IMPLICATIONS OF *RBCL* PHYLOGENY FOR HISTORICAL BIOGEOGRAPHY OF GENUS *MERCURIALIS* L.: ESTIMATING AGE AND CENTER OF ORIGIN

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Abstract - The aim of this study was to address questions concerning the historical biogeography of the genus *Mercurialis* in the subfamily Acalyphoideae. Applying a molecular clock to obtained *rbcL* phylogeny, we estimated the minimal age of divergence of genus *Mercurialis* to ~65-66 Ma, placing it at the Cretaceous/Paleogene boundary. We used ancestral area analysis and dispersal-vicariance analysis to infer the center of origin of the genus. Contrary to previous hypothesis, our results show that *Mercurialis* originated in Indomalaya and migrated westward, while the Mediterranean area was most probably the center of ecological diversification and further speciation. Evolutionary events of vicariance and dispersals were reconstructed in a proposed scenario of divergence of *Mercurialis* within Acalyphoideae.

Key Words: *Mercurialis*, Acalyphoideae, molecular clock, center of origin, ancestral area analysis, dispersal-vicariance analysis, historical biogeography

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INTRODUCTION

The genus *Mercurialis* L. (Euphorbiaceae *s. s.*; Wurdack et al., 2005), with its 10 species, is considered one of the best models for addressing fundamental questions in plant evolution; it is currently used in a wide variety of studies (e.g. Obbard et al., 2006; Cvetković & Jovanović, 2007; Vandepitte et al., 2009). The classification of this genus varies among authors, but most often it has been united with other herbaceous genera (*Leidesia*, *Seidelia*, *Dysopsis*) in the subtribe Mercurialinae of the Acalypheae tribe (Pax, 1914; Webster, 1975, 1994). This view, however, has changed with thorough molecular systematics surveys of the whole family. *Mercurialis* is now recognized as part of the acalyphoid "A2" clade (Wurdack et al., 2005; Tokuoka, 2007; Kabouw et al., 2008), the sole member of the subtribe Mercurialinae, distant to other herbaceous genera.

The distribution pattern differs as well: *Mercurialis* has a disjunct Palearctic distribution, with the majority of the species occupying Europe,

NW Africa and parts of Central Asia, and one species being native to temperate regions of East Asia and Malaysia (Mukerji, 1936; Webster, 1994; Qiu & Gilbert, 2008). Other herbaceous genera are South African, and related genera of the A2 clade are mostly Central African and Madagascan (Webster, 1994). Phylogenetic surveys pointed to perennial *M. leiocarpa* as the most basal species in the genus (Krähenbühl & Küpfer, 1995; Krähenbühl et al., 2002; Obbard et al., 2006). In major acalyphoid lineages, most basal species have African or Indomalayan distribution (Wurdack et al., 2005, Tokuoka & Tobe, 2006); *Mercurialis leiocarpa* is the exception, having Eastern Asian distribution (from Nepal to Japan; Qiu & Gilbert, 2008).

Modern historical biogeography includes a variety of comparative biological methods that investigate spatial aspects of the history of biodiversity (Cox & Moore, 2005; Lomolino et al., 2006). The reconstruction of the history of distributions is based on phylogenetic hypotheses, and includes phylogeny reconstruction, establishing the age of origin (Page & Holmes, 1998), as well as

the center of origin of different lineages (ancestral area; Bremer, 1992). To the best of our knowledge, there have been no attempts so far to determine the age of origin of the genus *Mercurialis*, although the age of the family Euphorbiaceae has been estimated (Davis et al., 2005). On the other hand, hypotheses concerning the origin of the disjunct distribution of the genus were proposed previously (e.g. Mukerji, 1936), but these need to be checked against modern phylogenetic reconstructions. Mukerji (1936) proposed the western Mediterranean area as the center of origin of the genus, as this is the area with the greatest number of native species. According to this scenario, the genus migrated eastward to Asia and the apparent disjunct distribution is due to the incomplete records of Central Asian flora.

Krähenbühl et al. (2002) proposed vicariance as an explanation to the current cytogeographical pattern in the genus *Mercurialis*. They considered the east Asiatic species *M. leiocarpa* and SE European *M. ovata* as vicariants derived from an ancestral diploid (2n=16) species. It should be mentioned, however, that this and other genetic surveys (Krähenbühl & Küpfer, 1995; Obbard et al., 2006) did not take into account the geographic distribution of presumably related genera.

As a phylogenetic framework is crucial for biogeographical analysis (Muellner et al., 2008), gene sequences that show fine resolution for studied taxa are used for reconstructing phylogeny. In this respect, the plastid gene *rbcL* was shown to provide sufficient phylogenetic information for Euphorbiaceae (Wurdack et al., 2005; Tokuoka, 2007).

The aims of this study were: i) to estimate the age of the genus *Mercurialis* by molecular clock on *rbcL* cladogram; ii) to identify the center of origin of the genus with an area-based biogeographical and event-based approach; iii) to clarify the biogeographical background and propose a scenario of dispersal/vicariance events that lead to the divergence of the genus *Mercurialis* within subfamily Acalyphoideae.

MATERIALS AND METHODS

A phylogenetic survey of *Mercurialis leiocarpa* and 10 additional species chosen to represent basal lineages in the most basal clades of subfamily Acalyphoideae *s.s.* (ALCH – Alchorneoids, A1, A2, A3; Wurdack et al., 2005; Tokuoka & Tobe, 2006), was conducted using the gene *rbcL*. Sequence data was downloaded from GenBank (http://www.ncbi.nlm.nih.gov/Genbank/); a list of species with GenBank accession numbers is given in Table 1.

Phylogenetic analyses were conducted in MEGA4 (Tamura et al., 2007). The evolutionary history was inferred using the Minimum Evolution method (Rzhetsky & Nei, 1992). The bootstrap consensus tree inferred from 1000 replicates is taken to represent the evolutionary history of the taxa analyzed (Felsenstein, 1985). The evolutionary distances were computed using the Maximum Composite Likelihood method (Tamura et al., 2004) and are in the units of the number of base substitutions per site. The ME tree was searched using the Close-Neighbor-Interchange (CNI) algorithm (Nei & Kumar, 2000) at a search level of 3. The neighbor-joining algorithm (Saitou & Nei, 1987) was used to generate the initial tree. All positions containing gaps and missing data were eliminated from the dataset (Complete deletion option). There were a total of 1320 positions in the final dataset. The branching pattern within the tribe on the bootstrap consensus tree was compared to previous tree topologies (Wurdack et al., 2005; Tokuoka & Tobe, 2006).

A molecular clock was calculated to establish the age of origin of the genus *Mercurialis*. The molecular clock was calibrated on a linearized cladogram assuming equal evolutionary rates in all lineages (Takezaki et al., 2004). The basal divergence time was set to 85 Ma, according to Davis et al. (2005). This age was plotted against historical geographical background to infer the center of origin of genus.

Table 1. List of species of Acalyphoideae *s.s.* used in this study, with their classification, distribution and GenBank accession numbers. Classification and distribution is given according to Webster (1994), while clades are given according to Wurdack et al. (2005).

Species	(Sub)tribe/clade	Distribution	GenBank AN
Pseudagrostistachys ugandensis	Agrostistachydeae/ ALCH	West Africa, East Africa	AY794966
Cyttaranthus congolensis	Agrostistachydeae/ ALCH	West Africa	AY794965
Mareyopsis longifolia	Claoxylinae/ ALCH	West Africa	AY794961
Blumeodendron tokbrai	Blumeodendrinae/ A1	Indomalaya	AJ418805
Spathiostemon javensis	Lasiococcinae/ A3	Indomalaya	AY788176
Homonoia riparia	Lasiococcinae/ A3	East Asia, Indomalaya	AY794978
Mareya micrantha	Claoxylinae/ A3	West Africa	AB267924
Crotonogynopsis usambarica	Adelieae/ A3	West Africa, East Africa	AY794972
Mercurialis leiocarpa	Mercurialinae/ A2	East Asia, Indomalaya, Europe-Mediterranean	AB233867
Erythrococca anomala	Claoxylinae/ A2	West Africa, East Africa	AB267918
Discoclaoxylon hexandrum	Claoxylinae/ A2	West Africa	AY794945

The centers of origin for all clades within the cladogram were inferred with an area-based biogeographical approach (ancestral area analysis; Bremer, 1992) and an event-based approach (dispersal-vicariance analysis, performed in DIVA; Ronquist, 1996).

Dispersal-vicariance analysis (Ronquist, 1997) is currently the most popular and the most widely-used method for the reconstruction of evolutionary events in historical biogeography, though it is not flawless. We took into account possible shortcomings and recommendations on how to

avoid them (Kodandaramaiah, 2010) by including an outgroup, by not constraining the number of maximum ancestral areas, and by consideration of the distances between the areas and the probabilities of dispersals among them.

RESULTS AND DISCUSSION

The reconstructed phylogeny of taxa chosen to represent the basal lineages of the subfamily Acalyphoideae *s.s.* is shown in Fig. 1. The topology of the obtained bootstrap consensus tree slightly differs from previously published cladograms

(Wurdack et al., 2005; Tokuoka & Tobe, 2006; Tokuoka, 2007) in showing the A3 clade to be paraphyletic, although with a little bootstrap support for one of subclades (African genera *Crotonogynopsis* and *Mareya*, bootstrap value 44).

Based on the molecular clock, we estimated the minimal age of divergence of the genus *Mercurialis* to ~65-66 Ma (Fig. 1), placing it at the end of Maastrichtian age and the boundary of Cretaceous and Paleogene. At this time the supercontinent Gondwana was well fragmented, with Greater India rapidly drifting towards southern Laurasia (Dèzes, 1999). All Gondwanan continents were still close enough for plants to migrate between them (Schatz, 1996). At the calculated time of divergence of *Mercurialis,* the paleotropical land masses consisted of Africa, Madagascar, Greater India, Australia and Western Malaysia (Schatz, 1996).

The vicariance hypothesis proposed to explain the current cytogeographical pattern (Krähenbühl et al., 2002) implied that the ancestral distribution of the genus corresponded to contemporary distributions of *M. ovata* and *M. leiocarpa*, i.e. temperate regions of Eurasia. Alternatively, the genus may have had western Mediterranean (Mukerji, 1936) or paleotropical origin (concordant with other acalyphoid lineages).

By applying Bremer's (1992) ancestral area analysis to the cladogram of basal acalyphoid species (Figure 1), the center of origin of *Mercurialis* (and the whole clade A2) could not be determined (Table 2). The analysis of optimal distribution for the most recent common ancestor of *Mercurialis* and the rest of A2 genera performed in DIVA (Ronquist, 1996) was also inconclusive (Table 3).

However, detailed dispersal-vicariance analysis in DIVA gave more conclusive output. Analysis of the frequency of vicariance events showed a possible vicariance event between West Africa and the Indomalaya/East Asia area (observed frequency 0.667). The last time these land masses were close enough was the time of the Madagascar-Great India

Table 2. Estimation of the centers of origin using ancestral area analysis (Bremer, 1992); most probable ancestral areas are underlined. G – number of necessary gains under forward Camin–Sokal parsimony; L – number of necessary losses under reverse Camin–Sokal parsimony; AA – ancestral area probability (G/L – quotients rescaled to a maximum value of 1); A1, A2, A3 – clades of Acalyphoideae *s. s.* defined by Wurdack et al., 2005.

Clade	Area	G	L	G/L	AA
Acalyphoideae *s. s.*					
	W Africa	3	3	1.00	1.00
	E Africa	3	6	0.50	0.50
	Indomalaya	3	3	1.00	1.00
	E Asia	2	5	0.40	0.40
A1+A2+A3					
	W Africa	2	3	0.67	0.44
	E Africa	2	5	0.40	0.27
	Indomalaya	3	2	1.50	1.00
	E Asia	2	4	0.50	0.33
A2+A3					
	W Africa	2	2	1.00	1.00
	E Africa	2	4	0.50	0.50
	Indomalaya	2	2	1.00	1.00
	E Asia	2	3	0.67	0.67
A2					
	W Africa	1	1	1.00	1.00
	E Africa	1	2	0.50	0.50
	Indomalaya	1	1	1.00	1.00
	E Asia	1	1	1.00	1.00

separation – about 90-85 Ma (Schatz 1996). This vicariance event could have produced two lineages of Acalyphoideae *s.s.*: Alchorneoids (ALCH) and clades A1–A3, which is in agreement with the established ancestral areas for these lineages (Table 2, Table 3). In Fig. 1, this vicariance event is shown as a dot on the cladogram. Alchorneoids diversified in Africa,

Table 3. Optimal reconstruction of the centers of origin and observed frequencies of dispersal events between areas (DIVA, Ronquist, 1996); ALCH, A1, A2, A3 – clades of Acalyphoideae *s. s.* defined by Wurdack et al., 2005.

Clade	Alternative optimal centres of origin
Acalyphoideae *s.s.*	W Africa + Indomalaya / W Africa + E Africa + Indomalaya
ALCH	W Africa / W Africa + E Africa
A1+A2+A3	Indomalaya
A2+A3	W Africa / W Africa + Indomalaya / W Africa + Indomalaya + E Asia
A2	W Africa + Indomalaya / W Africa + E Asia / W Africa + Indomalaya + E Asia

Long distance dispersals (from → to)	Frequency, in observed geological time
W Africa → Indomalaya	0.167
Indomalaya → W Africa	1.000

Short distance dispersals (from → to)	Frequency, in observed geological time
W Africa → E Africa	2.500
E Africa → W Africa	0.500
Indomalaya → E Asia	1.333
E Asia → Indomalaya	0.167

and the rest of the subfamily in Indomalaya. Indomalaya was made up of two separate land masses – Greater India and Western Malaysia, which established a direct contact only after India had collided with Laurasia (~45 Ma, Schatz 1996). Therefore, indication of Indomalayan distribution as ancestral one means that the two original land masses are equally probable as the center of diversification of acalyphoid clades A1-A3.

A previous scenario included dispersal events as well – short-distance dispersals (between West and East Africa, and between Indomalaya and East Asia) and long-distance dispersals (between Africa and Indomalaya). The optimal reconstruction

obtained by DIVA required 7 dispersals, two of which were long-distance dispersals (across the prime barrier – ocean). Asymmetric dispersal frequencies are the most conclusive, as they show the direction of dispersals. The most important asymmetric dispersal frequencies observed in DIVA were between West Africa and Indomalaya, and between Indomalaya and East Asia (Table 3). The frequencies were more in favor of Indomalaya being ancestral, so this asymmetry demonstrates that dispersals arose from Indomalaya to other areas. Thus, the Indomalayan region served as the center of dispersal towards East Asia and Africa. Based on the cladogram and optimal ancestral areas (Fig. 1, Table 3) two events of long-distance dispersal could be pointed out: in clade A3 (divergence of the African genera *Mareya* and *Crotonogynopsis*) and in clade A2 (divergence of the African genera from ancestors of *Mercurialis*).

The close connection of Eurasian *Mercurialis* with mostly-African A2 genera may be the result of ancient vicariance between West Africa and Indomalaya, or the divergence of A2 genera after long-distance dispersal towards Africa. Similar dispersals from Indomalaya to Africa have also occurred in the neighboring A1 clade (Kulju et al., 2007). The vicariant scenario therein was rejected for the relative young age of A1 clade.

Our results confirm the dispersal alternative in A2 clade also, but the more exact scenario of A2/*Mercurialis* divergence can only be obtained by a thorough phytogeographical study of African A2 genera accompanied with a careful revision of fossil data. Unraveling the phylogeny of the genus *Claoxylon*, with the species distributed from Madagascar to Hawaii but absent from Africa, could be most informative in this matter.

According to Wilson & Rosen (1998) the most enduring explanation of a high diversity area is that it represents the center of origin. Mukerji (1936) proposed the Western Mediterranean area as the center of origin of *Mercurialis*. However, this scenario is contrasted with the ancestral area analysis and the dispersal scenario we obtained.

Also, recent phylogenetic surveys of the genus have shown that the Mediterranean area is home to derived species of *Mercurialis*, rather than to basal ones (e.g. Krähenbühl et al., 2002). Our results show that the genus *Mercurialis* originated in area of Southeastern or Eastern Asia and migrated westward; the Mediterranean area is most probably the center of ecological diversification and speciation of annual and non-rhizomatous species.

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ИМПЛИКАЦИЈЕ *rbcL* ФИЛОГЕНИЈЕ НА ИСТОРИЈСКУ БИОГЕОГРАФИЈУ РОДА *MERCURIALIS* L.: ПРОЦЕНА СТАРОСТИ И ЦЕНТРА ПОСТАНКА

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Циљ овог рада био је да одговоримо на поједина питања историјске биогеографије рода *Mercurialis* унутар потфамилије Acalyphoideae (Euphorbiaceae). Реконструкција филогеније извршена је на основу података о секвенцама пластидног гена *rbcL*. Методом молекулског сата одређена је старост рода (време дивергенције) на пре око 65–66 милиона година (граница креде и палеогена). Центар порекла рода одређен је аналитичким методама које се заснивају на биогеографском приступу сарееним ареалима и могућим еволуционим догађајима дисерзије и викаријантне специјације. Насупрот претходним хипотезама, наши резултати указују на индомалајско порекло рода *Mercurialis*, одакле је мигрирао ка западу. Област Медитерана, коју карактерише висок биодиверзитет врста овог рода, је врло вероватно центар екоошке дивергенције и касније специјације. Реконструкција сценарија настанка рода *Mercuialis* укључила је и објашњење еволуционих догађаја у ширем контексту, у оквиру најстаријих клада потфамилије Acalyphoideae.