# REPRODUCTIVE BIOLOGY, MORPHOLOGICAL TAXONOMY, BIOGEOGRAPHY AND MOLECULAR PHYLOGENY OF *AGLAIA* LOUR. (MELIACEAE): THE MONOGRAPHIC APPROACH TO A LARGE GENUS OF TROPICAL TREES

*Caroline M. Pannell[1]*

ABSTRACT

The molecular revolution has given us new opportunities to explore species relationships, evolution and historical biogeography. It is at its most powerful when combined with studies of the living plants in the field and information gleaned from the many thousands of herbarium specimens that go into preparing comprehensive taxonomic revisions.

For the genus *Aglaia*, a genus of more than 100 species, morphological, distributional and biological information has been combined with the history of plate tectonics in the Indo-Malayan Australasian Archipelago, molecular phylogenies and historical biogeographical analyses. Hypotheses for the origin, expansion and species radiation since its origin c. 24 million years ago have been proposed. The tribe Aglaieae was the first monophyletic plant group for which a fully resolved, fossil-dated phylogenetic tree was published. Subsequent studies of some other groups of plants and animals have revealed similar patterns of dispersal, establishment and radiation in the region. The comprehensive nature of the research carried out on this medium-sized genus of tropical rain forest trees has contributed and continues to contribute to an understanding of the Sunda-Sahul floristic interchange and the species radiation that follows dispersal between these continental shelves.

The genus is found mainly in lowland tropical rain forests from the Western Ghats of India to Samoa and from southern China to tropical Australia, with its greatest diversity in Malesia. In SE Asia section *Aglaia* is dispersed by mammals, especially greater and lesser apes (orang-utan, siamang and gibbons). This section of the genus has diversified in New Guinea without its primate dispersers and with no obvious alternative disperser. No marsupial is known to be an efficient seed-disperser. The other two sections of the genus, section *Amoora* and section *Neoaglaia*, are bird-dispersed. The coastal and estuarine species, *Aglaia cucullata*, almost certainly sometimes survives a sea journey. This may partly explain its morphological uniformity over a wide geographical area, from Bangladesh to New Guinea.

## INTRODUCTION

The thousands of islands in the Indo-Malayan Australasian Archipelago (IAA) and their complicated tectonic history have made the region into a vast natural laboratory for evolution. In tropical forests, at least 50% and often more than 75% of the tree species produce fleshy fruits adapted for bird or mammal consumption and dispersal (Howe & Smallwood, 1982). Seeds have been dispersed across the deep seas between the islands

1. Caroline M. Pannell is a Research Associate in Plant Taxonomy at the Department of Plant Sciences, University of Oxford, and a Visiting Research Fellow at Queen's University Belfast, Marine Laboratory.
Address: Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK.
Email: carolinempannell@gmail.com

of Wallacea and have germinated, established and colonised virgin land masses, such as New Guinea on the Sahul continental shelf, after it arrived in tropical latitudes and gradually became dry land. These colonisations were followed by species radiations, stimulated at least partly by the selective pressure of the contrasting faunas of the east and the west of the IAA. Most of the large island of New Guinea was submerged when it entered tropical latitudes. "The area of dry land exposed above sea level gradually increased, from only a small eastern portion of the island less than 12 million years ago. It eventually achieved its current size and position less than 4 million years ago." (R. Hall, pers. comm.)

> *"From approximately 20 Mya, New Guinea began to emerge from the sea, probably as small islands along the northern edge, but most of the area that is now mountains was shallow sea … the islands of the Banda Arc, notably Timor and Seram, emerged in the past two million years from depths of several kilometers to elevations of more than three kilometers. At the same time, even higher mountains rose to form the Central Ranges of New Guinea, and most of that island emerged from the ocean. New Guinea has never been closer to the Sunda Shelf than it is at present, but the two have always been separated by ocean"* (Toussaint *et al.*, 2014).

*Aglaia* is almost entirely a lowland rain forest genus. In SE Asia one section of the genus is dispersed by mammals, especially greater and lesser apes. This section has diversified in New Guinea without its primate dispersers and with no obvious alternative disperser. No marsupial is known to be an efficient seed disperser. The other two sections of the genus are bird-dispersed.

Research into this large woody genus has contributed to our understanding of speciation and historical biogeography in the IAA. Information has accumulated and been interpreted in a biological and biogeographical context over many years of monographic work on this species-rich and common genus of lowland rain forest trees. *Aglaia* is the largest genus in the mahogany family (Meliaceae), with at least 120 species. A combination of ecological field work, morphological taxonomy and macro- and micro-molecular studies have led to a better understanding of species delimitations, evolutionary radiations, dispersal and colonisation of new territory and of its historical biogeography.

Before this work began, in 1977, the genus was viewed with horror by taxonomists and dismissed as consisting of swarms of species, common in SE Asian rain forests, with little or no ecological difference between the species and scant morphological characters for distinguishing them in the herbarium (Hopkins *et al.*, 1998, p. 152). Van Steenis (1957) described the genus as notorious for its "colossal, solid blocks of species, many of which show an undesirably low degree of good morphological characteristics". He recommended that the possibility that it might be apomictic should be investigated.

## METHODS

Initial headway with this large, taxonomically intractable genus of trees was made by finding out as much as possible about its reproductive biology during periods of up to one year in the field, focusing largely on one forest site, Kuala Lompat, in Krau Wildlife Reserve, Peninsular Malaysia. The reproductive biology of a dozen sympatric species was observed, measured and documented for six years.

Description of the initial results of my field work was complicated by the chaotic state of its taxonomy at the time. There had been no attempt at a monographic revision for 100 years, since C. de Candolle (1878). A revision of the species in Peninsular Malaysia was therefore added to the research project, so that ecological results could be attached to existing species names or new species recognised (Pannell, 1980). After that, a revision of the entire genus throughout its range was begun, based on examination of about 10,000 herbarium specimens. The 800 names attributed to *Aglaia* and the other genera (notably *Amoora* Roxb.), considered by Pennington & Styles (1979) to be synonymous with it, were placed. All extant type specimens were seen and the basionyms typified. The patterns of morphological variation and the distribution of all species was described.

The resulting monograph provided a unique opportunity on which to base phytochemical and DNA investigations. The published revision, the detailed knowledge of species and their variability, and the monographer's ongoing involvement with the genus in the herbarium and in the field provided a comprehensive framework in which to interpret the results of these investigations. In addition, the characteristic indumentum types found in *Aglaia*, their density and distribution makes identification of sterile collections possible, so that the material used in these further investigations could be named and the resulting work interpreted accurately, even if fertile material had not been collected. Detailed documentation of the unresolved taxa in the genus also meant that apparently anomalous results could be understood in the context of the need for more characters and information (molecular, morphological and ecological) to achieve better resolution of these taxa.

## RESULTS

The initial ecological field work produced a functional explanation for at least some of the morphological characters that are used in the classification of the genus, along with ecological explanations for the coexistence of many species in one small area of forest. It also provided clues to the selective forces that might have been at least partly responsible for speciation in the genus.

By 1992 a comprehensive alpha-taxonomic treatment of *Aglaia* had been completed and published (Pannell, 1992). This monograph, of the entire genus throughout its range, makes *Aglaia* the only genus in the IAA to have been revised in its entirety. This attracted the attention of other scientists, in ecological, biogeographical and molecular

disciplines. Their investigations have, in turn, improved our knowledge of the biology of the genus and occasionally led to the recognition and description of new species. *Aglaia* has become a model genus for understanding biological and historical processes in the plants of the IAA.

In order to complete the monograph of this notoriously intractable genus, however, compromises had to be made. With the material and information available, it was not possible to resolve all the taxonomic problems encountered. In 1992, 114 species were recognised, but it was clear that at least a third of these were not uniform either morpho-logically or biologically. The morphological variation and its geographical pattern was therefore documented for each of these species and one or two stars assigned to the variable (*) and complex (**) species, according to the extent of the morphological variation observed (see Table 2 and notes at the end of the individual species descriptions in Pannell, 1992, updated in Table 2 in Pannell, 2004).

Fruit structure and mode of dispersal fell into two main syndromes in *Aglaia* (Pannell, 1997a; Hopkins *et al.,* 1998). In the fruits of section *Aglaia*, the fibrous inedible pericarp is broken open or peeled off by a mammal disperser in order to gain access to the succulent aril. The seeds of *A. elliptica* Blume (section *Aglaia*), for example, are 28 mm long and 14 mm wide, small enough to be swallowed whole by primates and other mammals. In sections *Amoora* and *Neoaglaia* the fruit is dehiscent and the seeds, surrounded by a lipid-rich aril, are exposed and accessible to birds. In both cases, the dispersers swallow the seeds whole and excrete or regurgitate them some time later, cleaned of the fleshy aril. The seeds of *A. teysmanniana* (Miq.) Miq. (section *Neoaglaia*), dispersed by small birds such as broadbills and bulbuls to larger ones such as magpies, are 15 mm long and 10 mm wide. Those of *A. erythrosperma* Pannell (section *Amoora*), dispersed by hornbills and possibly pigeons, are 50 mm long, 35 mm wide and 20 mm through (Pannell & Kozioł, 1987). The cassowary-dispersed *Aglaia mackiana* Pannell has possibly the largest seeds (105 mm long, 70 mm wide and 60 mm through) swallowed by any bird.

ALFRED RUSSEL WALLACE, 'WALLACE'S LINE', DISPERSAL SYNDROMES
AND DISTRIBUTION PATTERNS IN *AGLAIA*

During his travels in the Malay Archipelago, Wallace was surprised by his first encounter with Australian vertebrates when he crossed from Bali to Lombok, across the narrow Straits of Lombok, in June 1856. He described the turbulent water in this 15 km wide sea channel with these words:

> *"This violent surf is probably in some way dependent on the swell of the great southern ocean, and the violent currents that flow through the Straits of Lombock. These are so uncertain that vessels preparing to anchor in the bay are sometimes suddenly swept away into the straits, and are not able to get back again for a fortnight. What sea-men call the 'ripples' are also very violent in*

*the straits, the sea appearing to boil and foam and dance like the rapids below a cataract; vessels are swept about helpless, and small ones are occasionally swamped in the finest weather and under the brightest skies. I felt considerably relieved when all my boxes and myself had passed in safety through the devouring surf, which the natives look upon with some pride, saying that their sea 'is always hungry, and eats up everything it can'"* (Wallace, 1869).

Since Wallace was taking soundings of the ocean depth as he crossed the strait, he was aware that the sea in the channel was much deeper than on the Sunda continental shelf that he had just left. An even greater surprise awaited him on landing on the island of Lombok. He observed that

*"Birds were plentiful and very interesting, and I now saw for the first time many Australian forms that are quite absent from the islands westward. Small white cockatoos were abundant, and their loud screams, conspicuous white color, and pretty yellow crests, rendered them a very important feature in the landscape. This is the most westerly point on the globe where any of the family are to be found"* (Wallace, 1869).

Later, when he reached Sulawesi by steamship, he recorded the westernmost limit in the Malay Archipelago of marsupial mammals. The precise position of the faunal boundary
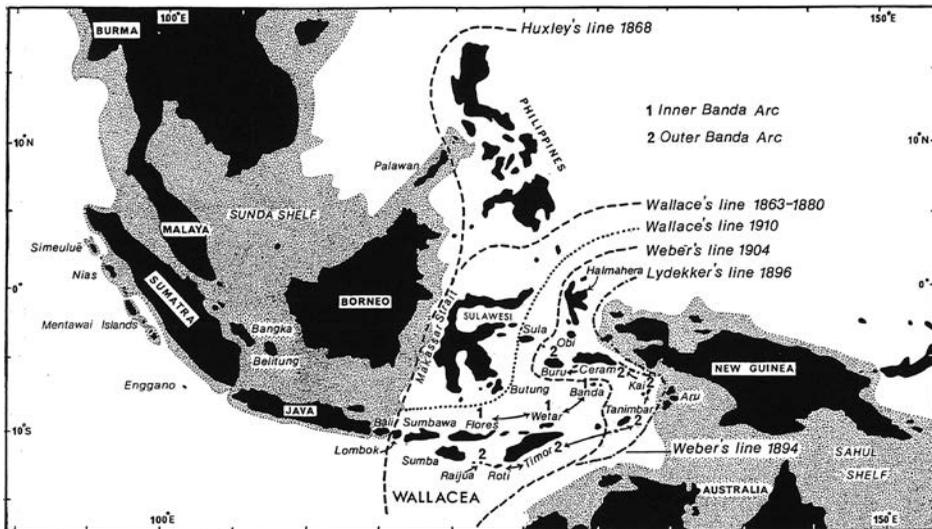


Fig. 1   Map, partly based on Figs 2-1, 2-4, 4-7 and 4-9 in Whitmore (1981), showing the faunal boundaries in the Malay Archipelago. Taken together, these define the region known as Wallacea that lies between the Sunda and Sahul continental shelves. The Missouri Botanical Garden Press has granted permission to reproduce Figure 1 from "Patterns of speciation in Africa, Madagascar, and the tropical Far East: Regional faunas and cryptic evolution in vertebrate-dispersed plants" in *Modern Systematic Studies in African Botany*, Pannell & White 1988: 642.

was different in different animal groups. The main geographical divisions for animals recognised by Alfred Russel Wallace and his successors in the late 19th and early 20th centuries are shown in Fig. 1. Taken together, they delimit the margins of the Sunda and Sahul shelves and are drawn at various positions in between, in the area of deep ocean and islands between these two continental shelves. This part of the Malay Archipelago has become known as Wallacea.

These boundaries are much less distinct in plants at the level of major taxonomic groups down to family and genus, so that Wallace's Line and the other faunal boundaries have traditionally been considered to be less significant for plants than for animals. However, detailed information of the distribution of all species had not been available for any large genus of plants until the monograph of *Aglaia* was published (Pannell, 1992). Mapping the complete range of all species, even with their numerous unresolved taxa, revealed a clear demarcation at the species level along Lydekker's Line. A large proportion of *Aglaia* species in Sundaland crosses Wallace's Line into Wallacea, but their distribution does not extend to the east of Lydekker's Line. A different suite of species, younger in age (see Muellner *et al.*, 2008; Grudinski *et al.*, 2014a), is found in Australasia and the Western Pacific. This pattern of distribution of *Aglaia* species is reflected in the limits of the distribution of some of the major fruit-eating vertebrates in the region. Most importantly, nearly all the non-flying, fruit-eating placental mammals and many families of fruit-eating birds reach their eastern limit at or west of Lydekker's Line. Marsupial mammals are only found as far west as Sulawesi. There are no marsupials west of Wallace's Line. Birds of paradise, bower birds and the large flightless cassowaries are confined to the east of Lydekker's Line (Pannell & White, 1988).

Only ten species of *Aglaia* occur in all three regions: SE Asia, Wallacea and Australasia. All but one of these species fall into the complex or variable species categories. Molecular phylogenies indicate that these species are probably made up of a mixture of related and unrelated entities that have converged in morphological characters. The only exception is *Aglaia cucullata* (Roxb.) Pellegr. It shows little morphological variation and is thought to be dispersed by sea, at least sometimes (Pannell, 2013). Australasian material of this species has not yet been sequenced. Of the remaining 100-plus species in the genus, three are found on both sides of Lydekker's Line. Only 13 species, therefore, transgress Lydekker's Line. With further morphological and molecular analysis, most of these are likely to be resolved into separate species that are confined to one side, east or west, of Lydekker's Line.

By combining what was known about seed dispersal in *Aglaia* (Pannell & Kozioł, 1987) and the distribution of vertebrates in the Malay Archipelago, we predicted that species endemic to the east of Lydekker's Line would be dispersed by birds or mammals that were also endemic to the region (Pannell & White, 1988). The discovery by Andrew Mack that the dwarf cassowary was responsible for almost all seed dispersal of an unknown and undescribed species of *Aglaia* from Papua New Guinea (Mack, 1997; 2014) was the first example of such a switch in dispersers. It represented a modification

of the bird-dispersal syndrome (Pannell, 1997b; Hopkins *et al.*, 1998). In SE Asia the bird-dispersed fruits dehisce on the tree, held in infructescences of one to a few fruits, on a short peduncle, close to a sturdy perching branch from which the bird disperser can extract the exposed arillate seed. The red colour of the aril contrasts with the exposed white inner pericarp and brick-red, pink, yellow or white outer pericarp. In this dwarf cassowary dispersed *Aglaia*, named *A. mackiana* Pannell (Pannell, 1997b), the much larger fruits fall to the ground and shatter, scattering the large seeds (105 mm long, 70 mm wide and 60 mm through). The red colour of the aril contrasts with the large white attachment scar and makes the seed conspicuous on the ground where the large, flightless cassowary picks it up and swallows it whole. The size, falling to the ground and distribution of attracting coloration are all differences from the arboreal bird-dispersal syndrome.

   Primates and other fruit-eating placental mammals, such as elephants, tigers, deer and sunbears, are absent from east of Lydekker's Line. It is not known what replaces them as seed dispersers for indehiscent section *Aglaia* fruits in Australasia. In contrast to the apes of SE Asia, arboreal marsupials are less mobile, and none is known to have a high proportion of fruits in its diet, except for those that destroy most of the seeds they consume. Fruit bats are equally diverse on both sides of Lydekker's Line but, so far, have only been implicated in the dispersal of two species of *Aglaia* in islands of the south-western Pacific (Wiles & Fujita, 1992; Rainey *et al.*, 1995). In spite of this apparent absence of seed dispersers for section *Aglaia*, a different suite of species, younger in age, is found in Australasia and the south-western Pacific. It seems that these have arisen since the original colonisation of Australasia by *Aglaia*. It is likely that there are modifications of the mammal-dispersal syndrome in this section that have not yet been observed or described. Although some bird families implicated in dispersal of seeds from dehiscent fruits in *Aglaia* sections *Amoora* and *Neoglaia* are confined to west of Wallace's Line (broadbills, for example) or decline markedly in numbers (only one hornbill species is known from New Guinea), endemic families such as birds of paradise and bower birds take seeds at the lower end of the size spectrum, while pigeons, corvids and others are capable of swallowing larger seeds. Cassowaries swallow much larger seeds than any other bird.

LONG-DISTANCE DISPERSAL OF *AGLAIA* BETWEEN THE SUNDA AND SAHUL CONTINENTAL SHELVES

Two groups of seed dispersers are present throughout the distribution of *Aglaia*. These are fruit bats (Pteropodidae) and fruit doves (*Ducula* and *Ptilinopus*). Either group could have been responsible for dispersing *Aglaia* seeds across expanses of deep sea in Wallacea, to or from Australasia, but only the fruit doves are known to swallow the seeds. They are therefore the most likely candidates for long-distance dispersal of these plants.

MOLECULAR PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF *AGLAIA*

The combination of a published comprehensive taxonomic revision throughout the range of the genus, expertise in identifying sterile specimens and hands-on involvement of the monographer providing accurately identified material for further investigations makes the genus uniquely suited for employing molecular methods to explore the evolutionary history of lowland tropical rain forest trees in the IAA.

Molecular phylogenies (Muellner *et al.*, 2005; Grudinski *et al.*, 2014a) have added to the knowledge of the genus *Aglaia* by estimating its approximate age to be 24 million years old, and its origin and centre of diversity to be in Sundaland (or mainland Asia). The biogeographical analyses (Muellner *et al.*, 2008; Grudinski *et al*., 2014b) suggest that *Aglaia* reached New Guinea from the west less than 12 million years ago, Australia five million years ago and Fiji three million years ago. The level of endemism in the genus in these relatively recently colonised eastern regions is higher than in the west of its range: nearly 50% in New Guinea (at least 16 out of at least 36 species), 33% in Australia (four out of 12), 80% in Fiji (eight out of ten). Without the expertise built up over many years of research on this genus, the published monograph and flora accounts and my identification of new, often sterile material, the plant names applied to the molecular formulae and DNA sequences would be inaccurate. Interpretations based on incorrectly named plant material would be misleading and non-repeatable.

In recent years, molecular studies have uncovered cryptic species with restricted distributions in other groups of organisms (Lohman *et al.*, 2011; Deiner *et al.*, 2011). Such cryptic species were suspected in *Aglaia* three decades ago from the morphological and geographical patterns of variation observed in the genus (Pannell & White, 1988). The more recent molecular phylogenies and chronograms (Muellner *et al.*, 2005, 2008; Grudinski, 2014a & b) suggest that the complex and variable species are not monophyletic, and many entities to the east of Lydekker's Line fall into a separate clade from those they most resemble in Wallacea and/or SE Asia. The appearance of different samples from the same complex or variable species in different parts of the molecular phylogenies make it seem likely that at least some of the variation in these species is the result of convergence in morphological characters between distantly related entities. The next phase of morphological and molecular research will be to attempt to resolve the variable and complex species morphologically and to test any new classification with more DNA sequencing, followed by even more comprehensive phylogenies than the most recent one by Grudinski *et al*. (2014a).

When the morphological, distributional and biological information was combined with the history of plate tectonics in the region, molecular phylogenies and historical biogeography analyses, a pattern of origin, expansion and species radiation in this genus through the last 24 million years emerged. Subsequent studies of other groups of plants and animals revealed a similar pattern of movement across Wallacea, now known as the Sunda-Sahul floristic interchange (Crayn *et al.*, 2015), with a range of timings from 33 million years for Euphorbiaceae (Van Welzen *et al.*, 2014) to 1

(0.1–1.2) million years for one clade of *Begonia* L. (Thomas *et al.*, 2012). All available phylogenies of plant groups for the region were included in Crayn *et al.* (2015) giving a synthesis of available information on the timing and direction of movement of plant groups across Wallacea, between the Sunda and Sahul continental shelves.

### CONCLUSION: WHAT NEXT?

A more powerful dataset for exploring the evolution and historical biogeography of this representative group of trees from the IAA, in deep and shallow time, would be achieved by combining improved morphological species delimitations (possibly resulting in recognition of up to 200 species of *Aglaia*). More molecular work to produce phylogenies with better resolution and support would enable even more informative biogeographical analyses than have already been produced. By recognising the larger number of species of more restricted range, it is hoped that the polyphyly that complicates the existing phylogenies and introduces error into the biogeographical analyses will be wholly or partially eliminated. In that way, more progress can be made in understanding the biogeography, patterns of diversification and even convergence between distantly related species. Then *Aglaia* will continue to advance our understanding of the biodiversity and evolutionary history of rain forest ecosystems in the context of two of the major zoogeographic regions of the world.

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