Kristýna Hlavatá

Biogeography of the subfamily Alpinioideae

Biogeografie podčeledi Alpinioideae

Bakalářská práce

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Prohlášení:

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V Praze dne 13. 5. 2012

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Abstract

This work aims to summarise the recent knowledge of the distribution of the subfamily Alpinioideae and suggest the possible patterns of distribution and dispersal for individual genera, particularly for South-East Asia, where the majority of genera is found. Alpinioideae is a quite recently established and unresolved group and some of its genera are polyphyletic. The main part of the subfamily is distributed throughout South-East Asia to Australia and Oceania, two genera (*Aframomum* and *Renealmia*) are found in Africa and the genus *Renealmia* has undergone long-distance dispersal to South America. Three genera (*Leptosolena, Paramomum* and *Siamanthus*) are monotypic endemics. Alpinioideae is further divided into the tribes Alpinieae and Riedelieae.

Keywords: Biogeography, Alpinioideae

Abstrakt

Tato práce si klade za cíl shrnout současné poznatky o rozšíření podčeledi Alpinioideae a navrhnout možné vzorce rozšíření a disperze jednotlivých druhů, a to zejména pro jihovýchodní Asii, kde se nalézá většina druhů. Alpinioideae jsou poměrně nedávno zavedenou a nevyřešenou skupinou a některé z rodů jsou polyfyletické. Hlavní část podčeledi je rozšířena v jihovýchodní Asii až po Austrálii a Oceánii, dva rody (*Aframomum* a *Renealmia*) se vyskytují v Africe a rod *Renealmia* se pomocí disperze na dlouhou vzdálenost rozšířil do Jižní Ameriky. Tři rody (*Leptosolena, Paramomum* a *Siamanthus*) jsou monotypické endemity. Alpinioideae se dále dělí na kmeny Alpinieae a Riedelieae.

Klíčová slova: Biogeografie, Alpinioideae
Table of Contents

Abstract – Abstrakt........................................................................................................2
Acknowledgement...........................................................................................................5
Introduction....................................................................................................................5
Methods.........................................................................................................................6

Table 1. An overview of previously used names in Alpinioideae....................................7

1. Biogeography of Southeast Asia.............................................................................8
   1.1 The abiotic conditions.........................................................................................8
   1.2 Patterns of migration........................................................................................9

2. Zingiberaceae..........................................................................................................10
   2.1 Description........................................................................................................10
   2.2 Phylogeny..........................................................................................................10
   2.3 Problems of classification................................................................................11
   2.4 Distribution........................................................................................................11

3. Alpinioideae............................................................................................................12
   3.1 Description........................................................................................................12
   3.2 Phylogeny..........................................................................................................12

4. Genera in Alpinioideae, their description and distribution....................................14
   4.1 Aframomum.......................................................................................................14
      4.1.1 Description..................................................................................................14
      4.1.2 Distribution...............................................................................................14
      4.1.3 Centres of diversity and possible patterns of dispersal..............................15
   4.2 Alpinia.................................................................................................................15
      4.2.1 Description..................................................................................................15
      4.2.2 Distribution...............................................................................................16
      4.2.3 Centres of diversity and possible patterns of dispersal..............................18
   4.3 Amomum............................................................................................................18
      4.3.1 Description..................................................................................................18
      4.3.2 Distribution...............................................................................................18
      4.3.3 Centres of diversity and possible patterns of dispersal..............................19
   4.4 Burbidgea...........................................................................................................19
      4.4.1 Description..................................................................................................19
      4.4.2 Distribution...............................................................................................19
      4.4.3 Centres of diversity and possible patterns of dispersal..............................20
   4.5 Cyphostigma.....................................................................................................20
      4.5.1 Description..................................................................................................20
      4.5.2 Distribution...............................................................................................20
   4.6 Elettaria..............................................................................................................20
      4.6.1 Description..................................................................................................20
      4.6.2 Distribution...............................................................................................20
      4.6.3 Centres of diversity and possible patterns of dispersal..............................21
   4.7 Elettariopsis......................................................................................................21
      4.7.1 Description..................................................................................................21
      4.7.2 Distribution...............................................................................................21
      4.7.3 Centres of diversity and possible patterns of dispersal..............................22
   4.8 Edlingera...........................................................................................................22
      4.8.1 Description..................................................................................................22
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Introduction

The Zingiberaceae are a difficult and to the present day largely unresolved group which has been intensively researched during the last few decades. The most comprehensive monography on Zingiberaceae was written by Schumann in 1904, more than a century ago. Since then there has been a number of different classifications proposed, but to the recent day this group is not fully resolved. The development of molecular methods and phylogenetics moved the research to a new level, but it also gave rise to new questions.

The subfamily Alpinioideae has been established quite recently (2002) and the internal relationships of the group are still partly unresolved. Some of the largest genera such as Alpinia or Amomum are polyphyletic, which makes even the genus definition problematic. Furthermore, the taxonomic revision in most regions of South-East Asia is still very poor and new species are still being discovered in the less accessible areas. Those places are problematic to access not only because of the physical obstructions arising from the character of the tropical biomes, but often also due to lack of understanding for the research by the local inhabitants or even the government (and lack of funding for the research projects).

This work attempts to map the distribution of the subfamily Alpinioideae and suggest the centres of diversity for each the included genera. It describes the evolution of phylogeny of both Zingiberaceae and Alpinioideae and focuses mainly on the region of South-East Asia, where lies the centre of diversity of Alpinioideae. As the subfamily has not yet been revised and the sources are therefore inconsistent, this work can only be an approximation; however, I hope that it will at least cast some light on this complex and unfortunately not yet well explored group.
Methods

As this work is based on bibliographic search, most of the publications were obtained from botanical libraries of the Faculty of Sciences, Institute of Botany ASCR and the Czech Botanical Society; some were downloaded from Internet databases, mostly JSTOR (http://www.jstor.org) and Web of Knowledge (http://apps.webofknowledge.com) or found on the Internet for free download (such as the articles published in Nordic Journal of Botany).

The main publications used were Chong et al. 2009; Holttum 1950; Hooker 1984; Hutchinson et al. 1968; Klopper et al. 2006; Lamxay 2001; Larsen 2005; Larsen and Larsen 2006; Lecomte 1942; Maas 1977; Newman et al. unpubl.; Newman et al. 2004; Noltie 1994; Ohwi 1965; Sabu et al. 2004 (website), Schumann 1904; Thonner 1908; Wu et al. 1994+ (website).

The information on diversity of Alpinioideae is spread through publications from various times, and as the species and genus concepts changed over time (Table 1), the authors use different concepts depending on when they wrote the work or what concept seemed most suitable to them (for example, Phạm in Cay Co Viet Nam, 1999 uses the old concept for Etlingera, although the new concept by Smith was already published in 1986).

Some of the more comprehensive publications are already very old (The Flora of British India 1894, Flore générale de l’Indochine 1908-1942) and their revisions are often nonexistent or still in making, particularly for Zingiberaceae (Flora Malesiana). I tried to mitigate this problem by choosing publications written after the year 1904, using Schumann’s concept as the basis; I made an exception with The Flora of British India, as it covers most of the region where Alpinioideae occurs, but as the genus concepts are different and many species had not yet been found by then, it is used rather as a comparison to the recent knowledge offered, for example, by the online checklist Gingers of India compiled by Sabu et al. (2004). I had also conducted research in order to compare the taxonomic concepts in different sources, for which I used the World Checklist database (http://apps.kew.org/wcsp/).

Another problem is that newer publications concerning South-East Asia, especially those published by local publishers (such as Etlingera of Borneo), are often difficult to obtain in the Czech Republic. This can sometimes be solved if the checklist or flora exists in an electronic version or in the form of an Internet database.

The most recent publication covering an area with majority of diversity of Alpinioideae is the work of Newman et al. (2004). The geographical division of Malesia (a biogeographic region which includes Sundaland, Wallacea, the Philippines, New Guinea and the Bismarck Archipelago) in this thesis was modelled after this publication, which uses the third level
areas of the TDWG (International Working Group on Taxonomic Databases for Plant Sciences) standard world geographical scheme. This work, however, attempts to describe the distribution of the chosen genera in individual countries; therefore, the occurrence of genera in the areas stated by the abovementioned work was always noted down for the particular state. It should be noted that by „Thailand“, they mean only the provinces of Narathiwat, Pattani, Satun, Songkhla and Yala; the distributions for Thailand were therefore taken from the book *Gingers of Thailand* by Larsen and Larsen (2006).

The result of this work is represented by two tables listing the numbers of species for individual genera according to the main publications and describing the numbers of species in individual regions. Maps were made in order to illustrate the distribution patterns of the genera. Some localities are not marked in the map (the Mascarene Islands, Micronesia, Hawaii) as they were not drawn in the map or out of its range. For some genera (*Renealmia, Aframomum*) the maps are only approximate as I did not find more specific data for their distribution.

Table 1. An overview of previously used names for the genera in Alpinioideae. Compiled from Newman et al. (2004), *Index Nominum Genericorum* (Farr and Zijlstra 1996+) and the *Zingiberaceae Resource Centre* (Newman, Škorničková and Pullan 2012).

<table>
<thead>
<tr>
<th>Current name</th>
<th>Previously used names (if any)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpinia Roxb. (1810)</td>
<td>-</td>
</tr>
<tr>
<td>Amomum Roxb. (1820)</td>
<td>Cardamomum Kunze (1891), Paramomum S.Q. Tong (1985)</td>
</tr>
<tr>
<td>Burbidgea Hook. f. (1879)</td>
<td>-</td>
</tr>
<tr>
<td>Cyphostigma Benth. (1882)</td>
<td>-</td>
</tr>
<tr>
<td>Élellaria Maton (1811)</td>
<td>Matonia J. Stephenson et J.M. Churchil (1831)</td>
</tr>
<tr>
<td>Elettariopsis Baker (1892)</td>
<td>-</td>
</tr>
<tr>
<td>Etlingera Giseke (1792)</td>
<td>Geanthus Reinw. (1826), Diracodes Blume (1827), Achasma Griff. (1851), Nicolaia Horan. (1862), Cardamomum Kunze (1891), Hornstedtia Sect. Phaeomeria Ridl. (1899)</td>
</tr>
<tr>
<td>Geostachys (Baker) Ridl. (1899)</td>
<td>Conamomum Ridl. (1899), Corenophila Ridl. (1909)</td>
</tr>
<tr>
<td>Hornstedia Retz. (1791)</td>
<td>Greenwaya Giseke (1792), Donacodes Blume (1827), Stenochasma Griff. (1851), Cardamomum Kunze (1891)</td>
</tr>
<tr>
<td>Leptosolina C.Presl. (1827)</td>
<td>-</td>
</tr>
<tr>
<td>Paramomum</td>
<td>-</td>
</tr>
<tr>
<td>Plagiostachys Ridl. (1899)</td>
<td>Cardamomum Kunze (1891)</td>
</tr>
<tr>
<td>Pleuranthodium (K.Schum.) R.M.Smith (1991)</td>
<td>-</td>
</tr>
<tr>
<td>Renealmia L. (1782)</td>
<td>Alpinia longepetiola Gagnep. (1906)</td>
</tr>
<tr>
<td>Siamanthus K.Larsen &amp; Mood (1998)</td>
<td>-</td>
</tr>
<tr>
<td>Siliquamomum Baillon (1895)</td>
<td>-</td>
</tr>
<tr>
<td>Vanoverberghia Merr. (1912)</td>
<td>-</td>
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</tbody>
</table>
1. Biogeography of South-East Asia

1.1 The abiotic conditions

The vegetation and the growing season are in SE Asia determined mainly by the abundance and seasonality of rainfall. The region has a monsoonal climate, which developed after the rise of the Tibetan plateau some 30 Ma and intensified about 10 Ma (Morley 2007, Berger 2009; cited in Woodruff, 2010). The first monsoon arrives in summer from southwest, bringing moisture from the Indian Ocean. If there is a second monsoon, it occurs in winter in the reverse direction. This monsoon is typically drier. After the summer monsoon follows a hot dry season lasting 1-7 months. The monsoon pattern is disrupted every 4-6 years by ENSO (El Niño Southern Oscillation) events, which are associated with drought and increased fire frequency (Berger 2009, Taylor 2010; cited in Woodruff 2010). The annual mean rainfall oscillates between 1,000 and 3,000 mm from the continental SE Asia to southern Borneo, with a few isolated super-wet spots. In accordance with this pattern, the productivity of the forest increases by as much as 200 Mg C/ha (million grams of carbon per hectare) from the north to the south (Brown et al. 2001; cited in Woodruff 2010).

The largest geographic feature of South-East Asia, the Sunda Shelf plains, has been flooded by the sea for the last 14 Kyr (Woodruff 2010). During the first half of the Tertiary the sea levels were about 25 m higher than today (Haywood et al. 2009, Naish and Wilson 2009; cited in Woodruff 2010) and the climate was warm and humid. The high sea levels caused the Thai-Malay peninsula to appear as “an island chain with water gaps separating the pre-Tertiary mountains of continental Asia from those in peninsula Malaysia, Sumatra and Borneo” (Woodruff 2010, p. 922). As opposed to that, when the sea levels fell lower than -30 m the Sunda Shelf was exposed, providing habitat between continental Asia, Borneo and Bali. This state was almost continuous for most of the last 2 Myr, and land bridges connecting the continent and present day islands were quite usual (Woodruff 2010). There were many large lakes in SE Asia during Pleistocene, of which only Tonle Sap (Cambodia) remained until the recent day as the others were located on the exposed Sunda Shelf and were submerged as the sea levels rose (Sathiamurthy and Voris 2006; cited in Woodruff 2010).
Plant dispersals to and from the Sunda region have been mainly controlled by climate since the Eocene. The ever-wet rain forest climates became widespread at about 20 Ma in the early Miocene, at which time they extended northward as far as Japan (Morley 1998).

As Woodruff (2010) states, according to the study of Cannon et al. (2009) who modelled the changes in distribution of major forest types (lowland evergreen rainforest, upland forest above 1,000 m and coastal mangrove forest) during the cooler phases of the last full glacial cycle the forests expanded rather than contracted (Woodruff 2010). They found that lowland and montane forests of Sundaland were more extensive during most of the glacial period; for example, the upland forest was 2-3 times more extensive than it is in the present. They concluded that today’s rainforests are refugial as opposed to those of earlier periods and their behaviour is opposite of those in temperate regions (Cannon et al. 2009; cited in Woodruff 2010).

1.2 Patterns of migration

A number of studies had been conducted to find out the biogeographic patterns in South-East Asia, some of them on individual genera, some on a larger group of organisms. A comprehensive study by Turner, Hovenkamp and Van Welzen (2001), carried out on two large data sets of both plants and animals, states that while there are two general patterns to be expected – one of South-East Asian elements expanding into Australian areas, and the other one of Australian elements expanding in the reverse direction – they are, in fact, very weakly supported by their research and do not allow general conclusion.

Another study has been carried out on the genus *Orchidantha* (*Lowiaceae*) to explore its chromosome numbers and their biogeographic implications (Song et al. 2004). The family *Lowiaceae* is monogeneric and is the only family in Zingiberales restricted to a single continent. The authors state that while *Orchidantha* was regarded as relict by Larsen (1966), no conclusions can be drawn from the distribution of extant *Orchidantha*. They suggest that the genus may have originated in South Africa, perhaps before India broke away from Africa, and then migrated into Asia; the common ancestor is now extinct (Song et al. 2004).

A study conducted by Thomas et al. (2012) on the dispersal of the genus *Begonia* suggests that this genus had undergone initial diversification in continental Asia and dispersed eastwards to Malesia, where it further diversified during the Pliocene. This second diversification was aided by the orogenesis and cyclic variance in the Pliocene and Pleistocene, which offered a wider range of habitats.
A comprehensive study of the biogeography of mammals in South-East Asia (Heaney 1986) notes that more endemic species occur on isolated and geologically old oceanic islands, particularly on the Philippines, where speciation may have exceeded colonization in contribution to species number.

2. Zingiberaceae

2.1 Description

The Zingiberaceae (gingers) is a family in the order Zingiberales containing around 50 genera and over 1200 species; some authors estimate as much as 1500 species (Van Royen 1979).

The gingers are often used in medicine or as spices (e.g. Zingiber officinalis, Alpinia galanga, Curcuma sp.) as they contain ethereal oils. Some species are also used as ornamental plants (e.g. Alpinia, Etlingera, or Hedychium). They are perennial flowering plants with creeping rhizomes which can be tuberous or horizontal and distichous leaves whose sheaths overlap, forming a pseudostem. The plane of distichy is parallel to the rhizome (with exceptions). Some of them may be epiphytic (e.g. some species of the genus Burbidgea).

The flowers are zygomorphic, arranged in branched inflorescences with deciduous bracts arranged in a spiral. The flower usually has only one fertile stamen. The labellum, which is the distinguishing morphological feature of the Zingiberaceae flower, is formed by the fusion of two lateral staminodes of the inner whorl (Missouri Botanical Garden 1995-2012). Their ovary is inferior, topped by two nectaries, and the stigma is funnel-shaped. The fruit is a fleshy capsule with the exotesta composed of fimbriiform cells.

2.2 Phylogeny

The family Zingiberaceae was first established by Bentham and Hooker in 1883 as Zingibereae, a tribe of the family Scitamineae; this tribe was renamed Zingiberaceae and raised to the status of a family as early as 1889 by Petersen (Kress 1990).

The original classification instilled by Petersen was followed by others for many years (Schumann 1904, Holttum 1950, Burtt and Smith 1972, Larsen et al., 1998; cited in Kress 2002) and divided Zingiberaceae into four tribes: Alpinieae, comprising 25 genera, Hedychieae (22 genera), Globbeae (four genera) and Zingibereae (one genus). The classification was based mainly on morphological characteristics (e.g. the plane of distichy, morphological traits of the ovary), but these characteristics were either divided between more tribes or were not shared by all the taxa in one tribus. The family originally included
Costaceae as well, but as it had a number of distinctive characters, such as the lack of aromatic oils, branched aerial stems, and spiral monostichous phylotaxy, it was later classified as a sister group of the *Zingiberaceae* (Kress 2002).

With the development of molecular techniques the family *Zingiberaceae* was assessed again by Kress *et al.* (2002). They sampled 140 species in 41 genera from all four tribes (former classification) of the *Zingiberaceae*, using the genus *Siphonochilus* as the outgroup, and analysed the ITS and matK regions. Based on these analyses they suggested four subfamilies Alpinioideae, Zingiberoideae, Siphonochiloideae and Tamijioideae. Of these, Alpinioideae contained the former Alpinieae, Zingiberoideae comprised the former Hedychieae, Globbeae and Zingibereae, Siphonochiloideae contained the genus *Siphonochilus* and Tamijioideae the genus *Tamijia* (see Appendix 1).

### 2.3 Problems of classification

The main problem with studying tropical plants in general is usually the lack of herbarium specimens in tropical countries. With *Zingiberaceae*, this problem is intensified by the difficulty of specimen preservation. The flowers, which are probably the most important feature in the determination of gingers, fade already after about 24 hours; the inflorescence is mucilaginous and as such impossible to preserve as a dried specimen so that the important characteristics would still remain recognisable. For this reason the fruits and flowers of *Zingiberaceae* are usually preserved in alcohol; however, specimens in older collections lack these parts altogether, which impedes their determination. It is also difficult to ensure that specimens grown at botanical gardens in western countries will have all the necessary conditions for flowering. Holttum (1950) notes that the constancy of form in *Zingiberaceae* flowers also creates a problem for their classification, as it is difficult to distinguish the groups within *Zingiberaceae* on the basis of their floral structure.

### 2.4 Distribution

The family has pantropical distribution (Fig. 2) with the centre of diversity in South and South-East Asia; one species, *Renealmia*, occurs in South America, four species (*Aframomum, Aulotandra, Siphonochilus* and *Renealmia*) in Africa, and some in subtropical and warm-temperate Asia (ZipcodeZoo.com 2004-2012).

Gingers grow in rainforest undergrowth, often in habitats disrupted by human activity, from low to high altitudes. The Alpinioideae are evergreen, but in Zingibereae the upper part of the
plant dies during the dry season and only the rhizome survives in the ground (Škorničková 2007).

![Figure 2. The distribution of Zingiberaceae](http://www.mobot.org/mobot/research/apweb/orders/zingiberalesweb.htm)

3. Alpinioideae

3.1 Description

The Alpinioideae are distinguished from Zingiberoidae by the absence or reduction of the two lateral staminodes and have a plane of distichy perpendicular to that of the growth of the rhizome. Also, as opposed to the Zingiberoidae, they are perennial and do not have a dormant period (Kress 2002).

Alpinioideae contains about twenty genera and over 600 species; the number of species is likely to grow as new ones are still being discovered in the less revised areas. It is also possible that the number of genera will grow as well, as the greatest genus *Alpinia* is polyphyletic (Rangsiruji *et al.* 2000) and may with new revisions break up into smaller groups as it had been in the past.

3.2 Phylogeny

The subfamily Alpinioideae was first suggested by W. J. Kress in his molecular study of the *Zingiberaceae* phylogeny (Kress 2002) as a new taxon comprising the tribe Alpinieae used in the previous classification (Petersen 1889). Kress, however, made an exception for the genus *Tamijia*, which was originally placed in Alpinieae based on the orientation of the plane of
distichy (Sakai and Nagamasu 2000). Kress argued that this classification was uncertain and suggested it as a special subfamily Tamijieae based on the new molecular data.

Kress divided Alpinioideae further into tribes Alpinieae and Riedelieae. Alpinieae comprised most of the genera, encompassing taxa distributed in Asia, Africa, and the Americas. His results supported further division of Alpinieae into two subclades, the Riedelia clade and the Etlingera clade, but as the three largest genera of Alpinieae (Alpinia, Amomum and Etlingera) are polyphyletic, these two clades were not given formal taxonomic status in his study (Kress 2002). The tribe Riedelieae contains the four genera Burbidgea, Pleuranthodium, Riedelia and Siamanthus. All four genera are united by having “long, slender silique-like capsules that open by longitudinal slits to the base” (Kress 2002) and “nectary pits” on the dorsal midrib of the leaf blade. The latter trait had been described before for three of the four genera (Smith 1972, Larsen and Mood 1998; cited in Kress 2002) and Kress in his study confirmed its presence in the remaining genus, Pleuranthodium, as well (Kress 2002).

The placement of the genus Siliquamomum had been stated as incertae sedis by Kress in 2002; later it had been placed as a sister group to the Alpinia Rafflesiana clade, but described as poorly supported, with the Bayesian analysis placing Siliquamomum basal to the Alpinieae (Kress 2005).

The latest phylogenetic analysis of Alpinioideae, focusing on the genus Etlingera, has been done by Pedersen (2004), who analysed the nuclear and plastid DNA. His results support most of the results obtained by Kress (2002), such as the monophyly of Zingiberoideae or the placement of Siamanthus in Alpinioideae. The study also supports the monophyly of Etlingera and divides it into two clades (the former Geanthus and the other genera). However, the monophyly of Alpinioideae is neither supported nor disproved. In contrast with Kress (2002), he states that the Renealmia clade is not sister to the other groups of Alpinieae (the Etlingera clade), but a part of the basal polytomy, and that Amomum does not belong to the Renealmia clade. He also claims that Amomum is monophyletic and is a sister group to Hornstedtia and Etlingera.

In 2006, a study had been conducted by Harris et al. which resulted in the transfer of the genus Aulotandra from Alpinioideae to Siphonochiloideae based on its ITS and trnL-F data, which indicated that it was closely related to Siphonochilus.
4. Genera in Alpinioideae, their description and distribution

4.1 Aframomum

4.1.1 Description

*Aframomum* is the largest genus of African *Zingiberaceae* comprising about 80 species (Harris *et al.* 2000). It was established by Schumann (1904) and it included the African species of *Amomum*; at that time, only 41 species were known. Recently, 54 accepted species are recognized (*The Plant List* 2010).

There are three main flower types in *Aframomum*, representing different pollinators (birds, bees and butterflies). There is quite a lot of morphological variation in the plants; for example, stilt roots may be present or absent and the ligule and leaves vary in size, texture and shape (Harris *et al.* 2000).

Harris *et al.* (2000), who studied the radiation in *Aframomum* based on ITS variation, note that in comparison to *Alpinia*, which has similar characteristics (large size, wide area of distribution, great morphological variability and the same ploidy level 2n=48), the amount of ITS variation in *Aframomum* is six times smaller. They explain this anomaly by the possibility of existence of factors which have accelerated morphological variation; the diversity in *Aframomum* would then have quite recent origin, which would be reflected in ITS variation.

4.1.2 Distribution

“The range of the genus is from Senegal to Ethiopia in the north and Angola and Madagascar in the south, it is also found on the Gulf of Guinea Islands, São Tomé and Príncipe” (Harris *et al.* 2000, p. 378). According to Thonner (1908), all species of *Aframomum* occur in the tropics and some species are grown as ornamental.

In *Flora of West Tropical Africa* (Hutchinson *et al.* 1968), 20 species are listed, occurring in Nigeria, Fernando Pó (today’s Bioko Island), Senegal, Guinea, Sierra Leone, Ivory Coast, Ghana, West Cameroon, Libya, Dahomey (now Republic of Benin), and Republic of Togo.
In Sub-Saharan Africa, Klopper et al. (2006) list 58 species. The species *A. albiflorum* and *A. angustifolium* grow in Zimbabwe and in Mozambique in the understorey and at forest margins (Hyde, Wursten and Ballings 2012; Hyde et al. 2012). Other species are found in Tanzania and Malawi (Hyde, Wursten and Ballings 2012). One indigenous species is found in Madagascar (Madagascar Catalogue 2012).

**4.1.3 Centres of diversity and possible patterns of dispersal**

From the evidence given it is difficult to find a centre of diversity for *Aframomum*. The most species (58, see Table 2) are listed for Sub-Saharan Africa in general; only one species is found in Madagascar and only two in Mozambique and Zimbabwe, which would indicate that the possible centre of diversity lies rather in western or south-western Africa. However, more detailed information needs to be obtained in order to find out the patterns of distribution for this genus.

**4.2 Alpinia**

**4.2.1 Description**

*Alpinia* is the most diversified and probably the most explored genus in the Alpinioideae. It contains about 230 species distributed from Sri Lanka through India, China, Japan and South-East Asia as far as Australia and the Caroline Islands (Larsen et al. 1998, Smith 1960; cited in Kress 2005); some species are cultivated or invasive in a number of neotropical countries as well.

*Alpinia* is polyphyletic and serves rather as a collective genus for species whose classification is yet uncertain. There had been several attempts at determining its phylogeny and it is possible that in the future, with better taxonomic revision, this genus will break down into more small groups as it had been in the past.

![Figure 4. Condensed tree of the Alpinioideae showing the six clades of Alpinia. (Kress et al. 2005).](image)
The oldest division of *Alpinia* was done by Baker in *Flora of British India* (1884). At that time, thirty species were known worldwide. Baker took into account seventeen species occurring from Sri Lanka to Singapore and divided them into two subgenera and two sections. Later, Schumann (1904) in *Das Pflanzenreich* divided *Alpinia* into five subgenera and 27 sections; eight of these have recently been transferred into different genera, leaving five subgenera and 19 sections (Kress *et al.* 2005).

The most recent study was carried out by Kress *et al.* in 2005, when the genus was tested with the use of molecular methods (analysis of the plastid *matK* region and the nuclear internal transcribed spacer) to compare the results with the previous study by Smith (1990). The authors divided *Alpinia* into six monophyletic clades which only partly corresponded with those established by Smith (1990) and Schumann (1904): 1. the *Fax* clade, 2. the *Galanga* clade, 3. the *Carolinensis* clade, 4. the *Zerumbet* clade, 5. the *Eubractea* clade, and 6. the *Rafflesiana* clade (*Fig. 3*).

The plants have a terminal inflorescence on leafy shoots, pollinated by bees, birds or bats. There is a frequent occurrence of flexistyly, a special flowering mechanism. In flexistyloous flowers, the style is either raised above the open anthers and descends during midday (cataflexistyloous flowers) or is curved downwards and during midday lengthens and rises up (anaflexistyloous flowers). Flexistyly promotes outcrossing and helps maintain diversity (Li 2001).

*Alpinia* usually occurs in forests from low to mid-elevation places. The plants grow in clumps; they are usually one to three meters tall but may reach up to 8 metres. Some species (e.g. *Alpinia japonica*, the northmost occurring species) are able to survive below-zero temperatures (Kress 2005).

### 4.2.2 Distribution

*Flora of Australia Online* (2009) describes *Alpinia* as “widely distributed throughout Indo-Malesia to New Guinea, the Solomon Islands, Fiji, Samoa”. Larsen (2005) recognises over 200 species and notes that most of them are found in Malesia, about 60 in China and the Indochinese region (Wu and Larsen 2000, cited in Larsen 2005) and that *Alpinia* has two centres of diversity, one in central Malesia and the other in the northern monsoon region.

Of the 51 species occurring in China, 35 are endemic (Wu *et al.* 1994+). Twelve species are found in Taiwan (Peng 2004+).
Cay Co Viet Nam lists 11 species of Alpinia, but also six species of Catimbium, one Cenolophon and two Languas, which have been included in Alpinia; this in total gives 20 species (see Table 2). However, Languas galanga and L. officinarum are listed only as cultivated (Pham 1999).

Of the three species found in Bhutan, A. calcarata and A. malaccensis are probably not native as they are widely cultivated through India (Noltie 1994). Two of the seven species listed by Burtt and Smith (1983) in Sri Lanka are noted as “probably endemic”, these being A. fax and A. rufescens. The species Alpinia galanga occurs in Sri Lanka, but it is not native. Later, Senaratna (2001) lists the same species, but already notes two cultivated species, these being A. galanga and newly A. calcarata.

In Singapore, seven species are listed, of which 3 are listed as “cultivated only”, 3 as extinct, one as critically endangered (A. aquatica) and one as casual (A. galanga) (Chong et al. 2009). The Checklist of the Zingiberaceae of Malesia, however, lists only 4 species for Singapore (Newman et al. 2004).

Nine species are known from Fiji (Smith 1979), of which 5 are endemic to Fiji and 4 are listed as cultivated, some of them naturalised. The only species found on the Marquesas is A. purpurata, which is cultivated there (Wagner and Lorence 2002).

One species, A. zerumbet, is also known to occur in South and Sub-Saharan Africa (Germishuizen and Meyer 2003, Germishuizen et al. 2006, Klopper et al. 2006).

In Australia this genus is distributed in Queensland and New South Wales. The published Flora of Australia listed six species in Australia, of which four were described as endemic; after the transfer of Alpinia racemigera to Pleuranthodium, the more recent Australian Plant Census lists five species (Flora of Australia Online 2009).

A. purpurata and A. zerumbet are found also in Puerto Rico and on the Virgin Islands (Acevedo-Rodríguez and Strong 2005).

Figure 5. The distribution of Alpinia.
4.2.3 Centres of diversity and possible patterns of dispersal

As can be seen from the map (Fig. 2), the distribution of Alpinia follows the pattern suggested by Larsen (2005). One of the centres of diversity is undoubtedly Indonesia, where the most (74) species occur (Table 3). The other centre is found in China (51 species), where a large portion of the local Alpinia is endemic (35 species). Other species-rich areas include Malaysia, Papua New Guinea and the Bismarck Archipelago, and the Philippines; this probably illustrates the dispersal of the Indonesian species of Alpinia. The areas adjacent to China contain a lesser number of species than those bordering Indonesia, and some (Bhutan and Nepal) contain only a few species. This seems to indicate that the dispersal from China is slower than from Indonesia. Only a small number of species (4) is found in Japan; this is probably caused by the sea barrier separating it from the mainland. Only five species are found in Singapore, which probably due to the small size of the country.

4.3 Amomum

4.3.1 Description

The pseudostems grow in a clump or in greater intervals from the rhizome. The inflorescence is radical, sometimes partially subterranean; the bracteoles are usually described as tubular, but Lamxay (2011) argues that on most plants he examined the bracteoles were open, ovate or lanceolate, or absent. The flowers are trimerous with a clawed labellum and the lateral staminodes may be present or absent (Lamxay 2011).

A phylogenetic analysis of Amomum has been done by Xia et al. in 2004. In Cambodia, Laos and Vietnam, Amomum has been revised recently by Lamxay (2011).

4.3.2 Distribution

Amomum contains about 90 species, distributed from India and China throughout South-East Asia to Australia (Flora of Australia Online 2009). Larsen (2005) lists about 150 species and
mentions “many new species from N Borneo”; he places the centres of diversity in Borneo, where most species are found, and China-Indochina, where about a third of species is found. Hooker (1894) describes about 150 species in total in the Old world.

Ten of the Indian species are endemics (Sabu et al. 2004). Four species are listed by Noltie in the *Flora of Bhutan* in South Bhutan, Sikkim and Darjeeling. However, only two species had been securely determined as native and occurring in Bhutan, namely *A. subulatum* and *A. dealbatum*. Of the ten species in Sri Lanka, eight are endemic. *A. acuminatum* is hyper-endemic, known only from Ekaneligoda in Ratnapura District (Burtt and Smith 1983; Senaratna 2001).

In Thailand, fifteen species were recognised by Larsen in 1996 before the genus was revised for Thailand, with a note that at least four new species are known. Recently, 16 species of *Amomum* are stated to occur in Thailand (Larsen and Larsen 2006). Two species are recognised in Singapore, of which *A. hastilabium* is listed as extinct and *A. xanthophlebium* as critically endangered (Chong et al. 2009).

*Flora of Australia Online* (2009) lists two species of *Amomum* for Australia, of which one is endemic: *A. queenslandicum*, which grows in northern Queensland and New Guinea, and *A. dallachyi*, which is endemic in northern Queensland. Both species are found in rainforests. (*Flora of Australia Online* 2009)

### 4.3.3 Centres of diversity and possible patterns of dispersal

The diversity centre of *Amomum* seems to lie in Malaysia, where most of the species are found, rather than in Indonesia (Borneo) as suggested by Larsen (2005).

#### 4.5 Burbidgea

##### 4.5.1 Description

This genus belongs to the tribe Riedelieae and is further divided by floral structure into two groups. Five accepted species are recognised at present (*The Plant List* 2010). However, Larsen (2005) lists 8 species.

##### 4.5.2 Distribution

*Burbidgea* occurs in the Malaysian Peninsula and in Borneo (Smithsonian Institution 2012).
4.5.3 Centres of diversity and possible patterns of dispersal

Malaysia is probably the centre of diversity, as five species are found here and only two in Indonesia. The dispersal probably occurs towards Indonesia.

4.6 Cyphostigma

4.6.1 Description

This is a monotypic genus represented by the species *C. pulchellum*. Burtt and Smith (1983) note that Schumann (1904) distinguished two species of *Cyphostigma*, *C. peicellatum*, which was characterised by broader, oblong leaves and pedicellate flowers, and *C. pulchellum*; however, he only examined specimens with a single leaf, whereas in plants with more leaves the later leaves are narrower.

4.6.2 Distribution

*Cyphostigma* is endemic to Sri Lanka, where it grows in forests up to 1000 m elevation (Smithsonian Institution 2012). The species *Cyphostigma kandariense*, which occurs in Malesia, is stated by Newman et al. (2004) to be probably transferred in the future to *Elettaria* or *Elettariopsis*.

4.7 Elettaria

4.7.1 Description

According to *The Plant List* (2010), this genus comprises 11 accepted species. However, Newman et al. (2004) list 12 species in Malesia (nine are found in Malaysia and five in Indonesia). Larsen (2005) lists 7 species of *Elettaria*, which are found in Malesia.

4.7.2 Distribution

The species *E. cardamomum* is stated to grow in Vietnam (Pham 1999), Myanmar (Kress et al. 2003), Sri Lanka (Senaratna 2001), the Mascarene Islands (Bosser 1983), Fiji (Smith 1979), Costa Rica (Hammel et al. 2003), and even in tropical Africa (Thonner 1908). In the floras of some of these countries it is noted that the species is only cultivated, as in Fiji (Smith 1909). It is also listed by Hooker (1984) as growing in British India, more particularly in...
“Malabar” (probably the former Malabar District), and cultivated in Ceylon (Sri Lanka). The *Gingers of India* database lists *E. cardamomum* as “probably native in South India” (Sabu *et al.* 2004).

However, Smithsonian Institution (2012) describes *E. cardamomum* as “endemic to Sri Lanka, but much cultivated in India and Guatemala, and naturalized in East Africa (Tanzania)”, which could indicate that this species had before been wrongly listed as native to abovementioned countries. The wide cultivation of this species is due to the use of its fruits as a spice (green cardamom).

In the *Handbook to the Flora of Ceylon*, *E. cardamomum* is listed as native in Sri Lanka, with two varieties, var. *cardamomum* and var. *major* (Burtt and Smith 1983).

4.7.3 Centres of diversity and possible patterns of dispersal

The diversity centre of this genus seems to lie in Malesia, probably in Malaysia, as there are the most species to be found (9 species listed by Newman *et al.* 2004). The most widespread species is undoubtedly *E. cardamomum*, which has dispersed or was brought to a number of other countries due to its cultivation as a spice.

4.8 Elettariopsis

4.8.1 Description

In *Elettariopsis* the inflorescence grows from the base of the pseudostem; the flowers are white or pinkish. The lateral staminodes are absent or very short (Hooker 1894). According to *The Plant List* (2010), so far 18 accepted species of this genus are known.

4.8.2 Distribution

*Elettariopsis* is found in China, Indonesia, Laos, Malaysia, Thailand, and Vietnam (Wu *et al.* 1994+).

Larsen (2005) lists ten species in Malesia. Newman *et al.* (2004) list nine species, but they note that the species *Cyphostigma kandariense* may be transferred to *Elettariopsis* (or *Elettaria*), which would increase the count to 10 species.
In China this genus is represented by one species, *E. monophylla*. It grows on forest floors from near sea level to 100 m in Hainan. In the Flora of British India this species is listed as *Amomum monophyllum* (Wu et al. 1994+).

*E. curtisii* is found in Singapore, where it is critically endangered (Chong et al. 2009).

4.8.3 Centres of diversity and possible patterns of dispersal

This genus seems to have its centre of diversity in Malaysia, where so far the most (9) species have been found. Other species-rich areas are Thailand and Laos. The number of species is however likely to change as new species are still being discovered and the genus is in need of revision.

4.9 Etlingera

4.9.1 Description

This genus covers the previous genera *Achasma*, *Geanthus* and *Nicolaia* on the basis of shared morphological characters of the bracts, bracteoles and labellum (Burtt and Smith 1986). A phylogenetic study by Pedersen (2004) confirms this establishment and places *Hornstedtia* as sister group to *Etlingera*. According to Larsen (2005), the genus comprises about 80 species distributed from Southern Himalayas throughout South-East Asia to North Queensland.

4.9.2 Distribution

Of the three species found in China, *E. elatior* is said to be cultivated as an ornamental plant with the possibility of naturalization in forests in lower elevations. *Etlingera elatior* is listed as cultivated in Sri Lanka by Senaratna (2001). It is also found in Micronesia (Wagner et al. 2012) and in Puerto Rico and the Virgin Islands (Acevedo-Rodriguez and Strong 2005). The species *E. ceyuga* is naturalised in the Hawaiian Islands (Wagner et al. 2005).

Three species are found in Singapore, of which *E. elatior* is listed as cultivated, *E. littoralis* as extinct, and *E. punica* as critically endangered (Chong et al. 2009). Poulsen (2006) lists 40 species in Borneo, of which 85% (34 species) are endemic. He also notes that the most
species-rich areas are Gunung Kinabalu, Sabah, and Gunung Mulu NP, Sarawak; these places offer a wide range of habitats and elevations.

In Australia, only one species, *E. australasica*, is found; it is endemic to north-eastern Cape York Peninsula in Queensland, Australia (*Flora of Australia Online* 2010).

4.9.3 Centres of diversity and possible patterns of dispersal

Both Poulsen (2004) and Larsen (2005) place the main centre of diversity in Borneo. The results shown in Table 3 support this statement, as Indonesia contains the most (34) species. However, only four less species are found in Malaysia, 10 of these in the Malay Peninsula (Table 2). The third area with most species is Thailand (12 species). The dispersal of *Etlingera* seems to occur in north-west direction, over Malaysia to the mainland.

4.10 *Geocharis*

4.10.1 Description

*Geocharis* is distinguishable by the lateral staminodes joined to the filament (Holttum 1950).

4.10.2 Distribution

*Geocharis* occurs from West Malaysia and Sumatra to Borneo and the Philippines (Smithsonian Institution 2012). Holttum (1950) lists two species in Peninsular Malaysia. Six accepted species are known recently (*The Plant List* 2010).

4.10.3 Centres of diversity and possible patterns of dispersal

The diversity centre of *Geocharis* probably lies in Malaysia, where 3 species are found (Table 3).

4.11 *Geostachys*

4.11.1 Description

This genus has a rhizome which is supported above ground by stilt roots (Larsen 2005). It may be related to *Amomum*.
4.11.2 Distribution

Holttum (1950) places the diversity centre of Geostachys in Peninsular Malaysia, where 12 species are found. According to Larsen (2005), all species are “endemics in montane forests above 800 m”. Schumann (1904) lists 5 species, Holttum (1950) already 14; in 2005 at least 24 species were known, including 10 species endemic to Thailand, Cambodia, Vietnam, Sumatra, and Borneo (Larsen 2005).

The Smithsonian Institution (2012) lists only seven species of Geostachys occurring in South Vietnam and Thailand, West Malaysia to Sumatra, and Borneo, and notes that “most species are from the Malay Peninsula”.

4.11.3 Centres of diversity and possible patterns of dispersal

The centre of diversity of Geostachys probably lies in Malaysia, as the number of species there is the highest (12 species). Thailand has the most species after Malaysia (5 species) and only two species are found in Indonesia. The dispersal of Geostachys seems to occur mainly in the north-west direction, further into the mainland rather than to the Malesian region.

4.12 Hornstedtia

4.12.1 Description

This genus counts about 50 species distributed from Malesia to north-east Australia. There are few Malaysian species, some of which are found in southern Thailand (Larsen 2005). They are tall herbs with a stout rhizome and terminal congested inflorescence with white, yellow, orange or red flowers (Smithsonian Institution 2012). The Plant List (2010) lists 32 accepted species.

4.12.2 Distribution

The two species of Hornstedtia found in China, H. hainanensis and H. tibetica, are both endemic (Wu et al. 1994+). In Thailand this genus is represented by four species (H. conica, H. leonurus, H. minor and H. scyphifera) (Larsen and Larsen 2006). Of the three species growing in Singapore, H. conica and H. leonurus are listed as critically endangered and H. scyphifera as vulnerable (Chong et al. 2009).
In Cambodia, Laos and Vietnam occurs only *H. sanhan*, which is found in Vietnam (Newman *et al.* unpubl.). Only one species, *H. scottiana* grows in Australia; it is found in the rainforest in north-eastern Queensland (*Flora of Australia Online* 2009).

In the work of Newman *et al.* (2004), two species occurring in Indonesia are cross-referred to *Amomum* and two to *Elettaria* (raising the count of Indonesian *Hornstedtia* to 22) and one species growing in the Philippines is cross-referred to *Amomum* (raising the number of Philippine *Hornstedtia* to 7) (see Table 2). Those species are listed as accepted names in both *Hornstedtia* and *Amomum* and were therefore tallied down for both of these genera.

4.12.4 Centres of diversity and possible patterns of dispersal

From the available information it can be discerned that the diversity centre of *Hornstedtia* seems to lie in Indonesia; the genus had probably dispersed from this centre mainly to the east to Malaysia, the Philippines and Papua New Guinea and some dispersal occurred also in the western (Singapore, India), northern (China, Vietnam) and southern (Australia) directions.

4.13 Leptosolena

4.13.1 Description

This is a monotypic genus restored from *Alpinia leptosolena* K.Schum. (Larsen 2005). The species *L. haenkei* was described by Funakoshi *et al.* (2005) and compared with the uncertain second species, *L. insignis*. They concluded that the two species are conspecific and *L. insignis* is a synonym. They also confirmed that *Leptosolena* forms a clade with *Vanoverberghia* and *Alpinia* species from the Philippines and Oceania.

4.13.2 Distribution

*Leptosolena haenkei* is endemic to the Philippines.
4.14 Paramomum

This is a monotypic genus. The only species *P. petaloideum* is found in tropical SW China (Wu *et al.* 1994+). It is similar in morphology to *Costus*, but in contrary to *Costus* it has an open sheath and the labellum is not joined with the stamen at the base in a short tube. The fruit is a capsule with black arillate seeds (Smithsonian Institution 2012).

4.15 Plagiostachys

4.15.1 Description

*Plagiostachys* includes about 25 species found mainly in the Malesian region; two species (one undescribed) grow in Thailand, and one is endemic to south China. He also notes that the endemic species form a narrow “tail” in the continental monsoon region (Larsen 2005). According to *The Plant List* (2010), 27 accepted species are known to exist.

A phylogenetic study conducted by Julius *et al.* (2008) divided *Plagiostachys* into three subclades recognisable by the morphology of the inflorescence and the capsules, which were different from the previous classification by Smith in 1985. They proposed that *Plagiostachys* remains an independent genus, but did not resolve its phylogenetic position.

4.15.2 Distribution

The only species found in China is *P. austrosinensis*, which is endemic to China (Wu *et al.* 2004). In Thailand, only *P. albilora* is known to occur (Larsen and Larsen 2006). Two species (*P. lateralis*, *P. mucida*) are listed for Singapore, but both as extinct (Chong *et al.* 2009).

Quite recently a new species, *P. nicobarica* was described from the Nicobar Islands, India. It is also the only species of *Plagiostachys* which is found in India (Sabu *et al.* 2008).

4.15.3 Centres of diversity and possible patterns of dispersal

From the information listed above, it would seem that the diversity centre of *Plagiostachys* lies in Malaysia, from where it had first dispersed to the Philippines and to Indonesia and then to Singapore and Nicobar Islands.

Figure 4.15 The distribution of *Plagiostachys*. 
4.16 Pleuranthodium

4.16.1 Description
This genus was previously known as Psychanthus (Smith 1990b). The Plant List (2010) lists 23 accepted species at the present.

4.16.2 Distribution
Larsen (2005) lists 25 species of Pleuranthodium occurring from east Malesia to northern Australia. In Australia the distribution of this genus is restricted to one species, P. racemigerum, occurring in rainforests in northern Queensland. This species was previously treated under Alpinia racemigera (Flora of Australia Online 2009).

4.16.3 Centres of diversity and possible patterns of dispersal
The centre of diversity of Pleuranthodium is probably found in Papua New Guinea, as the most (17) species are found here (Table 3).

4.17 Renealmia

4.17.1 Description
Renealmia is the only pantropic genus in the Alpinioideae, which is due to its long-distance dispersal (Särkinen et al. 2007). Maas (1977) lists 75 species in total, of which ca 25 occur in tropical Africa, ca 55 in the Neotropics, and 18 are endangered or rare. In New World it occurs from North Mexico over Cuba and the Bahamas to Bolivia and South Brazil in forest clearings, along streams or along large rivers, at altitudes from sea-level up to 2500 m. Two species (R. ferruginea, R. alticola) are reported to occur in altitudes up to 3000 m (Maas 1977). Särkinen et al. (2007) list only 15 species in Africa and 61 in the Neotropics.

Renealmia is divided into four neotropical and two African groups and is closely related to Amomum, Aframomum and Elettariopsis (Jannes 2009)
4.17.2 Distribution
In Costa Rica 14 species are found, of which one species, *R. costaricensis*, is endemic (Hammel *et al.* 2003). Twelve species are found in Peru (Macbride 1963).

In *Flora Fanerogâmica da Ilha do Cardoso* only one species, *R. petasites*, is listed (Instituto de Botânica de São Paulo 2007). Three species of *Renealmia* are found in Puerto Rico and the Virgin Islands (Acevedo-Rodriguez and Strong 2005).

Thonner (1908) lists 15 species, which all occur in Central Africa. Hutchinson *et al.* (1968) list 6 species of *Renealmia* occurring in tropical west Africa; of those, 3 are found in Ivory Coast, 2 in Libya, 2 in Cameroon, 2 in south Nigeria, 2 in Gabon, two on Fernando Pó (today’s Bioko Island, Equatorial Guinea) and one in Congo. Two more species are listed as imperfectly known (destroyed at Berlin), these being *R. albo-rosea*, which grows in west Cameroun, and *R. macrocolea*, which is found in the Republic of Togo.

4.17.3 Centres of diversity and possible patterns of dispersal
The centre of diversity of *Renealmia* probably lies in the neotropical region, where occurs the main portion of species (55). From the information available, closer specification is at the moment impossible to determine.

4.18 Riedelia

4.18.1 Description
This genus comprises 75 accepted species (The Plant List 2010). Larsen (2005) lists 60 species occurring from east Malesia to northern Australia.

4.18.2 Distribution
All species are found in Malesia, namely in East Malaysia, Papua New Guinea, the Bismarck Archipelago and the Moluccas (Newman *et al.* 2004).

4.18.3 Centres of diversity and possible patterns of dispersal
As can be seen in Table 3, Riedelia seems to have two centres of diversity – one in Indonesia (47 sp.) and the second in Papua New Guinea (41 sp.). It is interesting that no species are found in Malaysia. The dispersal probably occurred in the direction from Indonesia to Papua New Guinea.
4.19 Siamanthus
This is a monotypic genus represented by the species *S. siliquosus*, which had been described by Larsen and Mood in 1998. It has a bilabial floral structure different from most *Zingiberaceae* (Larsen 2005).

The Smithsonian Institution (2012) lists *Siliquamomum* as endemic to the Narathiwat province of South Thailand, but according to M. F. Newman (pers. comm. 2012) this genus had been described from a specimen sold in a market, and the original location where *Siamanthus* grows is yet unknown.

4.20 Siliquamomum

4.20.1 Description
This genus was first described from North Vietnam. Larsen (2005) describes *Siliquamomum* as a monotypic genus occurring in North Vietnam and adjacent southern China; it has been placed as *incertae sedis* by Kress et al. (2002). In 2010, another species, *S. oreodoxa*, has been discovered by Ly et al. Larsen (2005) also notes that it may be related to *Siamanthus* despite different floral morphology.

4.20.2 Distribution
The two known species so far are *S. tonkinense* and *S. oreodoxa* (Newman et al. unpubl.). *S. tonkinense* is found in North Vietnam and South-East Yunnan (Pham 1999; Wu et al. 1994+; Smithsonian Institution 2012). It is mentioned already by Gagnepain (1942). *S. oreodoxa* grows in Vietnam (IPNI 2005).

4.20.3 Centres of diversity and possible patterns of dispersal
The diversity centre of this genus apparently lies in Vietnam, as it is endemic to Vietnam and southern China.

4.21 Vanoverberghia
This is a small genus occurring in Taiwan and in the Philippines (Larsen 2005). In Taiwan occurs *V.
sasakiana, which is endemic to Lanyu Island (Peng 2004+). In the Philippines grows the species V. sepulchrei (Newman et al. 2004).

5. Results
Most of the greater genera in Alpinioideae have their centre of diversity in Malaysia; the second most species-rich area is Indonesia. The diversity centres of the rest of the genera are found on the Philippines (Leptosolena, Vanoverberghia), in Papua New Guinea (Pleuranthodium), in Vietnam (Siliquamomum) and in Thailand (Siamanthus). An interesting case is Riedelia, whose centre of diversity seems to lie in both Papua New Guinea and Indonesia, as these areas differ only by six species (Table 3), and Pleuranthodium, whose centre of diversity apparently lies in Papua New Guinea.

The most endemic species are found on the Philippines, which is in accordance with the study of Heaney (1986), who states that speciation is on the Philippines responsible for a greater number of species than colonisation.

The two genera Aframomum and Renealmia are an exception in that they have no representatives in South-East Asia, where lies the centre of diversity of the group; their diversity centres are unclear from the information given, but it is probable that the diversity centre of Aframomum lies in tropical west Africa.

The overall pattern of dispersal of the Alpinioideae seems to be mostly to the north-west and west from the diversity centre. Some species (Alpinia, Amomum) expand also to the south to Australia.

For a more thorough and more precise biogeographic analysis, more detailed information is required. For larger countries such as India, China or Thailand it would be better to note the number of species for individual states or provinces to obtain more specific data. The polyphyletic genera will need to be divided into monophyletic groups and analyse these groups separately for better clarity. Finally, revisions of the individual genera are needed to be made for the whole area of distribution of the genus to obtain consistent sources for future biogeographic research; until then, it is possible that some species occurring in different states may be conspecific and the information is therefore inaccurate.
Table 2. Distributions of Alpinioideae according to the floras of individual regions. c = cultivated only, e = endemic, n = native, orn. = ornamental. The numbers of accepted species were taken from The Plant List (2010). Species listed under the genus names Achasma, Nicolaia and Geanthus were tallied down for Etlingera; the genus Phaeomeria (in Holttum 1950, Pham 1999) was treated likewise. For genera with doubtful species, these species were for better clarity included to the total count.

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Genus/Country | total Alpinioideae | 892 | 10 | 65 | 8 | 113 | 58 | 3 | 4 | 46 | 37 | 4 | 32 | 79 | 3 |

1 The species A. seimundii is listed by Holttum as doubtful.
2 Twenty-eight species are listed by Hooker (1984) under Etlingera, sect. Euamomum. Here they have been included in Amomum.
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<td>Vanoverberghia</td>
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<td>Total sp.</td>
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<td>58</td>
<td>8</td>
<td>46</td>
<td>247</td>
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<td>174</td>
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<td>79</td>
<td>109</td>
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Conclusion

In this work, the distribution and phylogeny of the subfamily Alpinioideae have been researched and described. From the information available so far we can conclude that the most species-rich areas for the Alpinioideae lie in Malesia, particularly in Malaysia, Indonesia and possibly Papua New Guinea. From these areas the genera have dispersed mainly in the western and eastern direction. Some genera expanded as far as tropical Africa and the genus *Renealmia*, which is the only genus in the Alpinioideae to occur in both paleotropics and neotropics, had undergone a long-distance oceanic dispersal.

Endemic species and genera of the Alpinioideae seem to occur frequently in the peripheral area of the group’s distribution, such as in China (*Paramomum*), Vietnam (*Siliquamomum*) or the Philippines (*Leptosolena*).

The largest genus, *Alpinia*, which is polyphyletic and serves as a collective genus, seems to be the most widespread of the genera. It is probably partly due to the cultivation of some species as ornamental and their subsequent naturalization. In Africa the largest genus is *Aframomum*, which has probably undergone rapid radiation in Africa quite recently.

This work tries to summarize most of the available information; however, as can be seen from the level of inconsistency in (not only) generic and species concepts, a revision of most genera and the whole subfamily Alpinioideae and a more thorough research is needed in order to fully resolve the group’s internal relationships and to understand its biogeographic patterns. Until then, this work remains only an approximation of the patterns of biodiversity in the Alpinioideae.


Appendices

Appendix 1. The phylogeny of the family *Zingiberaceae*. (Kress et al. 2002)