



Dedicated to the memory of
C. F. A. CHRISTENSEN

DEDICATION

CARL FREDRICK ALBERT CHRISTENSEN (1872–1942) was the founder of modern fern taxonomy. To appreciate the scope of his work, it is necessary to understand the confusions of thought on the subject which persisted through the 19th century and were still evident in the summary prepared (by DIELS) for ENGLER & PRANTL's *Pflanzenfamilien* in 1899. CHRISTENSEN's first great work was his *Index Filicum* (1905–6) in which he listed all known fern binomials and also relegated many to synonymy. In the main he adopted the classification and nomenclature of DIELS. While preparing the Index he came to realize that many generic concepts accepted in the Index were unnatural or confused. This was especially evident in the great complex of species which he listed under the name *Dryopteris*. He next made a study of the tropical American species of that complex, and in so doing discovered how to separate them into natural groups (1913, 1920). At the time I first made contact with him (about 1925) he had begun to study ferns of the Old World tropics. I maintained a regular correspondence with him from 1925 to 1940, and sent him many specimens for identification. I also met him in Europe in 1930, 1934 and 1938 and had long discussions with him. I benefited from his wisdom also indirectly through the publications of R. C. CHING, who studied with CHRISTENSEN in 1929–1932 and applied CHRISTENSEN's ideas to Chinese and Indian ferns in an important series of papers in the 1930s. CHRISTENSEN's identifications of my collections and his comments upon them were the basis on which my own work was built; in the present Series of Flora Malesiana I have tried to extend his methods and his ideas to a much wider range of species than he could have encountered. To him I am profoundly grateful, and I am concerned also to acknowledge my debt, through him, to some perceptive earlier workers, notably G. H. METTENIUS and JOHN SMITH.

The objectives of any scheme of biological classification are to show natural relationships and to provide a means for the identification of individual organisms. It has sometimes been suggested that only the latter objective is important, and that a 'practical' scheme is all that is needed. The history of fern classification has shown that artificial schemes, made without thought as to relationships, do not work; and distribution-maps based on such schemes are meaningless. Fern classification as understood today should be based not only on gross-morphological characters but also on microscopical characters pertaining to the fern's anatomy, indument, spores, gametophytes, etc., and on cytotaxonomy.

There can be no doubt that existing ferns have originated through a process of evolution. They have therefore an inbuilt classification, and our object is to find it; the nearer we get to it, the nearer we are to the practical aspect of taxonomy. Fossils provide no clear evidence of the progress of the evolution of the great majority of leptosporangiate ferns. In most cases our only evidence for this is the natural relationships shown by taxonomy. We now have reached the stage at which most Malesian species can be allocated to definable natural groups which may have generic rank; most genera can also be associated in groups which appear to be natural; but it is often not yet clear how groups of genera are inter-related. For example, within the family *Thelypteridaceae* I cannot see a definite pattern of inter-relationships between the groups of genera which I have recognized. For a better understanding of this wider problem, genera throughout the tropics need to be taken into consideration; such an undertaking is beyond the scope of Flora Malesiana Series II, but I believe that this Series has presented a great deal of new evidence on which wider considerations may be based.

Some botanists appear to think that a Flora is not the place for discussion of such questions. I disagree with that idea. Floras and taxonomic monographs always appear to account for everything, owing to the nature of their presentation. But in fact there are always gaps and uncertainties, especially in tropical Floras; some indication of this should be given; no classification can be final.

FLORA MALESIANA

Even within groups of ferns already dealt with in Flora Malesiana, much more information is needed. For example, existing specimens do not show clearly the distinctions between species in the genus *Plesioneuron* (*Thelypteridaceae*). There is a great need for new collections made by persons who have specialist knowledge and are prepared to undertake prolonged critical search. After the publication of my book on the ferns of Malaya, BETTY MOLESWORTH ALLEN, by persistent collecting, discovered nearly twenty additional species including representatives of three additional genera.

The genera of LINNAEUS, which should be the basis of fern classification, are very crudely defined, and are only useful through agreement as to their typification. He did not notice indusia, upon which J. E. SMITH (1793) was the first to base new generic concepts, but SMITH also was not a critical observer. Within a few years, several other authors extended his observations and proposed new generic names, some not well distinguished, and in 1801 SWARTZ and BERNHARDI noted (more exactly than SMITH) the differences between annulate (or gyrate) and exannulate sporangia. These observations were collated by SWARTZ in his *Synopsis Filicum* (1806) where he separated the genera of *Osmundaceae*, *Schizaeaceae* and *Gleicheniaceae* as spuriously gyrate, distinguishing the annulate genera (*Polypodiaceae*) solely by the form of indusia and the form and position of sori where indusia were lacking. An extreme example of the artificial nature of some genera proposed at this period is *Belvisia* MIRBEL (1802) which, in addition to the recognized type *B. spicata* (L.) MIRBEL (*Polypodiaceae*) included species now allocated to *Actiniopteris*, *Schizaea*, *Asplenium* and *Ceratopteris*.

Simultaneous with SWARTZ, SCHKUHR was producing the first good series of illustrations of ferns (1804–1809). When one makes a drawing of a plant with the intention of accuracy, one often notices hitherto neglected characters. This was true of SCHKUHR, who observed and commented upon many details, especially of hairs, which have, since CHRISTENSEN, become recognized as important key characters. He noticed the jointed (septate) hairs of *Ctenitis villosa* (L.) COPEL., and portrayed accurately the equally long unicellular hairs on the indusia of a species of *Christella*, though he did not comment on the latter. In some cases he illustrated venation clearly and accurately, in others indistinctly or casually. Some of SCHKUHR's drawings were made from living plants, but most were from dried specimens.

HOOKE and GREVILLE's *Icones Filicum* (1827–1831) was the next illustrated work. The plates were better executed (by GREVILLE) than SCHKUHR's and one can also detect a gradual increase of interest in detail as the series progressed. For example, plate 5 depicts *Ceterach pedunculatum* and plate 6 *Grammitis decurrens*, but in neither case are any details of venation shown; both species are now placed in the genus *Colysis* PRESL (*Polypodiaceae*). Plate 125 shows *Polypodium irioides*, with enlarged details of venation well observed. Simultaneous with HOOKE and GREVILLE, BLUME (1829–1830) was publishing the wonderful plates 1–65 of his *Flora Javae, Filices*, in which details are, on the whole, even more carefully dealt with. His subdivision of *Polypodium* is important.

H. SCHOTT, at the imperial palace of Schönbrunn, had living fern plants in his care and published (1834) a short series of excellent engravings illustrating new genera, showing much more detail than HOOKE and GREVILLE; some of these were certainly based on living plants, in particular his *Nephrodium* which shows very exactly capitate hairs and the elongate unicellular glands which are present on the stalks of sporangia, noted by no-one else until I made drawings of them in Singapore in 1943 (published 1971). Between 1840 and 1851 G. KUNZE published a series of illustrations which he regarded as a continuation of SCHKUHR's. He was in charge of the Botanic Garden at Leipzig, in which was the best collection of living ferns in Europe (soon to be surpassed by Kew). His successor at Leipzig, G. H. METTENIUS, inherited KUNZE's living collections

Dedication

and herbarium, and on their basis prepared a new system of classification of ferns (1856) with plates often showing new details. He subsequently prepared monographs describing all known species of several major genera, after which he began observations on the collections from Malasia in the Rijksherbarium. He had previously misinterpreted some of BLUME's species through not having seen authentic specimens, and corrected some of them in the *Ann. Mus. Bot. Lugd.-Bat.*; he also incorporated new basic observations on several genera. While engaged on the latter work, he died of cholera in 1866 at the age of 42. Had he lived longer, he would have changed the course of pteridological thinking; I will revert to him later.

C. B. PRESL was given the task of describing the collections made by HAENKE on the Malaspina Expedition; these included many specimens of ferns from the Philippines (described in 1825). As a result PRESL became interested in the classification of ferns, and realized that characters other than those of sori needed to be taken into account. In 1836 he published *Tentamen Pteridographiae*, comprising a new scheme of classification in which the arrangements of vascular tissue, and of venation, had an important place. His work is illustrated by many small drawings showing details of venation in relation to sori, in most cases quite accurately. His later publication (1848) showing arrangement of vascular strands in the stipes of ferns is not so well observed. PRESL's emphasis on venation led him to associate together species of very diverse relationship, but it was a beginning of new thought.

At the same time JOHN SMITH of Kew had been taking an interest in the cultivated tropical ferns in his charge, many raised (as at Leipzig) from spores from herbarium specimens. He was in touch with ROBERT BROWN, who had made some original observations on the venation of ferns when describing his own Australian specimens and also some collected by HORSFIELD in Java. SMITH was also in touch with FRANCIS BAUER, the Kew botanical artist, and supplied him with living fern plants and herbarium specimens, from which BAUER prepared a beautiful set of forty plates. These were submitted to W. J. HOOKER (then at Glasgow) who arranged for them to be published and added more, prepared by W. H. FITCH, 120 plates in all, finalized after HOOKER came himself to Kew. Many of the genera are those of PRESL, but twenty were newly named and described by JOHN SMITH. SMITH himself had prepared a new scheme of classification independently of PRESL, finding much agreement between their ideas when the *Tentamen* appeared; he collated his nomenclature with PRESL's and his scheme was published by HOOKER in 1841-1843. JOHN SMITH continued to study ferns, and to add to the collection of living plants at Kew. By 1865, when he was obliged through failing sight to retire, he had seen more than 1000 species of ferns in a living condition, of which he published a list in 1866. The final summary of his ideas, resulting from continued observation of living plants, appeared in 1875 and will be considered later.

Having published *Genera Filicum*, HOOKER planned *Species Filicum*, in which he proposed to describe all known species of ferns. For this, he had to re-consider the question of classification, and concluded that PRESL had proposed too many genera; the result was that HOOKER's genera in *Species Filicum* are almost the same as those of SWARTZ. The work was published in five volumes over a period of twenty years (1844-1864); HOOKER planned to follow it with a summary in one volume, to be called *Synopsis Filicum*. He died just as the first part of the latter was printed. J. D. HOOKER, who succeeded his father at Kew, engaged J. G. BAKER to continue the *Synopsis* on the lines planned, and this was completed in 1868 (second edition, with many additions by BAKER, in 1874). In 1891 BAKER published a summary of new ferns discovered since 1874, still with the same set of genera.

HOOKER's *Species Filicum* was illustrated by 304 excellent plates prepared by W. H. FITCH (often two species on one plate). These show clearly and accurately details of venation and

FLORA MALESIANA

indusia, but rarely any smaller structures. In his descriptions HOOKER rarely described details of hairs or scales. He thought such details unimportant; his main objective (see Vol. 3, p. 3) was 'to assist the tyro in the verification of genera and species . . . natural habit is often a safer guide than minute microscopic characters'. He placed most exindusiate species of Thelypteroid, Tectarioid and Dryopteroid ferns in the genus *Polypodium*, but some in *Gymnogramme* and *Meniscium*; *Dictyocline* was merged with *Hemionitis*. He could not understand how JOHN SMITH could believe *Brainea* to be closely related to *Blechnum*, though it differs from *Blechnum* only in the absence of indusia. He placed *Brainea* between *Gymnogramme* (which included the diverse genera *Selliguea* and *Syngamma*) and *Meniscium*. His refusal to examine details led him to include in one species specimens which show great diversity in what are now considered to be significant characters. He united most of FÉE's species of *Lomariopsis* (including also *Teratophyllum* METT.), thus including several distinct Malesian species in *Acrostichum sorbifolium* L., of which the type came from the West Indies. His confusions in the synonymy of Thelypteroid ferns are very numerous, and can only be understood by reference to his herbarium. BAKER's descriptions of ferns discovered after HOOKER's death are even less satisfactory than HOOKER's and often do not serve to identify specimens with any certainty.

The remaining authors who proposed new schemes of classification were FÉE (1852) and T. MOORE (1857). FÉE's works were all admirably illustrated and his numerous plates show many significant details, but not always accurately. For example, in tab. XXI A, fig. 2 he was the first to show a transverse section of the stipe of *Pleocnemia* (*sensu* HOLTUM 1974), but the accompanying figure of venation in an allied species (fig. 1) is not accurate and fails to show the distinctive sinus-teeth. Neither FÉE nor any earlier author (so far as I have observed) shows the distinctive row of four cells on one side of the sporangia of leptosporangiate ferns. FÉE attempted to use the number of cells in the annulus as a generic character, but this is rarely practicable. His scheme is more elaborate than PRESL's but is no nearer to a natural arrangement by present standards. He has *Phegopteris* as a genus separate from *Polypodium*, but in the same group of genera, not with its true allies, which are in other groups. Under the tribe *Acrosticheae* he has an astonishing diversity of genera.

THOMAS MOORE's scheme is accompanied by good small drawings to show diagnostic characters. For example, he shows the difference in venation between *Stenochlaena* and *Lomariopsis*, not noticed by FÉE. But his scheme only differs in minor features from that of PRESL.

MILDE in 1866 made important observations of scales and stipe-anatomy showing a clear distinction between *Asplenium* and *Athyrium* (including *Diplazium*); he elaborated these in 1870. METTENIUS had noted that previous attempts to distinguish these genera were unsatisfactory, and HOOKER denied that any clear distinction was possible (and in 1928 BOWER still copied HOOKER's statement). In my judgement (HOLTUM 1947) *Asplenium* and *Athyrium* are not very closely related.

R. H. BEDDOME did not propose a new scheme of classification, but during the years 1856–1882 he made a more intensive field study of ferns in a tropical region than any previous author. He was critical of HOOKER's genera and made some minor alterations in them for purposes of his Handbook (1883, with Supplement 1892), though still accepting the main scheme (his preface hinted that more needed changing). His work covered the Malay Peninsula and so is important for Flora Malesiana (he also accepted HOOKER's misidentification of some Indian ferns with species in Java).

JOHN SMITH's *Historia Filicum* (1875) proposed a new scheme based on much study of living plants subsequent to his first one (1841). He did not use a microscope, and rarely refers to details of structure of sporangia, scales *etc.*, but from observation of his plants he did learn much that

Dedication

HOOKER never understood. I will refer later to some of his insights in a discussion of the work of DIELS, SMITH and METTENIUS, both observers of living plants, were the only authors of their period who (apparently independently) separated *Phegopteris*, *Dictyopteris* and other terrestrial exindusiate ferns from the alliance of *Polypodium* and transferred them to one including *Aspidium*. Both authors maintained separate genera for the exindusiate ferns, but JOHN SMITH admitted that probably some species were placed in *Phegopteris* and *Dictyopteris* merely because the only known specimens had old sori from which indusia might have fallen. Presumably he still thought the idea of uniting indusiate and exindusiate species in one genus too revolutionary. It should be noted that both METTENIUS and SMITH had a mixture of Thelypteroid, Tectarioid and Dryopteroid ferns in their genera, whether indusiate or not; and SMITH kept *Meniscium* (*Thelypteridaceae*) far from his Aspidioid ferns. The major advance in thinking was that indusiate and exindusiate species could be closely allied; this was something HOOKER refused to consider.

In this connection, the history of *Pleocnemia leuzeana* (GAUD.) PRESL is instructive. GAUDICHAUD described the species (from the Moluccas) in the genus *Polypodium* because its sori were exindusiate. PRESL founded a new genus based on the combination of a particular vein-pattern with circular exindusiate sori. Later CUMING collected specimens in Luzon which were similar in venation and general aspect, but some of them had indusiate sori. HOOKER, who had illustrated the genus *Pleocnemia* as exindusiate (Gen. Fil. t. 70A, copied from PRESL) published drawings made from two of CUMING's specimens, one sterile and one showing indusiate sori (t. 97), and stated that this gave him an opportunity to correct his previous 'error' in reporting that *P. leuzeana* was exindusiate. But CUMING made four different collections (all seen by HOOKER) which are now known to represent three distinct species, two of them indusiate, one exindusiate, all different from the type specimen of *P. leuzeana*. HOOKER assumed that some specimens had lost the indusia which they originally possessed. FÉE had specimens of the same collections from CUMING, and speculated (1852, p. 311) on the strange fact that different plants of the same species could have, or lack, indusia. BEDDOME, examining plants of *Pleocnemia* from N.E. India which are in fact exindusiate (as seen from young sori) and belong to a species different from all three in the Philippines, thought that his Indian specimens must have lost their indusia and figured a fertile leaflet from a Philippine specimen (Ferns Br. India, t. 134). COPELAND in 1960 (p. 310) still only recognized one species in the Philippines, noting that the indusia are 'sometimes fugacious'. Recent collections from Mt Makiling, at the foot of which COPELAND spent several years, confirm that CUMING's three species are distinct. The fronds are very large, so that only small parts can be put on herbarium sheets, and the stipe-scales (usually absent from herbaria) are distinctive. But herbarium specimens do show enough peculiar details if one knows what to look for, and the sum of these characters is sufficient to indicate that these species (and some others) form a genus distinct from *Tectaria* (to which COPELAND referred *P. leuzeana*), though the venation-pattern of *Pleocnemia* does occur in some species of the former. The sinus-teeth, which project out of the plane of the frond and are very conspicuous in living plants, were not noted by anyone except GAUDICHAUD until I re-defined the genus (HOLTUM 1951, 1974); there are also distinctive glands (noted by METTENIUS but not by others). The petiolar vascular structure, also peculiar, was figured by FÉE (1852, t. 21A fig. 2) and mentioned by no-one else.

It was details such as the presence and nature of scales, hairs and glands on pinnae that METTENIUS noted; these have subsequently been found to be significant diagnostically, and they give METTENIUS's specific descriptions a significance that is often lacking in BAKER's. METTENIUS maintained large genera, perhaps (like CHRISTENSEN at a later time) because he did not want to publish new binomials until he was more sure of them; he subdivided his large genera much more

FLORA MALESIANA

intelligently than HOOKER, and made improvements in subdivision in his works published in 1864. DIELS erred in ignoring several important observations made by METTENIUS.

The situation near the end of the century was that in most cases clear distinctions between groups of genera, and often even between genera now known not to be closely related, had not been discovered. This was due to a failure to understand that similar structures, whether of venation or sori, could have come into existence along different evolutionary lines. It is very clear that this is true of a simple type of anastomosis, seen in such genera as *Acrostichum* (*s.str.*), *Pteris*, *Elaphoglossum*, *Lomagramma*, *Taenitis*, *Lindsaea* and *Hemionitis*; in *Pteris*, *Lindsaea* and *Elaphoglossum* most species have free veins. The vein-pattern in *Tectaria* (*Aspidium* of *Ind. Fil.* 1905) and *Microsorium* (a segregate from *Polypodium*) is closely similar; in Malaya I found that up to 1955 a species of *Tectaria* had been included by all authors in *Polypodium*. It is also evident that acrostichoid ferns belong to several different alliances; and the acrostichoid condition is not exactly definable, so that authors disagreed in assigning genera to it. The sori of *Davallia* and *Microlepia* are very similar, but in other respects the plants are very different. An extreme case is *Heterogonium* PRESL, which I believe to be a natural genus (HOLTUM 1949); some species have indusia, some not; some species have free veins, some have anastomoses; some have separate indusiate sori, some are acrostichoid.

So the problem is to look for characters which may be a better guide to relationship than vein-patterns and sori. MILDE had shown the way by distinguishing between *Diplazium* and *Asplenium* on the basis of scales combined with vascular anatomy of the stipe. SMITH had noted that *Polypodiaceae* (*s.str.*) and the *Davallia* group of genera have a creeping caudex with stipes jointed to the dorsal surface of it; he coined the term *Eremobrya* for ferns of this habit; other ferns he called *Desmobrya*. The two terms were first defined in 1855. By this standard the ferns included by CHING (1940) and HOLTUM (1947) in *Grammitidaceae* are separate from *Polypodiaceae*. METTENIUS also found that the spores of the two groups differ (see below on DIELS 1899).

HERMANN CHRIST (1833–1933) was a lawyer who throughout a long life was actively interested in plants. He began to publish papers on ferns in 1890, and in 1897 produced *Die Farnkräuter der Erde*, an attempt to give a more balanced view of the more important species throughout the world than HOOKER and BAKER. He recognized the nature of the problem stated in the preceding paragraph, but did not manage to do much towards solving it. He placed *Aspidium* and *Phegopteris* (still separate genera, on the model of METTENIUS) in a family *Aspidiaceae*, distinct from *Polypodiaceae*, but under both *Aspidium* and *Phegopteris* had a great mixture of species not closely allied. In *Polypodiaceae*, tribe *Acrosticheae*, he had much confusion, especially in the genus *Stenochlaena* (see HOLTUM 1978, pp. 261, 266); some of this was copied by DIELS. His later work also showed lack of critical insight. In his monograph of *Elaphoglossum* (1899) he tried to subdivide the genus on characters of venation, but did not examine the veins carefully and the result is confusion; in his paper of 1907 on the Philippine species of *Dryopteris* (the composite genus of *Ind. Fil.* 1905) he did not make good descriptions nor understand relationships between species. He did not know of MILDE's work.

The century closed with the volume of ENGLER & PRANTL's *Pflanzenfamilien* covering vascular cryptogams, in which DIELS dealt with almost all the ferns (1899–1900). His *Polypodiaceae* consisted of nine tribes. He transferred several genera of the tribe *Acrosticheae* of some previous authors to *Aspidieae*, but mixed together Aspidioid and Polypodioid species under *Polybotrya*. He placed the Polypodioid genus *Platyserium* in *Acrosticheae*. He united *Phegopteris* with *Aspidium* but had a great mixture of species in it; his treatment only adds more confusion to an already very confused situation. He did understand MILDE's work, but he failed to notice some important observations made by METTENIUS and JOHN SMITH, of which the following are three examples.

Dedication

1. *Gleicheniaceae*. PRESL based his primary division of *Gleichenia* (*sens.lat.*) on the position of the sori on the veins, stating that in *Eu-Gleichenia* the sori were terminal, in all other cases dorsal on the veins. This division was copied by HOOKER, CHRIST and DIELS; but in 1856 METTENIUS had stated that the sori are *not* terminal in *Eu-Gleichenia*, and had repeated this in 1863. In the latter paper he divided *Gleichenia* into three subgenera, stating that two of them agreed in scales and in sporangia, the third (*Dicranopteris*) differing in both these structures. This was ignored by DIELS, who did not cite the paper of 1863 and mixed together in one subgenus species of *Dicranopteris* with those which differed both in scales and in sporangia. When preparing an account of the family for Flora Malesiana (HOLTUM 1959) I failed to notice METTENIUS 1863 and repeated his observations, differing only in the recognition of *Dicranopteris* as a genus distinct from *Gleichenia*, the latter having three subgenera; this is certainly the important division.

2. *Stenochlaena* and *Lomariopsis*. In 1875 (p. 140) JOHN SMITH stated the distinctions between these two genera (he had united them in 1841 and subsequently discovered the difference through observation of living plants). METTENIUS still included them in the same genus (1869, in a posthumous paper edited by KUHN) but in separate sections, and he established a new genus *Teratophyllum*, distinct from both, with two species. DIELS united *Stenochlaena*, *Lomariopsis* and one species of *Teratophyllum* in one genus (in the tribe *Aspleneae*) which he divided into two sections: *Eu-Stenochlaena* comprising the whole of *Lomariopsis* and *Teratophyllum aculeatum* (BL.) METT., and *Cafraria*, which consisted only of *S. tenuifolia*; the latter differs from the type species *S. palustris* (BURM.) BEDD. in having bipinnate fertile fronds and in little else. This is an absurdly unnatural division. DIELS included the second species of *Teratophyllum* (*T. articulatum* (J.SM.) METT.) in *Polybotrya* (tribe *Aspidieae*).

3. *Grammitidaceae*. This family was recognized as distinct by CHING in 1940; for fuller details see also HOLTUM 1947 and 1955. DIELS placed all species of the family in *Polypodium sect. Eu-Polypodium*, mixing them indiscriminately with true *Polypodium* species, except *Prosaptia* PRESL which he included in *Davallia*. BLUME in 1830, though retaining them in *Polypodium*, had already distinguished these ferns as 'spurious' in that genus. METTENIUS (1866) distinguished them in *Polypodium* as Div. 1, *Sphaerosporeae*, placing true *Polypodium* in Div. 2, *Nephrosporeae*; he did not mention *Prosaptia* in this paper, but had previously placed it with *Davallia*. As above noted, JOHN SMITH placed most Grammitoid ferns in his division *Desmobrya*, and thus separated them from *Polypodium*, but somehow he included *Prosaptia* (with the closely related *Cryptosorus*) in *Eremobrya*; he did however note that their sori were very different from those of *Davallia*. For some reason which is not at present understood, Grammitoid ferns are difficult to maintain in cultivation, and not one of them appears in JOHN SMITH's list of species which he had seen alive; this probably accounts for his mistake in placing *Prosaptia* with *Polypodium*. METTENIUS always noted the peculiar hairs on plants of *Grammitidaceae*, and also the hairs on scales and setae on sporangia, where these occur (true *Polypodiaceae* never have these characters). When he died in 1866 he was just beginning to see the significance of such structures.

Towards the middle of the 19th century academic botanists realized that taxonomic study, of the limited and formal kind which still prevailed, did not deal with important aspects of the life of plants. So they started 'scientific botany', but they made the mistake of thinking that taxonomy was an out-dated activity; many such botanists still persist in that mistake. What was needed was a better taxonomy, not its abandonment. This was especially true of tropical plants in general, and most ferns are tropical; significant facts about these plants had often not been put on record, or if recorded (such as the hairs figured by SCHKUHR) had not been understood. As 'scientific' botany diverged more and more from taxonomy, the shortcomings of the latter were less and less understood. A factor in this process was, and still is, the binomial system of nomenclature.

FLORA MALESIANA

Valid names consist of two parts, a generic name and a specific epithet. Thus one must know the correct genus if one wishes to describe a new species. But in the case of tropical plants, which were very little known to earlier authors, it was impossible to be sure of generic concepts, which changed with increasing knowledge. Thus the binomial system, in theory, imposed an impossible condition for naming new species. In practice, this situation was avoided by allowing taxonomists to make the best guess they could, with permission afterwards to change the generic name if later knowledge so indicated. Morphologists rightly wished to study plant-structures not mentioned in taxonomic descriptions; taxonomists were slow to realize the need for this as a help to better taxonomy. An outstanding exception was METTENIUS, who published important works on lateral buds on ferns (1860), on the morphology and anatomy of *Angiopteris* in comparison with other ferns (1863A) and on *Hymenophyllaceae* (1864B).

Morphologists who have not a wide knowledge of taxonomy are apt to think that any species is representative of the generic name it bears, and thus are liable to have erroneous ideas about genera (especially where such genera are still not clearly defined), and may be misled into making wrong comparisons or invalid statements about phylogeny. In view of the above discussion on the history of taxonomic study of the leptosporangiate ferns, it is evident that most 19th century taxonomy was an inadequate guide to morphologists. The most important morphologists were GOEBEL and BOWER. BOWER began his studies in the 1880s, mainly on the more primitive ferns. When he came to his summary on the leptosporangiate ferns (1928) he quoted GOEBEL's comparison of their study to wandering in a dark and trackless forest, but he did not know enough about existing information which could have provided him with some guiding light. He did not know of the work of MILDE and discussed the possible evolution of the sorus of *Asplenium* by reference to a species of *Diplazium*. He discussed *Stenochlaena*, which he interpreted according to the confused statement by CHRIST, and described the anatomy of the rhizome, but the material he described belonged to a species of *Lomariopsis*, as he could have learned from JOHN SMITH. He placed *Phyllitis* in a group separate from *Asplenium*, not knowing that natural hybrids between the two existed. He accepted CHRIST's comparison of *Elaphoglossum* with *Syngamma*, though the resemblance between the two is very superficial. He accepted the idea that the sorus of *Microlepia* was marginal in phyletic origin, but did not realize that this might also be true of *Cyathea* and *Dryopteris*. He insisted that *Deparia* was a natural genus, though each of the species included in it shows an alliance to a different group of ferns. He had not looked at CHRISTENSEN's dismemberment of '*Dryopteris*' and accepted a phyletic sequence (fig. 663 on p. 132) which derives the vein-pattern of *Bolbitis* (then still included in *Leptochilus*) from the condition of a Thelypteroid fern. But he did have a better understanding of the Gymnogrammoid ferns. GOEBEL had far more understanding than BOWER, having spent at least two periods of study in Java (BOWER never went to the tropics), but he did not keep in touch with CHRISTENSEN's work.

As above noted, CHRISTENSEN made a systematic study of all the tropical American species included in the comprehensive *Dryopteris* of *Index Filicum*. In so doing he followed the example of METTENIUS in looking for details of dermal appendages, but more critically and more consistently than METTENIUS had done; he had also a much wider range of species to examine. In this process he discovered that the many species could be separated into groups according to the nature of their hairs; he rightly insisted that groups distinguished in this way show also many other differences of a less easily definable character. CHING (1936, p. 243) added the distinctive character of vascular anatomy of the stipe of Thelypteroid ferns, in which they constantly differ from *Ctenitis* and *Dryopteris* (*s.str.*), as indeed METTENIUS had noted in his discussion of *Aspidium* in 1864. CHRISTENSEN (1911) expressed the opinion that some of the groups he had distinguished should be regarded as good genera, but he retained them in *Dryopteris* because he wished to

Dedication

examine species of the Old World before publishing new combinations. This work of CHRISTENSEN's was a turning-point in fern taxonomy. R. C. CHING applied CHRISTENSEN's ideas to ferns of southeast Asia, clearing up much previous confusion. But *Thelypteridaceae* are far more abundant and more diversified in Malesia than in mainland Asia. When writing my book on the ferns of Malaya (1955) I adopted CHING's generic concepts but stated (p. 236) that the resulting arrangement was not a natural one. I made new observations, especially of glands and hairs on sporangia (some not then published) but could not see my way to a good re-arrangement on the basis of the limited number of species in Malaya. It was only when I looked at all species in Malesia, mainland Asia and the Pacific (and also many previously unnamed collections), noting in detail structures not mentioned in earlier descriptions, that I was able to see how to improve on CHING's scheme, and to establish new genera peculiar to the Old World. CHING's work and mine (presented in the present volume) are built on CHRISTENSEN's methods and on his insights.

CHRISTENSEN subsequently identified a number of collections of ferns from Malesia and Asia (including my Kinabalu ferns, 1934) and wrote a fern flora of Madagascar (1932); in so doing he examined a large number of type specimens which had not been well described and published new information about them. The nomenclature in my book of 1955 was largely dependent on his observations on types. In 1939 he contributed a chapter on the classification of ferns to VERDOORN's *Manual of Pteridology*. This contains many new ideas, the result of his wide-ranging studies; from it one can judge the progress made since 1905, largely due to his own work and thought. His last work was a fern flora of Samoa, published after his death (1943). Owing to the stress of the war situation, no adequate obituary notice was published.

Pteridology in Malesia. The first considerable field work was on the ferns of Java, summarized by BLUME in 1828 and elaborated with excellent illustrations in 1829–30 (additional plates were published in 1847 and 1851). Little more was published until RACIBORSKI went to Bogor and undertook new field studies in West Java, summarized in his book of 1898; his descriptions are better than most of their time and his ecological information is valuable. A few years later, VAN ALDERWERELT VAN ROSENBURGH began fern studies covering the whole of Malesia by collating all existing descriptions, most of them too brief or too inaccurate to form a good basis for the keys which he prepared. In the main he followed the nomenclature of *Index Filicum*, but he wanted more clear-cut distinctions between genera as a better guide to identification, and so he adopted an artificial system. He reverted to a comprehensive tribe *Acrosticheae*, and a tribe *Phegopterideae* widely separated from *Aspidieae*; he revived *Pleocnemia* PRESL and included in it some Thelypteroid ferns. After completing his *Handbook* (1908) he continued a critical study of the specimens in the herbarium at Bogor, including many new collections, also plants in cultivation. He published descriptions of these in a series of papers, those up to 1917 being summarized in his *Supplement*. These new and amplified descriptions show a careful examination of much detail not previously recorded, including observations on spores; many of his new species are still recognized in the present work.

In Malaya H. N. RIDLEY made large new collections in the years 1888–1911, but his published work on them (1926) is very uncritical; his generic and specific descriptions are confused and sometimes inaccurate; the names he wrote on herbarium specimens at Kew are often wrong. Thus his statements on distribution of species are also often wrong. It is sometimes impossible to know the basis of such statements because often he did not write names on herbarium sheets in Singapore; I re-arranged the sheets without noting in which covers RIDLEY had placed them. RIDLEY's work on ferns is therefore usually ignored in *Flora Malesiana* except for his new names.

E. B. COPELAND (1873–1964) began a study of ferns in 1893 but soon specialized in plant

FLORA MALESIANA

physiology. He went to the Philippines in 1903 and during the years to 1917 made extensive field studies of ferns, also naming and describing collections made by others from the Philippines and other parts of Malesia. Between 1917 and 1928 he was concerned with rice cultivation in California; after that most of his active life was devoted to ferns. I have elsewhere (HOLTUM 1973) summarized his work, which culminated in his *Genera Filicum* (1947). His observations on Philippine ferns, based on the same classification, were not published until 1960. He was the first person to understand that HOOKER's genera *Cyathea*, *Hemitelia* and *Alsophila* were unnatural, but his revised scheme for *Cyatheaceae* in 1947 was little better because he did not examine the detailed structure of scales. Similarly, in dealing with *Thelypteridaceae* (which he did not recognize as a distinct family) he did not look carefully at hairs and glands; his descriptions of species are little better than BAKER's. His floristic work suffered also because he did not see the types of many of the older species and misconstrued some of them; this however does not excuse his failure to distinguish between *Sphaerostephanos penniger* (HOOK.) HOLTUM and *Pneumatopteris truncata* (POIR.) HOLTUM (as named in the present work). Yet in *Hymenophyllaceae* he did make very careful detailed observations of structure, which were very fully illustrated (COPELAND 1933, 1937, 1938). His families *Pteridaceae* and *Aspidiaceae* of 1947 are both confused mixtures which are still not fully disentangled. In general, COPELAND's failure was due to not looking for significant characters. His statement that the generic separation of *Gymnocarpium dryopteris* NEWM. from *Phegopteris connectilis* (MICHX) WATT was hardly possible is an illustration of this.

Simultaneously with COPELAND's work in the Philippines, C. A. BACKER (from 1905) was making large collections of ferns, as part of his general herbarium of the flora of Java. He collaborated with O. POSTHUMUS, who had specialized on ferns and had made many collections in several other islands also, in the production of a fern flora of Java (1939). The nomenclature follows that of the third supplement of *Index Filicum*. In general, this is a considerable advance on VAN ALDERWERELT, though the descriptions of species in complex genera are not as good as VAN ALDERWERELT's later ones. In *Cyatheaceae* the genera are not well distinguished and the specific descriptions are very inadequate; the authors could have learned much from METTENIUS (1863B). In *Dryopteris* no attempt is made to separate Thelypteroid species from the rest. The Grammitoid ferns are not separated from Polypodioids. The citation of synonyms is often uncritical. The work is of value mainly for its ecological information, but where species have been confused (e.g. under *Dryopteris uliginosa*) ecological information is also confused.

The present situation. At the beginning of this volume (p. ii, 1959) I presented a tentative list of genera, remarking that much new information would arise in the course of study in the production of the present Flora, and that new ideas on classification would probably emerge. I refrained from assigning the majority of genera of leptosporangiate ferns to families. In part 2 (1963) I showed *Dicksonia* and *Cyathea* to be much more nearly allied than I had thought in 1959. The inter-relations between genera there presented still appear sound, but the assignment of genera to families is still uncertain. In part 3 (1971) K. U. KRAMER presented a major revision of the genera of the *Lindsaea* group, clarifying distinctions between them and making a new subdivision of *Lindsaea*. Part 4, on the *Lomariopsis* group (as delimited by me in 1947) included much new information, especially on *Elaphoglossum* and *Bolbitis*, with a revised account of my earlier work on the other genera. The present part attempts a new subdivision and conspectus of the *Thelypteris* group of genera, which is so sharply distinct from other groups that I judge it to deserve family status. This decision commits us in some measure to the ultimate recognition of other families, but for this we still need more evidence. I think that the elaborate arrangement of PICHI SERMOLLI (1977) is premature, though it is much nearer to being natural than COPELAND's of 1947.

Dedication

We need more information about significant characters, and to be useful they must be available for all species; but no-one can tell in advance which characters will be significant. Since MANTON's book of 1950 the observation of chromosome numbers in a great range of ferns has provided important new evidence; but chromosome number by itself, without evidence of conformity with some quite different characters, can be misleading, and the proportion with species with known chromosome numbers is still relatively small in some genera and not easily augmented. As a result of the work by MANTON and others it has become clear that phenomena like hybridization and polyploidization — formerly regarded to be extremely rare in ferns — commonly occur also in tropical ferns. The impact of cytotaxonomic work on fern classification has recently been thoughtfully dealt with by LOVIS (1977) and WALKER (1979). KLEKOWSKI (1979) has contributed much to our knowledge of the reproductive biology of the ferns also in relation to polyploidy.

Morphologists can provide useful suggestions for characters of possible significance. Morphology and taxonomy are interdependent; morphology without a good taxonomy may arrive at wrong conclusions; taxonomy without the stimulus of morphology may miss important distinguishing characters. Features which have recently been shown to be of great significance for fern classification are stomata (VAN COTTHEM, 1970) and spores (LUGARDON, 1971). Gametophytes, formerly a neglected item, are important and often indicate relationships within the larger groups of ferns.

In the end, a practical taxonomy must rest on a limited number of characters which are observable without very elaborate equipment, which is one reason why uninformed academic botanists regard it as unscientific. I hope and believe that this Flora is producing new contributions to that end.

Work now in progress for further instalments of Flora Malesiana Series II is as follows. Dr E. HENNIPMAN, with collaborators, has begun a study of *Polypodiaceae* (*s.str.*); Prof. K. IWATSUKI is making progress with *Hymenophyllaceae*; Mr G. J. DE JONCHEERE is working on the *Davallia* group; Dr B. S. CROXALL is studying the complexities of *Grammitidaceae*; Prof. K. U. KRAMER has started on *Pteris*, which seems to me to be an isolated genus; Prof. T. C. CHAMBERS has made a world monograph of the genus *Blechnum* and it is hoped that he will be able to deal with the *Blechnum* group for Flora Malesiana; Mr A. C. JERMY is working on the complex genus *Selaginella*.

Of the other genera, *Dennstaedtia* is of basic importance. It is more diversified in the Philippines, New Guinea and the Pacific than in any other part of the world and, as the fronds are very large, existing herbarium material often does not give full information about them; more field work, by people who know what to look for, is needed. The most complex groups still not dealt with are those of *Tectaria* and *Athyrium*, the latter being very difficult, with need of much new observation, especially of scales. I have made studies of two genera of the *Tectaria* group and propose to continue with that group if I am able to do so. The *Adiantum* group (as listed in 1959) is complex, but not so well developed in Malesia as in drier climates, and is more dependent on studies of plants in such climates than are most other groups. This is true also of the *Dryopteris* group, which is mainly temperate in distribution.

December 1979

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FLORA MALESIANA

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