

9 Time Estimates and Historical Biogeography of the Primarily Woody Boraginales⁸

Abstract

Hypotheses on the origin of the current distribution patterns and bicontinental disjunctions of Cordiaceae, Ehretiaceae, and Heliotropiaceae (Primarily Woody Boraginales) are tested by pairwise comparison of KIMURA 2-parameter (K2P) distances. Estimated absolute dates of fossils and geological events (plate tectonics, climate changes) were used for calibration of the molecular clock. A mid Cretaceous origin of the Primarily Woody Boraginales as basal representatives of the asterids is proposed with an early diversification in South America. Plate tectonics seem to play a minor role in the historical biogeography of the Primarily Woody Boraginales. Most disjunctions are best explained by long-distance dispersal based on the abundant occurrence of drupaceous fruits and their potential for endozoochoria. Furthermore, migrations and extinctions appear to have played a considerable role in the formation of current distributions.

9.1 Introduction

Cordiaceae, Ehretiaceae, and Heliotropiaceae are the primarily woody taxa of the Boraginales and comprise a total of approximately 1000 species. These three taxa plus the parasitic Lennoaceae appear to be closely allied on the basis both of molecular (BÖHLE & HILGER 1997, GOTTSCHLING *et al.* 2001, GOTTSCHLING & HILGER in prep.) and of morphological data (DIANE *et al.* 2002b). Centres of species diversity are on the remnants of the Gondwana continent, i.e., South America, Africa, and India (to Australasia). There are few Laurasian taxa (namely in *Ehretia* and *Heliotropium*). Geographical range depends strongly on climatic conditions: The plants grow mainly in a tropical or subtropical climate, only very few species of *Heliotropium* have reached the temperate and Mediterranean regions. Parameters such as minimal temperature and water availability are limiting factors.

Neither the exact systematic placement of the Boraginales in their current circumscription (GOTTSCHLING *et al.* 2001), nor their geological origin have so far been established conclusively.

⁸ Manuscript submitted as GOTTSCHLING M, HH HILGER, N DIANE & M WEIGEND (subm.): Time estimates and historical biogeography of the Primarily Woody Boraginales: Ehretiaceae, Cordiaceae, and Heliotropiaceae. Int J Plant Sci

Own contributions: Collecting plants (partly), molecular calculations, time estimates, writing manuscript, drawings.

In all larger surveys of angiosperm phylogeny (e.g., CHASE *et al.* 1993, ALBACH *et al.* 2001), the taxon Boraginales has an isolated placement with a rather basal position in the Euasterid I clade. WIKSTRÖM *et al.* (2001) dated the origin of Boraginales into the late Cretaceous [77–81 million years ago (MYA)] and the origin of the Euasterid I clade into the mid Cretaceous (approximately 110 MYA).

The phylogenies of the core Ehretiaceae (GOTTSCHLING & HILGER 2001), Cordiaceae (GOTTSCHLING *et al.* in prep. a), and Heliotropiaceae (DIANE *et al.* 2002a) are well-understood, and hypotheses on the historical biogeography have been proposed. In all three taxa several cases of intercontinental disjunctions at various taxonomical levels are documented (Figs. 9-1 to 9-8). Three reasons for such disjunctions are conceivable: movement of continents (plate tectonics), (short-step) migration and extinction, and long-distance dispersal. While until recently historical biogeography has been largely a matter of conjecture, it has now found a powerful tool in the combination of cladistic analyses and molecular clock investigations. Calculating pairwise distances has turned out to be useful in estimating divergence rates (e.g., RENNER *et al.* 2000, MALCOMBER 2002, SOLTIS *et al.* 2002), although molecular clock estimations of separation events should be treated with caution (compare SANDERSON 1998). Under the assumption of constant substitution rates (over the time range under consideration) a rough dating of separation events is possible. The molecular clock is calibrated with previously known and independently derived absolute dates of, e.g., geological events (such as the separation of South America and Africa), climatic change, and fossils, all of which are relevant to this study (Table 7, appendix).

Some aspects of historical biogeography of the Primarily Woody Boraginales have been previously discussed: 1. plate tectonics has been proposed for, e.g., explaining the bicontinental distribution of *Bourreria* (Ehretiaceae, Fig. 9-3, GOTTSCHLING & HILGER 2001); 2. long-distance dispersal for the Old World/New World distribution of the subclades *Sebestena* (Cordiaceae, Fig. 9-5, GOTTSCHLING *et al.* in prep. a) and *Tournefortia* (Heliotropiaceae, Fig. 9-7, DIANE *et al.* 2002a), and for the colonisation of Laurasia by the *Ehretia* II subclade (Ehretiaceae, Fig. 9-1, GOTTSCHLING & HILGER 2001); 3. migration and extinction have been suggested as causal for the Central American–East Asian disjunction of the *Ehretia* II subclade (Ehretiaceae, Fig. 9-1, GOTTSCHLING & HILGER 2001; GOTTSCHLING *et al.* 2002). Putative long-distance dispersal by endozoochory is readily explained by the prevalence of drupaceous (Figs. 1-11 and 1-12, albeit often very large) fruits in the groups here studied.

In this present study, we intend to investigate the historical biogeography of Heliotropiaceae, Cordiaceae, and Ehretiaceae more rigorously by dating internal nodes, while previous studies relied largely on more or less circumstantial evidence. The approximate absolute ages of the diversification events and the relative importance of the different historical processes for the generation of the current distribution patterns are evaluated. We use KIMURA 2-parameter (K2P) distances of sequences of the first Internal Transcribed Spacer (ITS1) to investigate evolutionary rates.

9.2 Materials and Methods

For maximum likelihood trees, 39 species belonging to the Primarily Woody Boraginales have been investigated and are listed in Table 1 (appendix). Outgroup choice is based on detailed phylogenetic studies (GOTTSCHLING & HILGER 2001, DIANE *et al.* 2002a, GOTTSCHLING *et al.* in prep. a). *Rochefortia acanthophora* is used for a user specified outgroup comparison of the *Ehretia/Bourreria* phylogeny, *Varronia bullata* for the remainders of Cordiaceae, and *Tournefortia salzmannii* for the remainder of Heliotropiaceae. DNA extraction, PCR, purification, and sequencing followed standard protocols (GOTTSCHLING & HILGER 2001, DIANE *et al.* 2002a).

The sequences were manually aligned using Se-AL v2.0a72 (RAMBAUT 2001). The complete data matrices are available in NEXUS format on request. Clock and non-clock likelihood analyses (HKY85 model) were performed using PAUP* 4.0b1 (SWOFFORD 1998) for Power Macintosh PC. Heuristic searches were run in PAUP without changes from the default settings (starting trees obtained by neighbor joining). Bootstrap analyses (parsimony with heuristic searches) were also performed using PAUP with 1000 replicates (each with 10 random sequence addition replications) and without further changes from the default settings.

To assess the severity of rate heterogeneity among sequences, likelihood ratio tests (LRT; FELSENSTEIN 1981, SANDERSON 1998) were calculated, which compared the likelihoods of clock and non-clock versions of trees obtained under the same model. The significance of this value is judged by comparing it to a χ^2 distribution with n degrees of freedom (df), where n is the number of taxa used in an analysis minus 2.

K2P distances were obtained from pairwise distances also implemented in PAUP and are available on request. Calibration of the molecular clock by geological events and fossils follows the instructions given by RENNER *et al.* (2000), absolute dates used are given in Table 7 (appendix). Standard deviation (SD) were computed with $SD(p) = [p*(1-p)/N]^{1/2}$, where p is the proportion of nucleotides substituted (i.e., K2P distances) and N the total number of nucleotides in the alignment.

Wherever possible, the dating of the phylogenies was undertaken on the basis of fossils. Fossil leaves from the Cordiaceae that can be associated with the *Myxa* subclade were reported from the Asian Eocene (CHELEBAJEVA 1984), but there are no clear apomorphies with the *Myxa* subclade. Fossil pollen of Heliotropiaceae was described from the Central American Oligocene (GRAHAM & JARZEN 1969). If this really is Heliotropiaceae pollen (and homoplasy is generally high in pollen shape), then it has to be associated with the *Tournefortia* subclade, the only group with this specific (clavate) pollen type. The only fossils, which can be clearly placed and dated, are from the *Ehretia* II subclade of Ehretiaceae (GOTTSCHLING *et al.* 2002). The oldest of these fossil endocarps (fruit remnants) were described from the European Eocene (London Clay flora; CHANDLER 1961, 1964). The divergence rate calculated from these *Ehretia* fossils were also used in time estimates of Cordiaceae and Heliotropiaceae.

9.3 Results

Likelihood analyses under both clock and non-clock assumption of Ehretiaceae, Cordiaceae, and Heliotropiaceae yielded single optimal trees with identical topologies (Figs. 9-9 to 9-11). The likelihoods of the trees and the LRTs are given in Table 8 (appendix). Calculated divergence rates per million year (MY) vary between $7.82*10^{-4}$ and $22.04*10^{-4}$ (Tables 9 to 11, appendix).

Ehretiaceae: *Ehretia* and *Bourreria* constitute the core Ehretiaceae and are monophyletic sistergroups (Fig. 9-9). *Ehretia* comprises two subclades, *Ehretia* I and *Ehretia* II. The New World species group of the *Ehretia* II subclade is paraphyletic, and the subclade shows a

Laurasian distribution with a Central American/East Asian disjunction (Fig. 9-1). Sequence divergence is low in the *Ehretia* I subclade (not shown) distributed in Africa, Asia, and Australia (Fig. 9-2). *Bourreria* falls into two monophyletic sister groups, a New World clade and an Old World clade (Fig. 9-3). For Ehretiaceae we investigated four alternative calibrations (Fig. 9-9, Table 9, appendix).

Cordiaceae: Cordiaceae comprise of four major subclades, of which *Varronia* and *Collococcus* are indigenous to the New World exclusively (Figs. 9-4, 9-10), while in the subclades *Sebestena* (Fig. 9-5) and *Myxa* additionally Old World representatives are found. Within Cordiaceae the New World species groups are paraphyletic, while Old World species groups are monophyletic. For Cordiaceae we explored five alternative calibrations (Fig. 9-10, Table 10, appendix).

Heliotropiaceae: Heliotropiaceae comprise of six major subclades (Fig. 9-11), three of which have a New World distribution exclusively (Fig. 9-6): *Cyphocyema*, *Heliothamnus*, and *Heliotropium* II. As in Cordiaceae, New World taxa are paraphyletic within Heliotropiaceae, while Old World species groups represent three subclades: *Orthostachys* (Fig. 9-8), *Heliotropium* I (Fig. 9-6), and *Tournefortia* (Fig. 9-7). We explored five alternative calibrations on Heliotropiaceae (Fig. 9-11, Table 11, appendix).

9.4 Discussion

Likelihood trees and divergence rates. The topologies of the likelihood analyses agree with the phylogenies developed in previous studies (GOTTSCHLING & HILGER 2001, DIANE *et al.* 2002a, GOTTSCHLING *et al.* in prep. a). The nodes investigated are mostly well-supported both by molecular and/or by morphological data (Table 12, appendix). The results of the LRTs (Table 8, appendix) justify the use of ITS1 sequence divergence in the ingroup to estimate absolute divergence rates from branch lengths.

We found very few published divergence rates based on fossils or geological events for the First Internal Transcribed Spacer (ITS1). Ignoring implausible scenarios (see below) we obtain divergence rates between 14.08×10^{-4} and 21.16×10^{-4} per MY, which is in the range of the data published for other taxa [highest: 53×10^{-4} per MY for *Gossypium* (Malvaceae, WENDEL *et al.* 1995); lowest: 3.5×10^{-4} per MY for Winteraceae (SUH *et al.* 1993)].

Reliability of the fossils. Using fossils for the calibration of the molecular clock implies two major problems: correct systematic placement and absolute dating. The *Ehretia* fossils from the London Clay (CHANDLER 1961, 1964) can be unequivocally associated with the *Ehretia* II subclade (Ehretiaceae, GOTTSCHLING *et al.* 2002). These fossils are very similar to the endocarps of extant East Asian *Ehretia acuminata* (REID 1923) and show crucial apomorphies (GOTTSCHLING *et al.* 2002, GOTTSCHLING & HILGER *et al.* 2002). The fossils of the London Clay

flora have been dated within a rather narrow time frame into the early Eocene (49 to 52 MYA, COLLINSON 1983).

In contrast, the fossils described from Cordiaceae and Heliotropiaceae are rather ambiguous and should be used with caution. Although the fossil leaves associated with *Cordia* (CHELEBAJEVA 1984) are very similar to those of extant representatives of the *Myxa* subclade (e.g., *C. monoica*, *C. myxa*), they do not share any apomorphies with the latter. Furthermore, there is no information about the associated flora in the fossil record. The problems arising with the *Cordia* fossils do not concern the dating of the fossils (Eocene) and our time estimates (Table 10: line 3, appendix) but implies a dramatic range extension of *Cordia* far from its current stenotropic distribution.

The pollen from Heliotropiaceae associated with the *Tournefortia* subclade (GRAHAM & JARZEN 1969) share characters not found elsewhere in the Boraginales, but clavate pollen is abundant in many unrelated plant groups. A systematic placement within Heliotropiaceae should be treated with some reservation, while no other fossils from the same time are available. The main problem arising with the calibration with these fossils are the high values for our time estimates (Table 11: line 2, appendix), but especially in Heliotropiaceae the assumption of a constant molecular clock may be doubted because of widely different life histories from annuals to trees with dramatically different generation times [generation-time effect in, e.g., *Sidalcea* (Malvaceae, ANDREASEN & BALDWIN 2001)].

Plausibility of time estimates. Different calibrations yield widely different age estimates. Some estimates can be clearly disregarded, e.g., those that yield ages distinctly younger than the oldest known fossils are obviously incorrect. Using, e.g., the value computed for the Boraginales by WIKSTRÖM *et al.* (2001) as minimum age for the *Ehretia/Bourreria* phylogeny leads to an estimation for the *Ehretia* II subclade (Ehretiaceae, Table 9: line 4, appendix) that is younger than the geological age of the London Clay flora. On the other hand, we must consider the earliest known angiosperms that are dated almost to the Jurassic/Cretaceous boundary (BRENNER 1996, SUN *et al.* 1998). The Boraginales as representatives of the basal asterids (e.g., CHASE *et al.* 1993, ALBACH *et al.* 2001) cannot have diversified before the mid Cretaceous. Calibrating the separation of the bicontinental *Myxa* subclade (Cordiaceae) by plate tectonics thus implies a Late Jurassic origin of the ingroup (Table 10: line 1, appendix), which is implausible.

Our time estimates are relatively high as compared to other studies, which investigated mostly temperate plants (e.g., SUH *et al.* 1993: Winteraceae, XIANG *et al.* 2000: representatives of, e.g., Bignoniaceae, Berberidaceae, Cornaceae, RENNER *et al.* 2000: Atherospermataceae). In contrast, studies on tropical, woody plant groups are scarce [e.g., RENNER & MEYER 2001: Melastomataceae, MALCOMBER 2002: *Gaertnera* (Rubiaceae)]. Our estimated geological ages are higher than those proposed by WIKSTRÖM *et al.* (2001). But, *Ehretia* (with unambiguous fossils) was not included in their molecular taxon sampling (only the herbaceous Boraginales

Borago and *Hydrophyllum*), which may be causal for the differences between their and our time estimation.

Plate tectonics. Plate tectonics seem to have played a minor role for the current distribution of the Primarily Woody Boraginales. Although our time estimates indicate a relatively high age for all three groups, the values are too low for plate tectonics to have had a major impact on even the lowest nodes. Our initial assumption that the bicontinental distribution of *Bourreria* is due to plate tectonics (GOTTSCHLING & HILGER 2001) can now be rejected (see below).

The time estimate for Heliotropiaceae calibrated to 30 MY with the *Tournefortia* pollen suggests two disjunct taxa old enough to be separated by plate tectonics (Figs. 9-6 to 9-8, Table 11: line 2, appendix): the *Orthostachys* subclade and *Heliotropium s.str.* However, this estimate pushes the age of the ingroup (node A) back to the late Jurassic, which is, again, implausible. Using the divergence rate from the Ehretiaceae in calculating ages for the Heliotropiaceae indicates an early Tertiary origin for both, the *Orthostachys* subclade and *Heliotropium s.str.*, and a mid Cretaceous origin of the ingroup. The alternative time estimates thus strongly suggest that it is much more likely that the fossil *Tournefortia* pollen has been incorrectly determined than that the Heliotropiaceae were already highly diversified in the Cretaceous.

Long-distance dispersal. Most taxa in Ehretiaceae, Cordiaceae, but fewer in Heliotropiaceae have drupes dispersed by animals such as birds and small mammals (endozoochory), which is likely the main mechanism for long-distance dispersal in the Primarily Woody Boraginales. Also, corky endocarps (found in Cordiaceae) or air filled sterile chambers in the fruits (found in Heliotropiaceae: FÖRTHNER 1998, DIANE *et al.* 2002a) improve the chances for hydrochory, especially in coastal species (found in all three groups). Detailed observations on seed dispersal are lacking for the Primarily Woody Boraginales or are based on mere circumstantial evidence (e.g., RIDLEY 1930, SNOW 1981, SCOTT & MARTIN 1984). Regular long-distance dispersal is evidently not observed (narrow endemism and clear geographical ranges in many taxa), but sporadic long-distance dispersal is plausible, especially when the long time spans available are considered.

Ehretia (Ehretiaceae) falls into two monophyletic groups: a Gondwanan subclade *Ehretia* I and a primarily Laurasian subclade *Ehretia* II (GOTTSCHLING & HILGER 2001). Our time estimates calibrated with the *Ehretia* fossils (Table 9: line 3, appendix) suggest that *Ehretia* as such is younger (91 MY) than the opening of the Tethys, and that the *Ehretia* II subclade is younger (50 MY) than the opening of the North Atlantic. The assumption of the *Ehretia* II subclade as Laurasian genoelement (Fig. 9-1) is well-supported by: 1. the monophyly of the clade based both on molecular and on morphological data (GOTTSCHLING & HILGER 2001); 2. the presence of fossils from the European Tertiary (CHANDLER 1964, GOTTSCHLING *et al.* 2002); 3. the absence from South America (the main centre of diversity of the Primarily Woody Boraginales). This argues for a single colonisation event of the Laurasian region by long-distance dispersal

(probably endozoochoria) in the early Tertiary. It is more likely that the *Ehretia* II subclade originated in North America rather than in Europe since the New World species group is paraphyletic and appear to represent the ancestral species complex (Fig. 9-9). Whether temporary Paleocene land bridges or at least ‘stepping stones’ between North and South America were involved (e.g., RAVEN & AXELROD 1974, PITMAN *et al.* 1993) remains unclear. Centres of diversity of the *Ehretia* I subclade are in Sub-Saharan Africa, India, and Eastern Asia (Fig. 9-2). Calibration with the *Ehretia* fossils yields an age of 36 MY for this clade, much too young for any separation event by plate tectonics. Therefore, migration (probably combined with long-distance dispersal) is likely in agreement with the climatic history of Africa, Asia, and Australia (RAVEN & AXELROD 1974).

The bicontinental disjunction of *Bourreria* (Ehretiaceae, Figs. 9-3, 9-9) has been interpreted as a Gondwana distribution separated by the split of South America and Africa (GOTTSCHLING & HILGER 2001). The current distribution could then be explained by the very narrow ecological requirements of these plants that lead to extinction in larger parts of South America and in Western Africa due to the Tertiary climatic history (e.g., RAVEN & AXELROD 1974). The time estimates provided by this study reject this view (Table 9: lines 1, 3, appendix): Calibration with the *Ehretia* fossils yields 40 MY for *Bourreria* (including New World and Old World species), and thus long-distance dispersal renders the best explanation for the bicontinental distribution.

Cordiaceae falls into four major clades (Figs. 9-4 and 9-5, 9-10), two of which are restricted to the New World (the *Collococcus* subclade and *Varronia*), while the *Myxa* subclade comprises two monophyletic assemblages, a New World clade and an Old World clade. Our time estimates (Table 10: lines 3 to 5, appendix) rule out plate tectonics as cause for this disjunction: Plausible values indicate an age near the Cretaceous/Tertiary boundary or lower for the *Myxa* subclade, and thus imply that long-distance dispersal has taken place. Old World *Cordia subcordata* (East Africa, Australasia), a typical coastal plant of the *Sebestena* subclade, is nested in a paraphyletic New World (Caribbean) clade (GOTTSCHLING *et al.* in prep. a). Our data suggest a Neogene origin of these plants (calibrated with the leaf fossils of the *Myxa* subclade and with the divergence rate of the Ehretiaceae, Table 9: lines 3, 5, appendix), indicating, again, long-distance dispersal as an explanation of the disjunction. As suggested by JOHNSTON (1951) the floating fruits with a corky endocarp (found in species such as *C. subcordata*) probably facilitated dispersal by ocean currents (hydrochoria). Equatorial currents from tropical Western America westwards through Melanesia to Southern India and Africa were probably responsible for this dispersal, since representatives of the *Sebestena* subclade are absent from West Africa (compare a similar mechanism proposed for *Cycas*: DEHGAN & YUEN 1983).

In Heliotropiaceae the Old World/New World disjunctions in *Heliotropium s.str.* (Fig. 9-6) and the *Orthostachys* subclade (Fig. 9-8) are also likely to go back to long-distance dispersal, since plate tectonics is an implausible explanation. The paraphyletic New World and the few monophyletic Old World species of the *Tournefortia* subclade (DIANE *et al.* 2002a) are

morphologically little diversified. We therefore assume a low geological age of this group and recent long-distance dispersal from the New World westwards to the Old World (Fig. 9-7), which is in agreement with our time estimate (Table 11: line 4, appendix). Probable time estimates indicate a Tertiary (Oligocene or Miocene) age of the *Tournefortia* subclade as has also been hypothesised for the bicontinental disjunction of the *Sebestena* subclade (Cordiaceae, with a similar distribution pattern). The occurrence of a few *Heliotropium s.str.* species in Australia (Fig. 9-6) is also best explained by long-distance dispersal (possibly by the Westwind Drift in the Indian Ocean).

The representatives of the *Orthostachys* subclade (Heliotropiaceae) grow in the Americas (most species in South America, paraphyletic group), Africa, India, and Australia (Fig. 9-8). Probable time estimates (Table 11: lines 4 and 5, appendix) indicate an origin of this clade in the early Tertiary. Since the numerous species in Australia (monophyletic group) seem to be nested in the Old World species group (unpubl. data) a migration route from South America to Australia *via* Antarctica can be rejected in this case. Dispersal from the New World was initially to Africa, with a subsequent migration to Australia, where a massive recent radiation and diversification has taken place (CRAVEN 1996).

Ancient tropical land bridges (migrations and extinctions). Several ancient land bridges have been proposed as migration routes for plants between continents such as 1. the ‘Thulean bridge’ (‘Atlantic track’) connecting North America and Europe in the Eocene (e.g., GRAY 1878, WOLFE 1981, TIFFNEY 1985a, b, MAI 1995); 2. ‘Beringia’ (‘Pacific track’) connecting Asia and North America in the Eocene and later (e.g., RAVEN & AXELROD 1974, TIFFNEY 1985a); 3. a connection between Australia and South America *via* Antarctica (e.g., THORNE 1972, TAKHTAJAN 1986) probably until the Oligocene (RAVEN & AXELROD 1974, PITMAN *et al.* 1993). Especially the ‘Thulean bridge’ has been made responsible for migrations of temperate plant groups, but also for migrations of tropical plant groups including taxa, which currently have an apparent Gondwana distribution (i.e., subsequently went extinct in the northern hemisphere: DAVIS *et al.* 2002). Although this explanation cannot be ruled out for the core Ehretiaceae (*Bourreria*, *Ehretia* I subclade), Cordiaceae (*Myxa* subclade), and Heliotropiaceae (*Orthostachys* subclade, *Heliotropium s.str.*), there is neither unambiguous evidence from fossils nor are there any relic endemics in Laurasia (which could indicate a formerly more widespread distribution). Any discussion of a role of land bridges explaining current disjunctions remains conjecture in the Primarily Woody Boraginales.

The bicontinental disjunction of the *Ehretia* II subclade (Central America and East Asia, Fig. 9-1) is the only case with possible evidence for such a migration *via* the Atlantic track. MAI (1995) lists several tropical taxa with similar current distributions and fossils from the European Tertiary. Dating the *Ehretia* II subclade by fossils (50 MY) suggests its diversification in the early Tertiary. The separation of one lineage of the (paraphyletic) New World and the Old World species groups is consequently based both on the separation of North America and Eurasia (plate

tectonics) and on the climate history in Europe during the Tertiary as suggested in GOTTSCHLING & HILGER (2001). This separation event is dated into the mid Tertiary by our time estimates (about 38 MY for node F in Table 9: line 3, appendix), a time much older than assumed for other disjunct, mostly temperate Laurasian taxa (e.g., XIANG *et al.* 2000). Nevertheless, this value corresponds very well to the geological dating of the breakdown of the coherent tropical vegetation belt proposed by TIFFNEY (1985a). Since the European fossils are very similar to extant Asian and Australian *Ehretia acuminata*, they have been associated with the Old World species group of the *Ehretia* II subclade (REID 1923, GOTTSCHLING *et al.* 2002). However, our estimates suggest an age of the Old World species group younger than the fossils from the Eocene indicating a relationship of these fossils rather with the New World species group.

Conclusion. We cannot say how many Boraginales became extinct at the Cretaceous/Tertiary boundary, but based on the historical biogeography provided by this study, we can assume not only one lineage of the Primarily Woody Boraginales surviving this large extinction. In the contrary, we are able to reconstruct 1. from the Ehretiaceae (Fig. 9-9, Table 9: lines 2 and 3, appendix): *Ehretia* (about 80 MY) and its sistergroup (*Bourreria*, no support by our time estimates) must have been in existence as well as the sistergroup of both *Ehretia* and *Bourreria* (here represented by *Rochefortia*); 2. from the Cordiaceae (Fig. 9-10, Table 10: lines 3 to 5, appendix): *Cordia* (about 80 MY), and its sistergroup (*Varronia*) must have been in existence consequently; 3. from the Heliotropiaceae (Fig. 9-11, Table 11: line 4, appendix): one lineage comprising *Heliotropium s.str.* and the *Orthostachys* subclade (about 100 MY), and its sistergroup (*Cyphocyema* subclade) must have been in existence. Our data suggest at least seven lineages of Primarily Woody Boraginales survived the Cretaceous/Tertiary boundary. We want to contrast the mass extinction with a large-scale survival, at least of the Boraginales as basal representatives of the asterids (thus indicating the K/T boundary not as dramatic for plants as for animals).

Our time estimates suggest a mid Cretaceous origin of Ehretiaceae, Cordiaceae, and Heliotropiaceae. Based on the high diversity and paraphyly of New World species group we assume a South America origin of the Primarily Woody Boraginales. While plate tectonics seem to have played a minor role (separation of the *Ehretia* II subclade by the split of North America and Eurasia) for the plants under investigation, cases of migration and extinction based on climatic change (*Ehretia* II) and especially long-distance dispersal (e.g., *Sebestena* subclade of Cordiaceae, *Tournefortia* subclade of Heliotropiaceae), probably at early stages of the separation of the continents (*Myxa* subclade of Cordiaceae, *Orthostachys* subclade of Heliotropiaceae, *Heliotropium s.str.*) can be proposed. Hypotheses on distribution patterns and disjunctions cannot be explained monocausally by plate tectonics, migration and extinction, or long-distance dispersal. On the contrary, we have to investigate their relative frequencies and to analyse each single case carefully. Typically, historical biogeography may have components of all three mechanisms.