RESEARCH PAPER

PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF THE ORDER PANDANALES

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ABSTRACT. Reconstruction of the dispersal history and formation of modern ranges of various taxa is one of the actual problems of modern biogeography. Molecular genetic biogeography based on the analysis of phylogenetic relationships of taxa of different levels began to develop actively at the end of the XX century. Currently, this method is the most objective and represents the basis for reconstruction of scenarios of the origin and dispersal of various groups of plants.

Due to recent transformation of views on the phylogenetic relationships of Pandanales, the reconstruction of tracks and modes of dispersal of representatives of the order Pandanales becomes an actual task.

Representatives of all 5 families of Pandanales sensu APG IV were selected for the study and two cladograms were constructed.

Based on the molecular-genetic cladistic method the region of hypothetical origin and probable dispersal scenarios of the families of the order Pandanales were determined. The order Pandanales is treated as originated in Laurasia and its differentiation began on the territory of Tibet. Dispersal of the representatives of the basal family Velloziaceae took place by long-distance transport via the Bering Land Bridge to South America (approximately 115 Mya). Velloziaceae dispersed in the New World vicariously in South America, then it was distributed to sub-Atlantic Africa by long-distance transport, and finally also vicariously to the east, south and north of the continent. It is shown, that the modern range of the representatives of rest Pandanales is the result of both types of dispersal – vicariously and long-distance transport.

KEYWORDS: phylogenetic biogeography, dispersal history, molecular genetic analysis, phylogeny, Pandanales

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INTRODUCTION

At the end of the 20th century, due to the expansion of technological capabilities of molecular genetic research, phylogenetic biogeography began its active development. Phylogenetic biogeography is based now on the analysis of the phylogenetic relationships of taxa at different levels. This method is currently the most objective and is used as the basis for reconstructions of scenarios of the origin and dispersal history of different taxa of plants, as well as other living organisms (Heads 2012; Heads 2013).

In the APG IV system the families Velloziaceae, Triuridaceae, Stemonaceae, Pandanaceae and Cyclanthaceae were included in the order Pandanales. Earlier, most of these families were not considered to be related (Hutchinson 1973; Cronquist 1981; Thorne 2000; Takhtajan 2009). For example, the family Triuridaceae was considered in a separate monotypic subclass Triurididae and the family Stemonaceae was treated as closely related to Smilacaceae (Takhtajan 1987).

Within Pandanales the Velloziaceae clade (5–10 genera; 250 species) is basal. It is distributed in sub-Saharan Africa, south-western Arabia, western Madagascar, eastern Tibet, eastern, northern and central South America and Panama. Most Velloziaceae usually grow on granite or quartzite rocks, on sandy or stony soils, in more or less arid habitats (Takhtajan 1982; Kubitzki 1998a). Many species of *Vellozia* occur only on soils rich in iron in the form of hematite (Takhtajan, 1982). Some *Vellozia* species are well adapted to the unique Brazilian landscapes, their seeds are able to remain in the soil for long periods of time and maintain high germination rates. Thus, representatives of *Vellozia* form long-term stable soil seed banks, which play an important role in restoring disturbed plant communities (Garcia et al. 2017). Some representatives of the genera *Xerophyta* and *Nanuza* can survive severe drought to the point of complete leaf desiccation, consuming moisture only in the form of a dew. Almost all species of Velloziaceae are more or less xerophytic, whereas *Talbotia* is a true mesophyte (Takhtajian 1982; Kubitzki 1998a).

The next branched clade of Pandanales is the family Triuridaceae (5–9 genera; 70 species). It has a pantropical distribution, and also found in Japan and in the Midwest of the United States. Some genera are distributed in subtropical regions, including *Peltophyllum* in Argentina and Paraguay and *Sciaphila* in Japan (Maas-Van De Kamer and Weustenfeld 1998). Triuridaceae are achlorophyllous, saprophytic (mycoheterotrophic) herbaceous plants with obligate endomycorrhiza (Merckx et al. 2013). This mode of nutrition allows Triuridaceae to inhabit shaded conditions, and obtain carbon from symbionts but not from photosynthesis (Mennes et al. 2013). Triuridaceae inhabit dense and humid forests, under a closed canopy, at the base of large trees or along the banks of rivers, at altitudes ranging from 200 to 2200 m. Less commonly they are found in temporarily flooded forests, forests on coral sands, in bamboo thickets or on termite mounds (*Sciaphila purpurea* Benth., *S. africana* Becc.). They often grow in close association with other mycotrophic plants from different families (Mies-Van De Kamer and Weustenfeld 1998; Merckx et al. 2013).

The next step in the evolution of the order is the divergence of the family Stemonaceae (4 genera; 30 species). Its representatives are distributed in Malaysia, northeastern Australia, Sri Lanka, south of the Indian Peninsula, Japan (except Hokkaido Island), southern China, Indochina Peninsula and south-eastern USA. Stemonaceae inhabit tropical and subtropical highland forests, they occur on hillsides or in valleys, in shady areas and often in scrub vegetation (Velgorskaya 1982). In general, the representatives of the family prefer dry sandy or clay soils, but occasionally occur in wet areas on muddy soils in depressions in the foothills and lowlands (*Stemona tuberosa* Lour., *Pentastemona* spp.), some species of *Stemona* and *Stichoneuron* are distributed at altitudes up to 1800 m (Velgorskaya 1982; Kubitzki 1998b; Kubitzki 1998c). In Japan, *Croomia* species are often found in plantations of *Cryptomeria japonica* (Thunb. ex L. f.) D. Don. *Croomia pauciflora* (Nutt.) Torr. grows on dry, loose soils along riverbanks in the shade of forests (Vielgorskaya 1982). Seeds of representatives of most Stemonaceae have arillus or elaiosomes, which may indicate an adaptation to zoochoria. The seeds of some Stemonaceae species are light and dangle from the fruit by a long funiculus, and can probably be dispersed by wind (Velgorskaya 1982). Seeds of *Croomia* have a thick shell, which may contribute to hydrochoria (Kubitzki 1998b).

The family Stemonaceae is basal to the two sister terminal families of Pandanales – Pandanaceae (Palaeotropics; 5 genera; 750-900 species) and Cyclanthaceae (Neotropics; 12 genera; 230 species). Pandanaceae representatives are distributed from the sea level and up to altitude of ca. 3000 m on a variety of substrates: granites, limestones, ultrabasic, muddy, peaty or clay substrates. They also often participate in littoral mangrove communities or grow as epiphytes in rainforests (Stone et al. 1998). Representatives of the largest genus, *Pandanus*, are most commonly found along the shores of tropical lowlands. *Pandanus* species have an almost universal adaptability to different habitats. In addition to coasts and swamps, it is found in drier lowlands, mountainous and even high-altitude forests, on coral reefs and limestone cliffs, on the slopes of volcanoes, and in savannas (Grushvitsky 1982). Pandanaceae diaspores are dispersed by birds, mammals, sometimes turtles, and freshwater or ocean currents (Cox 1990; Stone et al. 1998). Almost all representatives of Cyclanthaceae are growing in wet and more or less shady habitats (tropical rainforests). The epiphytic Cyclanthaceae (61% of the family) dominate the epiphytic communities of the Neotropics, with only two other flowering plant families, Orchidaceae and Marcgraviaceae, having a similar ecological role (Gentry and Dodson 1987). The often brilliantly coloured spadices of Cyclanthaceae is probably an adaptation to endozoochoria (Harling et al. 1998), the agents of which are bats (Croat 1978; Hammel and Wilder 1989), monkeys (Croat 1978; Gentry and Dodson 1987) and birds (Olson and Blum 1968). Furthermore, ballistochoria (Hammel 1986) and barochoria (Hammel and Wilder 1989; Eriksson 1995) have been also described in some species of Carludovicoideae.

With the current reassessment of Pandanales phylogeny, the reconstruction of its dispersal history becomes an actual task of plant biogeography. In order to determine the region of hypothetical origin and probable dispersal scenarios of the families of Pandanales families, the representatives of all 5 families from 30 genera of the order Pandanales (sensu APG IV) were selected for conducting a phylogenetic phytogeographic reconstruction based on a molecular genetic cladistic methods of investigation.

MATERIALS AND METHODS

The cladistic method proposed by W. Hennig in 1950 was used in the present study (Crisci et al. 2003; Lukashov 2009; Hall 2011; Wiley and Lieberman 2011).

Thirty seven species from 30 genera from all five families of the order Pandanales were used in the present study (Table A.1). The sequences of four different markers were selected for each species, – matR (mitochondrial DNA), 18S (ribosomal RNA), atpA (chloroplast DNA), matK (chloroplast DNA). Since the selected nucleotide sequences had different lengths and some deletions, the multiple sequence alignment was performed using the Clustal Omega algorithm (Lukashov 2009; Sievers et al. 2011; Wiley and Lieberman 2011; Judd et al. 2016). Then, the concatenation of 4 markers to one sequence (18s–atpA–matK–matR) was made in Mega X program (Kumar et al. 2018), after which the consensus molecular genetic cladogram of Pandanales was obtained (Fig. 1).

Evolutionary models were formed in the MrBayes 3.2 program (Ronquist et al. 2012) using Bayesian inference by 4 genes for 3000000 generations. Samples were taken every 100 generations and 25% were discarded in the burning. For 18S and matR markers, the Kimura two-parameter model (Kimura 1980) was used. For atpA and matK the General time reversal (GTR) model was used (Nei, Kumar, 2000). Optimal models were selected in TOPALi v2 (Milne et al. 2009). Six species of *Dioscorea* (Dioscoreaceae–Dioscoreales, sister order to Pandanales sensu APG IV) were selected as an outgroup.

In order to clarify the relationship between representatives of the basal family Velloziaceae, we constructed a separate molecular genetic cladogram. The nucleotide sequences of three markers representing 9 species from 9 narrowly considered genera of Velloziaceae were selected from GenBank (Table A.2): two plastid (atpB with spacer atpB-rbcL and tRNA-Leu (trnL) with spacer trnL-F), and one ribosomal (5.8S ribosomal RNA with two internal spacers – 1 and 2).

Multiple sequence alignment was carried out using the Clustal X 2.0 program (Larkin et al. 2007), after which the consensus molecular genetic cladogram was obtained (Fig. 2). Evolutionary models were constructed in the Mega7 7.0.26 program (Kumar et al. 2016) using the maximum likelihood statistical method based on the Tamura 3-parameter model (Tamura 1992). The consensus cladograms were obtained using bootstrap analysis with 1000 replicates (Felsenstein 1985). The *Stemona tuberosa* Lour. from the closely related family Stemonaceae (Chase et al. 2016) was selected as an outgroup.

The charts of the correlation of the phylogenetic relationships of Pandanales genera and their geographical distribution were presented for each family separately: Velloziaceae (Fig. 3); Triuridaceae (Fig. 4); Stemonaceae (Fig. 5); Pandanaceae (Fig. 6) and Cyclanthaceae (Fig. 7).

RESULTS

As a result of our research, cladograms were obtained (Fig. 1, 2). The resulting cladograms are generally supported with high bootstrap index at most nodes. Velloziaceae is shown to be basal in Pandanales (Fig. 1). The next phylogenetic event was the separation of the clade Triuridaceae from other families. Later Stemonaceae clade and two sister terminal families – Pandanaceae and Cyclanthaceae – separated (Fig 1).

Phylogeny of Velloziaceae

The Tibetan genus *Acanthochlamys* is the most basal in Velloziaceae (Fig. 2). At the next step the American genus *Barbaceniopsis* and all other genera diverged into two branches. The first branch includes two sister African genera *Talbotia–Xerophyta*, which are basal to all other genera. Later these genera become diverged into two sister clades – *Nanuza–Vellozia* and *Pleurostima–Barbacenia–Burlemarxia*, both of which are American.

Phylogeny of Triuridaceae

In the family Triuridaceae, the Cameroon-Tanzanian clade *Kihansia–Kupea* is basal (Fig. 1, 4). It is followed by a polytomy giving rise to three clades: (1) *Seychellaria* – a genus distributed in Madagascar, Seychelles and Tanzania, (2) *Sciaphila* – a pantropical genus, and (3) *Lacandonia–Triuris* clade, whose representatives are distributed in Central America and tropical regions of South America.

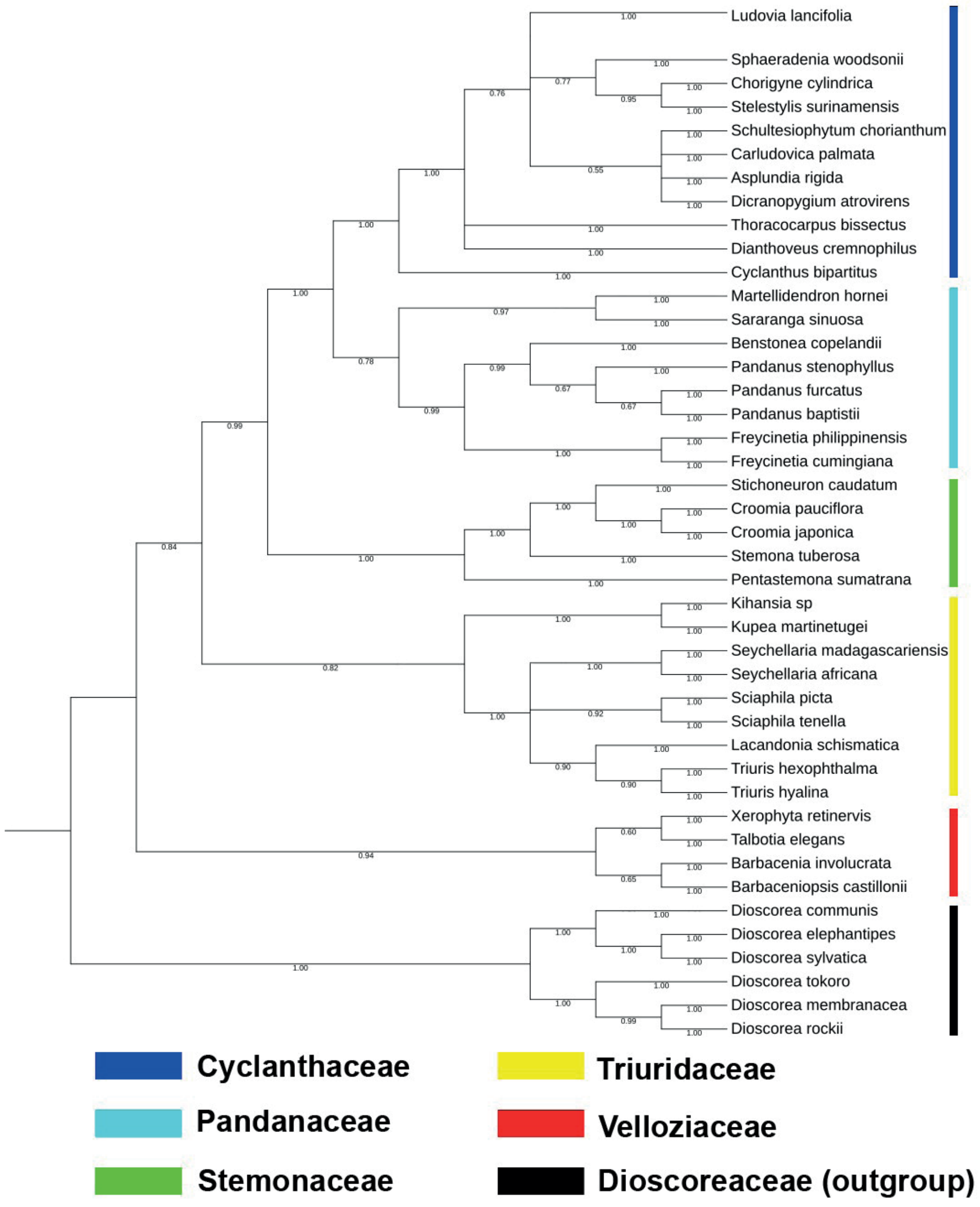

Fig. 1. Molecular genetic cladogram of Pandanales

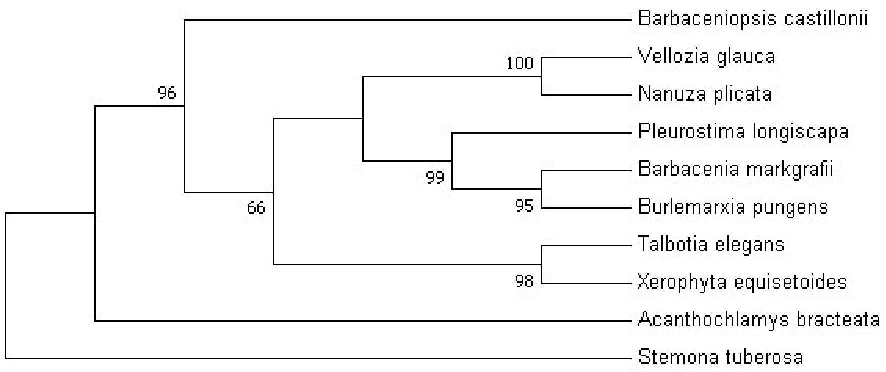

Fig. 2. Molecular genetic cladogram of Velloziaceae

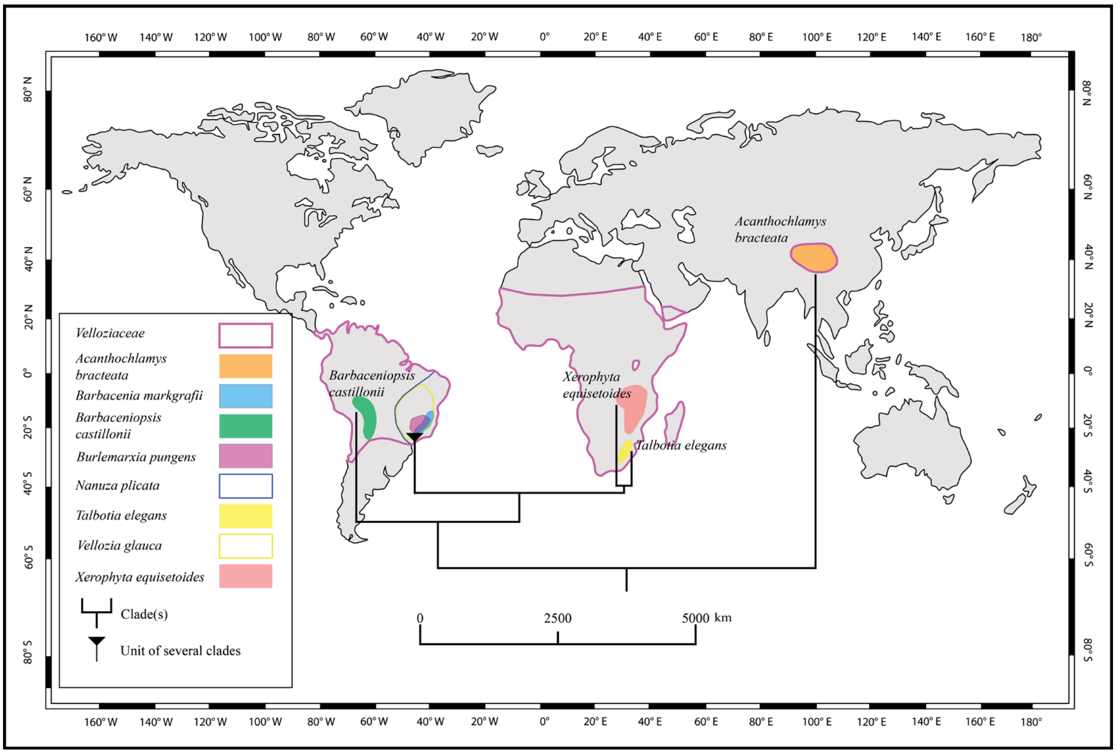

Fig. 3. Correlation of phylogeny of Velloziaceae genera and their distribution

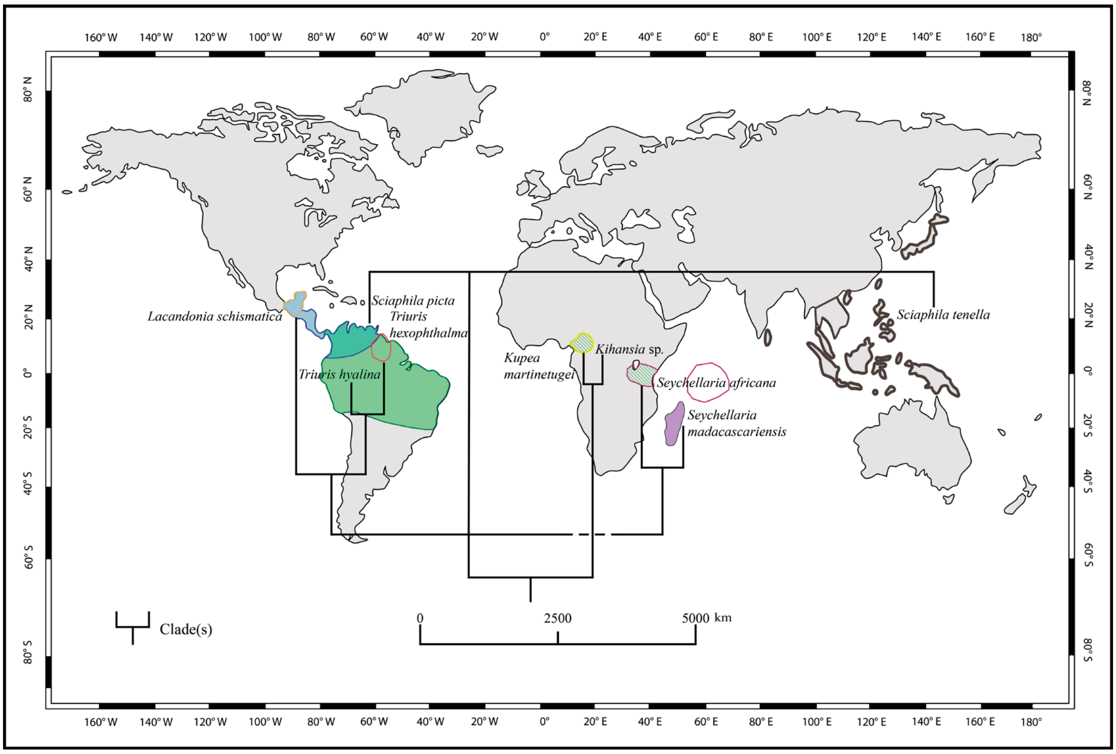

Fig. 4. Correlation of phylogeny of Triuridaceae genera and their distribution

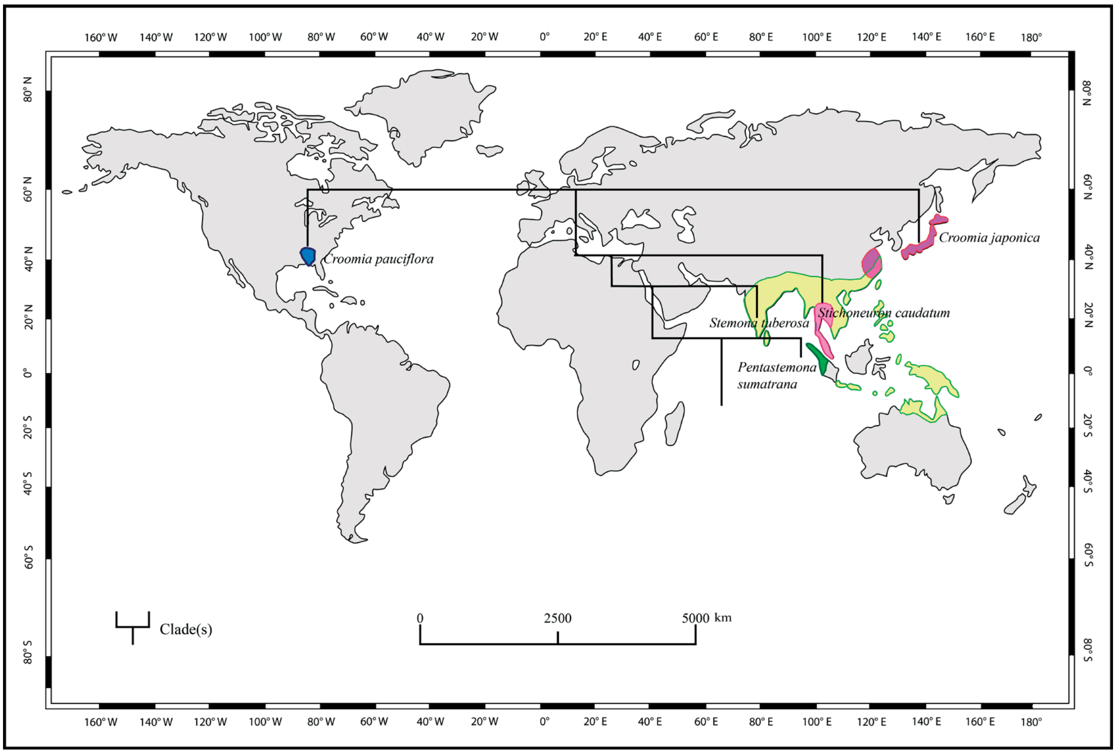

Fig. 5. Correlation of phylogeny of Stemonaceae genera and their distribution

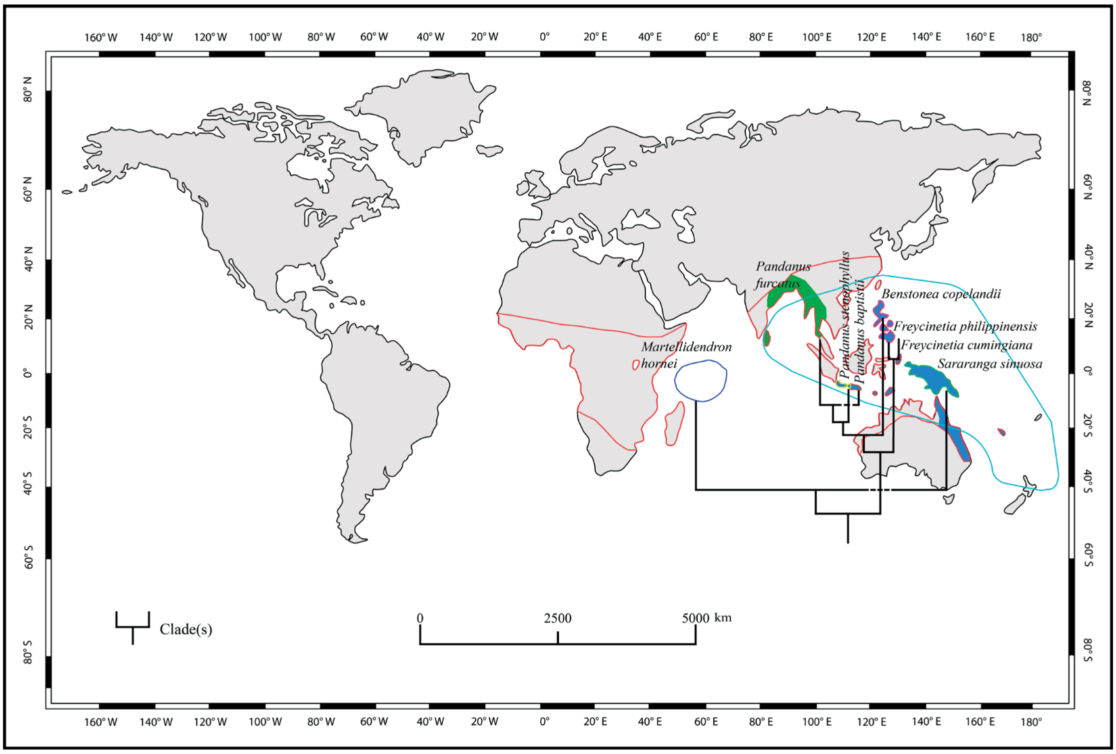

Fig. 6. Correlation of phylogeny of Pandanaceae genera and their distribution

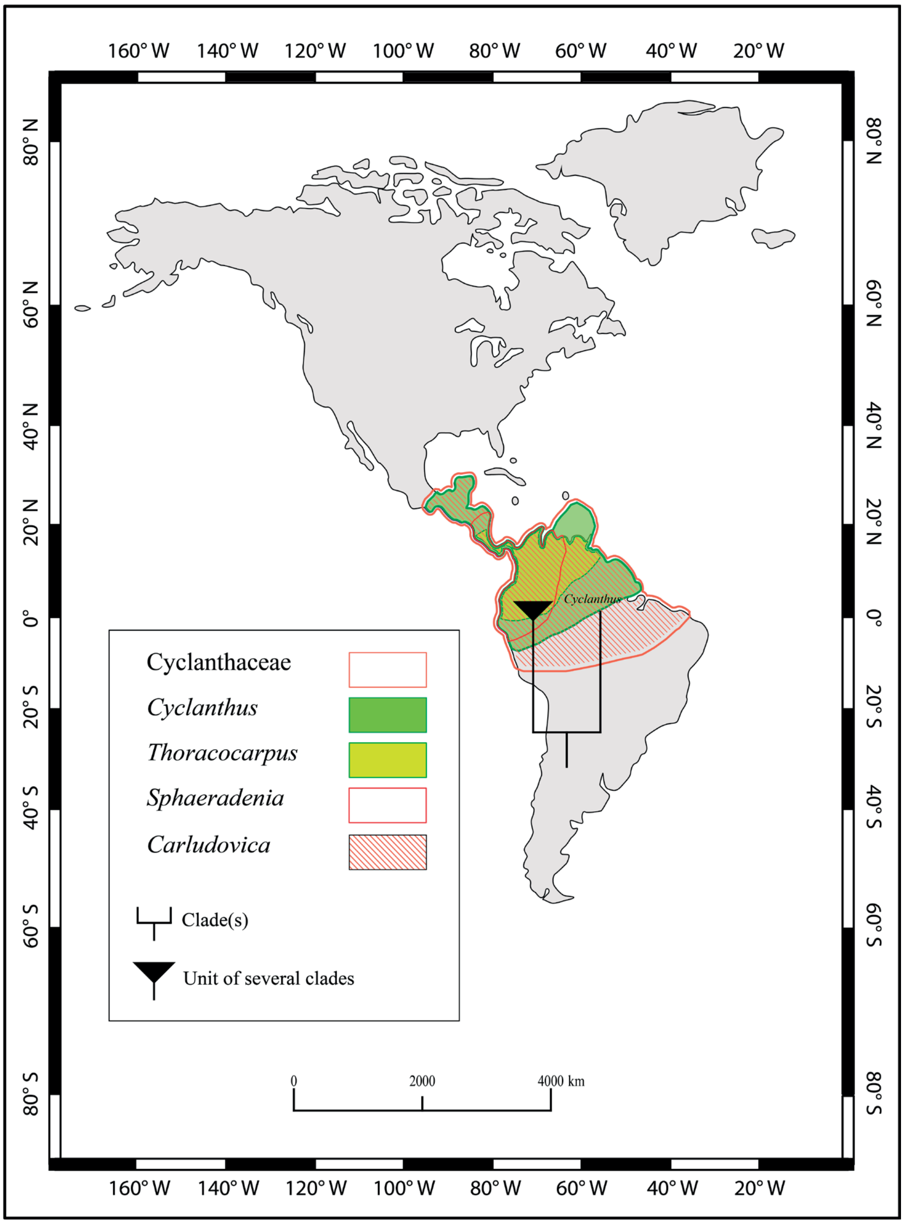

Fig. 7. Correlation of phylogeny of Cyclanthaceae genera and their distribution

Phylogeny of Stemonaceae

The genus *Pentastemona*, the endemic of Sumatra, is the basal in Stemonaceae family (Fig. 1, 5). Then the genus *Stemona*, which is widespread in the Paleotropics, diverged from the other genera of the family. The final bifurcation resulted in two sister clades: *Stichoneuron* (continental Southeast Asia) and *Croomia* (East Asia and Southeastern United States).

Phylogeny of Pandanaceae

The clade *Martellidendron–Sararanga* (Madagascar, Seychelles, New Guinea, Philippines) is basal in Pandanaceae (Fig. 1, 6). The clades of *Freycinetia* (from Sri Lanka to the Marquesas Islands, including Hawaii, Australia and New Zealand) and *Benstonea–Pandanus* (both Paleotropics) diverged at the next steps.

Phylogeny of Cyclanthaceae

The basal position in the neotropical family Cyclanthaceae was occupied by the representative of a separate monotypic subfamily – *Cyclanthus bipartitus* Poit. ex A.Rich. (Fig. 1, 7), which is distributed from northern Guatemala through Central America, the Lesser Antilles and Trinidad Island to Chile and Brazil. Polytomies were observed three times during the next evolutionary steps in the family, which may indicate the recent evolutionary divergence between the genera. (1) The first polytomy is the split of the rest genera (subfamily Carludovicoideae) into three clades: *Thoracocarpus, Dianthoveus* and all other genera. (2) The second polytomy is the split of the remaining genera into three clades as follows: *Ludovia, Sphaeradenia–Chorigyne–Stelestylis* and all other genera. (3) The third polytomy occurred at the final step and of four genera became separated: *Asplundia, Dicranopygium, Schultesiophytum* and *Carludovica*.

DISCUSSION

According to the cladogram of Pandanales, the family Velloziaceae occupies the basal position (Fig. 1). Due to the fact that the Asian genus Acanthochlamys is basal within Velloziaceae, it is suggested that the region of the hypothetical origin of the Pandanales order could be Tibet.

Phylogenetic biogeography of Velloziaceae

After the separation of *Acanthochlamys*, the basal genus of Velloziaceae, the bifurcation of the second order resulted in origin of the American genus *Barbaceniopsis* and all other genera (distributed in Neotropics and Africa). Their areas of distribution could be formed as the result of long-distance transport from Tibet to America via the existing bridge between Asia and North America (Fig. 8) around 115-100 Mya (Scotese et al. 1988; Wu 1988). After that, dispersal probably took place via the incipient Atlantic Ocean to West Africa (Scotese et al. 1988; Scotese 2014). Further on in Africa, vicarious dispersal in two directions is most probable: eastwards to the east coast of the continent (*Talbotia*) and on to Madagascar and northwards to the Arabian Peninsula (*Xerophyta*). In South America a vicarious dispersal probably occurred to the north and northeast of the continent (Fig. 8). The proposed dispersal scenario (scenario #1) suggest that the Velloziaceae originated in Laurasia, then dispersed by long-distance transport at early stages of their history via Americas to Africa and later vicariously from West Africa to east coast of the continent and to the Arabian Peninsula. Such interpretation of Velloziaceae phytogeographic history contrasts with earlier studies (Mello-Silva et al. 2011), which suggested a Gondwanan origin of Velloziaceae and recognized their modern distribution (almost exclusively) as the result of vicariance (scenario #2). This alternative interpretation (scenario #2) of the dispersal history of Velloziaceae (Mello-Silva et al. 2011) is also probable as far as more than 90% of the representatives of the family is currently distributed in the New World, two genera (*Talbotia, Xerophyta*) distributed in Africa, Madagascar and southern Arabia and only one monotypic genus in Tibet. Based on this, it can be assumed that Velloziaceae originates in the Neotropics (i. e. in Gondwana). At the same time a third scenario (scenario #3) of Velloziaceae dispersal history could be assumed. The range disjunction of the family is generally indicative of the relict nature of the taxa and molecular studies suggest that the Velloziaceae originated around 115 Mya, which is comparable to the early dicotyledons (Mello-Silva et al. 2011). So, during the Upper Cretaceous, representatives of the family could migrate from Tibet to Africa via Arabia and then from West Africa via the Atlantic to South America, where they found more suitable ecological niches.

Phylogenetic biogeography of Triuridaceae

After the separation of Triuridaceae from other Pandanales, probably in Tibet (where the basal family Velloziaceae originated), the long-distance dispersal to the Americas via the Bering Land Bridge is assumed (Fig. 9) around 100–90 Mya (Gandolfo et al. 2002; Scotese 2014), which was followed by their expansion to South America and then to Africa. In Africa the basal clade of Triuridaceae – *Kihansia–Kupea* diverged from the main tree. The representatives of *Kihansia* are distributed in Cameroon and Tanzania, whereas the studied species of *Kupea, K. martinetugei* Cheek & S.A.Williams, is distributed only in Cameroon. The revealed topology and the ranges of the basal representatives of Triuridaceae (Fig. 4) may indicate a Laurasian-Gondwanan origin of the family. The origin of Triuridaceae revealed in the present study is also supported by fossil records of plants with a high degree of attribution to Triuridaceae, reported from the modern territory of the USA and dated to 90–94 Mya (Gandolfo et al. 2002). The pantropical genus *Sciaphila*, the next clade (Fig. 4), dispersed from central West Africa in two directions (Fig. 9): (1) vicariously to north-east Africa and then – eastward via the tropical regions of Eurasia to the South-East Asia and Japan; (2) by long-distance transport to Central America. The representatives of *Seychellaria* diverge from the main tree in next turn and dispersed vicariously from central West Africa eastwards to Tanzania, Madagascar and the Seychelles. The studied representatives of the *Lacandonia–Triuris* clade dispersed vicariously, most probably, from the place of hypothetical separation from the other Triuridaceae in central West Africa into northern South America. Then they dispersed there westward via the continent to the Pacific coast, southward in South America to the boundary of the tropics, southwestward to northern Argentina and northward into Central America to the Yucatan Peninsula and the Antilles (Fig. 9).

Phylogenetic biogeography of Stemonaceae

Pentastemona, the basal genus of Stemonaceae, is distributed in North Sumatra (Fig. 5). Based on this the Stemonaceae most probably originated in West Malesia. The next stage of the evolution of the family was the differentiation of the palaeotropical genus *Stemona*, which dispersal from West Malesia supposedly took place vicariously in two directions. (1) South-eastwards via the Sunda Islands to North Australia and then eastwards along the continent to Cape York Peninsula, westwards along the northern coast of Australia and then southwards to the south-west of Australia. (2) Northward via continental South-East Asia to the tropical border, then eastward to the coast of the Taiwan Strait and westward to the Indian Peninsula. And then southward to the Indian Ocean coast and Sri Lanka Island (Fig. 10). After the branching of the terminal clade *Croomia* in tropical East Asia vicarious dispersal most likely took place northwards along the Eurasian coast to the northern cost of the East China Sea and later eastwards to the Japanese islands. The further dispersal of *Croomia* representatives was realised by long-distance transport via the Kuril Islands, the Kamchatka Peninsula and possibly via the Bering Land Bridge to North America and further southwestward (Fig. 10).

Disjunction of the ranges of closely related species has traditionally been described for representatives of various taxa, including early dicotyledons. The conservation of morphological peculiarities among taxa with such disjunctions can be the result of morphological stasis and/or low evolutionary rates (Wen 2001). This can be the reason of the morphological similarities between closely related taxa native to East Asia and eastern North America (Wen 2001). For example, one part of the species of the genus *Magnolia* sect. *Rytidospermum* is distributed in eastern Asia and the other in eastern North America. Such disjunction explained by the relatively recent differentiation of species (Eocene-Miocene) and their further migration, particularly via the Bering Land Bridge (Tiffney 1985; Qiu et al. 1995).

Phylogenetic biogeography of Pandanaceae

A clade of two sister genera, *Martellidendron* (Madagascar and Seychelles) and *Sararanga* (Philippines and New Guinea), is basal in Pandanaceae. Thus, it is possible to assume hypothetical origin of the family in Madagascar or in New Guinea. Both variants indicate a south-east Gondwanan origin of the Pandanaceae. At the first stage, after the separation from other Pandanales, representatives of Pandanaceae most probably dispersed vicariously from hypothetical range of origin in East Africa via the southern Arabian Peninsula and the Indian subcontinent into south-east Asia, where the genera *Benstonea, Pandanus* and *Freycinetia* became differentiated (Fig. 11). Then, also vicariously, they continued to disperse southwards to the north coast of Australia and southeastwards to New Guinea. Thereafter, some species of *Pandanus* repopulated Africa, probably by long-distance transport (from South-East Asia). Such dispersal tracks can be explained by the prolonged germ activity of *Pandanus* hydrochorous diaspores (Gallaher et al. 2015). Later the African *Pandanus* species vicariously dispersed westwards to the Atlantic coast of Africa and southwards to the continental margins (Fig. 11).

The Gondwanan origin of the family war earlier suggested by other researchers and it is supported hypothesis by the fossil evidence (Callmander and Laivao 2002; Callmander et al. 2003; Nadaf et al. 2012). Recent study of the biogeography of Pandanaceae, based on molecular data, has proposed that dispersal of most species occurred by long-distance transport in the late Eocene, i. e. after the divergence of the Gondwana continents (Gallaher et al. 2015).

Phylogenetic biogeography of Cyclanthaceae

The family Cyclanthaceae is most probably originated in south-west Gondwana, as the basal genus *Cyclanthus* is distributed in northern South America and Central America.

After the basal clade of Cyclanthaceae separated, polytomies of clades: *Dianthoveus, Thoracocarpus* and all other Cyclanthaceae occurred. There representatives of these clades were distributed vicariously from northern South America southwards to the tropical border in Brazil and south-westwards to northern Argentina (Fig. 12). The diversity hotspot of Cyclanthaceae is Central America, where up to 90% of the species of Cyclanthaceae are distributed. After the differentiation of the genera *Dianthoveus* and *Thoracocarpus*, polytomy has three times occurred in the family, indicating close genetic relations between different genera and their recent evolutionary divergence.

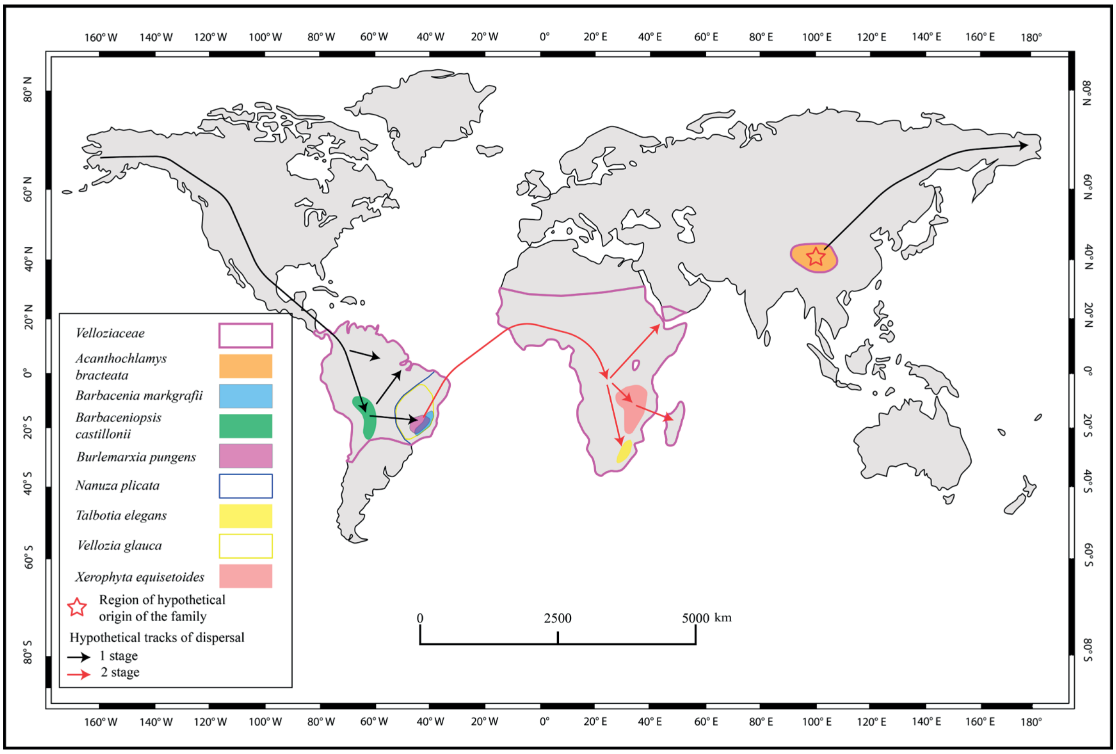

Fig. 8. The region of hypothetical origin and probable dispersal tracks of Velloziaceae

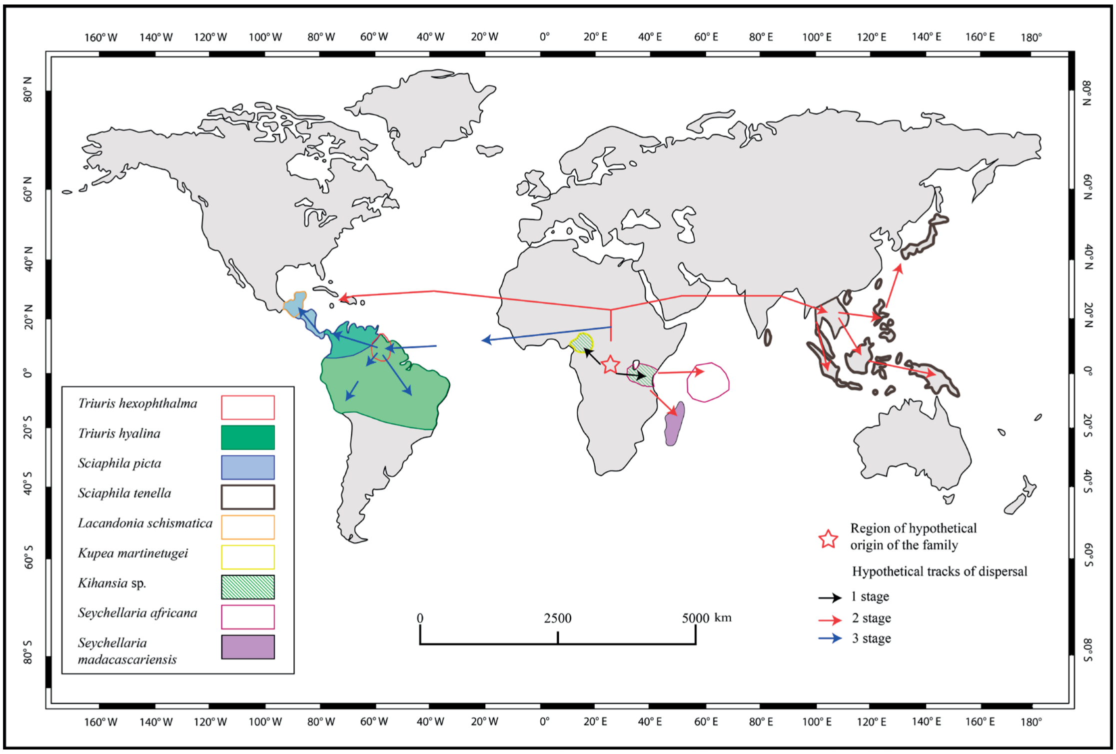

Fig. 9. The region of hypothetical origin and probable dispersal tracks of Triuridaceae

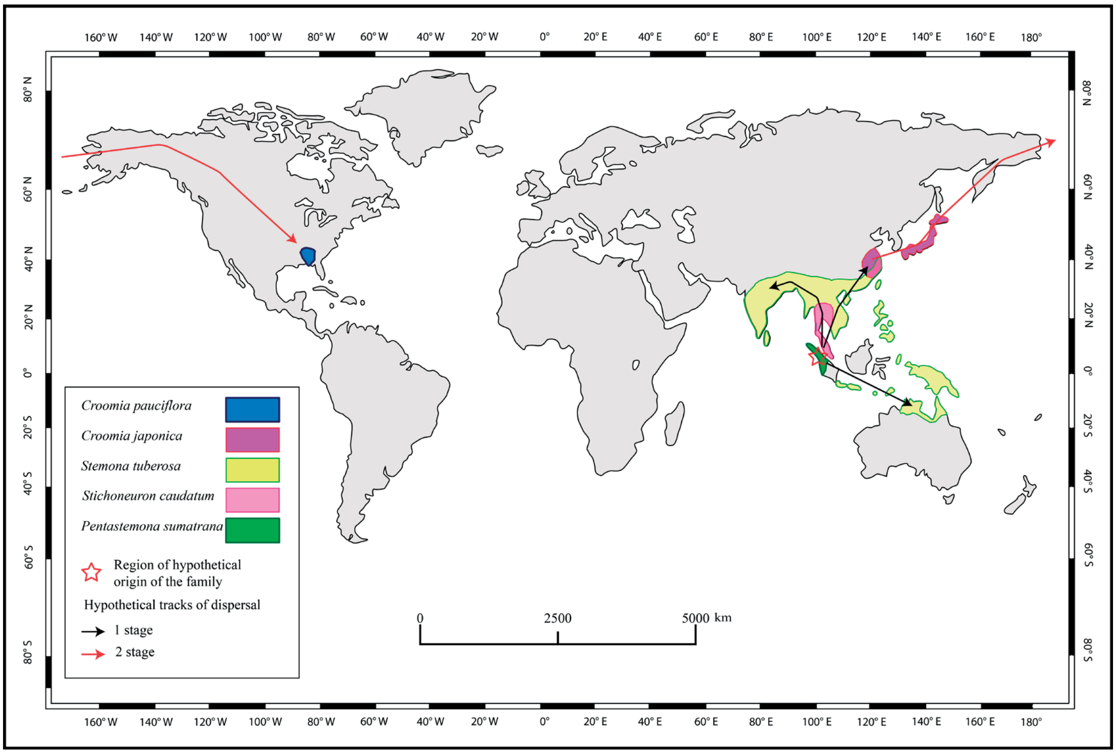

Fig. 10. The region of hypothetical origin and probable dispersal tracks of Stemonaceae

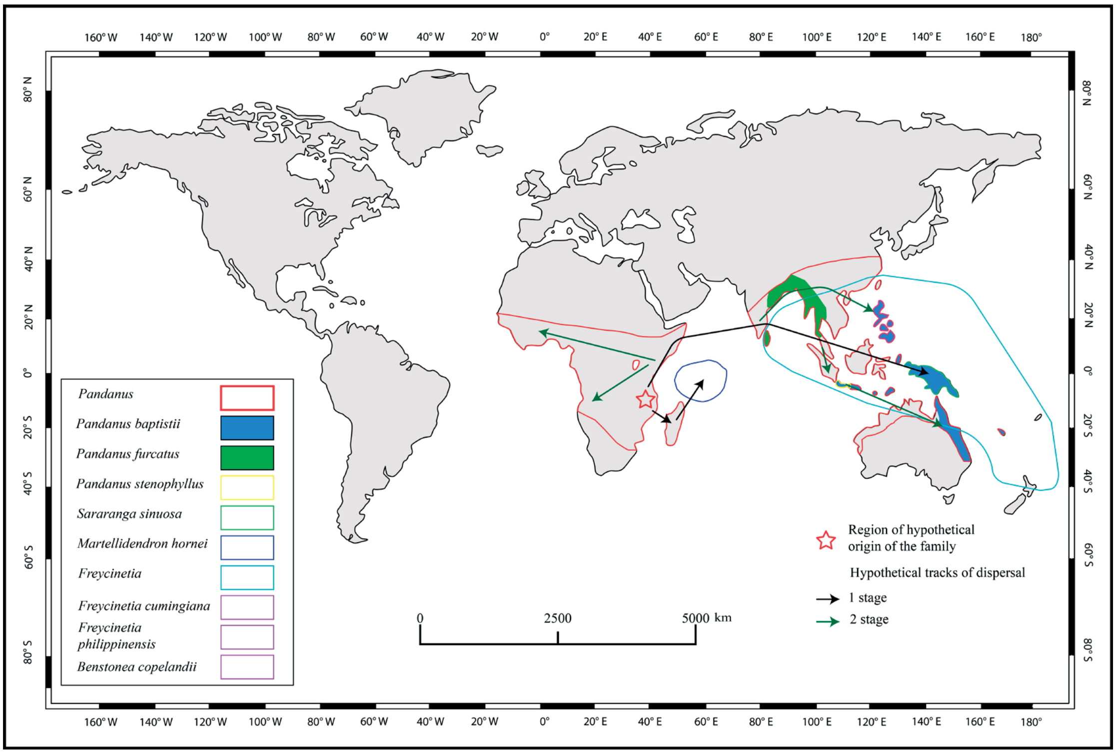

Fig. 11. The region of hypothetical origin and probable dispersal tracks of Pandanaceae

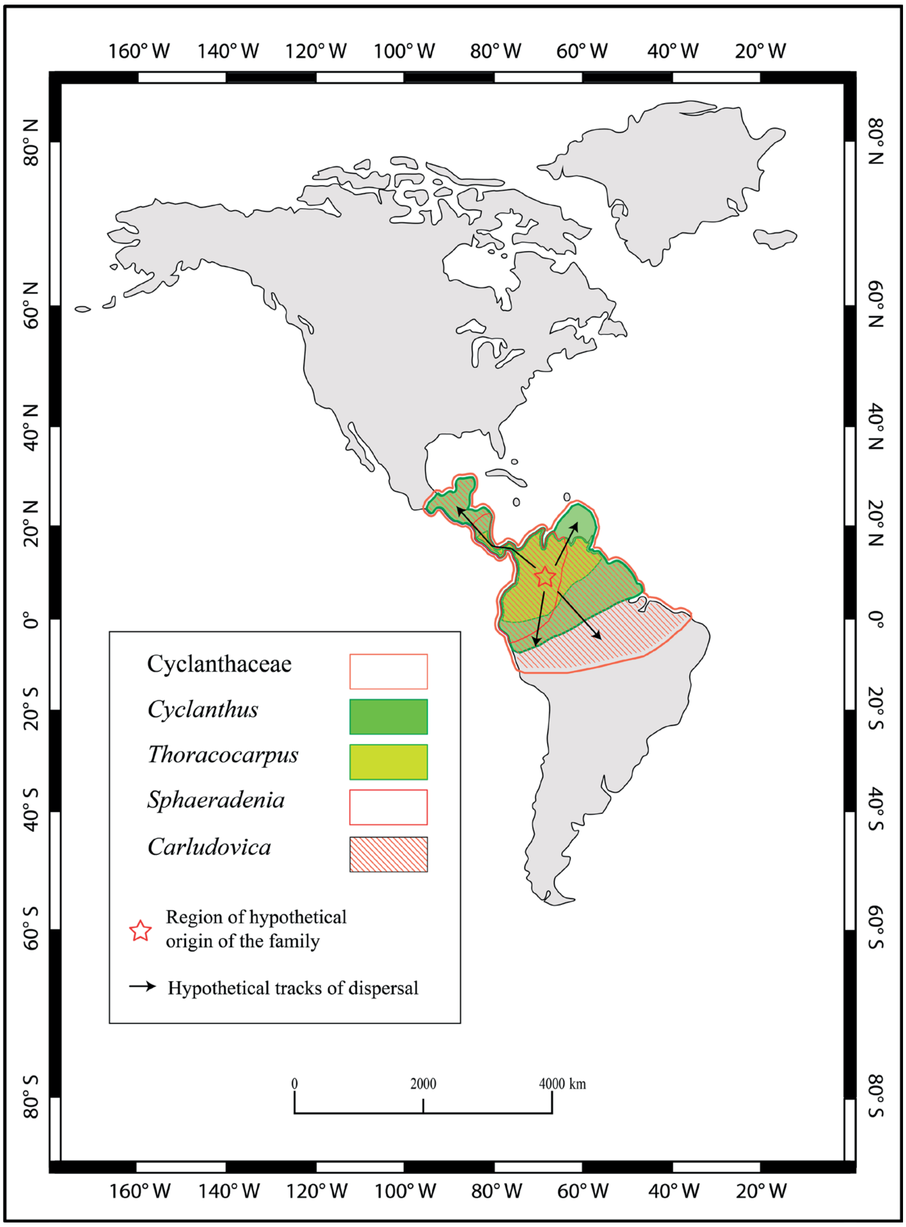

Fig. 12. The region of hypothetical origin and probable dispersal tracks of Cyclanthaceae

CONCLUSIONS

1. The order Pandanales is treated as originated in Laurasia and its differentiation began on the territory of Tibet.

2. Dispersal of the representatives of the basal family Velloziaceae took place by long-distance transport via the Bering Land Bridge to South America (approximately 115 Mya).

3. Velloziaceae dispersed in the New World vicariously in South America, then in was distributed to sub-Atlantic Africa by long-distance transport, and finally also vicariously to the east, south and north of the continent.

4. Triuridaceae, which probably originated in Africa, first dispersed vicariously along the several tracks of the tropical parts of the continent. Later two phylogenetic lines of Triuridaceae distributed to South America by long-distance transport on one side and probably vicariously – to South and South-East Asia, to North Australia and Oceania on the other.

5. Stemonaceae, having been differentiated from others Pandanales, probably, in South Malesia, dispersed vicariously from there in several tracks. Along the east track – to the coast of the Asian continent and then on to the Japanese islands; to the south-west to Hindustan and on to the island of Sri Lanka; to the south-east to the Philippines, Borneo, New Guinea and north-east Australia. Later the Stemonaceae dispersed from East Asia by long-distance transport via the Bering Land Bridge to the New World and reached eastern North America.

6. The family Pandanaceae probably diverged from the other Pandanales in West Africa. Later the representatives of the family vicariously dispersed eastwards into south-east Asia, northern Australia and New Zealand. Representatives of *Pandanus*, the largest genus in Pandanales, supposedly repopulated Africa (from south-east Asia) by long-distance transport.

7. Cyclanthaceae probably originated in south-west Gondwana (in northern South America or in Central America). The distribution of the representatives of the family most likely took place in South America vicariously: southwards to the tropical border of Brazil and south-westwards to northern Argentina.

In order to verify and clarify proposed scenario of Pandanales dispersal history the detailed comparative-morphological analysis (including studies of the carpological characters – the most conservative and, hence, informative in phylogenetic reconstructions) should be carried out. Furthermore, a detailed palaeobotanical data is needed that could verify the direction of dispersal tracks and the region of the hypothetical origin especially of the basal family Velloziaceae. ■

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APPENDICES

Table A.1. Access codes for sequences used in present investigation in the gene bank database (GenBank).

Species	18S	atpA	matK	matR
Cyclanthaceae				
Asplundia rigida (Aubl.) Harling	KF264477.1	KF258578.1	–	KF258199.1
Carludovica palmata Ruiz & Pav.	AF293756.1	KF258586.1	AB088793.1	KF258204.1
Chorigyne cylindrica R. Erikss.	–	MT054857.1	MT046143.1	MT054502.1
Cyclanthus bipartitus Poit. ex A. Rich.	AF168837.1	KF258587.1	KT205206.1	MT054505.1
Dicranopygium atrovirens (H. Wendl.) Harling	KF264481.1	KF258588.1	–	KF258203.1
Schultesiophytum chorianthum Harling	–	MT054861.1	MT046149.1	MT054506.1
Sphaeradenia woodsonii Harling	–	MT054868.1	MT046150.1	MT054513.1
Stelestylis surinamensis Harling	–	MT054867.1	MT046151.1	MT054512.1
Dianthoveus cremnophilus Hammel & G. J. Wilder		MT054864.1	MT046144.1	MT054509.1
Ludovia lancifolia Brongn.	KF264482.1	KF258589.1	MT046146.1	KF258202.1
Thoracocarpus bissectus (Vell.) Harling	–	MT054865.1	MT046152.1	MT054510.1
Pandanaceae				
Benstonea copelandii (Merr.) Callm. & Buerki	–	MT054880.1	–	MT054525.1
Freycinetia philippinensis Hemsl.	KF298381.1	KF298288.1	–	KF298294.1
Freycinetia cumingiana Gaudich.	KF298366.1	KF298287.1	–	KF298293.1
Martellidendron hornei (Balf. f.) Callm. & Chassot	–	MT054878.1	MT046147.1	MT054523.1
Pandanus furcatus Roxb.	KF298358.1	KF298307.1	KR531333.1	KF298321.1
Pandanus baptistii Misonne	KF298360.1	KF298305.1		KF298319.1
Pandanus stenophyllus Kurz ex Miq.	KF298353.1	KF298313.1	–	KF298327.1
Sararanga sinuosa Hemsl.	–	MT054881.1	KT204605.1	MT054526.1
Triuridaceae				
Kihansia sp. Sainge 1620	KF197095.1	KF197072.1	–	KF197113.1
Kupea martinetugei Cheek & S. A. Williams	KF197093.1	KF298372.1	–	KF197110.1
Triuris hexophthalma Maas	KF264487.1	KF258585.1	–	KF258197.1
Triuris hyalina Miers	KF264488.1	KF258581.1	–	
Sciaphila picta Miers	KF197084.1	–	–	KF197106.1
Sciaphila tenella Blume	KF264484.1	–	–	KF258194.1
Seychellaria africana Vollesen	KF264485.1	KF258584.1	–	KF258195.1
Seychellaria madagascariensis C. H. Wright	KF264486.1	–	–	KF258196.1
Lacandonia schismatica E. Martínez & Ramos	–	AY299794.1	–	–
Stemonaceae				
Croomia japonica Miq.	AF309408.1	MT054875.1	KT204663.1	MT054520.1
Croomia pauciflora (Nutt.) Torr.	AF168835.1	AF197708.1	KP083061.1	AF197735.1
Pentastemona sumatrana Steenis	KF264490.1	MT054873.1	KT205057.1	MT054518.1
Stemona tuberosa Lour.	AB429262.1	MT054874.1	KT204764.1	MT054519.1

Stichoneuron caudatum Ridl.	AF168875.1	KT204947.1	KT205006.1	MT054521.1
Velloziaceae				
Talbotia elegans Balf.	KF197080.1	KF197075.1	MT046154.1	MT054515.1
Barbacenia involucrata L. B. Sm.	–	MT054869.1	MT046141.1	MT054514.1
Xerophyta retinervis Baker	–	MT054871.1	KT204806.1	MT054516.1
Barbaceniopsis castillonii (Hauman) Ibisch	–	MT054872.1	MT046142.1	MT054517.1
Dioscoreaceae (outgroup)				
Dioscorea membranacea Pierre ex Prain & Burkill	–	MT054854.1	AY957598.1	MT054499.1
Dioscorea rockii Prain & Burkill	DQ786090.1	EU421029.1	AY972488.1	KF264495.1
Dioscorea elephantipes (L'Hér.) Engl.	FJ215767.1	FJ215777.1	KR086958.1	KY554897.1
Dioscorea tokoro Makino ex Miyabe	DQ786088.1	FJ215776.1	HQ637586.1	KY554895.1
Dioscorea sylvatica Eckl.	FJ215768.1	FJ215778.1	KR086976.1	KY554898.1
Dioscorea communis (L.) Caddick & Wilkin	EU186223.1	AY277804.1	HM850486.1	KF298370.1

Table A.2. Access codes for sequences used in present investigation in the gene bank database (GenBank)

Species	5.8s rib. RNA	AtpB	tRNA-Leu (trnL)
Talbotia elegans Balf.	JN016957.1	JN017009.1	JN016905.1
Vellozia glauca Pohl	JN016972.1	JN017024.1	JN016920.1
Barbacenia markgrafii Schulze-Menz	JN016942.1	JN016994.1	JN016890.1
Xerophyta equisetoides Baker	JN016986.1	JN017038.1	JN016934.1
Barbaceniopsis castillonii (Hauman) Ibisch	JN016945.1	JN016997.1	JN016893.1
Acanthochlamys bracteata P. C. Kao	JN016937.1	JN016989.1	JN016885.1
Pleurostima longiscapa (Goethart & Henrard) N. L. Menezes	JN016953.1	JN017005.1	JN016901.1
Nanuza plicata (Mart.) L. B. Sm. & Ayensu	JN016951.1	JN017003.1	JN016899.1
Burlemarxia pungens N. L. Menezes & Semir	JN016947.1	JN016999.1	JN016895.1
Stemona tuberosa Lour.	KF298348.1	JQ733661.1	JQ733892.1