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# Trans-Atlantic, trans-Pacific and trans-Indian Ocean dispersal in the small Gondwanan Laurales family Hernandiaceae

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## ABSTRACT

**Aim** To investigate the historical biogeography of the pantropical flowering plant family Hernandiaceae (Laurales), which today comprises 62 species in five genera.

**Location** Hernandiaceae occur in Africa (9 species), Madagascar (4), the Neotropics (25), Australia (3), southern China, Indochina, Malesia, and on numerous Pacific Islands (32). These numbers include two widespread species, *Hernandia nymphaeifolia*, which ranges from East Africa to the Ogasawara Islands and New Caledonia, and *Gyrocarpus americanus*, thought to have a pantropical range.

**Methods** We sampled 37 species from all genera, the widespread ones with multiple accessions, for a chloroplast DNA matrix of 2210 aligned nucleotides, and used maximum likelihood to infer species relationships. Divergence time estimation relied on an uncorrelated-rates relaxed molecular clock calibrated with outgroup fossils of Lauraceae and Monimiaceae.

**Results** The deepest split in the family is between a predominantly African–Madagascan–Malesian lineage comprising *Hazomalania*, *Hernandia* and *Illigera*, and an African–Neotropical lineage comprising *Gyrocarpus* and *Sparattanthelium*; this split may be 122 (110–134) Myr old. The stem lineages of the five genera date back at least to the Palaeocene, but six splits associated with transoceanic range disjunctions date only to the Oligocene and Miocene, implying long-distance dispersal. It is inferred that *Hernandia beninensis* reached the West African islands of São Tomé and Bioko from the West Indies or the Guianas; *Hernandia* dispersed across the Pacific; and *Illigera madagascariensis* reached Madagascar from across the Indian Ocean.

**Main conclusions** The disjunct ranges and divergence times of sister clades in the Hernandiaceae are partly congruent with the break-up of West Gondwana, but mostly with later transoceanic dispersal. An exceptional ability to establish following prolonged oceanic dispersal may be largely responsible for the evolutionary persistence of this small clade.

## Keywords

Gondwana, Hernandiaceae, historical biogeography, Laurales, long-distance dispersal, molecular clock, transoceanic disjunctions.

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## INTRODUCTION

Over the past 15 years, molecular phylogenies have supported, or newly suggested, hundreds of cases of transoceanic range expansion (de Queiroz, 2004; Renner, 2004, 2005a; Crisp *et al.*, 2009; Gehrke & Linder, 2009). As a result, dispersal across expanses of ocean has now become widely accepted as an

explanation for range disjunctions among close relatives, even though the actual mechanisms remain largely unknown (Nathan *et al.*, 2003, 2008). Dispersal to new areas may reduce the incidence of lineage extinction, and it is well known that some ancient flowering plant lineages, such as Amborellaceae (one species in New Caledonia), Monimiaceae (about 200 species throughout the tropics), and Trimeniaceae (eight

species in Sulawesi, Australia and the south-west Pacific), have species on relatively remote islands, where competition may be reduced (Cox & Ricklefs, 1977; Whittaker & Fernández-Palacios, 2007). A similarly small and ancient angiosperm family is the Hernandiaceae, a clade of 62 species in five genera that is close to Lauraceae and Monimiaceae (Kubitzki, 1969; Renner & Chanderbali, 2000), families dating back to the Upper Cretaceous (Eklund, 2000; von Balthazar *et al.*, 2007; Dettmann *et al.*, 2009).

The strikingly disjunct ranges of Hernandiaceae have long been explained by a combination of Gondwana break-up and transoceanic dispersal (Good, 1953; Kubitzki, 1969; White, 1983; the latter stressing dispersal over vicariance). All 62 species of Hernandiaceae are woody. Nine occur in Africa, four in Madagascar, 25 in the Neotropics, three in Australia, and 32 in southern China, Indochina, Malesia and throughout the Pacific, which gives a total of 73 because two species occur in three or four continents. These widespread species are *Gyrocarpus americanus*, which is found in Central and South America, Africa, Madagascar, the Malesian region and Australia, and *Hernandia nymphaeifolia*, which occurs from East Africa and Madagascar to New Caledonia and the Ogasawara Islands. In the only monograph of Hernandiaceae, Kubitzki (1969) hypothesized five long-distance dispersal events, namely three across the southern Pacific to the Neotropics, one from Southeast Asia to Africa/Madagascar, and one from the Guianas to West Africa. At the same time, Kubitzki attributed the presence of 'primitive' species, such as *Hazomalania voyronii* in Madagascar or *Hernandia albiflora* in Australia, to the break-up of East Gondwana (Madagascar, India, Australia and Antarctica). This combination of seemingly ancient phylogenetic divergences and strikingly disjunct ranges in a clade of a mere five genera makes the Hernandiaceae biogeographically interesting. Here we use a chloroplast phylogeny that includes 37 of the family's 62 species and relaxed molecular clock dating to study the ages of the various range disjunctions. We also test the monophyly of the pantropically distributed species *Gyrocarpus americanus*.

## MATERIALS AND METHODS

### Taxon sampling, DNA sequencing, alignment and phylogenetic analyses

We included 37 species from all five genera, following the taxonomic concepts of relevant treatments (Kubitzki, 1993; Espejo Serna, 1997; van Proosdij, 2007; Li *et al.*, 2008). Specifically, we sampled four of the five species of *Gyrocarpus* (*Gyrocarpus mocinnoi* Espejo could not be obtained), the single species of *Hazomalania*, 12 of c. 22 species of *Hernandia*, 11 of 22 species of *Illigera*, and nine of the 12–13 species of *Sparattanthelium*. The missing 11 species of *Illigera* occur in China and Indochina, except for *Illigera novoguineensis* (see Discussion); the missing species of *Sparattanthelium* all occur in South America; and the missing species of *Hernandia* occur in Cuba (*Hernandia cubensis*), Jamaica (*Hernandia jamaicen-*

*sis*), Polynesia (*Hernandia drakeana*, *Hernandia ternarii*, *Hernandia olivacea*, *Hernandia stokesii*), Haiti (*Hernandia obovata*), Tahiti (*Hernandia tahitensis*), Indochina (*Hernandia khasiana*) and Sumatra (*Hernandia trifoliata*). Widespread species were represented by several accessions each, and the complete matrix comprised 50 ingroup and six outgroup accessions. Species circumscriptions in *Sparattanthelium* are doubtful (Kubitzki, 1969), and the genus is much in need of a revision. Phylogenetic trees were rooted with representatives of Monimiaceae and Lauraceae selected to span the roots of these families (Renner & Chanderbali, 2000).

Total genomic DNA was isolated from herbarium specimens or, more rarely, silica-dried leaves with a commercial plant DNA extraction kit (NucleoSpin, Macherey-Nagel, Düren, Germany), following the manufacturer's instructions. Based on previous work that explored phylogenetically useful loci in the Laurales (e.g. Renner, 1999; Renner & Chanderbali, 2000), we amplified the *trnT-trnL* and *trnL-trnF* intergenic spacers using Taberlet *et al.*'s (1991) universal primers a and b, and e and f. Primers for the *psbA-trnH* intergenic spacer were those of Sang *et al.* (1997). Polymerase chain reactions followed standard protocols, using Taq DNA polymerase. For recalcitrant material, we used a more reactive polymerase (Phusion High Fidelity PCR Kit, Finnzymes, Espoo, Finland) according to the manufacturer's protocol. Products were purified with standard clean-up kits, and sequencing relied on Big Dye Terminator kits (Applied Biosystems, Foster City, CA, USA) and an ABI 3130 Genetic Analyzer. Sequence assembly of forward and reverse strands was carried out in SEQUENCHER 4.6 (Gene Codes, Ann Arbor, MI, USA) or BIOEDIT (Hall, 1999), all sequences were BLAST-searched in GenBank, and sequences were then aligned by eye in SEQUENCHER or in MESQUITE (Maddison & Maddison, 2009).

The aligned *trnT-trnL* matrix comprised 848 nucleotides, of which we excluded 60 dubiously homologous positions in microsatellite regions. The aligned *trnL-trnF* matrix comprised 556 nucleotides, of which 43 were excluded. The aligned *psbA-trnH* matrix comprised 1369 nucleotides, with 460 excluded. The combined matrix thus had 2210 positions. Because of several difficult-to-align regions of repeated motifs, an additional alignment was created with the recently developed program PRANK (Löytynoja & Goldman, 2005, 2008), which creates extremely conservative alignments. The initial neighbour-joining guide tree that PRANK uses for optimization was built from the manual alignment. The PRANK alignment had a length of 3756 characters.

Maximum likelihood (ML) tree searches and bootstrapping (100 replicates) relied on RAXML and used the GTR +  $\Gamma$  substitution model, with four gamma rate categories and model parameters estimated directly during runs (Stamatakis, 2006; Stamatakis *et al.*, 2008).

### Molecular clock analyses

Divergence times were inferred using BEAST (Drummond & Rambaut, 2007). The matrix used for dating included 2167

nucleotides for 46 accessions, representing 36 species of Hernandiaceae (the doubtfully identified *Illigera* cf. *glabra* was not included) and the six outgroups. BEAST analyses relied on the GTR +  $\Gamma$  substitution model, a Yule tree prior, with rate variation across branches uncorrelated and lognormally distributed. Markov chains were run for between 1 and 10 million generations (burn-in 10%), with parameters sampled every 200th or 500th step. Results from individual runs were combined as recommended, and effective sample sizes (analysed in the TRACER tool) for all relevant estimated parameters were well above 100.

Although Berry (1936, 1937a,b, 1939, 1945a,b) attributed a series of fossil leaves and fruits from the Miocene of Brazil, Ecuador, Colombia and Venezuela to *Hernandia* and *Sparattanthelium*, more recent research has shown that these fossils could as well represent Malvaceae subfam. Sterculioideae, and that one of Berry's beautifully preserved '*Gyrocarpus*' fruits represents the Malpighiaceae genus *Tetrapteris* (R. Burnham, University of Michigan, Ann Arbor, pers. comm., January 2001). Similarly, a Miocene leaf from New Zealand might represent Sterculioideae or Hernandiaceae (Pole, 1996). We therefore resorted to outgroup fossil calibration and two calibration schemes to cross-validate inferences. Scheme A involved a strict clock calibrated with an age of 109 Myr for the trichotomy of Hernandiaceae, Lauraceae and Monimiaceae, based on the oldest fossils of lauraceous affinity (von Balthazar *et al.*, 2007). Scheme B was a relaxed clock model with two prior age constraints. One constraint was applied to the Monimiaceae crown group and took the shape of a lognormal distribution with a minimal age of 71 Myr and a 95% confidence interval that allowed the node to be up to 83 Myr old, based on the oldest woods attributed to *Hedycaryoxylon*, *Hortonioxylon*, *Monimioxylon* and *Xymaloxylon*, which are from the Campanian, 83–71 Ma (Poole & Gottwald, 2001). The second constraint was applied to the Hernandiaceae, Lauraceae, Monimiaceae trichotomy and took the shape of a normal distribution with a mean of 121 Ma and SD of 6, such that the 2.5% and the 97.5% quantiles lay between 109 Ma, the age of the oldest lauraceous fossils (von Balthazar *et al.*, 2007), and 133 Ma, the minimal age of angiosperms (Hughes, 1994). Node heights were summarized on the highest likelihood tree. We also ran an analysis without the nucleotide data in order to sample from the joint prior distribution and to assess the decisiveness of the data. Results indicated that the posterior distributions obtained from the data departed from the prior distributions (indicating informative data).

To convert stratigraphic ages into absolute ages, we used the geological time-scale of Ogg (2008).

### Biogeographic analysis

For biogeographic analysis, we used ancestral area reconstruction, relying on parsimony inference as implemented in MESQUITE (Maddison & Maddison, 2009). Geographic regions were coded and treated as an unordered multi-state character,

using the following six states: (1) America, (2) Africa (including Madagascar and offshore islands), (3) Asia, (4) Malesia, (5) Australia, and (6) Pacific Islands.

### RESULTS

In all, 116 sequences were newly generated for this study and added to the 44 available from previous work (Renner, 1999; Renner & Chanderbali, 2000). Table 1 lists all DNA sources, along with their geographic origin, distributional range, species name and authority, and GenBank accession numbers. The combined matrix of the chloroplast spacers *trnT-trnL*, *trnL-trnF* and *psbA-trnH* comprises 2210 characters (with indels treated as missing data except for one clearly synapomorphic gap in two accessions of *Sparattanthelium wonotoboense*). Figure 1 shows a maximum likelihood tree that includes all 50 ingroup accessions. The major clades, which correspond to the traditional higher taxa in the family (genera and subfamilies), are well supported, whereas most within-genus divergences are short-branched, even where they involve large geographic disjunctions. The deepest split in the family is between *Gyrocarpus* and *Sparattanthelium* on the one hand and *Hazomalania*, *Hernandia*, and *Illigera* on the other. The position of *Hazomalania* as sister to either *Illigera* or *Hernandia* is not resolved. The tree obtained from the PRANK alignment yielded the same topology as obtained from the manual alignment, but with slightly higher bootstrap support values (Fig. 1).

The oldest divergence in the family (between *Gyrocarpus* and *Sparattanthelium* versus *Hazomalania*, *Hernandia* and *Illigera*) corresponds to a minimum age of 112 (89–130) Myr (Fig. 2). The four highlighted parts of the tree (Fig. 2) and corresponding maps (a)–(d) depict some of the inferred dispersal events, with arrows indicating directions, and balls being used where a direction could not be inferred owing to a polytomy or unclear outgroup information. Figure 2(a) (boxed clade and map to the right) shows the relationships and disjunction between the Australian, Pacific and American species of *Hernandia*; Fig. 2(b) depicts the disjunction between the American *Hernandia sonora* and *Hernandia guianensis* and the African *Hernandia beninensis*; Fig. 2(c) shows the disjunction between the African and Asian/Malesian lineage of *Illigera*; and Fig. 2(d) depicts the divergence between the Asian/Malesian clade of *Illigera* and Madagascar/African *Illigera madagascariensis*.

Ages obtained for the biogeographically interesting divergence events under a strict clock model versus a relaxed clock model are shown in Fig. 3. Generally, the ages obtained from the strict clock are somewhat younger than those from the relaxed clock. However, in 11 of 13 nodes, one of the inferred ages lies within the confidence interval of the alternative clock model, and in seven nodes both do. The two nodes where the strict and the relaxed clock yield different ages are the crown group of *Illigera* (but even in this case confidence intervals overlap) and the crown group of Monimiaceae. Based on the median ages from the relaxed clock (Fig. 3), the crown group

**Table 1** Species names and authorities, herbarium vouchers, geographic provenience and GenBank accession numbers for the material included in this study. Herbarium acronyms follow the Index Herbariorum at <http://scweb.nybg.org/science2/IndexHerbariorum.asp>. Generic types are marked with an asterisk before the name.

Species	Herbarium vouchers and their geographic origin	Taxon distribution	trnT-trnL spacer	trnL-trnF spacer	psbA-trnH spacer
<i>Gyrocarpus americanus</i> subsp. <i>africanus</i> Kubitzki	S.S. Renner 2714 (MO), Tanzania, Amani Nature Reserve	Angola, Ethiopia, Mozambique, Namibia, Republic of South Africa, Tanzania, Zambia, Zimbabwe	GQ131096	GQ258825	GQ131062
<i>Gyrocarpus americanus</i> subsp. <i>africanus</i> Kubitzki	H. Kolberg 1174 (WIND), Namibia, near Tsumeb		GQ131097	GQ258826	GQ131063
* <i>Gyrocarpus americanus</i> subsp. <i>americanus</i> Jacq.	M.W. Chase 317 (NCU), Sri Lanka, Bot. Gard. Peradeniya	Australia (Queensland), Cocos Islands, Colombia, El Salvador, Fiji, Guatemala, Honduras, India, Kenya, Lesser Sunda Islands, Malaysia, New Caledonia, New Guinea, Nicaragua, Philippines, Samoa, Solomon Islands, Java, Tahiti, Tanzania, Tonga, Vanuatu, Venezuela, Vietnam	AF129025	AF012397	AF129054
* <i>Gyrocarpus americanus</i> subsp. <i>americanus</i> Jacq.	C. Vogl 3 (M), Venezuela, Maracay		GQ131095	GQ131031	GQ131061
<i>Gyrocarpus americanus</i> subsp. <i>glaber</i> Kubitzki	S.G. Razafimandimbison 595 (TAN), Madagascar, Toliara, Betioky, Special reserve Bezaha Mahafaly, near 'Station forestiere'	Madagascar	GQ131098	GQ131032	GQ131064
<i>Gyrocarpus angustifolius</i> (Verdc.) Thulin	M. Thulin 6378 (UPS), Somalia, Shabeellaha Dhexe	Ethiopia, Kenya, Somalia	GQ131099	GQ131033	GQ131065
<i>Gyrocarpus hababensis</i> Chiov.	J.J.E. De Wilde 7273 (UPS), Ethiopia, c. 95 km south of Harrar, west of Daletti	Djibouti, Eritrea, Ethiopia, Kenya, Somalia	GQ131100	GQ131034	GQ131066
<i>Gyrocarpus jatrophifolius</i> Domin	N.A. Zamora & B. Hammel 1883 (CR, MO), Costa Rica, San Jose, Mora	Costa Rica, Mexico	AF233597	AF232026	GQ131067
<i>Gyrocarpus jatrophifolius</i> Domin	M. Olson 800 (MEXU), Mexico, Chiapas	Costa Rica, Mexico	GQ131094	GQ131030	GQ131060
* <i>Hazomalantia voyronii</i> (Jum.) Capuron	S.G. Razafimandimbison 590 (TAN), Madagascar, Toliara, Sakaraha, Zombitsy National Park	Madagascar	GQ131108	GQ131044	GQ131078
<i>Hernandia albiflora</i> (C. T. White) Kubitzki	R.L. Jago 4689 (CNS), Australia, Queensland, Daintree Rainforest, Cape Tribulation	Australia (Queensland)	AF233598	AF232027	GQ131068
<i>Hernandia beninensis</i> Welw. ex Ficalho	M. Gen Madureira 22 (LISC), São Tomé Island	Bioko, São Tomé	–	GQ131036	GQ131070
<i>Hernandia bivalvis</i> Benth.	L. Bird 52 (BRI), Australia, Queensland, Pine Mt., near Ipswich	Australia (Queensland)	GQ131103	GQ131038	–
<i>Hernandia didymantha</i> Donn. Sm.	R. Aguilar 5590 (INB), Costa Rica, La Selva	Costa Rica	GQ131101	GQ131035	GQ131069
<i>Hernandia guianensis</i> Aubl.	S.S. Renner 2833 (M), cultivated at Bot. Gard. Munich, seed probably from Venezuela	Brazil (Amazonas), Trinidad, Venezuela	AF233599	AF232028	AF261993
<i>Hernandia lychinifera</i> Grayum & N. A. Zamora	W.S. Alverson & D. Rubio 2238 (MO), Ecuador, Los Rios	Ecuador	GQ131106	GQ131042	GQ131074

Table 1 Continued

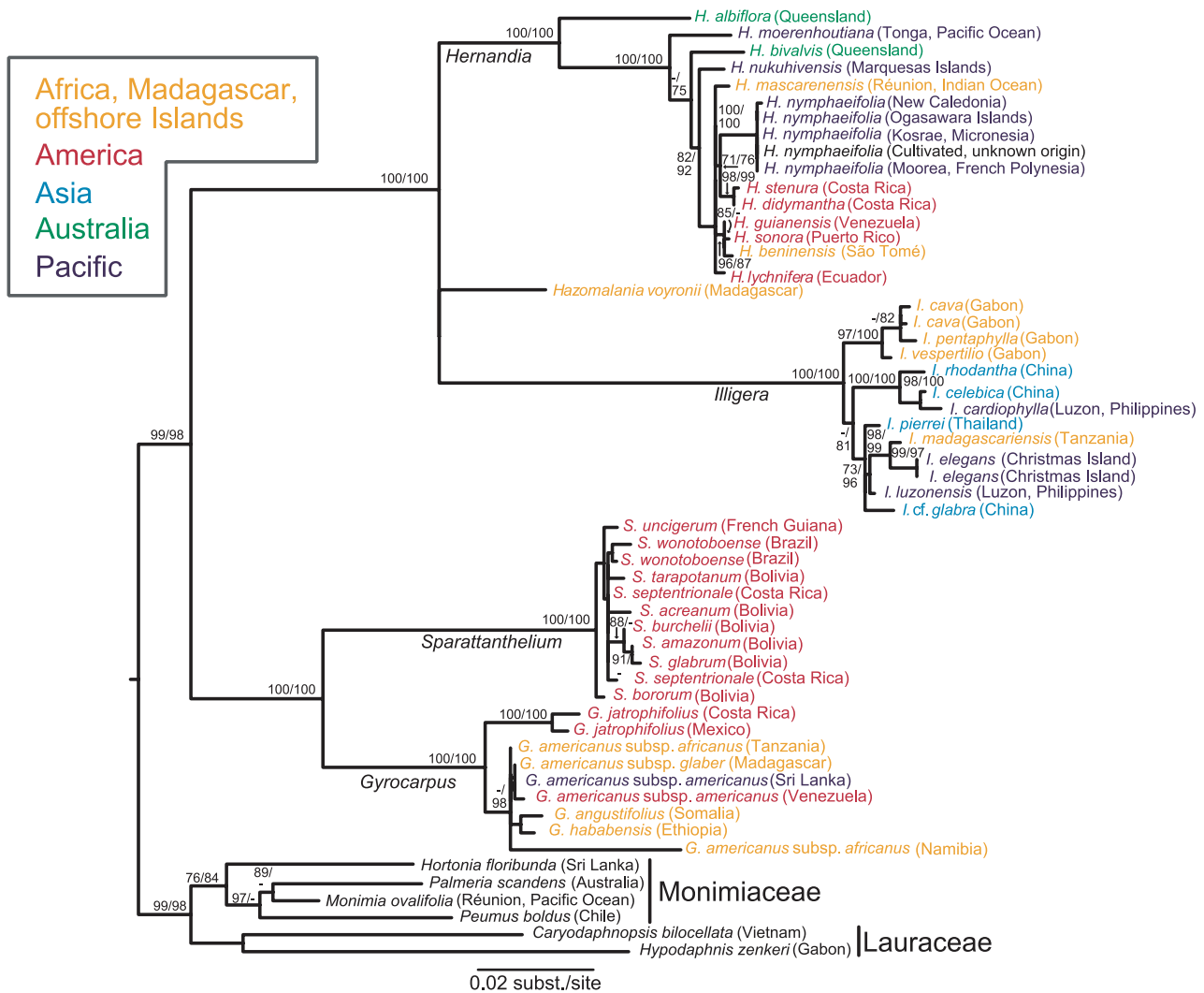
Species	Herbarium vouchers and their geographic origin	Taxon distribution	<i>trnT-trnL</i> spacer	<i>trnL-trnF</i> spacer	<i>psbA-trnH</i> spacer
<i>Hernandia mascarenensis</i> (Meisn.) Kubitzki	D. Strasberg sin. num. (REU), Réunion, Marelongue Nature Reserve	Mascarene Islands: Mauritius and Réunion	GQ131104	GQ131039	GQ131072
<i>Hernandia moerenhoutiana</i> Guill.	R. Whitten 6 January 1984 (BRI 395791), cultivated at Bot. Gard. Brisbane, originally coll. by Vera Scarf-Johnson on Tonga	Cook Islands, Fiji, Solomon Islands, Samoa, Santa Cruz Island, Tahiti, Tonga,	AF129026	AF052198, GQ131040	AF129055
<i>Hernandia nukuhivensis</i> F. Br.	D. Lorence 6267 (PTBG), cultivated at Natl. Trop. Bot. Gard. Hawai'i (950692), seeds collected on Nuku Hiva, Marquesas	Nuku Hiva (Marquesas Islands)	GQ131105	GQ131041	GQ131073
<i>Hernandia nymphaeifolia</i> (C. Presl) Kubitzki (incl. <i>Hernandia peltata</i> Meisn. in DC.)	D. Lorence 7598 (MO, PTBG), cultivated at Natl. Trop. Bot. Gard. (740137-001) from seed collected from cultivated plants on Kauai, parent plant from Moorea, French Polynesia	Andaman Islands, Borneo, Cambodia, Cocos Islands, Comoros, Java, Kenya, Lakshadweep, Lesser Sunda Islands, Madagascar, Malaysia, Maldives, Maluku Islands, Mascarene Islands, New Caledonia, New Guinea, Nicobar Islands, Philippines, Ryukyu Islands, Seychelles, Sri Lanka, Sulawesi, Sumatra, Taiwan, Tanzania, Thailand, Vietnam	GQ258836	GQ258827	GQ131075
<i>Hernandia nymphaeifolia</i> (C. Presl) Kubitzki (incl. <i>Hernandia peltata</i> Meisn. in DC.)	R. Kreutzer P/0130 (M), cultivated at Bot. Gard. Munich (flowered in July 2005)		AF233601	AF232030	AF261994, GQ131076
<i>Hernandia nymphaeifolia</i> (C. Presl) Kubitzki (incl. <i>Hernandia peltata</i> Meisn. in DC.)	D. Lorence 7734 (MO), cultivated at Natl. Trop. Bot. Gard. (960860) from seeds coll. in Kosrae, Micronesia		GQ258837	GQ258828	GQ258841
<i>Hernandia nymphaeifolia</i> (C. Presl) Kubitzki (incl. <i>Hernandia peltata</i> Meisn. in DC.)	G. McPherson & J. Munzinger 18278 (MO), New Caledonia, Province du Sud		GQ258838	GQ258829	GQ258842
<i>Hernandia nymphaeifolia</i> (C. Presl) Kubitzki (incl. <i>Hernandia peltata</i> Meisn. in DC.)	T. Fujita KITA 01135, Japan, Ogasawara Islands, Kita Iwo Jima, Ishino Village		-	-	GQ258843
<i>Hernandia peltata</i> Meisn. in DC.) * <i>Hernandia sonora</i> L.	J. Ramirez sin. num., Puerto Rico, Rio Piedras Arboretum	Antilles, Costa Rica, Guatemala, Honduras, Mexico	GQ131107	GQ131043	GQ131077
<i>Hernandia stenura</i> Standl.	R. Aguilar 5592 (INB), Costa Rica, La Selva	Costa Rica, Guatemala, Honduras, Mexico	GQ131102	GQ131037	GQ131071

Table 1 Continued

Species	Herbarium vouchers and their geographic origin	Taxon distribution	trnT-trnL spacer	trnL-trnF spacer	psbA-trnH spacer
<i>Illigera cava</i> Breteler & Wieringa	(1) J. Wieringa, T. Nzabi & J.-N. Bousiengui 4407 (WAG) (TYPE), Gabon, Ngoumié, near Ikobey (2) J. Wieringa, T. Nzabi & J.-N. Bousiengui 4647 (WAG) (Paratype), Gabon, Ngoumié, near M'bigou	Congo, Gabon	(1) – (2) GQ131109	(1) GQ131045 (2) GQ131046	(1) GQ131079 (2) GQ131080
<i>Illigera cardiophylla</i> Merr.	H. Hallier sin. num. (HBC), Philippines, Southern Luzon	Philippines	GQ131114	GQ131052	GQ131087
<i>Illigera celebica</i> Miq.	C.J. Chen sin. num. (HITBC), China, Yunnan, Menglun Natural Reserve, near Xishuangbanna Trop. Bot. Gard.	Borneo, Cambodia, New Guinea, Philippines, Southern China, Sulawesi, Thailand, Vietnam	AY786129, GQ131115	AY786140, GQ131053	GQ131088
<i>Illigera elegans</i> Duyfjes	(1) D.J. Du Puy Cl. 46 (CBG), Christmas Island (2) B.A. Mitchell 129 (CBG), Christmas Island	Christmas Island, Southern Java	(1) – (2) –	(1) – (2) GQ131050	(1) GQ131085 (2) GQ131084
<i>Illigera</i> cf. <i>glabra</i> Y.R. Li	J. Wen <i>et al.</i> 2133 (US), China, Yunnan, Yingjiang	China, West Yunnan	GQ131117	GQ131055	GQ131090
<i>Illigera luzonensis</i> (Presl) Merr.	E. Fernando 1602 (LBC), Philippines, Makiling Forest Reserve	Ishigaki (Ryukyu Islands), Philippines, Taiwan	AF129030	AF052199	AF129057
<i>Illigera madagascariensis</i> H. Perrier	B. Mhoro 5696 (MO), Tanzania, Morogoro, Ulanga	Madagascar, Tanzania	GQ131112	GQ131049	GQ131083
<i>Illigera pentaphylla</i> Welw.	J.J. Wieringa, T. Nzabi & J.-N. Bousiengui 4634 (WAG), Gabon, Ngoumié, near M'bigou	Angola, Cameroon, Central African Republic, Congo, Côte d'Ivoire, Gabon, Ghana, Guinea, western Kenya, Liberia, Nigeria, Sierra Leone, western Tanzania, Uganda	GQ131111	GQ131048	GQ131082
<i>Illigera pierrei</i> Gagnep.	J.F. Maxwell 01-12 (CMU, MO), Thailand, Khao-Yai-National-Park, Nakorn Nayok Provinz	Thailand, Vietnam	GQ131113	GQ131051	GQ131086
<i>Illigera rhodantha</i> Hance	Y. Hua-Gu 115-15 (IBSC, MO), China, Guangdong, Guangzhou	Cambodia, Laos, Vietnam	GQ131116	GQ131054	GQ131089
<i>Illigera vesperitilo</i> (Benth.) Baker f.	J.J. Wieringa, T. Nzabi & J.-N. Bousiengui 4578 (WAG), Gabon, Ngoumié, near Mimongo	Cameroon, Côte d'Ivoire, Gabon, Ghana, Liberia, Sierra Leone,	GQ131110	GQ131047	GQ131081
<i>Sparattanthelium acreanum</i> Pilger	D. Daly 6567 (LPB), Bolivia, Beni, José Ballivián Province	Bolivia, Brazil	GQ258839	GQ258830	GQ258844

Table 1 Continued

Species	Herbarium vouchers and their geographic origin	Taxon distribution	<i>trnT-trnL</i> spacer	<i>trnL-trnF</i> spacer	<i>psbA-trnH</i> spacer
<i>Sparattanthelium amazonum</i> Mart.	S. Bergeron 365 (LPB), Bolivia, Beni Province, Marmoré, Alto Ivón	Bolivia, Brazil, Guatemala, Honduras	–	GQ258831	GQ258845
<i>Sparattanthelium bororum</i> Mart.	S. Beck 12235 (LPB), Bolivia, Nuflo de Chávez	Bolivia, Brazil	–	GQ258832	GQ258846
<i>Sparattanthelium burchellii</i> Rusby	S. Beck 20113 (LPB), Bolivia, Pando	Bolivia	–	GQ258833	GQ258847
<i>Sparattanthelium glabrum</i> Rusby	S. Beck 19338 (LPB), Bolivia, Pando	Bolivia, Brazil, Colombia, Peru	–	GQ258834	GQ258848
<i>Sparattanthelium septentrionale</i> Sandw.	(1) R. Aguilar 5589 (INB), Costa Rica, La elva (2) B. Hammel 22270 (INB), Costa Rica, Puntarenas, Camaronal, Reserva biológica Carara	Costa Rica, Mexico	(1) AF232031 (2) GQ131027	(1) AF232031 (2) GQ131027	(1) GQ131056 (2) GQ131057
<i>Sparattanthelium tarapotanum</i> Meisn. in Mart.	G. Caity 138 (LPB), Bolivia, Beni	Brazil, Peru	GQ258840	GQ258835	GQ258849
<i>Sparattanthelium uncigerum</i> (Meisn.) Kubitzki	M.F. Prévost 4096 (MO), French Guiana, Cayenne	French Guiana, Suriname	GQ131092	GQ131028	GQ131058
<i>Sparattanthelium wonotoense</i> Kosterm.	(1) S.S. Renner 2832 (M), cultivated at Munich Bot. Gard. (97/1311w), from seed collected by K. Kubitzki, Brazil, Roraima, Boa Vista = K. Kubitzki & T. Feuener 97-21 (HBG) (2) W. Rodrigues 9140 (INPA), Brazil (Amazonas), Manaus, Adolpho Ducke Forest	Brazil, British Guiana, Suriname	(1) AF129043	(1) AF053342	(1) AF129070
<i>Caryodaphnopsis bilocellata</i> van der Werff & N. K. Dao	H. van der Werff <i>et al.</i> 14195 (MO), Vietnam, Ninh Binh	Vietnam	AF232603	AF232032	AF261995
<i>Hortonia floribunda</i> Wight ex Arn.	V. Karunaratne s.n., Sri Lanka, wild-collected at Hakgala, cultivated at Peradeniya BG	Sri Lanka	AF129028	AF040683	AF129071
<i>Hypodaphnis zenkeri</i> Stapf	G. McPherson 16184 (MO), Gabon, Ogooué-Ivindo	Cameroon, Gabon	AF232607	AF232036	AF261998
<i>Monimia ovalifolia</i> Thou.	D. Strasberg 417 (REU), Réunion Island	Réunion	AF129038	AF054896	AF129065
<i>Palmeria scandens</i> F. Muell.	J. Bradford <i>et al.</i> 878 (MO), Australia, New South Wales	New South Wales to Northern Queensland	AF129040	AF052200	AF129067
<i>Peumus boldus</i> Molina	Cultivated at Edinburgh Bot. Gard. (19870707)	Chile, Patagonian part of Argentina	AF129041	AF012403	AF129068



**Figure 1** Maximum likelihood (ML) tree for Hernandiaceae and outgroups obtained from 2210 aligned nucleotides of chloroplast DNA. Values at the nodes indicate ML bootstrap support > 70 from the manual alignment followed by support from the PRANK alignment (both from 100 replicates). *Hazomalania* was placed in a polytomy with *Illigera* and *Hernandia* because its sister group relationship with each has no statistical support. Countries listed refer to the origin of the respective voucher. Complete species ranges are given in Table 1.

of *Gyrocarpus* dates to 31 Ma, that of *Hernandia* to 50 Ma, that of *Illigera* to 27 Ma, and that of *Sparattanthelium* to 14 Ma. The divergence of *Hazomalania* from *Illigera* or *Hernandia* dates minimally to the Selandian (Palaeocene).

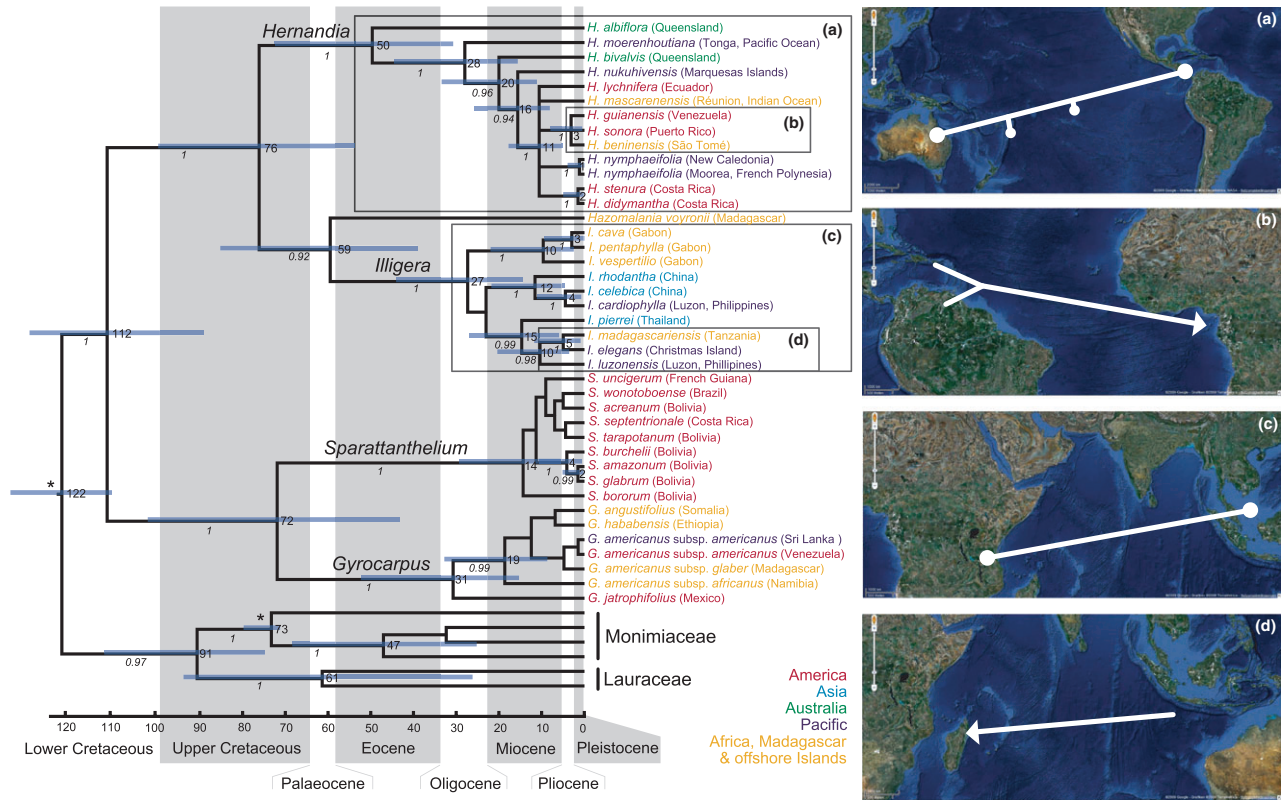
As regards the pantropical species *Gyrocarpus americanus* (Kubitzki, 1969), the molecular data show that two African species, *Gyrocarpus angustifolius* and *Gyrocarpus hababensis*, are embedded among accessions of *G. americanus* in a clade that has 98% bootstrap support (Fig. 1). The other extremely widespread species, *Hernandia nymphaeifolia*, represented by four accessions from New Caledonia, Micronesia, French Polynesia and the Ogasawara Islands, so far is monophyletic; however, we lack samples of this species from Madagascar, Kenya and Tanzania.

Parsimony-based ancestral area reconstruction (data not shown) yielded South America as the region for the common

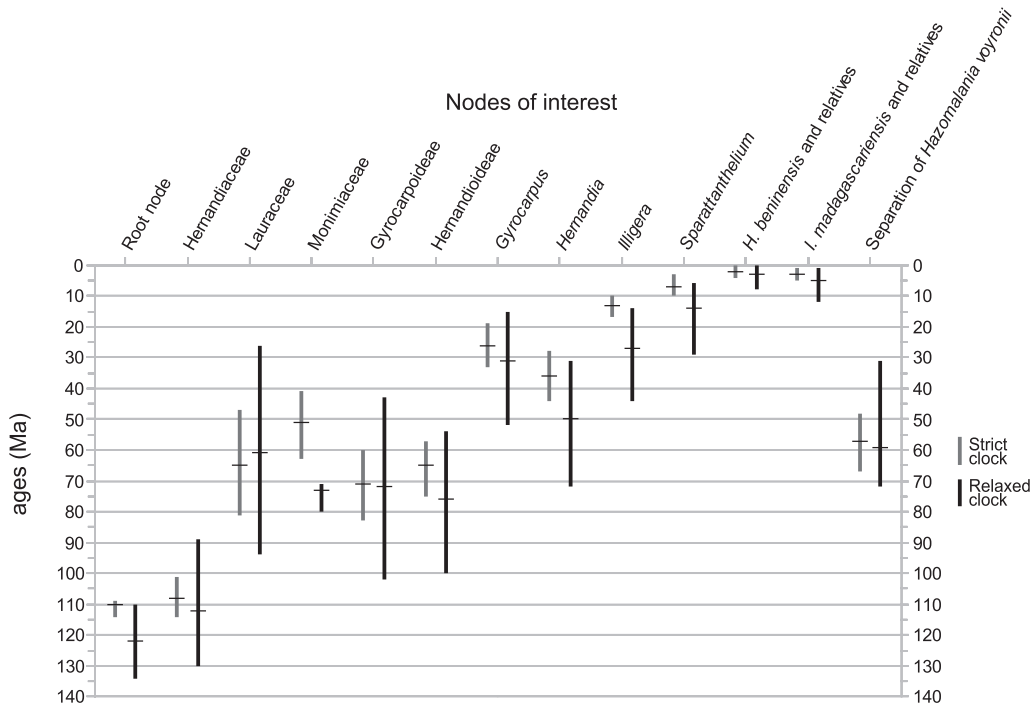
ancestor of *Sparattanthelium*, America or Africa for *Gyrocarpus* as well as for the *Gyrocarpus/Sparattanthelium* clade, and no clear ancestral areas for *Illigera*, *Hazomalania* and *Hernandia*.

## DISCUSSION

The deepest divergence in Hernandiaceae is between the South American/African *Gyrocarpus* and *Sparattanthelium* and the mainly African/Asian *Hernandia*, *Hazomalania* and *Illigera*. This split is 112 (89–130) Myr old and corresponds to the former families Gyrocarpaceae and Hernandiaceae, now the subfamilies Gyrocarpoideae and Hernandioideae (Shutts, 1960; Kubitzki, 1969; Takhtajan, 1987). Other evidence that Hernandiaceae are about 100 Myr old comes from the angiosperm-wide molecular clock study of Wikström *et al.* (2001, their table 2, ML-branch length column), who dated the



**Figure 2** Chronogram for 46 accessions from 36 species of Hernandiaceae obtained under a relaxed clock model with two calibration points (marked by asterisks). Node heights are the median ages, with 95% posterior density intervals shown as grey bars. Maps (a) to (d) on the right show the respective dispersal events in the chronogram. Arrows indicate the inferred dispersal direction; balls are used when the direction is unclear.



**Figure 3** Estimated node ages for the crown groups or splits named along the top under a strict clock (grey bars) and a relaxed clock (black bars), each with 95% confidence intervals. Horizontal lines indicate median values (cf. Fig. 2).

divergence of *Gyrocarpus* (the only Hernandiaceae included) from the remaining Laurales in their tree as  $95 \pm 7$  Myr old. The only calibration used in this analysis was the divergence of Fagales from Cucurbitales, which was set to 90 Ma, based on the oldest Fagales fossils.

Given the Cretaceous age and occurrence of the Hernandiaceae outgroups Monimiaceae and Lauraceae in both Laurasia and Gondwana (Eklund, 2000; Poole & Gottwald, 2001; Renner, 2005b for a summary), the geographic origin of Hernandiaceae cannot be inferred with confidence. Without the benefit of a molecular species tree and divergence dating, Kubitzki (1969) hypothesized that Hernandiaceae originated in East Gondwana. This was probably based mostly on the Madagascan species *Hazomalania voyronii* (in 1969 still classified as *Hernandia voyronii*), which combines the apically hinged anther valves of *Gyrocarpus* and *Sparattanthelium* with features otherwise found in *Hernandia*. Kubitzki thought that the break-up of East Gondwana left *Hazomalania* isolated on Madagascar as a kind of ancient relict, while the remainder of *Hernandia* diversified in Australia, giving rise to *H. albiflora* and *H. bivalvis* (compare our Fig. 1). This scenario is unlikely, however, because the movement of Madagascar relative to Africa began in the middle Jurassic, about the same time as the initial break-up of Gondwana. Sea-floor spreading ceased when Madagascar assumed its present position in the Early Cretaceous. These events greatly pre-date the evolution of *Hazomalania* (Fig. 2), whether it diverged from *Illigera* or from *Hernandia*.

Even if the break-up of East Gondwana pre-dates the evolution of Hernandiaceae, the deepest split in the family does coincide with the break-up of West Gondwana (South America and Africa), which occurred 100–110 Ma (McLoughlin, 2001; Lomolino *et al.*, 2006). The common ancestor of *Gyrocarpus* and *Sparattanthelium* (i.e. the Gyrocarpoideae) is inferred to be 72 (43–102) Myr old and could have evolved in South America. *Sparattanthelium* is now endemic in South America, whereas *Gyrocarpus* is widespread as a result of long-distance dispersal. Long-distance dispersal has long been postulated for *G. americanus* (Guppy, 1906; Good, 1953; Kubitzki, 1969; White, 1983) and is supported by our molecular clock age estimates (Fig. 2). Kubitzki also thought that *Gyrocarpus jatrophifolius* diverged from African 'ancestral stock' before the break-up of Africa and South America, but this is rejected by the inferred 31 (15–52) Ma estimate for the divergence of this species from the remaining species of *Gyrocarpus* (Fig. 2).

Within his broadly conceived species *G. americanus*, Kubitzki (1969) distinguished eight subspecies, namely three in Madagascar, one each in tropical East and West Africa, one in tropical Australia, and one in Malesia, with the eighth being the typical subspecies *G. americanus* subsp. *americanus* supposedly originating in the Palaeotropics and having reached the Neotropics via trans-Pacific dispersal. Most of these subspecies are rarely collected or are not recognized as such, and we could not obtain sequences for all of them. With the current sampling, the monophyly of *G. americanus* remains

unclear: the African *G. angustifolius* and *G. hababensis* (Burger, 1990; Thulin, 1991) are part of a polytomy with different accessions of *G. americanus* (Fig. 1).

Other biogeographically interesting findings concern *Hernandia* and *Illigera*. Kubitzki (1969) subdivided core *Hernandia* (excluding *H. voyronii* and *H. albiflora*) into three species groups, based mainly on fruit and leaf shape, and hypothesized that all three reached Central America from Polynesia, giving rise to the eight species of *Hernandia* in Central America and the Greater Antilles (one of them described after Kubitzki's treatment; Grayum & Zamora, 1991). Although our data do not support Kubitzki's species groups, his inference of trans-Pacific and trans-Atlantic dispersal within *Hernandia* appears correct (Fig. 2a,b). Specifically, Kubitzki hypothesized that *H. guianensis* from Trinidad, Venezuela and the Guianas might be a progenitor of *H. beninensis*, endemic on São Tomé and Bioko – the former an oceanic island *c.* 14 Myr old and the latter connected to Africa during the most recent glacial period, 10,000 years ago (Lee *et al.*, 1994). The ML tree topology and dates from the molecular clocks fit with this hypothesis. However, *H. beninensis* and *H. guianensis* are in a trichotomy with *H. sonora* from the Greater Antilles, a species that Sprague (1909–1910) suspected might be the progenitor of *H. beninensis*. Another example of a relatively young divergence is *H. mascarenensis*, endemic on Mauritius and Réunion, which are 7–8 and 2–3 Myr old, respectively (McDougall, 1971).

Whereas *Hernandia* exhibits both trans-Pacific and trans-Atlantic dispersal events, *Illigera* includes two trans-Indian Ocean dispersals. The older of these involves the separation of the Asian and African *Illigera* lineages (Fig. 2c), the latter today comprising three species, namely *Illigera cava* in Gabon and Congo, *Illigera vespertilio* from Sierra Leone to West Ghana and south to Gabon, and *Illigera pentaphylla* from Sierra Leone to western Kenya and Tanzania (Breteler & Wieringa, 2008). The more recent of the two inferred trans-Indian Ocean dispersal events involves the sister species pair *Illigera elegans* and *I. madagascariensis* (Fig. 2d). The inferred young age (*c.* 3 Ma) rejects Kubitzki's (1969) suggestion that *I. madagascariensis* might date back to the break-up of East Gondwana. However, when Kubitzki did his study, the Christmas Island species, *I. elegans* (Duyfjes, 1994), was not yet known, and so he was comparing *I. madagascariensis* only to *I. novoguineensis* from New Guinea, with which it shares similar stamens (as does *I. elegans*). We could not include *I. novoguineensis* because the type of this species is lost, and the species has not been re-collected for about 100 years (Takeuchi, 2000). Simulated Eocene wind currents and surface ocean currents show that Madagascar has for a long time been at the heart of the strongest gyre on Earth, implying that rafting across the Indian Ocean may have been a dominant means of overseas dispersal in the Cenozoic era (Ali & Huber, 2010; the focus of this study is the arrival in Madagascar from Africa, but the shown data for currents cover the entire Indian Ocean).

Relative to its size (62 species), Hernandiaceae includes a striking number of transoceanic disjunctions resulting from

long-distance dispersal, and if we had included the 10 species of *Hernandia* from Cuba, Jamaica, Polynesia, Haiti, Tahiti, Indochina and Sumatra (Materials and Methods), we might have inferred an even greater number of old or recent long-distance dispersal events. However, none of the inferred east-to-west or west-to-east dispersal events is unique. Dispersal from the Caribbean or South America to São Tomé has been inferred also for the otherwise Neotropical genus *Cayaponia* (Cucurbitaceae), which has a single West African species estimated to be 2–5 Myr old (Duchen & Renner, in press). Another 109 trans-Atlantic distributions at the genus level are listed in Renner (2004) of which many also appear due to long-distance dispersal. Disjunct ranges that encompass the tropical Pacific and the Neotropics are known from at least 20 angiosperm genera or tribes (van Steenis, 1962; Heads, 2003; M. Heads, Buffalo Museum of Science, pers. comm., August 2009), and there is evidence for a specific New Caledonia–Melanesia–tropical South America track (Heads, 2006, 2009). Dispersal between Madagascar, Indian Ocean islands, Malesia and Australia has long been regarded as a fact (Thorne, 1973), and at least nine African–Asian–Australian genus-level clades have been dated with molecular clocks (reviewed in Li *et al.*, 2009). Divergence times inferred in these studies range from 2 to 35 Ma, and, as in Hernandiaceae, diaspore dispersal apparently occurred in both directions, east to west and west to east.

Depending on the species, Hernandiaceae fruits are dispersed by wind, bats, birds, fresh water or salt water (Guppy, 1906; Ridley, 1930; van der Pijl, 1957; Kubitzki, 1969; White, 1983; Hacker, 1990), but the mechanism of crossing oceans may have been floating mats of vegetation (Van Duzer, 2004, 2006). Hernandiaceae flowers are pollinated by bees or flies (in the nectar-offering flowers of *Illigera* and *Hernandia*) or by wind (in the small flowers of *Sparattanthelium* and *Gyrocarpus*). Little or nothing is known about soil requirements, mycorrhizal associations and other niche parameters. It is clear, however, that the widespread species of Hernandiaceae are capable of establishing and persisting under an unusually broad range of conditions. White (1983, p. 402), who studied *Gyrocarpus* in Africa, summarized his findings thus, 'Ecologically, *G. americanus* is very versatile. It occurs in a wide range of forests, woodlands, bushlands, and thickets.'

## CONCLUSIONS

The balanced shape of the Hernandiaceae phylogeny (Fig. 1) is unusual. The consensus from several reviews (cited in Heard & Mooers, 2002) is that, in real phylogenies, sister lineages tend to differ in diversity. Often there are a few early-diverging (usually species-poor) lineages, followed by one or a few species-rich crown clades. Computer simulation of diversification shows that random mass extinctions, coupled with evolving among-lineage variation in speciation rates, increase the imbalance of phylogenetic trees. That the two deepest lineages of the Hernandiaceae have persisted and repeatedly produced recent small radiations may partly be the result of an

above-average ability to establish successfully following long-distance dispersal to geographically isolated regions, which may have retarded extinction while at the same time providing opportunities for radiations into new habitats.

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## BIOSKETCHES

**Ingo Michalak** is currently a PhD student in Frankfurt, where he is working on the evolution of *Fosterella* (Bromeliaceae). This study represents his diploma thesis.

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**Susanne S. Renner** is a professor of biology at the University of Munich and director of the herbarium and botanical garden. This study on Hernandiaceae is part of a broader focus on the biogeography of the basal angiosperm clade Laurales.

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