Species Delimitation in Neotropical *Urera* Guadich.

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Abstract

Urera Gaudich. is a member of the Urticaceae that occurs globally and is particularly prevalent in the tropics. There has been significant confusion in the circumscription of individual taxa in the genus. This is due to two factors. Firstly, the genus has had little attention paid to it taxonomically since the 1850s. Additionally, it is morphologically diverse. *Urera baccifera* (L.) Gaudich. ex Wedd. occurs throughout the Neotropics and is known to have a particularly diverse morphology. By using molecular phylogenies and examining the morphology of specimens across Central and South America, this study seeks to determine if the currently accepted *Urera baccifera* is made up of multiple species. The morphological study finds four distinct morphospecies, however these are not supported by the molecular work, which uses ITS and *trn*L-F gene regions. The phylogenies do show a degree of geographic structure within closely related *U. baccifera* clades and sees a movement into seasonally dry tropical forests. These genetic geographic distinctions may be the result of adaptations to movement to different biomes. Further study on divergence timing and dispersal methods of the species is necessary.

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Introduction

Urticaceae

The Urticaceae comprises ca 55 genera and over 2000 species. It is globally distributed, primarily occurring in the tropics, though also found in temperate habitats (Kim *et al.*, 2015; Wu *et al.*, 2015). Morphologically, Urticaceae is diverse and difficult to delimit taxonomically due to frequent homoplasy amongst morphological characters (Wu *et al.*, 2015; Wells, 2017). Despite this, there are a number of unifying characters that include highly reduced unisexual flowers (Friis, 1989) and a pistil with a single stigma (Wu *et al.*, 2013).

Urticaceae comprises six tribes: Boehmerieae Gaudich., Elatostemateae Gaudich., Forsskaoleeae Gaudich., Parietarieae Gaudich., Urticeae Lam. & DC, and Cecropieae Gaudich (Kim *et al.*, 2015). Of these, *Urera* Gaudich. belongs to the Urticeae tribe (Kim *et al.*, 2015). The Urticeae are diverse with respect to habit and fruit morphology (Kim *et al.*, 2015). Unifying characters include the presence of stinging hairs and female flowers with four tepals (Kim *et al.*, 2015). Additionally, Urticeae are typically found in disturbed and lightly disturbed habitats (Monro, pers. comm.).

Urera Gaudich.

Urera is comprised of 122 legitimate names worldwide, according to the Plants of the World (POWO, 2017), which correspond to ca 35 taxa at the species rank (Friis, 1993; Steinmann, 2005; Monro and Rodríguez, 2009; Kim *et al.*, 2015).

Urera has a pantropical distribution and is found in Africa, Madagascar, North and South America and Hawaii (Friis, 1993; Kim *et al.*, 2015), though not found in Asia (Monro and Rodríguez, 2009). It is found in mesic or riparian habits, often in areas that have experienced disturbance (Steinmann, 2005; Monro and Rodríguez, 2009; Kim *et al.*, 2015). There are exceptions to this, where some taxa, such as *Urera baccifera* (L.) Gaudich. ex Wedd. and *Urera nitida* (Vell.) Brack., are found in dry forests in Central American and southeastern South America, respectively (Monro, pers. comm.).

Urera was first published by Gaudichaud-Beaupré (1826) to account for variation seen in the existing taxa *Urtica* L. This description was based off of 9 collections from Gaudichaud-Beaupré: *Urtica baccifera* L., *Urtica acuminata* Poir., *Urtica gigantea* Poir., *Urtica alceifolia* Poir., *Urtica palmata* Frossk., *Urtica horrida* Kunth, *Urtica lamiifolia* Juss., *Urtica parietariafolia* H. Deless, and *Urtica frutescens* H. Deless. Gaudichaud-Beaupré also references three other taxa of which he is less sure, including: *Urtica ficifolia* Savig., *Urtica madagascariensis* Juss and *Obetia*.

Prior to a study on the Mesoamerican (Mexico to the Panama/Colombia border) *Urera* by Monro and Rodríguez (2009), there was much confusion regarding species delimitation within the genus. Burger (1977), in his treatment of *Urera* for *Flora Costaricencis* wrote that "[*Urera* presents] some of the most perplexing patterns of variation that the neotropical flora has to offer." An observation that is supported by Monro and Rodríguez (2009) who found that most Mesoamerican *Urera* herbarium specimens had been misidentified.

Much of this confusion can be attributed to the fact that *Urera* has been largely neglected since the 1850s. Weddell published the *Monographie de la Familles des Urticees*, *Tome IX* in 1856 and since then most accounts of the taxon can be found in local floras (Friis, 1985; Wagner, Herbst and Sohmer, 1990; Steinmann, 2005; Monro and Rodríguez, 2009), which, while useful, do not provide a comprehensive view of the genus.

Urera was recently recovered as a polyphyletic group in a study of the Urticeae tribe from Kim et al. (2015). Within this report, *Urera* was separated into three distinct groups that aligned with its geographic distribution: one group found in tropical Africa, with the other two groups both occurring in the tropical Americas. From these groups, the neotropical taxa were further divided, with *Urera baccifera* appearing separately from the rest of the sampled neotropical taxa (Kim *et al.*, 2015). The authors cite *U. baccifera*'s unique morphology, noting that the taxon is easily differentiated from the rest of the American *Ureras.*

A later study by Wells (2017) sought to further examine these findings and included *Urera laciniata* Wedd., another neotropical *Urera*. Once again *Urera* was found to be a polyphyletic group. In addition to this confirmation, *U. baccifera* and *U. laciniata* were found to be a monophyletic clade, sister taxa to the rest of the American *Ureras*. This report also found support for subclades within both *U. baccifera* and *U. laciniata* (Wells, 2017).

Gaudichaud-Beaupré's original description of the genus notes alternate leaves and flowers divided into four or five parts (Gaudichaud-Beaupré, 1826). Steinmann (2005), reports that the majority of *Urera* taxa are dioecious and found monoecy to be rare in the neotropical taxa. Furthermore, the genus is noted for its "fleshy persistent perianth and the mostly penicillate-capitate stigma," (Friis, 1993). *Urera* also has glabrous pistillodes, stinging hairs with bulbous bases which are almost always present, and intrapetiolar stipules (Killip, 1960; Monro and Rodríguez, 2009; Kim *et al.*, 2015). Additionally, the presence of cystoliths on both the adaxial and abaxial leaf surfaces and their shape, linear or punctiform, and arrangement can be a valuable character (Friis, 1989; Steinmann, 2005). The inflorescences of *Urera* taxa are generally branched panicles in which the length of the entire inflorescence can be a distinguishing character.

Many characters within the taxon are homoplasious with various characters appearing multiple times in a given tree. This is apparent in an unpublished master's thesis from Wells (2017), where like character states such as leaf outline and stipule position appear in various clades throughout the produced tree. Within the more localized accounts there have been calls for a full review of the genus (Killip, 1960; Burger, 1977; Friis, 1989, 1993), in order to reduce the confusion surrounding this taxa.

Ingroup taxa

Urera baccifera and *Urera laciniata* have a distinct and variable morphology when compared to the rest of the neotropical *Urera* taxa. This variation has resulted in the description of several new species.: *Urera armigera* Miq., *Urera denticulata* Miq., *Urera horrida* (Kunth) Miq., *Urera nitida*, *Urera rugosa* Rusby, and *Urera viridisetosa* Rusby. Each of which attempt to address in some way an aspect of the wide morphology of *U. baccifera*

Additionally, *Urera baccifera* and *Urera laciniata* have similarities within their morphology, as noted by Monro & Rodríguez (2009) and Wells (2017). Wells (2017) points to the lack of woodiness in the branchlets of the two taxa, resulting in flattened stems in herbarium collections. The main stems of these taxa are almost entirely pith and appear to contain no true wood (Wells, 2017). They each possess bulbed hairs that can become lignified, appearing as spines (Wells, 2017; pers. obs.).

Previous studies (Monro, 2006; Wu *et al.*, 2013) have demonstrated that *Urera baccifera* and *Urera laciniata* are distinct clades and this correlates well with the aforementioned morphological differences. Wells et al. (in prep.) also show that the ingroup taxa are sister to the rest of the American *Urera*.

The neotropical *Ureras* have been poorly studied in the last century, with *Urera baccifera* and *Urera laciniata* as the least studied (Burger, 1977), yet most morphologically distinct (Wells, 2017). Burger (1977) posits that this under collection is due to their large spines and *U. baccifera's* characteristic as one of the worst stinging plants in Central America.

Urera baccifera (L.) Gaudich. ex Wedd.

Urera baccifera was first described by Linnaeus (1763) as *Urtica baccifera*, based on an illustration of *Urtica* by Plumier (1760) from the West Indies. The species was later moved into *Urera* by Gaudichaud-Beaupré (1826) based on specimens collected during his expedition on *l'Uranie* (1817-1820). The name was validly published by Weddell in 1852 in his review of the genus. An epitype for *Urera baccifera* was designated in 2009 by Monro and Rodríguez based on a specimen from 1898.

Given the significant variation in leaf morphology and habit across its range (Weddell, 1852, 1856; Killip, 1960; Burger, 1977; Monro and Rodríguez, 2009; Wells, 2017), it might be assumed that the species delimitation is in need of revision. Weddell described three varieties: α, β, and γ in his treatment of the species in his monograph and later publications (Weddell, 1852, 1856, 1869). Variety α is described as having leaves that are widely ovate to oblong-ovate, with a scabrous adaxial surface. This variety does not appear in the 1869 review of Urticaceae. Variety β is described as having widely ovate or almost circular leaves, with a prickly adaxial surface. Variety γ was described as having lanceolate-oblong leaves (Weddell, 1852; Stearn, 1992). Weddell also considers *Urtica armigera* C. Presl to be variety γ (Weddell, 1852).

Urera baccifera has many distinguishing characteristics (figure 1). The taxon is noted for its sharply stinging spines and prominently toothed leaf margin (Killip, 1960; Burger, 1977; Kim *et al.*, 2015) differentiating it from other neotropical *Urera* taxa such as *Urera caracasana* (Jacq.) Griseb. (Kim *et al.*, 2015) As with the rest of the genus, *U. baccifera* releases a gray latex when the stem is cut (Monro and Rodríguez, 2009). Additionally, the species produces single seeded fruits, however the fruits of *U. baccifera* are larger than most other taxa (Monro, pers. comm). In Brazil, these fruits have been seen to be distributed by birds and monkeys (Galetti and Pedroni, 1994; Galetti and Pizo, 1996; Dutra, Freitas and Oliveira, 2006).

The specific epithet *baccifera* literally translates to “berry-bearing” (Stearn, 1992), referring to the fruits produced by the fleshy perianth. The local name “chichicaste,” is derived from a Nahuat word meaning “to vibrate,” (Monro and Rodríguez, 2009) and is the common name most often associated with *Urera baccifera*.

Figure 1 - Examples of *Urera baccifera* collected throughout Central and South America.

Urera baccifera is distributed throughout Central America and into South America where its range extends to Argentina (figure 2) (Killip, 1960; Martins *et al.*, 2009). The species is less shade tolerant than other *Urera* taxa and is found growing in all soil types and substrates. In particular, the taxon is noted for its association with moderately disturbed sites and riparian habitats (Monro, pers. comm.).

The species has been widely used in Central and South America as a "living fence" (Burger, 1977; Monro and Rodríguez, 2009; Mannion and Menezes, 2010). It is also used regionally in traditional medicine, noted for treating body aches and muscular pain (Giovannini, 2015), as well as having been studied by western medicine as a possible treatment for Herpes-simplex virus and for its levels of antioxidants (Martins *et al.*, 2009; Monro and Rodríguez, 2009; Mannion and Menezes, 2010). Additionally, Gindri et al. (2014) found high levels of oxalic acid in *U. baccifera*, which the authors postulate could be a cause for the stinging effects of the hairs.

Figure 2 - Distribution of *Urera baccifera*.

Urera armigera Miq.

Urera armigera was described by Miquel in the *Flora Brasiliensis* (Miquel, 1853) (figure 3). Weddell considered *Urera armigera* a synonym of one of his *Urera baccifera* varieties (Weddell, 1852, 1856, 1869).

From Miquel's description, *U. armigera* is a tree with leaves that are pubescent on the abaxial surface. The inflorescence is axillary with a short petiole (Miquel, 1853). Noticeably absent from the description is a mention of any kind of stinging hairs or spines. However, the specific epithet is likely an amalgamation of the Latin word *armatus*, meaning equipped or armed (Stearn, 1992), and the suffix -ger, meaning carrying or bearing (Stearn, 1992), referring to spines or stinging hairs.

Figure *3* - Holotype of *Urera armigera* collected in Brazil.

Urera armigera has been collected in Brazil (de Rooij, 1975). It is found primarily in disturbed riparian habitats.

Urera rugosa Rusby

Urera rugosa was first described in 1901 by Rusby. The type specimen was collected in 1885 in Bolivia at 2440 m (figure 4). The species was delimited by the presence of spines and stinging hairs confined to the inflorescence, a coarsely dentate leaf margin and prominent abaxial venation, globose berries and a short, stout style (Rusby, 1901). The specific epithet *rugosa* means wrinkled (Stearn, 1992). The taxa has been listed as occurring in Bolivia and Brazil (Rusby, 1901; Jørgensen *et al.*, 2014, GBIF, Tropicos.org). Still accepted as of the 1990s (Foster, 1958; Killeen, Garcia and Beck, 1993), the name was placed in synonym with *Urera baccifera* in 2014 by Jørgensen et al. (2014) .

Figure 4 - Holotype of *Urera rugosa*, a synonym of *U. baccifera.*

Urera nitida (Vell) Brack

Urera nitida was described by Vellozo (1827) as *Urtica nitida* and subsequently recombined with *Urera* by Brack (1987). The name has been accepted in numerous publications (Pederneiras *et al.*, 2011; Gaglioti and Romaniuc-Neto, 2012). Other authors consider *Urtica nitida* as a synonym of *Urera baccifera* (Monro and Rodríguez, 2009).

U. nitida is described as a small shrub with stems that release latex when cut (Pederneiras *et al.*, 2011). Leaves are elliptic to oblong and spines and stinging hairs are present throughout (Pederneiras *et al.*, 2011; Gaglioti and Romaniuc-Neto, 2012). Gaglioti and Romaniuc-Neto (2012) list the taxon as endemic to Brazil, however other reports list it as occurring throughout the neotropics (Pederneiras *et al.*, 2011). Occurrences of the taxa in the Global Biodiversity Information Facility (GBIF) are predominantly found in southeastern

Brazil, however a small number are also noted in central and northern South America. The specific epithet *nitida* means shining or polished (Stearn, 1992)

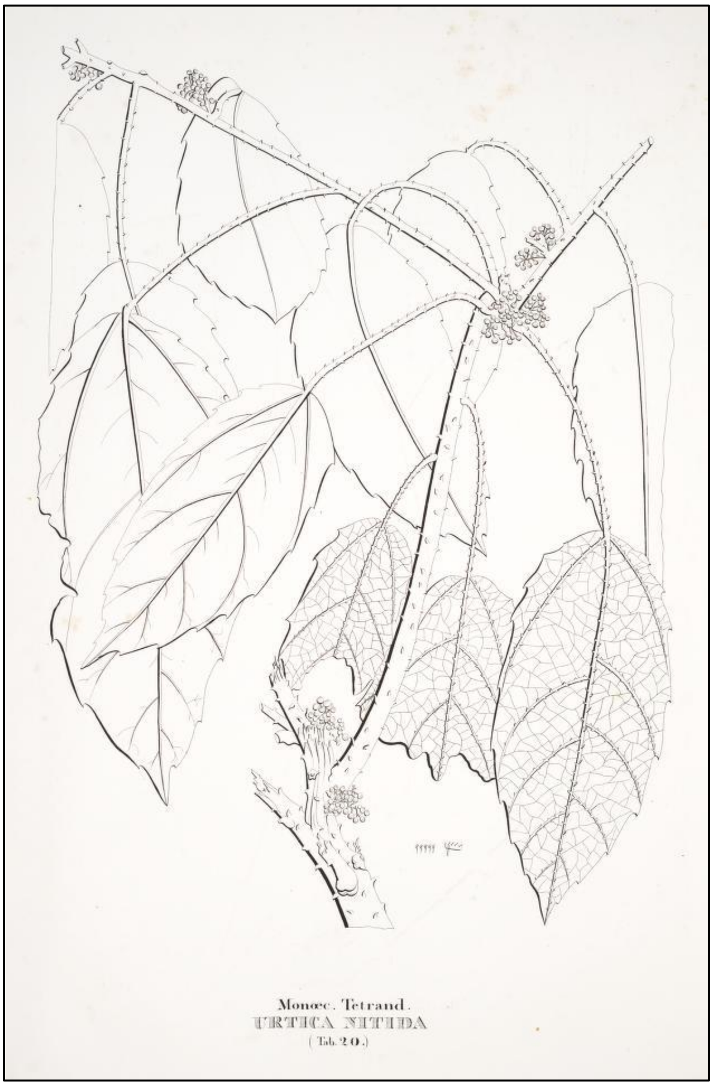

Figure 5 - Type illustration of *Urera nitida*.

Figure 6 - Neotype of *Urera denticulata* collected in Brazil.

Urera denticulata Miq.

Urera denticulata was first described in 1853 by Miquel. No type is specified in the description, however a neotype was designated by Monro and Rodríguez (2009) of a collection from Brazil (figure 6). The specific epithet *denticulata* is derived from the Latin *denticulatus* meaning “denticulate, with very small teeth,” (Stearn, 1992).

From Miquel’s original description, *U. denticulata* has oblong leaves the length of the petiole. Additionally, the leaves have a dentate margin. The inflorescence of the taxa are in axillary cymes, with minutely divided bracts (Miquel, 1853). According to Miquel’s description (1853), the taxa is found in forests of Brazil (GBIF, Tropicos.org).

Urera horrida (Kunth) Miq.

Urtica horrida was described by Karl Sigismund Kunth in 1817. A lectotype of *Urtica horrida* was designated by de Rooij (1975) from a collection of Humboldt’s from Colombia. The basionym was recombined and moved into the genus *Urera* by Miquel in 1853 (Miquel, 1853). The specific epithet *horrida* comes from the Latin *horridus* meaning “sticking out, prickly, rough, bristly,” (Stearn, 1992).

As seen in the type specimen (figure 7), the taxa has ovate leaves with cordate bases (Kunth, 1817). Additionally, the abaxial lamina surface is described as tomentose. As the name suggests, the taxon is noted for having stinging spines. Kunth’s description notes the taxa had been seen growing along river banks (Kunth, 1817). Additionally, it is found in northern and eastern South America (Kunth, 1817; de Rooij, 1975).

Figure 7 - Type of *Urera horrida* collected in Colombia.

Urera viridisetosa Rusby.

Urera viridisetosa was published by Rusby in 1927. The type specimen was collected in Bolivia in 1921 by White (figure 8).

The description of the *U. viritdisetosa* notes the dense prickles on the stem, petiole, and leaf veins (Rusby, 1927). Additionally, Rusby (1927) notes the leaves as being broadly ovate with a tomentose abaxial surface. The specific epithet *viridisetosa* is derived from the Latin prefix *viridi* meaning green (Stearn, 1992), and the adjective *setosus* meaning bristly (Stearn, 1992), referring to the deep-green leaf surface and dense prickles noted in the description (Rusby, 1927)

The type specimen was collected in Bolivia (Rusby, 1927), while the taxon has been noted as occurring in Panama as well (GBIF).

Figure 8 - Holotype of *Urera viridisetosa* collected in Bolivia.

Urera laciniata Wedd.

Urera laciniata was first described by Weddell (1852). The type specimen on which Weddell based the description, was collected in 1844 by Goudot in Colombia (figure 9). The specific epithet *laciniata* is derived from laciniate meaning “slashed; cut into narrow pointed lobes” (Fernald, 1950), referring to the distinguishable leaf shape.

This species is noted for its deeply lobed leaves and asymmetrical fruit (Monro and Rodríguez, 2009). Additionally, it is known to be densely covered in spines along the branches (Killip, 1960) and to release a white latex when the stem is cut (Monro and Rodríguez, 2009). Additionally, *U. laciniata* has ligulate stigma (pers. obs.).

The taxon grows in riverside scrub and in disturbed forest (Monro, pers. comm.). *U. laciniata* has been found from sea-level to elevations of 2600 m (Tropicos.org). The taxon occurs in Central and South America, from Honduras to Bolivia (Figure 10) (Burger, 1977; Monro and Rodríguez, 2009).

Urera laciniata is used as a traditional medicinal. In Peru it is used to treat malaria and ulcers (Céline *et al.*, 2009), in Ecuador to treat body aches and muscular pain (Giovannini, 2015).

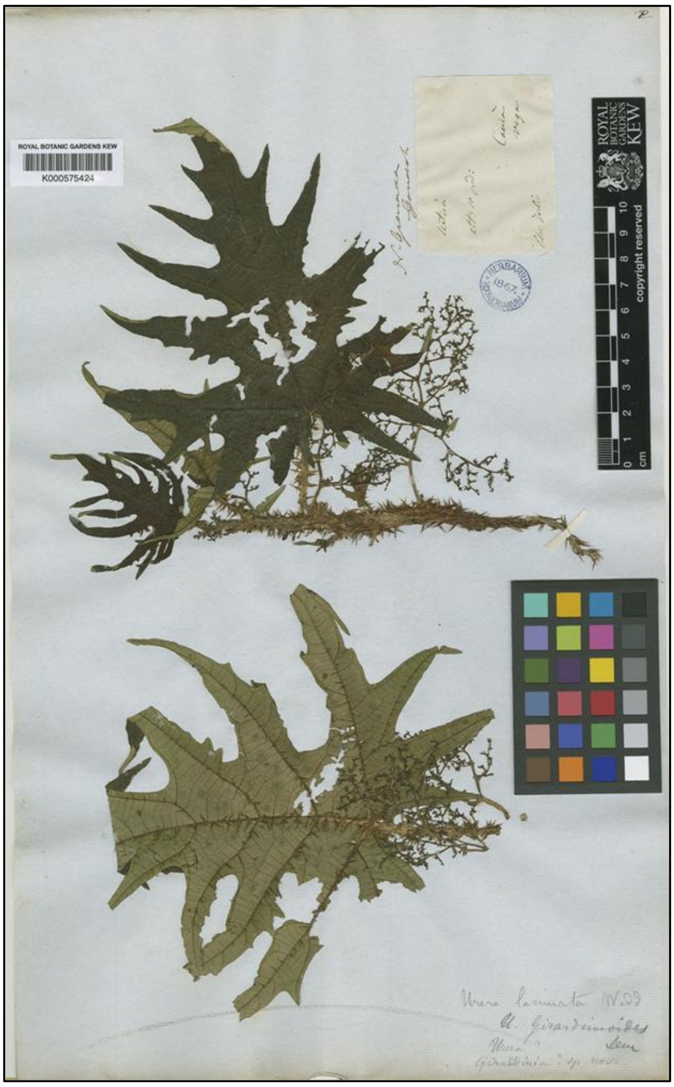

Figure 9 - Syntype of *Urera laciniata* collected in Colombia.

Figure 10 - Distribution of *Urera laciniata*.

Biogeography

The ingroup taxa are traditionally found in disturbed, riparian habitats (Monro and Rodríguez, 2009) at elevations ranging from sea level to 2600 m (Monro and Rodríguez, 2009, Tropicos.org). Taxa occurring in riparian habitats require a perpetual water supply (Mligo, 2017). Additionally, these areas experience frequent disturbance often due to human activity (Perry *et al.*, 2011).

Markedly different from riparian habitats, *U. baccifera* is also noted to be growing in dry, rocky outcrops, with one herbarium specimen referencing the *campos ruprestres* region in Brazil (pers. obs.). *Campos ruprestres* habitats are characterized by rocky outcrops and non-rocky areas of soil with varying depths that can be found in the Caatinga, Cerrado, and Atlantic rainforest of Brazil (Zappi *et al.*, 2017; Mucina, 2018). Based on the ecoregions delineated by Dinerstein et al. (2017) and herbarium label collection data, *U. baccifera* appears to grow in other dry environments such as the Caatinga and Cerrado.

Study Aims

It is clear that *Urera baccifera* and its associated taxa are in need of a comprehensive study, and this report aims to address a small piece of the confusion regarding species delimitation. Phylogenies produced in recent years (Kim *et al.*, 2015; Wells, 2017) have illustrated *Urera baccifera* and *Urera laciniata*'s unique relationship with the rest of the American *Ureras*. While closely related, each has a distinct morphology. In addition, *U. baccifera* has a variable morphology that has resulted in the publication of multiple names attempting to address different parts of the morphology. Finally, each taxa occurs throughout the Caribbean, and Central and South America. This variability will be addressed through a review of morphological characters and phylogenetic analyses. With these analyses, the specific aims of the study are to:

- Confirm the relationship between *Urera baccifera* and *Urera laciniata* as seen in previous studies, and
- Determine if there is more than one genetically and morphologically distinct species within what is currently accepted as *Urera baccifera,* and

Achieving these aims will allow for a clearer picture of species delimitation within the neotropical *Ureras*. In addition, they will provide a greater understanding of the current distribution of the taxa and its movement throughout the Caribbean and Central and South America

Methods

Morphology

Initial morphospecies were established using vegetative and floral characters based on personal observation and a review of the relevant literature. Herbarium specimens from the British Museum (BM), Royal Botanic Gardens, Kew (K), and Royal Botanic Garden Edinburgh (E) were observed in order to make these classifications. Each herbarium's collection was examined looking at all specimens of *U. baccifera*, *U. laciniata*, and those only identified to the genus level from the Caribbean, and Central and South America. Additionally, flowers and fruits were rehydrated in order to dissect them for further examination. All specimens were grouped into one of four morphospecies, primarily based vegetative characters, such as leaf shape and base.

Character Selection

Characters were selected after a review of the literature and images of type specimen, in addition to personal observations of herbarium material from BM, E, and K. Character states were then established based on variations across the examined specimens, based on Hawkins et al.'s (1997) findings that characters and character states should be treated separately in order to determine a hypothesis of primary homology.

In addition to character states previously noted as informative (outlined below), characters observed as having significant variation were also included for analysis. For example, previous studies have not included characters such as the shape of the leaf base as an informative character. Within the sampled accessions, however, there is significant variation in this character, leading to its inclusion.

Characters Selected

Characters selected included the overall habit/size, leaf shape, leaf base shape, the leaf margin, the pubescence on the abaxial leaf surface, stipule fusion, stigma shape, and the type of hairs found on the stem (table 1). Significant variation was not seen in characters noted as informative by others studies such as stem woodiness and morphology of fruits (Bonsen and Welle, 1984; Monro and Rodríguez, 2009). The characters included were limited, based on the argument of Scotland et al. (2003) that an increase in characters sampled can lead to an increased number of ambiguous characters.

Habit

There was variation in the habit of the assorted specimen, however designations such as tree, small tree, or shrub, were inconsistent across herbarium label data. As such, the lignification of the main stem is examined. Specimen were considered lignified if described on their herbarium label as a tree or shrub. Those described as herbs were considered not lignified.

Leaf morphological characters

The most significant morphological variation amongst the sampled specimens was in the leaf morphology. Leaf morphology has been noted as an informative character in the distinction of species (Monro and Rodríguez, 2009; Wells, 2017). The leaves of those identified as *U. baccifera* and *Urera* sp. had an overall elliptic or ovate shape, whereas *Urera laciniata* has deeply lobed leaves.

There is also variation within the leaf base of the sampled accession, with attenuate, cordate, and truncate bases seen.

The leaves, too, all had some degree of toothing on the margin, a character noted by Monro and Rodríguez (2009). Within the sampled accessions this ranged from forward facing serrate teeth to outward facing dentate teeth. The leaves of *U. laciniata* are lobed and occasionally have irregular dentation.

Finally, the abaxial lamina surface was either glabrous or pubescent.

Stipules

Kim et al. (2015) found that the stipules in the Urticeae tend to be partially fused and intrapetiolar. There was variation seen in the degrees of fusion in the stipules of the sampled accessions. Some were entire, others were almost entirely fused with a bifid apex. The stipules of *U. laciniata* have been noted to be mostly free, but partially fused at the base (Burger, 1977), however this character was not observed on the assembled specimen.

Cystolith arrangement on the adaxial surface

The arrangement of cystoliths on the adaxial lamina surface is a noted interspecific diagnostic character of *Urera* (Steinmann, 2005). Cystoliths on this surface had either a random or organized arrangement. Of the organized cystoliths, they were either arranged around bulbed hairs on the lamina surface or arranged linearly along veins.

Bulbed Hairs

Stinging hairs are a character found across the Urticeae tribe and are also an informative character (Weddell, 1852; Steinmann, 2005). *Urera baccifera* and *Urera laciniata* are no exception. In addition to these stinging hairs, the taxa often also have hairs on the stem that become lignified, similar to spines.

Bulbed hairs were seen with varying degrees of frequency on the midrib, petiole, and inflorescence.

Inflorescence

Within *Urera* there are differences seen in the symmetry of the inflorescence. Descriptions of *U. baccifera* note the inflorescence as a branched panicle (Burger, 1977; Steinmann, 2005). This does not encompass the possible variation of the structure, which could be have symmetrical or asymmetrical branching. Also, some inflorescences appeared to appressed to the stem, while others had an apparent peduncle.

Stigma Shape

Stigmas across the Urticaceae are relatively variable, with Chen (1985) illustrating 11 different stigma variations throughout the family. Present within the observed neotropical *Urera* were capitate stigmas and ligulate stigmas.

Fruit

The fruit of *U. baccifera* are noted for being achenes surrounded by fleshy perianth parts (Killip, 1960; Burger, 1977; Monro and Rodríguez, 2009).

Character	States			
Main Stem	Lignified	Non-lignified		
Leaf Shape	Ovate	Elliptic	Oblong	Obovate
Leaf Base	Cordate	Truncate	Attenuate	
Leaf Margin 1	Entire	Toothed		
Leaf Margin 2	Dentate	Serrate	n/a	
Lobes	Lobed	Unlobed		
Abaxial Lamina Surface	Pubescent	Glabrous		
Cystolith Arrangement 1	Organized	Random		
Cystolith Arrangement 2	Linear	Radial	n/a	
Stinging Hairs on Midrib	Present	Absent		
Stinging Hairs on Petiole	Present	Absent		
Stinging Hairs on Stem 1	Present	Absent	n/a	
Stinging Hairs on Stem 2	Lignified	Bulbed hair		
Stipule Shape	Entire	Bifid apex		
Inflorescence	Appressed to stem	Away from stem with apparent peduncle		
Inflorescence Symmetry	Symmetrical	Asymmetrical		
Presence of Bulbed Hairs on Inflorescence	Present	Absent		
Stigma Shape	Capitate	Ligulate		
Fruit	Becoming fleshy	Not fleshy		

Table 1 – Morphological characters and character states

Molecular

DNA extractions were taken from 54 herbarium specimens (Appendix 2) from the herbaria of the British Museum (BM) and the Royal Botanic Gardens, Kew (K). Preference was not given to specimen of any particular age, following the findings of Särkinen et al. (2012).

Taxon Sampling

Geographic Coverage

Herbarium specimens were chosen from across the geographic and altitudinal range of *Urera baccifera* and *Urera laciniata*. The northern limit found in the sampled *U. baccifera* specimen is southern Mexico and the southern limit is central Paraguay. Of the *U. laciniata* sampled the northern limit was central Costa Rica and the southern limit was northern Bolivia.

Morphological Coverage

Initial observations based on vegetative and floral characters guided the selections of morphology. Leaf shape, leaf base, abaxial lamina surface, presence and density of stinging hairs on stems, petioles, and lamina surface, in addition to the branching of the inflorescence and fruit size were considered in these selections.

Taxonomic Coverage

Specimen identified as *Urera baccifera*, *Urera laciniata*, and *Urera* sp. based on their determinations on each herbarium sheet were selected for extraction. Also included were specimen that match the descriptions of *Urera nitida* and *Urera rugosa* but are currently identified on their label as *Urera baccifera*.

Genome Region Selection

ITS

This study was conducted using the internal transcribed spacer region (ITS) of the 18S-5.8S-26S nuclear ribosomal cistron. The region is useful for phylogenetic reconstruction as it is an easy to find gene that repeats often, making it easy to isolate. Additionally, the "high copy number and the small size of the target DNA fragment facilitate ITS amplification by PCR, even permitting the use of ancient material [and] herbarium specimens," (Álvarez and Wendel, 2003). Additionally, Särkinen and Staats et al. (2012) found that short fragments are often abundant in the DNA extracted from herbarium material. All material in this study is derived from herbarium specimens, in which the drying method, which can significantly affect DNA yield (Särkinen, Staats, *et al.*, 2012), is typically unknown. Given these factors, the use of ITS is crucial in successfully obtaining and sequencing possibly degraded DNA.

*trn*L-F

Additional analysis was run using *trn*L-F sequences. With the introduction of universal markers, the *trn*L intron has become one of the most commonly used chloroplast markers (Quandt *et al.*, 2004). It is used to look at diversity in various taxonomic levels, including infraspecific and generic (Quandt *et al.*, 2004; Agostini, Echeverrigaray and Souza-Chies, 2012). *trn*L-F is an intergenic spacer that has shown "high sequence similarity among defined groups of taxa, such as angiosperms" (Quandt *et al.*, 2004). Sytsama et al. (2002) noted that *trn*L-F was an effective region in the analysis of various families of the Rosales, making it an useful region in finding resolution among the urticalean rosids. Through use of this region, in a combined analysis with the ndh-F region, Urticaceae was found to be strongly monophyletic

(Sytsma *et al.*, 2002). Additionally, Kim et al. (2015) used the plastid region in order to assess generic relationships within the tribe Urticeae.

DNA Extractions

Following protocols established by the STS office at the Royal Botanic Garden Edinburgh, less than 20 mg of leaf material was removed from samples of each herbarium sheet. The material was then placed in individual tubes where a small ball bearing was added to assist in the homogenization process. Using a Mixer Mill the samples were macerated for four minutes in order for them to be ground into a fine powder.

In order to extract the DNA from the samples, a QIAGEN DNeasy kit was used and the manufacturer's protocol was followed. AP1 buffer was added to the macerated sample tissue. The mixture was then incubated for 1 hour at 65°C in a Thermomixer, lysing the cells. P3 buffer was then added to the lysate and was incubated for 5 minutes on ice, precipitating detergents, proteins, and polysaccharides. The lysate was centrifuged for 5 minutes and then pipetted into a QIAshredder Mini spin column, where it was centrifuged again for 2 minutes. The flow-through was then added to a new collection tube where AW1 buffer was added to the cleared lysate. This was transferred to DNeasy spin column, which was then centrifuged for 1 minute. The flow-through from this process was discarded. Using the same spin column, the remainder of the sample was processed. With the DNA collected on the spin column filter, the column was added to a new tube where AW2 buffer was added and then centrifuged for 1 minute. The flow-through was discarded and additional AW2 buffer was added, centrifuged, and the subsequent flow-through was once again discarded. Once the flow-through was discarded, the spin column was centrifuged again in order to dry the membrane. The spin column was added to a new tube where AE buffer was pipetted onto the DNeasy membrane. This was incubated at room temperature for 5 minutes, after which it was centrifuged for 1 minute to elute.

The extracted DNA was then prepped to run through a polymerase chain reaction (PCR) using a Master Mix (Appendix 1a). The samples were then run through a PCR for 35 cycles (Appendix 1b).

Once run through the PCR, the samples were then run through a gel electrophoresis on a 2% agarose gel for 45 minutes at 80V. The gels were then run through a Syngene G:BOX F3 Fluorescence Imaging System in order to visualize the bands produced in the gel electrophoresis, using GeneSys Image Acquisition Software.

To prepare the PCR product of the successful runs for sequencing, the product was purified using ExoSAP IT (GE Healthcare). The PCR product was mixed with ExoSAP IT and incubated at 37°C for 15 minutes then heated at 80°C for 15 minutes.

Following the ExoSAP, the DNA template was prepared for a sequencing PCR. Individual Master Mixes were made for the forward and reverse primers, ITS 4 and ITS 5 respectively (Appendix 1c).

Once prepared the Master Mix was aliquoted to each DNA sample. The following PCR was run to prepare the samples for sequencing (Appendix 1d). Prepared samples were sent to Edinburgh Genomics for sequencing.

Phylogeny

The raw sequences were assembled and edited using Geneious 11.1.4 (Kearse *et al.*, 2012). The assembled sequences were aligned using MAFFT version 7 (Katoh, Rozewicki and Yamada, 2017), an online alignment algorithm. Following this alignment, the sequences were further edited manually using Bioedit v7.2.5 (Hall, 1999). In order to be read in the Phylogenetic Analysis Using Parsimony (PAUP) (Swofford, 2003), MrBayes (Ronquist *et al.*, 2012), and Randomized Axelerated Maximum Likelihood (RAxML) (Stamatakis, 2014), the alignment was converted to nexus files and a phylip file using the online format converter, ALTER (Glez-Peña *et al.*, 2010).

An outgroup was selected using previously sequenced data from various other *Urera* species, occurring in Central and South America (Wells, 2017).

Using PAUP, a parsimony heuristic search and a parsimony bootstrap analysis were run. The heuristic search was run with 10,000 replicates. Tree bisection and reconnection (TBR) was used as the branch swapping method. This search produced all of the most parsimonious trees and strict, semi-strict, and Adams consensus trees. Bootstrap analyses were run, with 10,000 replicates, to determine support for the clades of the parsimonious trees. Additional heuristic and bootstrap analyses were carried out in which the ITS1 and ITS2 internal transcribed spacers and 5.8s rDNA were partitioned, using Yakota et al. (1989) as reference for the nucleotide sequence, producing a strict and majority rule consensus trees.

Further analysis was done to determine the Maximum Likelihood trees. The initial DNA alignment was converted to a Phylip file using ALTER. The maximum likelihood was determined by running a Randomized Axelerated Maximum Likelihood analysis (Stamatakis, 2014). A general time reversible (GTR) model with a gamma distribution of rates was used to model DNA evolution. Additionally, 1000 bootstrap samples were used.

Bayesian analysis was run using MrBayes version v. 3.2.6 x64 using default priors. The best fit model was determined to be GTR+I by Akaike's Information Criterion (AIC) using MrModeltest (Nylander, 2004). Four Markov chain Monte Carlo (mcmc) chains were run for three million generations, where trees were sampled every 1000 generations. A 10% burn-in rate was assumed.

Finally, analysis was run combining the above ITS data and previously sequenced *trn*L-F data (Wells, 2017). Using PAUP, a partition homogeneity test was run to determine congruence within the combined dataset. Once established, the previously described parsimony protocol was followed. Using this combined data, a maximum likelihood analysis was also run using the above methods.

Combined Morphological Analysis

Characters identified in the morphological review were used to carry out a mixed morphological and molecular analysis. Multiple vegetative and floral characters were scored and added to the alignments. With this addition, another Bayesian analysis was run using MrBayes version v. 3.2.6 x64 using default priors. A GTR model with gamma was used. Additionally, four Markov chain Monte Carlo chains were run for three million generations, with trees sampled every 1000 generations. A 25% burn-in rate was assumed.

Biogeography

Using ArcMap 10.5.1, specimens of both *U. baccifera* and *U. laciniata* were mapped based on coordinate data provided on the herbarium labels. Additional specimens were plotted by assigning coordinate values based on locality information. All data points were projected in World Geodetic System 1984 (WGS). These points were overlaid on a map of Ecoregions2017©Resolve (Dinerstein et al., 2017).

Results

Molecular

Of the 54 specimens of *Urera baccifera* and *Urera laciniata* sampled from herbarium material, DNA was successfully extracted and sequenced from 32 individual accessions, with three *U. laciniatas* and 29 *U. bacciferas*. This data was supplemented in the phylogenetic analysis with data from Wells (2017). Sample age did not appear to affect the success of obtaining DNA from specific samples, with successful sequences coming from specimens collected from the mid-nineteenth century to the early twenty first century, aligning with the findings of Särkinen et al. (2012).

Phylogeny

Numerous analyses were run using a variety of methods as outlined in the section above. While there were multiple well supported clades, only one showed an affinity for a distinct morphology. In addition to the variable morphology seen within the clades, there were no distinct differences in the clades in any of the characters that previous reports have noted as good species indicators, such as the presence and shape of cystoliths. Finally, there was some degree of geographic signaling in the supported clades.

ITS

The below figure (figure 11) shows the Bayesian analysis of the sequenced ITS data, with the posterior probability values of the Bayesian analysis displayed (PP) and the bootstrap values from Maximum Likelihood (ML) and a Parsimony Heuristic (MP) search. The analyses were almost entirely congruent, with strong support values in each tree for the present clades. Each analysis showed strong support for clade C, the *Urera laciniata* clade (PP 100/ML 100/MP 100), as well as the two larger *Urera baccifera* clades, A (PP 100/ML 86/MP 82.9) and B (PP 100/ML 85/MP 95.1), and two smaller clades, D (PP 99/ML 64/MP 64.4) and E (PP 100/ML 72/MP 70.5), which only have two accessions each. These five clades, however, only account for 53% of the sampled specimens, with the rest appearing as a polytomy.

In the maximum likelihood analysis, baccifera13896 is found to be a sister to the rest of clade A. There is little separating this accession from the rest of the clade morphologically, however it does occur at a higher elevation than the rest of the specimens in the clade. Additionally, this accession was collected in Colombia, distinct from the rest of the clade, however it is found, like other members of the clade in a riparian habitat.

On each tree within clade B, two accessions, baccifera3930 and baccifera2107, appear as strongly supported sisters (PP 100/ML 88/MP 86.2) to the rest of the clade. These two specimens both occur in Brazil on calcareous substrates. Both are small shrubs with pink inflorescences, differentiating these two from the rest of the clade which have white to light green inflorescences.

Two subsequent taxa occur in clade B: *Urera nitida* and *Urera rugosa*. These three accessions were identified as *U. baccifera* on their herbarium labels. However, the morphology of these accessions aligned with the descriptions of *U. nitida* and *U. rugosa*, which, as their confused taxonomic histories show, are very similar to *U. baccifera*. The placement of these three accessions in the *Urera baccifera* clade B is strongly supported, though, and not as separate species.

Clade C also contained two sister accessions, laciniata3905 and laciniata221 (PP 99/ML 70/MP 63). Each accession occurs in Peru and are shrubs with green flowers, however their location and morphological features are indistinct when compared to the rest of the clade.

The placement of clade C is problematic, however. Despite the strong support for it in all of the analyses, clade C is comprised of accessions all identified as *Urera laciniata*. Previous studies have found *U. laciniata* to be closely related to, yet genetically distinct from, *Urera baccifera*.

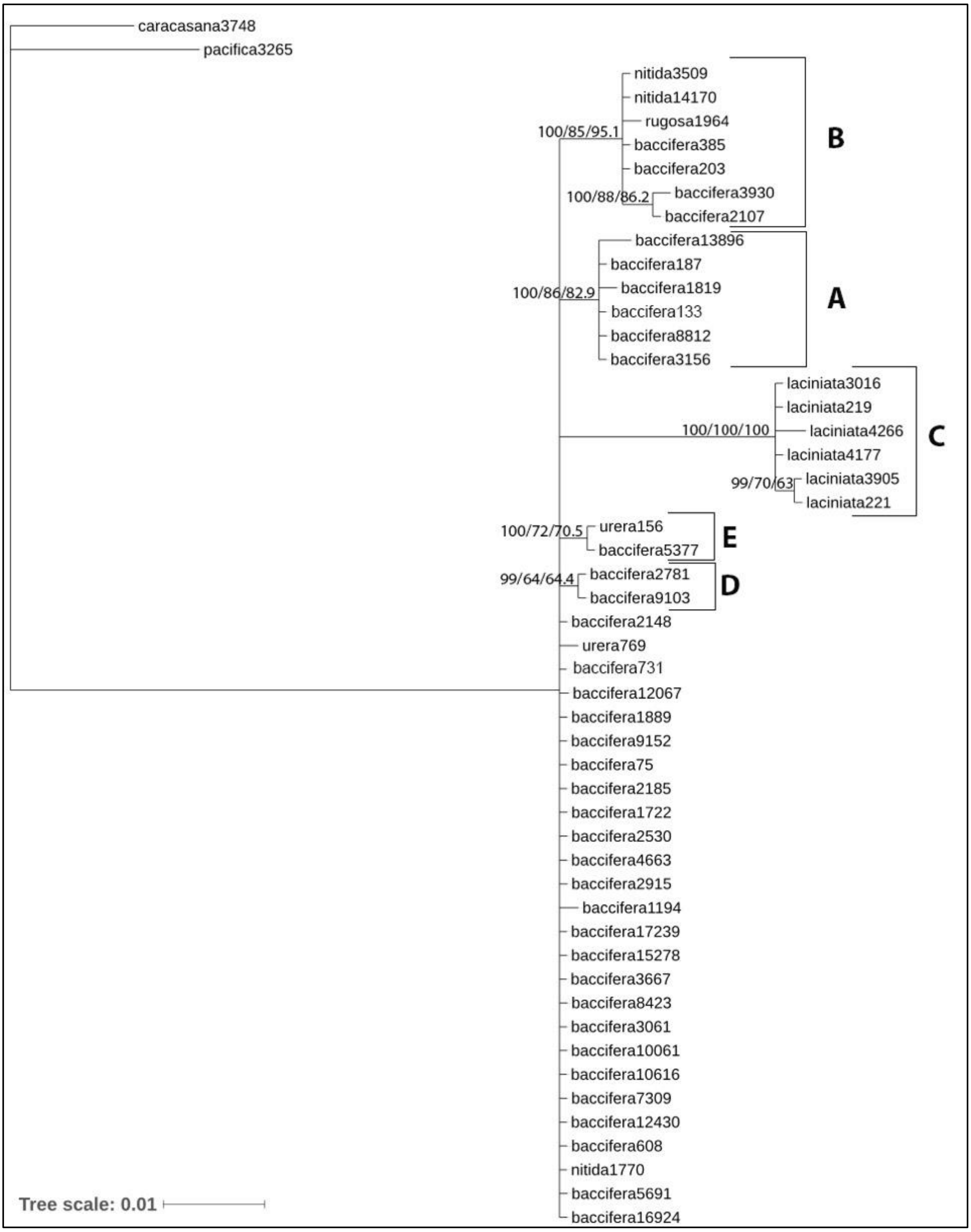

Figure 11 - A phylogram based on a Bayesian analysis.
Support values for clades within *Urera baccifera* include Posterior Probability values (PP) from Bayesian analysis, bootstrap values from a maximum likelihood analysis (ML), and bootstrap values from a heuristic search of most parsimonious trees (MP) (PP/ML/MP). Letters indicate the supported clade.

Combined *trn*L-F and ITS

In an analysis that combined ITS and *trn*L-F sequences (figure 12), three of the five clades seen in the ITS tree, Clade A (ML 82/MP 82), Clade B (ML 89/MP 96) and Clade C (ML 100/MP 100), were supported with strong support values.

Clades D (ML 57/MP 64) and E (ML 72/ML 66) were supported by this analysis, however with low support values. *trn*L-F data was not available for these accessions, and as such, the analysis was run with these four accessions coded for missing data in the *trn*L-F region. Due to their low support values, these two clades were collapsed and made part of the larger *U. baccifera* polytomy.

The sister groups within clades B and C were also supported by this analysis. The sister accessions in clade B were two of the accessions with available *trn*L-F data. However, this grouping had lower support in this analysis, with a maximum likelihood bootstrap value of 82 and parsimony bootstrap value of 90. The sister specimens in clade C, however, had stronger support with a maximum likelihood bootstrap value of 84 and parsimony bootstrap value of 64. *trn*L-F data was not available for laciniata4177, one of the two accessions within this group.

Despite the additional region, no further resolution was seen within the remaining accessions.

Combined Morphological and ITS

A combined Bayesian analysis of 19 morphological characters and ITS data (figure 13) has a similar topology to the previous two analyses, with strong support for all five clades, Clade A (100), Clade B (100), Clade C (100), Clade D (99), and Clade E (100). Additionally, this combined analysis shows support for the sister groups within clades B (100) and C (98).

Partitioned

A Bayesian analysis in which the ITS data was partitioned based on the ITS1 and 2 regions, as well as the 5.8s rDNA region, found all five clades have high support values (figure 14). Clades A, B, C, and E had posterior probability values of 100 and clade D with a posterior probability of 99. The two sister groups in clades B and C are also well supported here, with posterior probability values of 100 and 99, respectively. Moreover, this tree had the same topology as the unpartitioned ITS data.

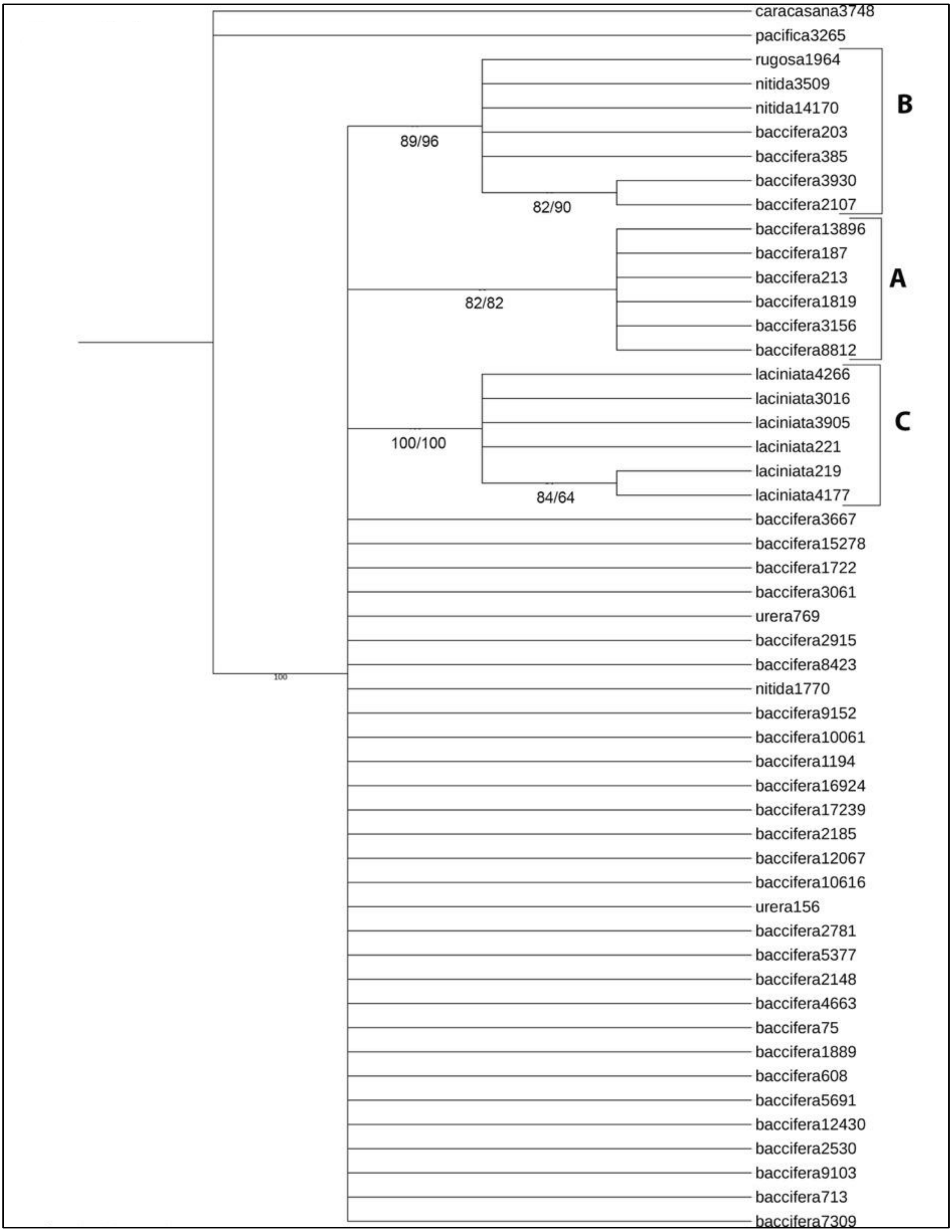

Figure 12 - Combined analysis of ITS and *trn*L-F data.
Tree from maximum likelihood analysis with bootstrap values from maximum likelihood (ML) and maximum parsimony (MP) analyses (ML/MP).

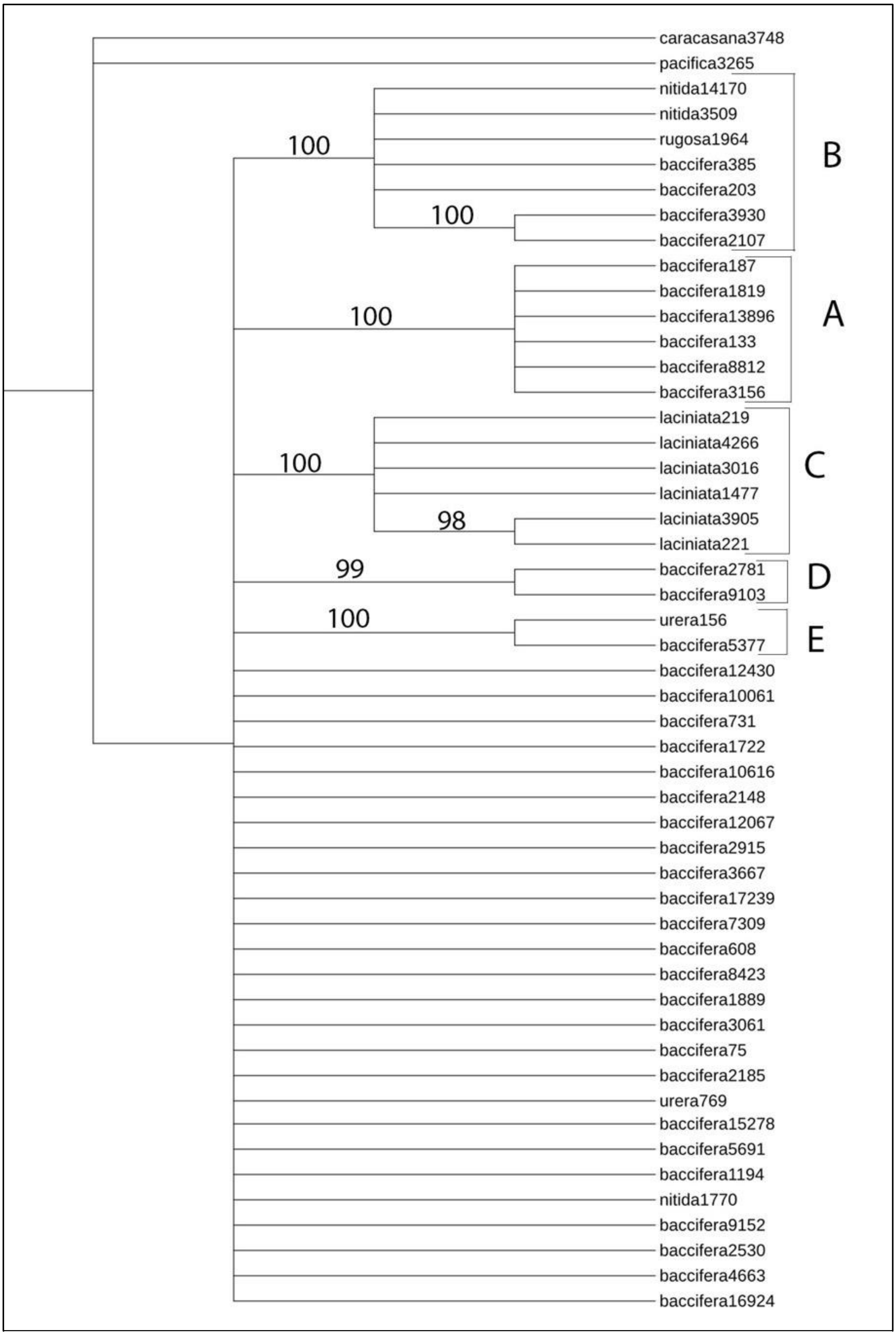

Figure 13 - Bayesian analysis of combined ITS data and coded morphological characters with posterior probability values.

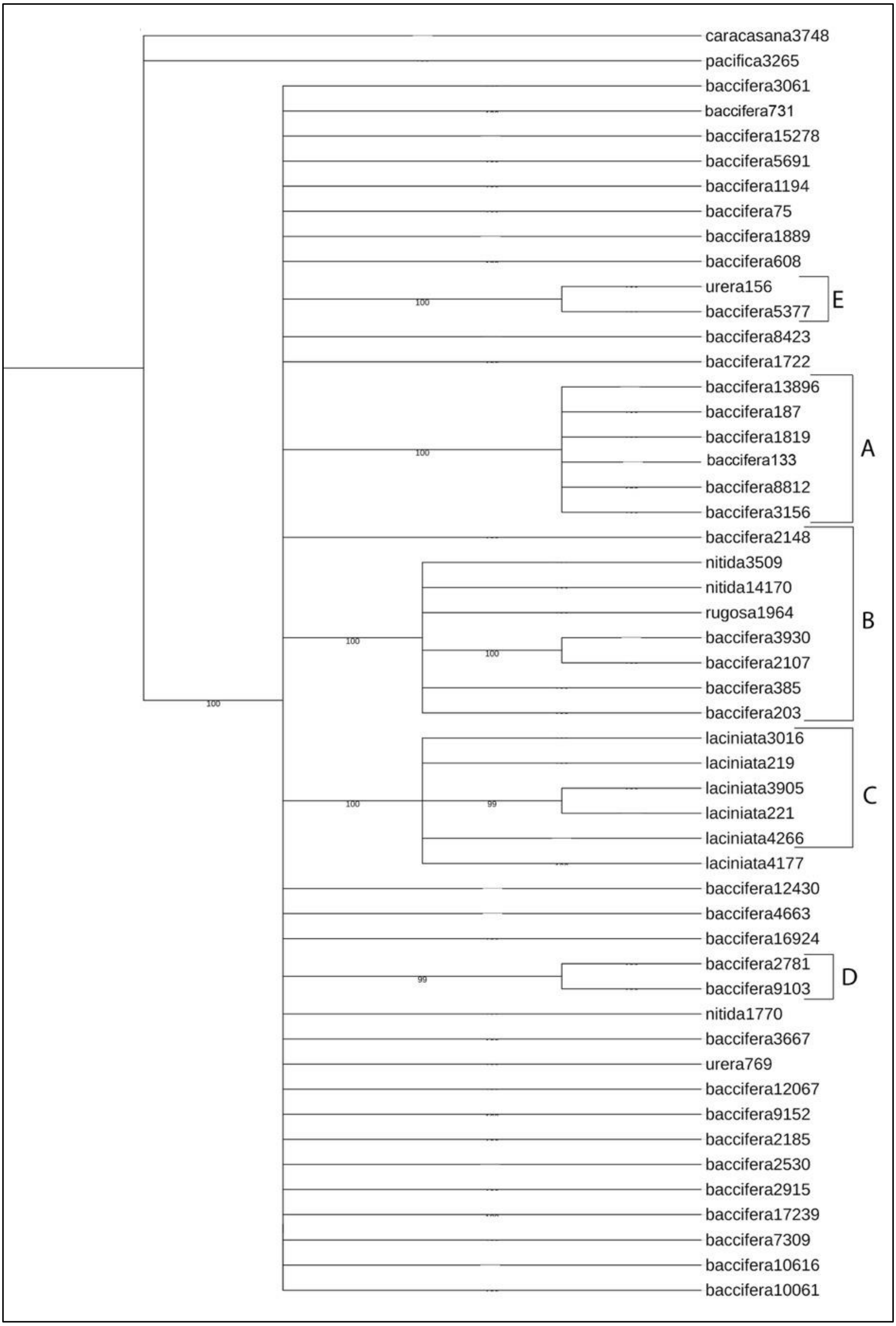

Figure 14 - Bayesian analysis of partitioned ITS data with Posterior Probability values.

Morphological Review

Based on the morphological review of vegetative and floral characters of the 272 assembled *Urera* specimens, four morphospecies were apparent prior to the phylogenetic analysis. The most notable variation was seen in leaf shape, margin, base, and pubescence on the abaxial surface. These characters have been noted for their variability throughout the literature (Weddell, 1852, 1856, 1869; Killip, 1960; Burger, 1977). Little variation was seen in the habit, presence of spines on assorted surfaces, in the symmetry of the inflorescence, and shape of the stigma.

Using the characters outline in the methods, morphospecies were delineated prior to the phylogenetic analysis. This was done by assessing the *Urera* specimens and determining groupings based on a majority consensus of characters. This was done in order to establish a hypothesis of morphologically distinct possible species currently classified in *U. baccifera*.

These four morphospecies were delineated as follows:

1. Elliptic to oblong leaves without lobes with serrate or dentate margins and attenuate to truncate bases, stipules entire or with a bifid apex. Generally glabrous abaxial surface, with bulbed hairs present on the stem, midrib, and petiole. Vines, shrubs, or small trees. (figure 15)
2. Ovate to obovate leaves without lobes with serrate or dentate margins and truncate bases, stipules entire or with a bifid apex. Generally glabrous abaxial surface with bulbed hairs on the petiole and midrib, if present, bulbed hairs on stem occasionally becoming lignified. Mostly shrubs. (figure 16)
3. Ovate leaves without lobes with serrate or dentate margins and cordate bases, stipules entire. Abaxial surface pubescent, with bulbed hairs on midrib and stem. Shrubs and herbs. (figure 17)
4. Broadly ovate, lobed leaves with entire or irregular dentation and truncate bases, stipules not seen. Abaxial surface glabrous, with bulbed hairs on the stem, petiole, and midrib, sometimes absent. Trees and shrubs. (figure 18)

Figure 15 - Examples of Morphospecies One, collected in Peru.

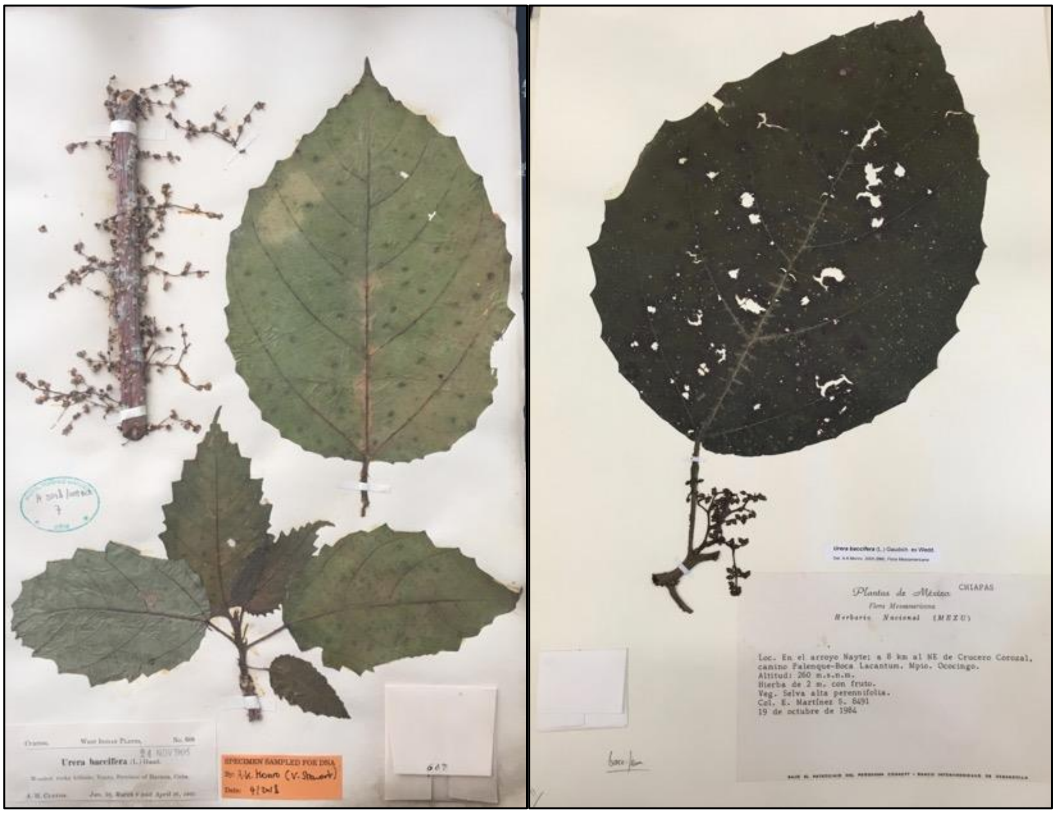

Figure 16 - Examples of Morphospecies Two, collected in Cuba and Mexico.

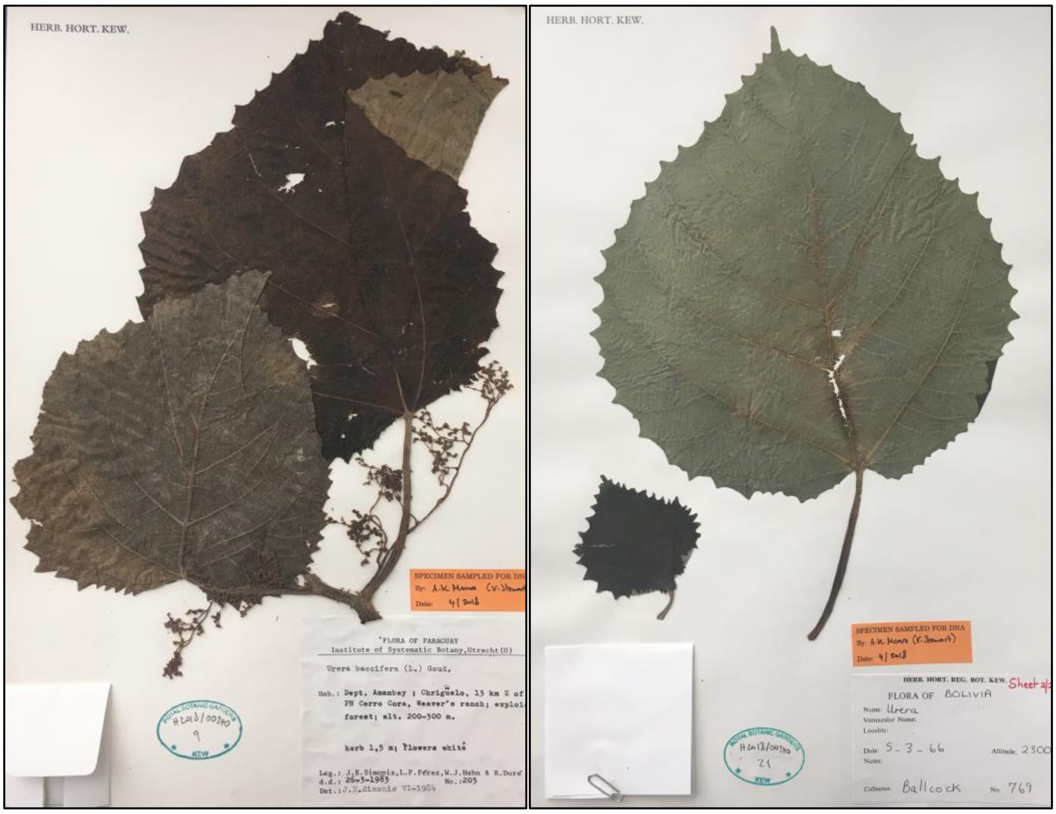

Figure 17 - Examples of Morphospecies Three, collected in Paraguay and Bolivia.

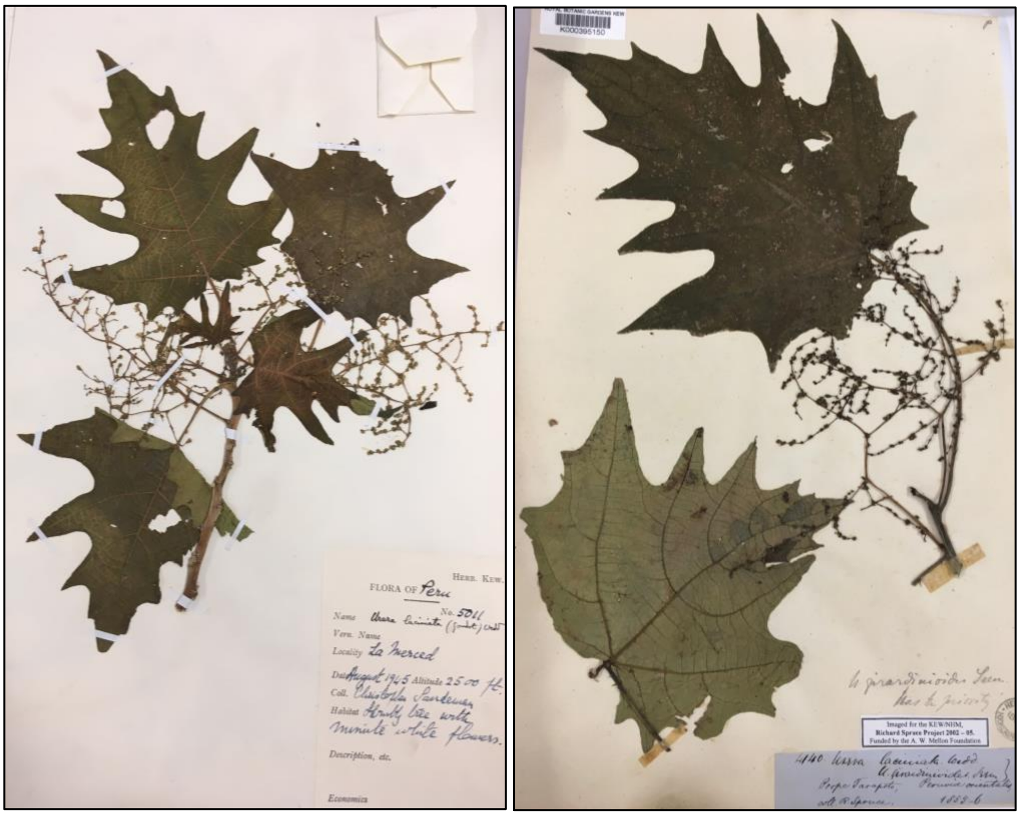

Figure 18 - Examples of Morphospecies Four, collected in Peru.

All four morphospecies are found throughout the Caribbean and Central and South America in a variety of habitats and elevations. Morphospecies Two and Three are similar in their morphologies to Weddell's α and β varieties (Weddell, 1852). The two distinct differences in the morphospecies in the delineation in this study, however, are the shape of the leaf base and the pubescence of the abaxial surface, characters not addressed in Weddell's description (1852). Morphospecies One has similarities to Weddell's variety γ, which describes the variety as having lanceolate-oblong leaves (Weddell, 1852).

Morphospecies Three also aligns with parts of Kunth's description of *Urera horrida*. In particular the description of the leaves, which are described as having a cordate base and tomentose abaxial surface (Kunth, 1817).

Morphospecies Four aligns with the type of *Urera laciniata*. The sampled *U. laciniata*'s were collected primarily in eastern South America, however, *U. laciniata* has been collected throughout Central and South America, with its range extending from Costa Rica to Peru (Burger, 1977).

U. laciniata and *U. baccifera* have been noted as being morphologically similar, however, there is divergence in terms of leaf morphology and their stigmas. The leaves of *U. laciniata* are deeply lobed, whereas *U. baccifera* lacks any lobes. *U. baccifera* does regularly have dentate margins, though occasionally the margins are entire. Alternatively, the margin of *U. laciniata* leaves are generally entire, with some rare, irregular dentation. Finally, there is variation in the stigmas of the two taxa. The stigma of *U. laciniata* is ligulate and covered in multicellular hairs, though one plane is glabrous (pers. obs.) (figure 19). The stigma of *U. baccifera* is capitate, it is also covered in multicellular hairs, though they are only at the top of the stigma (pers. obs.) (figure 20).

Figure 19 – Ligulate stigma of *Urera laciniata*

Figure 20 - Capitate stigma of *Urera baccifera*

Of the observed specimens 116 were a part of Morphospecies One, 60 in Morphospecies Two, 66 in Morphospecies Three, and 25 in Morphospecies Four (Appendix 3).

Placement of Characters Based on Phylogeny

Mapping the outlined characters on the cladogram of the combined morphological/ITS analysis found all characters to be homoplastic (figure 21). Additionally, only Morphospecies Four was supported by the phylogeny, in clade C.

Habit

A majority of the sampled accessions had lignified main stems across the clades and within the wider polytomy. Three accessions were described as herbs by their collector, which occurred in clade A, B, and the polytomy.

Leaf morphological characters

Leaf shape was variable across the clades. Clade A contained ovate and obovate leaves. Within clade B there were ovate and oblong leaves. Clade C had broadly ovate leaves. Clades D and E had ovate leaves, however each of these clades comprised of only two accessions each. Elliptic, oblong, and ovate leaves were seen throughout the specimen in the larger polytomy.

The shape of the leaf base varied throughout the tree. Within clade A base shapes included cordate and truncate, however truncate bases were the majority. Clade B had leaves with attenuate, cordate, and truncate bases. The majority of specimen in clade C had cordate bases, with one having an attenuate base. Both clades D and E had cordate bases. The bases of the rest of the specimen in the polytomy also included these three shapes.

All accessions in clades A, B, D, and E and in the rest of the polytomy are not lobed, whereas all specimens in clade C are. Additionally, each member of clade A, B, D, and E and the polytomy had toothed margins. Two specimen in clade C had entire margins, whereas the rest had irregular dentation in the lobes. Of the clades with teeth, there was variation in the type of toothing in each accession. All accessions in clade A have dentate margins. There was variation between dentate and serrate margins in clades B, D, and E.

The pubescence on the abaxial lamina surface also varied throughout the tree. Clade A and clade B had accessions with both pubescent and glabrous surfaces. The accessions of clade C and clade E had only glabrous adaxial surfaces. And each specimen in clade D had a pubescent abaxial surface. Pubescent and glabrous abaxial surfaces appear throughout the rest of the polytomy.

Cystolith Arrangement

Arrangement of cystoliths on the adaxial lamina surface varied across the tree. The cystoliths of clades A and C were all randomly arranged. Within clade B there was variation where cystoliths were randomly arranged or arranged in an organized manner. The organized cystoliths in clade B were arranged radially around the bulbed hairs and arranged linearly. The cystoliths of the accessions of clade D were organized and arranged radially around the bulbed hairs. The specimen of clade E had cystoliths that were either arranged linearly or randomly. The majority of the remaining specimen had randomly arranged cystoliths. One accession (baccifera2148), however, had cystoliths arranged linearly.

Bulbed Hairs

The presence of stinging hairs on the midrib varied. All accessions of clades A B, and D, where visible, had stinging hairs on the midrib on the abaxial side of the leaves. Clade C contains two accessions with visible stinging hairs on the midrib and one where stinging hairs were not seen, the abaxial surface was not visible in the remaining accessions. The midrib of only once accession in clade E (baccifera5377) was visible and it did not have stinging hairs present. The majority of remaining specimen had stinging hairs on the midrib, while two did not (baccifera731 and baccifera10616).

Stinging hairs on the petiole were also variable. Clades A, C, D, and E had a mixture of petioles with stinging hairs and petioles without stinging hairs. Clade B, of the accessions visible, all had petioles with stinging hairs.

Only two accessions in clade A (baccifera1819 and baccifera133) had stinging hairs on the stem, both of which are lignified. All specimen in clade B had stinging hairs on the stem, of these only one had stinging hairs that were not lignified (nitida3509). Half of the accessions in clade C had stinging hairs on the stem which were lignified, the remainder did not have stinging hairs on the stem. Both accessions of clade D had stinging hairs on the stem, however the hairs on one had lignified, while the others had not. One accessions in clade E (baccifera5377) had stinging hairs on the stem which were lignified. There was variation in these characters across the rest of the polytomy.

Stipules

Stipules shape varied across the clades, however stipules were not visible on many of the accessions. Only two specimens in both clades A (baccifera1819 and baccifera3156) and B (nitida14170 and baccifera203) had visible stipules, one with a bifid apex and one that was entire in each clade. Stipules were not visible in clade C. Stipules were only visible on one of the two accessions in both clades D and E, both entire. Although sparsely seen, where available there was a range of stipules that were entire or had a bifid apex in the rest of the polytomy.

Inflorescence

A majority of the sampled accessions had inflorescences with an apparent peduncle. One accession each in clade A (baccifera3156), clade C (laciniata3016), clade D (baccifera9103) and one in the polytomy (baccifera1722) had inflorescences that appeared to appressed to the stem.

The majority of inflorescences had a symmetrical branching pattern, seen in clades A, B, D, and E and the polytomy. Two accessions in clade C (laciniata219 and laciniata1477) and one in the wider polytomy (baccifera10061) had asymmetrical branching patterns.

All inflorescences in clades A, D, and E and in the polytomy had bulbed hairs on the rachis. One accession in clade B (baccifera385) did not appear to have bulbed hairs on the rachis. The specimen in clade C had a mixture of inflorescences with bulbed hairs and ones without.

Stigma

Where visible, stigma shape was the most consistent character across the entire tree. Ligulate stigmas were found only in clade C, with the rest of the specimen of clades A, B, D, E, and the rest of the polytomy having capitate stigma.

Fruit

In accessions where present, the fruit of clades A, B, D, and E and in the polytomy become fleshy. One accession with fruit in clade C (laciniata4266) did not appear fleshy.

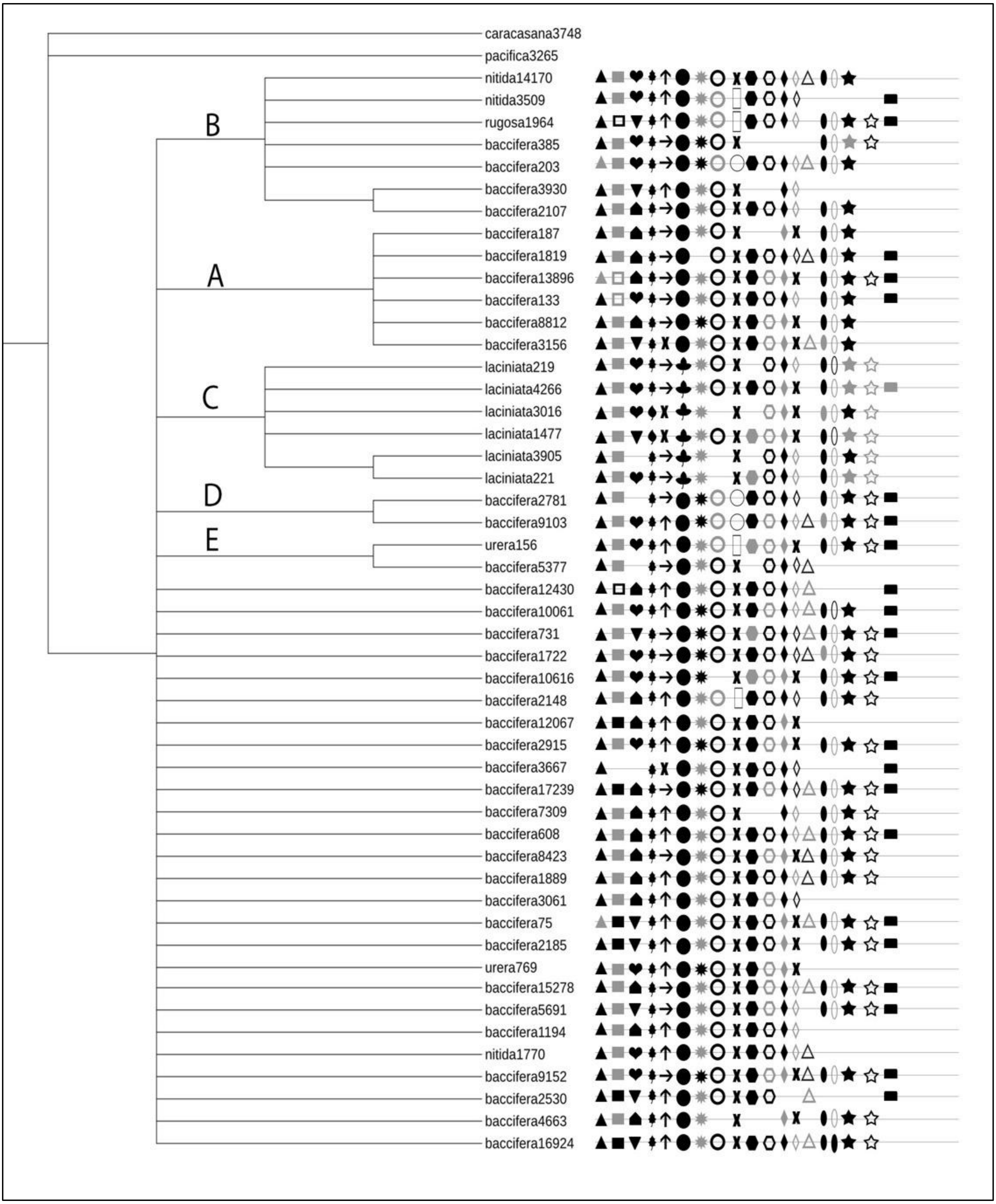

Figure 20 - Mapped morphological characters on the combined character/ITS Bayesian analysis tree. Legend on following page.

Characters	States			
1. Main Stem	Lignified	Non-lignified		
2. Leaf Shape	Ovate	Elliptic	Oblong	Obovate
3. Leaf Base	Cordate	Truncate	Attenuate	
4. Leaf Margin 1	Entire	Toothed		
5. Leaf Margin 2	Dentate	Serrate	n/a X	
6. Lobes	Lobed	Unlobed		
7. Abaxial Lamina Surface	Pubescent	Glabrous		
8. Cystolith Arrangement 1	Organized	Random		
9. Cystolith Arrangement 2	Linear	Radial	n/a **X**	
10. Stinging Hairs – midrib	Present	Absent		
11. Stinging Hairs – petiole	Present	Absent		
12. Stinging Hairs – stem 1	Present	Absent		
13. Stinging Hairs – stem 2	Lignified	Bulbed Hair	n/a **X**	
14. Stipule Shape	Entire	Bifid Apex		
15. Inflorescence	Appressed to Stem	With apparent peduncle		
16. Inflorescence Symmetry	Symmetrical	Asymmetrical		
17. Bulbed Hairs on Inflorescence	Present	Absent		
18. Stigma Shape	Capitate	Ligulate		
19. Fruit	Becoming Fleshy	Fleshy-ness not present		

Table 1 - Legend for mapped morphological character tree (Figure 21).

Biogeography/Ecology

Three of the *Urera baccifera* clades, A, B and E, show some geographic signaling (figure 22).

Figure 21 - Distribution of the sampled accessions of *Urera baccifera*. Accessions not found in one of the supported clades represented by blue dots.

The majority of individuals in clade A are located in tropical moist broadleaf forests, with one, baccifera1819, occurring in tropical dry broadleaf forest, as defined by Dinerstein et al. (2017). Additionally, they are found from 600–2600 m above sea level.

Clade B is found in eastern Paraguay and southwestern Brazil. These accessions are located in a variety of biomes, including tropical moist broadleaf forests, tropical dry broadleaf forests, and tropical grasslands, savannas, and shrublands (Dinerstein *et al.*, 2017). Being outside of the Andes, clade B occurs at lower elevations, ranging from 200–1100 m above sea level.

Clade D is found in Bolivia and Belize, growing in tropical moist broadleaf forest (Dinerstein *et al.*, 2017). The Bolivian specimen is found at 1500 m, and there is no available elevation data for the Belizean specimen. Clade E occurs in Ecuador in tropical moist broadleaf forest (Dinerstein *et al.*, 2017) with a wide elevation range of 325–1150 m.

The remainder of the *Urera baccifera* accessions are found across the Caribbean and Central and South America, reaching as far north as southern Mexico and as far south as southern Brazil. They are found predominately in tropical moist broadleaf forests, with some accessions occurring in biomes including tropical dry broadleaf forests, tropical coniferous forests, and tropical grasslands, savannas, and shrublands (Dinerstein *et al.*, 2017).

The *Urera laciniata* clade, clade C, is found in eastern South America, predominantly in Peru, with additional accessions occurring in Bolivia, Costa Rica, and Ecuador (figure 23). Individuals are found growing in tropical moist broadleaf forest and montane grassland and shrubland (Dinerstein *et al.*, 2017). The one accession occurring in montane grass- and shrubland, occurs just outside of the boarder of the tropical moist broadleaf forest, which is likely due to the resolution of the ecoregions map (Dinerstein *et al.*, 2017). The individuals of this clade are found from 250–1150 m.

The specific ecoregions, as defined by Dinerstein et al. (2017), as well as habitat information from herbarium sheets, of each accession can be found in appendix 4.

Figure 22 - Distribution of sampled accessions of *Urera laciniata.*

Discussion

The above analyses found five strongly supported, monophyletic clades within one large polytomy. There is evidence that there is correlation between these clades and geography, morphology, and ecology. For example, clades A, B, and E showed a degree of geographical structure, whereas clade C, *Urera laciniata*, was morphologically distinct, and clade B and its subclade showed an affinity for areas of seasonally dry forests, particularly in southern Brazil and eastern Paraguay. Clades A, B, D, and E fit within the larger species concept of *Urera baccifera* of a single species with a wide range and variable morphology.

A similar result was found by Wakasugi et al. (2017) regarding *Geranium yesoense* Franch. et Sav. in Japan. Prior to Wakasugi et al.'s (2017) study there were three varieties of the taxon based on leaf morphology and pubescence on the sepals, though these characters had never been quantified objectively. The results of *G. yesoense* study, which was based on ITS and *trn*L-F sequences, found strong support for geographic groupings of the sampled accessions, but with a range of morphological characters within each clade, much like what is seen here with *Urera baccifera*. The variability of the morphology prevented the authors from creating groupings based on the geography. The authors postulated that these groupings may have diverged too recently to see significant genetic changes or that the variable morphology was the result of the ecotypes in which the individual accessions occurred, a result of allopatric speciation. Ultimately the authors chose to synonymize the three varieties with the specific epithet (Wakasugi *et al.*, 2017).

Geography& Dispersal

Urera baccifera is found throughout the Caribbean and Central and South America. Clade A is found solely in western Central and South America in the Andean region and beyond, whereas clade B is found in the east in Brazil and Paraguay. Clade E occurs in the northeastern portion of the Andes. Accessions in the wider polytomy were found throughout the Caribbean and Central and South America. These specimen occurred in close proximity to clades A, D, and E, however no other sampled accessions were found near clade B. The widespread dispersal of *U. baccifera* is likely due to its dispersal mechanisms.

Urera taxa, including *U. baccifera*, have fleshy fruits that are presumed to be dispersed by animals (Killip, 1960; Friis, 1989, 1993; Kim *et al.*, 2015). In *U. baccifera* these fruits are large, white berries, borne on infructescences covered with relatively stout stinging hairs (figure 24), a character not seen in other American *Urera*, excluding *U. laciniata* (Monro, pers. comm.).

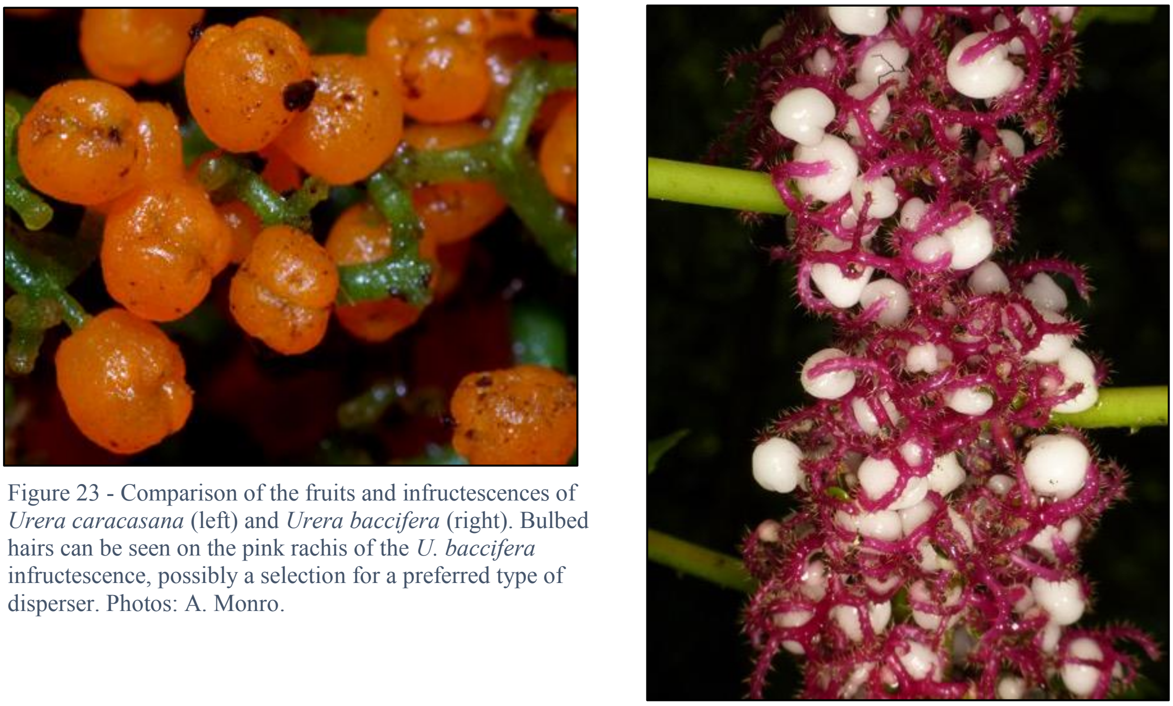

Figure 23 - Comparison of the fruits and infructescences of *Urera caracasana* (left) and *Urera baccifera* (right). Bulbed hairs can be seen on the pink rachis of the *U. baccifera* infructescence, possibly a selection for a preferred type of disperser. Photos: A. Monro.

The presence of the stinging hairs on the infructescence suggests that the species is selecting for a preferred group of dispersers and attempting to exclude others. Birds have been reported feeding on the fruit of *U. baccifera* (Galetti and Pizo, 1996), suggesting that they are unaffected by the stinging hairs and are able to obtain the fruit, whereas a small mammal would get stung (Monro, pers. comm.). Small mammals are too large to avoid the stinging hairs on the infructescence and have sensitive noses, whereas a bird's beak would be unaffected by the stinging hairs (Monro, pers, comm.). Galetti and Pizo (1996), found seven bird species in Brazil consuming the fruit of *U. baccifera*. Of these seven, *Vireo olivaceus* (L.) migrates from northern North America in order to winter in South America (Callo, Morton and Stutchbury, 2013). This suggests a mechanism for *U. baccifera* seeds to disperse across long distances, as Nathan et al. (2008) found that migratory animals are more likely to transport seeds across dispersal barriers. In addition to dispersal by birds, *Urera baccifera* is used by humans as a natural fence, which Burger (1977) posits is the reason for the widespread dispersal of the taxon. Both of the outlined dispersal mechanisms disrupt the accumulation of local genetic differences, suggesting another mechanism is the cause for the genetic distinction between the clades.

Effects of Dispersal

If the flow of genes continues between these widespread populations of *Urera baccifera*, then the morphology will likely remain variable. Morphological variation between different populations indicates a migration of alleles through gene flow (Dewoody, Trewin and Taylor, 2015), a process which is maintained by seed and pollen dispersal (Kremer *et al.*, 2012). Additionally, the efficacy of gene flow in maintaining variation between populations is tempered by the strength of selection pressures (Lynn and Waldren, 2001).

Within these populations, it is unclear if these are relictual differences or if they are recently evolved. However, if they are recently evolved, the fact that genetic differences are accumulating in these geographically distinct clades, suggests that this gene flow may be slowing or has become cut off in some way (Clegg and Phillimore, 2010). As gene flow slows or stops, further genetic differences will begin to occur through genetic drift or natural selection. When gene flow is occurring, genetic divergence between populations is impeded (Huang *et al.*, 2014). Additionally, adaptive genetic changes can only be maintained when the pressures of selection and genetic drift are stronger than that of gene flow (Volis and Zhang, 2010). This can ultimately lead to genetically and morphologically distinct species, specifically adapted to the habitat into which the population has moved (Lynn and Waldren, 2001; Huang *et al.*, 2014).

Divergence

Särkinen et al. (2012) argue that geographically isolated clades in the Andean region indicate an old divergence between clades. Clade A is found in the Andes, however it appears throughout the region and into Central America. This distribution implies that the clade is not geographically isolated and therefore may have diverged more recently.

The study by Särkinen et al. (2012) noted that these divergences could be the result of dispersal limitations due to geographic barriers. Given *U. baccifera*'s dispersal by birds, it is not limited by these factors, allowing gene flow between populations. This implies a different mechanism causing genetic distinction and divergence from the remaining sampled specimens.

Additionally, it has been noted in prior studies that some groups begin genetic divergence before expressing morphological differences (Gill *et al.*, 2016), which could be the case for the well supported clades A, B, and E. Smith et al. (2018) suggest that recently diverged populations often lag behind in terms of full genomic independence from the original population, which if sampled early in the speciation process may result in paraphyletic progenitor species. This lack of morphological difference and paraphyly as a result of allopatric speciation reflects the problem with the instance of monophyly in taxonomic decisions, as outlined by Brummitt (2002). The imposition of monophyly may result in the splitting of a grouping that does not have easily identifiable characters, which Brummitt argues is an important factor in support of recognizing paraphyletic taxa (Brummitt, 2002).

Morphology

One of the only clades to present a similar morphology across all specimens examined was clade C, which contained *Urera laciniata*. *U. laciniata* is distinct from the rest of the sampled accessions in its lobed leaves and elongated stigma.

Previous studies from Wells (2017) and an unpublished report from Kew have found the taxon to be a part of a well-supported monophyletic clade, in which it is sister to *Urera baccifera*. The current placement within this larger *Urera baccifera* polytomy is likely due to a limited number of outgroups, which were used to address low resolution and support values. Further analyses with a greater number of outgroups could confirm *U. laciniata's* placement and relationship with *U. baccifera*.

The specimens of Clade D also have similarities in terms of their morphology, though the clade is only comprised of two accessions. Both specimens have ovate leaves with cordate bases with a pubescent abaxial lamina surface and cystoliths arranged radially around the bulbed hairs on the adaxial lamina surface. This homogeneity is of note particularly because the two accessions that comprise the clade, baccifera2781 and baccifera9103, occur over a wide distance from each other, with one in southern Central America and the other in central South America. They both occur in moist broadleaf forests, in riparian habitats, on or associated with limestone (herbarium label data; Monro, pers. comm). The above characters unite clade D, however, they occur in other neotropical *Ureras*. Additionally, *U. baccifera* is noted as growing in tropical moist forests and have been recorded in Belize and Bolivia (de Rooij, 1975; Burger, 1977; Monro and Rodríguez, 2009).

Given the geographic disjunction, but like biome and morphology, it is unclear what the factors are for the affinity between the clade D specimen. Further sampling within the regions in which they occur is necessary.

A majority of the characters sampled are homoplastic and can be found throughout the tree (figure 20). An exception to this, though, is clade C, where characters such as lobed leaves and ligulate stigma were exclusively found. This tendency towards homoplasy, is similar to the results of a study from Monro (2006). The Monro study (2006) on *Pilea*, another member of the Urticaceae, found that the majority of the morphological characters used for species delimitation were homoplastic. Monro (2006) suggests that this may have been the result of reversals and convergences of morphological characters, which may be the cause in *Urera* as well.

Paraphyletic species

As these genetic changes occur and *Urera baccifera* fragments into individual monophyletic clades, a paraphyletic *U. baccifera* group may form with multiple good species within it. The concept of species is controversial, and what defines a good species, is even more controversial still (Mallet, 1996; Shaw, 1996; Amitani, 2015). Amitani (2015) outlines arguments that a "good species" is one that is judged based on more than one criterion, such as phylogenetics, geography, ecology, and morphology, and that the more criteria satisfied by the group, the more confident one can be in defining that species. Following this argument, within this study of *Urera*, the clades currently only differentiate themselves based on one or two criteria, making defining them as "good species" difficult.

The prevailing rule in taxonomy currently is that all valid species concepts must be based on monophyly (Abdelaziz et al., 2011). Brummitt (2002) argues, however, that insistence upon monophyly does not always work and that paraphyletic taxa are acceptable. His report cites an example in which Cactaceae is found to be nested within the Portulaceae and the subsequent suggestion that because of this Portulaceae be split. Brummitt describes Portulaceae as an easily recognizable family with no characters that would neatly divide it. Brummitt argues because of the family's morphology, paraphyly alone is not enough to justify making a taxonomic change.

We recover distinct genetic groups within the wider, accepted *Urera baccifera*. However, these clades cannot be separated morphologically, with the exception of clade C. It is currently impossible to identify these remaining clades without a molecular study. Therefore, they cannot be described as new species within the current method of species description that relies on morphological distinction, as their descriptions would match the wider *U. baccifera* description.

However, following the argument that these clades have diverged recently, then perhaps distinguishing morphological characters have not begun to be expressed yet. If this study was to be revisited in the future and the analyses were run again using samples collected years in the future, there is a possibility the clades from this study would resolve themselves in the resulting trees in a monophyletic manner. Additionally, these specimen would have the time to further evolve morphologically distinct characteristics. This further study could be achieved through the use of next generation sequencing to look at the entire genome, which would allow for further insight into the taxa and its relationships.

If these geographic groupings persist in these regions, they will continue to adapt to their habitats. Within these adaptations, it is possible that morphological heterogeneity will appear within these groups or that further distinctions could be made based on geography or habitat.

Biome

Clade B shows a correlation with seasonally dry tropical forests in eastern South America, in a region referred to as the dry diagonal. The dry diagonal is an area ranging from the Caatinga in northeastern Brazil, to the Cerrado in central and southeastern Brazil, down through the Chaco of Argentina, Bolivia, and Paraguay, to the eastern edge of the Andes mountains (Santos-Silva *et al.*, 2013). This area is known for its low levels of precipitation and high seasonality (Santos-Silva *et al.*, 2013). However, accessions of this clade are also found in the Brazilian Atlantic forests (herbarium label data). The dry diagonal region was shaped during the Pleistocene, prior to which the Atlantic Forest biome spread across that region (Souza, Lima-Ribeiro and Solferini, 2015). This previously shared climatic conditions could indicate clade B's presence in both biomes.

While these areas are also characterized as being seasonally dry tropical forests, they are notably drier than the areas in which Clade A appears. Antonelli et al. (2018) found in many dispersal events that when they occurred across biomes, there was a tendency for the transition to be from wet to dry habitats.

Antonelli et al. (2018) also noted that, though not always true, many taxa disperse widely and in doing so adapt to significant regional and ecological shifts (Antonelli *et al.*, 2018). *U. baccifera* is most often described as occurring in riparian habitats, areas where access to water is perpetual (Mligo, 2017). However, clade B has made the transition into a drier habitat. Most of the accessions within this clade are described as occurring in rocky habitats, with no mention of riparian conditions. The accessions within this clade, however, do not show morphological signs of adaptation to a dry environment. However, these adaptations are occasionally anatomical or physiological (Aisha *et al.*, 2016), characters that could be examined in future study. As a result, clade B would need to develop adaptions to survive in this environment in which water is less common in order to establish itself as a viable population.

Despite the moderate frequency of this trend from wet to dry in the neotropics, dispersal across distinct biomes and establishing successfully therein is a rare global phenomenon (Antonelli *et al.*, 2018).

Translating my results into taxonomic actions

I believe that there are multiple names for what may be just a few species. From this study, it is clear that *Urera baccifera* and *Urera laciniata* are morphologically distinct species, with Wells (2017) supporting this claim molecularly. Additionally, there is a chance that there are good species within *Urera baccifera*, however, they cannot currently be distinguished morphologically (table 2). In this instance, due to the geographic range of *U. baccifera,* morphological distinction is crucial as specimens within the supported clades occur in similar regions to those in the polytomy and to specimens examined in the larger morphological review (figure 25).

	Distinct Morphology	Distinct Geographic Range	Distinct Ecology	Distinct Genetics
Clade A		X		X
Clade B		X	X	X
Clade C	X			X
Clade D				X
Clade E		X		X

Table 2 – Criteria for a good species based on argument outlined in Amintani (2015) and which each clade satisfies

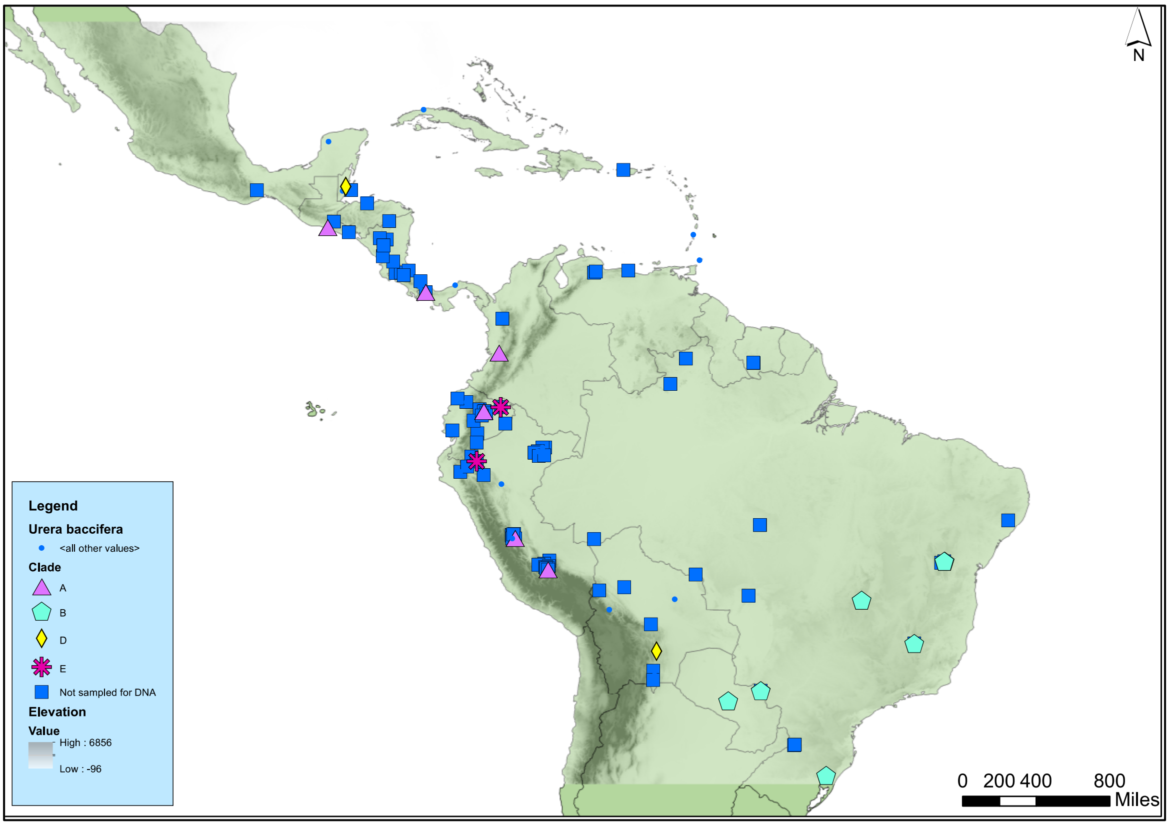

Figure 24 - Distribution of *Urera baccifera* including location data for specimen examined in the morphological review, but not sampled for DNA.

Additionally, there are multiple names, that, based on their type specimen, are likely synonyms of *U. baccifera*. There is a disjunction between the number of published names and the number of taxa that likely exist for this assemblage. Moreover, there is not a clear molecular signal for the wide variation seen in the morphology of *U. baccifera*. Together, these facts make taxonomic decisions about the wider *Urera baccifera* difficult to make with certainty. As a result, these names should be synonymized with *U. baccifera*.

Urera baccifera synonyms

Three accessions found in Clade B (nitida3509, nitida14170, and rugosa1964) and one within the wider polytomy (nitida1770) closely resembled the morphologies of two other *Urera* taxa: *Urera nitida* and *Urera rugosa*.

The three *U. nitida* accessions each had oblong to ovate leaf blades, in addition to stinging hairs along the stem, petioles, and veins on the abaxial lamina surface, matching the type illustration of the taxon (figure 26).

The *U. rugosa* specimen had a weak, light brown branch, stout petioles, a dentate margin and an adaxial surface that is darker green than the abaxial surface, as seen on the type specimen from Rusby (1901).

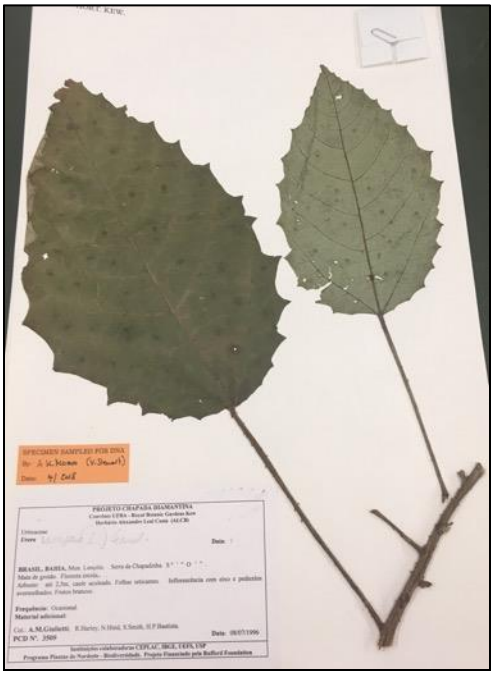

Figure 25 - Collection of *U. baccifera* (left) that closely matches the type illustration of *U. nitida* (right).

The placement of these accessions in clade B and the wider polytomy, suggests that they are in fact representatives of *U. baccifera*. *U. rugosa* is currently accepted as a synonym of *U. baccifera* (Jørgensen *et al.*, 2014) and the placement of rugosa1964 suggests that the name should remain a synonym.

The relationship between *U. nitida* and *U. baccifera* is more complicated (Monro and Rodríguez, 2009; Pederneiras *et al.*, 2011; Gaglioti and Romaniuc-Neto, 2012), as outlined in the introduction. That the placement of these three accessions (nitida14170, nitida3509, and nitida1770) had strong support values throughout multiple analyses suggests that the name may be better classified as a synonym of *U. baccifera* than as a separate species. Additionally, the remaining accessions in clade B do not match the type illustration of *U. nitida*, signifying that this clade should remain *U. baccifera*.

Further sampling of accessions of these taxa is necessary in order to further delineate these taxa and understand their scope throughout the Caribbean and Central and South America.

Although not addressed in the phylogenetic analysis, based on the morphologies outlined in their original descriptions *Urera denticulata*, *Urera horrida,* and *Urera viridisetosa* are all likely synonyms of *Urera baccifera*. *Urera denticulata* has oblong/elliptic leaves with dentate margins and inflorescences as axillary cymes, based on the neotype designated by Monro and Rodríguez (2009) (figure 6). These characteristics are also found in descriptions of *U. baccifera* (Killip, 1960; Burger, 1977; Kim *et al.*, 2015).

Urera horrida is noted in its original description as having ovate leaves with cordate bases, as seen on the lectotype specimen (figure 7). Kunth's (1817) original description of the taxon also describes a tomentose abaxial surface, which cannot be seen on the lectotype. Some specimen of *U. baccifera* are also noted for their soft, densely pubescent abaxial lamina surface (pers. obs.), in addition to having ovate leaves with cordate bases (Weddell, 1852, 1856, 1869; Killip, 1960; Burger, 1977)

The type specimen of *U. viridisetosa* (figure 8) has dense stinging hairs on the stem, petiole, and leaf veins, in addition to ovate leaves with a tomentose abaxial surface. In addition to the leaf shape and abaxial surface descriptions, *U. baccifera* is also noted for the significant amount of stinging hairs across its stems, petioles, and leaves (Killip, 1960; Burger, 1977; Kim *et al.*, 2015).

Naming Without Morphological Support

No new species can be described with both morphological and molecular support, however, the variation in the clades can be seen within their alignments.

A recent argument has been presented supporting the description of species using solely DNA data. Cook et al. (2010) propose that solely DNA species descriptions could be valid descriptions. The authors point to the use of DNA in taxonomic decisions, whether explicitly explained or not, and suggest that it could be another way to describe species and to make managing biodiversity more efficient. They do recognize the drawbacks though, particularly the idea that DNA-only descriptions will make identification more challenging. This argument is countered, however, with the idea that many morphology based identifications are also challenging and can be just as time consuming and cost prohibitive as identification based solely on DNA. The other major weakness of DNA-only descriptions is that the reference databases necessary to make this a successful reality do not exist yet (Cook et al., 2010). Given the controversial nature of this taxonomic choice, this method will not be used to propose new species from the currently accepted *Urera baccifera* polytomy.

Taxonomic Units From Phylogenies

1a. Leaves without lobes, capitate stigma, gray latex when stem is cut……………………………………………………………………..…. *Urera baccifera*
1b. Leaves with lobes, ligulate stigma, white latex when stem is cut…………………………………………………………...………. *Urera laciniata*

Urera baccifera (L.) Gaudich. Ex Wedd.

(Adapted from Killip, 1960, Burger 1977, and Monro & Rodríguez 2009 with personal observations)

Urera baccifera (L.) Gaud. Voy. Uran. Bot. 497. 1826.
Urtica baccifera L. Sp. P1. ed. 2. 1398. 1762.; *Urera armigera* Miq. Fl. Bras. 4(1): 192. 1853; *Urera baccifera* var. *horrida* (Kunth) Wedd. Arch. Mus. His. Nat. 9(1-2): 151. 1856-1857; *Urera denticulata* Miq. Fl. Bras. 4(1): 192. 1853; *Urera horrida* (Kunth) Miq. Fl. Bras. 4(1): 192. 1853; *Urera rugosa* Rusby Bull. Torrey Bot. Club 28: 310. 1901; *Urera viridisetosa* Rusby Mem. New York Bot. Gard. 7: 232. 1927; *Urtica armigera* C. Presl Abh. Königl. Böhm. Ges. Wiss., ser. 5 3: 540. 1845; *Urtica grandidentata* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5 2: 296. 1851; *Urtica horrida* Kunth Nov. Gen. Sp. (quarto ed.) 2: 41. 1817.; *Urtica nitida* Vell. Fl. Flumin. Icon. 10: tab 20. 1827

Type: Plumier, Pl. Amer.: tab. 260. 1760.
Epitype: Jamaica. Stony Hill, 13 Mar. 1898, *Fawcett 7177*

Dioecious, large herb, or shrub or small tree, 0.5 - 4 m. high. Stem usually covered with short, urticating hairs, occasionally lignified, gray latex when cut (not seen). Stipules intrapetiolar, occasionally with bifid apex. Leaves alternate, petiole 2-17 (21) cm long, laminae ovate to elliptic, up to 35 cm. long and 22 cm. wide; base attenuate, cordate, or truncate, apex acute; margin dentate to serrate. Adaxial surface with urticating hairs and cystoliths, randomly arranged, linearly arranged, or radially arranged around bulbed hairs, rarely glabrous, abaxial surface glabrous to velutinous, urticating hairs on midrib and occasionally secondary and tertiary veins. Inflorescence branched cyme, in an axillary position. Staminate flowers tetramerous, white to pink. Pistillate flowers tetramerous, white to red, purple. Fruit achenes subtended by fleshy perianth parts, white to light purple, 0.3-0.4 cm long, 0.1-0. 3 cm wide.

Flowering Time: Year round
Ecology: Disturbed open areas, riparian zones, rocky outcrops, montane forests. On limestone and sandstone.
Altitudinal Range: 200-2600 m
Distribution: Neotropics: Honduras, El Salvador, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia, Brazil

Specimen Seen:
Caribbean: *Cuba*: Curtiss 608 (K!); *Puerto Rico*: Axelrod 8423 (K!); *St. Vincent*: Smith 1194 (K!); *Tobago*: Sandwith 1889 (K!)
Central America: *Belize*: Gentle 2781 (K!) (as British Honduras), Whitefoord 106016 (BM!); *Costa Rica*: Taylor 187 (MO); *El Salvador*: Sandoval 1819 (MO); *Honduras*: Gentle

2781 (K!), Monro 3016 (BM!); *Mexico*: Darwin 2148 (BM!), Campos 3667 (BM); *Panama*: Hampshire 133 (BM!), Monro 4663 (BM), Croat 12430 (MO)
South America: *Bolivia*: Wood 9103 (K!), Serrano 7309 (BM!), Krukoff 10061 (K), Ballcock 769 (K!), Cayola 2530 (BM),; *Brazil*: Zappi 2107 (K), Harley 14170 (K!), Giulietti 3509 (K!), Milliken 1722 (K!), Dubs 1770 (K!), Kirkbride 3930 (US), Wasum 385 (US); *Colombia*: Cuatrecasas 13896 (K!); *Ecuador*: Quishpe 156 (K!), Freire 5377 (BM!), Zak 3156 (BM!), Rios 75 (K); *Peru*: Nuñez 8812 (BM!, K!), Vasquez 16924 (K!), Rojas 2185 (BM!), Valenzuela 2915 (BM!), Valenzuela 9152 (BM!), Vasquez 12067 (BM!), Pennington 17239 (K), Rojas 731 (BM!, K!); *Venezuela*: Meier 5691 (BM!), Meier 15278 (BM!)

Urera laciniata Wedd.

(Adapted from Killip, 1960 and Burger, 1977 with personal observations)
Urera laciniata (Goudot) Wedd. in Ann. Sci. Nat. III. 18:203. 1852.
Urtica laciniata Goudot, ex Wedd. loc. cit., as synonym.; *Urera girardiniodes* Seem. Bot. Voy. Herald 194. 1854.

Type: J. Goudot, s.n., Colombia, Nouvelle Grenade. "Quindui", La Bolsa, 1844.
Lectotype: de Rooij, M.J.M. 1975. Urticaceae. 5(1): 308. n A. A. Pulle (ed.) Fl. Suriname. Koninlijke Vereeninging Indisch Instituut, Amsterdam.

Dioecious, small tree, sparsely branched shrub, or large herb, 1-5m tall. Stem hollow with minute hairs and stinging bulbed, occasionally lignified, white latex when cut (not seen). Stipules intrapetiolar, paired or partly fused near base (not seen). Leaves alternate, petiole 6-15 cm long, laminae broadly ovate, 15-30 cm long and wide, base cordate, apex acute; margin deeply lobed, lobes entire to irregularly dentate, apex acute. Adaxial surface with bulbed, urticating hairs and punctiform cystoliths, rarely with spines on laminae surface, abaxial surface with cystoliths and spines on midrib and secondary veins. Inflorescence branched panicle, in an axillary position, to 30 cm. Staminate flowers tetramerous in clusters, white to green. Pistillate flowers white to green, style and stigma possibly layered, difficult to differentiate. Fruit achene subtended by 2 perianth parts, 0.2 cm long, 0.1 cm wide.

Flowering Time: Year round
Ecology: Disturbed areas, riparian habitats, premontane forest
Altitudinal Range: 250-1150 m
Distribution: Neotropics: Costa Rica, Suriname, Colombia, Peru, Bolivia

Specimen Seen:
Central America: *Costa Rica*: Skutch 4266 (K!)
South America: *Bolivia*: Macia 4326 (BM), Araujo 1477 (K!), Araujo 3016 (BM); *Colombia*: Holton 219 (K!) *Peru*: Huaman 221 (BM), Monteagudo 3905 (K!); *Suriname*: Lindeman 5660 (K!)

Further Study & Conclusions

Based on the findings of this study, *Urera baccifera* is one, large, widespread, morphologically diverse taxon, a fact supported by various analyses that produced multiple topographically identical phylogenies. The heterogenous morphology of the species could be used to separate the taxon into multiple morphospecies, however molecular data has shown that these species are not supported on a genetic level. This is an important reminder for the importance of molecular data in taxonomy, as a source for critical evaluation of other phenomena such as morphology, geographic range, or ecological affinities.

The initial examination of this group found morphological distinctions that were not supported by the molecular phylogeny, with the exception of the *U. laciniata* group. The remaining clades do, however, show signs of geographic structure. Additionally, one clade (B) has made a biome shift into seasonally dry tropical forests. Creating a dated phylogeny would be a useful tool in assessing the clades supported in this study. This would allow for an understanding of divergence between the clades, which could give clues as to how these clades have ended up in their current regions.

Sampling for this study was relatively limited. Increasing the number of samples could result in an increase in resolution and adding a more complete look at *trn*L-F data could lead to more conclusive evidence. Additionally, sampling the type specimen of the associated names would provide strong evidence for the relationships between *U. baccifera* and these additional taxa. Further research is needed to make a conclusive argument about the presence of distinct groups within what is currently considered *Urera baccifera*.

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Appendix

Appendix 1a – PCR MasterMix recipe

Reagent	Volume/sample
H2O	8.7 µl
dNTPs	2 µl
10xBuffer	2 µl
MgCL2	0.6 µl
Forward primer – ITS4	0.75 µl
Reverse primer – ITS5	0.75 µl
5x TBT-PAR	4 µl
Taq	1 µl
DNA template	1 µl

Appendix 1b – PCR Program

Temperature	Time	
95°C	4 min	
94°C	30 sec	35 cycles
50°C	30 sec	
72°C	2 min	
72°C	7 min	
10°C	forever	

Appendix 1c- Sequencing Master Mix Recipe

Reagents	Volume/sample
dH_2O	6.68 µl
5x BigDye Buffer	2 µl
10 µM Primer (ITS4 or ITS5)	0.32 µl
BigDye Mix	0.5 µl
Template DNA	1 µl

Appendix 1d – Sequencing PCR

Temperature	Time	
95°C	30 sec	25 cycles
50°C	20 sec	
60°C	4 min	
4°C	forever	

Appendix 2 - Sequences Specimens

Name	Collector	Collector Number	Country	Extracted	Sequenced	Hebrarium	EDNA Number
Urera baccifera	A.H. Curtiss	608	Cuba	x	x	K	EDNA18-0051366
Urera baccifera	Alvarez, Aida, J. Machuca, A. Zamora, & V. Huaraca	1883	Ecuador	x		BM	EDNA18-0051518
Urera baccifera	Campos V, Alvaro & R. Torres	3667	Mexico	x	x	BM	EDNA18-0051522
Urera baccifera	Campos, J., W. Vargas, & L. Saavedra	3876	Peru	x		BM	EDNA18-0051452
Urera baccifera	Clark, John L., Y. Troya	681	Ecuador	x		BM	EDNA18-0051515
Urera baccifera	Darwin, S. E. Sundell & D. White	2148	Mexico	x	x	BM	EDNA18-0051523
Urera baccifera	de Miche, C.	RM2745	Bolivia	x		K	EDNA18-0051294
Urera baccifera	F. Axelrod	8423	Puerto Rico	x	x	K	EDNA18-0051365
Urera baccifera	Freire, Efrain & F. Chavez	5377	Ecuador	x	x	BM	EDNA18-0051447
Urera baccifera	Garcia, Alberto R. & Esteban Martinez	47	Mexico	x		BM	EDNA18-0051519
Urera baccifera	H. van der Werff, B. Gray, R. Vasquez, R. Rojas	15481	Peru	x		K	EDNA18-0051369
Urera baccifera	H.H. Smith	1194	n/a	x	x	K	EDNA18-0051380
Urera baccifera	Hampshire, R.J. & C. Whitefoord	133	Panama	x	x	BM	EDNA18-0051521
Urera baccifera	Herrera C., Gerardo, S. Koemar, & B. Allen	9995	Suriname	x		BM	EDNA18-0051511
Urera baccifera	J. Cuatrecasas	13896	Colombi	x	x	K	EDNA18-0051375
Urera baccifera	J.E. Simonis, L.F. Pérez, W.J. Hahn, R. Duré	203	Paraguay	x	x	K	EDNA18-0051457
Urera baccifera	J.R.I Wood	9103	Bolivia	x	x	K	EDNA18-0051455
Urera baccifera	J.R.I Wood	12565	Bolivia	x		K	EDNA18-0051460
Urera baccifera	Meier, W & A. Cordido	17330	Venezuela	x		BM	EDNA18-0051451
Urera baccifera	Meier, W & G. Forbes	15278	Venezuela	x	x	BM	EDNA18-0051517
Urera baccifera	Meier, W., L. Cortez, & D. Eisner	5691	Venezuela	x	x	BM	EDNA18-0051514
Urera baccifera	Monro, A.	3016	El Salvador	x		BM	EDNA18-0051445
Urera baccifera	Nunez, P. & F. Motocanchi	8812	Peru	x	x	BM	EDNA18-0051449
Urera baccifera	NY Sandwith	1889	Tobago	x	x	K	EDNA18-0051367
Urera baccifera	P. Nunez V, F. Motocanchi	8812	Peru	x		K	EDNA18-0051370
Urera baccifera	P.H. Gentle	2781	Belize (British Honduras)	x	x	K	EDNA18-0051293
Urera baccifera	Pipoly, John J., N. Jaramillo & R. Ortiz	12438	Peru	x		BM	EDNA18-0051453
Urera baccifera	R. Vasquez	16924	Peru	x	x	K	EDNA18-0051378
Urera baccifera	Rojas, R., J. Lingan, K. Meza, A. Pena	2185	Peru	x		BM	EDNA18-0051297

Appendix 2 - Sequences Specimens

Name	Collector	Collector Number	Country	Extracted	Sequenced	Hebrarium	EDNA Number
Urera baccifera	Rojas, R., R. Vasquez, J. Campos, S. Flores, T. Mark, & O. Diaz	731	Peru	x	x	BM	EDNA18-0051295
Urera baccifera	Serrano, M., A. Lliully & J. Villalobos	7309	Bolivia	x	x	BM	EDNA18-0051516
Urera baccifera	Valenzuela, L., E. Suclli, G. Calatayud, I. Huamantupa, N. Suarez, & F. Zamora	9152	Peru	x	x	BM	EDNA18-0051450
Urera baccifera	Valenzuela, L., E. Suclli, I. Huamantupa, A Carazas	2915	Peru	x	x	BM	EDNA18-0051290
Urera baccifera	van der Werff, Henk, B. Gray, E. Freire & M. Tirado	13002	Ecuador	x		BM	EDNA18-0051512
Urera baccifera	van der Werff, Henk, B. Gray, E. Freire & M. Tirado	13028	Ecuador	x		BM	EDNA18-0051513
Urera baccifera	van der Werff, Henk, B. Gray, R. Vasquez, R. Rojas	15481	Peru	x		BM	EDNA18-0051296
Urera baccifera	Vasquez, R & N. Jaramillo	12067	Peru	x	x	BM	EDNA18-0051510
Urera baccifera	Whitefoord, C & Quiroz, V	106016	Belize	x	x	BM	EDNA18-0051446
Urera baccifera	Whitefoord, Caroline	1613	Belize	x		BM	EDNA18-0051520
Urera baccifera	William Milliken	1722	Brazil	x	x	K	EDNA18-0051376
Urera baccifera	Zak, Vlastimil & J. Jaramillo	3156	Ecuador	x	x	BM	EDNA18-0051448
Urera laciniata	A. Araujo et al	1477	Bolivia	x	x	K	EDNA18-0051291
Urera laciniata	A.F. Skutch	4266	Costa Rica	x	x	K	EDNA18-0051368
Urera laciniata	Holton	219	n/a	x	x	K	EDNA18-0051379
Urera laciniata	J.C. Lindeman	5660	Suriname	x		K	EDNA18-0051454
Urera nitida?	A.M. Giulietti	3509	Brazil	x	x	K	EDNA18-0051458
Urera nitida?	B. Dubs	1770	Brazil	x	x	K	EDNA18-0051456
Urera nitida?	R. Harley	14170	Brazil	x	x	K	EDNA18-0051292
Urera rugosa?	B. Balansa	1964	Paraguay	x	x	K	EDNA18-0051377
Urera sp.	Ballcock	769	Bolivia	x	x	K	EDNA18-0051371
Urera sp.	G. Martinelli, G.M Barrese, S. Mayo, H.C. de Lima, A. Mayo, M.P.M de Lima	7596	Brazil	x		K	EDNA18-0051459
Urera sp.	V. Zak & J. Jaramillo	3742	Ecuador	x		K	EDNA18-0051372
Urera sp.	W. Galiano, E. Suclli, P. Nunez, A. Rodriguez, V. Chama	6114	Peru	x		K	EDNA18-0051374
Urera sp.	W. Quishpe, C. Chimbo, A. Jimenez	156	Ecuador	x	x	K	EDNA18-0051373

Appendix 3 - Morphospecies Classification

Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	Araquistain, M., & P. Moreno	2863	Nicaragua	BM	1
Urera baccifera	Balansa, B.	1964	Paraguay	K	1
Urera baccifera	Bang, A. Miguel	1209	Bolivia	BM	1
Urera baccifera	Bang, A. Miguel	1209	Bolivia	K	1
Urera baccifera	Berg, G.	00000	Brazil	K	1
Urera baccifera	Broadway, W.E.	6127	Trinidad	K	1
Urera baccifera	Burchell	947	Brazil	K	1
Urera baccifera	Burchell	4742	Brazil	K	1
Urera baccifera	Calatayud, G., I. Huamantupa, B. Gonzales	2866	Peru	BM	1
Urera baccifera	Camp, W.H.	E-3567	Ecuador	K	1
Urera baccifera	Campos V, Alvaro & R. Torres	3667	Mexico	BM	1
Urera baccifera	Campos, J., W. Vargas, & L. Saavedra	3876	Peru	BM	1
Urera baccifera	Campos, J., W. Vargas, & L. Saaverda	3876	Peru	K	1
Urera baccifera	Caranqui, Jorge, E. Toapanta, T. Croat	731	Ecuador	BM	1
Urera baccifera	Carvalho, Andre M. de, G. Bromley	266	Brazil	K	1
Urera baccifera	Cayola, L., G. Chive, I. Loza, M. Cornejo, E. Ticona, A. Fuentes	2530	Bolivia	BM	1
Urera baccifera	Coello, F. & A. Freire	30766	Ecuador	K	1
Urera baccifera	Coronado, Indiana, M. Barrios & F. Rojas	1297	Nicaragua	BM	1
Urera baccifera	Croat, Thomas B	17444	Peru	K	1
Urera baccifera	Croat, Thomas B.	68307	Costa Rica	BM	1
Urera baccifera	Croat, Thomas B., L. Hannon, G. Walhert, T. Katan Jua	90442	Ecuador	BM	1
Urera baccifera	Curtis, A.H.	608	Cuba	E	1
Urera baccifera	Daly, D.C., J.D. Mitchell, F.C.S. Walthier, L.B. Assis, L.S. Saraiva, M.E.M. Braga	11980	Brazil	K	1
Urera baccifera	Darwin, S.; E. Sundell & D. White	2148	Mexico	BM	1
Urera baccifera	de Queiroz, D.P., Lemos & Lobo	1766	Brazil	K	1
Urera baccifera	dos Santos, T.S., S. Mori, L.A. Mattos Silva	3330	Brazil	K	1
Urera baccifera	Evans, Randy, S. Koemar, E. Wittenberg	3460	Suriname	K	1
Urera baccifera	Farfan, J., A. Carazas, J. Tito, L. Vargas, B. Rado	1759	Peru	K	1
Urera baccifera	Fiebrig, K.	5115	Paraguay	K	1
Urera sp.	Fiebrig, K.	5735	Paraguay	E	1
Urera baccifera	Figueiredo, L., K. Andrade	100	Brazil	K	1
Urera baccifera	Forest Dept of British Guiana	5132	British Guiana	K	1
Urera baccifera	Garcia, Alberto R. & Esteban Martinez	47	Mexico	BM	1
Urera baccifera	Gaumer, G.F.	936	Mexico	BM	1
Urera baccifera	Gentry, A.L., R. Vasquez, N. Jaramillo	65814	Peru	K	1

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Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	Glaziou, A.	13210	Brazil	K	1
Urera baccifera	Glaziou, A.	14276	Brazil	K	1
Urera baccifera	Glaziou, M.	11556	Brazil	K	1
Urera baccifera	Grubb, P.J., J.R. Lloyd, T.D. Pennington, & T.C. Whitmore	1043	Ecuador	K	1
Urera baccifera	Hampshire, R.J. & C. Whitefoord	133	Panama	BM	1
Urera baccifera	Harley, R.M., C.M. Sakuragui, P.T. Sano, S. Atkins, & V.C. Souza	14170	Brazil	K	1
Urera baccifera	Hassler, E.	11541a	Paraguay	K	1
Urera baccifera	Herrara C., Gerardo, S. Koemar, & B. Allen	9995	Suriname	K	1
Urera baccifera	Herrera Ch., Gerardo	360	Costa Rica	BM	1
Urera baccifera	Jack, J.G.	5270	Cuba	K	1
Urera baccifera	Klein	292-179	Brazil	K	1
Urera baccifera	Klug, G	4029	Peru	BM	1
Urera baccifera	Krapovickas, A. & A. Schinini	39230	Bolivia	K	1
Urera sp.	Leitao F, H.F., G. Shepherd, J.Y. Tamashiro, & K. Yamamoto	13.116	Brazil	E	1
Urera baccifera	Lero, G.C.	47	Bolivia	K	1
Urera baccifera	Liesner, Ronald L.	26275	Honduras	BM	1
Urera baccifera	Maas, P.J.M., C.C. Berg, & R.L. Dressler	2736	Panama	K	1
Urera baccifera	Meier, W., L. Cortez, & D. Eisner	5691	Venezuela	BM	1
Urera baccifera	Meiers	4573	Brazil	K	1
Urera baccifera	Melo, A., G.A. Gomes-Costa, M.A. Chagas, & S.O. Santos	523	Brazil	K	1
Urera baccifera	Mexia, Y.	4679	Brazil	K	1
Urera baccifera	Milliken	205		K	1
Urera baccifera	Moreno, Pedro P	238	Nicaragua	BM	1
Urera baccifera	Moreno, Pedro P	24124	Nicaragua	BM	1
Urera baccifera	Mori, S.A. & A.M. de Carvalho	12007	Brazil	K	1
Urera baccifera	n/a	k000973198	Brazil	K	1
Urera baccifera	Oliveira, M., S.S. Lira, M.C. Tscha, A.B. Marcon	81	Brazil	K	1
Urera baccifera	Ortiz V, E., F. Mellado N, R. Francis J, J. Mateo M	187	Peru	K	1
Urera baccifera	Ortiz, R.T.	383	Guatemala	BM	1
Urera baccifera	Pabst, G.	22729	Brazil	K	1
Urera baccifera	Peck, M.E.	504	Belize (British Honduras)	K	1

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Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	Pedersen, T.M.	11005	Panama	K	1
Urera baccifera	Pennington,T.D. & A. Daza	17239	Peru	K	1
Urera baccifera	Perea, J., R. Francis, H. Cristobal, E. Camavilca	1609	Peru	BM	1
Urera baccifera	Pipoly, John J., N. Jaramillo & R. Ortiz	12438	Peru	BM	1
Urera baccifera	Prance, G.T., P.J.M. Maas, A.A. Atchley, W.C. Steward, D.B. Woolcott, D.F. Coelho, O.P. Monteiro, W.S. Pinheiro, & J.F. Ramos	13384	Brazil	K	1
Urera baccifera	Rios, M	75	Ecuador	K	1
Urera baccifera	Robinson	103		K	1
Urera baccifera	Robles, R.	1119	Costa Rica	BM	1
Urera baccifera	Rodal, M.J.N., M.F. Sales, & C. Zickel	566	Brazil	K	1
Urera baccifera	Rojas, R., J. Lingan, K. Meza, A. Pena	2185	Peru	BM	1
Urera baccifera	Rojas, R., K. Meza, J. Lingan, E. Camavilca & M. Villaran	1832	Peru	K	1
Urera baccifera	Rojas, R., R. Vasquez, J. Campos, S. Flores, T. Mark, & O. Diaz	731	Peru	BM	1
Urera baccifera	Rugel, F.	254	Cuba	K	1
Urera baccifera	Sales de Melo, M.R.C., E.V. Freire	156	Brazil	K	1
Urera baccifera	Sales, M.F., M.J.N. Rodal, M.C. Tscha	641	Brazil	K	1
Urera baccifera	Sandino, J.C.	570	Nicaragua	BM	1
Urera baccifera	Sandino, J.C.	1749	Nicaragua	BM	1
Urera baccifera	Sandino, J.C.	2736	Nicaragua	BM	1
Urera baccifera	Schott	796		BM	1
Urera baccifera	Seeman	495	Panama	BM	1
Urera baccifera	Seeman	495	Panama	K	1
Urera baccifera	Seidel, R., D. Vaquiata, E. Vargas	7248	Bolivia	K	1
Urera baccifera	Smith	1442		K	1
Urera baccifera var. horrida	Smith, J.D.	1775	Guatemala	K	1
Urera baccifera	Spruce 1640, R.	1640	Brazil	K	1
Urera sp.	Spruce, R.	1640	Brazil	E	1
Urera baccifera	Stevens, W.D.; E. Martinez S., H. Droege & A.N. Diaz	25612	Guatemala	BM	1
Urera baccifera	Tate, R.	395	Nicaragua	BM	1
Urera baccifera	Ule, E.	9330	Peru	K	1
Urera baccifera	Valenzuela, L., E. Suclli, G. Calatayud, A Carazas	7515	Peru	BM	1
Urera baccifera	Vasquez, R.	12244	Peru	K	1
Urera baccifera	Vasquez, R.	28202	Peru	BM	1

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Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	Vasquez, R.	28202	Peru	K	1
Urera baccifera	Vasquez, R. & G. Criollo	1803	Peru	K	1
Urera baccifera	Vasquez, R. & N. Jaramillo	12067	Peru	BM	1
Urera baccifera	Vasquez, R. & N. Jaramillo	12067	Peru	K	1
Urera baccifera	Vasquez, R. & N. Jaramillo	12228	Peru	K	1
Urera baccifera	Vasquez, R. & N. Jaramillo	12241	Peru	K	1
Urera baccifera	Vasquez, R. & N. Jaramillo	16924	Peru	K	1
Urera baccifera	Vasquez, R. & N. Jaramillo	17267	Peru	K	1
Urera baccifera	Vasquez, R., A. Monteagudo, A. Pena, J. Mateo, & V. Flores	30958	Peru	K	1
Urera baccifera	Vasquez, R., A. Monteagudo, A. Pena, V. Flores, & G. Castillo	32091	Peru	K	1
Urera baccifera	Vasquez, R., R. Rojas, & A. Pena	22654	Peru	K	1
Urera baccifera	Vasquez, R., S. Marchand, & N. Jaramillo	11932	Peru	K	1
Urera baccifera	Vitorio	139375	Brazil	K	1
Urera baccifera	Whitefoord, C. & A. Eddy	249	Panama	BM	1
Urera baccifera	Whitefoord, Caroline	1613	Belize	BM	1
Urera baccifera	Wij	404	Jamaica	K	1
Urera baccifera	Williams	685		K	1
Urera baccifera	Wood, J.R.I.	12565	Bolivia	K	1
Urera baccifera	Wright, C.	527	Cuba	K	1
Urera baccifera	Zappi, D.C.	2107	Brazil	K	1
Urera baccifera	Alvarez, Aida, J. Machuca, A. Zamora, & V. Huaraca	1883	Ecuador	BM	2
Urera baccifera	Argent, G.C.G. & Burbidge, R.B.	67	Ecuador	E	2
Urera baccifera	Axelrod, F	8423	Puerto Rico	K	2
Urera baccifera	Ayala, F.	2181	Peru	BM	2
Urera baccifera	Bang, A. Miguel	1209	Bolivia	E	2
Urera baccifera	Bang, A. Miguel	1609	Bolivia	BM	2
Urera baccifera	Bang, A. Miguel	1609	Bolivia	E	2
Urera baccifera	Burger, W.	4161	Costa Rica	BM	2
Urera baccifera	Clark, John L. & T. Nunez	1572	Ecuador	BM	2
Urera sp.	Clark, John L., Y. Troya	681	Ecuador	BM	2
Urera baccifera	Colque, O., I. Lineo, & F. Hilarson	521	Bolivia	BM	2
Urera baccifera	Cuatrecasas, J.	13896	Colombia	K	2
Urera baccifera	Curtis, A.H.	608	Cuba	K	2
Urera baccifera	Dubs, B.	1770	Brazil	K	2
Urera baccifera	Dwyer, John D.	2414	Panama	K	2
Urera baccifera	Eggers	690	Puerto Rico	K	2

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Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	Eiten, George, L.T. Eiten, G.M. Felippe, J.M. de Freitas Campos	3141	Brazil	K	2
Urera baccifera	Evans, Randy, K. Koemar, & E. Wittenberg	3460	Suriname	BM	2
Urera baccifera	Fendler, A.	1276	Venezuela	K	2
Urera baccifera	Freire, E. & F. Chavez	5377	Ecuador	BM	2
Urera baccifera	Friedrichsttae	s.n.	St. Thomas	K	2
Urera baccifera	Fuertes, P.	3	Domincan Republic	E	2
Urera baccifera	Gaumer, G.F.	936	Mexico	E	2
Urera baccifera	Giulietti, A.M., R. Harley, N. Hind, S. Smith, H.P. Bautista	3509	Brazil	K	2
Urera baccifera	Gutierrez V., G. & F. A. Barkley	17C121	Colombia	BM	2
Urera baccifera	Hawkins, T.	1119	Belize	BM	2
Urera baccifera	Herrera C., Gerardo, S. Koemar, & B. Allen	9995	Suriname	BM	2
Urera baccifera	Jacquemont, V.	s.n.	Haiti	K	2
Urera baccifera	Lewis, W.H., J.D. Dwyer, T.S. Elias, & K.R. Robertson	941	Panama	K	2
Urera baccifera	Maguire	42018		K	2
Urera baccifera	Martinelli, G.	204560	Brazil	K	2
Urera baccifera	Meier, W & A. Cordido	17330	Venezuela	BM	2
Urera baccifera	Milliken, W.	549	Brazil	E	2
Urera baccifera	Monro, A.K.	671	Belize	BM	2
Urera baccifera	Pedraza-Penalosa, P., J. Betancur, M. Sundue, G. Giraldo, M. Jaimes, E. Tineo, M. Londono, A. Duque, & L. Arias	2671	Colombia	K	2
Urera baccifera	Peterson, P.M. & C.R. Annable	6969	Panama	K	2
Urera baccifera	Philipson, W.R., J.M. Idrobo, A. Fernandez	1453	Colombia	BM	2
Urera baccifera	Quishpe, W., C. Chimbo, & A. Jimenez	156	Ecuador	K	2
Urera baccifera	Rambo, B.	49487	Brazil	E	2
Urera baccifera	Rojas, R., C. Mateo, E. Jimenez & C. Rojas	1065	Peru	K	2
Urera baccifera	Rojas, R., K. Meza, J. Lingan, E. Camavilca, & M. Villaran	1832	Peru	BM	2
Urera baccifera	Sandwith, N.Y.	1889	Tobago	K	2
Urera baccifera	Serrano, M., A. Lliully & J. Villalobos	7309	Bolivia	BM	2
Urera baccifera	Serrano, M., R. Lozano, & F. Cardoso	1543	Bolivia	BM	2
Urera baccifera	Sintenis	2358		K	2
Urera baccifera	Smith, G.W.	1194	St. Vincent	K	2
Urera baccifera	Van der werff, H., B. Gray, R. Vasquez, & R. Rojas	15481	Peru	K	2
Urera baccifera	van der Werff, Henk & E. Gudino	11188	Ecuador	BM	2

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Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	van der Werff, Henk, B. Gray, E. Freire & M. Tirado	13002	Ecuador	BM	2
Urera baccifera	van der Werff, Henk, B. Gray, E. Freire & M. Tirado	13028	Ecuador	BM	2
Urera baccifera	van der Werff, Henk, B. Gray, R. Vasquez, R. Rojas	15481	Peru	BM	2
Urera baccifera	Vargas, Homero	3610	Ecuador	BM	2
Urera baccifera	Vasquez, R., R. Rojas, & A. Pena	22487	Peru	K	2
Urera baccifera	Vasquez, R., R. Rojas, & A. Pena	22654	Peru	BM	2
Urera baccifera	Vasquez, R., R. Rojas, & A. Pena	22671	Peru	K	2
Urera baccifera	Wallnofer, B., & M. Henzel	114-16388	Peru	K	2
Urera baccifera	Whitefoord, C.	1613	Belize	BM	2
Urera baccifera	Whitefoord, C. & A. Eddy	249	Panama	BM	2
Urera baccifera	Zak, V., & J. Jaramillo	3742	Ecuador	K	2
Urera baccifera	Zak, Vlastimil & J. Jaramillo	3156	Ecuador	BM	2
Urera baccifera	Balansa, B.	1975	Paraguay	K	3
Urera baccifera	Ballcock	769	Bolivia	K	3
Urera baccifera	Bang, A. Miguel	1609	Bolivia	K	3
Urera baccifera	Castroviejo, S., J. Cuadras, & M. Velayos	7261	Panama	K	3
Urera baccifera	Chavez de Miche, R.	RM2745	Bolivia	K	3
Urera baccifera	de Bruijn, J.	1164	Venezuela	K	3
Urera baccifera	Driver	77	n/a	K	3
Urera baccifera	Dusen, P.	33/43	Brazil	K	3
Urera baccifera	Eggers	5727	Tobago	K	3
Urera baccifera	Estrada, Armando	548	Costa Rica	K	3
Urera baccifera	Eyerdam, W.J.	25212	Bolivia	K	3
Urera baccifera	Ferrucci, S., R. Vanni, & L. Ferraro	123	Argentina	K	3
Urera baccifera	Fiebrig, K.	6075	Paraguay	E	3
Urera baccifera	Fiebrig, K.	6183	Paraguay	K	3
Urera baccifera	Galeotti, H	375	Mexico	K	3
Urera baccifera	Galiano, W., E. Suclli, P. Nunez, A. Rodriguez, & V. Chama	6114	Peru	BM	3
Urera baccifera	Galiano, W., E. Suclli, P. Nunez, A. Rodriguez, & V. Chama	6114	Peru	K	3
Urera baccifera	Gentle, P.H.	2781	Belize (British Honduras)	K	3
Urera baccifera	Hassler, E.	3132	Paraguay	K	3
Urera baccifera	Hassler, E.	11541	Paraguay	K	3
Urera baccifera	Heller, A.A.	6138	Puerto Rico	E	3

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Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	Hincle	1042		K	3
Urera baccifera	Holton	258		K	3
Urera baccifera	Huamantupa, I., G. Calatayud, J. Tito, B. Rado, R. Ayerbe	10442	Peru	BM	3
Urera baccifera	Keller, H.A. & G.T. Prance	3293	Argentina	K	3
Urera baccifera	Klug, G	4029	Peru	K	3
Urera baccifera	Krukoff, R.A.	10061	Bolivia	K	3
Urera baccifera	L. Valenzuela, J. Farfan, & I. Huamantupa	6611	Peru	K	3
Urera baccifera	Lewis, W.H., W.H. Blackwell Jr., J.L. Hawker, J.W. Nowicke, R.L. Oliver, J.E. Ridgway, A.G. Robyns, & S.E. Verhoek	3046	Panama	K	3
Urera baccifera	Lindeman, J.C.	1573	Suriname	K	3
Urera baccifera	Lozano	1960		K	3
Urera baccifera	Martinez S., E	8491	Mexico	BM	3
Urera baccifera	Meier, W & G. Forbes	15278	Venezuela	BM	3
Urera baccifera	Milliken, W.	549	Brazil	K	3
Urera baccifera	Milliken, W.	1722	Brazil	K	3
Urera baccifera	Milliken, W.	1785	Brazil	K	3
Urera baccifera	Monro, A.K.	3016	El Salvador	BM	3
Urera baccifera	Monro, A.K. & S. Cafferty	4663	Panama	BM	3
Urera baccifera	Morong, T.	663	Paraguay	K	3
Urera baccifera	Neill, David & Paul C. Vincelli	3589	Nicaragua	BM	3
Urera baccifera	Nunez, P. & F. Motocanchi	8812	Peru	BM	3
Urera baccifera	Nunez, P. & F. Motocanchi	8812	Peru	K	3
Urera baccifera	Nunez, P., E. Bengoa & A. Rodriguez	11866	Peru	BM	3
Urera baccifera	Nunez, P., E. Bengoa, & A. Rodriguez	11866	Peru	K	3
Urera baccifera	Pedersen, T.M.	1314	Argentina	E	3
Urera baccifera	Pedersen, T.M.	1314	Argentina	K	3
Urera baccifera	Perry, A.	675	Bolivia	K	3
Urera baccifera	Rojas, R., R. Vasquez, J. Campos, S. Flores, T. Mark, & O. Diaz	731	Peru	K	3
Urera baccifera	Rusby, H.H.	1467	Bolivia	BM	3
Urera baccifera	Rusby, H.H.	1467	Bolivia	K	3
Urera baccifera	Sandwith, N.Y.	1889	Tobago	K	3
Urera baccifera	Sasaki, D.	1487	Brazil	K	3
Urera baccifera	Sasaki, D., Henicka, G.S., T.J.C. Andre, & J.H. Piva	1488	Brazil	K	3
Urera baccifera	Sellow	1548	Brazil	K	3
Urera baccifera	Serrano, M., & J. Villalobos	7447	Bolivia	BM	3

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Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera baccifera	Simonis, J.E., L.F. Perez, W.J. Hahn & R. Dure	203	Paraguay	K	3
Urera caracasana	Smith, J.D.	2976	Guatemala	K	3
Urera baccifera	Spruce, R.	sn		E	3
Urera baccifera	Tate, R.	395 (305)	Nicaragua	K	3
Urera sp.	Triana, J.	884	New Grenada	E	3
Urera baccifera	Tweedie	837		K	3
Urera baccifera	Uzquiano	24		K	3
Urera baccifera	Valenzuela, L., E. Suclli, G. Calatayud, I. Huamantupa, N. Suarez, & F. Zamora	9152	Peru	BM	3
Urera baccifera	Valenzuela, L., E. Suclli, I. Huamantupa, A Carazas	2915	Peru	BM	3
Urera baccifera	van der Werff, H., R. Vasquez, B. Gray, & J. Campos	16487	Peru	K	3
Urera baccifera	Vanni, R., J. Davina, M. de Pompert, & A. Radovancich	783	Argentina	K	3
Urera baccifera	Whitefoord, C & Quiroz, V	106016	Belize	BM	3
Urera baccifera	Wood, J.R.I.	9103	Bolivia	K	3
Urera baccifera	Woolston, A.H.	1094	Paraguay	K	3
Urera laciniata	Acevedo-Rdgz, P., P. Nunez & M.E. Chuspe	9721	Peru	K	4
Urera laciniata	Araujo-M, A., P. Gismondi, & N. Flores	1477	Bolivia	K	4
Urera laciniata	Asplund, Erik	18842	Ecuador	K	4
Urera laciniata	Bang, A. Miguel	1247	Bolivia	K	4
Urera laciniata	Belshaw, Charles M.	3342	Peru	K	4
Urera laciniata	Campos, J., & W. Vargas	3932	Peru	K	4
Urera laciniata	Ceron M, Carlos E.,	2053	Ecuador	K	4
Urera laciniata	Farfan, J., A. Carazas, W. Argandona	1159	Peru	K	4
Urera laciniata	Goudot, J.	s.n.	Colombia	K	4
Urera laciniata	Holton, I.F.	219	n/a	K	4
Urera laciniata	Lindeman, J.C.	5660	Suriname	K	4
Urera laciniata	Mexia, Ynes	8326	Peru	K	4
Urera laciniata	Monro, A.K., R.T. Pennington, & A. Daza	3993	Peru	E	4
Urera laciniata	Monteagudo, A., C. Mateo & G. Ortuiz	3905	Peru	K	4
Urera laciniata	Pennington, T.D. & A. Daza	16675	Peru	K	4
Urera laciniata	Peterson, P.M. & C.R. Annable	6853	Panama	K	4
Urera laciniata	Sandeman, Christofer	5011	Peru	K	4
Urera laciniata	Seeman	1867	n/a	K	4
Urera laciniata	Skutch, A.F.	4266	Costa Rica	K	4
Urera laciniata	Spruce, R.	4140	Peru	K	4

Appendix 3 - Morphospecies Classification

Name	Collector	Collector Number	Country	Herbarium	Morphospecies
Urera laciniata	Suclli, E., V. Chama, J. La Torre, A. Astete, A. Carazas, & B. Titto	2399	Peru	K	4
Urera laciniata	Vargas, L., A Portugal, & J. Torrez	1337	Bolivia	K	4
Urera laciniata	Vasquez, R., Ch. Davidson, Sh. Davidson, J. Farfan, E. Suclli, & A. Pena	33060	Peru	K	4
Urera laciniata	Vigo, Jose Shunke	6173	Peru	K	4
Urera laciniata	White	965	Bolivia	K	4

Appendix 4 - Ecoregions and Habitat Information

Clade	Name	Collector	Coll No.	Biome	Ecoregion	Habitat info from label	Translation
A	Urera baccifera	Cuatrecasas, J.	13896	Tropical & subtropical moist broadleaf forest	Northwest Andean montane forests	hoya del rio Calima	Basin of Calima river
A	Urera baccifera	Zak, V.	3156	Tropical & subtropical moist broadleaf forest	Eastern Cordillera Real montane forests	en las orillas del rio hollin	On the banks of the Hollin River
A	Urera baccifera	Ortiz, V.	187	Tropical & subtropical moist broadleaf forest	Peruvian Yungas	bosque montano interior	Interior montane forest
A	Urera baccifera	Nunez, P.	8812	Tropical & subtropical moist broadleaf forest	Peruvian Yungas		
A	Urera baccifera	Hampshire, R.J.	133	Tropical & subtropical moist broadleaf forest	Talamancan montane forests	Cloud forest	
A	Urera baccifera	Sandoval, E.	1819	Tropical & subtropical dry broadleaf forest	Central American dry forests	n/a	
B	Urera baccifera	Wasum, R.	385	Tropical & subtropical moist broadleaf forest	Araucaria moist forests	Forest interior	
B	Urera rugosa	Balansa, B.	1964	Tropical & subtropical grasslands, savannas & shrublands	Humid chaco	n/a	
B	Urera nitida	Giulietti, A.M.	3509	Tropical & subtropical dry broadleaf forest	Caatinga	Floresta umida	Humid forest
B	Urera baccifera	Kirkbride, J.H.	3930	Tropical & subtropical grasslands, savannas & shrublands	Cerrado	In deciduous forest on calcareous rocks with thin organic soil	

Appendix 4 - Ecoregions and Habitat Information

Clade	Name	Collector	Coll No.	Biome	Ecoregion	Habitat info from label	Translation
B	Urera baccifera	Harley, R.M.	14170	Tropical & subtropical dry broadleaf forest	Caatinga	Area de campo rupeste com escarpas rochosas ingremes e fendas onde ocorre mata com palmeiras e algumas epifitae	Area of campos rupeste field with rocky escarpments inlets and cracks where it occurs forest with palm trees and some epifitae
B	Urera baccifera	Zappi, D.C.	2107	Tropical & subtropical moist broadleaf forest	Bahia interior forest	Afloramento rochoso e mata seca a Norte de Faz	Rocky outcrop and dry forest north of Faz
B	Urera baccifera	Simonis, J.E.	203	Tropical & subtropical moist broadleaf forest	Alto Paraná Atlantic forests	Exploited forest	
D	Urera baccifera	Gentle, P.H.	2781	Tropical & subtropical moist broadleaf forest	Petén-Veracruz moist forests	N/a	
D	Urera baccifera	Wood, J.R.I.	9103	Tropical & subtropical moist broadleaf forest	Southern Andean Yungas	In moist broad-leaved forest near a small river, in valley	
E	Urera baccifera	Freire, E.	5377	Tropical & subtropical moist broadleaf forest	Napo moist forests	Bosque maduro, relieve plano	Mature forest, flat relief
E	Urera baccifera	Quishpe, W.	156	Tropical & subtropical moist broadleaf forest	Ucayali moist forests	Bosque muy humedo premontano. Substrato de roca arensica.	Very wet premontane forest. Substrate of sandstone.

Appendix 4 - Ecoregions and Habitat Information

Clade	Name	Collector	Coll No.	Biome	Ecoregion	Habitat info from label	Translation
C	Urera laciniata	Vargas, L.	1337	Tropical & subtropical moist broadleaf forest	Bolivian Yungas	n/a	
C	Urera laciniata	Araujo-M, P.	1477	Tropical & subtropical moist broadleaf forest	Bolivian Yungas	Bosque amazonico perandino	Preandean Amazonian forest
C	Urera laciniata	Araujo-M, A.	3016	Tropical & subtropical moist broadleaf forest	Bolivian Yungas	Bosque amazonico perandino	Preandean Amazonian forest
C	Urera laciniata	Skutch, A.F.	4266	Tropical & subtropical moist broadleaf forest	Isthmian-Pacific moist forests	Beside river	
C	Urera laciniata	Ceron, M.	2053	n/a	n/a	Bosque muy humedo tropical; disturbado	Very humid tropical forest; disturbed
C	Urera laciniata	Monteagudo, A.	3905	Tropical & subtropical moist broadleaf forest	Peruvian Yungas	Primary forest	
C	Urera laciniata	Monro, A.K.	3993	Tropical & subtropical moist broadleaf forest	Peruvian Yungas	Tropical wet forest, disturbed	
C	Urera laciniata	Acevedo-Rdgz, P.	9721	Tropical & subtropical moist broadleaf forest	Southwest Amazon moist forests	Primary lowland non-flooded tall forest intermixed with Guadua (bamboo)	
C	Urera laciniata	Suclli, E.	2399	Tropical & subtropical moist broadleaf forest	Southwest Amazon moist forests	Bosque humedo intervenido	Disturbed humid horest

Appendix 4 - Ecoregions and Habitat Information

Clade	Name	Collector	Coll No.	Biome	Ecoregion	Habitat info from label	Translation
C	Urera laciniata	Farfan, J.	1159	Montane grasslands & shrublands	Central Andean wet puna	Bosque secundario	Secondary forest
C	Urera laciniata	Vasquez, R.	33060	Tropical & subtropical moist broadleaf forest	Peruvian Yungas	Bosque primario sobre colina	Primary forest on hill
C	Urera laciniata	Campos, J.	3932	Tropical & subtropical moist broadleaf forest	Eastern Cordillera Real montane forests	n/a	
C	Urera laciniata	Pennington, T.D.	16675	Tropical & subtropical moist broadleaf forest	Ucayali moist forests	Forest at foot of steep slopes	
C	Urera laciniata	Huamán, A.P.M. & C. Rojas	221	Tropical & subtropical moist broadleaf forest	Ucayali moist forests	Secondary forest on roadside	