

# Infra-familial phylogeny of Urticaceae, using chloroplast sequence data

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**Abstract.** Recent studies of the phylogeny of the Urticales have suggested that Cecropiaceae, at least in part, should be included within Urticaceae. To evaluate phylogenetic relationship between these two taxa, together with the consequences on tribal concepts (of the Urticaceae) of including any part of Cecropiaceae within Urticaceae, we analysed sequence variation for larger databases of both *rbcL* and *trnL-F* sequences. We conclude that the circumscription of Urticaceae needs to be broadened to include taxa of Cecropiaceae, with Urticeae here expanded to include *Poikilospermum*. The tribal placement of *Cecropia* and *Coussapoa* (both Cecropiaceae) remains unclear but their affinities are with the Forsskaoleae, Parietarieae and Boehmerieae. The circumscription of Boehmerieae should be changed to exclude *Myriocarpa*, with the latter genus exhibiting a strong relationship with Elatostemeae. The intratribal structure of the Elatostemeae is unclear because of the uncertainty of the position of *Myriocarpa*, but there is a strong suggestion that the tribe consists of two sister taxa, one of Elatostemeae *sensu stricto*, including *Elatostema* and *Procris*, and the other consisting of *Lecanthus* and *Pilea*. It is reconfirmed that *Pellionia* should not be recognised as a distinct genus and is here regarded as a synonym of *Procris*, rather than part of the synonymy of *Elatostema*, as previously suggested. *Boehmeria*, *Cypholophus* and *Laportea* as currently circumscribed are all paraphyletic. There are three evolutionary lineages in the Urticaceae revealed by our study, namely (1) Boehmerieae–Cecropieae–Forsskaoleae–Parietarieae, (2) Urticeae and (3) Elatostemeae.

## Introduction

The taxa circumscribed in the Urticaceae, Moraceae and Cecropiaceae have been commonly regarded as very closely related to each other and have been united into one group by various authors, from Gaudichaud (1830) until Bentham and Hooker (1883). However, Weddell (1854, 1856, 1869), Engler (1894) and until recently, all subsequent taxonomists have recognised these three groups as distinct families, with Weddell's circumscription remaining remarkably unchallenged, being widely followed and supported by later researchers (e.g. Berg 1977, 1989; Friis 1989, 1993). Berg (1977, 1989) provided an overview of the macromorphological characters that are useful for distinguishing these families from each other. Friis (1989, 1993) briefly discussed ordinal relationships based on previous classical taxonomic approaches.

Modern phylogenetic studies involving the Urticaceae have mostly concentrated on ordinal relationships, with the circumscription of the Urticales remaining relatively stable since the middle of 1800s when Weddell (1856) included Artocarpeae, Cannabineae, Moreae, Ulmaceae and Urticaceae in the order. This classification was used by Dahlgren (1989), Thorne (1992) and Takhtajan (1997). Cronquist (1968, 1981) united Urticaceae with Moraceae, Cannabaceae, Ulmaceae and Barbeyaceae, largely on the basis of the single ovule,

stipules usually present, nodes tri- or multilacunar, flowers clustered and perianth usually much reduced in size. The recent reconstructed higher-level phylogenies of Chase *et al.* (1993), using the DNA sequences of the chloroplast gene *rbcL*, support the monophyly of the Urticales with Cannabaceae, Moraceae, Ulmaceae and Urticaceae included. However, subsequent analyses including additional loci (Angiosperm Phylogeny Group 1998; Soltis *et al.* 2000; Stevens 2001+) and non-molecular data (Judd *et al.* 1999) have shown this group to be nested within the Rosales. All of these modern authors, by using morphological and molecular characters, consider Cannabaceae, Celtidaceae, Cecropiaceae, Moraceae and Ulmaceae to be the closest families to Urticaceae.

Sytsma *et al.* (2002) provided information on the family concepts and inter- and intrafamilial relationships within the Urticales based on chloroplast DNA sequences of *rbcL*, *trnL-F*, and *ndhF*. They examined a total of 85 taxa, of which there were 46 urticalean rosids and 39 taxa from other members of the Rosales, plus the Cucurbitales, Fabales, Fagales and Oxalidales. Their work supported the monophyly of Moraceae, Urticaceae (including Cecropiaceae) and Cannabaceae (including Celtidaceae), although support for the latter family was not as strong as support for the former two. Datwyler and

Weiblen (2004) studied the phylogeny of Moraceae (together with that of Cecropiaceae and Urticaceae), on the basis of *ndhF* sequence data, and concluded that the Cecropiaceae plus Urticaceae formed a strongly supported clade (100% bootstrap; +21 decay value); however, Cecropiaceae was paraphyletic owing to the position of *Poikilospermum*. Hadiah *et al.* (2003) also supported the monophyly of the Urticaceae on the basis of *rbcL* data and found strong support (with a 95% jackknife value) for a sister relationship between the Urticaceae and the clade comprising Moraceae and Cannabaceae. However, representatives of the Cecropiaceae were not included in their study. In a study of the phylogeny of the genus *Pilea* on the basis of *trnL-F* data, Monro (2006) examined 109 taxa (95 ingroup, mostly *Pilea* species; 14 outgroup; with non-urticalean taxa represented by *Trema integerrima*, Celtidaceae, and *Cecropia obtusifolia*, Cecropiaceae) and supported the conclusion of Sytsma *et al.* (2002) that *Poikilospermum* should be included within the Urticaceae; however, Datwyler and Weiblen (2004), by using *ndhF* data, placed this genus as sister to the family. Although both Sytsma *et al.* (2002) and Monro (2006) concluded that the Cecropiaceae is polyphyletic, the former authors concluded that both *Cecropia* (on the basis of *C. palmata*) and *Poikilospermum* arise within the Urticaceae, whereas, by inference, Monro concluded that *Cecropia* (on the basis of *C. obtusifolia*) is sister to this family. These conclusions differ from those of Friis (1989), who maintained the familial distinctness of the Cecropiaceae as proposed by Berg (1978; also refer Kubitzki 1993). The latter authors characterised the Cecropiaceae as having flowers with a basal ovary and stamens that are straight in bud or sometimes inflexed and straightening gradually at anthesis. They included the following genera within this family: *Cecropia*, *Coussapoa*, *Musanga*, *Myrianthus*, *Poikilospermum* and *Pourouma*.

Gaudichaud (1830) provided the first infra-familial classification of the Urticaceae (as 'Urticées vraies'). He grouped the genera of his 'True Urticaceae' into six tribes (refer Conn and Hadiah 2009), one of which included *Cecropia* and *Coussapoa* (as Cecropieae; regarded as Cecropiaceae, in part, *sensu* Berg 1978). Weddell (1854, 1856, 1869) provided a detailed circumscription of the five tribes that he recognised, namely Boehmerieae, Elatostemeae (initially as 'Lecantheae', later as 'Procridae'; refer Conn and Hadiah 2009), Forsskaoleeae (as 'Forskahleae'), Parietarieae and Urticeae (as 'Urearee'). As mentioned above, he separated *Cecropia* and *Coussapoa* from the Urticaceae and placed them in the separate family Cecropiaceae. Friis (1989, 1993) provided the most recent detailed comparison of morphological features of the Urticaceae at the familial, infra-familial and generic levels. His work provided broad support for and acceptance of Weddell's classification of the family and tribes. Friis (1989) characterised the Urticaceae as having flowers with a basal ovary and stamens that are elastically and simultaneously reflexing. Within the family, he circumscribed five tribes, namely Boehmerieae, Elatostemeae (as 'Lecantheae'), Forsskaoleeae (as 'Forsskaoleae'), Parietarieae and Urticeae. However, he questioned the distinctiveness of the Boehmerieae, Forsskaoleeae and Parietarieae, and suggested further work may lead to a taxonomic rearrangement at the

tribal level (Friis 1989). He also questioned the taxonomic position of *Myriocarpa* in the Boehmerieae.

A comparative carpological study of 45 genera or generic groupings of the Urticaceae by Kravtsova (2007) recognised three major lineages and these were proposed as new subfamilies, namely Boehmerioideae (characterised by having fruits 4- or 5-partite; integument of anthocarp mostly tubular; pericarp glabrous or hairy, incompletely sclerified; exocarp lacking hydrocites; and stinging hairs absent), Lecanthoideae (having fruits (2-)4- or 5-partite; integument of anthocarp fleshy; pericarp glabrous, incompletely sclerified; exocarp with many hydrocites; and stinging hairs absent) and Urticoideae (having fruits 4-partite; pericarp glabrous, mostly completely sclerified; exocarp with hydrocites often present; and stinging hairs usually present). Three tribes were recognised in the Boehmerioideae, namely Boehmerieae (with integument tubular and pericarp partially sclerified), Forsskaoleeae (as 'Forsskaoleae') (integument compact and closely acumbent) and Parietarieae (integument tubular and pericarp fully sclerified). Her placement of genera within these tribes is similar to that of Friis (1993), but with some notable exceptions. *Hemistylus* Benth. and *Rousselia* Gaudich. (=Parietarieae *sensu* Friis 1994) are included in the Boehmerieae (Kravtsova 2007), together with *Archiboehmeria* C.J.Chen. The Boehmerieae is divided into two subtribes, namely Boehmeriinae Kravtsova (with fruit wall containing only one conductive fascicle) and Myriocarpinae Kravtsova (with fruit wall containing only two conductive fascicles). The latter subtribe consists of *Myriocarpa* only). *Touchardia* Gaudich. (=Boehmerieae *sensu* Friis 1993) is moved to the new monogeneric tribe Touchardieae Kravtsova (characterised by drupiferous fruits) as part of the subfamily Lecanthoideae Kravtsova, together with Elatostemeae (as 'Lecantheae') (having nut-like fruits, rarely drupiferous). Kravtsova (2007) recognises both *Achudemia* Blume (= *Pilea sensu* Friis 1993) and *Pellionia* Gaudich (here regarded as a synonym of *Procris*) as distinct genera. The generic composition of the Urticoideae is identical to Urticeae (*sensu* Friis 1993).

Phylogenetic reconstruction of the Urticaceae by using morphological data (Beaman 2000, fig. 3-3), as part of a study of *Elatostema* from Mt Kinabalu (Malaysia), provided support for the monophyly of Elatostemeae (as 'Lecantheae') and Urticeae, but suggested that the Boehmerieae is polyphyletic. Hadiah *et al.* (2003) found no support for the monophyly of Boehmerieae or Elatostemeae (as 'Lecantheae') in their analysis of *rbcL* sequence data. *Myriocarpa longipes* was placed sister to Urticeae plus Elatostemeae with moderate support (79% jackknife), rather than with species of *Boehmeria* (Boehmerieae); *Pilea pumila* was grouped with *Urtica dioica* (89% jackknife) rather than with species of *Elatostema* and *Procris* (Elatostemeae). Likewise, on the basis of *trnL-F* data, Hadiah *et al.* (2003) found strong support (91% jackknife) for *Myriocarpa longipes* as sister to species of *Elatostema* and *Procris* (Elatostemeae). *Pilea* species were included with *Urtica dioica* (Urticeae) rather than with other species of Elatostemeae; however, there was no support for this clade (51% jackknife), possibly a consequence of the limited sample of *Pilea* used in their analysis. Monro (2006) concluded that the following two infra-familial groupings could be recognised within the Urticaceae: a clade including Boehmerieae (excluding *Myriocarpa*), Forsskaoleeae and

Parietarieae (Monro 2006, fig. 2, Clade I), and another clade including Elatostemeae (as 'Lecantheae'), Urticeae (including *Poikilospermum*) and *Myriocarpa* (Clade II). However, his results must be regarded as equivocal since Clade I has very weak support (Bootstrap 64%; Bremer decay value 2) and forms an unresolved clade that include *Cecropia obtusifolia* (previously regarded as a member of the distinct family Cecropiaceae, refer Berg 1978).

We report analyses of enlarged sequence databases of both *rbcl* and *trnL-F* sequences aimed at testing the infra-familial (tribal) concepts of the Urticaceae.

## Materials and methods

### Nomenclature

Family and generic names, species epithets and specific authorities follow IPNI (2004+). Tribal names within the Urticaceae follow Conn and Hadiyah (in press), a nomenclatural modification of Friis (1993).

### Taxon sampling

The Urticaceous taxa used in the present study represented each of the currently recognised tribes (as circumscribed by Friis 1993): namely, Boehmerieae (10 genera sampled: total genera in tribe = 19), Elatostemeae (four genera: total = 7), Forsskaoleeae (three genera: total = 4), Parietarieae (two genera: total = 5), and Urticeae (six genera: total = 10). Representatives of the Cecropiaceae were included because of the close relationship of these taxa with the Urticaceae (Sytsma *et al.* 2002) and their likely inclusion in the latter family. In particular, the sequence of *Cecropia palmata* (AF061196) used by Sytsma *et al.* (2002) was included in our analysis in order to test the position of this species on a larger taxon sample of Urticaceae, and also to test their placement of *Poikilospermum suaveolens* within the Elatostemeae rather than the Cecropiaceae. Preliminary parsimony analysis by us of the *rbcl* and *trnL-F* sequence data revealed that sequences attributed to '*Poikilospermum* sp. Woolliams' (taken from GenBank: AF500362, AF501617, respectively) were found to be from an unknown species of *Elatostema* subg. *Pellionia*. DNA was extracted from additional material (Orr s.n.) collected from plants of the same cultivated material originally collected by Woolliams from the Musgrave River, Central Province (Papua New Guinea). Both collections of this taxon (Woolliams 547 and Orr s.n.) refer to separate DNA extractions and are here referred to as '*Elatostema* sp. Woolliams' and '*Elatostema* sp. Orr', respectively. Since both chloroplast regions employed here are insufficiently variable to provide strong resolution of relationships within *Elatostema* (Hadiyah *et al.* 2003), representation of this genus was restricted to several species from each of the four subgenera of Schröter and Winkler (1935) so that the molecular diversity of the genus was well sampled. Likewise, representative species of *Pilea* were selected to sample the molecular diversity of the genus on the basis of the studies of Monro (2006). Sequence data of five purported species of the Forsskaoleeae were sourced from GenBank (Table 1), and one of these, cited as '*Didymodoxa caffra*' (AM235160) is here referred to as *Laportea peduncularis* (Urticeae). However, since the herbarium voucher (*Goldblatt 12582 & Porter*) held at MO is sterile and the NBG replicate was

not been located (Foster, pers. comm., 15 Aug 2007), this identification is tentative.

### Outgroup taxa

Trees obtained from the *rbcl* analysis were rooted on the more distant outgroup, Rosaceae, represented by *Prunus persica*, on the basis of the broad analyses of Soltis *et al.* (2000) and Sytsma *et al.* (2002). Those obtained from an analysis of the *trnL-F* database were rooted on representatives of Moraceae (three genera) and Cannabaceae (three genera), which have been shown to be the sister groups of Urticaceae in the same analyses.

### Molecular method

DNA was extracted from leaves dried in silica gel using the technique of Gilmore *et al.* (1993). The *rbcl* gene and the *trnL-F* region of the chloroplast genome were amplified and sequenced by using the techniques and primers detailed in Hadiyah *et al.* (2003). The latter region, which for simplicity is henceforth referred to as *trn*, includes the *trnL* intron, the *trnL-F* spacer and the intervening *trnL* exon. Details of vouchers, GenBank accessions for sequences and authorities for binomials are given in Table 1. Our data were supplemented by sequences available from GenBank (Table 1). Sequences were initially aligned manually in PAUP\* Version 4.0b10 (Swofford 2002), and the alignment was refined in MacClade Version 4.05 (Maddison and Maddison 2001). Insertions/deletions (indels) were positioned so as to best conform to the indel types of Golenberg *et al.* (1993) and, where informative, coded according to the 'simple' scheme of Simmons and Ochoterena (2000) and added to the database.

### Phylogenetic analyses

Heuristic searches were conducted in PAUP\* by using tree bisection reconnection branch swapping and 100 replicates of random taxon addition to search for multiple islands of most-parsimonious (MP) trees. Uninformative characters were deleted before analyses. Support for clades was estimated by both decay and bootstrap analyses. The former were conducted in PAUP\* with 100 replicates of random taxon addition on each constraint tree, using command files created in MacClade. Bootstrap analyses were also conducted in PAUP\* with character resampling selected, and 1000 replicates were performed; when the analysis could not be completed within available memory, branch-swapping was restricted to 100 trees per replicate and the number of replicates increased to 10 000. Bootstrap values  $\geq 95\%$  are interpreted as strong support, whereas values between 75 and 95% are interpreted as moderate support (as in Hadiyah *et al.* 2003). Constraint trees designed to test alternative topologies were constructed in MacClade, imported into PAUP and the analyses conducted as described above.

## Results

The *rbcl* database sequences of 34 members of the Cannabaceae, Cecropiaceae, Moraceae and Urticaceae were included in the database. A total of 26 sequences of Urticaceae was obtained, with taxa from the tribes Boehmerieae, Elatostemeae, Forsskaoleeae,

**Table 1.** List of voucher specimens from the *Urticales* and *Prunus persica* (*Rosaceae*) used for DNA extracts and GenBank numbers for sequences. The location of herbarium vouchers are cited, using standard abbreviations Holmgren and Holmgren (1998+), except Waimea is used as abbreviation for Waimea Valley Audubon Center, Hawaii, USA; institution abbreviated as 'Yemen' is unknown (refer Monro 2006). Herbarium vouchers are unknown for some GenBank sequences. √ refers to sequences extracted for the present study. Classification of *Urticaceae* follows Friis (1989, 1993)

Taxa	Voucher	<i>rbcL</i>	<i>trn</i> region
<b>CANNABACEAE</b>			
<i>Cannabis sativa</i> L.	Chase 2992, K	AJ390068	AJ390367
<i>Celtis iguanaea</i> (Jacq.) Sarg.	Whiteford 9350, BM		AY488673
<i>Humulus lupulus</i> L.	Westad s.n., WIS		AB033889 – intron AB033890 – spacer
<b>CECROPIACEAE</b>			
<i>Cecropia palmata</i> Willd.	Fairchild Bot. Gard. 3181, FTG	AF061196	AF501615
<i>C. obtusifolia</i> Bertol.	Monro 3767, BM		DQ179377
<i>Coussapoa ovalifolia</i> Trécul	Nee & Vargas 41774, WIS		AF501616
<i>Poikilospermum lanceolatum</i> (Trécul) Merr.	Stainton 6519, BM		DQ179374
<i>P. suaveolens</i> (Blume) Merr.	Hadijah 488, NSW	FJ432245	
	Conn 5086, NSW		FJ432260
<i>P.</i> sp.	Hadijah 171, NSW		FJ432261
<i>P.</i> sp.	Hadijah 489, NSW		FJ432262
<b>MORACEAE</b>			
<i>Dorstenia mannii</i> Hook.f.	Sytsma 7104, WIS	AF500349	AF501604
<i>D. psilurus</i> Welw.	Voucher unknown		AJ390365
<i>D.</i> sp.	Conn 5090, NSW		FJ432250
<i>Ficus benjamina</i> L.	Sytsma 7106, WIS		AF501605
<i>F. pretoriae</i> Burt Davy	Chase 2412, K	AJ390067	
<i>Morus alba</i> L.	Voucher unknown	D86319	
<i>M. rubra</i> L.	Morgan 2157, WS	U06812	
<i>Streblus pendulinus</i> (Endl.) F.Muell.	Morden 1689, BISH		AF501609
<b>ROSACEAE</b>			
<i>Prunus persica</i> (L.) Batsch	Voucher unknown	AF411493	
<b>URTICACEAE</b>			
<b>Boehmerieae</b>			
<i>Boehmeria biloba</i> Wedd.	Chase 2532, K	AJ390069	AJ390371
<i>B. calophleba</i> C.Moore & F.Muell.	Hadijah 393, NSW	AY208700	AY208723
<i>B. grandis</i> A.Heller	Morden 1120, BISH	AF500354	
<i>B. macrophylla</i> Homem.	Hadijah 394, NSW	AY208701	AY208722
<i>B. nivea</i> (L.) Gaudich.	UCBerkeleyBG 90.1116, UC	AF062005	AF501610
<i>B. platyphylla</i> D.Don	Ariyanti 20, NSW		FJ432251
<i>Cypholophus</i> sp. aff. <i>trapula</i> H.Winkler	Pullen 5962, BM		DQ179365
<i>C. macrocephalus</i> Wedd.	Conn 4386, NSW		FJ432254
<i>Debregeasia dichotoma</i> (Blume) Wedd.	Hadijah 361, NSW		FJ432255
<i>Gonostegia pentandra</i> Miq.	Conn 4549, NSW		FJ432252
<i>Leucosyke capitellata</i> Wedd.	Conn 4531, NSW		FJ432258
<i>Maoutia puya</i> Wedd.	Hadijah 173, NSW		FJ432259
<i>Myriocarpa longipes</i> Liebm.	Hadijah 395, NSW	AY208705	AY208724
<i>Nothocnide repanda</i> (Blume) Blume	Conn 4399, NSW		FJ432253
<i>Oreocnide</i> sp.	Conn 5093, NSW		FJ432275
<i>Pouzolzia longipes</i> Killip	Monro 4037, BM		DQ179368
<b>Elatostemeae</b>			
<i>Elatostema acuminatum</i> Brongn.	Hadijah 249, NSW	AY208702	AY208744
<i>E. backeri</i> H.Schroet.	Hadijah 146, NSW		FJ432268
<i>E. curtisii</i> (Ridley) H.Schroet.	Hadijah 427, NSW		AY208731
<i>E. grande</i> (Wedd.) P.S.Green	Brown 2000/20, NSW		FJ432269
<i>E. griffithianum</i> Hallier f.	Hadijah 351, NSW		AY208732
<i>E. integrifolium</i> Wedd.	Hadijah 242, NSW		AY208741
<i>E. macrophyllum</i> Brongn.	Hadijah 245, NSW		AY208739
<i>E. parvum</i> Blume ex Miq.	Hadijah 154, NSW	AY208703	AY208733
<i>E. pedunculosum</i> Miq.	Hadijah 312, NSW		AY208738
<i>E. repens</i> (Lour.) Hallier f. & H.Schroet.	Hadijah 445, NSW		AY208730

Table 1. (continued)

Taxa	Voucher	<i>rbcL</i>	<i>trn</i> region
<i>Elatostema rostratum</i> (Blume) Hassk.	Hadiah 144, NSW		AY208743
<i>E. sinuatum</i> (Blume) Hassk.	Conn 5087, NSW		FJ432270
<i>E. sp.</i> Woolliams	Woolliams 547, Waimea	AF500362	AF501617
<i>E. sp.</i> Orr	Orr s.n., NSW719905		FJ432271
<i>Lecanthus peduncularis</i> Wedd.	Voucher unknown		DQ179370
<i>Pellionia daveauana</i> N.E.Br. <sup>A</sup>	Sytsma 7105, WIS	AF500358	AF501612
<i>Pilea craspedodroma</i> A.K.Monro	Johns 10522, BM		AY756275
<i>P. depressa</i> Blume	Sytsma 7102, WIS	AF500359	
<i>P. johnsii</i> A.K.Monro	Edwards 4240, BM		AY756276
<i>P. longicaulis</i> Hand-Mazz.	Báise Expedition 01909, PE		DQ179363
<i>P. microphylla</i> (L.) Liebm.	Hadiah 398, NSW		AY208726
<i>P. nummulariifolia</i> Wedd.	Hadiah 389, NSW		AY208727
<i>P. peplodes</i> Hook. & Arn.	Conn 4566, NSW		FJ432267
<i>P. plataniflora</i> C.H.Wright	Gressitt 509, BM		DQ179349
<i>P. pumila</i> Liebm.	Voucher unknown	AF206811	
<i>P. stipulosa</i> Miq.	Hadiah 237, NSW		FJ432266
<i>P. tripartite</i> A.K.Monro	Monro 4181, BM		DQ176859
<i>Procris frutescens</i> Blume	Hadiah 149, NSW	AY208704	AY208728
<i>Procris insularis</i> H.Schroet.	Hadiah 390, NSW	AY208706	AY208729
<i>Procris pedunculata</i> (J.R.Forst. & G.Forst.) Wedd.	Conn 4568, NSW		FJ432273
<i>Procris ruhlandii</i> H.Schroet.	Ariyanti 19, NSW		FJ432272
<b>Forsskaoleae</b>			
<i>Didymodoxa capensis</i> (L.f.) Friis & Wilmot-Dear	Goldblatt 12893 & Manning, NSW		FJ432257
<i>Droguetia iners</i> Schweinf.	Wood Y-74–382, Yemen		DQ179371
<i>Forsskaolea tenacissima</i> L.	Thesiger s.n., BM		DQ179376
<i>F. sp.</i>	Goldblatt & Porter 12472, NBG	AM235162	
<b>Parietarieae</b>			
<i>Parietaria debilis</i> G.Forst.	Conn 4348, NSW		FJ432256
<i>Parietaria judaica</i> L.	Conn 4468, NSW	FJ432248	✓
<i>Parietaria pennsylvanica</i> Muhl. ex Willd.	Sytsma 6045, WIS	AF500357	AF501611
<i>Gesnouinia arborea</i> Gaudich.	Evrard 12088, BM		DQ179372
<b>Urticeae</b>			
<i>Dendrocide excelsa</i> (Wedd.) Chew	Klaphake s.n., NSW 718764		FJ432265
<i>D. sinuata</i> (Blume) Chew	Conn 4394, NSW	FJ432246	
<i>D. stimulans</i> (L.f.) Chew	Conn 4441, NSW	FJ432247	FJ432274
<i>Discocnide mexicana</i> (Leibm.) Chew	Gereau <i>et al.</i> 2205, B		DQ179369
<i>Hesperocnide tenella</i> Torr.	Pires 98-073, WIS	AF500355	
<i>Laportea canadensis</i> Gaudich.	Sytsma 6105, WIS	AF500356	
<i>L. peduncularis</i> (Wedd.) Chew	Goldblatt & Porter 12582, NBG	AM235160	
<i>L. sp.</i>	Conn 4497, NSW		FJ432263
<i>Urera glabra</i> Wedd.	Morden 1673, BISH	AF500360	AF501614
<i>U. laciniata</i> Wedd.	Voucher unknown		DQ179367
<i>Urtica dioica</i> L.	Hadiah 391, NSW	AY208707	AY208725
<i>U. urens</i> L.	Wiecek s.n., NSW722989	FJ432249	FJ432264

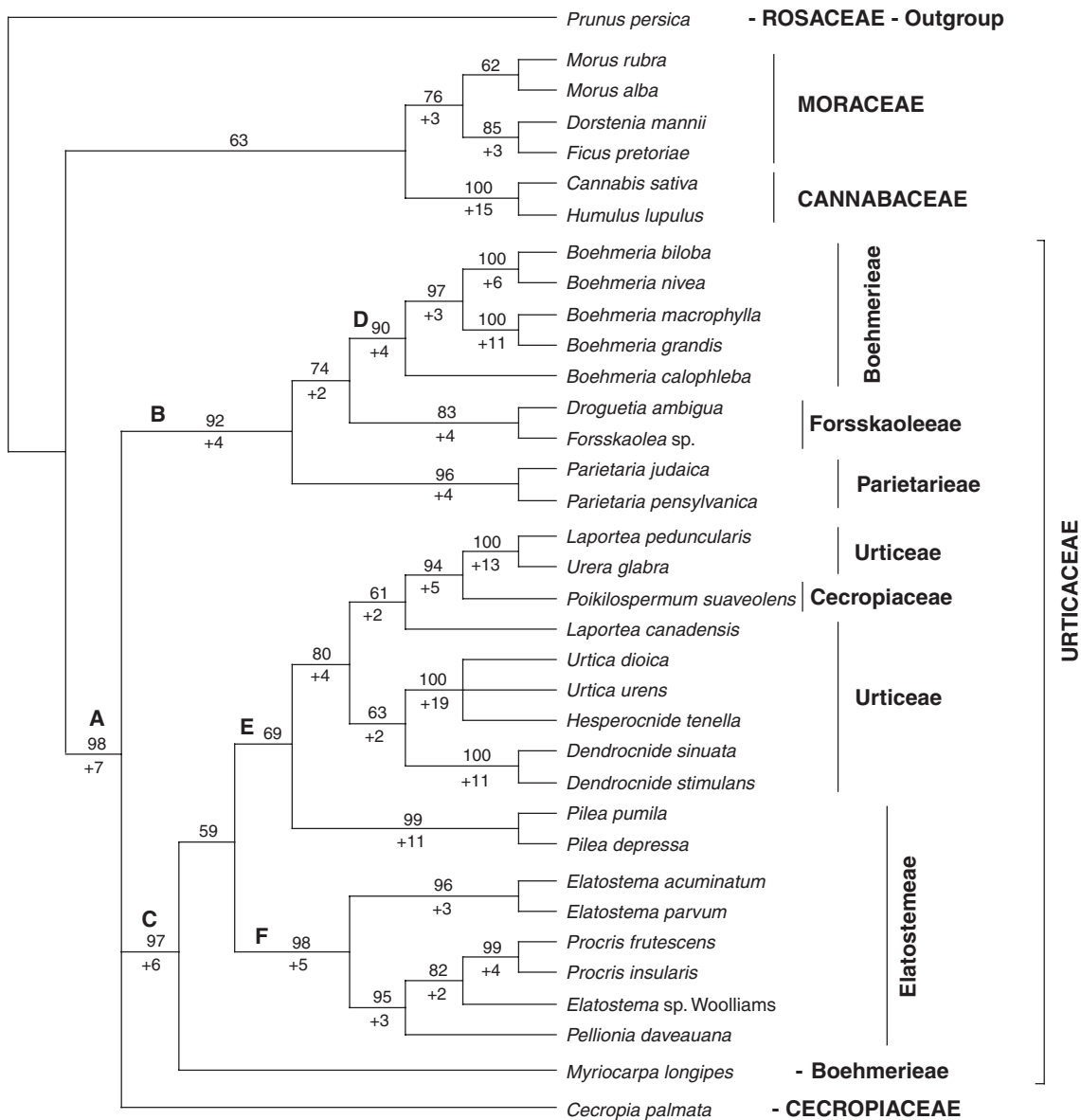
<sup>A</sup>This particular GenBank accession is referred to as *Pellionia daveauana* N.E.Br. in Sytsma *et al.* (2002); however, it is a synonym for *Elatostema repens* (Lour.) Hallier f. & H.Schroet. (Schröter and Winkler 1935, pp. 25–26).

Parietarieae and Urticeae represented in the dataset (Table 1). The aligned database totalled 1346 positions, of which 307 (22.8%) were variable and 177 (13.2%) parsimony informative. Missing sequence totalled 4.0% of the matrix.

Parsimony analysis found one island of four MP trees of 471 steps (RI = 0.71, RC = 0.36). The strict consensus tree is shown in Fig. 1. The Urticaceae and Cecropiaceae form a strongly supported clade (A; bootstrap 98%, decay value +7), within which there is a polytomy of the following three lineages: *Cecropia palmata* (Cecropiaceae); Clade B, comprising *Boehmeria* (Boehmeriaceae), Forsskaoleae and *Parietaria*

(Parietarieae); and Clade C, comprising Urticeae, Elatostemeae, *Myriocarpa longipes* (Boehmeriaceae) and *Poikilospermum* (Cecropiaceae).

Within Clade B, species of *Boehmeria* form a moderately supported clade (Clade D) (90%; +4) that is sister to the moderately supported *Droguetia ambigua* and *Forsskaolea sp.* (both Forsskaoleae) clade (83%; +4). The two representatives of *Parietaria* (Parietarieae) are strongly grouped (96%, +4). There is only weak support (74%; +2) for the sister relationship between the first two clades, but moderate support (92%; +4) for the entire clade. Within Clade C, representatives of Urticeae, *Pilea*



**Fig. 1.** Strict consensus tree of four equally parsimonious trees of 471 steps (RI=0.71, RC=0.36) found from heuristic searching of the *rbcL* database with 100 replicates of random taxon addition. Bootstrap percentages are shown above branches; decay values >1 below.

(Elatostemeae) and *Poikilospermum suaveolens* (Cecropiaceae) form a weakly supported Clade E (69%; +1). Although the link between *Pilea* and other members is very weak, the remainder of the mostly Urticeae + *Poikilospermum suaveolens* clade receives moderate support (80%, +4). The *Urtica* + *Hesperocnide* clade and the *Dendrocnide sinuata* + *D. stimulans* clade both receive 100% bootstrap support and high decay values (+19 and +11, respectively), and the inclusion of *Poikilospermum suaveolens* (Cecropiaceae) along with *Ureia glabra* and *Laportea peduncularis* (both Urticeae) is also well supported (94%; +5). However, the position of *Laportea canadensis* as sister to the latter three species renders *Laportea* as paraphyletic. Clade F is strongly supported (98%; +5), and includes remaining

representatives of Elatostemeae. The sister relationship between Clades E and F is very weak (59%, +1), but support for a close relationship of *Myriocarpa longipes* (Boehmerieae) to both E and F (Clade C) is robust (97%, +6).

#### The *trn* database

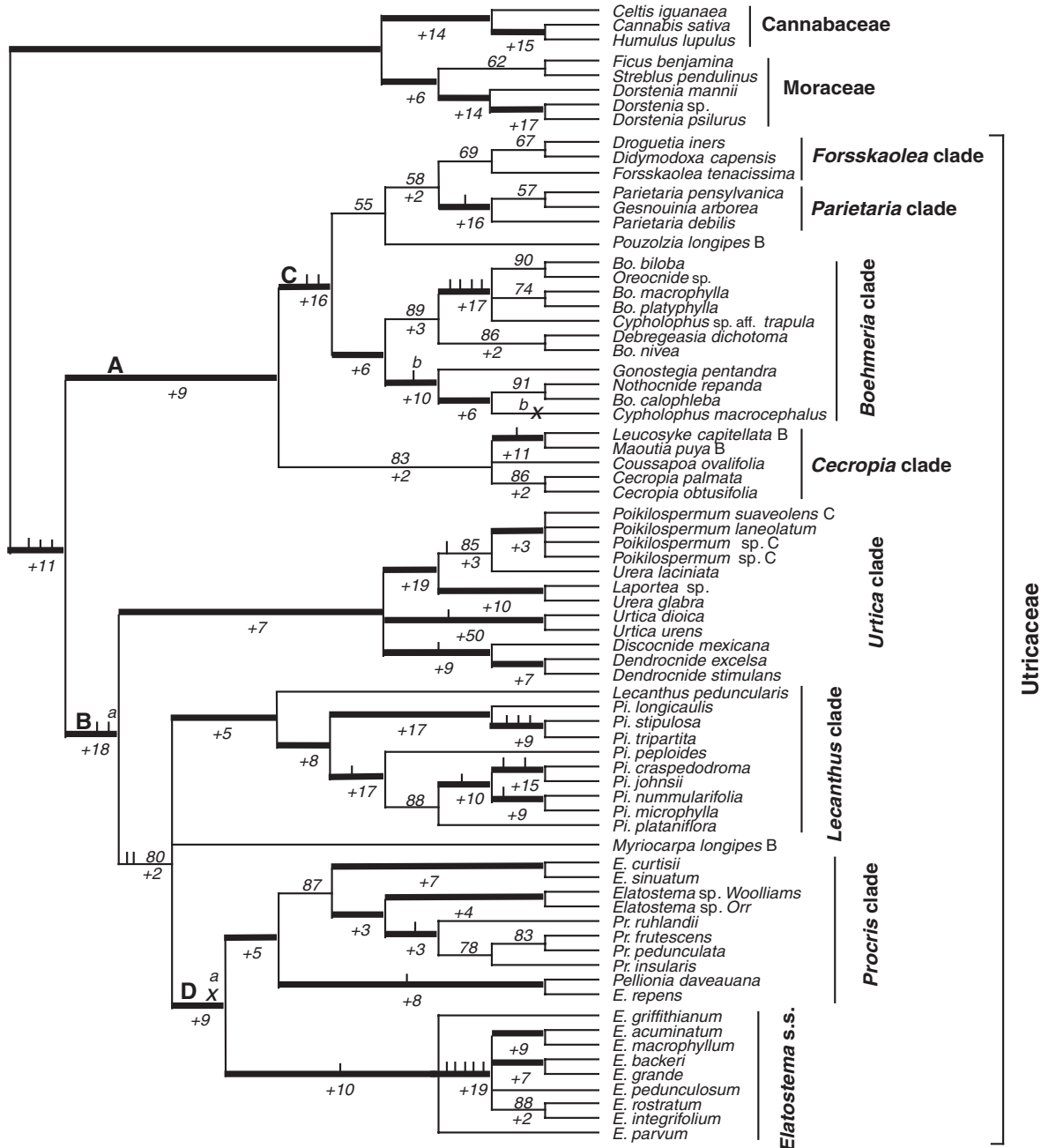
A total of 73 sequences for the *trn* region, representing 71 species of Cannabaceae, Cecropiaceae, Moraceae and Urticaceae (the latter represented by 55 species), were aligned to form a database of 1475 bp (Table 1). Missing sequence totalled 5.3% of the data matrix. Several short regions of dubious homology that included indels and totalled 18 bp were deleted before the analyses. Sixty-

five potentially informative indels, ranging from 1 to 149 bp, were scored and added to the database. The final data matrix consisted of 1494 characters.

In all, 726 (49.3%) characters were variable and 503 (34.2%) were parsimony informative. Parsimony analysis yielded a single island of 16200 MP trees of 1674 steps (RI=0.84, RC=0.53); the strict consensus is presented in Fig. 2. The

distributions of selected informative indels are mapped on the consensus tree.

All ingroup taxa are placed in a highly robust clade (100%; +11) comprising Urticaceae + Cecropiaceae. Within this, two robust major lineages labelled A and B are retrieved. Clade A (100%; +9) comprises all representatives of Forsskaoleae and Parietarieae, together with most of Boehmerieae and



**Fig. 2.** Strict consensus of a single island of 16 200 equally parsimonious trees of 1674 steps (RI=0.84; RC=0.53) found from heuristic searching of the *trnL-F* database by using 100 replicates of random taxon addition with branch-swapping on all trees. Thick branches received at least 95% bootstrap support; other values >50% are shown above branches; decay values >1 are shown below branches. Distribution of indels consistent with a single origin is mapped on tree; single bar, origin; x, reversal. A, B, indels showing reversals; B, Boehmerieae placed closer to other tribes; C, Cecropiaceae placed near to members of Urticeae; *Bo.*, *Boehmeria*; *E.*, *Elatostema*; *Pi.*, *Pilea*; *Pr.*, *Procris*.

Cecropiaceae. The first two tribes constitute monophyletic groups, whereas those members of Boehmerieae that are included in the clade are not grouped together. Clade B (100%, +18) includes the remaining Urticaceae plus *Poikilospermum* (Cecropiaceae).

Within Clade A, the genus *Boehmeria* and *Cypholophus* are both rendered paraphyletic as part of a strongly supported clade that includes *Debregeasia*, *Gonostegia* and *Oreocnide* (all members of the Boehmerieae). Within Clade B, the Urticeae forms a strongly supported *Urtica* clade (98%; +7) in which *Poikilospermum* is nested as sister to *Urera laciniata* (85%; +3), within a robust subclade (100%; +19) with *Urera glabra* and *Laportea* sp. Two other major lineages are present within Clade B and include the following: the *Lecanthus* clade, which receives strong support (97%, +5) and includes *Lecanthus pedunculata* and species of *Pilea*; and the strongly supported clade D (99%, +9). The latter consists of a strongly supported *Procris* clade (99%, +5) including *Pellionia daveauana*, the representatives of *Procris* and some species of *Elatostema*, and a robust clade comprising the remaining representatives of *Elatostema* (*Elatostema sensu stricto* clade; 100%, +10). *Myriocarpa longipes* (Boehmerieae) is placed in a polytomy with the *Lecanthus* clade and Clade D.

## Discussion

As shown in Fig. 2, indels provide considerable support to the topology: the distributions of 48 of the 65 informative indels are consistent with a unique origin, two more (*a* and *b*; refer Fig. 2, nodes 'B' and 'D', and within the *Boehmeria* subclade of Clade C, respectively) have a single origin but require one reversal (*x*). Whereas virtually all these indels arise on well supported branches, a single-base deletion at position 1378 and a seven-base insertion at position 1117 reinforce the moderately supported (80%, +2) resolution of Urticeae as the first diverging lineage within Clade B. Hence, the distributions of the overwhelming majority of scored indels are a perfect fit to the strict consensus tree.

### Phylogeny of *Poikilospermum*

In a broad analysis of urticalean rosids on the basis of *rbcL* data (Sytsma *et al.* 2002), *Poikilospermum*, a member of Cecropiaceae *sensu* Berg (1978), was placed sister to *Pellionia* (= *Elatostema sensu lato*), in tribe Elatostemeae. This conclusion conflicts with our analysis of *rbcL* data, in which *Poikilospermum suaveolens* was placed within Urticeae sister to the *Urera glabra*+*Laportea peduncularis* clade (Fig. 1). Our results concur with those of Monro (2006). However, the specimen of *Poikilospermum* sp. (AF500362) used by Sytsma *et al.* (2002) was incorrectly identified and, on the basis of inflorescence structure, is here regarded as an unknown species of *Elatostema* subg. *Pellionia* and is referred to as *Elatostema* sp. Woolliams. In Fig. 1, it is grouped with the representatives of *Procris* and *Pellionia daveauana* (a synonym of *Elatostema repens*). Therefore, after this correction of identity, the results obtained by Sytsma *et al.* (2002) for this taxon accord with our analysis.

Our analyses placed all four representative samples of *Poikilospermum* within the Urticeae on either *rbcL* or *trn* data (Figs 1 and 2). The status of *Poikilospermum* within the

Urticaceae has been a point of major disagreement. It was first included in this family by Miquel (1863), and this was widely followed by later authors (e.g. Weddell 1869; Baillon 1874; Engler 1894). Likewise, Chew (1963) revised the genus as a member of Urticaceae. However, Hutchinson (1967) placed it within Moraceae as the separate subfamily Conocephaloideae. Nevertheless, when Berg (1978) raised the Cecropieae (*sensu* Gaudichaud 1830) to family status, he included *Poikilospermum*. Subsequently, Berg (1989) admitted that it had some characters in common with Urticaceae, namely, the elongated 'urticaceous' cystoliths, similar wood anatomy to *Urera* (refer next paragraph), and similar inflorescences to those of *Debregeasia* (Boehmerieae). The higher-level classification systems developed by Cronquist (1988), Dahlgren (1989) and Takhtajan (1997) all recognised the new family and the position of this genus within it. Friis (1989, 1993) also excluded *Poikilospermum* from his accounts of the Urticaceae.

On the basis of research of wood and leaf anatomy, Bensen and ter Welle (1984) suggested that *Poikilospermum* should be placed within Urticaceae, close to *Nothocnide* (Boehmerieae), because both have unligified bands of axial parenchyma within their secondary growth. They also suggested that it possibly has a close relationship with *Dendrocnide* (which has more strongly developed unligified bands) and *Urera* (both Urticeae), as all three share dimorphic wood fibres that are regarded as a specialised feature. Similarly, Bigalke (1933) noted the similarities between *Poikilospermum* and members of the tribes Urticeae and Elatostemeae, in that they all have elongated cystoliths and do not have hooked hairs on the leaves. The placement of *Poikilospermum lanceolatum* sister to *Urera laciniata* (Fig. 2) reinforces these suggestions. We conclude that the genus *Poikilospermum* should be assigned to the tribe Urticeae.

### Taxonomic status of Cecropiaceae

Recent phylogenetic studies into Urticaceae and related families (e.g. Sytsma *et al.* 2002; Hadiah *et al.* 2003) have added significantly to our understanding of the phylogeny of the Urticaceae. Our analyses of *rbcL* and *trn* data strongly support the conclusion that the Urticaceae is paraphyletic with respect to Cecropiaceae. Constraint analyses revealed that enforcing a monophyletic Cecropiaceae (including *Poikilospermum*) and Urticaceae required an extra 15 steps on the *rbcL* MP tree, and an extra 62 steps on the *trn* tree. Even when excluding *Poikilospermum*, an extra seven steps are still required on the *trn* analysis to render Cecropiaceae monophyletic outside Urticaceae. Hence, our analyses do not support the recognition of Cecropiaceae as a distinct family intermediate between Moraceae and Urticaceae as proposed by Berg (1978) and Kubitzki (1993). Although the relationships of *Cecropia palmata* to the two main lineages in Urticaceae (B and C) are equivocal on the *rbcL* data (Fig. 1), the more informative *trn* data for a wider sample of taxa provide strong support (100%, +9) (Fig. 2, Clade A) for *Cecropia* and *Coussapoa* (together with *Leucosyke* and *Maoutia*) (*Cecropia* clade) being sister to the Boehmerieae + Forsskaoleae + Parietarieae lineage (Fig. 2, Clade C). This result accords with the placement of



*Cecropia palmata* as sister to *Boehmeria* and *Parietaria* in the *rbcL* analysis of Sytsma *et al.* (2002). We conclude that Cecropiaceae should be reduced to the synonymy of Urticaceae, which would render the Urticaceae monophyletic in both of our analyses.

#### Tribes of the Urticaceae

The monophyly of Forsskaoleeae is moderately supported on *rbcL* data (Fig. 1), but only weakly supported on *trn* data (Fig. 2). In comparison, Parietarieae is strongly supported in both datasets. However, the monophyly of Boehmerieae is not supported by either dataset. *Myriocarpa longipes* is clearly much more closely related to Urticeae and Elatostemeae (Figs 1 and 2). Constraint analyses revealed that an extra 21 steps were required on the *rbcL* tree to form a monophyletic Boehmerieae, and an additional 36 steps were needed on the *trn* tree. Hence, the molecular data provide strong evidence against the placement of this taxon in the Boehmerieae (*sensu* Friis 1993, Kravtsova 2007). Furthermore, the relationships of *Pouzolzia longipes* (Boehmerieae) are with representatives of the tribes Parietarieae and Forsskaoleeae rather than with Boehmerieae on the *trn* data (Fig. 2), although support for this is very weak (55%, +1). Similarly, *Leucosyke* sp. and *Maoutia puya* are placed closer to Cecropiaceae, although again with only moderate support. Constraint analysis revealed, however, that only four extra steps on a tree length of 1674 steps are required for these last two taxa to cluster with the *Boehmeria* clade on the *trn* data. Hence, although the limited sampling of Parietarieae and Forsskaoleeae suggests these tribes may be monophyletic, a wider study is required to test the monophyly of Boehmerieae excluding *Myriocarpa*. The *trn* analysis also suggests that further research is required to clarify generic concepts within Boehmerieae. The placement of members of several genera within the *Boehmeria* clade (e.g. *Boehmeria*, *Cypholophus*, *Debregeasia*, *Gonostegia* and *Nothocnide*; Fig. 2) renders *Boehmeria* and *Cypholophus* paraphyletic. The systematics of both of these genera are regarded as requiring extensive revision (Friis 1993), with the former genus currently being researched intensively by M. Thomas (K) and I. Friis (C).

The sister relationship between the Boehmerieae + Forsskaoleeae + Parietarieae clade and the *Cecropia* clade (Fig. 2) provides support for the recognition of *Cecropia* and *Coussapoa* (both Cecropiaceae) as members of the Urticaceae. However, formal recognition of the former Cecropiaceae, even as a more reduced taxonomic concept (here only including *Cecropia* and *Coussapoa*) is not supported, partly because the support for the *Cecropia* clade is not strong (83%; +2) and both *Leucosyke* and *Maoutia* (both Boehmerieae) are included. Furthermore, the phylogenies of the remaining genera in Cecropiaceae *sensu* Berg (1978), namely *Musanga*, *Myrianthus* and *Pourouma*, have yet to be evaluated. These genera are morphologically diverse. *Cecropia* and *Musanga* have peltate leaves, whereas the other two, like *Coussapoa*, have entire to subpalmate leaves. *Myrianthus* and *Pourouma* both have large fruits with more or less woody endocarps, whereas *Cecropia*, *Coussapoa* and *Musanga* have relatively small fruits with crustaceous endocarps (Kubitzki 1993). The

phylogenetic importance of these morphological differences is yet to be tested.

Relationships between Urticeae, Elatostemeae (*Elatostema sensu stricto*, *Procris* and *Lecanthus* clades) and *Myriocarpa longipes* are only very weakly resolved (59%; +1) on *rbcL* data (Fig. 1), and incompletely resolved on *trn* data (Fig. 2). In each case, *Myriocarpa* is robustly grouped with both tribes (Clade C: 97%, +6, Fig. 1; Clade B: 100%, +18, Fig. 2), being placed in a polytomy with Elatostemeae (Clade D and the *Lecanthus* clade) with only modest support (80%, +2) on *trn* data (Fig. 2). Although *M. longipes* displays a strong relationship with Urticeae and Elatostemeae, it is premature to propose a supra-generic classification for this genus. There is certainly no support for its inclusion in Boehmerieae as a separate subtribe, Myriocarpaceae, as proposed by Kravtsova (2007). Sequence data for additional species of *Myriocarpa* are required to gain a better understanding of its taxonomic position.

The circumscription of Elatostemeae is unclear because of the placement of *Pilea* with Urticeae (Fig. 1) and because of the unresolved position of *Myriocarpa longipes* (Boehmerieae) (Fig. 2). On the basis of *trn* data, a narrowly circumscribed Elatostemeae (including *Elatostema*, *Pellionia sensu* Wang 1980, and *Procris*) could be distinguished from the *Lecanthus* + *Pilea* group (*Lecanthus* clade). The placement of the other genera of Elatostemeae (*sensu* Friis 1993) is still to be determined, but morphologically, it is expected that *Meniscogyne* Gagnep. (a poorly known taxon) would be placed within the *Elatostema sensu stricto* clade based on its anisophyllous opposite leaves (hence appearing alternate) which are asymmetric and held close to the branches (subappressed), and female inflorescences which are discoid (modified into a membranous cupule). *Sarcopilea* Urban and possibly *Petelotiella* Gagnep. would be included along with *Lecanthus* and *Pilea* in *Lecanthus* clade, based on their mostly isophyllous, clearly opposite leaves that are mostly symmetric or almost so, with patent to subpatent leaves, and female inflorescences generally loosely cymose clusters. However, both *Sarcopilea* and *Petelotiella* have two free stipules, unlike the connate stipules of *Lecanthus* and *Pilea*.

The Urticeae is moderately supported by *rbcL* data (80%, +4) and strongly supported by *trn* data (98%, +7). Although relationships of genera within the tribe have not been evaluated in detail, there are some conclusions that can be reached on the basis of our analyses. Representatives of *Poikilospermum* form a strongly supported clade (98%; +3) that is clearly nested within the Urticeae, together with *Urera* and *Laportea* (100%; +19). Therefore, the former genus should be transferred from the Cecropiaceae to the Urticeae. *Dendrocnide* is placed sister to the *Hesperocnide* + *Urtica* clade on *rbcL* data (Fig. 1) and sister to *Discocnide* on *trn* data (Fig. 2), whereas *Laportea* is included within the *Urera* + *Poikilospermum* lineage (Figs 1 and 2). This supports the opinion of Chew (1969a, 1969b) that *Dendrocnide* and *Laportea* are distinct genera, rather than Weddell's (1869) conclusion that the two are congeneric. However, the topology does not support the contention (Chew 1965) that *Urera* is more closely related to *Dendrocnide* than to *Laportea*. The later genus is paraphyletic in Fig. 1, with *L. peduncularis* (AM235160, referred to as *Didymodoxa caffra* by Forest *et al.* 2007) forming a strong sister relationship with

*Urera glabra* (100%, +13), whereas *L. canadensis* forms a weakly supported clade (61%, +2) with *Poikilospermum suaveolens*, *Urera glabra* and *Laportea peduncularis*. Analyses that include additional species of *Laportea*, as well as other taxa of the Urticeae, and use the more informative *trn* region, are required to thoroughly test generic concepts and inter-relationships within the tribe. Furthermore, the uncertainty about the identity of AM235160 (refer above) requires further investigation of the affinities of *Didymodoxa caffra*.

## Conclusions

Phylogenetic analysis of the Urticales based on a larger set of *rbcL* and *trn* sequences showed congruence with the preliminary analyses of the Hadiah *et al.* (2003), and also with the analyses of Sytsma *et al.* (2002) and Monro (2006). Our analyses provide evidence to support the need for the circumscription of the Urticaceae to be broadened to include the Cecropiaceae as suggested by Sytsma *et al.* (2002). Furthermore, our analyses provide strong resolution of many of the tribal relationships within the family.

We concluded that *Myriocarpa* should not be classified in the Boehmerieae because, although unresolved, it has strong affinities with the Elatostemeae. The circumscription of Urticeae should be expanded to include *Poikilospermum*. There is strong support for the monophyly of Forsskaoleeae Gaudich. and Parietarieae Gaudich. The suprageneric classification of *Cecropia* and *Coussapoa* is unclear but their affinities are with the Forsskaoleeae, Parietarieae and Boehmerieae.

The circumscription of Boehmerieae Gaudich. should be changed to exclude *Myriocarpa*, with further work required to test the monophyly of remaining members, as well as generic concepts within the tribe. The phylogeny of *Myriocarpa* should be evaluated using additional species. Our analyses support the opinion of Chew (1969a, 1969b) that *Dendrocide* and *Laportea* are distinct genera. They also support the conclusion of Hadiah *et al.* (2003) that *Pellionia* should not be recognised as a distinct genus, contrary to Wang (1980). However, contrary to the former authors who placed this genus within *Elatostema*, it is here concluded that *Pellionia*, including *Elatostema* subgenus *Pellionia*, is a synonym of *Procris*.

Friis (1993) hypothesised that there are three evolutionary lines in the Urticaceae, namely, (1) Boehmerieae–Forsskaoleeae–Parietarieae (=Boehmerioideae *sensu* Kravtsova 2007), (2) Elatostemeae (as ‘Lecantheae’) (=Lecanthoideae *sensu* Kravtsova 2007) and (3) Urticeae (=Urticoideae *sensu* Kravtsova 2007). Our results lend some support to this hypothesis. We have presented clear evidence for the inclusion of *Cecropia* and *Coussapoa* within the first of these lineages. Although Kravtsova (2007) was the first to recognise the distinctiveness of *Myriocarpa* within the Boehmerieae, our data suggest that the affinities of this genus are closer to Elatostemeae. Finally, Urticeae is here expanded to include *Poikilospermum*.

## Acknowledgements

The authors thank Esti Ariyanti (Kebun Raya Purwodadi, Indonesia) for her field assistance and companionship in Sumatera (Indonesia); Frank Zich

(QRS, formerly Kebun Raya Indonesia) for field assistance in Jawa Barat and Bali; Adjun, Nanang Suryana and Rustandi (all Kebun Raya Cibodas, Indonesia) for field assistance in Jawa and for skilful cultivation of plants; Ruspandi (Kebun Raya Bogor, Indonesia) for assisting with initial identification. Dedy Darnaedi (then Director) and staff of Kebun Raya Bogor (Indonesia) provided considerable logistical field support for our field work in Sumatera (for JTH & BJC) and accommodation while in Bogor (for BJC). Kipiro Damas, Kaigube Fazang, Tory Kuria and Oliver Paul (all LAE) provided field support in Papua New Guinea. Margaret Heslewood and Andrew Perkins (both NSW) generously provided technical assistance and advice on DNA laboratory techniques. We thank the Directors and staff of the following herbaria for making collections available as loans and donations, namely A, BRI, CANB, E, K, L, LAE, MEL, MO and NY. David Orr, Waimea Valley Audubon Center, Hawaii provided a DNA sample and images of the living material of Woolliams 547. Peter Goldblatt (MO) and Suseth Foster (NBG) located a herbarium voucher of AM235160 (as cited in GenBank). Debby McGerty (NSW) kindly edited the figures for publication. Jeremy Bruhl (NE) provided us with a copy of the recent paper on the classification of the Urticaceae by T. I. Kravtsova and George Orel (University of Western Sydney) kindly translated the Russian text. One of us (JTH) was generously supported by a post-graduate AusAID scholarship.

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Manuscript received 4 October 2007, accepted 9 September 2008