RESEARCH PAPER

THE HISTORY OF DISTRIBUTION OF THE FAMILY LECYTHIDACEAE *S. L.*

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ABSTRACT. The modern distribution and dispersal history of the family Lecythidaceae s. l. present scientific interest so far as Lecythidaceae has a pantropical areal, thus forming several disjunctions, that may represent ancient continental contacts. Species of this family are distributed in Central America, firstly in the subequatorial and equatorial areas of South America, particularly, in Amazon Basin and some zones of Northern and Central Andes, in the equatorial forests of Congo Basin, along the Gulf of Guinea in Africa, and in South and Southeast Asia. Species of the family are also found in Australia and also in some Oceania Islands. According to modern data, the family, which is part of the order Ericales, includes 30 genera and 395 species [PoWO 2025]. The purpose of research is to point a hypothetical center of origin of the entire family and reconstruct the spreading routes of family species and genera. Several morphological and ecological features (mostly pollination and dissemination) of family representatives were analyzed and compiled. The molecular genetic data for selected taxa of Lecythidaceae s. l. was also analyzed and the results of reconstructing probable dispersal routes were compared with available paleobotanical materials. The resulting molecular genetic model was calibrated according to age of found fossils. The parsimony reconstruction of hypothetical dispersal tracks and dispersal ways of Lecythidaceae s. l. species and genera was based on a detailed calibrated model and became the result of this research. A hypothetical center of origin for the ancestor of the family Lecythidaceae s. l. was identified.

KEYWORDS: Phytogeography, Dispersal tracks, Molecular-genetic analyses, Calibration based on available paleobotanical data

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INTRODUCTION

The family Lecythidaceae *s. l.*, which is part of the order Ericales, includes 30 genera and 395 species. It has a pantropical range. Genera such as *Lecythis, Allantoma, Gustavia, Corythophora, Couratari, Couroupita, Grias, Cariniana, Bertholletia, Asteranthos* and *Eschweilera* are native to South America and are mostly found in Amazon basin, the territory of modern day Colombia, Venezuela, Guyana, Suriname and French Guiana, as well as eastern and central Brazil. Many species of these genera also grow in Central America. Species of the genera *Napoleonaea, Foetidia, Rhaptopetalum, Brazzeia, Scytopetalum,* and *Petersianthus* inhabit large areas of Central Africa, particularly the Congo River basin. Finally, the areal of species of *Barringtonia, Careya, Planchonia* and *Chydenanthus* covers Southeast Asia, Northern Australia, several islands in Oceania. Also, some species of the genus *Barringtonia* grow in Madagascar.

Species of the family Lecythidaceae *s. l.* are large and very large trees, up to 55 meters tall, such as *Bertholletia* [Prance & Mori 2004], or, more rare, small trees, or less commonly, shrubs. The leaves are always alternate and simple. The flowers of some species of the family Lecythidaceae *s. l.* form inflorescences, but many species have solitary flowers. The inflorescences are represented by simple racemes or panicles. Other types of inflorescences specific for the family can be named derivatives of panicles [Appel 1996]. The flowers are bisexual, can be actinomorphic or zygomorphic and have a peduncle or sessile bracts in the axil. Some species of the family, such as the genus *Napoleonaea*, present the formation of flowers directly on the stem – cauliflory [Prance 2004]. Sepals are usually 2 to 6 and they are often free, but sometimes (particularly in members of the subfamily Scytopetaloideae) they are fused into a single calyx, often thick and leathery. Petals are usually 3 to 6, but in several species, they are 8. The members' of the subfamily Napoleonaeoideae petals are fused into a ribbed corolla consisting of 30–35 segments, or true petals are absent, and the outer circle of sterilized stamens forms a pseudocorolla. The subfamily Scytopetaloideae species have no petals, but have an outer circle of sterile stamens that form a pseudocorolla. Lecythidaceae species have many stamens, from 10 to 1210 (possibly more), often fused at the bases of the filaments. The flowers form several whorls of stamens, sometimes fused at the base, and several whorls of morphologically similar staminodes. Often this partially fused androecium forms a cap, which has varying configurations. The gynoecium is coenocarpous; the ovary is usually inferior, although it can also be semiinferior (*Asteranthos, Crateranthos*) or superior (in species of Scytopetaloideae, except *Asteranthos*). It consists of 2, 3, 4, or 6, rarely 8, locules, each containing from 2 to a huge number of ovules. The fruits are indehiscent dry, leathery or even woody pyrenaria, or capsules, which often have a unique rounded "lid" [Prance & Mori 1978]. The embryo of Lecythidaceae *s. l.* species is usually large, straight or curved. Actinomorphic flowers of the family species are pollinated mostly by bees, but field observations of these plants have shown that some beetles and even bats also actively visit the flowers; however, this fact requires more detailed study [Prance & Mori 2004]. Species of the genus *Gustavia*, according on the available data, provide parts of the pollen as a "reward" for visiting bees, which further encourages them to visit the flowers [Mori & Boeke 1987]. The flowers of many species of the genus *Grias* secrete unique acids that have a special fragrance, which attracts pollinating beetles [Knudsen & Mori 1996]. Pollination processes of Lecythidaceae *s. l.* species, which have zygomorphic flowers, are more difficult. The specific ways depend mostly on the complexity and openness of the androecium, as well as on the benefit each flower of a particular species provides to the pollinating animal [Mori 1989]. For example, some species (*Lecythis zabucajo*) produce specific pollen grains in the open anther cap, and the others (*Corythophora rimosa*) produce such pollen in the closed cap. Some of species (*Lecythis corrugata*) produce a combination of pollen grains and nectar grains, which are located in the closed cap of the androecium. Finally, the most highly organized species (in particular, the genera *Eschweilera* and *Couratari*) offer pollinators nectar directly from the closed stamen cap [Prance & Mori 2004]. Visitors of these flowers are also mostly bees. However, there are at least two species with zygomorphic flowers (*Lecythis poiteaui, Lecythis barnebyi*) were visited by bats; however, this point requires further research and confirmation [Mori, Prance & Bolten 1978; Mori, Prance & Zeeuw 1990]. A detailed study of pollination processes didn't reveal any individual relationships between specific Lecythidaceae species and specific bee species, which are the most active pollinators. The only connection that exists in these relationships is that the pollinator must be large enough to open the anther cap (of course, only if it is closed) and have a long proboscis to reach the pollen and nectar located inside the cap [Prance & Mori 2004]. For example, species of such genera of bees and bumblebees as *Bombus, Centris, Epicharis, Eulaema* and *Xylocopa* often fly into the flowers of the genus *Bertholletia* [Mori & Prance 1990; Mori 1992]. The flowers of *Eschweilera pedicellata* are visited exclusively by bees of the tribe Euglossini, which are the only New World bees whose proboscis is long enough to extract pollen from the closed stamen cap. Due to the great variety of fruits, dissemination of different species of the family Lecythidaceae *s. l.* also differs in many forms and ways. Some species of the genus *Barringtonia* (in particular *B. racemosa* and *B. acutangula*) have large, but not dense, floating fruits, which, according to available data, are spreading by ocean currents, which explains the wide area of the genus. Many fruits of other genera are dispersed similarly, which suggests that one of the mostly used methods of dissemination of these plants is hydrochory. Fruits of many other genera, for example, *Couroupita, Grias* and *Gustavia*, have combined methods of dissemination. In particular, it was noted that after dehiscence of hard and heavy fruits, seeds that contained in the fruit are dispersed by many species of forest mammals (agouti or many species of monkeys), and seeds that fall into water are dispersed by fish [Prance & Mori 1978; 1979]. Other Lecythidaceae genera, such as *Cariniana* and *Couratari*, have dehiscent fruits with winged seeds inside, which represents anemochory. Also, the seeds of some species of the genus *Lecythis,* whose fruits also dehisce, are dispersed by bats [Prance & Mori 2004].

There is very little paleobotanical data that would allow us to talk about the origin of the entire family or its individual taxa. There are known finds of *Lecythidoanthus kugleri* [Berry 1924a; 1924b], whose flower has features of the species of subfamily Lecythidoideae. The age of this find is dated to the Miocene. Wood of the plant *Lecythioxylon brasiliense* [Milanez 1935], dated to the Cretaceous, was also described. In 1960, the possible ancestor of species of the subfamily Barringtonioideae, *Barringtonioxylon deccanense* [Shallom 1960], was described, as well as the closely related *Barringtonioxylon eopterocarpum*, which are dated to the Upper Cretaceous [Prakash & Dayal 1965]. In 1969, a fossil fruit from Colombia was described and it present morphological similarities to fruits of the genus *Eschweilera*. This plant was named *Lecythidopyxion girardonatum* [Huertas 1969]. Pollen from several extinct plants has also been found in India and Borneo, possibly of the genera *Barringtonia* and *Chidenanthus*, dating to the Eocene. Finally, some pollen was found in Cameroon, which is similar to pollen from the genera *Barringtonia* and *Planchonia* and also dating to the Eocene [Tsou 1994].

MATERIALS AND METHODS

To research the dispersal history of the family Lecythidaceae *s. l.* and to construct possible tracks, species included in different genera, presenting variety of morphological and ecological similarities and differences, and growing in different parts of the family's areal were selected for analysis. Thus, 40 species were analyzed, including a species from the outgroup: 5 species each from the genera *Lecythis* and *Barringtonia*, 3 species each from the genera *Gustavia, Grias, Napoleonaea,* and *Foetidia*, 2 species each from the genera *Couratari* and *Couroupita*, and 1 representative each from the genera *Allantoma, Corythophora, Bertholletia, Asteranthos, Rhaptopetalum, Scytopetalum, Petersianthus, Brazzeia, Careya, Cariniana, Eschweilera, Planchonia,* and *Chydenanthus*. The genera *Chytroma, Crateranthus, Guaiania, Imbiriba, Oubanguia, Pachylecythis, Pierrina, Scottmoria* and *Waimiria* were not studied analyzed due to the absent available material.

In our research, were used the cladistic method [Henning 1950]. The studied species, their areas, and the genes used in the research are listed below (Tab. 1).

Table 1. Access codes and ranges of the analyzed species

Species	Genes				Range
	trnL-trnF	matK	ndhF	rbcL	
Impatiens balsamina	EF649982.1	MN317471.1		MK526011.1	
Lecythis ampla	DQ418012.1		JN607452.1		Central America
Lecythis barnebyi	JN221947.1		JN607453.1		Central Amazon basin
Lecythis lurida	JN221958.1		JN607460.1		Amazon basin, Brazil Highlands
Lecythis minor	DQ418022.1		DQ388216.1		Central America, Guiana
Lecythis retusa	JN221972.1				Central Amazon basin
Allantoma lineata	DQ417929.1		JX164031.1	AF077657.1	Central Amazon basin, Guiana
Gustavia augusta	DQ418002.1		DQ388207.1	MF786277.1	Amazon basin
Gustavia monocaulis	DQ418008.1		DQ388206.1		Central America
Gustavia superba	DQ418010.1	GQ982005.1	DQ388199.1	GQ981755.1	Central America
Corythophora labriculata	DQ417943.1		DQ388190.1		Guiana Highland
Couratari calycina	DQ 417945.1		DQ388192.1	JQ626169.1	Guiana Highland
Couratari guianensis	DQ417946.1	JQ626563.1	DQ388193.1	JQ626273.1	Guiana Highland
Grias cauliflora	DQ417997.1		DQ388179.1	AF077652.1	Central America
Grias peruviana	DQ417999.1		DQ388178.1		North Andes
Grias multinervia	DQ417998.1		DQ388272.1		Central America, North Andes
Couroupita guianensis	DQ417951.1		DQ388182.1	AF022134.1	Amazon basin, Guiana Highland, Central America, North Andes
Couroupita nicaraguarensis	DQ417952.1		DQ388183.1		Central America, North Andes
Cariniana rubra			JX164036.1		Amazon basin, Brazil Highlands
Bertholletia excelsa	DQ417933.1		DQ388181.1	Z80178.1	Amazon basin, Guiana Highland
Asteranthos brasiliensis	AF077648.1			AF022133.1	Central Amazon basin
Eschweilera integrifolia	DQ417965.1		DQ388234.1		Central America, North Andes
Napoleonaea imperialis	DQ418031.1		AJ236258.1		Coast of Golf of Guinea and Congo basin
Napoleonaea heudelotii				MN366490.1	Coast of Golf of Guinea and Congo basin
Napoleonaea gabonensis		MN370170.1		MN366489.1	Coast of Golf of Guinea and Congo basin
Foetidia obliqua	DQ417995.1		DQ388176.1		East Africa, Madagascar or Mascarenes
Foetidia asymetrica				Z80183.1	Madagascar or Mascarenes
Foetidia mauritiana	DQ417996.1		DQ388177.1		Madagascar or Mascarenes
Rhaptopetalum coriaceum	DQ418037.1				Coast of Golf of Guinea and Congo basin
Scytopetalum klaineanum	DQ418038.1	KC627646.1	DQ388166.1	KC628275.1	Coast of Golf of Guinea and Congo basin
Petersianthus macrocarpus			DQ388172.1		Coast of Golf of Guinea and Congo basin
Brazzeia soyauxii		MN370172.1		MN366488.1	Coast of Golf of Guinea and Congo basin
Barringtonia acutangula		JN183985.1		AB925810.1	South Asia, Southeast Asia, Malesia, North Australia

Barringtonia asiatica	DQ417930.1	DQ924095.1	DQ924203.1	EU980812.1	South Asia, Southeast Asia, Malesia, North Australia, East Africa, Madagascar or Mascarenes
Barringtonia edulis	DQ417931.1		DQ388174.1		Melanesia
Barringtonia lanceolata				MG784924.1	Malesia
Barringtonia racemosa	DQ417932.1	KJ510928.1	DQ388175.1	MK529927.1	South Asia, Southeast Asia, Malesia, North Australia, East Africa, Madagascar or Mascarenes
Careya arborea	DQ924313.1	MG742305.1	DQ924204.1	AF077655.1	South Asia, Southeast Asia
Chydenanthus excelsus	DQ417940.1		DQ388173.1		Southeast Asia, Malesia
Planchonia careya		KM894763.1		KY661347.1	North Australia, Malesia

Information on the ranges was taken from literary sources [Takhtadzhyan 1978; MOBOT 2025]. To reach the stated purposes, in particular, to obtain an objective "cladistic picture", it is necessary to include a species that is not closely related to the studied taxa (i.e., not included in the studied group), but "in general" taxonomically close (usually more basal) in the list of studied taxa as an outgroup [Abramson 2013]. In this study, the species Impatiens *balsamina* L. from the family Balsaminaceae was used as an outgroup. In the process of constructing cladograms in this study, two methods were used, representing the relationships within the family Lecythidaceae *s. l.*, one of which is based on the analysis of molecular genetic data, and the second is used to establish hypothetical divergence times for specific clades and to calibrate the cladogram (the calibrated cladogram method). The molecular genetic method is based on the comparison of genetic characteristics, that is, the nucleotide sequences of individual DNA fragments in different taxa. The resulting cladogram is calibrated using available paleobotanical data and replenished with a visual representation of the ranges of the species included in it. For a more complete description of the processes involved in such analysis, it is necessary to describe these methods in more detail.

The molecular genetic analysis of analyzing taxa requires extensive data collection. Nucleotide sequences of four chloroplast markers were used for phylogenetic analysis. In our research, information of 40 species, including outgroup, was retrieved from the GenBank open database. These data are encoded in four sequence genes (the plastid maturase K gene (matK), the plastid ribulose bisphosphate carboxoxidase gene (rbcL), the plastid NADH dehydrogenase complex gene (ndhF), and the trnL-trnF spacer). These genes were not analyzed for every species, as information on some of them is missing in GenBank. Also, since each species was sequenced using different algorithms and for different purposes, the number of nitrogenous bases, as well as the start and end locations of the sequences, didn't match. So, before the analysis, multiple sequence alignment was done using the Clustal W algorithm [Larkin et al. 2007]. The steps of processing the nucleotide sequences were implemented in the MEGA 11 program. Gaps (empty regions without nitrogenous bases) were encoded with the "-" symbol, and regions with an unknown set of nitrogenous bases were encoded with the "?" symbol. The aligned and most informative regions of the nucleotide sequences were connected into single chains for each of the analyzed taxa, and then, in the MEGA 11 program, a cladogram of the studied species was constructed. It was used the Tajima-Nei model with the maximum parsimony method, which is based on establishing proximity by minimizing the number of transformations of each character (i.e., minimizing the number of nucleotide substitutions) [Lemey, Salemi & Vandamme 2009]. Branch reliability was assessed using the bootstrap method with a score of 5000 [Felsenstein 1985]. The number located on each branch indicates the percentage probability of the degree of the species relatedness. A probability greater than 70 is considered sufficient [Hillis & Bull 1993; Wiley & Lieberman 2011].

The calibrated cladogram method allows to determine the approximate divergence time of individual clades. The first step is to convert aligned nucleotide bases using the Clustal W method to the NEXUS (.nexus) format. MEGA 11 program allows to export alignment sessions to this format. Then, it is necessary to use the available paleobotanical data. For this purpose, divergence points of specific clades were specified in BEAUti ver. 2 Standard. These points were assigned a time corresponding to the geological period when these clades diverged, and they were also assigned a name identical to the Latin name of the fossil species Lecythidaceae *s. l.* To accurately calculate the data of the specified divergences, the corresponding taxa were placed on different sides of the bifurcation in the command field. The Strict Clock model was used as a model of evolutionary time. It assumes a correlation between the speed of evolution and the lengths of branches [Ferreira & Suchard 2008]. The JC69 model [Jukes & Cantor 1969], which compares the speed of appearance and substitution of mutations, was used as a replacement model. For the probability distribution of time intervals, the Yule model was used [Yule 1924; Simon 1955; Rose & Smith 2002]. The program also allows to choose a separate function for the probability distribution. The lognormal function was selected as the most optimal. For further calibration, the BEAST ver. 2.6.6 program was used. It constructed a large number of probable phylogenetic trees based on the available nucleotide base sequences and paleobotanical data. The number of such trees can be determined manually. So, a number of 500,000 models with a step of 1000 were selected. Then, it was necessary to reduce all the cladograms obtained during the analysis into a single "average", consensus cladogram. This was done using the program TreeAnnotator ver. 2.6.6. In this application, the percentage of pruning of the extreme probability trees for the next reduction was selected (it was equal to 20%). As a result of these operations, a file containing a single consensus phylogenetic tree was obtained. Finally, visualization of the result and stylization of the cladogram were done in the program FigTree ver. 1.4.4. The result was a calibrated cladogram, which also included paleobotanical data with the probable divergence times of individual clades from each other. The distribution of the time of evolutionary divergence is shown by the length of the lines at the bifurcation points.

Construction of area and distribution maps for analyzed taxa. A cartographic method was used to visualize the dispersal processes of taxa within the family Lecythidaceae *s. l.* The maps were created using QGIS ver. 3.22.6.

RESULTS

Molecular genetic model

Analyzing the model obtained using molecular-genetics data, a number of conclusions about the relationships between various species of the family Lecythidaceae *s. l.* was drawn and, based on these, probable routes of their dispersal (Fig. 1) were construct.

The configuration of the tree constructed using molecular-genetics data allows to divide it into several clades. The basalmost position includes three species of the genus *Napoleonaea*. According to structure, *N. heudelotii* and *N. imperialis* are more closely related than *N. gabonensis*, which is located in the most basal position of all the species analyzed. The second clade includes three African species of Lecythidaceae *s. l.* – *Rhaptopetalum coriaceum, Scytopetalum klaineanum*, and *Brazzeia soyauxii*, as well as one South American species, *Asteranthos brasiliensis*. The last two taxa, according to the model, are sister to each other, and then paraphyly is observed for the first two. The next clade includes all the species of the genus *Barringtonia*. It has a bifurcation, based on which it can be concluded that the species *B. edulis* and *B. asiatica*, as well as *B. acutangula* and *B. lanceolata*, are pairwise sister ones. The position between these pairs is contained with *B. racemosa*, which belongs to the same clade with the first two species and is more closely related to them than to the last two. Another clade has a bifurcation that pairwise unites four species. The first part of this bifurcation contains *Chydenanthus excelsus* and *Petersianthus macrocarpus,* indicating the close relationship between these genera. The second part contains *Careya arborea* and *Planchonia careya*. So, these genera can also be considered sister ones. The next clade includes three species of the genus *Foetidia*. *F. asymetrica* and *F. mauritiana* are located in a sister position, and *F. obliqua* is the most basal here. Next goes a clade that bifurcates into branches including two large Neotropical genera – *Gustavia* and *Grias*. The close relationship between these genera is also confirmed by some molecular-genetic studies [Mori et al. 2015]. *Gustavia monocaulis* and *G. superba* are sister genera, while *G. augusta* is located in a basal position. On the other side of this clade there is the genus *Grias*. *G. cauliflora* and *G. multinervia* are the sister species, with *G. peruviana*, which is the most basal.

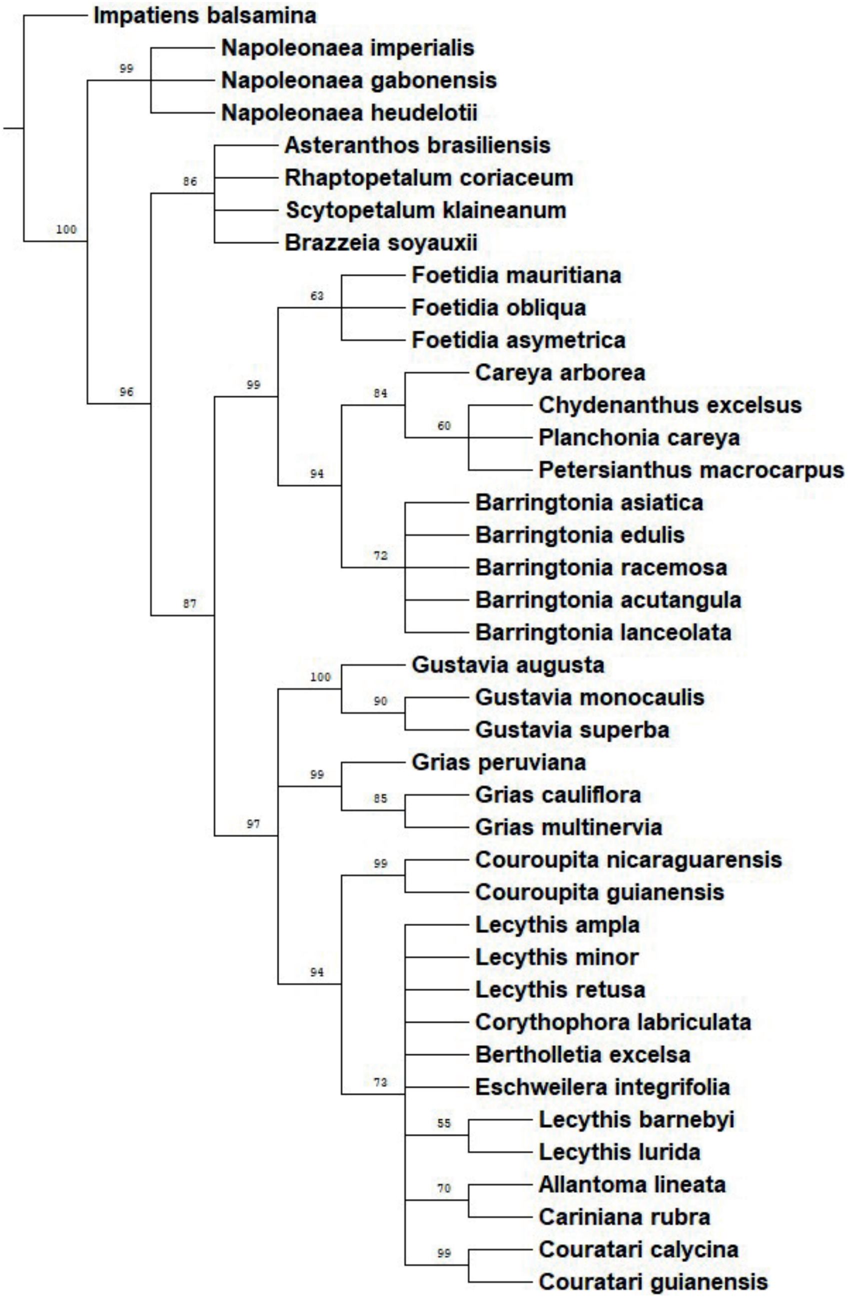

Fig. 1. Molecular genetic cladogram of *Lecythidaceae s. l.*

This topology confirms the close relationship between these two genera. The next two clades are configured in such a way that the species are located in sister positions. The first one includes two species of the genus *Couroupita*, particularly, *C. nicaraguarensis* and *C. guianensis*. The second one pairs two species of *Couratari (C. calycina* and *C. guianensis)*, as well as *Allantoma lineata* and *Cariniana rubra*, which are also very closely related, according to cladogram structure. Finally, the last clade includes several Neotropical species, which are also paired together to form four sister groups. The first one includes *Eschweilera integrifolia* and *Bertholletia excelsa*, which represent a high degree of closeness between these genera, and this point is also confirmed by other studies [Huang, Mori & Kelly 2015]. The second group includes one Lecythis species, *L. retusa*, which is sister to *Corythophora labriculata*. This configuration allows to conclude that *L. retusa* should be included into a separate genus (specifically, a separate one *Chytroma*), or the genus *Corythophora* should be included within *Lecythis s. l.* The next two groups consist only of *Lecythis* species. One group is formed by the sister species *L. barnebyi* and *L. lurida*, and the second one – by *L. ampla* and *L. minor*, which represents the close relationship between these species.

Calibrated molecular-genetic model. After calibrating the molecular-genetic cladogram, the new tree was constructed. Specific lines at bifurcation points indicate the time intervals when specific clades diverged. This model was built using paleobotanical materials. The age of the fossils and their morphological similarity to various taxa allowed to select specific bifurcation points and determine the minimum age of these divergences.

The resulting model (Fig. 2) allows to reconstruct hypothetical dispersal tracks of the family *Lecythidaceae s. l.* and the time in which they occurred.

The indicated geological periods correspond to the subdivisions of the International Stratigraphic Chart and the boundaries ratified by the IUGS (International Union of Geological Sciences) as of March 2008 [Ogg, Ogg & Gradstein 2008]. Based on the calibrated model, it can be concluded that the family diverged approximately 85 million years ago, in the Late Cretaceous. It was also at this time that species of the Napoleonoideae (the basal subfamily of Lecythidaceae) diverged. Then, the separation of the Scytopetaloideae subfamily into a separate clade occurred. According to the model, it was approximately 50 million years ago. Later, in the Paleocene, there was divergence, forming the ancestors of the modern subfamily Barringtonioideae. In the Eocene (approximately 41 million years ago), species of the subfamily Lecythidoideae separated. Finally, the last divergence, in the Oligocene, leaded to appearance of the ancestors of modern species included in subfamily Foetidioideae.

DISCUSSION

The analysis of hypothetical dispersal tracks of *Lecythidaceae s. l.* was based on several characteristic of its species. Certainly, the most important initial data for the reconstruction were the modern ranges (Fig. 3).

Their structure allows to reconstruct the possible taxa dispersal routes. Another important factor is the ecological conditions of modern species. Pollination and dissemination characteristics are key components of such reconstructions, as they often allow to determine the methods and ways of dispersal. Morphological similarities and differences make it possible to understand the degree of evolutionary relationship between individual taxa and to reconstruct some hypothetical processes that occurred with their vegetative and reproductive organs. However, in this research, the molecular-genetic cladogram is the foundation for reconstructing possible dispersal routes. Based on phylogenetic relationships, the basal group (closest to the "root" of the cladogram) was determined, the possible region of taxon formation, and the tracks of their dispersal were identified. The results of the molecular genetic model of the relationships between the taxa of *Lecythidaceae s. l.* confirm that the basal taxon is the genus *Napoleonaea*, which with the genus *Crateranthus*, grows in the Guinea-Congo floristic region. In particular, *Napoleonaea gabonensis* grows in the Congo River Delta region, *N. heudelotii* – in the western part of this region, on the coast of the Gulf of Guinea, and *N. imperialis* has a wide area, growing almost everywhere in Guinea-Congo region [Takhtadzhyan 1978]. This fact allow to consider the range of the subfamily Napoleonoideae the hypothetical region of origin of the whole family Lecythidaceae *s. l.* According to

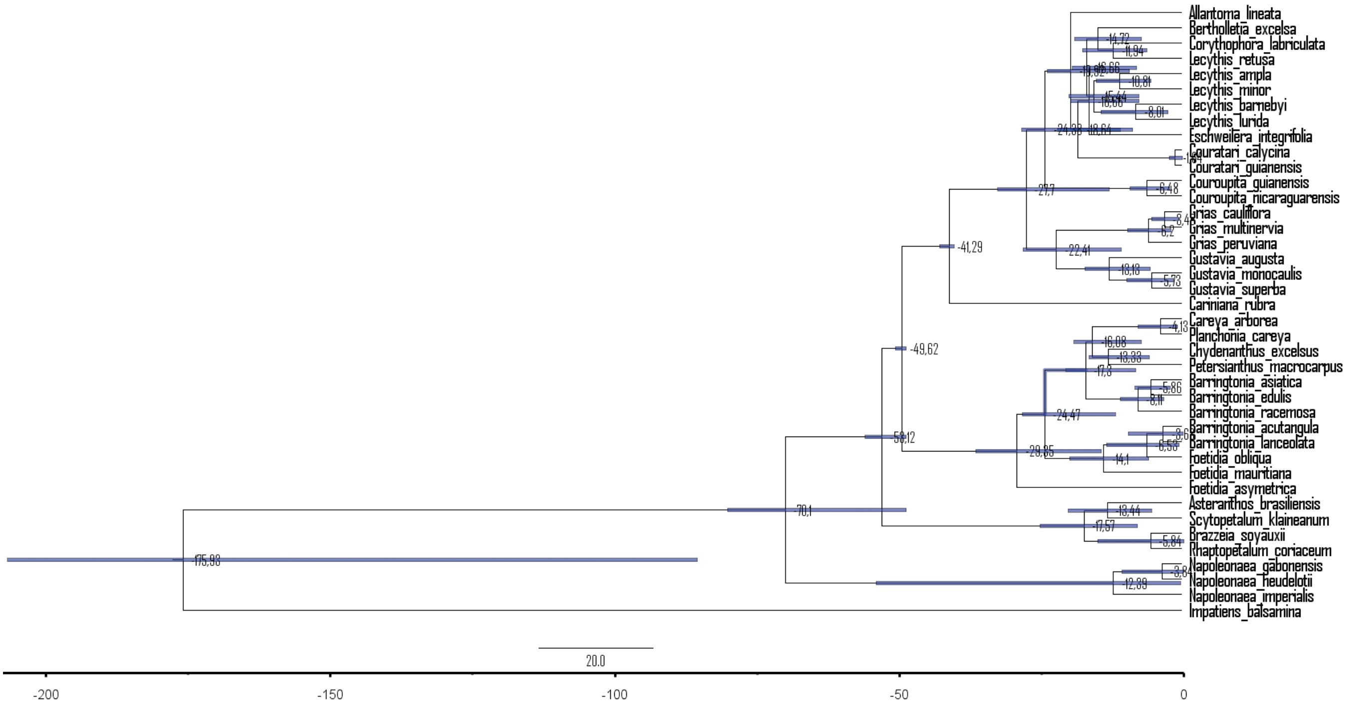

Fig. 2. Calibrated cladogram of *Lecythidaceae s. l.*

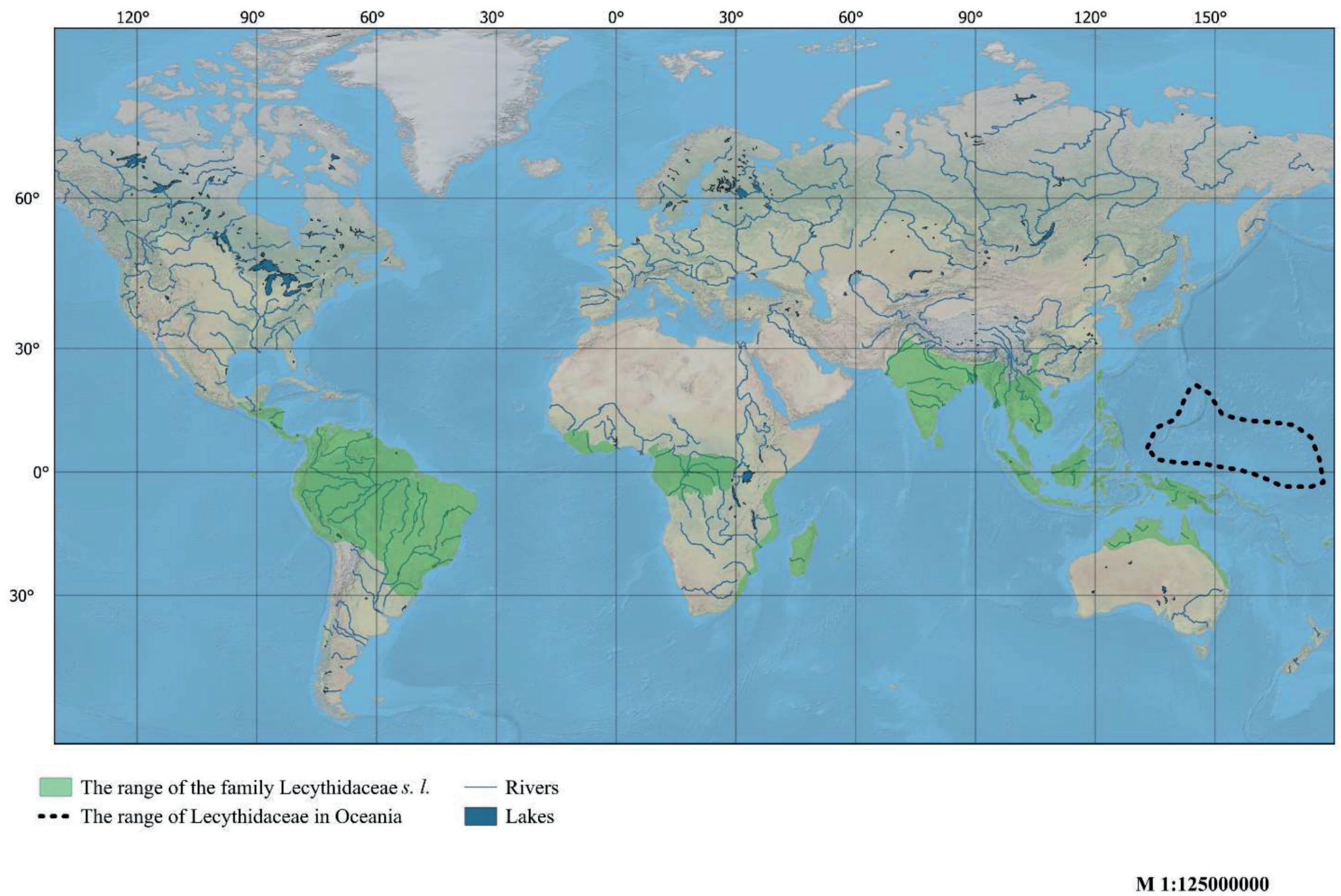

Fig. 3. Modern distribution of *Lecythidaceae s. l.*

paleobotanical data of *Barringtonioxylon* wood, dated to the Late Cretaceous and anatomically similar to the wood of all species of the family, the Late Cretaceous period could be considered the starting point for the further processes of distribution of Lecythidaceae *s. l.* taxa.

The subfamily closest to Napoleonoideae, based on the results of the model, is Scytopetaloideae. All of its species, with the exception of *Asteranthos brasiliensis*, also grow in the Guinea-Congo floristic region. So, *Rhaptopetalum coriaceum* inhabits the coast of the Gulf of Guinea, primarily in its western part, within the Congo basin [PoWO]. *Scytopetalum klaineanum* is distributed even more locally and is found only in Gabon, Congo, Cameroon, and Equatorial Guinea [PoWO]. *Brazzeia soyauxii* is distributed in the eastern and southern parts of the Guinea- Congo region [Takhtadzhyan 1978; PoWO], reaching the savannas. *Asteranthos brasiliensis* is the only species from the subfamily Scytopetaloideae reached South America [PoWO], particularly, the Central Amazon region (Fig. 4). Based on calibration data, this happened approximately 17 million years ago. The dispersal was by long-distance transport, i.e., anemochorous or animal disseminators. Paleobotanical data allow to suggest that this was a secondary colonization of South America by species of Lecythidaceae *s. l.*

The way to the east of Lecythidaceae was possibly difficult. Based on the results of a calibrated cladogram, this process may have begun approximately 50 million years ago. It was associated with the dispersal of species of the subfamily Barringtonioideae into Asia (Fig. 5).

The first two clades of this subfamily are represented only by Barringtonia. These mostly coastal ("peri-mangrove") plants began to spread eastward, colonizing large areas along the east coast of Africa. The range of *Barringtonia racemosa* covers East African coast from southern Kenya to northern South Africa, while *Barringtonia asiatica* spreads to eastern Tanzania, from where it reached Madagascar [PoWO]. Further, through Hindustan, the species of the genus *Barringtonia* reached Asia, where they became extremely widespread. Their range is bordered in the north by Himalayas, so their further path was to the east. Then they reached Indochina and Malesia. *Barringtonia acutangula* and *Barringtonia lanceolata* also grow there. Then species of the genus colonized Northern Australia, spreading along its coast in the Cape York and Arnhem Land peninsulas, where *B. racemosa, B. asiatica,* and *B. acutangula* also grow nowadays [PoWO]. Finally, the genus *Barringtonia* reached Melanesia *(B. edulis)*.

Species of another clade of the subfamily Barringtonioideae diverged much later, but still in Africa, about 17 million years ago. The range of the most basal genus in this clade, *Petersianthus*, consists of two parts. *Petersianthus macrocarpus*, separated from the main Barringtonioideae tracks, returned (or initially did not leave) to the Guinea-Congo region [Takhtadzhyan 1978] and spread there. Another species, *P. quadrialatus*, with other ones, reached Asia and further spread to the Philippines. Other taxa of the subfamily followed the main tracks. Species of the genus *Careya* (in particular, *C. arborea*) dispersed throughout Hindustan and Indochina. The genus *Chydenanthus* has a similar range, with the only exception that it is absent from Hindustan, but is widespread in Malesia (in particular, *Chydenanthus excelsus*) [PoWO]. The genus *Planchonia* dispersed throughout Malesia and, like some *Barringtonia* species, also reached Northern Australia.

Species of the subfamily Foetidioideae diverged from Barringtonioideae while they had not yet left Africa, approximately 29 million years ago. They remained on the East African coast, also reaching Madagascar and the Mascarene Islands, forming an isolated East African- Madagascar relict lineage. *Foetidia obliqua* occupies a small area of the Tanzanian coast and is also distributed in Madagascar, like *Foetidia asymetrica*. *Foetidia mauritiana*, however, is found only in the Mascarene Islands [PoWO].

Finally, another stage of the dispersal of Lecythidaceae *s. l.* is associated with their first entry into South America (Fig. 6).

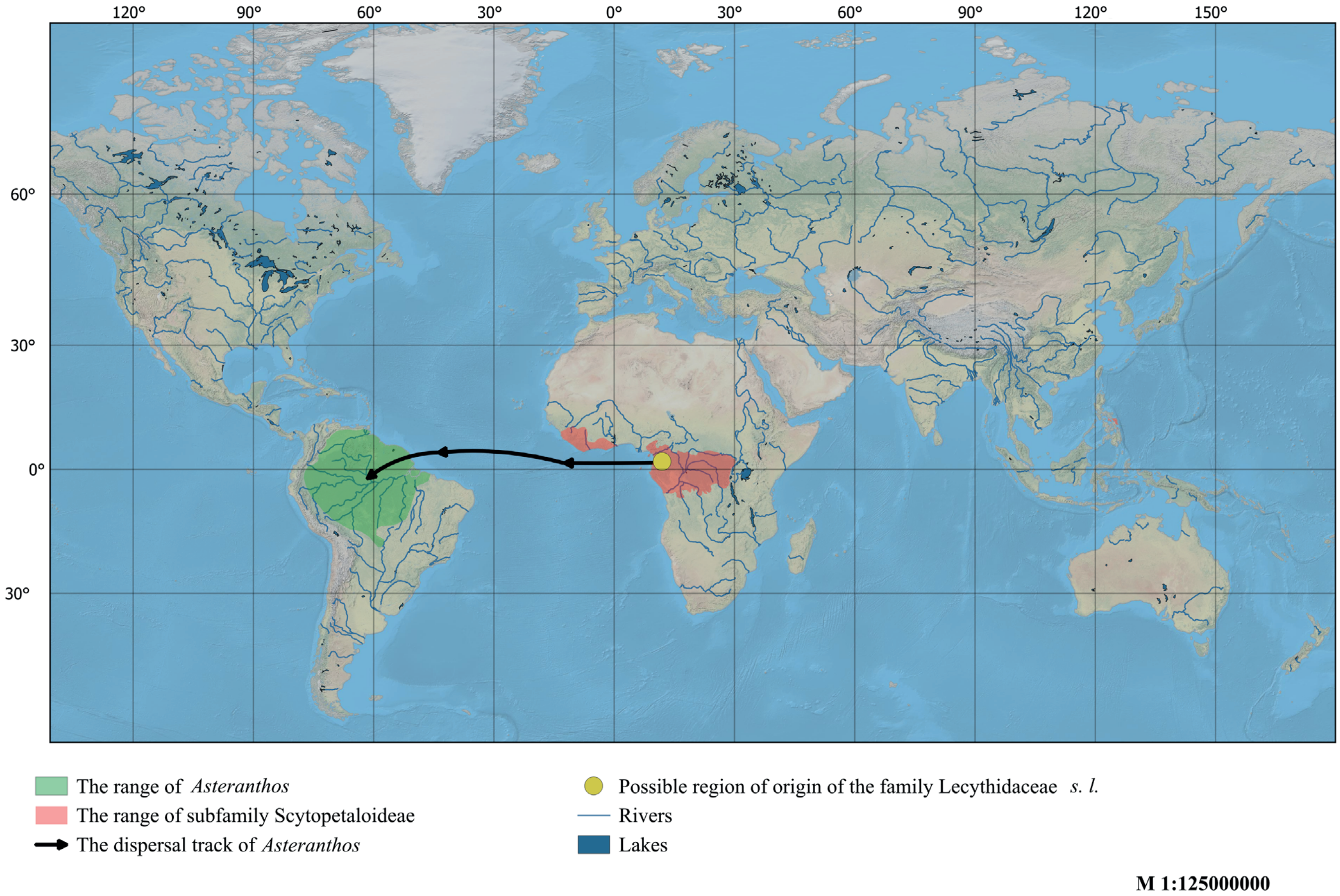

Fig. 4. Track of Scytopetaloideae to South America

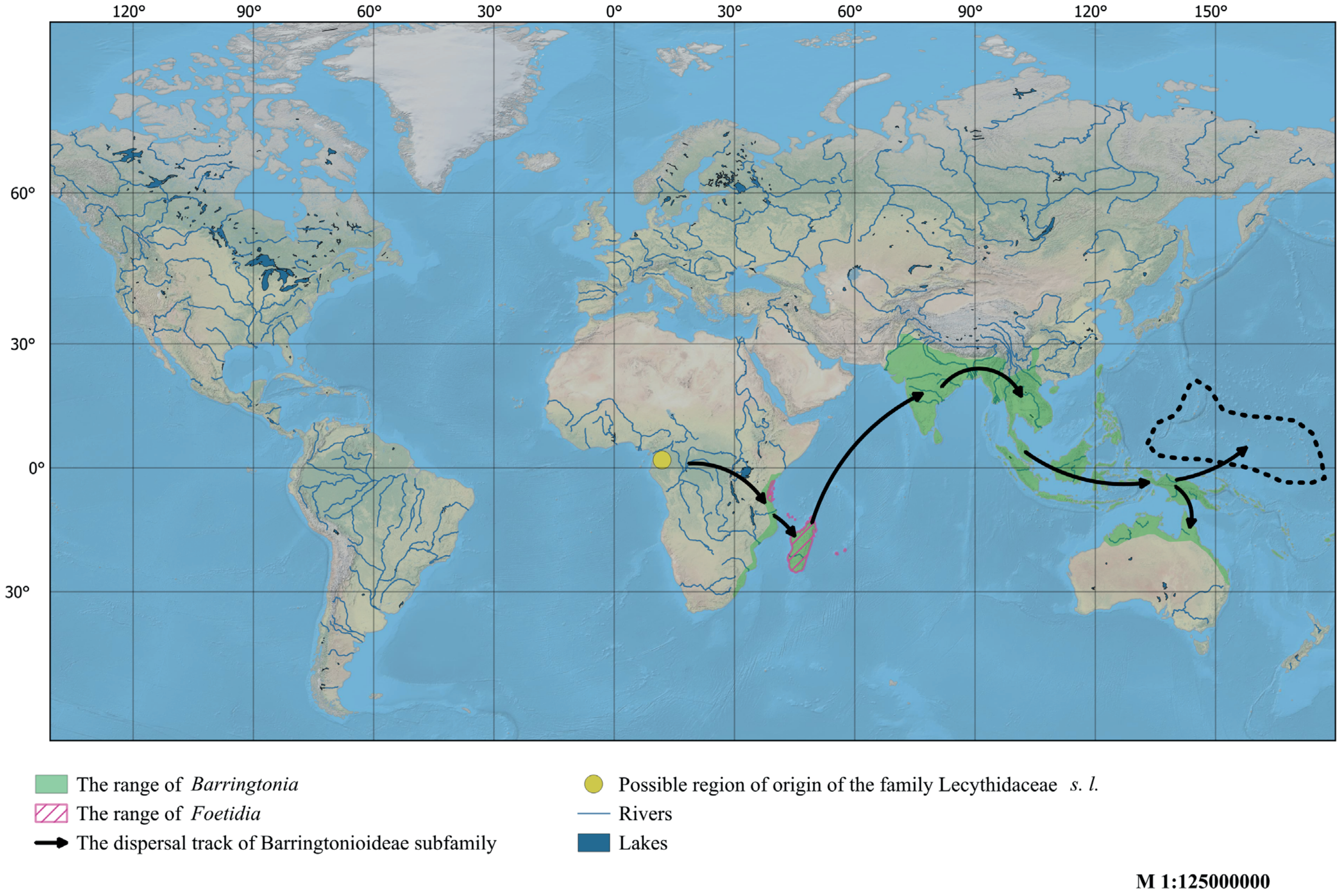

Fig. 5. Tracks of Barringtonioideae

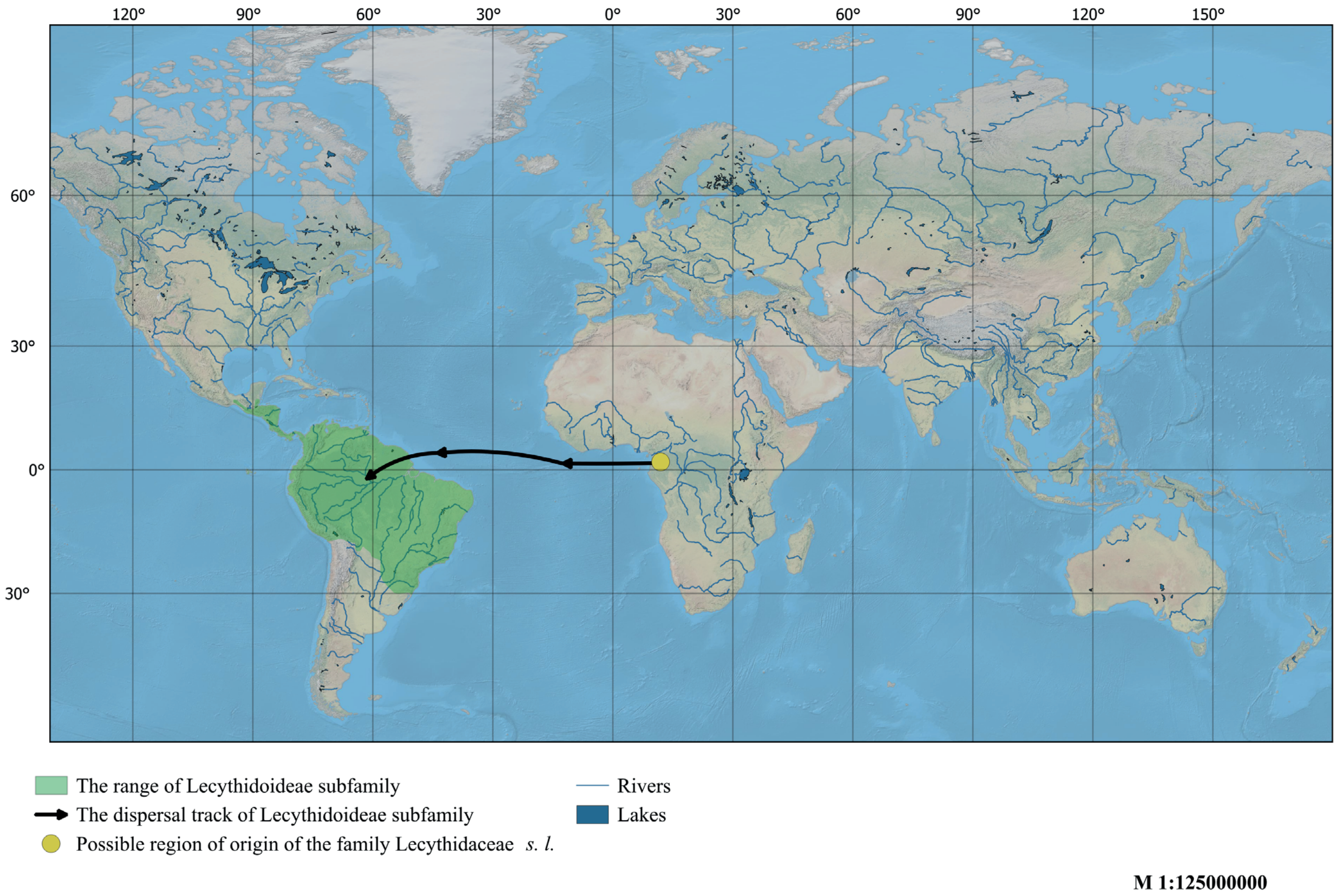

Fig. 6. Tracks of Lecythidoideae to South America

Based on the results of the calibrated cladogram, these events also began approximately 50 million years ago. Species of the Neotropical clade, which includes *Grias* and *Gustavia*, possibly were the first to complete this way, reaching the territory of the modern Brazilian Highlands and moving further west. *Grias* species dispersed mostly in mountainous regions, primarily in the Northern Andes (*Grias peruviana*), as well as in northern Amazonia *(Grias multinervia)* and Central America *(Grias multinervia, Grias cauliflora)*. Species of the genus Gustavia have spread extremely widely, both in Central America *(Gustavia monocaulis, Gustavia superba)*, the region of the Guiana Highlands and Amazonia *(Gustavia augusta)* and in the Northern Andes [PoWO].

Species of the genus *Couroupita*, another Neotropical clade, also have a wide distribution. They inhabited both mountainous and lowland regions. Specifically, *Couroupita nicaraguarensis* grows in the mountainous regions of Central America and extends into the northern Andes. *Couroupita guianensis* has an extremely wide range, covering territories from Central America to the southern borders of the Amazon basin [PoWO].

Genera included in another Neotropical clade covered large areas in the Guiana Highlands *(Couratari calycina, Couratari guianensis)*, but some reached regions of Central Amazonia *(Allantoma lineata)*. Others *(Cariniana rubra)* remained in the Brazilian Highlands and became among the few that colonized the steppe landscapes of the cerrado.

Finally, species of the "last" Neotropical clade adapted to a variety of environmental conditions. Some species colonized the mountainous regions of Central America and the Northern Andes *(Eschweilera integrifolia)*. Others spread widely across the Amazonian tropical rainforests *(Lecythis retusa, Lecythis barnebyi)*. Others colonized the steppe areas of the cerrado *(Lecythis lurida)*. And many went far north, reaching the Yucatan Peninsula *(Lecythis ampla, Lecythis minor)*.

CONCLUSIONS

The family Lecythidaceae s. l. hypothetically originated in Central Africa, where species of the basal subfamily Napoleonoideae grow. The family originated approximately 85 million years ago.

The first colonization of South America probably happened about 50 million years ago by species of the subfamily Lecythidoideae, which later spread extremely widely throughout the tropics of the New World.

The eastward dispersal of subfamily Barringtonioideae species from Africa also began 50 million years ago and followed several routes. Initially, species of the subfamily occupied large areas along the coast of East Africa, and then moved into Asia through Hindustan and Indochina peninsulas, spreading to Malesia, northern Australia, and Oceania.

Species of the subfamily Scytopetaloideae diverged at the earliest stages of the family's evolution, but dispersed beyond the region of its origin much later (about 17 million years ago): the only Neotropical species of the subfamily, *Asteranthos brasiliensis*, grows in Central Amazonia.

The dispersal of the subfamily Foetidioideae, the most recently diverged group, happened approximately 25±10 million years ago in East Africa, with the single genus *Foetidia* that reached Madagascar and the Mascarene Islands.

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