XI. AN EXCHANGE OF VIEWS ON THE CYATHEACEAE

When Dr. R.E. Holttum kindly submitted the following essay review of two papers on Cyatheaceae, a suggestion that Dr. R.M. Tryon be enabled to reply was welcomed by both pteridologists. The editor feels grateful to them for their contribution.

First Dr. R. E. H o l t t u m :

GASTONY,G.J. *Spore morphology in the Cyatheaceae. I. The perine and sporangial capacity: General considerations.* Amer. J. Bot. 61 (1974) 672-680.

GASTONY,G.J. & R.M.TRYON. *Ibid. II. The genera Lophosoria, Metaxya, Sphaeropteris, Alsophila and Nephelea.* Amer. J. Bot. 63 (1976) 735-758.

These two papers are important for Malesia because they deal in a comparative way with the sporangia and spores of species of Cyatheaceae in both Paleo- and Neotropics. The generic concepts accepted are those proposed by Dr. Tryon in Contr. Gray Herb. 200 (1970) 3-53 in a new scheme of classification of the family. In both papers now reviewed it is stated that the observations reported are in accord with this scheme, but to me they offer important evidence against it.

In The Ferns, vol. 2 (1926) F.O. Bower proposed the idea that Cyathea evolved from a Gleichenia-like ancestor, and that therefore the primitive Cyathea was exindusiate. This implies that the indusia in Cyathea are a new evolutionary development; and further, that other groups of ferns which are considered to be later developments of the Cyathea alliance have indusia which are not homologous with the indusia of ferns believed to be derived from the Dicksonia alliance, which Bower considered to have evolved from ancient Schizaeaceae. In my paper on the classification of ferns of 1947 (J. Linn. Soc. Bot. 53: 123-158) I called attention to the similarities between Cyathea and the Thelypteris group of genera; accepting Bower's theory of the origin of Cyathea, I then stated that thelypteroid indusia could not be homologous with those of Dryopteris, which appeared to me to be more nearly related to Dennstaedtia, a member of Bower's family Dicksoniaceae. But I did not feel very happy with the idea that indusia of Dryopteris, Tectaria and Thelypteris, which are so much alike, could not be regarded as homologous.

When I came to study the tree-ferns for Flora Malesiana I was fortunate in having the results of Dr. U. Sen's anatomical studies available to supplement my taxonomic survey. Dr. Sen suggested that the soral condition of Cyathea could best be accounted for by accepting Goebel's hypothesis (rejected by Bower) that the hemitelioid indusium in Cyathea could be regarded as having evolved from the condition of Dicksonia.

Dr. Sen also showed the close similarity in anatomy between Cyathea and Dicksonia. Putting together the ideas about sori and anatomy, I concluded that a rather close association between Cyathea and Dicksonia was a logical notion, whereas Bower had placed them far apart in his evolutionary scheme. Dicksonia is certainly the older group, with many fossils of Jurassic age, and it seems to me highly probable that Cyathea is a later offshoot from Dicksonioid ancestors. This conclusion has the advantage that it admits homology of indusia in the great majority of terrestrial ferns.

In 1970 Tryon rejected these ideas and reverted to Bower, regarding Cyathea sens. lat. as primitively exindusiate. He then followed Bower also in supposing that Lophosoria and Metaxya, which are exindusiate ferns with a primitive type of sporangium, are primitive allies of Cyathea; primitive because they have an indumentum of hairs only, not scales. But anyone who has studied the thelypteroid, tectarioid, dryopteroid and athyrioid ferns knows that there are many species which lack indusia though in other respects their generic assignment is clear. A loss of indusium has certainly taken place on many separate evolutionary lines. Why then cannot Lophosoria and Metaxya be regarded as ferns which have lost their indusia? Tryon does not mention this possibility.

Lophosoria looks to me like a reduced and exindusiate derivative of Dicksonia. It also has the same chromosome number as Dicksonia (65), whereas all species of Cyathea (including Sphaeropteris) so far investigated have the number 69. Now in Gastony and Tryon's latest paper the spores of Lophosoria are shown in beautiful SEM photographs to be extremely different from those of Cyathea and much more like Dicksonia. I see no evidence why Lophosoria should be regarded as a primitive cyatheoid fern. Tryon in 1970 reported evidence in Nephelea (a genus split off from Cyathea in America) of intermediates between hairs like those of Lophosoria and narrow scales; precisely the same kind of transition between Dicksonia-like hairs and scales can be seen in Malesian species of Cyathea subgenus Sphaeropteris.

Metaxya is very different in general morphology from Cyathea in all parts of the plant. It is also very peculiar in its high chromosome number (2n = 192) which is not closely related to either Cyathea or Dicksonia. Gastony and Tryon now for the first time show SEM photographs of Metaxya spores; they are extremely different from those of Lophosoria, thus reinforcing the evidence of morphology and cytology to show that Metaxya and Lophosoria are not closely related to each other. The existence of both genera seems to me irrelevant in considering the affinities and possible phylogeny of Cyathea.

In his paper of 1970, Tryon separated Sphaeropteris (the type of which is the New Zealand species Cyathea medullaris)

as a genus distinct from Cyathea, whereas in my arrangement it is placed as a subgenus. He included in it not only the South American species related to Cyathea horrida which I had indicated as apparently related to Malesian species (Fl. Males. ii 1, p. 124) but also another group of South American species the scales of some of which he illustrated on p. 19 (fig. 14-17). The figures show that these scales are not strictly conform (Tryon's term) and they lack merginal setae; thus they differ from the scales of true Sphaeropteris of Malesia. Some species of this alliance have hemitelioid sori, which do not occur in any Malesian species of Sphaeropteris. Now the beautiful series of SEM photographs of spores show that in spores also this group of species differ consistently from true Sphaeropteris. I believe that other kinds of evidence could be added, and I maintain that these species should be excluded from any group which bears the name Sphaeropteris, whether as genus or subgenus.

In Gastony's paper of 1974 he examines the spore content of sporangia and states (p. 676) "the family may be divided into two natural groups based on the number of spores [16 and 64] produced per sporangium". He implies that the division corresponds with Tryon's scheme of classification. But on p. 679 he lists several exceptions to this generalization, and in the joint paper of 1976 (p. 753) it is pointed out that these exceptions do not form a natural group. One of them is Cyathea capensis (which occurs both in S. Africa and in S. America) which Tryon and Gastony state has an "evident relationship to the paleotropical species of Holttum's Cyathea section Gymnosphaera" in its "extreme development of aphlebiae". But a majority of Malesian species (14 out of 18) of section Gymnosphaera have no "aphlebiae" (a term misapplied to the residual basal pinnae in Cyathea, which do not lack veins), and the form of "aphlebiae" is not constant in the four species which do possess them. The only species which have aphlebiae comparable to those of C. capensis are C. ramispina of North Borneo and the closely related Philippine C. atropurpurea. The species most closely related to these (as judged by other characters) is C. recommutata, the basal reduced pinnae of which are of a very different type. C. capensis differs from all species of sect. Gymnosphaera in its hemitelioid indusium, and the axes of its fronds do not have the very dark colour characteristic of Gymnosphaera; and there is other evidence that residual small basal pinnae are not solely confined to sect. Gymnosphaera.

In Dr. Tryon's original paper of 1970 he rejected Goebel's theory of the origin of the hemitelioid indusium in Cyathea from the inner indusium of Dicksonia, but failed to mention the principal argument in favour of Goebel's theory. This is the fact that all hemitelioid indusia (in a large number of

species in both the Old World and the New) are attached at the base of the sorus on the side remote from the margin of the leaflet, exactly where one would expect to find them on Goebel's theory. Dr. Tryon evades this fact by the vague statement that "moderately to well developed indusia that partially surround the base of the receptacle are called hemitelioid" (1970, p. 7). This omits the essential facts. He also fails to consider the stages of reduction of hemitelioid indusia which occur in many Malesian species; is the very small indusium of C. latebrosa to be considered primitive? It seems to me much more likely to be reduced from a larger primitive condition. If Dr. Tryon regards the indusia of Cyatheaceae as new evolutionary developments, how does he account for the various comparable indusia in the Thelypteris, Tectaria, Athyrium, Davallia and other groups of genera? It seems to me that all these indusia are homologous, and a consideration of all of them is relevant.

Finally, in self-defence, I would like to state the facts about the development of ideas as to the significance of scales in understanding classification within Cyatheaceae. I observed the distinction between setate and marginate scales (Tryon's terms) before 1930 during field work in Malaya, and used these characters in describing the Malayan species in a paper published in 1935 (Gard. Bull. Str. Settl. 8: 243-320) which is cited in my book on Malayan ferns but not noted by Tryon. I then knew that all species in Malaya had one type of scale or the other except C. latebrosa, which appeared to be peculiar. In 1953 I passed on this information to Gordon DeWolf, who made a careful examination of the scales of all Malayan species and showed me that C. latebrosa was not peculiar; its scales have a narrow fragile margin which is soon abraded and can only be seen on very young scales. DeWolf proposed the terms flabelloid and setiferous for the two types; I prefer flabelloid to Tryon's marginate (every scale has a margin) though the margins of some are hardly fan-like.

When I came to study the much larger number of species for Flora Malesiana, I discovered that they also could be separated into two groups on scale characters, but I discovered also that there are a number of associated characters which are consistently present, giving further confirmation of the distinctness of the two groups. Dr. Tryon has completely ignored these other characters, which is one reason why he has failed to notice the unnatural nature of his concept of Sphaeropteris. But I do not doubt that he has correctly distinguished some other South American groups, and in particular the group associated with the type species of Cyathea, thus showing that I was wrong to include a majority of Malesian species in Cyathea subg. Cyathea.

Dr. Tryon regards Sphaeropteris as the most primitive genus in Cyatheaceae, apart from Lophosoria and Metaxya. But some of the slight arguments he adduces in favour of this are based on the alien species. I would say that Sphaeropteris s.str. and Alsophila sensu Tryon represent separate evolutionary lines, but the fact that they both have a chromosome number 69 indicates that they are not very far apart. I think that the indusium in Sphaeropteris s.str., which is never hemitelioid, may be a new development, and I suggest that Dr. Tryon may be wrong in regarding some indusia in Cyathea s.str and in Alsophila as sphaeropteroid.

In Flora Malesiana I recognized a family Cyatheaceae which included Dicksonia as well as other genera. I now think that this was too broad a concept, and that the subfamilies should be raised to family rank; but I think that the general scheme of inter-relationships of groups is still valid, on available evidence. Thus I regard Cyathea and Dicksonia as more nearly related to each other than either is to Culcita, which for so long was confused with Dicksonia; but I suggest that any new review of this whole situation must take into account the possible relationships of Culcita to Dennstaedtia, of Cyathea and Dicksonia to Thelypteris and Tectaria. I feel sure that the broad concept of Cyatheaceae of Flora Malesiana represents a basic group to which a majority of other terrestrial ferns are allied.

Kew R.E. Holttum

Now the reply by Dr. R. M. T r y o n :

Studies on the American Cyatheaceae and on the classification of the family.

The impressive stature of tree ferns encountered during many field trips in the American tropics in the past twenty-five years initially motivated our study. The publication of Dr. Holttum's work on the Cyatheaceae in Flora Malesiana was a further stimulus for the preparation of a comparable systematic treatment for these plants in the Americas. Dr. Holttum's studies supply information on major groups, valuable descriptive data, and excellent illustrations. These aspects greatly facilitated a review of the paleotropical species and the integration of new data from the American Cyatheaceae. Six genera have been recognised in the scaly Cyatheaceae (R. Tryon, 1970): Alsophila, Sphaeropteris, Nephelea, Trichipteris, Cyathea and Cnemidaria. The first two are pan-tropic and correspond to Dr. Holttum's Cyathea subgenus Cyathea and subgenus Sphaeropteris, respectively, in Flora Malesiana. The other four are confined to the American tropics. To these may be added a new American subgenus of Sphaeropteris that is in

press (Windisch, 1977, b). The appropriate rank of these taxa is naturally a matter of judgement, but their reality as evolutionary groups seems well established. This work has been accomplished through the cooperative efforts of a group of collaborators investigating diverse aspects of the family.

I do not wish to pursue details of Dr. Holttum's commentary, but will remark on a few principal points and clarify some possible misunderstandings. In regard to the relationships of Lophosoria and Metaxya, I agree that these are isolated genera, not very close to any others, nor to each other. In my 1970 paper, I denied any direct ancestral relation of either to the scaly Cyatheaceae. They both have only trichomes on the stem and Lophosoria has large sporangia, primitive features with respect to the scaly Cyatheaceae. The intermediate type of indument Dr. Holttum refers to is in species of Sphaeropteris (not Nephelea), where his observations coincide with my own. The problem of the origin and possible loss of the indusium in tree ferns, and indeed the whole matter of the homology of the indusia of higher ferns, is a more complex one. New evidence has been presented in Cyathea fulva that the indusium develops from the vein sheath some distance from the margin (A. Tryon and Feldman, 1975). This must be considered along with Dr. Sen's contribution. Additional developmental studies are needed in the Cyatheaceae and also in the other genera Dr. Holttum discusses.

Dr. Gastony does not simply imply that the division of the Cyatheaceae into two natural groups corresponds to my scheme of classification, as stated in the review. Rather, his analysis carefully indicates (1974, 1976) how this infra-familial division relates to the genera in my (1970) phyletic chart, notes the occurrence of the more primitive spore numbers which are fortunately still evident in some Alsophila species, and explains the phyletic significance of these exceptional spore numbers. Dr. Gastony is presently completing the third and final paper on the spores of the Cyatheaceae (Trichipteris, Cyathea, Cnemidaria) and he has in progress a comparative study of the spores of the dicksonioid and dennstaedtioid genera. We prefer not to comment on the palynological evidence of relationships among these genera until this study is completed.

I wish to emphasise the recent progress made in the taxonomy of the Cyatheaceae, rather than dwell on differences of opinion on the elusive course of evolution. There is still much to do, but for the first time there is a taxonomic framework encompassing the species of the paleo- and the neotropics. The work of Dr. Holttum on these plants is a major contribution to our knowledge of the group and has been a stimulus for additional studies.

The following are the principal papers resulting from our

work on the classification of the family and on the American genera. This effort has been directed toward the development of a broad base of data on the family.

Arnold Arboretum, Cambridge, Mass. R. Tryon

BARRINGTON,D.S. *A revision of Trichipteris (Cyatheaceae).* Ph.D. Thesis, Harvard University (1973).

CONANT,D.S. *Hybrids in American Cyatheaceae.* Rhodora 77 (1975) 441-455.

----- *Ecogeographic and systematic studies in American Cyatheaceae.* Ph.D. Thesis, Harvard University (1976) (includes a revision of American Alsophila).

GASTONY,G.J. *A revision of the fern genus Nephelea.* Contr. Gray Herb. 203 (1973) 81-148.

----- *Spore morphology in the Cyatheaceae. I. The perine and sporangial capacity: general considerations.* Amer. J. Bot. 61 (1974) 672-680.

----- & R.TRYON. *Spore morphology in the Cyatheaceae. II. The genera Lophosoria, Metaxya, Sphaeropteris, Alsophila and Nephelea.* Amer. J. Bot. 63 (1976) 738-758.

LUCANSKY,T.W. *Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. I. Metaxya and Lophosoria, and II. Squamate genera.* Amer. J. Bot. 61 (1974) 464-471 and 472-480.

----- & R.A.WHITE. *Comparative studies of the nodal and vascular anatomy of neotropical Cyatheaceae. III. Nodal and petiole patterns; summary and conclusions.* Amer. J. Bot. 61 (1974) 818-828.

----- & ----- *Comparative ontogenetic studies in young sporophytes of tree ferns. I. A primitive and an advanced taxon.* Amer. J. Bot. 63 (1976) 463-472.

RIBA,R. *Revision monographica del complejo Alsophila Swartziana Martius (Cyatheaceae).* Ann. Inst. Biol. Univ. Mex. 38, ser. Bot. 1 (1967) 61-100 (the Trichipteris armata group).

STOLZE,R.G. *A taxonomic revision of the genus Cnemidaria (Cyatheaceae).* Fieldiana: Bot. 37 (1974) 1-98.

TRYON,A.F. & L.J.FELDMAN. *Tree fern indusia: studies of development and diversity.* Canad. J. Bot. 53 (1975) 2260-2273.

TRYON,R. *The classification of the Cyatheaceae.* Contr. Gray Herb. 200 (1970) 3-53.

----- *The American tree ferns allied to Sphaeropteris horrida.* Rhodora 73 (1971) 1-19.

----- *A revision of the genus Cyathea.* Contr. Gray Herb. 206 (1976) 19-98.

----- & G.J.GASTONY. *The biogeography of endemism in the Cyatheaceae.* Fern Gazette 11 (1975) 73-79.

WINDISCH,P.G. *Filices novae austroamericanae. I.* Bradea 1 (1973) 371-376 (Sphaeropteris species).
----- *Filices novae austroamericanae. II.* Bradea 2 (1976) 57-60 (Sphaeropteris species).
----- (a) *The systematics of the group of Sphaeropteris hirsuta (Cyatheaceae).* Mem. New York Bot. Gard. (1977, in press).
----- (b) *Synopsis of the genus Sphaeropteris (Cyatheaceae), with a revision of the neotropical exindusiate species.* Bot. Jahrb. (1977, in press).

THE GOLDEN CHICKEN DECEASED

The Cibotium barametz depicted on the cover of FMBulletin number 28, with an explanation on *page 2303*, was still in good health in the summer of 1976, almost 3¾ years after its reception into Professor O. Kranendonk's house at Amsterdam in September 1972. Then the family went on holidays, and the 'golden chicken sit' forgot to water it, during the extremely hot days of July. It never recovered from this set-back, which made the vessels shrivel, and caused a sad withering of its tail. Mrs. Kranendonk was able to prolong its life till January 1977, but then it was clear that there was no hope. Mrs. Kranendonk feels certain that it could have lived much longer, if the water supply had been continuous. Requiescat In Pace!