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THE SO-CALLED "MEGASPOROPHYLL" OF CYCAS — A MORPHOLOGICAL MISCONCEPTION. ITS BEARING ON THE PHYLOGENY AND THE CLASSIFICATION OF THE CYCADOPHYTA

A. D. J. MEEUSE

(*Hugo de Vries Laboratory, University of Amsterdam*)

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ABSTRACT

1. The morphological interpretation of the female reproductive organ of *Cycas*, traditionally a primitive form of a fertile leaf homologue or "megasporophyll", is reconsidered in the light of typological and phylogenetic evidence.
2. The inquiry into the nature of this so-called "megasporophyll" emphasizes its aberrant structure and in spite of the incongruity in appearance requires its homology with the female "strobilus" of all other Cycadales.
3. The homology of the "megasporophyll" with a cycadalean "strobilus" cannot be accepted without certain restrictions, because it is not subtended by a bract.
4. The paradoxal situation can only be explained by the pseudo-phyllosporous nature of the "megasporophyll" produced by the merging of a "strobilus" and its bract, the resulting structure, by exhibiting a mixture of the characteristics of both the axial ovuliferous organ and the foliar bract, assuming an unusual and typologically incongruous shape reminiscent of a teratological case.
5. The re-assessment of the phylogenetic and taxonomic relationships between the genus *Cycas* and the other *Cycadales* indicates that this aberrant form is advanced rather than primitive in respect of its near allies.
6. The alternative interpretation of the reproductive organs of the *Cycadales* has been discussed in connection with its bearing on the morphology and the phylogeny of other cycadopsid groups, and the existence since early Mesozoic times of an independent hologeny leading to the living cycads is postulated.
7. The diversity of the recent *Cycadales* most probably reflects an early separation of their ancient lineage into several minor lines of descent.

STATEMENT OF THE PROBLEM

By the turn of the century, especially after Čelakovsky's spirited defense of the "*Blattbuertigkeit der Eichen*", the previous controversy regarding the axial or foliar origin of the ovules seemed to be definitely settled in favour of the traditional "sporophyll" concept. The phytomorphologists had also found, in the form of the female reproductive organ of *Cycas*, a structure that answered admirably to their idea of a primitive "megasporophyll". Up to this day it is still the text book example of the postulated ovuliferous "sporophyll", defined as a leaf homologue, or a leaf metamorphosis, bearing marginal ovules. It also figures prominently in many leading manuals in a series of illustrations suggesting the derivation of the lateral scale-like appendages of the female reproductive structures, commonly referred to as "strobili" or "cones", of the other *Cycadales* from a "megasporophyll" of the *Cycas* type (see Fig. 1). Such a derivation presupposes the homology of the

ovule-bearing portions of the "megastrobili" with the entire female reproductive organ of *Cycas*, which reasoning was, as far as I can ascertain, never seriously challenged except by BREMEKAMP (1962, p. 129–130). I believe that Bremekamp hits the nail on the head when he states that the ovuliferous organ of *Cycas* is strongly reminiscent of a teratological case, because, I presume, it is not conformable to the

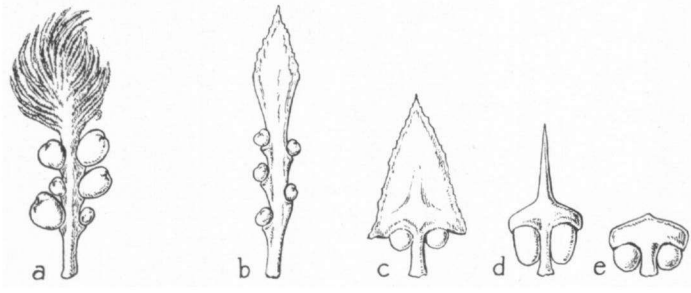

Fig. 1. Conventional typological derivation of the "cone-scale" of *Zamia* (e) from a so-called "megasporophyll" of *Cycas revoluta* (a) through *Cycas media* (b), *Dioon* (c) and *Macrozamia* (d).

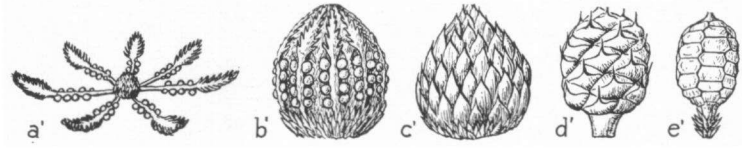

Fig. 2. Conventional typological derivation of a cycadaceous "cone" of *Zamia* (e') from a "cycle" (whorl) of individual "megasporophylls" of *Cycas revoluta* (a') through the suberect arrangement in *C. media* (b') and the "cones" of *Dioon* (c') and *Macrozamia* (d').

morphology of the male and female reproductive structures of all other cycads including the male specimens of *Cycas*. The purpose of this paper is to demonstrate that the conventional identification of the female reproductive organ of *Cycas* with a "megasporophyll" (defined as a leaf homologue bearing marginal ovules) is fallacious and to discuss the phylogenetic consequences of an alternative interpretation.

MORPHOLOGICAL AND PHYLOGENETIC IMPLICATIONS OF THE CONVENTIONAL INTERPRETATION

According to the "classical" criteria, the "megasporophyll" of *Cycas*, as a leaf homologue, is a lateral derivative of the main stem on which it is borne, whereas the "microsporophylls" of the male cone of *Cycas* and the "mega-" as well as the "microsporophylls" in all other genera of the *Cycadales* are lateral organs in respect of the axis of the 'strobili'. The 'megasporophylls' of *Cycas* are, accordingly, borne on an axis of the first order, but the cones or strobili being inserted in the axil of a leaf, their central axis is a cauline organ of the *second* order.

The phylogenetic relation between the ovuliferous organ of *Cycas* and the female cycadalean strobili is traditionally explained in the following manner (see also Fig. 2): a number of solitary "megasporophyls" borne as in *Cycas*, *i.e.*, helically arranged in pseudo-whorls on the main stem, is supposed to have occurred in the ancestral forms of the other genera. These megasporophylls are thought to have become more densely packed whilst the supporting portion of the stem became thinner and morphologically distinguishable from the stem of which it is an elongation, the sporophylls and their supporting axis thus assuming the shape of a distinct strobilus. The phylogenetic history of the male cones has never been discussed in a similar way as far as I am aware, but in view of the similarity in morphology between male and female cones I am entitled to presume that what is sauce for the goose is sauce for the gander, so that, on the analogy of the current explanation of the origin of the female strobilus, the male strobilus could not very well have developed in any other way but from scattered "sporophylls" borne in pseudo-whorls, exactly like their female counterparts. However, if the condition found in the female *Cycas* is the starting point of the evolution of the strobilus, the suggested derivation could only result in a *terminal* cone in the female as well as in the male specimens, the strobilus axis being simply an extension of the main stem, so that the actual *lateral* position of the cones requires some miraculous "shift" of the strobili from a terminal to a lateral position.

Another requisite of the postulated homology of the "megasporophyll" of *Cycas* with the ovuliferous appendages of the female strobili is the oligomerisation of the number of ovules from more than two in several species of *Cycas* to two. The palaeobotanic evidence favours a descent of the *Cycadales* from *Nilssoniales* which bore female reproductive structures of a type, described as *Beania*, with biovulate appendages (see Fig. 3). Leaving the morphological interpretation of this nilssonialean reproductive organ out of consideration for the moment, one must admit that it is a perfect prototype for all female strobili of the

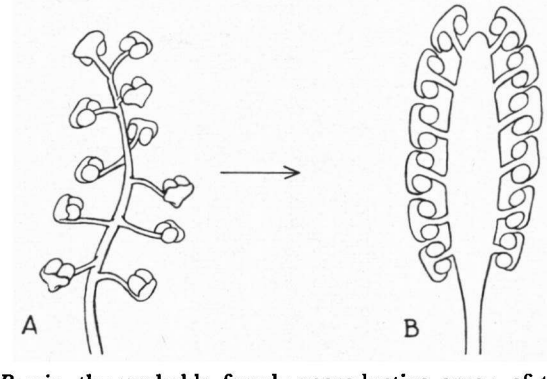

Fig. 3. A: *Beania*, the probable female reproductive organ of the Nilssoniales. B: *Microzamites*, a possible Cretaceous intermediate between Nilssoniales and Zamiaceae, female "cone" in semidiagrammatic longitudinal section.

recent cycads. However, this does not support a derivation of the *Cycadales* from an archetype resembling *Cycas* in the morphology of the reproductive organs, unless one accepts such a descent *via* a *Beania*-like form which requires a considerable antiquity of the *Cycas* type of plant. Although several workers such as ARNOLD (1953) have pointed out that the *Cycadales* as an old and rather varied group are rather unsurveyable as regards the relative degree of advancement of the individual taxa, there is no reason to consider *Cycas* to be a very primitive member. SCHUSTER (1931) and GAUSSEN (1944) even concluded, in spite of the conventional "primitive" condition of the female reproductive organ in *Cycas*, that this genus shows signs of being one of the most derived forms. If we accept *Cycas* as a fairly young taxon its so-called megasporophyll, if it is indeed primitive, appears to be incongruous with the advanced condition of the other characters of this genus and the assumption that the strobiloid female reproductive organ of the *Beania* type originated from a prototype represented by the "*megasporophyll*" of *Cycas* does not appeal to me. The female strobili of all other genera with their biovulate appendages and the male strobili of all genera including *Cycas* are evidently homologous with the strobiloid reproductive structures of the *Nilssoniales* and they can, accordingly, not very well have been directly derived from the ovuliferous organ of the type found in *Cycas* (as represented in Figs. 1 and 2). It is difficult to see how and where *Cycas* comes into the picture, especially if one has to account for the fact that the "megasporophyll" in several species of *Cycas* bears more than two ovules.

In spite of the diversity of the living cycads, they have so many morphological, anatomical and biological characters in common that there is a general consensus of opinion regarding their status as a "natural" group and, but for the aberrant morphology of its female reproductive organ, *Cycas* is not at all atypical or unusual. Its single aberrant feature is so much out of place that it strongly suggests an abnormality (Bremekamp), which opinion can be explicitly expressed by saying that one would *expect* the female *Cycas* to have strobili ("cones") like all other cycads and the ancient *Nilssoniales*, in other words, *that its so-called "megasporophyll" represents an abnormally developed whole cycadalean strobilus*. The consequences and implications of this alternative hypothesis must now be considered.

A PHYLOGENETIC INTERPRETATION OF THE CYCADALEAN "STROBILUS"

If *Cycas* is regarded as a specialised form the probable descent of the living cycads from Mesozoic ancestral stock enables a phylogenetic approach of the morphological interpretation of their reproductive organs (previously referred to as "strobili" or "cones") through the nilssonialean prototype represented by forms like *Beania*. The *Nilssoniales* and several more or less coetaneous related groups constitute what I have called *Protocycadopsida* (MEEUSE 1963a), *i.e.*, the intermediate plexus linking the Pteridosperms of glossopteridalean alliance and the more advanced Cycadopsids. A tentative semophylesis of the

genitalia of the *Protocycadopsida* will be discussed in detail elsewhere, so that only my conclusions will be given here. These organs consist of an axis, normally subtended by a bract (stegophyll), which bears essentially stalked, and in the female organ cupulated, aggregates of homologues of sporangia (groups of ovules or male synangia). The female synovulangia consist of several unitegmic ovules (*Caytonia*) or they are more or less reduced (to a single ovule in *Corystospermaceae*). In *Beania* not only an oligomerisation of the number of ovules to two had taken place, but the cupule, so strongly developed in *Caytonia*, also became rudimentary and is apparently represented by the recurved flap tipping the stalk of the synovulangium (see Fig. 3). The ovules are exposed and separated by the thickened apical portion of the stalk (synangiophore). In a forthcoming publication I shall explain why it is advisable to employ the term "gonoclad" rather than "strobilus" for such fertile axes, one of the reasons being the absence of bracts on these axes supporting the appendicular sporangium-bearing organs which are the derivatives of aggregated sporangiophores, and therefore, not of "foliar" origin.

The cone-like reproductive structures of the recent cycads can, accordingly, be concisely defined. The female one is a female gonoclad or *gynoclad* and the corresponding male organ an *androclad*. The male and female organs being fundamentally homologous and the female organ of *Cycas* thus being homologous with the strobiloid androclad of the male specimens of *Cycas*, the evidence seems to point strongly to the identity of the traditional "megasporophyll" of *Cycas* with a gynoclad, but, apart from its different *Gestalt*, it differs from all the gonoclads of the other *Cycadales* (including again the male specimens of *Cycas*) in one fundamental respect. A gonoclad is almost invariably subtended by a bract and this holds good for all the strobiliform gonoclads of the cycads, but not for the laminose ovuliferous organ of *Cycas*. Neither the comparative morphological nor the phylogenetic inquiry seems to be adequate to explain the peculiar characteristics of the so-called megasporophyll and the female *Cycas* plants still cannot be fitted into a general morphological pattern common to all *Cycadales*. The phylogenetic evidence indicates an *axial* organ, a homologue of a gynoclad which should be subtended by a bract, but we find a solitary laminose and bractless organ with several attributes of a leaf. This paradoxal situation could be taken to indicate that the "established" identification of the ovuliferous structure of *Cycas* with a megasporophyll, with a leaf homologue, stands unrefuted and that the phylogenetic evidence is misinterpreted if not worthless. This maintenance of the *status quo* would be a silent admittance of the soundness of the preconceived sporophyll concept which I do not endorse. The palaeobotanic records, to my mind, justify the assumption that the suggested semophylesis of the controversial organ is essentially correct and that it must be a derivative of a gonoclad, provided the discrepancy, the absence of a bract, can be satisfactorily accounted for.

The same paradoxal situation is encountered in the female genitalia (the "carpels") of the *Polycarpicae* and some other groups of the Angio-

sperms, the phylogenetic evidence being in this case equally in favour of an axial derivation of the ovules (MEEUSE 1963a) and the stumbling block also being the absence of a bract. MELVILLE (1960, 1962) has suggested a dual origin of the carpel through the adnation of a fertile axis to its subtending stegophyll and although his working hypothesis must be amended in several respects as I shall explain in a forthcoming publication, his postulate of a dual origin is essentially sound. The main difference between Melville's original deductions and my amended version is that he neglected the morpho- and histogenetic aspects altogether. The most important feature of the origin of such organs as "carpels" is that the merging of the two constituting organs is already completed in early developmental stages at the shoot apex. As I shall discuss this working hypothesis in detail elsewhere, only a brief explanation will be given here. The histogenetic development of a leaf and its axillary bud normally begins with the differentiation at the shoot apex of a combined leaf-bud primordium which later divides into two primordia by the formation of an adaxial (later axillary!) protuberance of the original single primordium. In fertile regions the subsidiary primordium develops into a gonoclad and the abaxial one into the subtending bract (or stegophyll). If, however, the splitting of the original single primordium of gonoclad and bract into an individual gonoclad primordium and a bract primordium is retarded or, in extreme cases, does not take place at all, the primordium remains a single entity combining the potencies of the two categories of primordia, so that, when such an undivided primordium develops into an organ, the resulting single morphological structure exhibits a mixture of the features of a foliar bract and its associated axial organ (the axillary gonoclad). The resulting organ has, accordingly, more or less the attributes of a teratological case and cannot be classified in one of the alternative categories of the classical morphology, because it is neither a completely axial (cauline) nor a strictly lateral (foliar) organ but a peculiar amalgamation which may develop some new characteristics. Mainly for historical reasons I have called this phenomenon *pseudo-phyllospory*. If this principle applies to the female *Cycas* plants, one must anticipate the merging of the characteristics of a radially symmetric strobiliform gonoclad bearing biovulate appendages with those of its stegophyll (that must resemble a pinnate cycad frond) and the actual morphology of the fertile organ of *Cycas* certainly fits the part of the veritable *chimaera* that one could visualise as the result of the combination of two such completely different structures. The ovules, borne in two rows along either margin in the proximal (lower) portion, and the absence of assimilatory pigments are indicative of its gynoclad nature, whereas its dorsiventral laminose shape and the more or less blade-like, serrate to pinnate distal portion betrays foliar characteristics, the unpaired condition of the ovules being one of the novel features.

The anatomy of the pseudo-megasporophyll of *Cycas* also shows a mixture of a cauline and a foliar stelar structure. BOUREAU (1946) was struck by the convergence in the anatomy of this organ and that of

the ovuliferous scales of the conifers. The latter, as we know from FLORIN's (1951) researches, are also fusion products of a bract and an axillary fertile axis, so that the similarity of the anatomical features reported by Boureau agrees with the suggested origin of the *Cycas* pseudosporophyll as an organ of dual nature combining axial and foliar characteristics.

The parallelism between the "carpels" of the *Polycarpicae* and the pseudo-sporophyll of *Cycas* is most elucidating, because the hologeny of the *Cycadales* provides tangible evidence of the origin of this organ from a gynoclad and the associated bract, whereas convincing corroborative palaeobotanic data are as yet lacking in the angiospermous lines of descent.

SOME VIEWS REGARDING THE PHYLOGENY AND RELATIONSHIPS OF THE CYCADOPHYTA

The phylogenetic history of the *Cycadales* being, in my opinion, sufficiently elucidated, the relations of this order with other groups of the *Cycadophyta* can be considered with a reasonable degree of confidence. For various reasons these relations have previously, I believe, not been properly understood. In the following tentative phylogeny some of these reasons will be mentioned and discussed, especially those cases which I consider to be based on erroneous premises and tend to confuse the issue.

Since FLORIN's (1931, 1933) work on the stomatal apparatus of gymnospermous groups another tradition became established, *viz.*, the recognition of the supposedly alternative haplocheilic and syndetocheilic types of stomata as an indication of the existence of two main evolutionary lines, a cycadalean and a bennettitalean, distinguished by their stomatal development. This difference is regarded by Florin and others as a very fundamental one, so that there has been a tendency to refer mesozoic form genera based on leaves to either the "cycadoid" or the "cycadeoid" (or bennettitalean) group, which suggests that there were only two main cycadopsid lineages. This rigid classification cannot be maintained, not only because the Jurassic *Pentoxylales*, which are indubitably of bennettitalean alliance, have stomata which have been variously interpreted as haplocheilic or syndetocheilic (VISHNU MITTRE 1957) and are apparently not strictly conformable to either pattern, but also because MAHESHWARI & VASIL (1961) have demonstrated that apparent haplo- and syndetocheilic conditions found in mature organs do not always reflect the mode of development. Form genera pertaining to detached fossil leaves can, accordingly, not be referred with any degree of certainty to one of the major cycadopsid taxa on the basis of the stomatal apparatus alone and such leaves may belong to protocycadopsids, to cycads, or to one of the bennettitalean groups including protangiosperms. A case relevant to the problem under discussion is the fossil known as *Bjuvia* or *Palaeocycas*, tentatively reconstructed by FLORIN (1933) and referred to the "cycads" chiefly on account of its type of stomatal apparatus and its peculiar laminose

reproductive organ reminiscent of a pseudo-sporophyll of *Cycas*. However, there is no cogent reason to accept this identification of the leaves as "cycadalean", the more so because they are entire, *i.e.*, of a type that is completely unknown in *Nilssoniales* and the living cycads but resembles certain bennettitalean phyllomes (*e.g.*, those of *Pentoxylales* and *Williamsonieae*) and the simple angiospermous leaf. As I am convinced of the comparatively recent advent of the *Cycas* type, the fairly ancient *Bjuvia* fructification is more likely to be a parallel development. It could be an example of early pseudo-phyllospory in one of the bennettitalean-protangiospermous groups of the *Cycadopsida*; in fact, Florin's reconstruction, to my mind, does not preclude the possibility of *Bjuvia* being a protangiosperm in the magnoliaceous line of descent. The inadequate factual palaeobotanic evidence renders any interpretation highly conjectural, but the available data point to a non-cycadoid rather than to a cycadoid nature of *Bjuvia*.

The apparently very diverse morphology of the reproductive organs of the various groups constituting the *Cycadopsida* has also been considered to be indicative of very fundamental differences between these groups. Some of them, such as the cycads, could be fitted into the Angiosperm-centred pattern of "phyllosporous" forms supposed to have "sporophylls", but the female reproductive organs of the *Cycadeoidales* and especially of the *Pentoxylales* are not conformable to this type. Some workers have laid the stress on the differences, some even to the extent of over-estimating them (Florin, as I have pointed out already), whereas other botanists have tried to bridge the gaps by suggesting the common derivation of diverse morphological structure from a common archetype. Needless to say, the morphological interpretation of the reproductive organs has been predominantly conservative and there has been no lack of attempts to derive all cycadopsid genitalia from some kind of a "sporophyll". It requires a considerable stretch of imagination to accept the far-fetched "derivations" of, *e.g.*, Chamberlain and Gaussen, who suggest a common semophyletic origin of the female reproductive organs of *Cycadales* and *Cycadeoidales* from a pteridospermous fertile frond (see Fig. 4) and of CHADEFAUD (1947) who, on paper, manipulates amphisporangiate "sporophylls" in such a way that they assume the shape of a "strobilus" of the *Cycadeoidales*. The paleobotanic records indicate that there must have been a large and rather varied mesozoic group of advanced pteridospermous taxa (the *Protocycadopsida*) which show distinct cycadopsid trends and must have been the basic stock of all higher cycadopsid groups including the Angiosperms. The divergent cycadopsid groups must each have rooted in one of the protocycadopsid taxa and their different evolutionary trends must already have been noticeable at the protocycadopsid level of organisation. The *Protocycadopsida* were more or less fern-like plants usually of low stature (and presumably often rhizomatous) with zoidiogamy. Their leaves were of various shapes, pinnate, bipinnate, bifurcate-pinnate, digitately compound and entire types being known. Their reproductive organs (gonoclads) were predominantly unisexual and borne monoeciously or

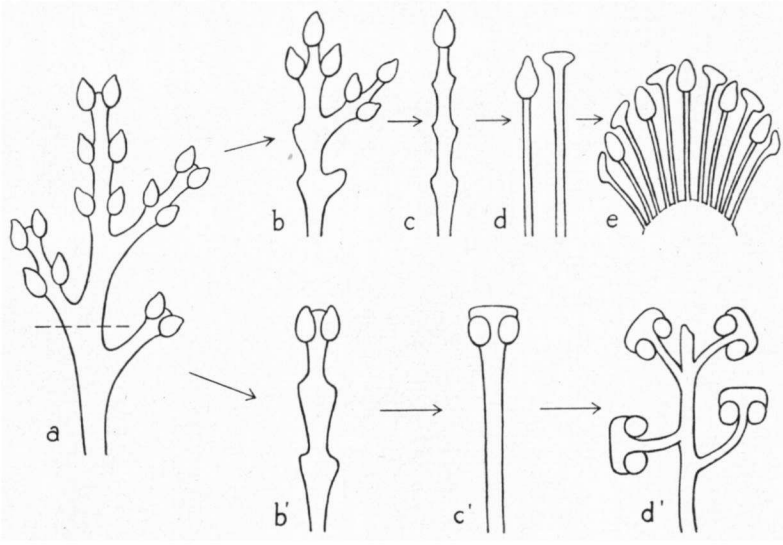

Fig. 4. Derivation of a female "strobilus" of *Cycadeoidales* (e) and a female cone of the *Cycadales* (d') from the same prototype (a, supposed to be a fertile pteridospermous frond) through the reduction of all but the terminal megasporangium, and a reduction to a few lateral ones, respectively (b, c, b', c' hypothetical intermediate stages), based on an idea originally suggested by Chamberlain and adopted by Gaussen.

dioeciously. The androclads supported a number of stalked microsynangia sometimes developed as flat laminose organs, the gynoclads cupulated aggregates of unitegmic ovules. Important differences existed in the female reproductive organs, the number of ovules in each cupule varying from several (*Caytoniaceae*) to one (*Corystospermaceae*). The pluri-ovulate cupule probably represents the most ancient condition which apparently died out with the *Caytoniales*. The *Nilssoniales* specialised in the direction of biovulate reduced cupules which condition survived in the recent *Cycadales* (*Cycas* excepted). The *Corystospermaceae* or very similar forms with solitary ovules and a well-developed cupule must have been the basic stock of the taxa of bennettitalean and protangiospermous affinities. Characteristic features of the higher cycadopsids are the development of additional protective coats of the ovules, siphonogamy and, ultimately, angiospermy, but the living cycads are essentially still protocycadopsid in their organisation, for — apart from several specialisations to be expected in such an ancient group and a marked tendency towards gigantism — they are not very far advanced beyond the nilssonialean level of evolution. The *Cycadales* apparently represent an independent hologeny which was already separated from other lineages at the protocycadopsid level, the *Nilssoniales* forming a well-defined taxon. The differences between the genera of the living cycads must also reflect an ancient differentiation, in other words, when the *Nilssoniales* became recog-

nisable as a group they must have had an independent phylogenetic history of sufficient duration to cause some diversity. The leaf shape may well be indicative of the development of different trends, so that *Stangeria* with its peculiar foliage resembling fern-fronds represents some minor lineage, *Bowenia* with bipinnate leaves another and the remaining genera at least a third. All things considered, the almost stemless forms (e.g., *Zamia*) are more primitive than the taller arborescent genera (*Encephalartos*, *Microcycas*, *Cycas*, etc.). At any rate, of all genera with once-pinnate leaves *Zamia* resembles the *Nilssoniales* most. The Cretaceous *Microzamites* (*Microzamia*) is indeed strikingly intermediate, exhibiting a female strobilus more compact than *Beania* and more loosely constructed than the female cone of *Zamia* (Fig. 3). Gaussen has attempted to evaluate the characters of the recent *Cycadales* numerically in order to obtain a kind of relative advancement index. His conclusion is that *Zamia*, *Bowenia* and *Stangeria* are the three most primitive genera and rate about equal, but in spite of the assessment of its female reproductive organ as "primitive", *Cycas* clearly stands out as the genus with the highest degree of advancement.

The views expressed in this paper fully endorse the general conclusions of Arnold's recent comprehensive summary of the *Cycadales* and of Gaussen's advancement index, but it is felt that the additional suggestions have eliminated some inconsistencies and may contribute to a better understanding of the phylogeny and morphology of these interesting "relics from an ancient past".

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