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GENERAL INTRODUCTION TO PAPERS ON ZINGIBERACEAE

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For just over two decades there has been a rising interest in the family Zingiberaceae. The first major event in this period was R. E. Holttum's much needed revision of the family as it occurs in the Malay Peninsula (Holttum, 1950). The importance of this paper, however, was far more than local: Holttum put forward ideas, especially on the importance of inflorescence structure, that affect the whole classification of the family; he also brought back into the limelight the very fine work that had been done by T. Valeton (1904–1921) at the Botanic Garden, Buitenzorg (Bogor). These studies of Holttum and of Valeton were based largely on the living plants (or on adequate material preserved in alcohol) and stand in a class apart. They showed up the enormous deficiencies that are inevitable in a herbarium investigation, such as that which was the basis for K. Schumann's account written for Das Pflanzenreich (1904).

Work at Edinburgh started in 1962 with the study of collections made in Sarawak by Burtt & Woods in a deliberate attempt to extend Holttum's classification geographically. The problems encountered in this work dictated its expansion into a more general survey and encouraged the building-up at Edinburgh of a collection of living plants and of flowers and inflorescences preserved in alcohol. In both fields we have received help from friends too numerous to name, but we wish to acknowledge a particular debt to Mr J. S. Womersley and his staff at the Division of Botany, Forest Dept., Lae, New Guinea.

We are also especially grateful to Dr G. Moggi, Firenze, for the loan of the types of many of K. Schumann's species based on Beccari's Bornean collections. The Director of the Botanic Garden Singapore has lent some of H. N. Ridley's types and others have kindly been sent on loan from Kew. The correlation of these sets of specimens has enabled us to identify much of the Sarawak material and to effect some reduction in the current list of names.

Work on the Zingiberaceae has brought us into contact with other students of the family, in particular with Professor Kai Larsen who is studying the family in the monsoon climate of Thailand (Larsen 1962—) and Dr Lim Siew-Ngo who has investigated the complicated genus *Globba* in the Malay Peninsula (Lim, Notes R.B.G. Edinb. 31: 243–285, 1972).

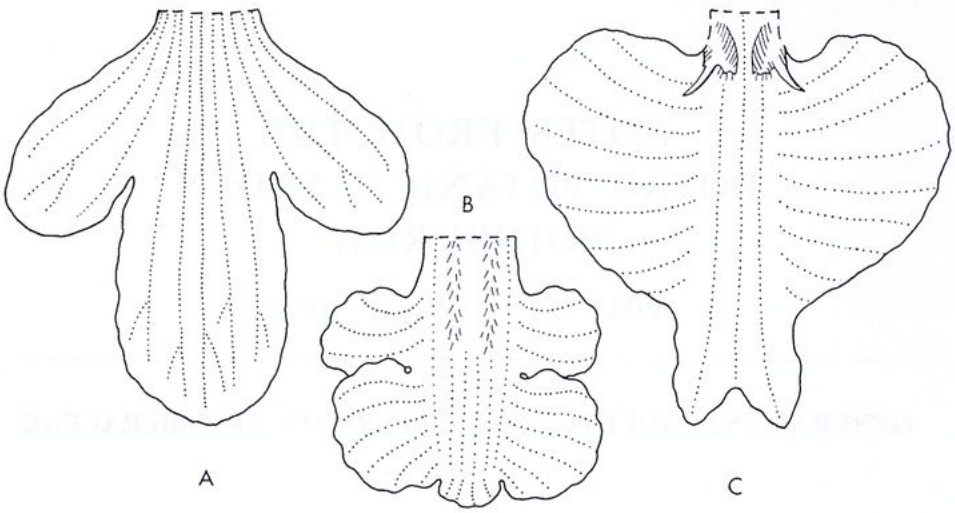

FIG. 1. Labellum types in Zingiberaceae: A, *Zingiber coloratum* x 2; B, *Alpinia purpurata* x 2; C, *Alpinia novae-pommeraniae* x 1.

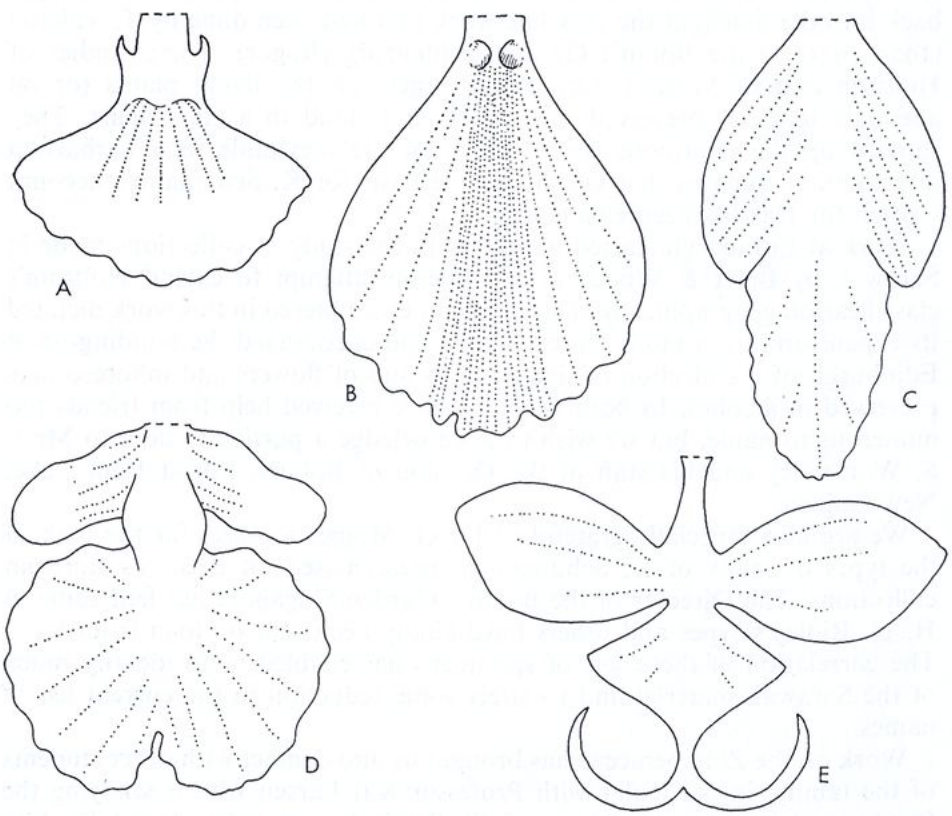

FIG. 2. Labellum types in Orchidaceae: A, *Aganisia cyanea* x 1; B, *Sobralia liliastrum* x 1; C, *Maxillaria trilosis* x 2; D. *Epidendrum atropurpureum* x 1; E, *Phalaenopsis amabilis* x 2.

In 1968 O. A. Olatunji, a research student at Edinburgh, was able to use the herbarium and living collections that had been brought together to extend the anatomical investigations made by P. B. Tomlinson (1956, 1969). Now that we all have papers ready for publication at the same time, it has seemed logical, and helpful to others, to present them between the same covers.

Studies in Zingiberaceae have been progressing on many different lines and it is not easy for everyone to keep in touch. A list of recent important papers that have come to my notice (chiefly those published since 1950) is therefore appended. This bibliography is surely incomplete and I shall be glad to receive additions to it.

Holttum (1950: 11–12) surveyed the various interpretations of the labellum of Zingiberaceae. Since then V. S. Rao and his associates have made extensive studies of serial sections and have concluded that the labellum is a double structure, formed from the two united antero-lateral staminodes of the inner whorl (Rao, Gupte & Karnik, 1954; Rao, 1970; Pai, 1965). On this view the median anterior stamen of the outer whorl is entirely suppressed. This view, which is that originally put forward by Payer (1857, 674, t. 144), fits well with the obviously bilobed labellum of a genus such as *Kaempferia* or *Burbidgea*, and the fact that Payer derived it from a species where the labellum is not bilobed (*Alpinia zerumbet*, but misidentified as *A. nutans*) adds to its probability. In any case the labellum acts very much as a unitary organ; the taxonomist would, however, be concerned if it were shown that the labellum did not have the same origin throughout the family: a view held by several authors including K. Schumann, though it seems not to have affected his classification.

The lips of Zingiberaceae and Orchidaceae must often serve a similar function in the floral mechanism. It is therefore illuminating to compare their form, for the labellum of Orchidaceae represents a single perianth member: its protean diversity owes nothing to the presence or absence of staminodes. In the first place, the tip of the labellum can be entire, bilobed or trilobed in both families. Secondly, the lower part of the orchid labellum is not infrequently expanded into two erect lateral lobes (fig. 2 C). Such lobes are very similar in general form to the "adnate staminodes" of *Zingiber* (fig. 1 A). Furthermore in many species of *Alpinia*, similar lobes are developed on the main part of the labellum, above those other structures which are usually interpreted as staminodes (fig. 1 C). It seems reasonable to conclude that those upstanding lateral lobes at the base of the labellum are functional.

Development at the base of the orchid labellum is almost at its simplest with the development of two lateral lobes. Much greater elaboration is known, the examples shown (fig. 2) being simply some that are comparable to conditions found in Zingiberaceae, where outgrowths at the base of the labellum are usually thought to represent the lateral staminodes. I have no intention of denying that possibility. The point being made is simply that in both Orchidaceae and Zingiberaceae the margin of the labellum towards its base is apparently a region of meristematic activity. It is easy to be persuaded that the free petaloid structures of *Hedychieae* (fig. 3 A, C) represent the lateral staminodes; but the situation in *Alpineae* is less convincing. The single or double tooth-like structures, tumid patches or rarer petaloid outgrowths (fig. 4) may, in some cases at least, be merely basal

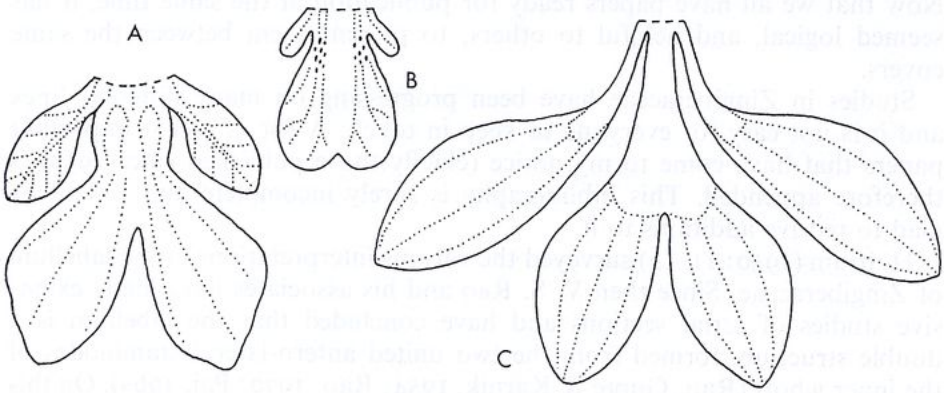

FIG. 3. Labellum types and lateral staminodes in the tribe Hedychieae: A, *Roscoea purpurea* x 1; B, *Scaphochlamys perakensis* x 2; C, *Kaempferia elegans* x 2.

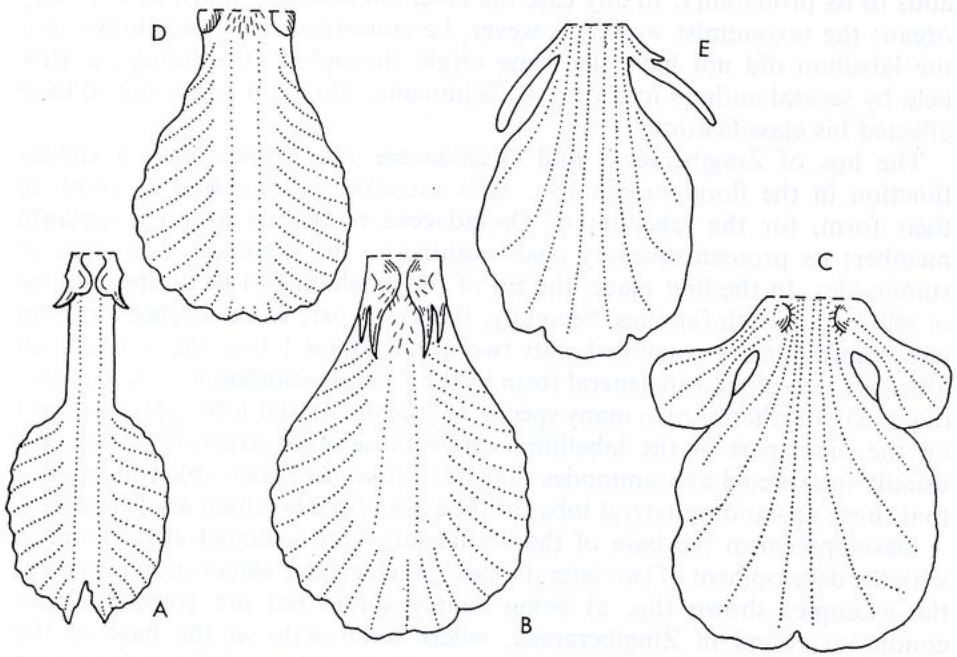

FIG. 4. Labellum types and lateral staminodes in Alpineae: A, *Alpinia galanga* x 2; B, *Amomum xanthophlebium* x 1; C, *Cenolophon oxymitrum* x 2; D, *Amomum* sp. (*B.* 5283) x 2; E, *Alpinia* sp. aff. *glabra* x 1.

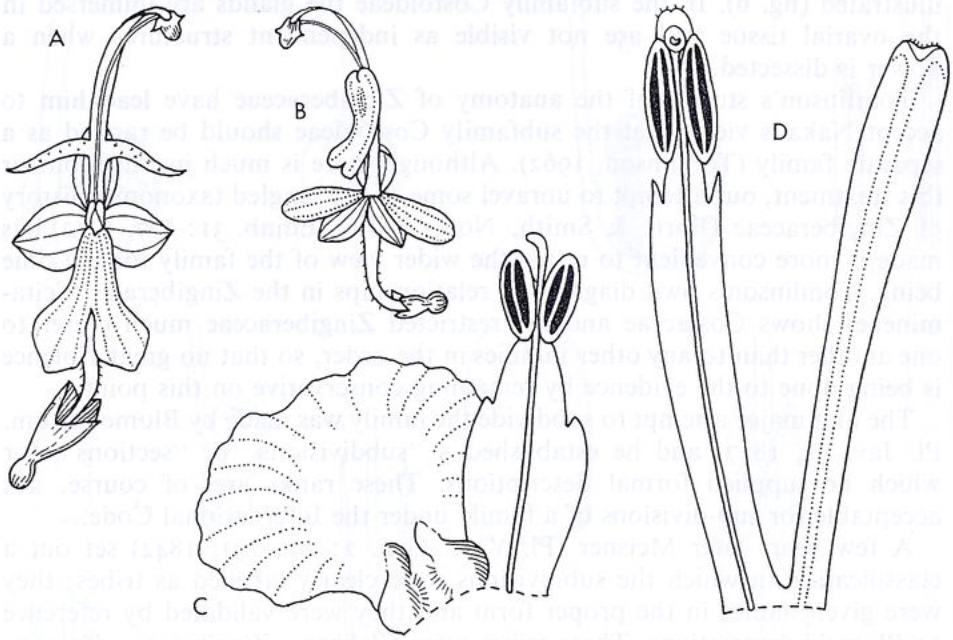

FIG. 5. A, *Mantisia wardii*, flower. B, *Globba leucantha*, flower. C, *Alpinia* sp. sect. *Psychanthus*, labellum and stamen. D, *Alpinia* sp. aff. *pulchra*. All x 2.

elaborations of the labellum without any significance in terms of morphological homology.

The lateral staminodes in Zingiberaceae have also been "recognized" as outgrowths of the filament of the fertile stamen. In *Globba* these are near the base of the long exserted filament, but in the very similar flower of *Mantisia* they occur half-way up the filament (fig. 5 A, B). In *Alpinia pulchra* and others there are two teeth on the side of the rather broad filament (fig. 5 D), and these teeth are regarded by both Ridley and K. Schumann as being staminodial. In *Alpinia* sect. *Psychanthus* (N.G.F. 49052) there are two teeth on the filament and also two lateral swellings at the base of the lip (fig. 5 C) just where in other species (e.g. *A. allughas*, *A. galanga*) the 'lateral staminodes' arise (fig. 4 A). It seems to me dangerous to attempt a morphological interpretation of mere tooth-like outgrowths of the filament; comparable teeth are well-known in *Allium*, where the idea that they represent the stipules of the filaments is a fancy which contributes nothing to their being understood.

It is now generally agreed that the epigynous glands are outgrowths of the upper surface of the ovary (Rao, 1963) and are not homologous with staminodes or stylodes. These ideas evidently derived from examination of those species where just two elongate glands are present. Had a more thorough survey preceded the formulation of such theories it would have been seen that such a condition is only one of several. Especially in the tribe *Alpineae* the nectarial structure may be more or less cupular or a massive gland of varying shapes: in neither case does it in the least suggest the missing floral members. A range of types found in Zingiberoideae is

illustrated (fig. 6). In the subfamily Costoideae the glands are immersed in the ovarial tissue and are not visible as independent structures when a flower is dissected.

Tomlinson's studies of the anatomy of Zingiberaceae have lead him to accept Nakai's views that the subfamily Costoideae should be ranked as a separate family (Tomlinson, 1962). Although there is much justification for this treatment, our attempt to unravel some of the tangled taxonomic history of Zingiberaceae (Burtt & Smith, Notes R.B.G. Edinb. 31: 177, 1972) has made it more convenient to retain the wider view of the family for the time being. Tomlinson's own diagram of relationships in the Zingiberales (Scitamineae) shows Costaceae and the restricted Zingiberaceae much closer to one another than to any other families in the order, so that no great violence is being done to the evidence by remaining conservative on this point.

The first major attempt to subdivide the family was made by Blume (Enum. Pl. Jav. 41, 1827) and he established 5 "subdivisions" or "sections", for which he supplied formal descriptions. These ranks are, of course, not acceptable for sub-divisions of a family under the International Code.

A few years later Meisner (Pl. Vasc. Gen. 2: 290–291, 1842) set out a classification in which the subdivisions were clearly labelled as tribes; they were given names in the proper form and they were validated by reference to Blume's descriptions. These tribes were *Globbeae*, *Zingibereae*, *Alpineae*, *Amomeae*, *Costeae*. Nowadays *Alpinia* and *Amomum* are not separated at tribal level, but recognition is given to a group of genera centred on *Hedychium*. The tribe *Hedychieae* dates from O. G. Petersen's account of the family in the first edition of Engler & Prantl, Die natürliche Pflanzenfamilien (1889).

It now seems desirable to accept Zingibereae as a tribe containing the genus *Zingiber* alone. The case for doing so is argued in detail in the next article. The tribes of Zingiberoideae will then be *Zingibereae*, *Globbeae*, *Hedychieae*, *Alpineae*. The acceptance of these tribes as a working basis does not imply satisfaction with their definitions.

Globbeae has usually been characterized by its unilocular ovary with parietal placentae. However, similar ovaries may be found in *Riedelia* (e.g. *R. ligulata* Ridl., *R.* aff. *subulicalyx* Val., N.G.F. 40168). Furthermore Rao & Gupte (1961, p. 139 & figs. 60, 61) have shown that the most basal part of the ovary of *Globba leucantha* has an axile placenta and septa reaching to the ovary wall: that is, it appears to be trilocular in transverse section: the placentae become parietal higher up. Throughout the family a mere handful of species has so far been examined critically from this point of view, but it seems clear that the distinction is by no means fundamental. Similar transitions between axile and parietal placentation are, of course, well known in quite unrelated groups, such as Ericaceae—*Pyroloideae* and *Monotropoideae* (cf. Pykko, 1969) or Scrophulariaceae (Hartl, 1956). The characteristic flower of *Globba*, with its long-exserted anther, suggests that it should be easy to find other distinctive features. However, the anther is long-exserted in species of *Hedychium* (*Hedychieae*) and in some species of *Alpinia* and in *Pommereschea* (*Alpineae*), but not in *Hemiorchis* (*Globbeae*).

Similarly the dividing line between *Hedychieae* and *Alpineae* is not easy to draw. The characteristically petaloid lateral staminodes of *Hedychieae* are occasionally quite small (e.g. in *Scaphochlamys perakensis*, fig. 3 B) whereas

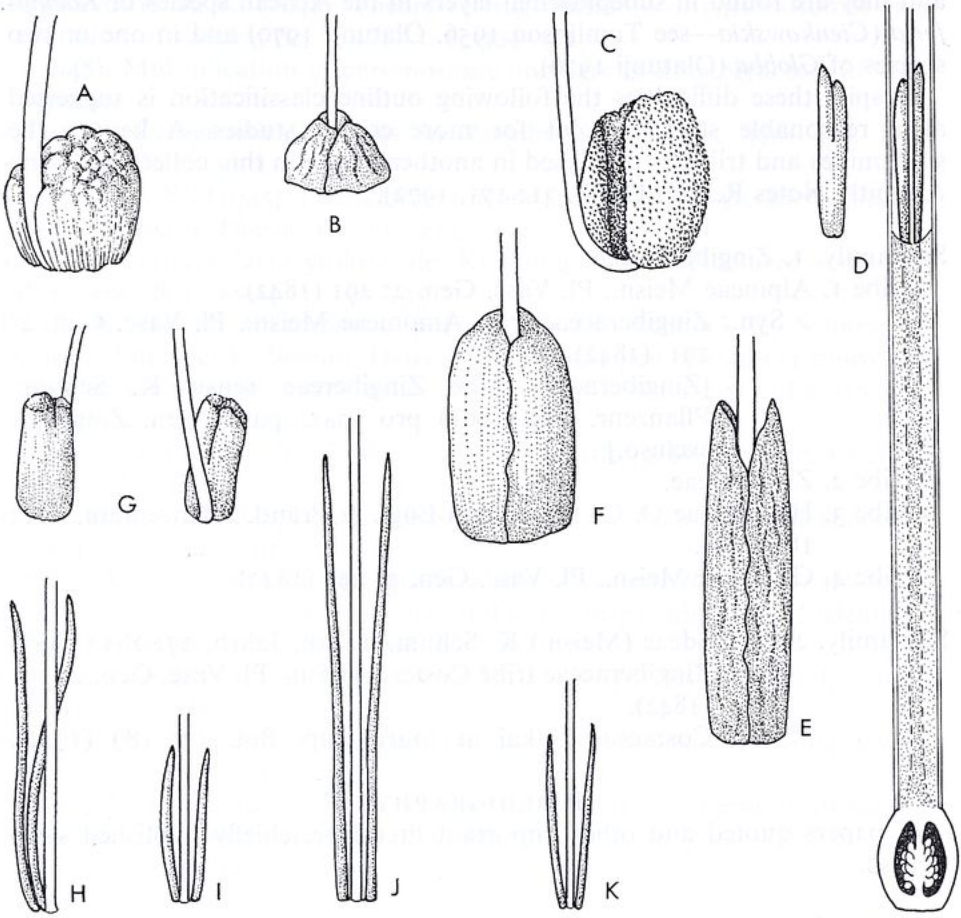

FIG. 6. Epigynous glands in Zingiberaceae: A, *Alpinia* sp. sect. *Pleuranthodium*; B, *Plagiostachys* sp.; C, *Riedelia lanata;* D, *Cyphostigma pedicellatum;* E, *Hornstedtia tomentosa;* F, *Cenolophon argenteum;* G, *Hedychium cylindricum;* H, *Roscoea purpurea;* I, *Caulokaempferia yunnanensis;* J, *Zingiber coloratum;* K, *Mantisia wardii.* A & C, lateral view; remainder abaxial. All x 9 except D (x 3).

those of *Alpineae* have already been seen (fig. 4 C, E) to be better developed sometimes than would be expected from the usual key character "lateral staminodes small or absent".

The plane of distichy of the leaves may be a more reliable difference (Weisse, 1932, 1933). It is parallel to the length of the rhizome in *Hedychieae*, transverse to it in *Alpineae*. Unfortunately it is too often unobservable on herbarium specimens to be convenient in use and but a small percentage of known species have yet been checked.

Tomlinson (1956, 1969) found that there were no fundamental anatomical differences distinguishing the tribes and the recent examination at Edinburgh of a wider range of material has merely confirmed this (Olatunji, 1970). Some features are certainly helpful. For instance, the presence of epidermal stegmata (cells containing a single large silica body) would seem to indicate tribe *Alpineae* with certainty. However, many species of *Alpineae* lack stegmata

and they are found in subepidermal layers in the African species of *Kaempferia* (*Cienkowskia*—see Tomlinson 1956, Olatunji 1970) and in one or two species of *Globba* (Olatunji 1970).

Despite these difficulties the following outline classification is suggested as a reasonable starting point for more critical studies. A key to the subfamilies and tribes is published in another article in this collection (Burtt & Smith, Notes R.B.G. Edinb. 31: 171, 1972).

Subfamily. 1. Zingiberoideae

Tribe 1. Alpineae Meisn., Pl. Vasc. Gen. 2: 291 (1842).

Syn.: Zingiberaceae tribe Amomeae Meisn., Pl. Vasc. Gen. 2: 291 (1842).

[Zingiberaceae tribe Zingibereae sensu K. Schum., Pflanzenr. 163 (1904) pro max. parte, gen. Zingibero excluso.]

Tribe 2. Zingibereae.

Tribe 3. Hedychieae O. G. Petersen in Engl. & Prantl, Pflanzenfam. 2, 6: 18 (1889).

Tribe 4. Globbeae Meisn., Pl. Vasc. Gen. 2: 291 (1842).

Subfamily. 2. Costoideae (Meisn.) K. Schum. in Bot. Jahrb. 27: 265 (1899).

Syn.: Zingiberaceae tribe Costeae Meisn., Pl. Vasc. Gen. 2: 291 (1842).

Costaceae Nakai in Journ. Jap. Bot. 17: 189 (1941).

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(ii) Both Ridley and K. Schumann published papers containing new Malesian species in 1899. They are: Ridley, H.N., in Journ. Straits Br. Roy. Asiatic Soc., 32: 85–184 (June) and Schumann, K., in Engler's Bot. Jahrb. 27: 259–350 (September).

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