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Chapter 7

Historical Biogeography of *Ficus* subsection *Urostigma* (Moraceae): Palaeotropical Intercontinental Disjunctions revisited

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Abstract

Aim: The historical biogeography of *Ficus* subsect. *Urostigma* is analysed with the aid of a dated phylogeny to investigate the spatio-temporal diversification patterns in Asia and to see which hypotheses could best explain the various Palaeotropical Intercontinental Disjunctions (PIDs).

Location: Tropics and subtropics worldwide with an emphasis on Africa, Madagascar and Asia up to Australia.

Methods: Estimates of divergence times of subsect. *Urostigma* were obtained using a Baysian relaxed clock analysis via the program BEAST using three calibration points. The output of beast was used to analyse the historical biogeographic patterns via the program rasp (S-DIVA option). The results were compared with existing geological knowledge.

Results: The taxon probably originated in Madagascar or Madagascar and India, and dispersed once (or twice) to Africa and once to Asia. From Asia dispersal finally covered Southeast Asia mainland, Malesia, Australia, Micronesia and the island chains in the West Pacific. Wallace's Line throught central Malesia was only crossed by widespread species, of which few sister species are endemic east of Wallace's Line. One (ancestral) species dispersed back from Asia to Africa.

Main conclusions: The combination of dates and area optimisations for the ancestral nodes of *Ficus* subsect. *Urostigma* show that the first PID could best be explained by species rafting on India to Asia, after which the majority of species evolved in Asia up to Australia. The second PID probably involved dispersal via south Asia and Arabia to Africa in the early Miocene before the worldwide climate cooled down and areas became drier. Dispersal over Wallace's Line in Malesia is mainly by widespread species from which only a few local endemics in east Malesia and Australia developed. The multiple samples per species indicated that especially African species developed quite early, 17-18 Ma, while the Malesian species are younger, usually less than 7 Ma.

Keywords: Africa, ancestral area reconstruction, Asia, dispersal, *Ficus* subsect. *Urostigma*, historical biogeography, Palaeotropical disjunction, vicariance.

Introduction

Ficus L. subsection *Urostigma* (Gasp.) Endl. is a group of figs that are mainly trees, many of which are hemi-epiphytic and they generally show intermittent growth and possess few aerial roots. The leaves are often deciduous, spirally arranged, and (sub)articulate (some African and Madagascan species lack the articulation). The inflorescences are borne below the leaves or on the spurs of older branches and the synconia (figs) change colour from white via pink and purple to finally black (Berg & Wiebes, 1992; Berg & Corner, 2005). The group was recently revised by Chantarasuwan et al. (2013) and phylogenetic analyses (Weiblen, 2000; Jousselin et al., 2003; Machado et al., 2005; Rønsted et al., 2005, 2008; Xu et al., 2011, Chantarasuwan et al., ms) showed that its composition had to be slightly altered. *Ficus amplissima* J.E.Sm. and *F. rumphii* Blume, placed by Berg (2004) in subsect. *Urostigma*, appeared to be part of subsect. *Conosycea* (Miq.) C.C.Berg. Chantarasuwan et al. (ms.) made this change.

Subsect. *Urostigma* in its present circumscription (Chantarasuwan et al., ms) is found in tropical Africa, Madagacascar and ranges in Asia from India to Japan and troughout the southern part of the Malay Archipelago to Australia and the west Pacific (Fig. 7-1). Most species are found in Asia, but a few are present in Africa or on Madagascar. These species are partly at the base of the cladogram, but also split off higher up in the cladogram. This means that dispersal between Asia and Africa happened several times, and probably via different pathways. Sirichamorn et al. (2014) gave a nice overview of four different theories explaining the disjunct distribution between Africa and Asia, the so-called Palaeotropical intercontinental disjunctions (PID): (1) Gondwanan taxa rifted on India from Africa (and Madagascar) to Southeast Asia ('Out of India' hypothesis; McKenna, 1973; Morley, 1998; Conti et al., 2002); (2) dispersal occurred via boreotropical forests during the Palaeocene and Eocene ('boreotropical' hypothesis; Wolfe, 1975; Morley, 2000, 2007); (3) long-distance dispersal (e.g., Li et al., 2009; Warren et al., 2010); and (4) overland dispersal between Asia and Africa via Arabia and south Asia during the first warm half of the Eocene (e.g., Zhou et al., 2012). A dated phylogeny of *F.* subsect. *Urostigma* will contribute to this discussion. The hypotheses are exclusive, also in time, thus several may apply to subsect. *Urostigma*. Continuing contributions to this discussion will show which hypotheses best explain the most common patterns. The dataset of subsect. *Urostigma* is rather unique for this purpose, 27 out of 31 species are included and often several samples per species.

The aims of the study are to date the phylogeny of *F.* subsect. *Urostigma*, to see how old some of the species are, to analyse the historical biogeography, and to see how the patterns found contribute to the discussions of PIDs and general Asian biogeography patterns.

Material and methods

Taxon sampling, DNA markers

The same taxa, with usually multiple samples per species (2-4 samples), and the same four genetic markers were used as in the phylogenetic analysis of Chantarasuwan et al. (ms). Three nuclear markers were used (ETS, 481 basepairs, G3dh, 779 bp, ITS, 815 bp) and one chloroplast marker (ncpGS, 599 bp). Also the same evolutionary models were applied, HKY+G except GTR+G for ETS. An overview of the samples and genbank accession numbers can be found in Chantarasuwan et al. (ms).

Dating

Calibration points were obtained from Xu et al. (2011, their table 7-2) and the dating was performed within a Bayesian framework with the program BEAST v.1.8.0 (Drummond & Rambaut, 2007; Drummond et al., 2012, 2013). BEAUTi (part of the BEAST package) was used to create the input file with the following settings: – four groups were defined: Alltaxa (mean age 86.67 Ma, corresponds with node 1, Genus *Ficus* in Table 7-2 of Xu et al., 2012), Ingroup (excl. *F. maxima* Mill., *F. tonduziii* Standl.; mean age 79.23 Ma = node 3 Other clades excluding section *Pharmacosycea* in Table 7-2 of Xu et al., 2012), subsect. *Urostigma* (mean age 35.53 Ma,= node 15 section *Urostigma* in Table 7-2 of Xu et al., 2012), section *Conosycea* (no age); – Yule process speciation, - an exponential relaxed clock, – random starting tree; – ucld prior set to uniform and those of Alltaxa, Ingroup, *Urostigma* also set to uniform (no indication exists about any distribution type of the ages for these groups: Ho, 2007), with as upper and lower bounds for Alltaxa = 136.83-60.00 Ma, Ingroup = 130.12-50.59 Ma, *Urostigma* = 60.54-18.13 Ma. All other priors were left to default. The analysis was run twice for a 100 million generations.

The results were tested for Effective Sampling Sizes (ESS values > 200) with TRACER v.1.6 (Rambaut & Drummond, 2009). TREEANNOTATOR (part of BEAST package) was used to find the Maximum Clade Credibility (MCC) tree and this cladogram was visualised with FIGTREE v.1.4.0 (Rambaut, 2009).

Ancestral area reconstruction

Twelve areas (Fig. 7-1) were discriminated based on the presence of endemic species (areas A, B, C, E, H, J, L) or areas of overlap in the various configurations of the distributions (D, F, G, I, K). Table 7-1 gives an overview of the distributions of all sampled species.

Parsimony-based Statistical Dispersal-Vicariance Analysis (S-DIVA) was used for the historical biogeographic analyses, which is based on dispersal-Vicariance Analysis (DIVA; Ronquist, 1997) and implemented in RASP v.2.0b (Yu et al., 2010, 2013). Every 1000th tree saved from the 100 million trees generated with BEAST were used as input tree, of which 10,000 were discarded as burn-in. The remaining cladograms were evaluated against the MCC tree by S-DIVA. Variable numbers of areas, ranging from 2-6, were optimised per node; higher numbers took too much computing time.

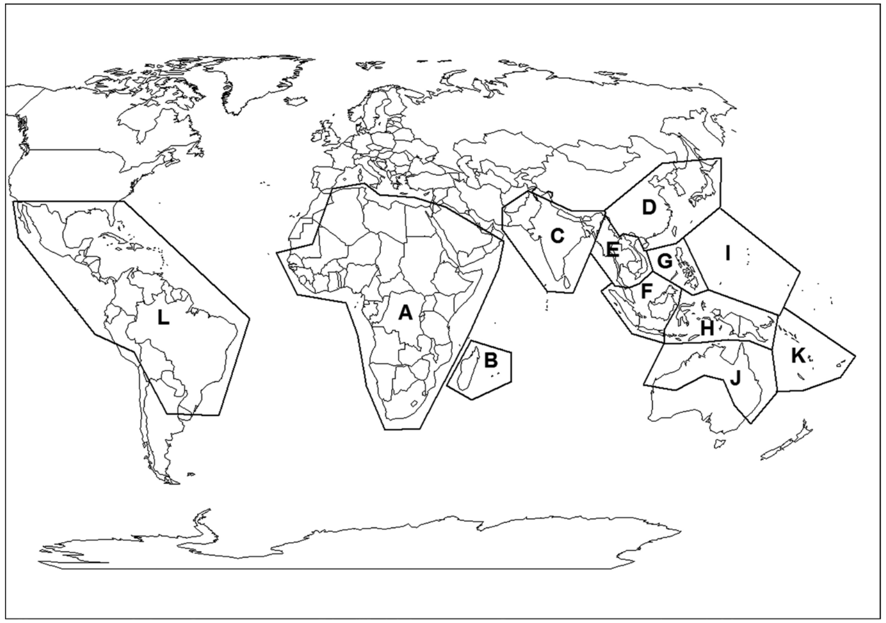

FIGURE7-1. Phytogeographic areas (Table 7-1) as used in the historical biogeographic analysis. A = Africa; B = Madagascar and surrounding islands; C = 'Greater' India; D = China, Japan; E = Southeast Asia; F = west Malesia; G = the Philippines; H = east Malesia; I = Micronesia; J = Australia; K = West Pacific.

Results

The dated phylogeny can be found in Fig. 7-1, the historical biogeographic analysis is shown in Fig. 7-3.

Probably subsection *Urostigma* originated between 61.2 (95% Highest Posterior Density interval [HPD]: 75.7-50.6; node 149 Fig. 7-3, Table 7-2) Ma, the stem node, and 51 (60.6-40.3; node 148 Fig. 7-3, Table 7-2) Ma, the crown node of the *Urostigma* clade. The first species to split of was *F. madagascariensis* C.C.Berg [c. 51 (60.6-40.3 Ma; node 148)], followed by *F. densifolia* Miq. [between 42.2 (72.5-30; node 147) and 8.5 (17.1-3.1) Ma; node 92]. Both species occur on Madagascar (area B; Fig. 7-1). Next, species (*F. cordata* Thunb., *F. lecardii* Warb., *F. verruculosa* Warb.) develop in Africa between 39.6 (50.7-28.8; node 146) Ma and 33.1 (46.1-18.8; node 145) Ma, followed by the first developments in Asia (*F. religiosa* L., *F. tsjakela* Burm. *F.* and '*F. pseudocaulocarpa*' Chantaras.) between 36.6 (50.7-28.8; node 139) and 28.3 (42.9-13.2; node 138) Ma (areas C, D, E, and later also G; Fig. 7-1),

Table 7-1. Phytogeographic areas and the distributions of the sampled species.

Phytogeographic areas

A = Africa
B = Mascarines
C = India s.l.: Pakistan, India, Sri Lanka, Nepal, Bhutan, Bangladesh
D = China, Japan
E = Southeast Asia (Myanmar, Thailand, Laos, Cambodia, Vietnam)
F = West Malesia (Malay Peninsula, Sumatra, Borneo, Java)
G = Philippines
H = East Malesia: Sulawesi, Lesser Sunda Islands, Moluccas, New Guinea
I = Micronesia
J = Australia
K = West Pacific
L = America

Species	**Distribution**
Ficus alongensis Gagnep.	DE
Ficus altissima Blume	CDEFGH
Ficus americana Aubl.	L
Ficus arnottiana (Miq.) Miq.	C
Ficus aurea Nutt.	L
Ficus benjamina L.	CDEFGHJK
Ficus brachypoda (Miq.) Miq.	J
Ficus bubu Warb.	A
Ficus caulocarpa (Miq.) Miq.	CDEFH
Ficus concinna (Miq.) Miq.	CDEFG
Ficus cordata Thunb.	A
Ficus densifolia Miq.	B
Ficus glabella Blume	EFGHJ
Ficus geniculata Kurz	CDE
Ficus geniculata Kurz var. *insignis* (Kurz) C.C.Berg	CEJ
Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg	EF
Ficus henneana Miq.	J
Ficus hookeriana Corner	CDE
Ficus ingens (Miq.) Miq.	A
Ficus lecardii Warb.	A
Ficus madagascariensis C.C.Berg	B
Ficus maxima Mill.	L
Ficus menabeensis H.Perrier	B
Ficus middletonii Chantaras.	CE
Ficus orthoneura H.Lév. & Vaniot	DE
Ficus pleurocarpa F.Muell.	J
Ficus prasinicarpa Elmer	GHK
Ficus prolixa G.Forst.	IK
'Ficus pseudocaulocarpa' Chantaras. (name still to be published)	G
Ficus pseudoconcinna Chantaras.	H
'Ficus pubipetiola' Chantaras. (name still to be published)	E
Ficus religiosa L.	CDE
Ficus rumphii Blume	CEFH
Ficus salicifolia Vahl	A
Ficus subpisocarpa Gagnep. subsp. *pubipoda* C.C.Berg	EF
Ficus superba Miq.	EFH
Ficus tonduzii Standl.	L
Ficus verruculosa Warb.	A
Ficus tsjakela Burm.f.	C
Ficus virens Aiton	CDEFGHIJ
Ficus wightiana (Miq.) Benth.	C

Table 7-2. Nodes (Figs. 2, 3) and their mean, earliest and youngest ages as estimated by the BEAST analysis of four molecular markers and three calibration points. In the last column the most likely S-DIVA optimisations for 2-6 areas per node.

Node	Mean age	Earliest	Youngest	S-DIVA optimisation(s)
77	6.65	13.11	1.94	E
78	12.37	20.81	5.65	E
79	20.2	31.18	11.1	BE
80	18.66	31.08	8.24	E
81	26.66	39.26	16.17	E
82	0.84	3.02	0	E
83	5.64	12.97	1.33	E
84	32.42	46.48	20.32	E
85	8.78	17.53	2.62	L
86	18.24	31.42	8.21	AL
87	10.86	24.65	2.22	J
88	34.53	49.67	20.21	2 areas: AJ; 3,4: AJL, JI, AJ; 5,6: AJL, AJ
89	43.87	59.15	29.47	2 areas: AE; 3: AEJ, EJL; 4-6: AEJL, AEJ
90	3.13	7.82	0.45	B
91	2.91	7.19	0.44	B
92	8.51	17.05	3.12	B
93	18.42	30.9	7.18	A
94	3.83	10.5	0.43	E
95	3.18	8.46	0.4	C
96	5.18	10.68	1.42	C
97	10.62	18.41	4.46	C
98	10.62	18.02	4.46	C
99	3.28	6.39	1.06	C
100	4.84	8.5	2.05	C
101	6.1	10.18	2.72	C
102	11.27	17.35	6.32	C
103	5.74	10.99	1.51	K, I
104	5.04	9.64	1.44	C
105	8.55	14.16	3.88	CI
106	14.65	21.27	8.94	C
107	1.57	4.63	0.07	E
108	3.09	9.54	0.27	CE
109	17.55	24.82	10.92	C
110	20.74	29	13.2	C
111	25.14	34.8	16.67	CE
112	2.16	5.58	0.24	J
113	7.41	14.54	2.41	CJ
114	12.1	21.45	5.15	C
115	15.55	26.35	6.9	2-6: all containing CG, CH, CK.
116	28.55	38.57	19.16	C
117	10.07	17.53	4.55	
118	4.61	10.16	1.05	E
119	15.39	23.97	8.38	E
120	4.77	11.66	0.72	H
121	19.1	28.56	11.13	EH
122	0.77	5.58	0.0	A
123	9.91	16.93	4.65	A
124	7.93	16.76	1.76	E
125	15.39	24.44	7.82	AE
126	19.41	29.27	10.93	E
127	26.33	32.7	13.9	E
128	1.00	4.53	0.0	E
129	10.58	20.15	3.93	E
130	8.73	18.25	1.77	E
131	17.15	30.82	8.23	E
132	26.33	36.02	17.57	E
133	31.36	41.59	21.8	CE
134	33.21	43.83	23.3	AC
135	3.61	8.62	0.64	C
136	7.68	16.34	2.3	C
137	1.96	7.44	0.02	CG
138	28.34	42.92	13.24	C
139	36.55	50.68	28.8	C
140	2.22	6.38	0.22	A
141	17.85	29.29	8.39	A
142	26.45	39.31	14.25	A
143	11.46	21.22	4.16	A
144	17.28	29.21	8.05	A
145	33.08	46.09	18.81	A
146	39.58	50.68	28.8	A
147	42.22	72.54	30.0	AB
148	51.31	60.59	40.3	B
149	61.17	75.71	50.59	2: A; 3,4: many, all B and usually A; 5: ABEJL, ABEJ; 6: ABEFJ, ABEFJL, ABEJ, ABEJL
150	0.93	4.82	0.0	L
151	69.92	92.61	60.0	2: EL; 3: AEL; 4:AEJL; 5:ABEJL; 6: ABEFJL, ABEJL

Table 7-2. Continued

while *F. salicifolia* Vahl develops again in Africa [area A, Fig. 7-1; between 33.2 (43.8-23.3; node 134) and 18.4 (30.9-7.2; node 93) Ma]. All further developments are in Asia, with one later return to Africa [*F. ingens* (Miq.) Miq., between 15.4 (24.4-7.8; node 125) and 9.9 (16.9-4.7; node 123) Ma]. One Asian clade [*F. subpisocarpa* Gagnep. var. *pubipoda* C.C.Berg up to *F. wightiana* (Miq.) Benth.] mainly occurs in Greater India (Area C, Fig. 7-1) and the other clade (*F. alongensis* Gagnep. to *F. hookeriana* Corner including the African *F. ingens*) in Southeast Asia (Area E, Fig. 7-1). One of the interesting dispersal barriers in Asia is Wallace's Line (Wallace, 1859; van Welzen et al., 2011), running from east of the Philippines, between Borneo and Sulawesi and between Bali and Lombok. *Ficus* subsection *Urostigma* crosses this line with several widespread species [*F. caulocarpa* (Miq.) Miq., *F. geniculata* Kurz var. *insignis* (Kurz) C.C.Berg, *F. glabella* Blume, *F. prasinicarpa* Elmer ex C.C. Berg, *F. superba* (Miq.)Miq., and *F. virens* Aiton]. The mainly Greater Indian clade (area C, Fig. 7-1; clade *F. subpisocarpa-F. wightiana*) has two species occurring east of Wallace's Line, *F. prolixa* G.Forst. [Micronesia and W. Pacific, areas I & K; dispersal between 8.6 (14.2-3.9; node 105) and 5.7 (11-1.5; node 103) Ma] and *F. henneana* Miq. [Australia, area J; dispersal between 7.4 (14.5-2.4; node 113) and 2.2 (5.6-0.24; node 112) Ma]. The mainly Southeast Asian clade (area E, Fig. 7-1; clade *F. alongensis–F. hookeriana*) has one species east of Wallace's Line, *F. pseudoconcinna* Chantaras. [E Malay Archipelago, area H; dispersal between 19.1 (28.6-11.1; node 121) Ma and present].

Discussion

Species ages

Usually several samples per species were used in the analyses. The dating (Fig. 7-2) shows that the species often developed quite early. The crown nodes of the African species with multiple samples, *F. cordata*, *F. lecardii* and *F. salicifolia*, are all between 20 and 13 Ma (Lower to middle Miocene), only the crown node of *F. verruculosa* is much younger (but its stem nodedates from the same period). The Asian species have crown nodes of c. 10 Ma to much younger, just like the Madagascan *F. densifolia*. Samonds et al. (2012) show that from 20 Ma onwards it becomes difficult for floating and swimming animals to reach Madagascar from Africa, because of changing winds and water currents, which might mean that the opposite, dispersal from Madagascar to Africa, may have been facilitated. In Asia, the eastern part of Malesia (Malay Archipelago; Raes & van Welzen, 2009), attached to west Malesia and emerged above sea level during especially the last 10 Ma (Hall, 2002, 2009, 2012), which may have catalysed speciation in *Ficus*.

S-DIVA optimisations

Five different S-DIVA analyses were run with a variable number of areas to be optimised per internal node ranging from two to six areas. Generally, the optimisations gave the same results for all nodes, the most likely of these are shown in Table 7-2 and Fig. 7-3. Only five nodes had (slightly) different optimisations, the result of allowing more areas per node: node 88, 89, 115,

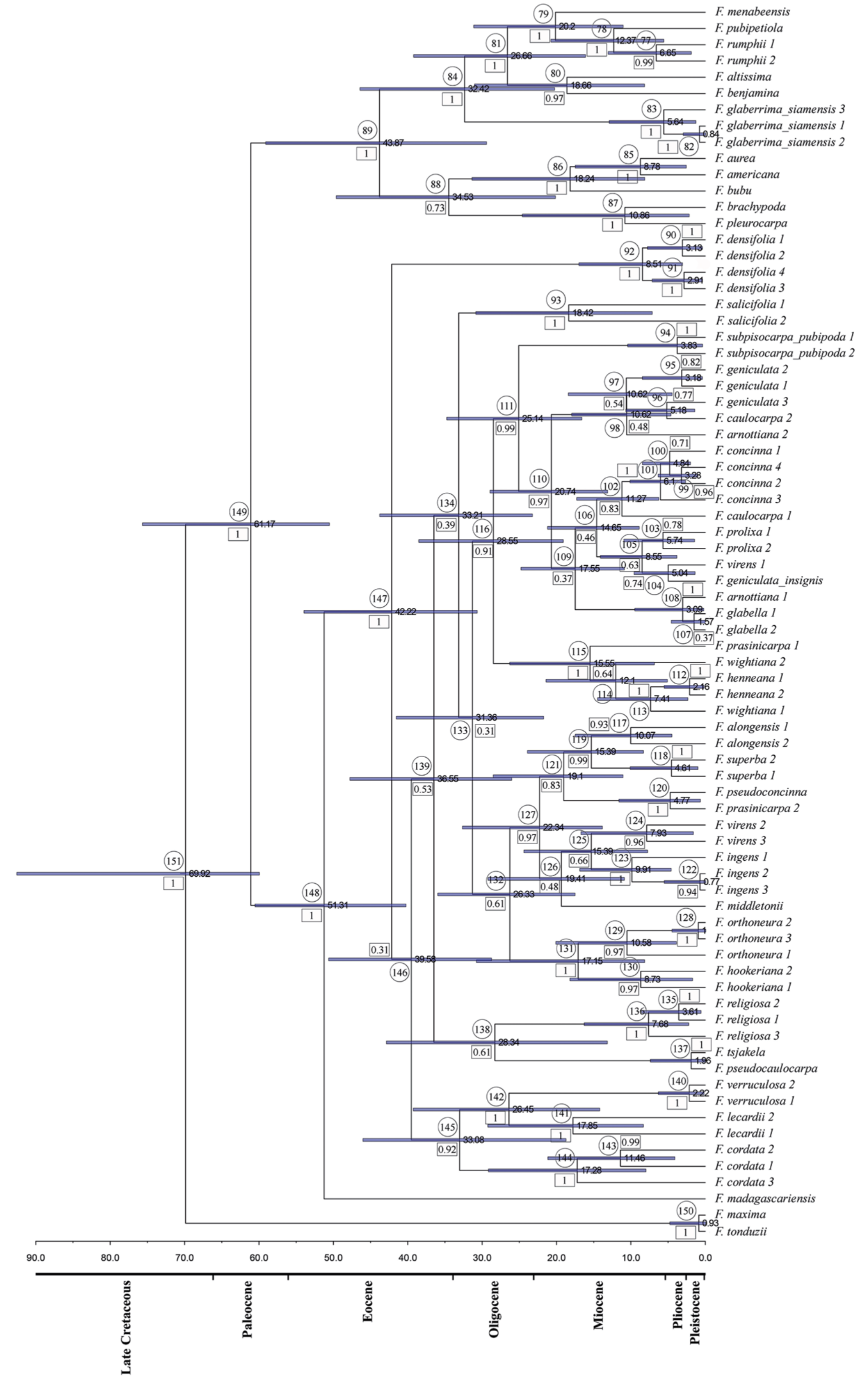

FIGURE7-2. Dated phylogeny. The numbers per node are the node number (in circles), the posterior probabilities (in square boxes) and the mean age of the nodes, the bars indicate the 95% Highest Posterior Density interval [HPD] (mean ages and HPD also summarised in Table 7-2).

149, 151 (Table 7-2, Fig. 7-3). Table 7-2 shows some of the possibilities for these nodes, in Fig. 7-3 a 'mean' area (the area in common) is shown. The optimisations of 149 and 151 can be ignored, these are the basal nodes and probably do not represent realistic ancestral areas, because of the insufficient sampling of the outgroups. The latter also applies to node 88 and 89, the outgroups are only partly represented. The variable node 115 (CH shown in Fig. 7-3) has, like nodes 105 (CI), 113 (CJ), 125 (AE), 134 (AC), an unlikely, disjunct optimisation. These are the result of the parsimony method used in DIVA (Ronquist, 1997), with no penalty for vicariance and sympatric speciation, and a penalty of 1 for dispersal and extinction. This results in internal nodes with wide distributions (like the nodes above), which can then be followed by vicariance in higher nodes.

Scenario

The first species that split off (*F. madagascariensis* and *F. densifolia*) occur on Madagascar (Fig. 7-3). The optimatisations of the basal internal nodes (Fig. 7-3: nodes 151, 149, 148, 147) show Madagascar (area B, Fig. 7-1) or Madagascar in combination with Africa (area A) and/or other areas. The latter form unrealistic ancestral areas, because South America, area L, and Australia, area J, had already split from Africa, starting c. 165 Ma, with a broad gap between Africa and South America at c. 135 Ma (Moyersoen, 2006; Samonds et al., 2012). This is much older than the age of the stem node of subsect. *Urostigma*, node 149, 61.2 (75.7-51) Ma (Fig. 7-2; Table 7-2). The breakup between Africa and the Madagascar- India-Seychelles complex (c. 130 Ma; Samonds et al., 2012) and the subsequent breaking up of the latter plate (c. 87.6 ± 0.6 Ma; Storey et al., 1995; Samonds et al., 2012) also predate the estimated age of origin of subsect. *Urostigma*. Thus, which distributions did the basal species and ancestors of subsect. *Urostigma* have? Most likely, the first species occurred on Madagascar (still present are *F. madagascariensis* and *F. densifolia*). From Madagascar there must have been dispersal to Africa as the clade *F. verruculosa*–*F.cordata* is African and slightly later, higher in the cladogram, *F. salicifolia* is also African. It is unclear if this was a single dispersal event or two events. The support for nodes 134 and 146 is low (posterior probabilities 039 and 0.31, respectively), thus *F. salicifolia* may have been part of the *F. verruculosa*–*F. cordata* clade. The latter (thus a single event) is more likely, because the wind and water currents favoured dispersal from Africa to Madagascar (Samonds et al., 2012). The figs of subsect. *Urostigma* are small, thus bird dispersal is likely and birds are relatively independent of wind directions.

How did subsect. *Urostigma* reach Asia? Two possibilities exist. The optimisation for node 134 (Fig. 7-3) is Africa-India (areas A, C), with an age 33.2 (43.8-23.3) Ma. India collided with Asia c. 35 Ma (Samonds et al., 2012). One possibility is dispersal from Africa via Arabia to India and then Asia. However, the connection Africa-Arabia-west Asia is younger, connection were the Meswa Bridge, c. 23.5 Ma, and the Gomphoterium Bridge, c. 18 Ma (Rögl, 1999). The optimisation of node 134 is caused by the position of

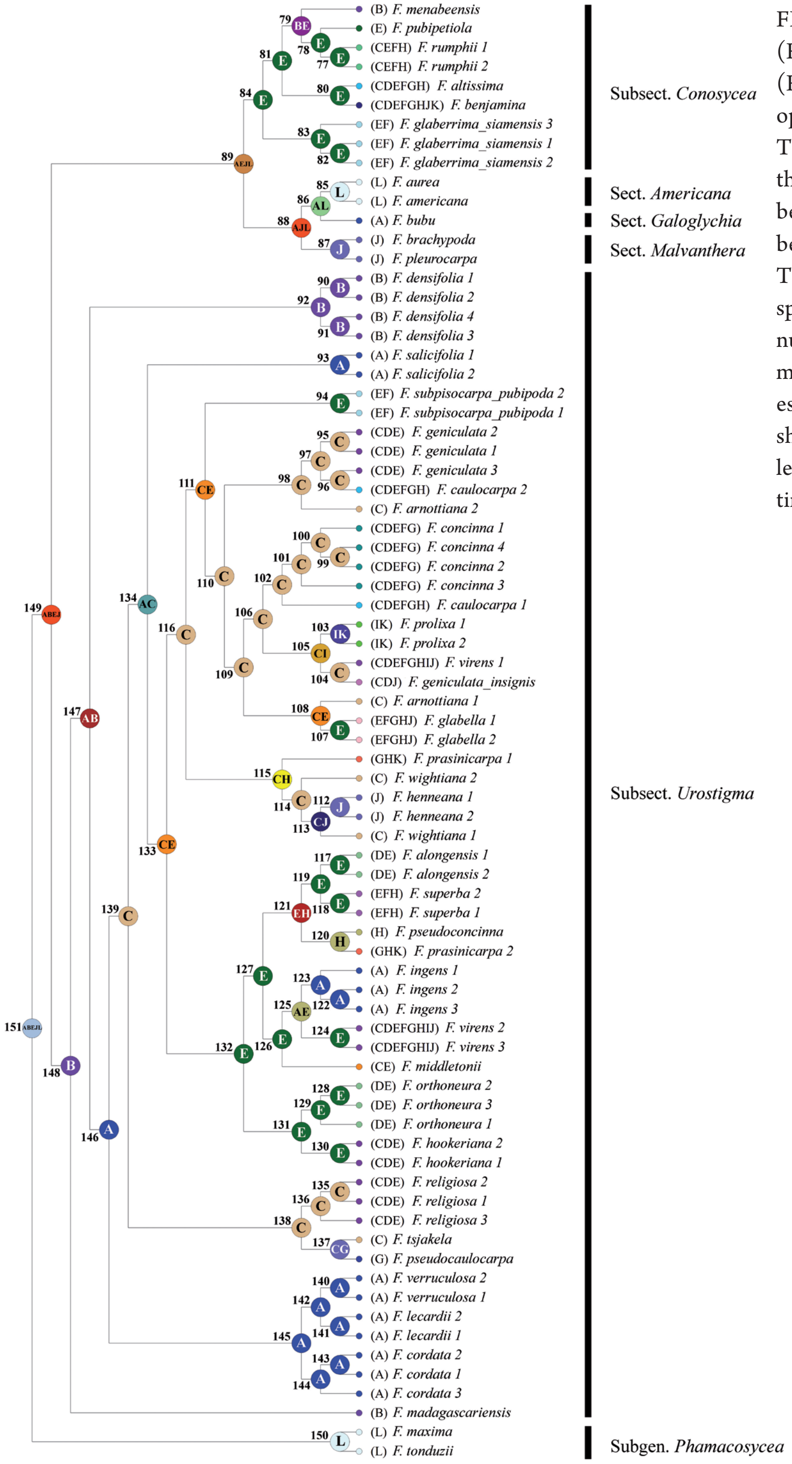

FIGURE 7-3. Phylogeny (Fig. 7-2) with the area (Fig. 7-1, Table 7-1) optimisations per node. The distributions of the species is indicated between brackets before the species names. The numbers corresponds with the node numbers. Only the optimisations with the highest probabilities are shown and the branch lengths do not indicate time as in Fig. 7-2.

F. salacifolia, and as already indicated above, a possibility with low likelihood. The other, more likely alternative of reaching Asia, is rifting with India. Briggs (1989) indicates that India, while moving to Asia, may have had a rather constant interchange of biodiversity with Africa and Asia, because it does not really harbour a typical, endemic flora and fauna. This is substantiated by Ali & Aitchison (2008), who show in various hypotheses dispersal, back and forth, between India and Madagascar, India and Africa and India and Asia. Ancestral species may already have been present on India next to Madagascar, or they dispersed from Madagascar to India after these two terranes had already split. After reaching Asia, the clade *F. religiosa–F. pseudoacaulocarpa* developed in mainly India, followed by two developments, one clade (*F. subpisocarpa–F. wightiana*) also mainly developed in India (area C, Fig. 7-1, but with many widespread species and an Australian endemic, see below) and the other clade (*F. alongensis F. hookeriana*) developed especially in southeast Asia (area E, Fig. 7-1, also with many widespread and east Malesian taxa). Spreading over Malesia is mainly by widespread species, all from west to east.

Wallace's line

Several species occur east of Wallace's line, and could only have reached their distributions by dispersal, either by themselves or via ancestral species. In the Southeast Asian clade *F. henneana* (node 112, Fig. 7-3) is endemic in Australia (area J, Fig. 7-1) with as sister species *F. wightiana* from India (area C; nodes 113, 114), together they are sister to *F. prasinicarpa 1* (node 115), found in the Philippines, east Malesia, and the west Pacific (areas G, H, K). It is difficult to explain the presence in Australian from a Southeast Asian origin (area C), which is more or less the optimisation for the internal nodes 113,114, 115. However, compared with the distribution of *F. prasinicarpa*, which occurs in adjacent areas, the dispersal to Australia is easy to explain and it occurred in a period (less than 20 Ma) that exchange between west Malesia and Australia was possible (van Welzen et al., 2014). *Ficus pseudoconcinna* Chantaras. is another species that occurs only east of Wallace's Line (east Malesia, area H, node 120), and its distribution overlaps with the closely related *F. prasinicarpa 2* (which crosses Wallace's Line), similar with *F. prolixa* (Micronesia, west Pacific, areas I, K, node 103), which partly overlaps with the distribution of its sister group consisting of the species *F. virens 1* and *F. geniculata* var. *insignis*.

Palaeotropical Intercontinental Disjunctions

The first PID is the dispersal from Africa/Madagascar to Asia, explained above as rifting on India ('Out of India' hypotheses, see Introduction). There is one more dispersal between Asia and Africa, from Asia to Africa. *Ficus ingens* (Miq.) Miq. is an African species and its sister species is *F. virens 2/3*, which occurs from India (area C) to Australia (area J). Their crown node (node 125) has as age 15.4 (24.4-7.8) Ma and the stem node (node 126) 19.4 (29.3-10.9) Ma. These ages are too young for the 'Out of Africa' hypothesis and the Boreal Forest hypothesis. Considering the fact that *F. ingens* occurs in the northern parts of India, the most likely hypothesis is dispersal via south Asia and Arabia to Africa. This is comparible with the genera Macaranga Thouars and Mallotus Lour. (Euphorbiaceae; van Welzen et al., 2014), which even earlier dispersed from Asia to Africa (c. 23 Ma) when the Arabian land bridges were still forming (Rögl, 1999). The dispersal of *Ficus* to Africa occurred when the Miocene climate was still warm and humid, before the Middle Miocene Climatic Optimum (c. 17-15 Ma; Zachos et al., 2001). Then forests were more extensive and conditions along the coastal areas favoured dispersal. The PIDs found for the legumes in Sirichamorn et al. (2014) also dispersed along the Asian-Arabian coast, these species are mangrove related.

Climate

During the different epochs that subsect. *Urostigma* existed the climate changed several times drastically from warm and wet to colder and drier. Moreover, the various contemporary species also inhabit a large variety of climates and soils. Seemingly, the figs can tolerate various climates, especially the widespread species. Most species occur in areas with a yearly dry monsoon (Chantarasuwan et al., 2013), adaptation to which may have helped survival. Areas like most of Africa, Madagascar, India, Southeast Asia, the Philippines, east Malesia, Australia, etc. have a dry spell during part of the year. In Malesia, most species occur in the southern part, areas with often a severe dry season (central and eastern Java, Lesser Sunda Islands; Chantarasuwan et al., 2013). In areas with a dry season, and usually deciduous trees, figs may form the last available food supply for animals like orang-utans (Sugardjito et al., 1987).

Dating

Xu et al. (2011) used fossil *Ficus achenes* (Collinson, 1989) of c. 60 Ma as calibration point and an artificial constraint on the root of 190 Ma (Lower Jurassic; otherwise the program BEAST did not work), even though the oldest known Angiosperm fossils were 130 Ma (Lower Cretaceous). Still, these apparently poor calibration points worked out quite well. Our data and scenario support (do not contradict) the dates found by Xu et al. (2011) and coincide with the various tectonic hypotheses.

Conclusions

The combination of dates and area optimisations for the ancestral nodes of *Ficus* subsect. *Urostigma* show that it likely originated in Madagascar and dispersed once or twice to Africa and rafted on India to Asia. In Asia many species became widespread, sometimes ranging from India to Micronesia and Australia, thus crossing Wallace's Line. Only few species are endemic to areas east of Wallace's Line. One reversed dispersal from Asia to Africa occurred in the early Miocene, probably along south Asia and Arabia.

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