cones apparently lost.

Synonymy, specimens and further discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Southern part of North Coast and extreme north of Central Coast, from Bulladelah district to Lake Macquarie, in sclerophyll forest, on rather siliceous soils.

In some respects this race has more resemblance to the geographically remote ssp. *pauli-guilielmi* than to the contiguous ssp. *plurinervia*, although it differs markedly from ssp. *pauli-guilielmi* in the long, rounded petioles. As stated above, the southern populations referred to ssp. *plurinervia* exhibit clinal approach to ssp. *flexuosa*.

Submature plants of *M. spiralis* with rather twisted fronds have often been referred to *M. flexuosa*, but true *M. pauli-guilielmi* ssp. *flexuosa* is distinguished by its fronds being twisted through at least two complete revolutions and by its concave pinnae. No area of contact with *M. spiralis* is known, but the two may well meet in the Wollombi Creek-Macdonald River district.

14. *M. FAWCETTII* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 120.

Typification: “On high ground on the upper part of the Richmond; discovered by C. Fawcett, Esq., P.[olice] M.[agistrate], . . . Only freshly-gathered leaves and old male cones have as yet been seen.” This is in herb. NSW, labelled: Upper Richmond River, New South Wales, C. Fawcett (NSW.40653), vegetative with male cone fragments. HOLOTYPE.

Synonymy, description, specimens and discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Farther North Coast and ranges, from Richmond River to Coff's Harbour, in dry or semi-wet sclerophyll forest on siliceous soils.

M. fawcettii, though closely related to *M. pauli-guilielmi*, the other species with twisted fronds, is isolated geographically and is clearly distinguished from all forms of *M. pauli-guilielmi* by its very broad, usually several-toothed pinnae. Whatever might happen if it were brought into contact with *M. pauli-guilielmi*, it is at the present time effectively isolated as a species. It overlaps *M. lucida* in distribution, but no contact has been observed.

The nomenclatural confusions which ensued from Mueller's association of specimens of *M. fawcettii* with the very different *M. miquelii* are discussed under the latter species and in the forthcoming *Flora of N.S.W.*, part 1.

III. *BOWENIA* Hook. ex Hook. f.

Hook. ex Hook. f.* in *Bot. Mag.*, 89 (1863), sub t.5398; *ibid.*, 98 (1872), sub t.6008; F. Muell., *Fragm. Phytogr. Austral.*, 5 (1866), 171; A.DC., *Prodr.*, 16, pt. 2 (1868),

* J. D. Hooker described the genus and species, but adopted names proposed though not published by W. J. Hooker, whom he again cited as author in 1872. Later authors, confused by this, have cited either “Hook.” or “Hook. f.”. Under the I.C.B.N. the correct citation is as given above.

524; Miq. in *Arch. Néerl.*, 3 (1868), 254, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 57; Benth., *Fl. Austral.*, 6 (1873), 254; Regel in *Acta Hort. Petrop.*, 4 (1876), 316; F. M. Bail., *Queensl. Fl.*, 5 (1902), 1507; Chamberlain in *Bot. Gaz.*, 54 (1912), 419; Schuster, *Pflanzenr.*, IV, i (1932), 85.

Typification: *B. spectabilis* Hook. ex Hook. f. TYPE SPECIES (the sole original species).

Caudex subterranean, tuberous, naked, from the crown repeatedly producing one to numerous short, slender, more or less determinate frond- and cone-bearing branches (sometimes themselves branched); all parts more or less pilose or pubescent when young, but glabrescent (except petiole-bases, cataphylls and sporophylls) with maturity. Cataphylls short, flat, ovate-triangular, interspersed among the frond-bases. Fronds 1-several on each slender branch, long-petiolate; decompound by pinnate (or at the end sometimes dichotomous) branching of the rhachis, the lowest branches sometimes approximate to appear quasi-palmate; rhachis somewhat curved but not twisted, base of petiole somewhat thickened, more or less hairy. Pinnules several to fairly numerous on each secondary rhachis (which is itself terminally expanded into a pinnule), spreading, inserted marginally but towards the adaxial side of the rhachis and more or less decurrent, not articulate, simple, entire or lacerate or toothed, obliquely ovate or lanceolate, contracted and more or less petiolulate at the base, with close quasi-parallel dichotomous venation, stomata confined to the lower surface. Cones of both sexes shortly stalked or sessile, terminal on the short determinate branches, with the spirals (parastichies) of sporophylls so arranged that the sporophylls form vertical rows (orthostichies); sporophylls peltate with expanded oblate-hexagonal terminally-compressed spineless ends. Male sporophylls with a very short stipes, a broadly obovate-cuneate lamina the proximal half of which has two collateral fertile areas on the undersurface, and a more or less hexagonal end compressed to lie in the vertical plane. Female sporophylls with a fleshy stipes, the two ovules borne on the inward-facing margins ("inner surface") of the expanded hexagonal end. Seeds with a fleshy outer coat, inner seed-coat hard. Taproot tuberous, producing apogeotropic as well as normal roots.

Chromosome number: $x = 9$ (Darlington and Wylie, 1955).

Endemic in north-eastern Australia (Queensland), with two species, centred on the Cairns and Rockhampton districts respectively, in open spaces in rainforest and in eucalypt forest (Text-figure 4).

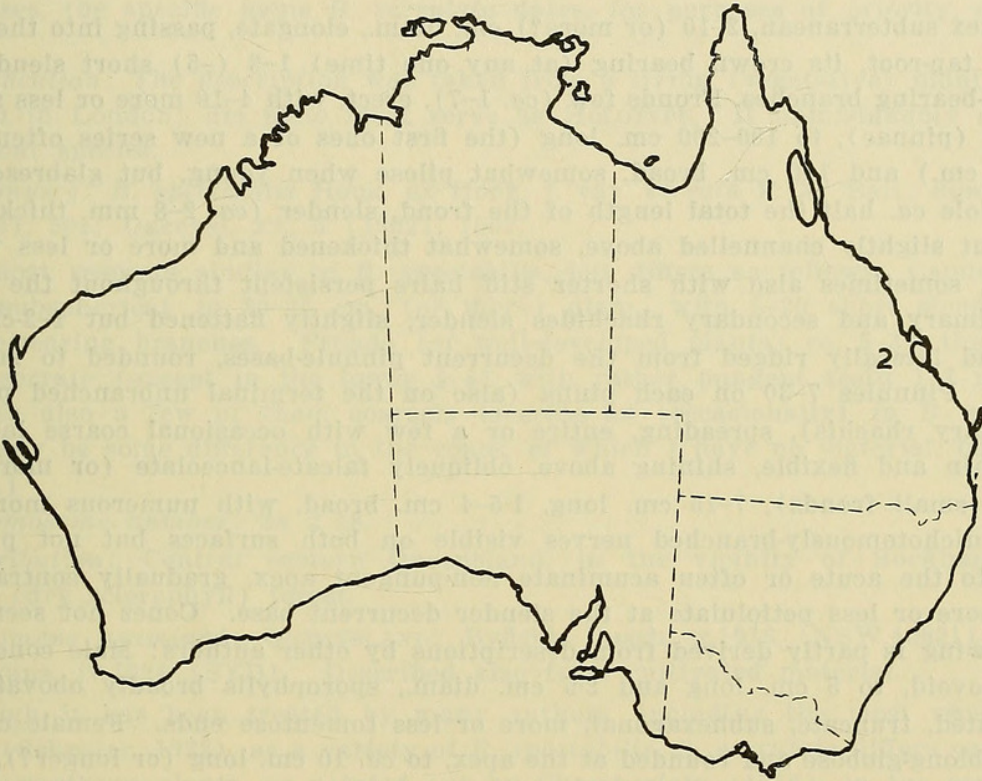
Bowenia is a very distinct genus among the Zamiaceae and has not been confused with any other. It possesses more advanced features than the other Australian genera and appears to be related to such American genera as *Zamia*, though some of the resemblances may be due to parallel evolution or convergence. Bentham's (1873) statement that it differs "from *Macrozamia* only in foliage and in the absence of the point to the cone-scales" is not true. The naked caudex, the system of short determinate branches, the terminal cone position, and the regular arrangement of the sporophylls are all very different from the characters of *Macrozamia*, to which *Bowenia* can be only very distantly related.

The decompound fronds distinguish *Bowenia* from all other cycad genera. In some species of *Macrozamia* and at times in *Stangeria* the pinnae are dichotomously divided, but the rhachis itself is undivided, so that the fronds may be described as simply pinnate with forking pinnae. In *Bowenia* the rhachis itself branches.

The fronds are usually described as bipinnate, but Schuster (1932) refers to the branching as dichotomous. In *Bowenia* the frond at maturity may certainly be justly called bipinnate; there is a median rhachis (continuous with the petiole) bearing on each side two to five lateral secondary rhachides which in turn bear the final segments (pinnules) on either side. (The lowest laterals may arise at almost the same point due to arrested intercalary growth during development, but the arrangement is still pinnate.) Beyond the most distal lateral rhachis the median rhachis itself bears pinnules directly (in some cases it forks apparently dichotomously, each branch then

bearing pinnules). However, there is little difference between primary and secondary rhachides and the junctions tend to be fork-like, though the median branch is the larger and, unlike the lateral, continues on to branch again.

In the light of conditions in other plant groups, this can be regarded as a stage in the evolutionary development of a pinnate (or a kind of monopodial) branching from dichotomy by the process of "overtopping" (*Übergipfelung*). This process must be understood, however, in a phylogenetic and not an ontogenetic sense. The frond is a *determinate* branch-system with the whole of its ramifications established in the bud stage, and later simply expanded by intercalary growth and cell enlargement. It is not strictly comparable with a normal branch-system enlarging by apical growth, though probably evolutionarily descended from such a system, as indeed all the fronds



Text-fig. 4.—Distribution of *Bowenia*: 1: *B. spectabilis*; 2: *B. serrulata*.

(leaves) of the various pteropsid lines may be. Similar conditions can be seen in various living and extinct fern groups and in the extinct Pteridosperms, and the beginnings of the trend are evident even in some of the ancient Psilophytales.

So far as the *Bowenia* frond is concerned, the significant point is that the ramifying process is less stereotyped than in such groups as Angiosperms or Conifers, so that more or less modified dichotomy can occur in various parts of the branching system. The same applies to other cycads, but usually less strikingly. In *Bowenia* the capacity for dichotomy and for overtopping has made possible a particular kind of frond specialization apparently suited to the environment. *Bowenia* is not a primitive cycad, and we need not assume that the decompound frond has been continuously retained during its evolutionary history. It may well be a secondary acquisition, which would remain possible so long as the mechanism for unstereotyped branching was not lost.

Both species have been cultivated to some extent as ornamentals, but are rather tender even in the Sydney climate.

Key to the Species.

1. Pinnules entire or a few of them irregularly lacerate. Caudex elongate, with 1-5 frond-bearing branches. N.E. Queensland 1. *B. spectabilis*.
- 1.* Pinnules regularly serrate. Caudex subspherical, with 5-20 frond-bearing branches. Central eastern Queensland 2. *B. serrulata*.

1. *B. SPECTABILIS* Hook. ex Hook. f. in *Bot. Mag.*, 89 (1863), sub t.5398; *ibid.*, 98 (1872), sub t.6008; F. Muell., *Fragm. Phytogr. Austral.*, 5 (1866), 171; A.DC., *Prodr.*, 16, pt. 2 (1868), 524; Miq. in *Arch. Néerl.*, 3 (1868), 254, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 57; Benth., *Fl. Austral.*, 6 (1873), 254; Regel in *Acta Hort. Petrop.*, 4 (1876), 316; F. M. Bail., *Queensl. Fl.*, 5 (1902), 1507, in part, excl. var.; Chamberlain in *Bot. Gaz.*, 54 (1912), 419; Domin in *Bibl. Bot.*, 20 (1915), 244; Schuster, *Pflanzenr.*, IV, i (1932), 85, in part, excl. var.

Typification: J. D. Hooker mentioned a specimen of *A. Cunningham's* from the Endeavour River, 1819, but stated that the description was made from a living plant with dried leaves and a male cone, from Rockingham Bay, sent by W. Hill to Kew in 1863. This material is thus the HOLOTYPE and is represented by *Bot. Mag.*, t.5398.

Caudex subterranean, 2-10 (or more?) cm. diam., elongate, passing into the elongate tuberous tap-root, its crown bearing (at any one time) 1-3 (-5) short slender frond- and cone-bearing branches. Fronds few (*ca.* 1-7), erect, with 4-10 more or less spreading branches (pinnae), to 100-200 cm. long (the first ones of a new series often smaller, from 40 cm.) and 100 cm. broad, somewhat pilose when young, but glabrescent with age; petiole *ca.* half the total length of the frond, slender (*ca.* 2-8 mm. thick), almost terete, but slightly channelled above, somewhat thickened and more or less villous at the base, sometimes also with shorter stiff hairs persistent throughout the proximal half; primary and secondary rhachides slender, slightly flattened but 1-2-channelled above and laterally ridged from the decurrent pinnule-bases, rounded to subangular beneath. Pinnules 7-30 on each pinna (also on the terminal unbranched portion of the primary rhachis), spreading, entire or a few with occasional coarse lacerations, rather thin and flexible, shining above, obliquely falcate-lanceolate (or more or less ovate on small fronds), 7-15 cm. long, 1.5-4 cm. broad, with numerous more or less parallel dichotomously-branched nerves visible on both surfaces but not prominent, tapered to the acute or often acuminate non-pungent apex, gradually contracted and finally more or less petiolulate at the slender decurrent base. Cones not seen mature, the following is partly derived from descriptions by other authors: Male cones shortly stalked, ovoid, to 5 cm. long and 2.5 cm. diam., sporophylls broadly obovate-cuneate with dilated, truncate, subhexagonal, more or less tomentose ends. Female cones sessile, oblong-globose and rounded at the apex, to *ca.* 10 cm. long (or longer?), 7-10 cm. diam.; sporophylls about 8-stichous, the expanded ends oblate-hexagonal (in the vertical plane), 3-5.5 cm. broad, *ca.* 1.5 cm. high, terminally more or less truncate-pyramidal with a central depression (said to be more or less tomentose but glabrescent in the immature example seen). Seeds to 3.2 cm. long, 1.8 cm. thick.

Chromosome number: $2n = 18$.

Distribution: Queensland: North-eastern coast and ranges from Cooktown to Rockingham Bay district, in the more open situations in and around rainforest.

Specimens examined: QUEENSLAND: Whyanbeel Creek, 7 miles north of Mossman, M. Tindale, 15.vii.1957 (NSW.42280); Cape Tribulation, W. W. Mason, i.1947 (NSW.40615); Yarrabah Mission, Trinity Bay near Cairns, P. R. Messmer, 16.vii.1952 (NSW.30535); Jordan's Creek, P. R. Messmer, 11.viii.1954 (NSW.30537); Babinda, W. W. Watts, vii.1913 (NSW.40618); Atherton district, per H. L. White, 1912 (NSW.40620); Malanda, C. T. White, i.1918 (NSW.40617); Geraldton, Johnstone River, S. W. Jackson, 1908 (NSW.40619); Rockingham Bay (NSW.40616).

The concept of *B. spectabilis* has been extended by some authors, including Schuster (1932), to include *B. serrulata*, but the latter differs in a number of characters and the two population-groups seem quite isolated (see below, under *B. serrulata*). According to Chamberlain (1912), *B. spectabilis* does not form dense stands like those of *B. serrulata*, and each plant produces fewer fronds. The species has been cultivated to some extent.

2. *B. serrulata* (W. Bull) Chamberlain in *Bot. Gaz.*, 54 (1912), 419.

Basionym: *B. spectabilis* Hook. ex Hook. f. [var.] *serrulata* W. Bull, *Catal.* (1878), 4, t.5.* [Chamberlain gave the citation "(André) Chamberlain, n. comb." and referred to *B. spectabilis* Hook. f. var. *serrulata* André, *Ill. Hort.*, 26 (1879), 184, t.366. However, André did not publish this as a new variety of his own; he cited it as "Hort. Angl." and his plate is identical with Bull's original, though he made no explicit reference to Bull. The same plate, with similar descriptions, and references to Bull's *Catalogue*, was reproduced also by T. Moore in *Florist and Pomologist* (July, 1878), 107, as "*Bowenia spectabilis serrulata*", as well as in *Gartenflora*, 27 (1878), 314, and in *Ill. Gartenz. Stuttgart*, 23 (1879), 99, t.15, as *B. spectabilis* var. *serrulata*. Since Bull's was the original valid publication of the variety from which the others were derived, it should be cited as the basionym. Despite the custom of citing the author of the variety in parentheses, the specific name *B. serrulata* dates, for purposes of priority, only from 1912.]

Typification: The description was taken from a living (vegetative) plant in Bull's collection in London; his plate must serve as HOLOTYPE. It unmistakably represents the present species.

Synonymy: *B. spectabilis* Hook. ex Hook. f. var. *serrata* F. M. Bail., *Syn. Queensl. Fl.* (1883), 501; *Queensl. Fl.*, 5 (1902), 1507.

In most respects similar to *B. spectabilis*, but differs as follows: Caudex subterranean, subspherical, to 20–25 cm. (or more) diam., with 5–20 short slender frond-bearing branches. Fronds (of well-developed plants) ca. 5–30, the pinnules sharply serrate (except in the lower $\frac{1}{4}$ – $\frac{1}{2}$) with rather pungent teeth 1–3 mm. long, sometimes also a few of them coarsely lacerate as (occasionally) in *B. spectabilis*. [There may be some difference in the cones, of which I have no material, but none is recorded.]

Chromosome number: $2n = 18$.

Distribution: Central eastern Queensland, in the vicinity of Rockhampton, in eucalypt (dry sclerophyll) forest.

Specimens examined: QUEENSLAND: Byfield, Busch, x.1916 (NSW.40621); Byfield, O. D. Evans, iv.1924 (SYD). Described also from cultivated material.

Though it has been treated by many authors, including the most recent monographer (Schuster, 1932), as a variety of *B. spectabilis*, *B. serrulata* differs consistently from the northern plants, as pointed out by Chamberlain (1912), in the serration of the pinnules (a condition quite distinct from the coarse laceration found in both species), the subspherical shape of the caudex and the more numerous frond-bearing branches. These characteristics are maintained in cultivation, given suitable conditions for full development (in pots, *B. serrulata* often grows poorly and produces few fronds). Furthermore, the populations are quite isolated in nature and occupy rather different ecological niches (unlike *B. spectabilis*, *B. serrulata* grows in rather dry sclerophyll forest and forms fairly dense and extensive stands). They thus agree with any reasonable concept of specific distinction, since each is now evolutionarily independent and differs materially from the other.

B. serrulata is sometimes grown in gardens and conservatories for its ornamental fronds.

INDEX OF NAMES.

Names accepted in this revision (Part II only) appear in SMALL CAPITALS, with reference to their numbers in the formal section (I, 1, etc.). Valid synonyms, in *italic*, are referred to their correct nomenclatural position (in roman) as determined by the identity of their types. Invalid *nomina nuda* and misapplications are not cited (for Schuster's misapplications see Table 1, p. 74). All epithets are decapitalized and terminations in "-i/-ii" are given in the

* I am indebted to Dr. R. Melville of the Royal Botanic Gardens, Kew, for copies of the descriptions in Bull's *Catalogue* and the Stuttgart *Gartenzeitung*. In *Index Londinensis* the entry in the latter publication is wrongly given as "*B. serrata*". In fact, it appeared as "*Bowenia spectabilis*, Hooker, var. *serrulata*". Previous to Bull's valid publication the trinomial appeared in *Gard. Chron.*, n.s., 8 (1877), 310, as a *nomen nudum*.

correct form as authorized by the I.C.B.N. (1956), irrespective of the original. Other misspellings are given in quotation marks.

BOWENIA Hook. ex Hook. f. (1863). III.

BOWENIA SERRULATA (W. Bull) Chamberlain (1912). III, 2.

B. SPECTABILIS Hook. ex Hook. f. (1863). III, 1.

B. spectabilis var. *serrata* F. M. Bail. (1883) = *B. serrulata*.

B. spectabilis [var.] *serrulata* W. Bull (1878) = *B. serrulata*.

Catakidozamia W. Hill (1865) = *Lepidozamia*.

Catakidozamia hopei W. Hill (1865) = *Lepidozamia hopei*.

Cycas riedlei Fisch. ex Gaudich. (1826) = *Macrozamia riedlei*.

Encephalartos sect. *Lepidozamia* (Regel) Miq. (1863) = *Lepidozamia*.

Encephalartos sect. *Macrozamia* Miq. (1863) = *Macrozamia* sect. *Macrozamia*.

Encephalartos sect. *Parazamia* Miq. (1863) = *Macrozamia* sect. *Parazamia*.

Encephalartos denisonii (C. Moore and F. Muell.) F. Muell (1859) = *Lepidozamia peroffskyana*.

E. douglasii F. Muell. (1883) = *Macrozamia miquelii*.

E. dyeri F. Muell. (1885) = *Macrozamia riedlei*.

E. fraseri (Miq.) Miq. (1863) = *Macrozamia riedlei*.

E. macdonnellii F. Muell. ex Miq. (1863), (*sphalm.* "*macdonelli*") = *Macrozamia macdonnellii*.

E. miquelii F. Muell. (1862) = *Macrozamia miquelii*.

E. moorei (F. Muell.) F. Muell. (August, 1881) = *Macrozamia moorei*.

E. oldfieldii Miq. (1863) = *Macrozamia riedlei*.

E. pauli-guilielmi (W. Hill and F. Muell.) F. Muell. (1859) = *Macrozamia pauli-guilielmi* ssp. *pauli-guilielmi*.

E. preissii (Lehm.) F. Muell. (1859) = *Macrozamia riedlei*.

E. spiralis (Salisb.) Lehm. (1834) = *Macrozamia spiralis*.

E. spiralis var. *diplomera* F. Muell. (1866) = *Macrozamia diplomera*.

E. spiralis var. *major* Miq. (1863) = *Macrozamia miquelii*.

LEPIDOZAMIA Regel (1857). I.

Lepidozamia denisonii (C. Moore and F. Muell.) Regel (1875) = *L. peroffskyana*.

LEPIDOZAMIA HOPEI Regel (1876). I, 1.

[*L. HOPEITES* (Cookson) L. Johnson (1959), *sp. foss.* See under I, 1.]

L. PEROFFSKYANA Regel (1857). I, 2.

MACROZAMIA Miq. (1842). II.

Macrozamia sect. *Genuinae* Miq. (1868), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Lepidozamia* (Regel) Miq. (1868) = *Lepidozamia*.

MACROZAMIA sect. MACROZAMIA. II, i.

Macrozamia sect. *Monoocidentales* Schuster (1932), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Monoorientales* Schuster (1932) *nom. illegit.* = *Lepidozamia*.

MACROZAMIA sect. PARAZAMIA (Miq.) Miq. (1868). II, ii.

Macrozamia sect. *Polyorientales* Schuster (1932), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Polyorientales* subsect. *Acutae* Schuster (1932) = *M.* sect. *Parazamia*.

Macrozamia sect. *Polyorientales* subsect. *Attenuatae* Schuster (1932), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Polyorientales* subsect. *Curvatae* Schuster (1932) = *M.* sect. *Parazamia*.

MACROZAMIA COMMUNIS L. Johnson (1959). II, 5.

M. corallipes Hook. f. (1872) = *M. spiralis*.

M. cylindrica C. Moore (1884) = *M. miquelii*.

M. denisonii C. Moore and F. Muell. (1858) = *Lepidozamia peroffskyana*.

M. denisonii var. *hopei* (W. Hill) Schuster (1932) = *Lepidozamia hopei*.

M. DIPLOMERA (F. Muell.) L. Johnson (1959). II, 6.

M. douglasii W. Hill ex F. M. Bail. (1883) = *M. miquelii*.

M. dyeri (F. Muell.) C. A. Gardn. (1930) = *M. riedlei*.

M. FAWCETTII C. Moore (1884). II, 14.

M. flexuosa C. Moore (1884) = *M. pauli-guilielmi* ssp. *flexuosa*.

M. fraseri Miq. (1842) = *M. riedlei*.

M. HETEROMERA C. Moore (1884). II, 11.

M. heteromera var. *dicranophylloides* Schuster (1932) = *M. stenomera*.

M. heteromera var. *glauca* C. Moore (1884) = *M. heteromera*.

M. heteromera var. *tenuifolia* C. Moore (1884) = *M. stenomera*.

M. heteromera var. *tenuifolia* Schuster (1932), *nom. illegit.* = *M. stenomera*.

M. heteromera var. *tenuifolia* f. *harmsii* Schuster (1932) = *M. heteromera*.

M. hopei W. Hill ex F. M. Bail. (1886) = *Lepidozamia hopei*.

[*M. hopeites* Cookson (1953), *sp. foss.* = *Lepidozamia hopeites*.]

M. LUCIDA L. Johnson (1959). II, 8.

M. MACDONNELLII (F. Muell. ex Miq.) A.DC. (1868). II, 3.

M. mackenzii Hort. ex Mast. (1877) = *M. miquelii*.

M. macleayi Miq. (1868) = *M. miquelii*.

M. MIQUELII (F. Muell.) A.DC. (1868). II, 4.

M. MOOREI F. Muell. (March, 1881). II, 1.

- M. mountperriensis* F. M. Bail. (1886) = *M. miquelii*.
M. oldfieldii (Miq.) A.DC. (1868) = *M. riedlei*.
M. PAULI-GUILIELMI W. Hill and F. Muell. (1859). II, 13.
M. PAULI-GUILIELMI ssp. *FLEXUOSA* (C. Moore) L. Johnson (1959). II, 13c.
M. PAULI-GUILIELMI ssp. *PAULI-GUILIELMI*. II, 13a.
M. PAULI-GUILIELMI ssp. *PLURINERVIA* L. Johnson (1959). II, 13b.
M. peroffskyana (Regel) Miq. (1868) = *Lepidozamia peroffskyana*.
M. PLATYRACHIS F. M. Bail. (1898). II, 7.
M. plumosa Hort. ex Mast. (May, 1875) = (probably) *M. pauli-guilielmi* ssp. *pauli-guilielmi*.
M. plumosa Hort. ex auct. anon. (June, 1875) = *M. pauli-guilielmi* ssp. *pauli-guilielmi*.
M. preissii Lehm. (1844) = *M. riedlei*.
M. preissii ssp. *dyeri* (F. Muell.) Schuster (1932) = *M. riedlei*.
M. RIEDLEI (Fisch. ex Gaudich.) C. A. Gardn. (1930), ("reidlei"). II, 2.
M. SECUNDA C. Moore (1884). II, 10.
M. secunda var. *dichotoma* C. Moore and Betcher (1893) = (probably) *M. heteromera* × *M. secunda*.
M. SPIRALIS (Salisb.) Miq. (1842). II, 9.
M. spiralis var. *?corallipes* (Hook. f.) Benth. (1873) = *M. spiralis*.
M. spiralis var. *?cylindracea* Benth. (1873) = *M. pauli-guilielmi* (ssp.?).
M. spiralis var. *cylindrica* Regel (1876), *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *cylindrica* (C. Moore) Maid. and Betcher (1916), *nom. illegit.* = *M. miquelii*.
M. spiralis var. *diplomera* (F. Muell.) A.DC. (1868) = *M. diplomera*.
M. spiralis var. *?diplomera* F. Muell. ex Benth. (1873) = *M. diplomera*.
M. spiralis var. *eximia* Regel (1876) *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *fawcettii* (C. Moore) Maid. and Betcher (1916) = *M. fawcettii*.
M. spiralis var. *flexuosa* (C. Moore) Maid. and Betcher (1916) = *M. pauli-guilielmi* ssp. *flexuosa*.
M. spiralis var. *fraseri* Regel (1876), *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *heteromera* (C. Moore) Maid. and Betcher (1916) = *M. heteromera*.
M. spiralis var. *hillii* Regel (1876), *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *?secunda* Benth. (1873) = *M. secunda*.
M. spiralis var. *secunda* (C. Moore) Maid. and Betcher (1916) = *M. secunda*.
M. STENOMERA L. Johnson (1959). II, 12.
[*M. tridentata* (Willd.) Regel. See list of excluded and dubious names, below.]
M. tridentata ssp. *cylindrica* (C. Moore) Schuster (1932) = *M. miquelii*.
M. tridentata ssp. *cylindrica* var. *corallipes* (Hook. f.) Schuster (1932) = *M. spiralis*.
M. tridentata ssp. *cylindrica* var. *corallipes* f. *dielsii* Schuster (1932) = *M. spiralis*.
M. tridentata ssp. *cylindrica* var. *corallipes* f. *vavilovii* Schuster (1932), *nom. dub.* = *M. miquelii* or *M. communis*.
M. tridentata ssp. *cylindrica* var. *corallipes* f. *wallsendensis* Schuster (1932) = *M. communis*.
[*M. tridentata* ssp. *cylindrica* var. *pungens* (Ait.) Schuster (1932), *nom. dub.* (quoad typ.) = *Encephalartos* sp. ?]
M. tridentata ssp. *cylindrica* var. *pungens* f. *diplomera* (F. Muell.) Schuster (1932) = *M. diplomera*.
M. tridentata ssp. *cylindrica* var. *pungens* f. *hillii* Schuster (1932), *nom. dub.* = *M. miquelii* or *M. communis*.
M. tridentata ssp. *cylindrica* var. *secunda* (C. Moore) Schuster (1932) = *M. secunda*.
M. tridentata ssp. *mountperriensis* (F. M. Bail.) Schuster (1932), ("mountperriensis"), = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *douglasii* (F. Muell.) Schuster (1932) = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *mackenzii* (Hort. ex Mast.) Schuster (1932) = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *miquelii* (F. Muell.) Schuster (1932), *nom. illegit.* = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *miquelii* f. *milkaui* Schuster (1932), *nom. illegit.* = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *miquelii* f. *oblongifolia* (Regel) Schuster (1932) = *M. miquelii*.
M. tridentata var. *oblongifolia* Regel (1876) = *M. miquelii*.
Zamia spiralis Salisb. (1796) = *Macrozamia spiralis*.

EXCLUDED AND DUBIOUS NAMES.

This list includes only names which are wholly dubious, possibly not being based on Australian plants at all. Names which can be placed to within a couple of species are included in the Index, above.

- Encephalartos pungens* (Ait.) Lehm., *nom. dub.* = *Encephalartos* sp.? See under II, 5 and 9.
E. tridentata (Willd.) Lehm., *nom. dub.* = *Macrozamia* or *Encephalartos* sp.? (juvenile). See under II, 4, 5 and 9.
Macrozamia tridentata (Willd.) Regel, *nom. dub.* (quoad basionym.) = *Macrozamia* or *Encephalartos* sp. (juvenile). See under II, 4, 5 and 9.

- M. tridentata* ssp. *cylindrica* var. *pungens* (Ait.) Schuster, nom. dub. (quoad basionym.) = *Encephalartos* sp.? See under II, 5 and 9.
Zamia pallida Salisb., nom. dub. = *Encephalartos* or *Macrozamia* sp.? (juvenile). See under II, 5.
Z. pungens Ait., nom. dub. = *Encephalartos* sp.? See under II, 5 and 9.
Z. tridentata Willd., nom. dub. = *Macrozamia* or *Encephalartos* sp.? (juvenile). See under II, 4, 5 and 9.

Acknowledgements.

My thanks are due to Mr. R. H. Anderson, Chief Botanist and Curator, National Herbarium, Royal Botanic Gardens, Sydney, for making this work possible, and to the past Directors of the Melbourne and Brisbane Herbaria for the opportunity to examine several specimens. Dr. Joyce Vickery has given generously of her time and experience in the discussion of some of the difficult matters of typification and nomenclature which abound in *Macrozamia*; responsibility for the decisions, however, rests with myself. Dr. R. Melville of Kew has been most helpful in sending me copies of obscure references. Miss D. P. Ragg, Librarian at the National Herbarium, has shown great patience and enterprise in obtaining many rare publications.

Dr. Isabel Cookson freely discussed with me her work on frond anatomy in *Macrozamia* and *Lepidozamia*, and some of her unpublished findings, though not specifically mentioned in this revision, have helped to influence and confirm my judgements. But for Mr. G. Chippendale, Botanist, Animal Industry Division, Alice Springs, I should not have been able to examine *Macrozamia macdonnellii* in the field. Mr. N. Forde had earlier sent me excellent material and photographs of this species. Finally, I thank all of my colleagues at the National Herbarium for co-operation in various ways, and particularly Mr. E. F. Constable, Official Collector, for his efforts and companionship in the field, especially in the re-discovery of the magnificent *M. moorei* in New South Wales.

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