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PHYLOGENETIC BIOGEOGRAPHY OF THE FAMILY MONIMIACEAE

ABSTRACT. A complex cladistic analysis of molecular and morphological data of the Monimiaceae family is carried out. The hypothetic modes of the family dispersal are reconstructed basing on the data received for the studied representatives of the Monimiaceae family from all parts of the range and available fossils data. The family supposedly originated in Africa and penetrated into South America via the Antarctic way, and through the Arabian Peninsula and Sri-Lanka to South-Eastern Asia, Australia, New Zealand, New Caledonia, and further then to Madagascar.

KEY WORDS: dispersal history, cladistic analysis, Monimiaceae, molecular data

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INTRODUCTION

Molecular phylogenetics is a synthetic natural science discipline. It reveals the relationship between organisms on the basis of the sequence of the fragments of the nucleic acids - DNA and RNA (Judd et al. 2016; Wiley and Lieberman 2011). The result of a molecular genetic analysis is a phylogenetic tree formalized in the form of a cladogram - a scheme of successive divergences of the evolving group. At the present time, the concept that the data of molecular genetic analysis reflect the hypothetical evolution of the studied organisms is considered to be generally accepted (Judd et al. 2016; Wiley and Lieberman 2011).

This method of molecular analysis is widely used in biogeography (Crisci et al.

2003; Heads 2012, 2013). The analysis of the evolutionary relationships of different taxa within the key groups of angiosperms allows reconstructing the processes of their distribution and making the models of transformation of biogeosystems in the time and space (Crisci et al. 2003). So, with the aim to reconstruct the origin of the current distribution of the Monimiaceae family one of the most polymorphic families among magnoliids (Perkins and Gilg 1901; Philipson 2003; Takhtajan 2009) basing on the complex molecular and morphological analysis, this study was initiated.

Recent taxonomic treatment of Monimiaceae recognizes 27—28 genera, which include 200—270 species (Philipson 1993; Stevenson 2001). The family comprises two subfamilies – Hortonioidae (with single

genus *Hortonia*) and *Monimioideae*, which includes three tribes: *Hedycaryeae* (7 genera – *Xymalos*, *Decarydendron*, *Ehippiandra*, *Tambourissa*, *Hedycarya*, *Kibaropsis*, *Levieria*), *Monimieae* (3 genera – *Peumus*, *Monimia*, *Palmeria*) and *Mollinedieae* (17 genera – *Austromatthaea*, *Endressia*, *Hemmantia*, *Matthaea*, *Stegantthera*, *Tetrasynandra*, *Hennecartia*, *Macropeplus*, *Macrotorus*, *Mollinedia*, *Grazielanthus*, *Wilkiea*, *Kairoa*, *Faika*, *Kibara*, *Parakibara*, *Lauterbachia*) (Philipson 1993; Renner 1998; Renner and Chanderbali 2000; Stevenson 2001).

The representatives of *Monimiaceae* are woody plants with opposite leaves lacking stipules and the inflorescences formed by monoecious or dioecious, mostly polymeric flowers (Perkins and Gilg 1901; Philipson 1986, 1993; Takhtajan 2009). The fruit of most *Monimiaceae* are free from each other or submerged into the receptacle drupes of *Laurus* type (mostly red, orange or black) or apocarpous berries (*Kibara*, *Stegantthera*) or inferior pyrenaria of *Ilex* type (*Tambourissa* only) (Romanov et al. 2007).

The representatives of the family *Monimiaceae* are mostly occurring in humid evergreen tropical and subtropical forests up to 3000 m above sea level and representing the forest subcanopy, lower woody level or making the forest canopy whereas some species are growing in dry forests and savannas (Lorence 1985; Philipson 1986, 1993; Whiffin and Foreman 2007). The reproductive biology of the representatives of *Monimiaceae* is studied insufficiently (Lorence 1985; Philipson 1986, 1993; Whiffin and Foreman 2007). The flowers are mostly small (up to 1 mm in diameter) and inconspicuous with strong smell, in multiflorous inflorescences and are mostly attractive for insects. Rarely the flowers are large and the segments of the perianth are petal-like (in *Tambourissa perrieri* Drake – up to 3,5 cm: (Lorence 1985)). The anther glands and cauliflory indicate the entomophilous syndrome of the flowers in most representatives of the family, on the other hand as well as the *Monimiaceae* representatives are mostly the plants of the understorey the anemophily is doubtful, but the data on any other visitors of the flowers

are absent. The fruits of *Monimiaceae* are attractive for birds and supposedly are distributed by them, nevertheless only for *Hedycarya arborea* J. R. Forst. & G. Forst these data are based on the observations in the wild (Philipson 1993).

The most of biological diversity of *Monimiaceae* is distributed in South-East Asia as well as in Eastern Australia (Fig. 1) with endemic genera *Austromatthaea*, *Endressia*, *Hemmantia*, *Stegantthera*, *Tetrasynandra* (and genus *Wilkiea*, which areal also covers the New Guinea) (Whiffin and Foreman 2007). The genera *Kairoa*, *Faika*, *Lauterbachia* are the endemics of New Guinea, where the genus *Kibara* is distributed both in New Guinea and on the islands in the broad region from Nicobar Islands and Thailand to Philippines and Queensland (Philipson 1986). The genera of *Monimiaceae* are widely distributed in Malesia in Philippines, Thailand, Malaya and Sumatra (*Stegantthera*) and in Sulawesi, Solomon Islands and Queensland (*Stegantthera*); whereas the genus *Parakibara* is the endemic of Halmahera Island (Philipson 1986). The genus *Mollinedia* is widely distributed in the New World (central and northern part of the South America), whereas the genus *Hennecartia* has narrower distribution (Paraguay, south Brazil, north-eastern Argentina); some genera (*Macropeplus*, *Macrotorus* and *Grazielanthus*) are distributed in south-east Brazil (Philipson 1993). Of particular interest is the distribution of the genera of *Monimieae*: the genus *Peumus* is distributed in South Chile, the genus *Monimia* occurs in Mauritius and Reunion, and the genus *Palmeria* is distributed in New Guinea, Sulawesi and Eastern Australia (Philipson 1993). In Africa, the family *Monimiaceae* is represented by the genus *Xymalos* (триба *Hedycaryeae*) with broad, but fragmented areal (Sudan, South Africa, the volcano Cameroon, Bioko Island) (Philipson 1993). There are three genera of the same tribe *Hedycaryeae* – *Decarydendron*, *Ehippiandra*, *Tambourissa* in Madagascar, whereas the last genus also occurs in the Mascarene Islands (Lorence 1985). The genus *Kibaropsis* is distributed at the New Caledonia, similar to *Hedycarya*, which is also occurs at the New Zealand, Eastern Australia and Fiji; the genus *Levieria*

is represented in Queensland, New Guinea and Sulawesi (Philipson 1993). The genus *Hortonia* (subfamily Hortonioideae) is the endemic of Ceylon Island (Perkins and Gilg 1901; Philipson 1993).

The fossil records of the family Monimiaceae are scarce (Fig. 2). The fossils from Upper Senonian deposits in the eastern part of the Cape Province – *Hedycaryoxylon hortonioides* Mädel (Renner et al. 2010),

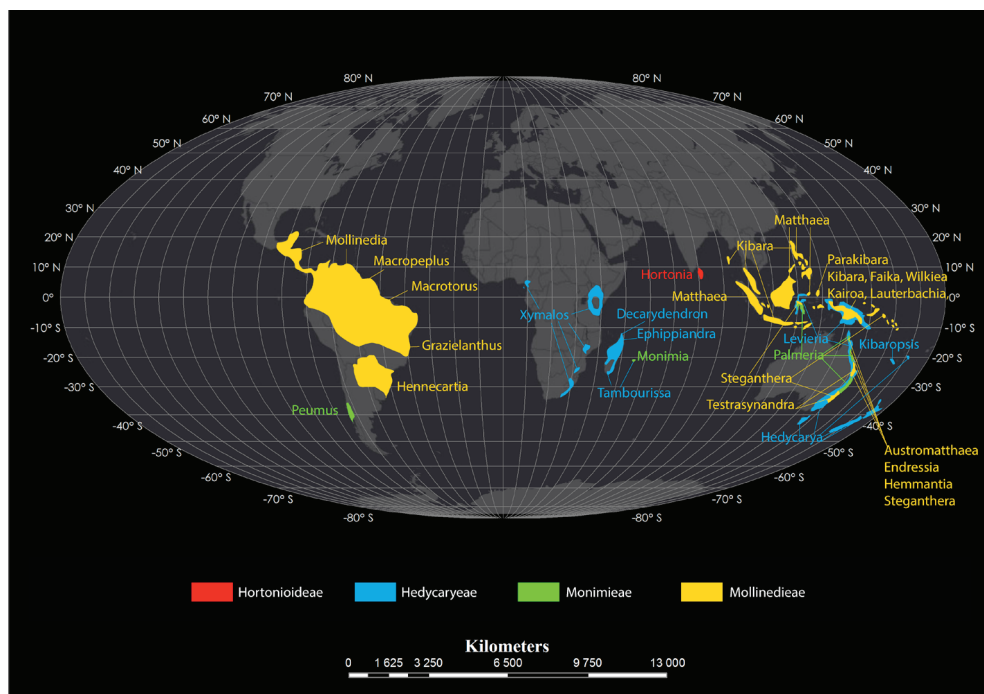


Fig. 1. The distribution of the family Monimiaceae

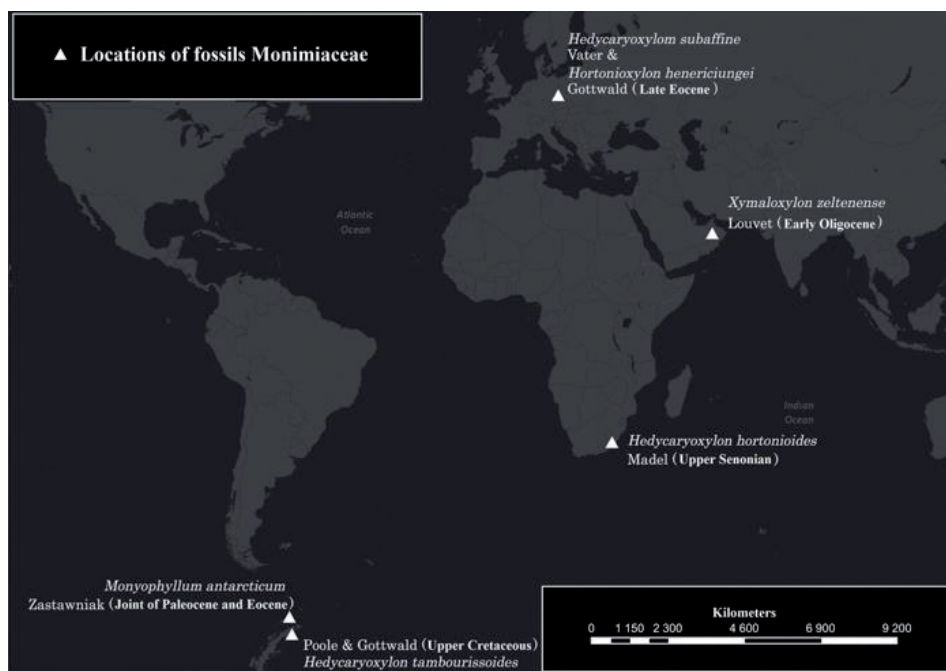


Fig. 2. Fossil representative of the family Monimiaceae

and those from Upper Cretaceous from the James Ross Island close to the Antarctic coasts – *Hedycaryoxylon tambourisoides* Poole & Gottwald (2001) are doubtlessly referred to Monimiaceae. The forest of fossil *Xymaloxylon zeltenense* Louvet are described from Oman (Knight and Wilf 2013). The Paleocene/Eocene leaves' reprints of *Monimiophyllum antarcticum* Zastawniak are found on the King Georgy Island at the Antarctic coasts (Renner et al. 2010). Interestingly, that *Hedycaryoxylon subaffine* Vater and *Hortoniioxylon henericiungeri* Gottwald found in the most northern Upper Eocene deposits of Germany are similar with modern *Hortonia* and *Hedycarya* (Renner et al. 2010).

Basing on the data on morphology, ecology and geography of Monimiaceae mentioned above it is a relatively complicated task to build a reliable concept of the processes of historical distribution of the family even with attraction of data of the molecular analysis (Renner and Chanderbali 2000; Renner et al. 2010). The aim of present work is to combine molecular and morphological data and compare this complex phylogenetic data with the data on the family Monimiaceae distribution in the present time and in the past and thus to propose a verified model of origin of their modern distribution.

MATERIALS AND METHODS

To reconstruct the history of origin of modern distribution of Monimiaceae the representatives of 18 genera of the family occurring in different parts of the areal were analyzed. The object of the research were (The Plant List 2016): *Hortonia floribunda* Wight ex Arnott, *Xymalos monospora* (Harv.) Baill.*, *Decarydendron ranomafanensis* Lorence & Razafim.*, *Ehippiandra madagascariensis* (Danguy) Lorence*, *Tambourissa amplifolia* (Bojer ex Tul.) A. DC.*, *Hedycarya arborea* J. R. Forst. & G. Forst.*, *H. angustifolia* A. Cunningh.*, *H. cupulata* Baill., *Kibaropsis caledonica* (Guillaumin) J. Jérémie, *Peumus boldus* Molina*, *Monimia amplexicaulis* Lorence, *Palmeria foremanii* Whiffin, *Austromatthaea elegans* L. S. Sm.*, *Steganthera maccooraia* (F.M. Bailey) P. K. Endress, *Hennecartia omphalandra* Poiss.*,

Macropeplus ligustrinus (Tul.) Perkins var. *friburgensis* Perkins, *Mollinedia widgrenii* A. DC., *Graziellanthus arkeocarpus* Peixoto & Per.-Moura, *Wilkiea huegeliana* (Tul.) A. DC.*, *Kibara moluccana* Boerl. ex Perkins*. *Gyrocarpus americanus* Jacq.* from the *Hernandiaceae* family (sister to Monimiaceae: (APG IV 2016; Stevens 2001)) was selected as an outgroup in the analysis (Fig. 3). The following genes were selected for the molecular analysis: ITS 1 (internal transcribed spacer 1), 5.8S rRNA (5.8S ribosomal RNA gene) and ITS 2 (internal transcribed spacer 2), which had been sequences in all studied species. The *rbcl* gene (ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit gene) was represented in GenBank (GenBank 2016) only for the taxa marked with an asterisk (*). The available molecular data were not enough for construction of a cladogram for all studied species, so the «molecular» and complex cladograms were built separately for two groups of taxa.

The principal method of the investigation is the construction of cladograms showing phylogenetic relationships by means of combination of molecular and morphological data of the taxa in Winclada program (Hall 2011; Wiens 2000; Wiley and Lieberman 2011). For the higher reliability of the reconstruction of the areal origin of Monimiaceae family three different models of phylogenetic relationships: molecular, morphological and the combined one.

Basing on the results of the nucleotide sequences analysis downloaded from the GenBank the «molecular-genetic» cladograms were built for 1) 20 species of Monimiaceae (Fig. 4) and 2) 11 species of Monimiaceae and *Gyrocarpus americanus* (Fig. 5). For estimation of the branch support of the cladograms the bootstrap analysis was conducted; the nodes with bootstrap values 80–100 are considered as highly supported, whereas the values of bootstrap > 65 are treated as acceptable (Hall 2011; Wiley and Lieberman, 2011).

With the aim to describe an alternative evolutionary scenario of the taxa involved in the present research the «morphological» cladogram was built (Fig. 6) basing on the

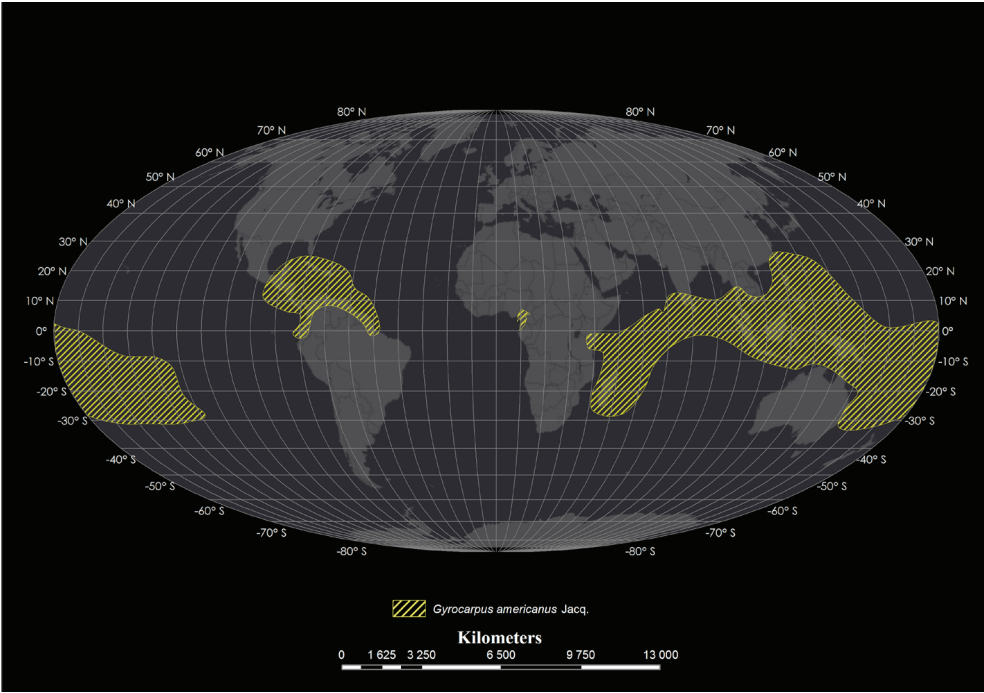


Fig. 3. The distribution of the *Gyrocarpus americanus*

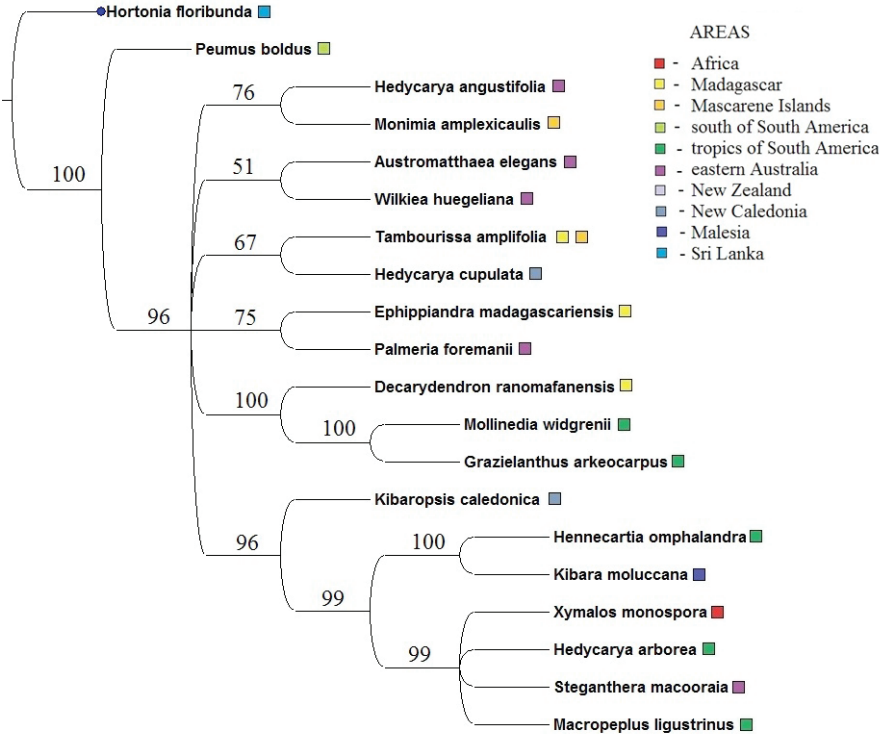


Fig. 4. Cladogram of Monimiaceae based on molecular data

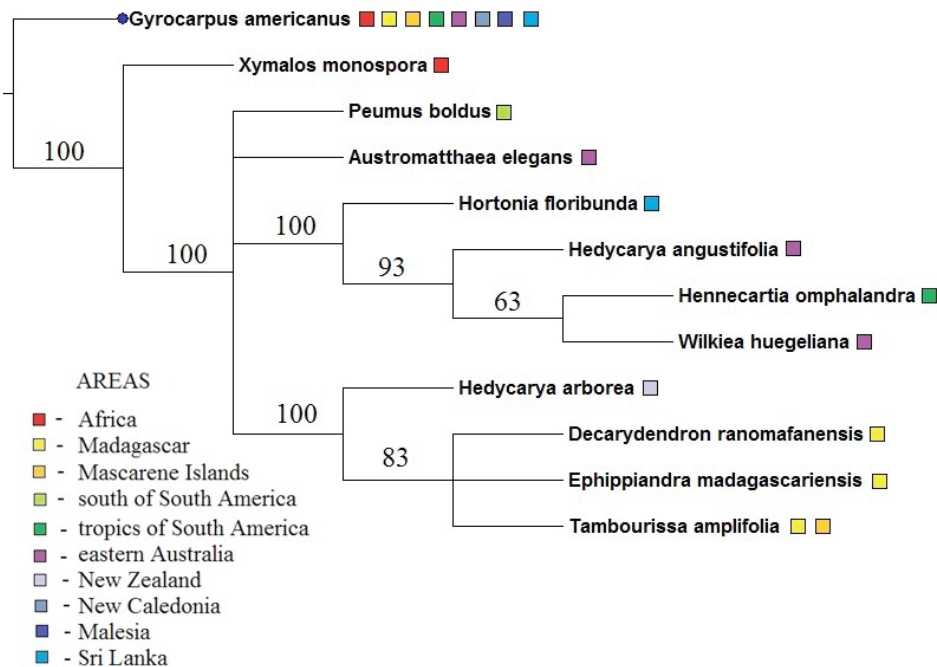


Fig. 5. Cladogram of Monimiaceae and Gyrocarpus (an outgroup) based on molecular data

tables of the morphological characters (Wiens 2000). Twenty-seven morphological characters were involved in the analysis, which are based on the original observations of plant morphology and the literature data (Lorence 1985; Money et al. 1950; Perkins and Gilg 1901; Philipson 1986; Philipson 1993). Both numerical (the number of perianth segments, stamens, carpels, cotyledons, etc.) and qualitative (the life form, leaf blade

structure, pericarp type, presence of fleshy appendages of the fruitlet, etc.) characters were selected.

The combined cladograms (Fig. 7) are based on the complex analysis of data matrix including both molecular and morphological data (Hall 2011; Judd et al. 2016; Wiley and Lieberman 2011).

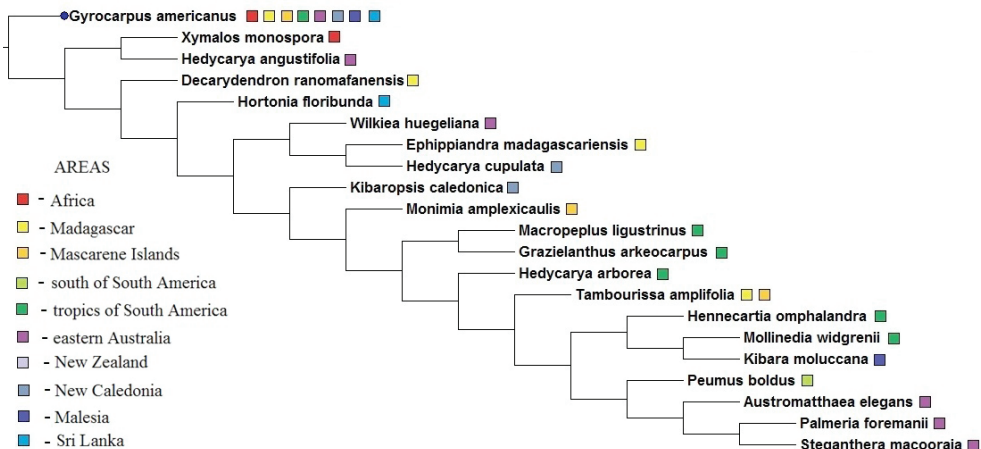


Fig. 6. Cladogram of Monimiaceae and Gyrocarpus (an outgroup) based on morphological data

RESULTS

The topology of «morphological» and «molecular» cladograms sufficiently differs – the «molecular» one provides better support for the genera delamination, whereas

Australia, Antarctic, Madagascar and India, the formation of the Monimiaceae areal proceeded as the result of long-distance dispersal (Crisci et al. 2003; Heads 2012, 2013; Renner et al. 2010), which is supported by our results.

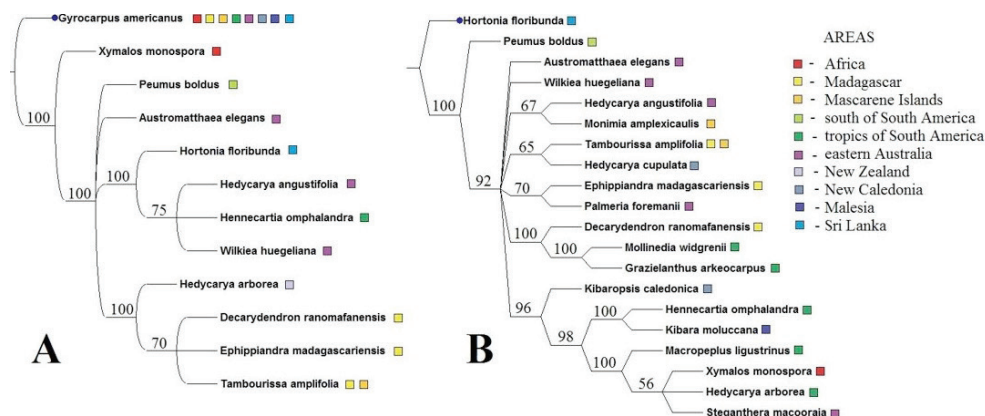


Fig. 7. Complex morpho-molecular cladogram with bootstrap indexes indicated

the «morphological» one includes less polytomies. So, the complex cladograms (Fig. 7), which usually have less faults (Hall 2011; Wiens 2000; Wiley and Lieberman, 2011) were analyzed. The topology of the complex cladograms sufficiently differ both from the molecular ones and from each other. In spite of the first complex cladogram (Fig. 7) includes less number of taxa in comparison with the second one, it is nevertheless is used as the base for the modelling of the original scenario of distribution of Monimiaceae as well as it includes the outgroup (the genus *Gyrocarpus*). Bootstrap index is more than 70 in all nodes, the cladogram includes less polytomies, and the basal (original in evolution) position of the recent African genus *Xymalos* concords with finding in South Africa of the oldest fossil records of Monimiaceae dated by Upper Cretaceous time (100 MYA) (Renner et al. 2010).

The early stages of distribution of the family Monimiaceae were supposedly realized by the «vicarious algorithm» (Crisci et al. 2003; Heads 2012, 2013) and were dependent on the splitting of the Western Gondwana – i.e. by the split of Africa and South America about 100–110 MYA (Renner et al. 2010). Later on the territories of the Eastern Gondwana, which included

DISCUSSION

The model of Monimiaceae distribution (Fig. 8) is based on the complex cladogram (Fig. 4) and available paleo botanical data. As well as the genus *Xymalos* is basal on the cladogram (Fig. 7) we suppose that Monimiaceae originated in Africa and started their distribution from there. The ancestor of recent genus *Xymalos* supposedly originate in the south of Africa and started distribution to the north of the continent (Fig. 8: 1). Supposedly about the same time in Upper Cretaceous Monimiaceae occupied South America (Fig. 8: 2) via Antarctica (Poole and Gottwald 2001), which brought to origin of the genus *Peumus*. Later, following the climate change, the areal of Monimiaceae in South America moved to the north (Fig. 8: 3), so the genera *Mollinedia*, *Grazielanthus*, *Hennecartia* and *Macropheplus* originated and became distributed on the continent.

The analysis of the fossil representatives of the family Monimiaceae from Oman allows to suppose, that to get to Australia from Africa fossil members of the family moved and distributed along the coasts of the Eastern Africa and South Asia (Fig. 8: 4), which is confirmed by occurring of

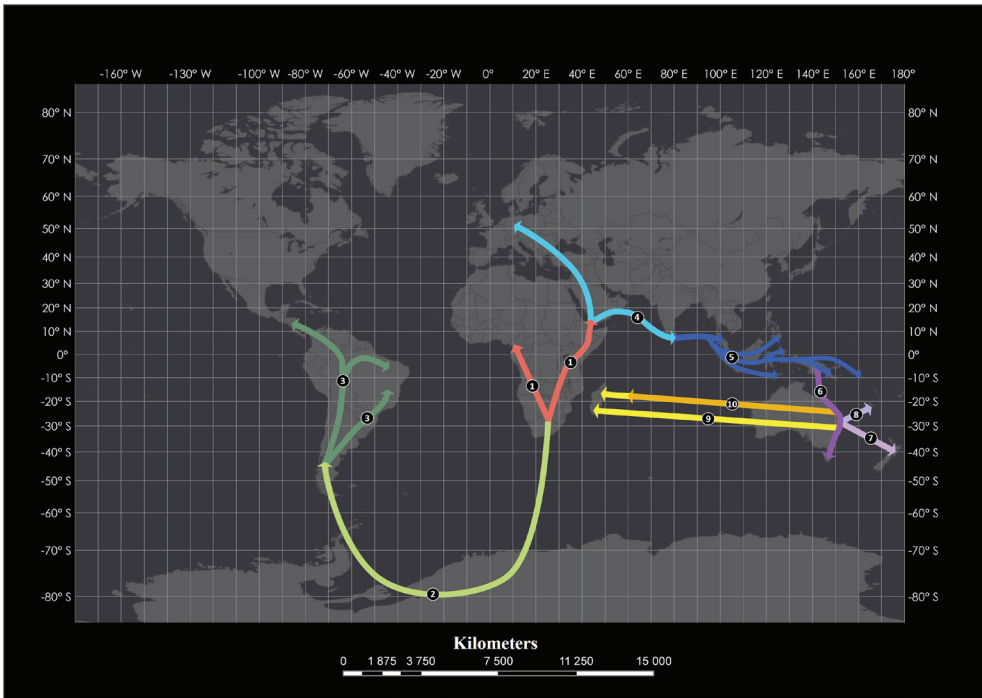


Fig. 8. The reconstruction of the history of formation of Monimiaceae current distribution

the archaic oligotypic genus *Hortonia* in Ceylon. The finding of the fossil records of the family in Germany indicate that yet in Upper Eocene Monimiaceae had broader distribution, and their areal included the Europe.

According to the model of phylogenetic relationships, the areal of the family Monimiaceae continued to expand to the East (Fig. 8: 5, 6) up to the recent Malesia (Kibara) and further up to Australia (*Hedycarya*, *Palmeria*, *Austromatthaea*, *Steganthera*, *Wilkiea*) (Whiffin and Foreman 2007). New Zealand and New Caledonia were populated with ancestors or representatives of the genus *Hedycarya* (Fig. 8: 7, 8). Madagascar (*Decarydendron*, *Ephippiandra*, and *Tambourissa*) and supposedly later Mascarene Islands (*Tambourissa* p.p.) were inhabited by New Caledonian or East Australian Monimiaceae (*Kibaropsis*, *Hedycarya*) (Figs. 8: 9, 10). The Monimiaceae in Australia could have a broader distribution before the period of aridization of the climate there and could inhabited Western Australia as well (now they are not represented there). During

Early Tertiary period, the disposition of the continents allowed to agents of dissemination to transport diaspores from Australia to Madagascar. The processes of distribution of the family Monimiaceae in the Eastern Hemisphere supposedly occurred due to long-distance dispersal of the diaspores (the fruits, fruitlets, separate seeds) by birds (Money et al. 1950).

CONCLUSION

The genus *Xymalos* – is the basal genus in Monimiaceae and its African distribution allows to treat Africa as the ancestral part of the areal of the family. The distribution of Monimiaceae to South America occurred through Antarctica before the end of Cretaceous period (Peumus); later the areal of the family in South America expanded to the north of the continent (genera *Mollinedia*, *Graziellanthus*, *Hennecartia*, *Macropeplus*). To get to the Eastern tropics hypothetical representatives of ancient Monimiaceae made a long way along the coasts of Eastern Africa, Arabia, South Asia (the genus *Hortonia* stopped its distribution at Ceylon) and further to the islands of Malesia (genus

Kibara) to Australia (genera *Hedycarya*, *Palmeria*, *Austromatthaea*, *Steganthera*, *Wilkia*). Monimiaceae representatives from Australia (by ancestors or representatives of the genus *Hedycarya*) occupied New Zealand. Madagascar (*Decarydendron*, *Ephippiandra*, and *Tambourissa*) and Mascarene Islands (*Tambourissa*) were occupied by Monimiaceae from New Caledonia (*Kibaropsis*, *Hedycarya*) and/or Australia (Eastern or Western).

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