Biogeography of *Aporosa* (Euphorbiaceae): testing a phylogenetic hypothesis using geology and distribution patterns

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Abstract

A cladistic analysis of the SE Asian angiosperm genus *Aporosa* (Euphorbiaceae) leads to a hypothesis about the possible formation of hybrid species on New Guinea. It is suggested that members of two different Sundanian lineages reached New Guinea independently and hybridized on contact. Distributional patterns and current interpretations of the geological evolution of the area confirm the possibility of two different pathways to New Guinea from Sundaland: one along the Outer Melanesian arc, and a second via the Banda arc.

Introduction

Aporosa is a genus of about 80 species of small trees which inhabit the tropical rain forests of SE Asia. Six species are found in the remnant forests of South India and Sri Lanka; the others are found from the Himalaya southwards into the Malay archipelago and onwards to the Solomon Islands. Borneo, with 30 species, of which 10 are endemic, and New Guinea, with probably up to 20 endemic species, many of which are still poorly known, are the main centres of diversity for *Aporosa* (Fig.1).

Aporosa has been revised and cladistically analysed (Schot, 1998). Shaping the cladogram for *Aporosa* has met with some difficulties. Some problems are caused by the size of the genus. There are 110 taxa, including 82 species, 8 varieties, 6 forms, 7 poorly known species, and a multiple outgroup. The number and quality of the available macromorphological characters which were used to build the data set presented another problem. *Aporosa* belongs to the subfamily Phyllanthoideae in the family Euphorbiaceae. The Phyllanthoideae comprise the paraphyletic part of the family as a whole, in which the more derived 'eu-Euphorbiaceae' are thought to nest. The main characteristic of the Phyllanthoideae is the lack of specialized characters. *Aporosa* conforms completely with this characterization; it is non-descript. The species are minimally distinct from each other and defined on combinations of characters. There are very few unique apomorphies. 83 multistate macromorphological characters can be scored for the 110 taxa. Of these characters, most turned out to be phylogenetically uninformative because of the recognition of combinations instead of unique characters.

Due to these two factors, cladistic analysis of *Aporosa* has yielded thousands of equally parsimonious solutions. It is impossible to make biologically meaningful choices among these; the accuracy of any one cladogram is probably very low. However, it was found that many of the ambiguities of the various solutions resulted from the placements of one category of taxa; part of the New Guinean species. These particular New Guinean species possess anomalous character combinations in comparison with the Sundanian species and the remainder of the New Guinean species. The character combinations that are found in the majority of species do not apply. The species vary interspecifically in characters that are stable in West Malesia and are stable for characters that vary interspe-
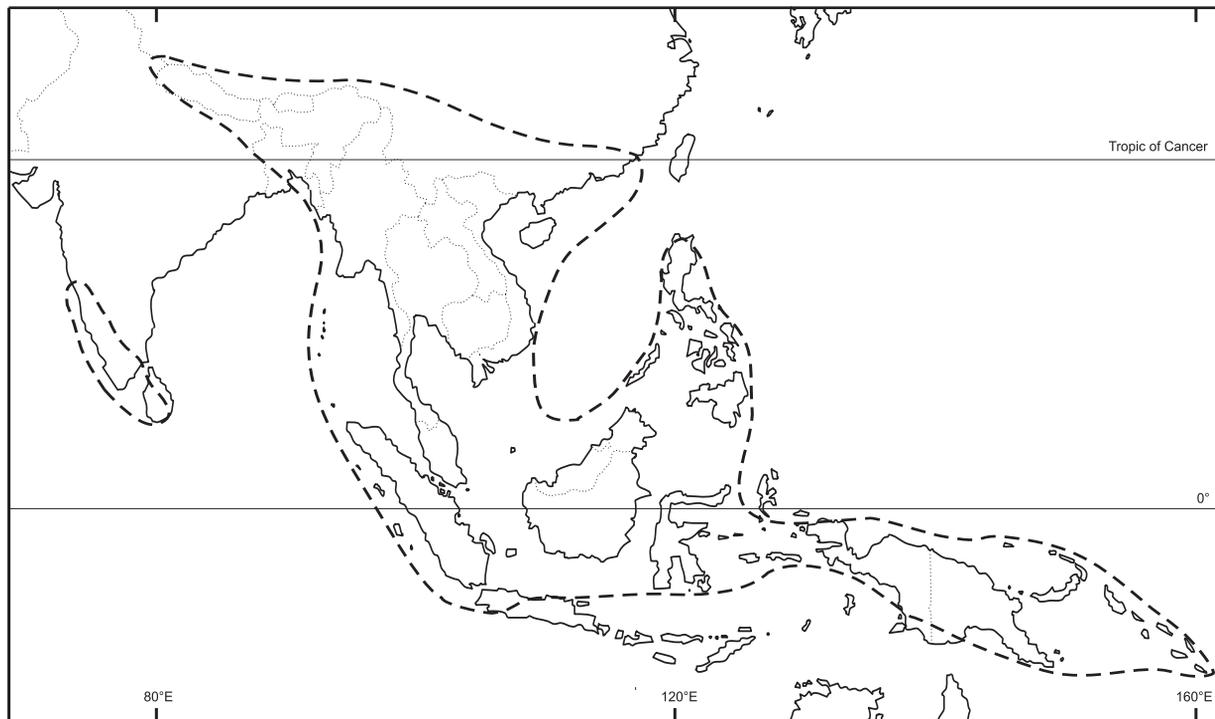
Fig.1. The distribution of *Aporosa*.

cifically in West Malesia. In an attempt to clarify some of the cladistic patterns, an analysis was conducted excluding these anomalous New Guinean taxa. This resulted in a strong reduction of the number of solutions. In consequence, it was hypothesized that the species that possess the anomalous character combinations and disrupt the cladogram might be the products of extensive hybrid speciation between unrelated lineages. The remaining New Guinean taxa, which were placed in two lineages in the cladogram when excluding the anomalous ones, are interpreted to represent the two parental clades that independently reached New Guinea and hybridized on contact.

In this paper I investigate whether historical biogeographical patterns support this hypothesis. First, I give a summary of the main phylogenetic patterns found in the cladistic analysis. Next, I describe the distributions of selected groups of *Aporosa* and try to identify those events in the geological evolutionary history of the Malay archipelago that could be relevant in the evolution of *Aporosa*. Comparison of the distributional pathways as suggested by the geology of the area with the phylogenetic patterns in *Aporosa* may then be used as independent test of the hypothesis of hybrid speciation.

Phylogenetic patterns in *Aporosa*

Cladistic analysis was undertaken with the computer program HENNIG86 (Farris, 1988). This program searches for the most parsimonious trees. These are calculated by looking for trees with the fewest character changes, or the highest consistency index (CI). The retention index (RI) is a measure of the quality of the characters.

The data matrix for *Aporosa* contained 110 taxa, of which 103 were taxa of *Aporosa* and seven were outgroup taxa, and 83 macromorphological characters. Analysis with the tree search commands 'mhennig*' and 'bb*' produced 875 trees of length 1428, CI 0.11, and RI 0.57. The selection of the characters and outgroup and the results of the analyses are treated in detail by Schot (1998). Here I give a brief outline of the procedures followed and the results. As can be seen, the CI and RI in the analysis are low. Since a CI and RI of 1.00 indicate perfect fit, the low CI and RI indicate that the found cladograms of *Aporosa* are untrustworthy. In addition, because an overflow of computer-memory was encountered during the search, more equally parsimonious trees are present. The possibility that the trees found are not the most parsimonious can not be ruled out.

To search for more equally parsimonious or more parsimonious trees various options of the phylogenetic analysis were changed. For instance, characters were weighted differently or only subsets were taken, the taxa were given in a different order, or other tree calculating commands were used. All various options resulted in even more different solutions. It was found that all trees shared a pattern in which 8 clusters of species could be identified, 3 of which were monophyletic groups. The other 5 components were in some analyses placed as paraphyletic tails to the monophyletic groups, and in other analyses as a monophyletic sister groups. Part of the species had no constant placement among the cladograms. Together a general pattern was formed consisting of three lineages, each containing one monophyletic group with one or more of the other components as its sister or paraphyletic tail and a changing compound of other taxa. An Adams consensus tree is given in Fig.2 showing these 8 clusters and the switching remainder. A ninth cluster in the lower half of Fig.2 is in my view a completely arbitrary clustering of incompletely known anomalous taxa and does not deserve recognition. I have simplified the tree by not naming the species in the clusters. They are named after the most common taxon in the cluster. Taxa not placed in any of the clusters are taxa that swap positions in the various solutions. Accolades with numbers indicate how the three lineages are formed. Note that some clusters and species switch between the lineages.

The Adams consensus tree of Fig.2 was calculated using PAUP 3.1.1 (Swofford, 1991) and all the cladograms found in the various analyses using the complete and unweighted set of characters. Adams consensus trees summarize the patterns found by checking the clades for identical elements. In contrast with the more often used strict consensus tree, an Adams consensus tree will thus not collapse clades in which one or a few taxa are missing in part of the solutions. For *Aporosa*, where some taxa are switching and some clusters of taxa are either paraphyletic or monophyletic, a strict consensus gives no solution at all. The Adams consensus tree moves the swapping taxa to a polytomy at the base and keeps the unchanging part of the clade intact. In this way, the consensus tree can be used for identifying the identical elements between the thousands of found solutions. However, it will sometimes show paraphyletic elements in a monophyletic configuration. Thus the 5 non-monophyletic clusters of species of Fig.2 are
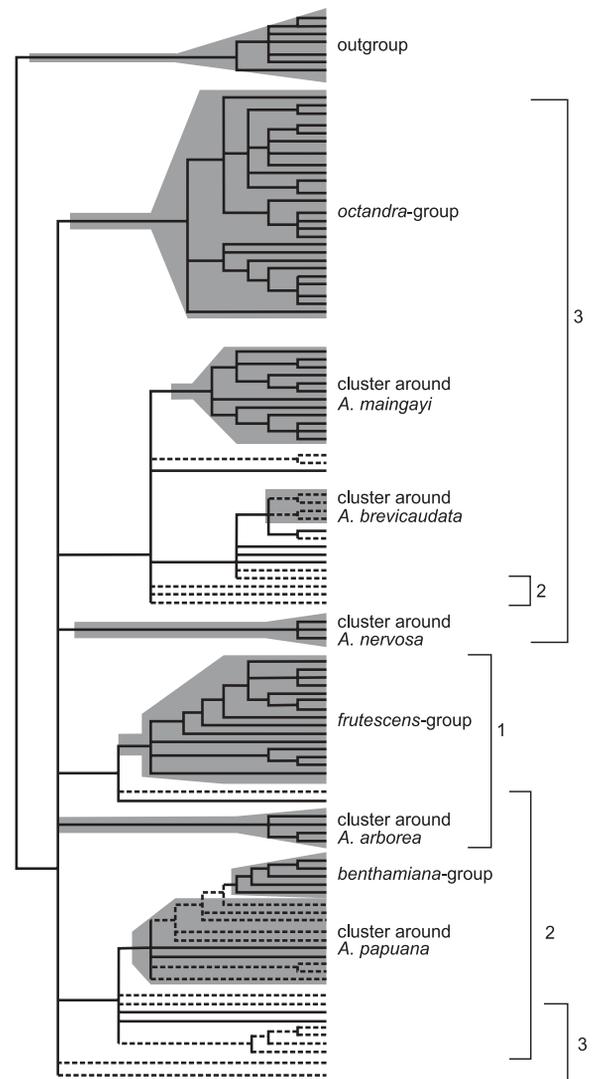

Fig.2. Adams consensus tree of the 4374 trees found in various phylogenetic analyses of *Aporosa*. For simplicity the names of taxa have been left out. Eight clusters of taxa can be identified: three named monophyletic groups and five paraphyletic components. Species not part of any of these components represent the ambiguous paraphyletic tail. The three lineages that were present are indicated by accolades on the right with numbers. Some taxa or clusters were variously placed. Asiatic and West Malesian species are in black, New Guinean species in dashed lines. Note the scattering of the New Guinean species.

depicted monophyletically only as a result of the Adams consensus technique. The three lineages do not show in the consensus tree, because their identical elements are the 8 clusters; the lineages themselves are formed of these clusters and a varying component of other taxa. They can be seen by studying the cladograms.

The three monophyletic groups are the *frutes-*

cens group, the *benthamiana* group, and the *octandra* group (Fig.2). The species of the first two groups occur on Sundaland, in the Malay peninsula, Sumatra, West Java, and Borneo, and some species reach the Philippines and NE Sulawesi. The *octandra* group is mainly found on the mainland of Asia. The six endemic species of Sri Lanka and South India all belong in this clade, and two species are widespread in West Malesia.

Two of the five paraphyletic components are rather large: the species around *A. papuana* and the species around *A. maingayi*. It is possible that these two components only show up in a paraphyletic configuration in part of the analyses because of the way in which the phylogenetic algorithm works. They may represent the local sister group to the last two monophyletic clades respectively. Because they do not possess a synapomorphy, parsimony analysis optimizes them in a pectinate diagram, but this is not necessarily accurate (Baum and Estabrook, 1996). *Aporosa maingayi* and its allies are Sundanian, *A. papuana* and allies New Guinean.

The remaining three smaller recognizable paraphyletic elements are the Sundanian species around *A. nervosa* and those around *A. arborea*, and the New Guinean species around *A. brevicaudata*. Together with the taxa without consistent placement they form the paraphyletic tail. Their configuration is ambiguous, and nothing can be said at this point about the taxa in it.

Biogeographically speaking, the pattern of the consensus tree shown in Fig.2 is disturbing: the distribution of the Sundanian and the New Guinean taxa in the paraphyletic tail is completely mixed. As seen in Fig.2, many of the New Guinean species (dashed lines) are interspersed among their Sundanian relatives (in black). Interpreted as biogeographical pathways, this would mean a constant coming and going between Sundaland and New Guinea. An evolutionary scenario with fewer dispersals might be more plausible.

To seek a less ambiguous pattern, and one with, preferably, the New Guinean taxa less scattered, further cladistic analyses were undertaken using only subsets of taxa. Taxa placed in the polytomies in the Adams consensus tree in Fig.2 are taxa that have ambiguous placements. It may clarify part of the phylogenetic relationships if such taxa are omitted from the analysis. Thus subanalyses were undertaken with various taxa of the basal polytomies excluded. One subanalysis (the others are treated by Schot, 1998)

was an analysis without the New Guinean taxa of the basal polytomy. These particular taxa are different from all West Malesian taxa and the remaining New Guinean taxa around *A. papuana* and *A. brevicaudata* in having an anomalous combination of the characters they are described on. The species can be identified by characters that vary within a species in Malesia, such as size differences, whereas characters that are used in West Malesia to delimit the species, such as inflorescence, are variable. It was found that excluding these taxa resulted in a strong reduction of the number of trees found. 24 trees were found with length 977, CI 0.17 and RI 0.53. Besides a reduction in the number of solutions, the ambiguity between the solutions decreased. Differences were only found in minor branches, resulting in a better resolved consensus among them. The other subanalyses with different taxa of the basal polytomy excluded did, in contrast to the analysis without the anomalous New Guinean taxa, not give fewer trees or a better solution of the consensus pattern.

This obvious improvement of the cladistic analysis when excluding part of the taxa led to the idea that these particular taxa were the main causes of disturbance of the phylogenetic patterns. The question then arises of what to do with the excluded New Guinean taxa. How should they be placed in the phylogeny of *Aporosa*? Where did they come from and why do they disrupt the phylogenetic pattern so much? The macromorphological characters of these species give an answer to this last question. The species are characterized by anomalous combinations of characters. The unchanging combinations as shown by the Sundanian species are disrupted and recombined. Additionally, more primitive characters are retained by these various New Guinean taxa. And finally, exceptional characters emerge that have no parallel within the genus. Such characteristics might indicate hybrid species (Rieseberg, 1995). Furthermore, when formed between distantly related lineages, hybrid species are expected to disrupt phylogenetic patterns (McDade, 1992). With this idea in mind the data set was analysed again, but now with only subsets of taxa and recoded characters. A new consensus tree, built by combining the various results of the subanalyses after excluding the anomalous New Guinean taxa, is given in Fig.3. The basic pattern is an Adams consensus tree, with polytomies solved as far as possible based on cladistic analyses of smaller groups. Not all polytomies could be solved in a trustworthy manner and
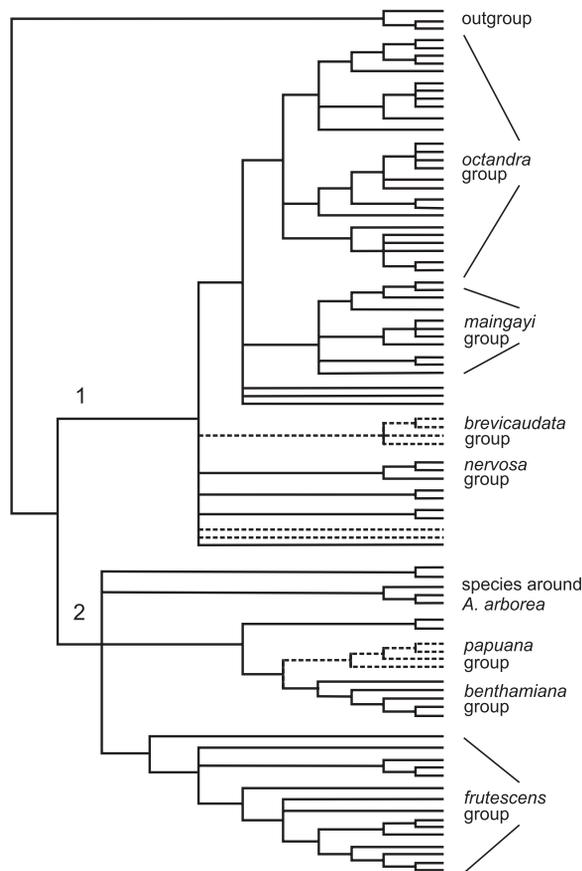
Fig.3. Accepted combined consensus tree for *Aporosa.* The names of the taxa are left out. The consensus tree was shaped on several subanalyses. The New Guinean taxa with anomalous character combinations are excluded. The remaining taxa settle into two lineages, indicated by numbers, each with a New Guinean component, shown in dashed lines. The eight components of Fig.2 are also indicated.

these were left as polytomies. However, only the broad picture is considered here. The separation of the remaining New Guinean species into two lineages was evident in other analyses as well and can be viewed with confidence.

Looking at the consensus tree of Fig.3 the broad picture that was found before with three intermingling lineages (Fig.2), has changed to consist of two distinctly separate lineages. Both contain one component of New Guinean species (Fig.3, dashed lines). One of the lineages contains the now monophyletic cluster with *A. papuana*, the other the cluster with *A. brevicaudata* and two further species, *A. nigropunctata* and *A. longicaudata.* Macromorphological characters and results of other subanalyses showed that these two species belonged to the ambiguously placed West Malesian species, rather than

to the anomalous New Guinean species. The clade with *A. papuana* shows a close relationship with the monophyletic *frutescens* and *benthamiana* groups and the cluster around *A. arborea*; the clade with *A. brevicaudata* is more related to the *octandra* group and the clusters around *A. maingayi* and *A. nervosa* and the remainder of the paraphyletic tail. In a biogeographic sense, only two colonization events from West Malesia to New Guinea now need to be proposed, which is a more parsimonious scheme than that mentioned above.

The phylogenetic pattern found with two independent lineages that occur on New Guinea supports the hypothesis that two distinct lineages colonized New Guinea. The fact that the pattern is disrupted by including the anomalous species is consistent with the hypothesis that these originated by hybridization events that followed the double colonization. Fig.3 shows the two possible parental lines to the hybrid species and their nearest West Malesian relatives. Next, distribution data can be studied to examine if the two New Guinean clades inhabit different areas and if the supposed hybrid species occur in their contact zones.

Distributions of *Aporosa*

The distributions of the New Guinean species are shown in Fig.4. The New Guinean species are divided into three groups: the two separate lineages in the cladogram of Fig.3 and the excluded putative hybrids. The species of the first clade consisted of the four species around *A. brevicaudata*, together with *A. nigropunctata* and *A. longicaudata.* Their distribution is depicted in Fig.4A. The species of the second lineage, the *papuana* group, are in Fig.4B. Fig.4C shows the distribution of the putative hybrid species.

The four species around *A. brevicaudata* are montane species of the central mountains ranging from the Arfak Mountains in the Bird's Head to Markham in the east. The two lowland species *A. longicaudata* and *A. nigropunctata* are found in the easterly and westerly adjacent lower parts of this range respectively. *Aporosa nigropunctata* also occurs sporadically in the Papuan peninsula (Fig.4A).

The *papuana* group consists of species of the lowland rain forests and seems mostly concentrated in north New Guinea, with one species, *A. brassii*, near the Vailala River on the southern side of the central mountains. *A. papuana* itself
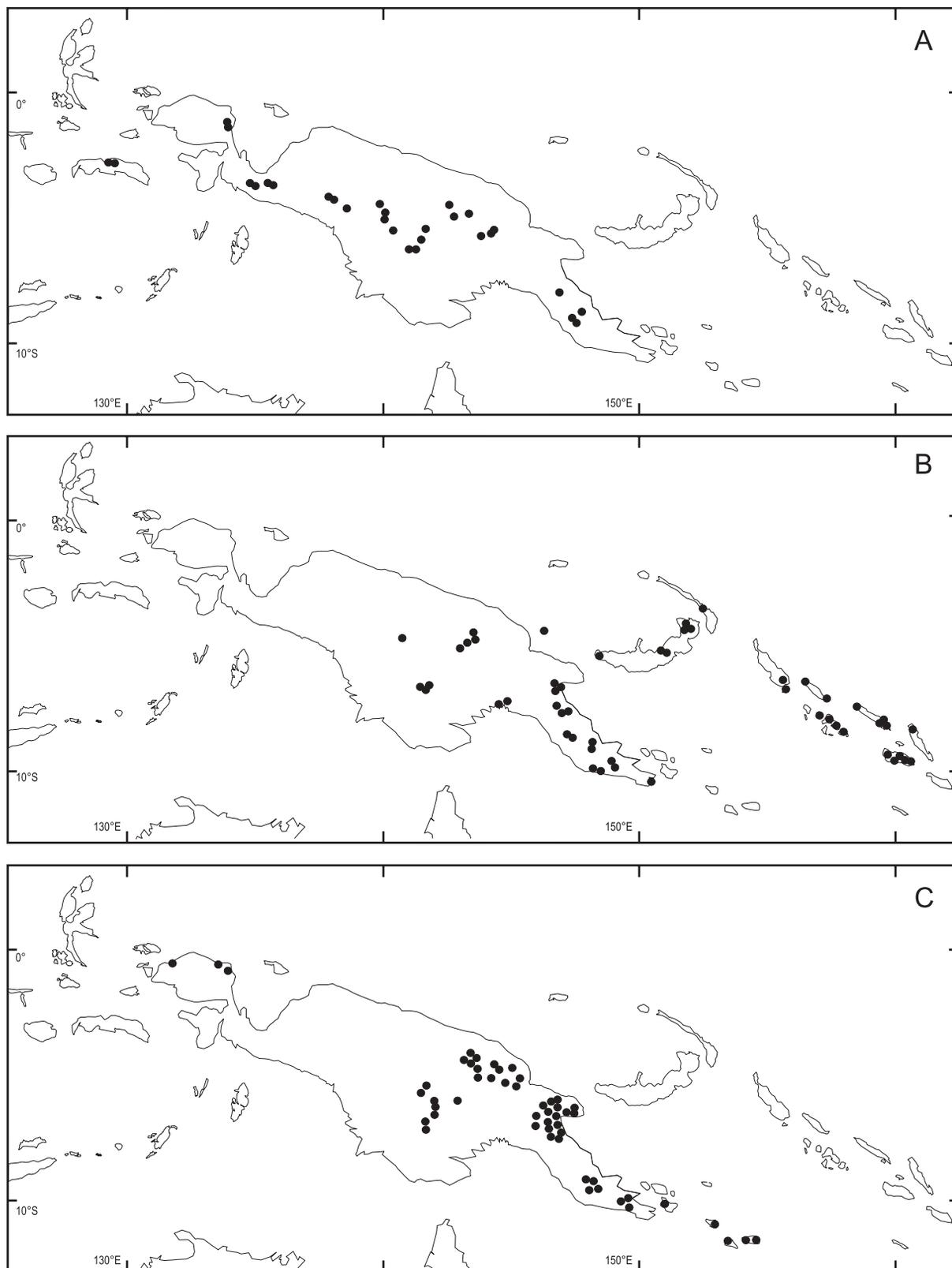
Fig.4. Distribution of the three groups of New Guinean species of *Aporosa*: A: the four species around *A. brevicaudata* with *A. nigropunctata* and *A. longicaudata;* B: the species around *A. papuana*; and C: the putative hybrids.

is widespread over north New Guinea, the Bismarck archipelago, and reaches the Solomon Islands. A few specimens have been found in the Papuan peninsula (Fig.4B).

The putative hybrids are found mostly in the Sepik area, the western part of the central mountain range and adjacent lowlands, and in the Owen Stanley range of the Papuan peninsula southwards into the Papuan Islands (Fig.4C). The places where this last group is found coincide largely with places where the first two groups co-occur. Thus, the hypothesis of hybridization is consistent with the distributional data. A third confirmation would be if historical geographical patterns allow at least two different ways and/or times to disperse from Sundaland to New Guinea. This is discussed next.

Relevant geological history

The Euphorbiaceae are assumed to have originated in the Cretaceous in the Old World tropics, since the largest number of primitive taxa of the basal subfamily Phyllanthoideae are found in Africa/Madagascar. From here they spread over America and the Malay archipelago (Webster, 1994). This may mean that *Aporosa*, whose greatest diversity is found in the tropical forests of Sundaland, originated in a time when the Sibumasu, East Malayan, and the SW Borneo block had already accreted to the Asian mainland (see Ridder-Numan, 1996, or Metcalfe, 1998 this volume, for a summary of the drifting sequences of the various terranes). This sets the starting point of this story at its earliest in the Cenozoic (Metcalfe, 1994). The onset of the collision of India in the early Eocene probably caused the clockwise rotations of the various islands on the Sunda shelf. This might have given *Aporosa* the chance to establish itself here over the next few million years, as is indicated by the mainly Sundaland distribution of the more primitive species of the genus (Fig.3).

The consensus tree shows that at least the species around *A. papuana* originated from West Malesian relatives; for the second New Guinean component this is hard to tell with the base of the lineage unresolved. My interpretation is that, after originating, the genus dispersed over the archipelago, including part of New Guinea. These species are those that are found in the polytomies. A later speciation event gave rise to the more derived resolved components, such as the three monophyletic groups. This included a second invasion of New Guinea

by the ancestor to the species around *A. papuana*.

An origin of the primitive *Aporosa* in New Guinea, which then spread to West Malesia and returned to New Guinea in the form of *A. papuana*, is less plausible, since the outgroup occurs in West Malesia. However, this would still require two separate pathways. Dispersal events to New Guinea became possible with the forming of the Tertiary island arc complex later in the Eocene and the arrival of Australia in Malesia in the Miocene (Boer, 1995). Since I am here mainly concerned with the possible distributional pathways for *Aporosa* to reach New Guinea from Sundaland, I will concentrate on the geological events in the period from the Eocene to recent that allowed dispersal from Asia to Australia (Fig.5).

Boer (1995) gives a summary of the most important geological events in Indo-Melanesia. The Indo-Melanesian part of the Tertiary island arc system started to develop about 40 million years ago. Remnants of this arc are found in parts of the central Philippines, northwest and east Sulawesi, and north and east New Guinea. This part has been termed the Outer Melanesian arc (OMA) in biogeographic studies and served as an important pathway for dispersal between SE Asia and Australia (Boer, 1995). At 30 Ma the OMA connected with SE Asia, possibly somewhere south of the Philippines and started breaking. At 20 Ma the Australian craton had arrived in the area and collided with the fragments of the OMA. Little is known of the amount of emergent land on this OMA; dispersal patterns of biota suggest that at times some dry land must have been present to allow colonization.

In southeast Indonesia the amalgamation of the various fragments of the Philippines and Sulawesi and the continuous movement of Australia was also felt (see Hall, 1998 this volume). According to Daly *et al.* (1991) at about 10 Ma the Banda arc bent and Buru-Seram rotated, initiating accretion of the northwest margin of Australia to south Indonesia (see also Burrett *et al.*, 1991). This might have opened connections of the Sunda island chain to Buru-Seram and onto the Bird's Head of New Guinea.

In the meantime, New Guinea itself was growing. Pigram and Davies (1987) reconstructed the accretion history of New Guinea (Fig.6). According to them fragments of the Tertiary arc chain were accreted onto the passive margin of the Australian craton in various steps. The Sepik terrane was the first to dock at 25 Ma, followed at 15 Ma and 10 Ma by the Composite East Papuan block and north New Guinea respectively.
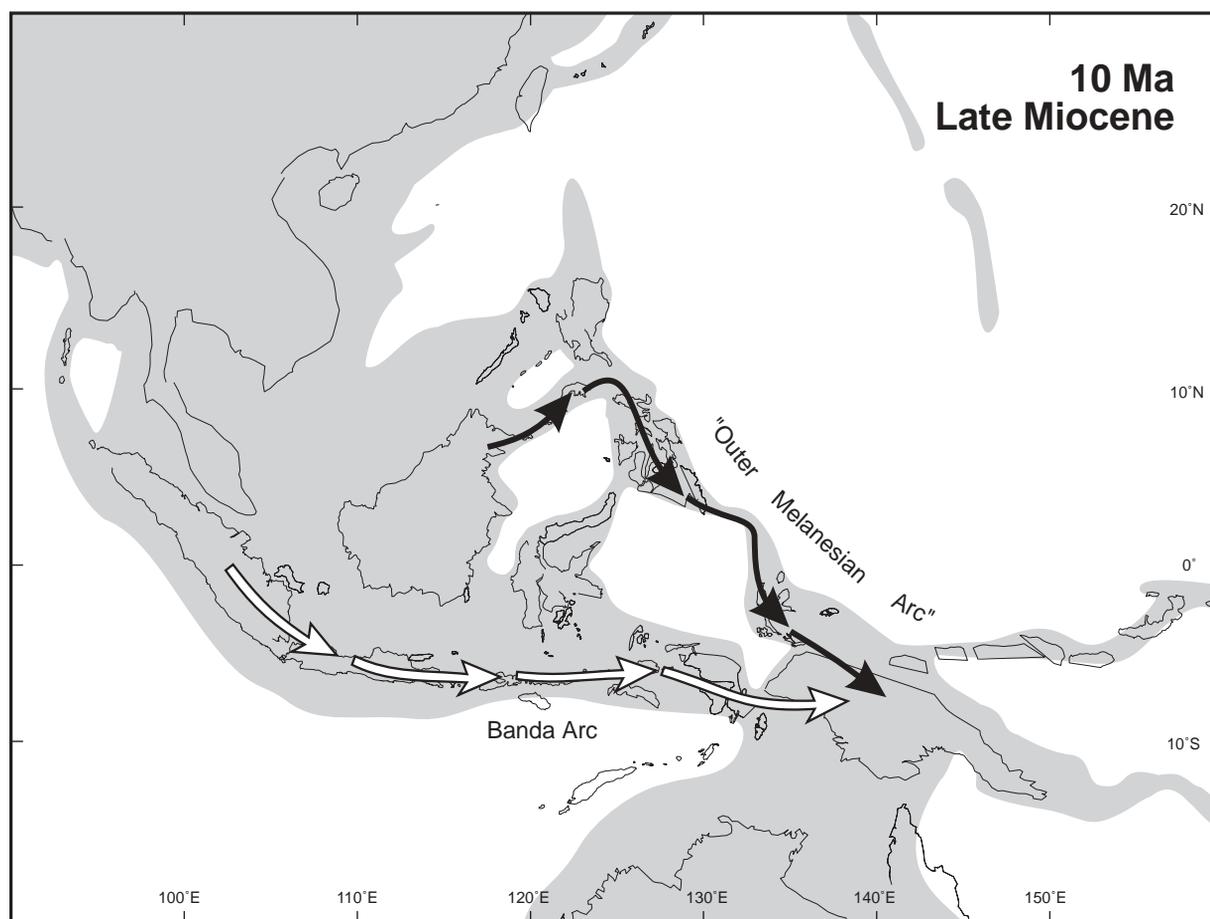
Fig.5. A geological reconstruction of SE Asia at 10 Ma. The two possible routes followed by *Aporosa* to disperse from Asia to Australia are indicated by arrows. Modified from Hall (1998 this volume).

In the west, the south Bird's Head was accreted at 10 Ma following the bending of the Banda arc and the rotation of Buru-Seram. At 2 Ma the Arfak Mountains in the north Bird's Head and the Solomon Island chain followed suit.

Two possible pathways can be supposed on the basis of these geological events. The first goes in the north along the fragments of the OMA between the Philippines, Moluccas, northern New Guinea, and New Guinea. A second dispersal route in the south could have followed the Sunda islands, Banda arc, Buru-Seram, to the south Bird's Head and, after docking at 10 Ma, to the rest of New Guinea (Fig.5).

Comparison of phylogenetic, distribution and geological patterns

With the phylogenetic patterns, the distribu-

tions, and the geological events we can try to complete the picture of the putative colonization events of *Aporosa* from Sundaland to New Guinea. The cladogram had two lineages (Fig.3). The New Guinean clade of the first lineage, the *brevicaudata* group with *A. nigropunctata* and *A. longicaudata* was concentrated mostly in the central mountain range, the Arfak Mountains, and some specimens in the Papuan peninsula (Fig.4A). This clade showed close relationships with the Asiatic *octandra* group, the Sundanian *maingayi group,* the Sindanian species around *A. nervosa,* and the unresolved part of the cladogram (Fig.3). The distribution of these relatives is shown in Fig.7A. The *octandra* group, which is the only clade found mainly on the mainland of Asia, is indicated by its derived position in the cladogram not to be relevant to the dispersal to New Guinea of the more primitive species. This
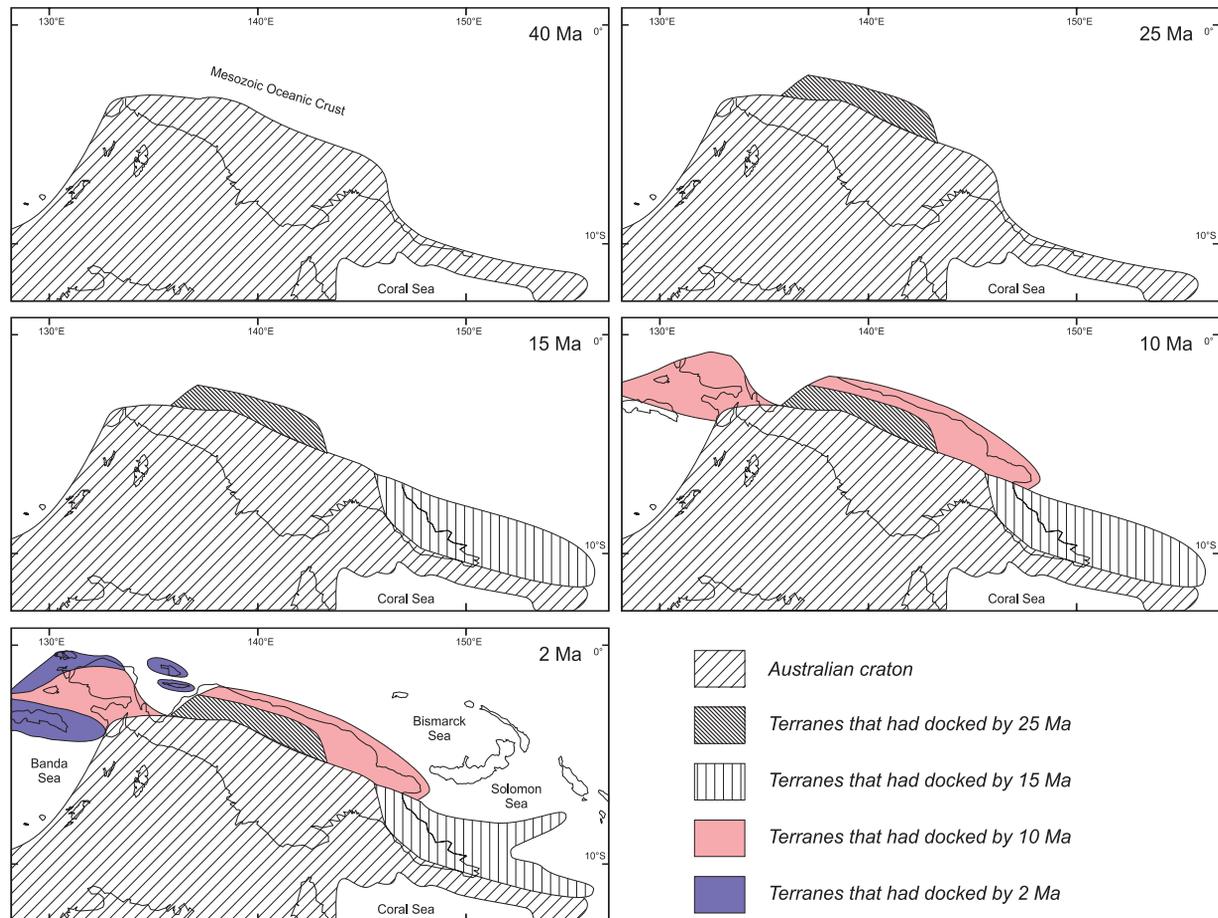
Fig.6. The accretion history of New Guinea as reconstructed by Pigram and Davies (1987).

group also contains the species nowadays found on Sulawesi. The *maingayi*, the *nervosa* clade, and the remainder contain 18 species which are found on peninsular Malaysia, Sumatra, Java, Borneo, the Philippines, and Buru-Ambon (Fig.7A). The main diversity is found in peninsular Malaysia and Borneo with 9 species in both, of which 3 are widespread in Sundaland. One species is found in the Philippines with a different variety on West Java. One species occurs in Buru and Ambon, and the last is a fragmentary specimen from the Philippines.

Coupled to the fact that some of the New Guinean relatives of this lineage occur in the Bird's Head, it is likely that this group reached New Guinea along the Banda arc, and spread over New Guinea when the Bird's Head came in close contact at approximately 10 Ma (Figs.5 and 6). The central mountain range of New Guinea, where the clade is still best represented, was al-

most certainly emergent at this time and onwards (Rangin *et al.*, 1990).

According to such a distributional pathway it might be expected that the lineage would also occur on the Lesser Sunda Islands. But they do not. This absence is explicable. *Aporosa* is mostly restricted to an ever-wet climate. However, nowadays the Lesser Sunda Islands and parts of Sulawesi and the Moluccas have a more or less seasonal climate (Steenis, 1979). Because of changing climates or ecological circumstances the range where the lineage once occurred may now be shrinking. The Buru-Ambonese *A. dendroidea*, the West Javanese *A. sphaeridiophora* var. *campanulata*, and the most northerly distributed *A. duthieana* are all little known species that might represent the boundaries of the distribution of this lineage in former times. Supporting this interpretation is the fact that *A. sphaeridiophora* var. *campa-*
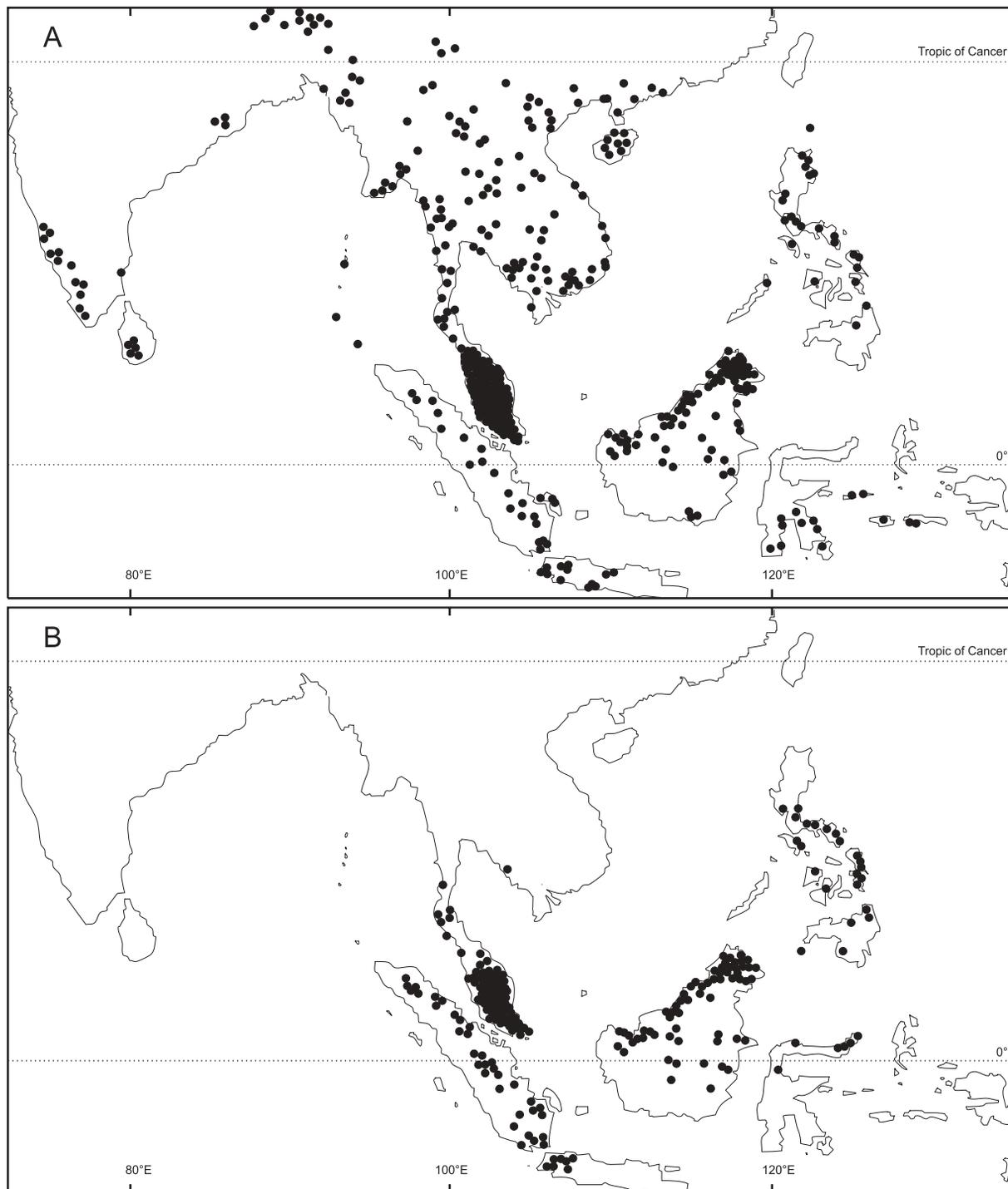
Fig. 7. Distribution of the West Malesian species of *Aporosa*. A: the *maingayi* and *nervosa* groups and the unresolved para-phyletic tail; and B: the *benthamiana*-group and the species allied to *A. arborea*.

nulata has never been collected again after the first few times in 1890 and is now almost certainly extinct. Considering this possible extinction of *A. sphaeridiophora* var. *campanulata* from Java, other extinct species may once have occupied the Lesser Sunda Islands, bridging the gap between Sumatra and Buru-Seram.

The New Guinean clade of the second lineage

is distributed in north New Guinea and the Solomon Islands (Fig.4B). The Sundanian relatives of this lineage, the *benthamiana* group, the *frutescens* group, and the species allied to *A. arborea* (Fig.3) are found in Sundaland, south Philippines, and the Minahassa peninsula of Sulawesi (Fig.7B). This pathway coincides with a dispersal along the OMA. The south Philippines were colonized from Borneo and from there to Minahassa. The lineage is absent from east Sulawesi, the Moluccas, and part of the Sepik district, but abundant again in north New Guinea, the Bismarck and Solomon Islands. Two aspects might play a role to effect this. The dispersal along the OMA may have been taking place only after the OMA became partly incorporated in the Indonesian archipelago, at about 10 Ma. Halmahera or other islands of the Moluccas now subjected to a seasonal climate may have functioned as stepping stones from Minahassa directly to north New Guinea. It is also possible that more *Aporosa* species occur on Sulawesi, which is one of the under-collected areas of Indonesia. But this would only strengthen the pathway. The possibility that such fragments may have served as stepping stones is also supported by the occurrence of two species of putative hybrid origin in the most northern part of the Bird's Head, which is thought to have docked to New Guinea at 2 Ma (Fig.6). This area might represent another more recent point of contact between the first lineage, which was present in south Bird's Head, and the second lineage, coming in along the OMA.

The larger part of the second lineage may have reached New Guinea with the North New Guinea terrane that docked at 10 Ma (Fig.6). Spreading from there over New Guinea it met in the central mountain range with the first lineage. Hybrids or introgression yielded species with various adaptations that were able to colonize different parts of New Guinea, like *A. ledermanniana* that established itself in the swamps along the Sepik River, or *A. petiolaris* and *A. hermaphrodita* that became locally thriving populations in the striction zones caused by the subsequent docking of Finisterre. Others spread over the Papuan peninsula and reached places neither lineage was able to colonize before, like *A. misimana* on the Papuan Islands. Next to the newly inhabited areas the non-hybrid species had established themselves in other parts before contact and were able to persist there, such as the major part of Irian Jaya for the first lineage and the Solomon Islands for the second lineage.

These distributions of the three groups also raise the possibility that the first lineage was earlier to reach central New Guinea, because the mountain ranges contain both first and hybrid taxa, but none of the second lineage. This could mean that the Bird's Head was earlier in docking than the North New Guinea terrane, or that climatological, oceanic currents, or the presence of appropriate land extensions were more favourable to promote a dispersal from the south. It remains an area that needs further study.

Conclusions

Geological events and distributional patterns support the phylogenetic hypothesis that two different lineages of *Aporosa* have reached New Guinea from Sundaland independently at approximately 10 Ma. One clade might have undertaken the journey along the Lesser Sunda Islands to the Banda arc and the Bird's Head, reaching the central mountain ranges of New Guinea when the Bird's Head came in close contact with the rest of New Guinea. The other lineage might have travelled along the Outer Melanesian arc from Mindanao, through the Moluccas, to north New Guinea and the Solomons. New Guinea was colonized with the arrival of the North New Guinea terrane, which possibly occurred slightly later than the colonization from the south.

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