11-18-2020

Trilepisium (Moraceae): Four New Species from Madagascar

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B.S., Biology, University of Missouri-St. Louis, 2018

A Thesis Submitted to The Graduate School at the University of Missouri-St. Louis
in partial fulfillment of the requirements for the degree
Master of Science in Biology

December
2022

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Abstract

Trilepisium is a genus of tree with two member species: *T. madagascariense* and *T. gymnandrum*. This genus shows diversity in habit and morphology greatly exceeding that expected of a genus with two member species. Concerted collection efforts since the last revision have suggested there are several unrecognized species within *Trilepisium* and a revision is needed. Chapter one of this thesis details the history of this taxanomically challenging genus and presents the results of our study of 600 Malagasy herbarium specimens. *Trilepisium* is more adequately circumscribed as containing 17 species, 11 of which are new to science. Chapter two contains descriptions of four of the newly delineated species for which adequate and fertile material was present: *T. littoralis*, *T. vohibensis*, *T. andapensis*, and *T. borealis*. Accompanying these descriptions are distribution maps for each species. All four species are of conservation concern, meeting the criteria for Endangered (EN) (IUCN, 2012).

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Note on the Formatting of Chapter Two

Chapter two of this thesis is formatted to the standard of the intended journal of publication. This chapter is intended to be published in the Journal Novon (Missouri Botanical Garden, 2022)

Citations

Missouri Botanical Garden 2022. *Submissions*

https://novon.mobot.org/index.php/novon/about/submissions

The Current State of Trilepisium in Madagascar

Trilepisium Thouars is a genus of evergreen trees in Moraceae characterized and distinct from other genera particularly by its unique inflorescence and fruits. The inflorescences of *Trilepisium* consist of several staminate flowers surrounding a single pistillate flower. The staminate flowers are greatly reduced, lacking any form of perianth, and consisting solely of numerous anthers (De Candolle 1825). Distinction between individual staminate flowers is difficult, as they consist solely of anthers; as a whole the anthers appear to form a large aggregation surrounding the single, central pistillate flower. This pistillate flower may or may not possess a corolla (Hutchinson and Rendle, 1916). When present, this corolla is always fused into a single tube. In the absence of a corolla, it may give the impression of a perfect flower, stamen surrounding styles, but the functional sexual parts are arranged in individual flowers. The drupaceous fruits of *Trilepisium* are often described as urn-like and the styles and scars from the anthers persist in mature fruits. The fruits are most frequently purple when mature, but may less frequently be other colors (Berg 1977). Both the inflorescences and fruits of *Trilepisium* are unique and set it apart from other members of Moraceae. *Trilepisium's* sister genus, *Bosqueiopsis,* has staminate flowers surrounding female flowers, however these staminate flowers possess a perianth and consist of 1 or 2 stamen per flower and produce orange fleshy fruits (Hauman, 1948). Like most of Moraceae, *Trilepisium* has a thick, white latex.

In Madagascar, *Trilepisium* trees are used for lumber, along with a red dye that can be extracted from the sap (Burkill, 1985). Additionally, the seeds can be eaten, usually when roasted (African Plant Database 2022). Finally extracts from the bark of *T. madagascariense* shows antidiarrheal traits (Teke et al. 2010) and possible antimicrobial properties (Ango et al., 2012). *Trilepisium* is found in forests throughout sub-Saharan Africa, and the southwest Indian Ocean, including Madagascar (Berg, 1977). In Madagascar this includes locations with rainfall varying from 3000mm to 300mm annually and substrates including sand, limestone, and swamps (Moat and Smith 2007). This genus does not have an IUCN Red List designation. However, given its wide distribution, if considered only a single species, *T. madagascariense* would be categorized as of Least Concern (LC). Without a clear picture of the genus, it is impossible to determine which populations or species are of conservation concern.

In Madagascar, Moraceae consists of 10 genera with and 40 currently accepted species (Schatz et al. 2021); only the genus *Trophis* is endemic. Very little is known about the evolutionary history of *Trilepisium*; and its origins and how it has dispersed geographically remains unknown. Both *Trilepisium* and its sister genus *Bosqueiopsis* likely diverged from a common ancestor on continental Africa; *Bosqueiopsis* only occurs in central Africa (Berg, 1977).This is further supported by genetic data showing *Trilepisium* and *Bosqueiopsis* as sister genera (Zhang et al., 2019). It seems likely that *Trilepisium* then dispersed to Madagascar, but molecular

data is needed to confirm. The bulk of morphological and ecological diversity within the genus, both morphologically and ecologically, occurs in Madagascar; on the African continent, the species is significantly less diverse (Berg 1977). In this thesis we describe four new species of *Trilepisium* endemic to Madagascar. These descriptions represent the first step towards a full revision of Malagasy *Trilepisium*. With what is currently known about diversity in continental Africa, this revision should provide a reasonable working taxonomy for the whole genus.

Trilepisium is a taxanomically challenging genus, with a history of varying revisions. Opinions have varied about the taxonomy of *Trilepisium*. Some authors have recognized multiple species (Hutchinson and Rendle, 1916; Humbert, 1948; LeBathie and Leandri, 1952), while Berg (1977) recognized only a single accepted species in Madagascar, *T. madagascariense* DC. A second species, *T. gymnandrum* Gerlach was published (Gerlach, 2000) based on material from the Seychelles; there have been no revisions of this genus since that publication that address the status of this Seychelles endemic. The delineation of *T. gymnandrum* came in response to work by Friedmann, who hypothesized three or four species of Malagasy *Trilepisium* and noted the differences between the Seychelles populations and Malagasy populations (1994).

The results from the current preliminary revision indicate that the diversity in Madagascar is best described as consisting of 17 species, four of which are new to

science and described here. The remaining material remains under study; some collections clearly represent additional species that are new to science, but it is not currently clear whether the available collections present adequate information for the description of these potentially new species.

Taxonomic History

Trilepisium was originally described by De Candolle, in 1825, from 3 specimens from Madagascar. De Candolle noted the caudate apex, 5-lobed calyx, 3 styles, and numerous stamen (1825). Since that time, three genera: *Trilepisium*, *Bosqueia* Thouars ex Baill, and *Pontya* Chevalier have been used to accommodate more than a dozen various species names currently considered to belong to *Trilepisium* (LeBathie and Leandri, 1952). There is great morphological and ecological diversity between the Malagasy collections of *Trilepisium*, especially among recent collections gathered since Berg's revision. These collections strongly suggest that there is more than a single species within Madagascar.

Berg (1977) revision of Malagasy *Trilepisium* recognized only a single species: *T. madagascariense,* but given the extent of morphological diversity among the collection he examined, he defined three broad groups of no taxonomic status based on morphological differences. These groups still frequently overlap to some degree. Group A contains strongly coriaceous leaves with an obtuse or acuminate

apex and fruit longer or shorter than 10cm, group B possesses coriaceous leaves with a long acuminate apex and fruit over 10 cm, and group C contains variable coriaceous or subcoriaceous leaves with fruit shorter or longer than 10 cm (Berg, 1977). It has been shown by other authors that such a broad species definition may not accurately reflect the diversity of a genus (Renner, 2016; Weber, 1977; Wright, 2012).

This study includes information from over 600 herbarium specimens including 222 from the Missouri Botanical Garden (MO), about 350 from the Natural History Museum in Paris (P), and about 40 from the Conservatoire et Jardin botaniques in Geneva (G). These numbers also include duplicates originally gathered by two herbaria in Madagascar, the National Zoological and Botanical Park (TAN) and the Forestry Department (TEF), as well as some collections from other herbaria when collections were available. These specimens represent the vast majority of all *Trilepisium* specimens gathered from Madagascar, most of which were gathered after Berg's revision. In contrast to the 600 specimens included in this study, Berg examined only about 100 Malagasy specimens during his revision (Berg 1977). The present study suggests that there are currently 17 species of *Trilepisium* found in Madagascar. Of these, 11 are new to science; five have available names from previously described species that Berg treated as synonyms of *T. madagascariense*. In chapter 2, we describe four of the newly circumscribed species, for which adequate herbarium material exists. The recognition of multiple previously unrecognized species results in a much more narrowly defined *T. madagascariense*. The most

interesting trend in the species appears to show an inverse correlation between leaf thickness and precipitation, with *T. occidentalis* and *T. borealis* possessing the thinnest leaves of the genus and the *T. littoralis* the thickest. A distribution map for the four new species is available in appendix A, produced with QGIS (QGIS.org 2022). Appendix B contains a table comparing variable characters between *T. madagascariense* and the four newly described species. An identification key for the four new species and the two currently recognized species is available in chapter 2. A brief overview of all 17 species and species hypotheses follows.

Prospective Species Recognized in this Analysis

According to the most recent literature (Berg,1977; Gerlach, 2000), there are the following two currently accepted species in *Trilepisium*, only one of which can be found in Madagascar:

T. madagascariense DC. This species is characterized by thin textured, elliptic leaves, a caudate apex, revolute margins, prominent knob-like leaf scars, ramified tertiary venation, reduced or absent higher order venation, small obovoid fruits, and 3 styles on the central pistillate flower (most of this genus only has 2 styles).

T. gymnandrum. The other currently accepted species, described from and apparently endemic to the Seychelles, is characterized by large oblong leaves with an acuminate apex, an obtuse leaf base, and well developed basal leaf nerves.

The following species were previously described, but synonymized with *T. madagascariense* by Berg. Our study of the available material gives evidence they should be recognized as separate species again. Updated descriptions of these species will be needed for a full revision of the genus.

T. boiviniana. This species consists of populations in Northwestern Madagascar in humid forests and on the island of Nosy-be characterized by thick acuminate leaves, with a dull abaxial surface, and a highly glossy adaxial surface. All 21 specimens are housed at Paris. The name *Bosqueia boiviniana* Baill. already exists and can be transferred to *Trilepisium* to accommodate this species.

T. occidentalis. This species consists of populations from dry western forests, preferring limestone substrates and characterized by chartaceous leaves, a stout midrib, reticulate tertiary venation, elliptic leaves, a flat margin, and red obovoid fruits at maturity. The type for this specimen is housed in Paris, with ten specimens at Missouri Botanical Garden and 30 specimens at Paris in total. The name *Bosqueia occidentalis* Leandri already exists and can be transferred to *Trilepisium* to accommodate this species.

T. manongarivensis. This species consists of populations from eastern humid forests around the Masoala peninsula at middle elevations. This species is distinct in its thick twigs, very large leaves, a caudate apex, prominent tertiary venation with higher order venation reduced or absent, a flat margin, and large obovoid fruits. The type is housed in Paris, along with 23 specimens. Four specimens are deposited at MO. The name *Bosqueia manongarivensis* Leandri already exists and can be transferred to *Trilepisium* to accommodate this species.

T. danguyana. This species consists of populations from humid Eastern forests, this species is characterized by prominent knob-like leaf scars, acuminate leaves, glossy abaxial and adaxial surfaces, a revolute leaf margin, ramified tertiary venation, small mature flowers and fruits. Known from 25 specimens all at Paris. The name *Bosqueia danguyana* Leandri already exists and can be transferred to *Trilepisium* to accommodate this species.

T. pyriformis. This species consists of a single population found on the island of Nosy-be characterized by small dark leaves with prominent reticulate venation on both leaf surfaces, an acuminate apex, and a non-revolute margin. This probable species is only known from four specimens, all at Paris. The name *Bosqueia thoursiana* var. *pyriformis* Baill. exists and can be transferred to *Trilepisium* and prompted to species to accommodate this species.

The following species hypotheses surfaced during examination of herbarium material. Further collections will be helpful for adequately describing these potential species; available herbarium material is currently lacking.

T. sp1. This species consists of populations from northern, high elevation sites and characterized by very narrow elliptic acuminate leaves, and very small mature flowers and fruits. This species is only known from three specimens, all of which are housed in Paris +.

T. sp2. This species consists of populations from low elevation, humid Northeastern forests distinguished by thin leaves with a caudate apex that remain bright green after drying, even when preserved in alcohol, straw colored mid-veins and reticulate venation. This probable new species is only known from two collections at Paris. Flowers and fruits are lacking from both specimens, making future description daunting without more material.

T. sp3. This species consists of a population from very dry southwestern forests characterized by obovoid leaf blades with a mucronulate apex, reduced venation, a flat margin that is not revolute, and small obovoid fruit. This probable new species is known from a single specimen at Paris. This specimen is fertile.

T. sp4. This species consists of populations from mid- to high-elevation humid Northeastern forests distinguished by thick, broad leaves, a strongly revolute margin, an obcordate apex, and spheroid fruits. All 13 specimens are at Paris.

T. sp5. This species consists of a population found near Tolanaro in southwestern Madagascar dry forests, characterized by a glossy adaxial leaf surface, caudate apex, and secondary and tertiary venation raised on the adaxial surface. The single known specimen is at Paris. Vegetative characters appear sufficient to describe this species adequately with a single specimen; however, any future description would benefit greatly from fertile specimens.

T. sp6. This species consists of a population from Zahamena National Park at 500-600m, characterized by large, rounded, obovoid leaves with a strongly revolute margin, and large spheroid fruit and known from only two specimens at Paris. While flowers are unknown, both specimens are fertile.

T. sp7. This species consists of a population from northern dry forest characterized by flaking bark, small caudate leaves, very fine venation, and medium obovoid fruits. The single known specimen is at Paris.

There are four additional new species, all known from adequate material for reasonably complete description. Full descriptions are contained in chapter 2.

T. littoralis Kelley. This species consists of coastal populations almost exclusively found on white sand in littoral forests along the eastern coast of Madagascar and distinguished by its thicker leaves, rounded and mucronulate apices, strongly revolute leaf margin, and a fused white corolla on its pistillate flowers. The type specimen is housed at Missouri Botanical Garden along with 34 other collections.

T. andapensis Kelley. This species consists of populations found on the eastern slopes of the Tsaratanana Massif and near Andapa in humid pre-montane and montane forests characterized by leaves with an acuminate apex, a pubescent inflorescence, and a red calyx. The type specimen is housed at Missouri Botanical Garden along with seven other collections.

T. borealis Kelley. This species consists of populations found in dry northern forests between 75m and 432m. This species is characterized by semi-coriaceous leaves, an acuminate leaf apex, non-revolute margins, reticulate venation, and a minutely pubescent inflorescence and corolla. The type specimen is housed at Missouri Botanical Garden, along with five other collections.

T. vohibensis Kelley. This species consists of populations known only from the humid Forêt de Vohibe in southeastern Madagascar characterized by a truncate leaf apex, glossy abaxial surface, and very slightly revolute margin. A single collection was found at 13m in an eastern littoral forest. The type specimen is at Missouri Botanical Garden along with two other collections.

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The following paper is being submitted to the journal Novon.

New Moraceae from Madagascar: Four new species of *Trilepisium*.

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Abstract. Four new species of *Trilepisium* (Moraceae), *T. littoralis* Kelley, *T. vohibensis* Kelley, *T. andapensis* Kelley, and *T. borealis* Kelley, are described from Madagascar. A phylogeny for this genus is not available, so the relationships of these species are unknown, but they are all distinctive morphologically and unlikely to be confused with other known species. Images of all type specimens and distribution maps are included. All species are considered to be of conservation concern and each is assigned to an IUCN Red List Category.

Key words: Trilepisium, Moraceae, Madagascar, IUCN Red List

The island of Madagascar is famous for its high levels of biological diversity. About 85% of all vascular plants found on the island are endemic (Goodman and Benstead, 2005; Callmander et al., 2011); when only considering trees and large shrubs this number rises to 96% (Schatz, 2000). This unusually high rate of endemism is likely due to the islands extremely prolonged isolation. Madagascar has been isolated from continental Africa and the Indian subcontinent for more than 85 million years (Ali and Aitchison., 2008). Additionally, the island boasts a wide range of habitats ranging from the eastern rain-forests, high central plateaus, to arid deserts in the southwest (Moat and Smith, 2007). This has led to numerous families and genera to greatly radiate and diversify after dispersing to the island. It is common to find numerous endemic species in a single genus with very limited ranges (Lowry et al., 2017; Applequist, 2020). Recent studies have increased the number of vascular plant species from Humbert's total of 7,900 (1959) to almost 14,000 (Schatz et al., 2022). Additionally, Madagascar's forests are one of the most threatened habitats in the world. The island has lost 80 % of its core forest (more than 1 km from a forest edge) overall (Harper et al. 2007) and 44% of the island's total forest since 1953 (Morelli et al., 2020). The combination of significant habitat loss and high rate of range-limited endemic species makes Madagascar a major conservation focus.

According to the Catalog of the Plants of Madagascar, Moraceae consists of 10 genera with 40 constituent species, with *Trophis* Browne being the only endemic genus (Schatz et al., 2021). *Trilepisium* Thouars is a genus of evergreen trees in

Moraceae, that appears to follow the same pattern of radiating into several range-limited species after reaching Madagascar. The genus is characterized and distinct from other genera by its unique inflorescence and fruits. The inflorescences of *Trilepisium* consist of several staminate flowers surrounding a single pistillate flower (De Candolle, 1825). The staminate flowers are greatly reduced, lacking any form of perianth, and consisting solely of numerous anthers. Distinction between individual staminate flowers is nearly impossible; as a whole, the anthers appear to form a large aggregation surrounding the single, central pistillate flower. This pistillate flower may possess a corolla. When present, this corolla is always fused into a single corolla tube. In the absence of a corolla, it may give the impression of a perfect flower, stamen surrounding styles, but the functional sexual parts are distributed in individual, unisexual flowers. The drupaceous fruits of *Trilepisium* are usually purple and retain the persistent styles and scars from abscised stamens; the shape is often described as urn-like (Berg, 1977).

Trilepisium has most recently been treated (Berg 1977) as monotypic and distributed throughout Madagascar and Africa. *Trilepisium* has been revised multiple times since its initial description by De Candolle (1825). Every treatment of this genus, except for that of Berg (1977), has recognized multiple species, even while opinions on the number of constituent species have varied (Hutchinson and Rendle, 1916; Humbert, 1948; LeBathie and Leandri, 1952).

The most recent taxonomic treatment (Berg, 1977) accepted only a single species, *T. madagascariense* DC. A second species, *T. gymnandrum* Gerlach, endemic to the Seychelles, has been published and generally accepted, but its status has not been reviewed in any recent revision. *Trilepisium* is found throughout sub-Saharan Africa, and Madagascar (Berg, 1977). Very little is known about the evolutionary history of the genus, such as its origins or how it has dispersed since splitting from its apparent sister genus *Bosqueiopsis*, however both genera likely diverged from a common ancestor on continental Africa (Zhang et al. 2019). The bulk of the diversity within the genus, both morphologically and ecologically occurs in Madagascar; on the African continent, the species is significantly less diverse (Berg 1977).

There are now about six times as many collections available as were included in Berg's study of the genus in Madagascar and the morphological diversity seems to agree with Friedmann's assessment (1994) that *Trilepisium* contains more than a single species in the country, so a revision of the genus in Madagascar was undertaken. This review of collections has revealed that there are clearly multiple species in Madagascar, both ecologically and morphologically distinct. These species each have distinctive morphological characteristics and are not easily confused with each other or *T. madagascariense*. We recognize 17 putative species, 11 of which are new to science; the six previously named species are: *T. occidentalis, T. bioviniana*, *T. manongarivensis*, *T. danguyana,* and *T. pyriformis*. Four new of the new species of

Trilepisium have adequate material already collected and are described as new species as a first step towards a revision of this taxonomically challenging genus. *Trilepisium littoralis* and *T. vohibensis* have distinctive apexes, rounded to mucronulate and truncate respectively. *Trilepisium andapensis* possesses a dark red calyx. *T. andapensis* and *T. borealis* both have pubescent inflorescences, but show a difference in hair length. *Trilepisium borealis* also stands distinct with its semi-coriaceous leaves which are noticeably thinner than other *Trilepisium* specimens, having a texture that bridges the gap between coriaceous and chartaceous.

Trilepisium Thouars. Gen Nov. Madagasc. 22 1806. TYPE SPECIES *Trilepisium madagascariense* DC. (P)

Synonyms

Bosqueia Baillon Gen Nov. Madagascar 1863 TYPE SPECIES *Bosqueia thoursiana*

Pontya A. Chev. Gen Nov. Madagasc. 1909 TYPE SPECIES *Pontya excelsa*

Discussion. Trilepisium as treated here follows the generic circumscription of Berg (1977). The collection of about five hundred additional specimens since the last revision has allowed for the discovery of morphological distinctions and subsequent recognition of additional species. An identification key for all described *Trilepisium* in Madagascar, including the four newly described species, and the only other species

in the Indian Ocean follows. With the description of these new species, *T. madagascariense* is more narrowly defined. The recognition of *T. littoralis* and *T. andapensis* accommodates virtually all individual specimens that lack a distinct acumen or caudex, placing such collections in the two newly described species. For IUCN conservation assessments, Area of Occupancy (AOO) was calculated with a grid size of 2km. This allows a maximum of 2 locations for a species to be considered Critically Endangered (CE) (IUCN, 2012).

Key for identification of all *Trilepisium* in Madagascar and the Indian Ocean

1. Leaf texture semi-coriaceous, or chartaceous, tertiary venation ramified

    2. Leaves elliptic and semi-coriaceous, fruits obovoid, northern dry forests……..

    ……..……...……..*T. borealis*

    2’. Leaves obovate and chartaceous, fruits spheroid, western dry forests near Mahajanga..…….…….....*T. occidentalis*

1’. Leaf texture coriaceous, tertiary venation usually ramified, sometimes reticulate

    3. Leaf apex not acuminate or caudate

        4. Leaf apex rounded to mucronulate, adaxial leaf surface dull, eastern littoral forests below 260m...……..……...…....*T. littoralis*

        4’. Leaf apex truncate, adaxial leaf surface glossy, central eastern forests above 650m……...…….…...……..*T. vohibensis*

    3’. Leaf apex acuminate or caudate

5. Adaxial surface glossy

6. Abaxial surface dull, found on Nosy-be…..…….....*T. bioviniana*

6’. Abaxial surface glossy, found in humid eastern forests…..*T. danguyana*

5’. Adaxial surface dull and matte

7. Tertiary venation reticulate, leaves dark, found on Nosy-be

……..……...……..*T. pyriformis*

7’. Tertiary venation ramified, leaves not dark

8. Twigs longitudinally grooved or ridged and >5mm in diameter…….……...…….…….…..*T. manongarivensis*

8. Twigs not longitudinally grooved or ridged and <5mm in diameter

9. Fruits larger than 15mm x 20mm, calyx dark red, wet northern mid-elevation forests near Andapa or the Tsaratana Massif……

…….…….……..…*T. andapensis*

9. Fruits smaller than 15mmx20mm, calyx usually green or brown

10. Leaves elliptic or obovate, leaf base cuneate…….

……....*T. madagascariense*

10’ Leaves ovate, leaf base obtuse, found in the Seychelles islands ……....*T. gymnandrum*

Trilepisium littoralis S. Kelley Sp. Nov. TYPE: Madagascar. Sava: Fiv; Vohémar, Fir: Tsarabaria, Fok: Manakana, a l’Est du Village d’Ambondrobe 13°42’35”S,

50°05’49”E, 12 March 2004, *Rabevohitra* 5129 (Holotype: MO!, Isotype: P!, TEF not seen).

Diagnosis. Trilepisium littoralis is distinguished from all species described here and from a more narrowly circumscribed *T. madagascariense* by its rounded or mucronulate apex and a revolute margin. It is distinguished from *T. vohibensis* by its dull leaf surfaces and a rounded or mucronulate apex instead of truncate apex; *T. littoralis* is found below 150m, while *T. vohibensis* is found above 650m.

Tree 4-20 (-22) m tall, twigs glabrous; leaf blades obovate, widest just below the apex, 3-10 cm long, 1-4.5 cm wide, the apex rounded to mucronulate, the base cuneate, the margin entire and revolute, the texture coriaceous, the venation brochidodromous, the midrib raised or even with the adaxial surface, raised on the abaxial surface, the secondary veins 4-6, the tertiary veins ramified and transverse; petioles 0.5-1 cm long, glabrous; stipules deciduous, 3-7 mm long, sheathing. Inflorescence an umbel 4-12 mm broad; flowers unisexual and sessile, with the inflorescence functionally bisexual; staminate flowers with the calyx absent, the corolla absent, the stamens numerous, the filaments 2 mm long, the anthers 1.5-2 mm long; pistillate flowers with the calyx absent, the corolla white, 3.5-4 mm long, 1-1.5mm wide 5-lobed, fused at base; styles 2, free, 5-6 mm long, stigma 1, clavate. Fruit drupaceous, yellow to green at maturity, 8-20 mm long, 4-8 mm in diameter.

Distribution and habitat. Trilepisium littoralis is found on white sand in littoral forests throughout Eastern Madagascar, from as far north as Vohemar, south to Tolanaro. Very rarely individuals can be found above 100m; the highest recorded elevation for this species is 260m.

IUCN Red List Category. With an Extent of Occurrence (EOO) of about 45,000km^2, *T. littoralis* would be considered provisionally of Least Concern (LC) (IUCN, 2012). Individuals have been collected from 35 known locations giving an Area of Occupancy (AOO) of 136km^2, below the threshold for Endangered (EN). The eastern littoral forests are subject to intense fragmentation and are one of the most threatened habitats in Madagascar (Consiglio et al., 2006; Lowry et al. 2008) Combined with the low AOO, this species meets the requirements for Endangered (EN).

Discussion. Trilepisium littoralis shows variability in the form of its leaf apexes. Most individuals have both rounded and mucronulate leaves on the same branch. The margin is also strongly revolute almost forming a tube in some individuals, whereas in other species magnification is needed to view this curling. Additionally, this species has a white corolla surrounding the female flower in each inflorescence. Aside from a handful of individuals, this species exists exclusively on the white sand littoral forests of Eastern Madagascar. Local names for this species include Fotsydity, Beronono, and Lipaty.

Etymology. *Trilepisium littoralis* is named after the white sand littoral forests the species grows on. This species is the only *Trilepisium* species to grow in the eastern littoral forests of Madagascar.

Paratypes. MADAGASCAR. **Anosy region**: Tolanaro, forest of Petriky, elev. 25m, 25°05'S, 46°52'E, 16 October 1989, *McPherson et al. 14130* (MO, TAN); Tolanaro, Forêt de Mandena, in Botanical Garden, elev. 25m, 24°57'S, 47°00'E, 25 October 1989, *McPherson et al. 14235* (MO, TAN); Fort-Dauphin, Mahatalaky, Belavenoko, S17 ou Agnalavao, 2.5 km a l'Est de Belavenoko, elev. 15 m, 24°51'47"S, 47°07'25"E, 27 February 2012, *Ratovoson 1838* (MO, P, TAN); Fort-Dauphin, Sainte Luce, Iabakoho, Ambanihazo, Andranomanga, a 500km du campement, elev. 13m, 24°40'23"S, 47°12'28"S, 19 November 2011, *Ramananjanahary et al. 412* (MO, P, TAN); District de Fort-Fauphin, Forêt de Mandena, 24°57'S, 47°00'E, 6 December, 1989, *Dumetz & McPherson 1128* (MO, TAN); Fok: Mandena, Fir: Ampasy, Fort-Dauphin, 24°56'07"S, 47°01'42"E, 21 December 2000, *Faliniaina et al. 90* (MO, TEF); Tolagnaro, Mahatalaky, Belavenoka, forêt littorale de Saint Luce, 24°47'S, 47°11'E, 28 September 2007, *Rabenantoandro 1825* (MO); District de Fort-Dauphin, Commune Mahatalaky, FKT Manafiafy Sainte Luce, Forêt de Beboaka, plot forestier S9b, a 2km Nord du campement QMM a Sainte Luce, elev. 23m, 24°45'56"S, 47°10'25"E, 01 March 2012, *Randrianaivo et al. 1982* (MO, P, TAN). **Vitovavy region**: Fiv: Nosy Varika,

Fir: Firaisana, Fok: Ambahy, foret sublittorale a l'Est du village d'Ambahy, 20°46'47"S, 48°29'05"E, 23 March 2003, *Rabevohitra 4708* (MO, P, TEF); Fiv: Nosy Varika, Fir: Ambahy, Sur sable d'Ambahy, elev. 3m, 20°48'07"S, 48°28'56"E, 11 December 2002, *Rabenantoadnro et al. 1171* (MO). **Atsinanana region**: Brickaville, Ambinaninony, Andranokoditra, Forêt littoral: Vohibola, elev. 0-10m, 18°33'35"S, 49°15'05"E, 26 October 2002, *Ranaivojaona et al. 441* (MO); Province Tamatave, RN5, ca. 5.0km S of Foulpointe, 12 December 1984, *Dorr & Bartnett 3405* (MO, TAN). **Analanjirofo region**: Fiv: Soanierana-Ivongo, Fir: Manompana, Fok: Antanambao-Ambodimanga, Forêt d'Antanambao-Ambodimanga, elev 13m, 16°59'27"S, 49°43'01"E, 6 October 2003, *Andrianarivelo et al. 36* (MO, P, TEF); Manambia, Parc National de Masoala, elev. 0m, 15°45'41"S, 49°59'40"E, 21 November 1994, *Rahajasoa et al. 957* (MO); Parc National de Masoala, Antalavia, 15°47'00"S, 50°02'00"E, 22 November 1994, *Rahajasoa et al. 962* (MO); District Fenerive-Est. Station forestiere de Tampolo, 10km Nord de Fenerive-Est. elev. 0-150m, 17°16'52"S, 49°24'44"E, 24 January 1995, *Raholivelo et al. 136* (MO);Tampolo, pres du village Tanambao-Tampolo, Fenoarivo-Est., elev. 0-5m, 17°17'S, 49°25'E, date unknown, *Ralimanana et al. 89* (MO, P, TAN); Fiv: Maroantsetra, Fir: Rantabe, Fok: Rantabe, elev. 5m, 15°44'01"S, 49°39'37"E, 20 February 2002, *Rabenantoandro et al. 917* (MO, TEF); District Fenerive, 24 April 1957, *S.F 16_930* (P); Fiv: Soanierana-Ivongo, Fir: Manompana, Fok: Tanambao, sublittoral forest 2km au Nord de Tanambao, 16°45'27"S, 49°43'10"E, 31 January 2004, *Rabevohitra 4953* (MO, P, TEF); Masoala Peninsula, south of the village of

Ambanizana, in the Andranobe River Watershed, between 400 and 1700m from the seashore, elev 110-260m, 15°40’24”S, 49°57’51”E, 24 November 1994, *Vasey & Velo 119* (MO, TAN); Tampolo (Masoala), Ambanizana, Anjahana, Maroantsetra, Forêt littoral de Tampolo, elev. 10m, 15°43’45”S, 49°57’38”E, 18 October 2001, *Randrianaivo 704* (MO); Tampolo, Fenerive, 5 January 1955, *S.F. 12_581* (MO, P, TEF); Fiv: Soanierana-Ivongo, Commune Rurale: Manompana, Forêt d’Antanambao-Ambodimanga, *16°46’24”S, 49°42’51”E,* 30 January 2003, *Rabevohitra et al. 4339* (MO, TEF), District Fenerive-Est. Station forestiere de Tampolo, 10km Nord de Fenerive-Est. elev. 0-150m, 17°16’52”S, 49°24’44”E, 25 January 1995, *Raholivelo et al. 255* (MO); District Fenerive, Ampasina, 7 February 1957, *S.F. 16_538* (P); Station forestiere de Tampolo, 9km N of Fenerive, Plot 1, elev 10m, 17°16’52”S, 49°24’44”E, 29 November 1994, *Schatz et al. 3630* (MO, P, TEF); Tampolo, 17°17’S, 49°25’E, 15 October 2001, *Rebevohitra et al. 3943* (MO); District Fenerice-Est. Station forestiere de Tampolo, 10 km Nord de Fenerive-Est. elev. 0-150m, 17°26’52”S, 49°24’44”E, 24 January 1995, *Raholivelo 140* (MO). **Sava region**: Parc National de Masoala Plot 1-B 15°35’00”S, 50°25’00”E, 22 September 1994, *Rahajasoa et al. 519* (MO, TAAN); Fiv. Vohémar, Fir: Fanambana, Forét de basse altitude s’Analava-Antsoha, elev. 61m, 13°35’44”S, 50°00’04”E, April 2001, *Rabenantoandro 484* (MO); Fiv. Vohémar, Fir: Tsarabaria, Fok: Manakana Forêt d’Ambondrobe, 13°42’46”S, 50°05’25”E, 18 May 2004, *Rabehevitra et al. 1061* (MO, P, TEF); Commune: Antalaha, Commune: Ambohitralanana, Fkt: Ambodirafia 15°16’02”S, 50°28’47”E, 10 December 2015, *Razanatsoa 649* (MO, P); Vohemar,

Binara Forest, 13°15’15”S, 49°37’14”E, 9 December 2004, *Hertiana RHS 514* (CAS, MO).

Trilepisium vohibensis S. Kelley Sp. Nov. TYPE: Madagascar. Antsinanana region: Vatomandry, Ambalabe, Ambinanindrano II, Forêt de Vohibe, piste vers Sahamahirana, elev. 661m, 19°09’40”S, 48°34’42”E, 20 January 2012, *Rakotoarivelo et al. 627* (Holotype: MO!, Isotype: P!, TAN not seen).

Diagnosis. Trilepisium vohibensis is distinguished from all species of the genus by its truncate leaf apex. It is distinguished from *T. borealis, T. littoralis, T. andapensis,* and some populations of *T. madagascariense* by its highly glossy abaxial leaf surface. It is also distinguished from *T. littoralis* by elevation. *T. vohibensis* occurs about 650m, while *T. littoralis* is found below 260m.

Tree to 16m tall, the twigs up to 3 mm in diameter, glabrous and striate. Leaves persistent, heteromorphic, leaf blades obovate, 2-4 cm long, 1.5-2 cm wide, the texture coriaceous, the apex truncate or occasionally rounded, the base cuneate, the margin entire, slightly revolute, the adaxial surface glabrous and glossy, the abaxial surface glabrous, the venation brochidodromous, the midvein raised on abaxial surface, ca. 1mm in width, the secondary veins 3-4 (-5), the tertiary veins ramified and transverse; stipules terminal, sheathing, ca. 1-3 mm long, deciduous;

petioles 2-4 (-6) mm long. Flowers unknown. Fruits drupaceous, obovoid, red at maturity, 1.5-2 cm long, 1-1.5 cm wide, the exocarp glabrous, the endocarp stony.

Distribution and habitat. Trilepisium vohibensis is only known from three collections, one from Zahamena National Park, one from the Forêt de Vohibe and one from the Forêt de Vohimana. All locations are part of the same contiguous wet mid-altitude (between 650m and 1100m) forest in eastern, central Madagascar. *Rakotoarivelo et al. 627* (MO!) has epiphytic bryophytes on the twigs, suggesting a wet habitat.

IUCN Red List Category. With only three collections, this species has an Area of Occupancy (AOO) of 12 km^2, below the threshold for Endangered (EN) (IUCN, 2012). Additionally, while some of these locations are protected, logging and agriculture present a habitat threat at the margins. This species should be considered Endangered (EN).

Discussion. Trilepisium vohibensis is most easily distinguished by its truncate apex and highly glossy upper leaf surface, making it identifiable from *T. littoralis*, whose surface is barely reflective and has a leaf apex that is never truncate. Additionally, *T. littoralis* has a strongly revolute margin, whereas the curl on the margins of *T.* vohibensis is difficult to see without magnification. It is not easily

confused with other *Trilepisium* specimens, which are often characterized by a caudate or acuminate leaf apex.

Etymology. The type specimen for *Trilepisium vohibensis* was collected in the Forêt de Vohibe. This species is thus named after that forest.

Paratypes. MADAGASCAR**. Alaotra-Mangoro**: Moramanga, Ambatovola, Ranovana, Forêt de Vohimana, elev. 800m, 18°55'13"S, 48°30'49"E, *Andriatsiferana 2560* (MO, P, TAN); Zahamena AP, elev. 1100m, 17°38'30"S, 48°38'24"E, date unknown *Ratovoson 683* (MO, TEF, CNARP).

Trilepisium andapensis S. Kelley Sp. Nov. TYPE: Madagascar. Sava region: Andapa, Ambodivohitra, Anjialavabe, versant ouest, elev.940m, 14°14'12"S, 49°23'05"E, 02 March 2006 *Rakotovao et al. 2770* (Holotype: MO, Isotype: P!, TAN not seen).

Diagnosis. Trilepisium andapensis is distinguished from all species of *Trilepisium* by its very large fruits (15-20 mm x 35-40 mm), twice the size of other fruits in the genus. Additionally, it possesses a dark red calyx, not reported elsewhere in the genus. This species has a pubescent calyx (and possibly corolla), but the hairs (0.5 mm) are significantly larger than *T. borealis* (0.1 mm). Furthermore, *T.*

andapensis has ramified venation easily visible to the fifth degree or higher, which is reduced or indistinct past the fourth degree in other *Trilepisium* species.

Tree to 18 m, the twigs ca. 2-4 mm in diameter, striate and glabrous. Leaves persistent, not heteromorphic, leaf blades obovate, 6-10 (-14) cm long, 2-4.5 (-6.5) cm wide, the apex acuminate, the acumen >1cm long, the base cuneate, the margin entire, the abaxial surface glabrous, the adaxial surface glabrous, the venation brochidodromous, major secondary veins 5-6, midvein raised on abaxial surface, depressed on abaxial surface, the tertiary venation ramified, higher order venation to the fifth degree ramified; stipules terminal, sheathing, ca. 5mm long, deciduous; petioles 7-10 (-13) mm long,. Mature flowers unknown. Inflorescences sessile; calyx present in emerging flowers, the color dark red, pubescent, the hairs >0.5 mm long; staminate flowers, the stamens numerous; pistillate flowers, corolla 5-lobed. fused at base, styles 2, free; stigma 1, clavate. Fruits drupaceous, obovoid, yellow maturing to green, 3.5-4 cm long, 1.5-2 cm wide, the exocarp glabrous, the endocarp stony.

Distribution and habitat. Trilepisium andapensis is found at high elevations, >900m, on the eastern slopes of the Tsaratanana Massif and also to the south, near Andapa. This species prefers wet montane and pre-montane forests.

IUCN Red List Category. Trilepisium andapensis has an Extent of Occurrence of about 500km^2, below the threshold for Endangered (EN) (IUCN, 2012).

Tsaratanana and Marojejy (near Andapa) are National Parks and are partially protected; at the margins and outside of these parks, logging and cultivation present habitat threats.

Discussion. Trilepisium andapensis occurs at high elevations in northern wet forests. It is not easily confused with any other species described in this paper. Its extremely large fruits, elongated leaves, and dark red calyx distinguish this species from *T. madagascarensis*. Only emerging flowers were available for observation.

Etymology. *Trilepisium andapensis* is named after the town and commune of Andapa, where several individuals have been found.

Paratypes. MADAGASCAR. **Sava region**: Sambava, Bevontro, Tsaratanana, Morafeno, foret dense humide de moyenne altitude d'Antsahandroboka, 10km au Sud-Ouest du village de Morafeno elev. 907m, 14°10'33"S, 49°18'38"E, 07 February 2007, *Rakotovao et al. 3450* (MO, G, P, TAN); Andapa, Doany, Andranomilolo, foret dense humide de moyenne altitude situee au pied du sommet d'Anjanaharibe "Nord", elev. 1407m, 14°18'16"S, 49°18'52"E, 22 November 2006, *Rakotovao et al. 3495* (MO, P, TAN); Andapa, Doany, Anjialavahely, Antsahabalika, situe a 10km vol d'oiseau au Nord d'Anjalava, elev. 1293m, 14°13'55"S, 49°22'42"E, 26 February 2006, *Ravelonarivo et al. 1623* (MO, P, TAN); Andapa, Anjialavabe, Ankiakabe, Foret humide d'Antsahaberaoka, elev. 957m 14°09'46"S, 49°22'34"E, 19 February

2007, *Razakamalala et al. 3282* (MO). **Diana region**: Reserve Naturelle Integrale de Tsaratanana, Beangona, Antsahabe River, Fok. Ambinany Beangona, Fir. Marotolana, Fiv. Ambanja, elev. 700-1100m, 14°00'45"S, 48°46'40"E, 25 July 2000 *Antilahimena et al. 497* (MO); Antsiranana, Reserve Naturelle Integrale de Tsaratanana, Valley of Antsahamanara River, Fir. Marotolana, Fiv. Ambanja, elev. 1100m, 14°02'51"S, 48°47'34"E, 30 November 2000, *Antilahimena et al. 683* (MO). **Sofia region**: Fiv. Bealanana, Commune, Mangindrano, Forêt de Befosa, a 4km du campement, aux environs des rivieres Ambinantelo, elev. 1214m, 14°12'47"S, 48°58'21"E, 18 February 2003, *Razafitsalama et al. 206* (MO, P, TAN, TEF).

Trilepisium borealis S. Kelley Sp. Nov. TYPE: Madagascar. Diana: Mosorolava, Ampombiantambo, Forêt d'Antsoroby, elev. 75m, 12°42'13"S, 48°58'12"E, 23 September 2007, *Ratovoson et al. 1352* (Holotype: MO!, Isotype; P!, CNARP not seen, TAN not seen).

Diagnosis. Trilepisium borealis is distinguished from all species of *Trilepisium* by its semi-coriaceous leaves, very visible reticulate tertiary and higher venation on the abaxial leaf surface, and pubescent calyx. The pubescence of this species (0.1mm) is noticeably shorter than that of *T. andapensis* (0.5mm). Additionally, it lacks the dark red calyx of *T. andapensis*.

Tree to 16m, twigs ca. 2 mm in diameter, fissured, persistent leaf scars. Leaves not heteromorphic, leaf blades elliptic, 3.5-6.5 cm long, 2-3.5 cm wide, the texture semi-coriaceous, the apex acuminate, the acumen ca. 5 mm long, the base cuneate to rounded, the margin entire, the abaxial surface glabrous, the adaxial surface glabrous, the venation brochidodromous, the midvein slightly raised on adaxial surface, major secondary veins 4-5, higher order veins reticulate, prominent and dark on abaxial surface; petioles 0.5-1 cm long. Inflorescence an umbel, the pedicels 0.5 mm long, minutely pubescent hairs >0.1 mm long; calyx absent; staminate flowers, the stamens numerous; pistillate flowers, corolla 5 lobed, fused at base, minutely pubescent, the hairs >0.1 mm long, fused at base, styles 2, free; stigma 1, clavate. Mature fruits unknown. Fruits drupaceous, obovoid, the exocarp glabrous, the endocarp stony.

Distribution and habitat. Trilepisium borealis is found in dry forests in the extreme north of Madagascar eastward to northern littoral forests. Collected specimens range in elevation from 13m to 430m.

IUCN Red List Category. Trilepisium borealis has an Extent of Occurrence (EOO) just less than 1000km^2, below the threshold for Endangered (EN) (IUCN, 2012). While some individuals were found within protected areas, all locations are experiencing significant levels of deforestation as a threat to habitat.

Discussion. This species is not easily confused with any other species within the genus. Unlike other species of *Trilepisium*, *T. borealis* has semi-coriaceous leaves with non-revolute margins. These leaves have the thickness and apparent pliability expected from coriaceous leaves, however they also are noticeably thinner and more brittle, possessing characteristics both coriaceous and chartaceous. Additionally, the thick, reticulate venation on the abaxial surface easily distinguishes this species from others within the genus.

Etymology. *Trilepisium borealis* derives its name from the Latin for North. This species encompasses all the most northern collections from Madagascar.

Paratypes. MADAGASCAR. **Diana region**: Fiv. Antsiranana II, environ de Réserve Spéciale d'Ankarana, a 80km au Sud d'Antsiranana par route RN6, a 4 ou 5 km a l'Est de l'ancien chantier du Colas, tout pres du village dAmbalabao, Forêt de Mahory, elev. 369-432m, 12°49'23"S, 49°16'26"E, 6 February 1996, *Andrianantoanina & Bezara 941* (MO); Fiv. Antsiranana II, Ramena, Andavakoera, Forêt de Marovalavelo, 3km a l'Ouest du village d'Andavakoera, elev. 185m, 12°20'12"S, 49°21'35"E, 24 February 2007, *Guittou 410* (MO, CNARP, P, TAN); Sahafary, a 12km a l'Est de la RN6, elev. 277m, 12°36'28"S, 49°27'24"E, 15 December 2004, *Rakotonandrasana 895* (MO, CNARP, P, TAN); Fiv: Antsiranana II, Mahavanona, Montagne de Francais, Ampitiliantsambo, elev. 221m, 12°23'17"S, 49°23'00"E, 10 June 2004, *Ramananjanahary et al. 6* (MO, CNARP, P, TAN). **Sava**

region: Sous prefecture: Vohemar, Commune: Nosibe, Fok: Anjiabe, Village: Anaborano, Forêt d'Analabe, elev. 13m, 13°04'06", 49°51'12"S, 9 December 2004, *Manjakahery & Sola 78* (MO, P, TEF).

Acknowledgments. I would like to thank Drs. Dunlap, Miller, and Muchhala for their guidance through the production of this thesis. I would also like to thank Drs. Lowry and Miller for their assistance in learning how to distinguish morphological characters and differences, Dr. Miller for his assistance in editing this manuscript, and Drs. Lowry and Phillipson for their assistance with the ecology and geography of Madagascar. This paper is partial fulfillment of requirements for an M.S. degree at the University of Missouri-St. Louis.

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Figure1: Type specimen for *Trilepisium littoralis*, Rabevohitra 5129 (MO)

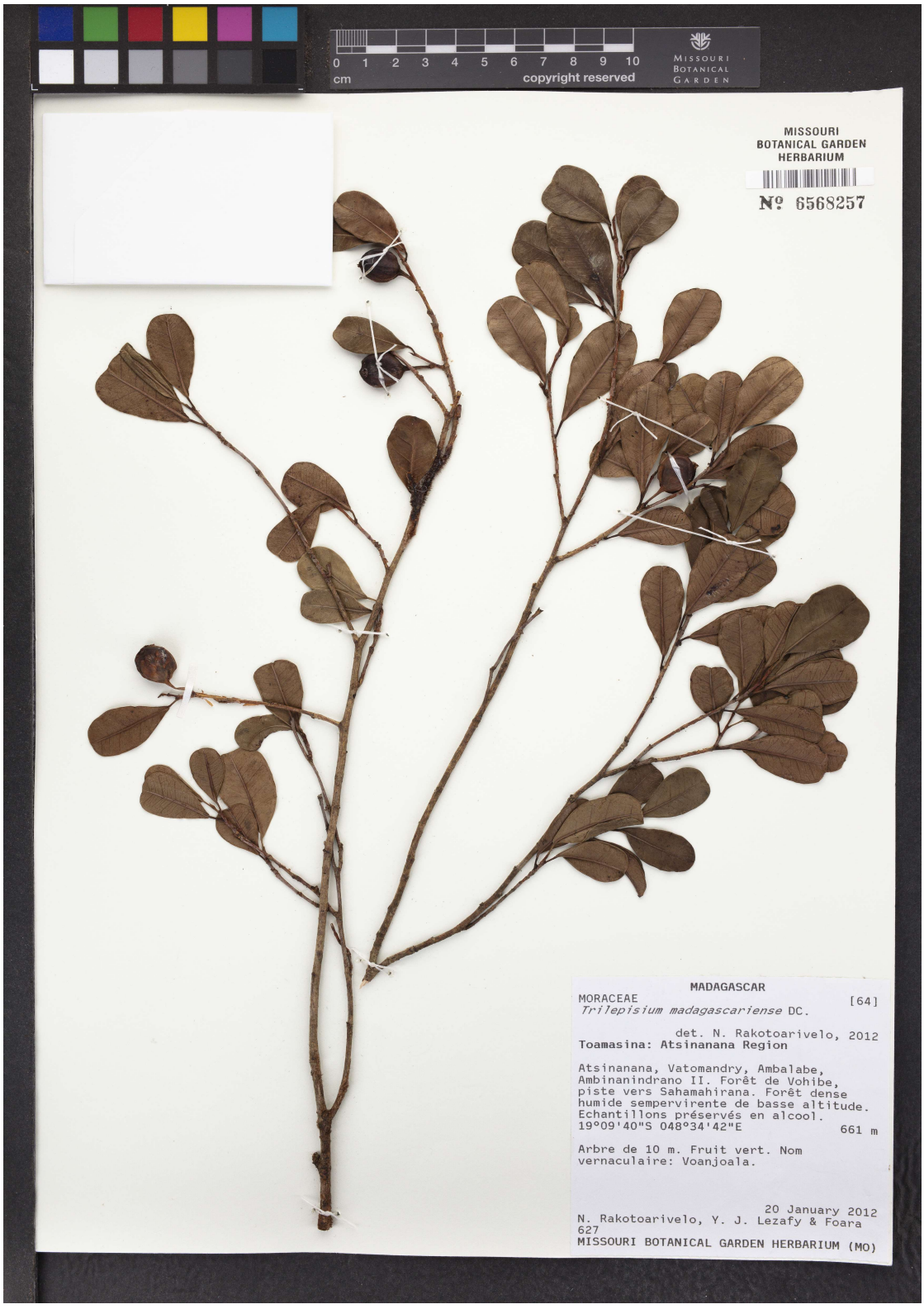


Figure 2: Type specimen for *Trilepisium vohibensis*, Rakotoarivelo 627 (MO)

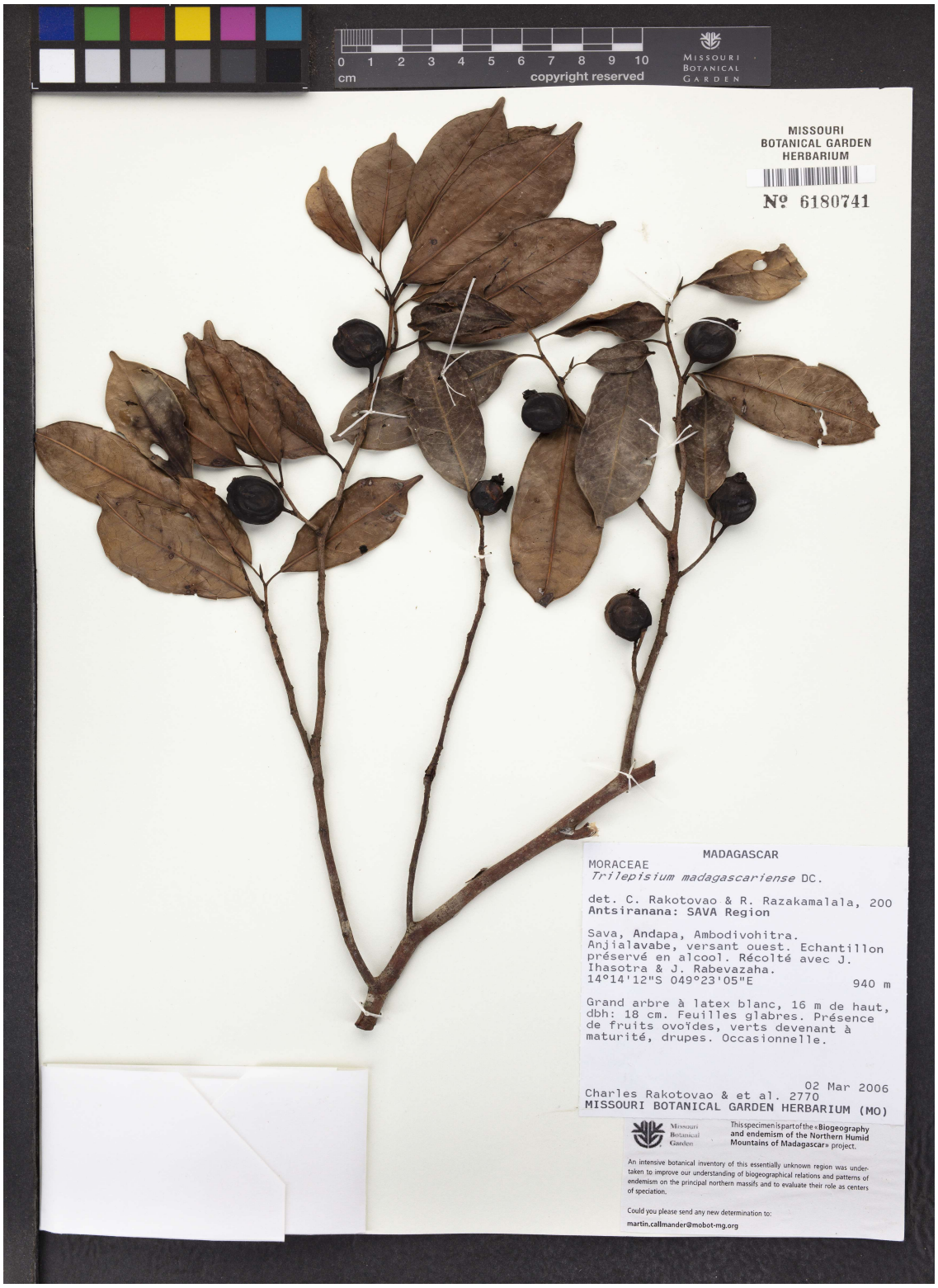


Figure 3: Type specimen for *Trilepisium andapensis*, Rakotovao 2770 (MO)

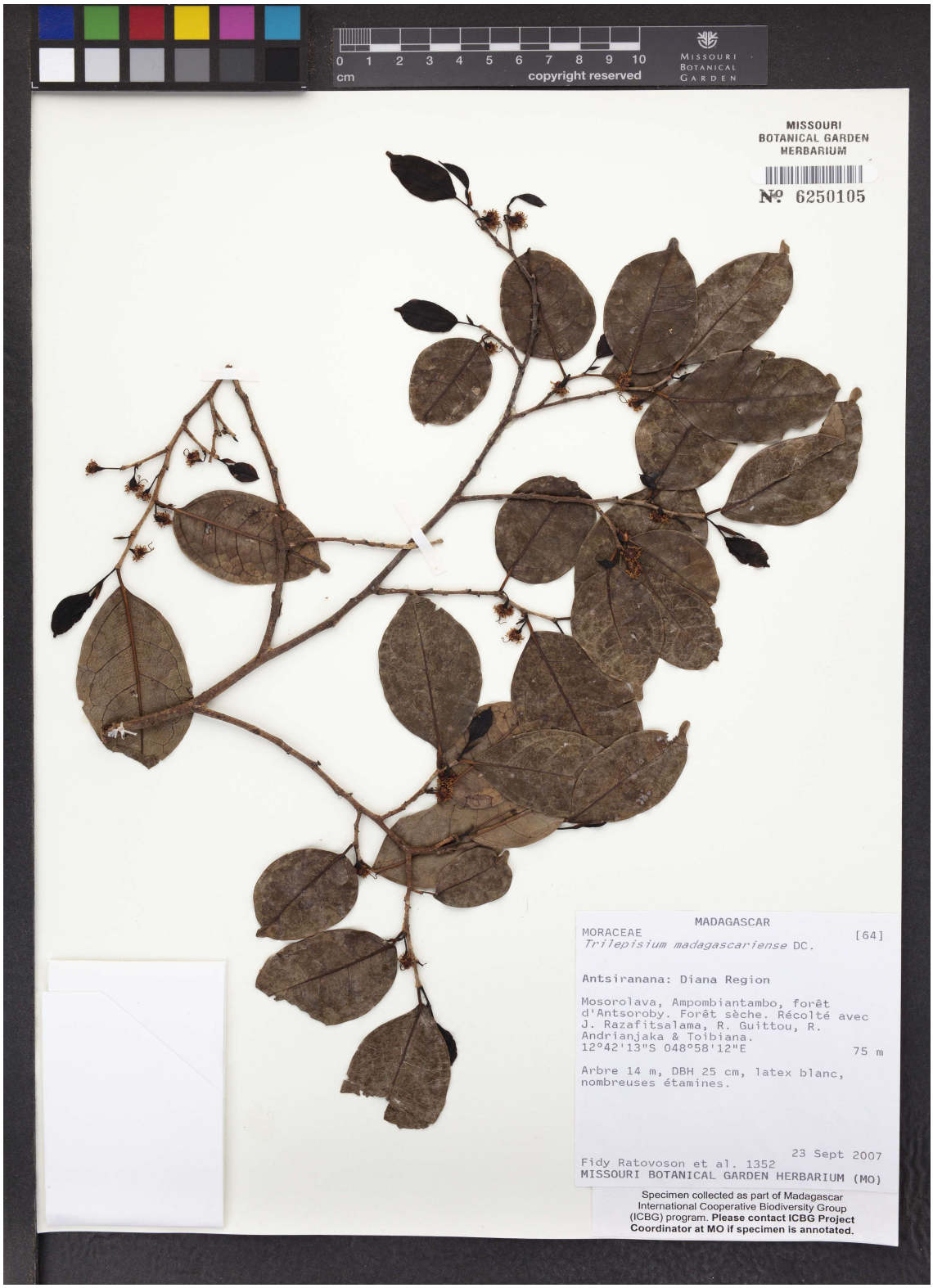
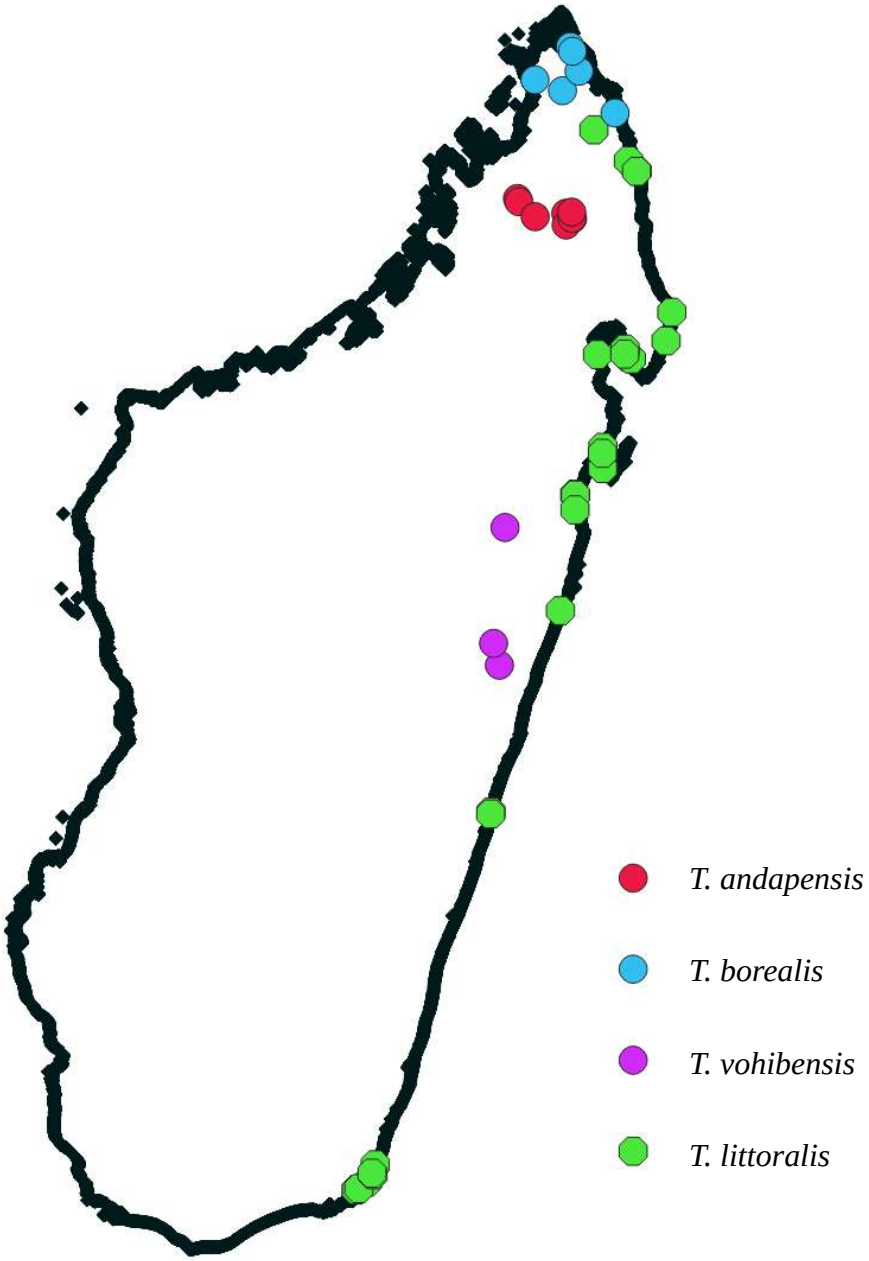


Figure 4: Type specimen for *Trilepisium borealis*, Ratovoson 1352 (MO)

Appendix A

Figure 5: Map of occurrence for the four newly described species in Madagascar: *T. littoralis*, *T. vohibensis*, *T. andapensis*, and *T. borealis*. Mapped collection records are from herbarium specimens housed at the Missouri Botanical Garden.



Appendix B

Table 1: Table of species level morphological characters

Species	T. madagascariense	T. littoralis	T. vohibensis	T. andapensis	T. borealis
Max Height	20-25m(-40m)	20 (22)m	16m	18m	16m
Leaf Scars	varies	absent	absent	absent	persistent
Leaf Shape	elliptic or obovate	obovate	obovate	obovate	elliptic
Widest Point	varies	just below apex	at apex	about ¼ below apex	midpoint
Leaf Texture	coriaceous or subcoriaceous	coriaceous	coriaceous	coriaceous	chartaceous
Max. Leaf Width	(0.5-)1.5-6.5(-8)cm	1-4cm	1.5-2cm	2-4.5(-6.5)cm	2-3.5cm
Mean Max Leaf Width		2.6cm	1.8cm	3.8cm	3cm
Max. Leaf Length	(1-)2-12(-18)	3-10cm	2-4cm	6-10(-14)cm	3.5-6.5cm
Mean Max Leaf Length		6.8cm	3.5cm	8.8cm	4.8cm
Leaf Apex	caudate, acuminate, rounded	rounded or mucronulate	truncate	acuminate, acumen >1cm	acuminate, acumen 5mm
Leaf margin	varies	strongly	slightly revolute	flat	flat
Secondary Veins	4-10(-12)	4-6	3-4(-5)	5-6	4-5
Tertiary Venation	varies	ramified	ramified	ramified	reticulate
4+ Venation	varies	reduced	reduced	ramified	reticulate
Petioles	3-15mm	5-10mm	2-4(-6)mm	7-10(-13)mm	5-10mm
Stipules	2-12mm	3-7mm	1-3mm	5mm	3-5mm
Inflorescence width	(2-)5-8(-10)mm	4-8mm	flowers unknown	mature flowers unknown	6-9mm
Pedicel	2-12mm	sessile	unknown	sessile	5mm
Pubescence	absent or present	absent	present, hairs >0.5mm	absent	present, hairs >0.1mm
Pistillate Corolla		white	unknown	dark red	color unknown
Styles	2 or 3	2	unknown	2	2
Max Fruit Width	1.5-15(-25)mm	4-12mm	10-15mm	15-20mm	unknown
Max Fruit Length	8-25(-30)mm	8-20mm	15-20mm	35-40mm	unknown

Table 2: Specimen data for *T. litoralis*

MO number	Rabevohitra 5129	Heritiana RHS 514	Razanatsoa 649	Rabehevitra 1061	Rabenantoandro 484
Other locations	P, TEF		P	P, TEF	
Height	12m	6m	10m	unknown	16m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	1-3mm	2-5mm	3-5mm	2-6mm	2-4mm
Leaf Scars	absent	absent	absent	absent	absent
Leaf Shape	obovate	obovate	obovate	obovate	obovate
Widest Point	just below apex	just below apex	just below apex	just below apex	just below apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	4cm	2.5cm	3cm	4cm	2cm
Max. Leaf Length	7cm	5.5cm	7cm	10cm	5.5cm
Leaf Apex	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate	rounded	rounded or mucronulate
Leaf margin	strongly revolute	strongly revolute	strongly revolute	strongly revolute	strongly revolute
Secondary Veins	4-6	4-5	4-5	5-6	4-5
Tertiary Venation	ramified	ramified	ramified	ramified	ramified
4+ Venation	reduced	reduced	reduced	reduced	reduced
Petioles	8-10mm	5-8mm	5-7mm	5-10mm	5-8mm
Stipules	4-7mm	absent	4mm	6-7mm	5mm
Inflorescence width	4-8mm	unknown	unknown	unknown	unknown
Pedicel	sessile	unknown	unknown	unknown	unknown
Pubescence	absent	unknown	unknown	unknown	unknown
Pistillate Corolla	white	unknown	unknown	unknown	unknown
Styles	2	unknown	unknown	unknown	unknown
Max Fruit Width	unknown	immature fruit	18mm	immature fruit	8mm
Max Fruit Length			20mm		19mm
notes		green fruit	red fruit		glossy upper surface

MO number	Rahajasoa 519	Raholivelo 140	Rabevohitra 3943	Schatz 3630	S.F. 16_538
Other locations	TAN				P, TEF
Height	10m	8m	18m	12m	unknown
twigs	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	2-5mm	2-5mm	2-4mm	1-3mm	1-2mm
Leaf Scars	absent	absent	absent	absent	absent
Leaf Shape	obovate	obovate	obovate	obovate	obovate
Widest Point	just below apex	just below apex	just below apex	just below apex	just below apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	2.3cm	3cm	2.5cm	2.5cm	3cm
Max. Leaf Length	6cm	8cm	5.5cm	7.5cm	7cm
Leaf Apex	rounded or mucronulate	rounded	rounded	rounded or mucronulate	rounded or mucronulate
Leaf margin	strongly revolute	strongly revolute	strongly revolute	strongly revolute	strongly revolute
Secondary Veins	5-6	4-5	4-6	4	4-5
Tertiary Venation	ramified	ramified	ramified	ramified	ramified
4+ Venation	reduced	reduced	reduced	reduced	reduced
Petioles	5-8mm	5-7mm	5-8mm	7-10mm	5-7mm
Stipules	3-4mm	5-6mm	3-5mm	4-7mm	absent
Inflorescence width	unknown	unknown	unknown	unknown	unknown
Pedicel	unknown	unknown	unknown	unknown	unknown
Pubescence	unknown	unknown	unknown	unknown	unknown
Pistillate Corolla	unknown	unknown	unknown	unknown	unknown
Styles	unknown	unknown	unknown	unknown	unknown
Max Fruit Width	unknown	unknown	unknown	immature fruit	8mm
Max Fruit Length					16mm
notes					Fotsydity

MO number	Raholivelo 255	Rabevohitra 4339	S.F 12_581	Randrianaivo 704	Vasey 119
Other locations		TEF	P, TEF		TAN
Height	15m	20m	unknown	15m	13m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	2-5mm	2-5mm	2mm	2-7mm	1-3mm
Leaf Scars	absent	absent	absent	persistent	persistent
Leaf Shape	obovate	obovate	obovate	obovate	obovate
Widest Point	just below apex	just below apex	just below apex	just below apex	just below apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	3cm	2.5cm	2cm	2cm	5cm
Max. Leaf Length	8cm	6cm	6cm	6cm	4cm
Leaf Apex	rounded or mucronulate	rounded	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate
Leaf margin	strongly revolute	strongly revolute	strongly revolute	strongly revolute	strongly revolute
Secondary Veins	5-6	4-5	4-6	4-6	4-5
Tertiary Venation	ramified	ramified	ramified	ramified	ramified
4+ Venation	reduced	reduced	reduced	reduced	reduced
Petioles	7-10mm	8-9mm	5-7mm	5-7mm	6-8mm
Stipules	3-5mm	5-6mm	absent	3-4mm	3mm
Inflorescence width	unknown	unknown	unknown	budding flowers	unknown
Pedicel	unknown	unknown	unknown	sessile	
Pubescence	unknown	unknown	unknown	absent	
Pistillate Corolla	unknown	unknown	unknown		
Styles	unknown	unknown	unknown		
Max Fruit Width	fruits in poor shape	8mm	unknown	unknown	immature fruits
Max Fruit Length		12mm			
notes					

MO number	Rabevohitra 4953	S.F. 16_930	Rabenantoandro 917	Ralimanana 89	Raholivelo 136
Other locations	P, TEF		TEF	P, TAN	
Height	22m	unknown	18m	14m	18m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	2-4mm	2mm	2-7mm	1-3mm	2-3mm
Leaf Scars	absent	absent	absent	absent	absent
Leaf Shape	obovate	obovate	obovate	obovate	obovate
Widest Point	just below apex	just below apex	just below apex	just below apex	just below apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	1.5cm	2.5cm	3cm	3cm	1cm
Max. Leaf Length	4cm	7.5cm	7.5cm	8cm	5.5cm
Leaf Apex	rounded or mucronulate	rounded	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate
Leaf margin	strongly revolute	strongly revolute	strongly revolute	strongly revolute	strongly revolute
Secondary Veins	4-6	4-6	5-6	5-6	4-6
Tertiary Venation	ramified	ramified	ramified	ramified	ramified
4+ Venation	reduced	reduced	reduced	reduced	reduced
Petioles	5-6mm	5-6mm	5-8mm	7-10mm	5-9mm
Stipules	4mm	5mm	3-4mm	4mm	6-7mm
Inflorescence width	unknown	most of flowers	unknown	budding flowers	unknown
Pedicel		missing		sessile	
Pubescence				absent	
Pistillate Corolla				present	
Styles		2		2	
Max Fruit Width	unknown	unknown	8mm	unknown	6mm
Max Fruit Length			12mm		12mm
notes		Fotsydity			

MO number	Rahajasoa 962	Rahajasoa 957	Andrianarivelo 36	Dorr 3405	Ranaivojaona 441
Other locations			P, TEF	TAN	
Height	16m	9m	7m	unknown	8m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	1-3mm	2-6mm	2-5mm	3mm	2-4mm
Leaf Scars	absent	absent	absent	persistent	absent
Leaf Shape	obovate	obovate	obovate	obovate	obovate
Widest Point	just below apex	just below apex	just below apex	just below apex	just below apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	3cm	1.5cm	1.5cm	2cm	3cm
Max. Leaf Length	8.5cm	5cm	5cm	6cm	7cm
Leaf Apex	rounded or mucronulate	rounded	rounded or mucronulate	rounded	rounded or mucronulate
Leaf margin	strongly revolute	strongly revolute	strongly revolute	strongly revolute	strongly revolute
Secondary Veins	4-6	4-5	4-5	4-5	4-5
Tertiary Venation	ramified	ramified	ramified	ramified	ramified
4+ Venation	reduced	reduced	reduced	reduced	reduced
Petioles	6-10mm	5-8mm	5-7mm	5-7mm	6-8mm
Stipules	7mm	6mm	4-5mm	absent	3mm
Inflorescence width	unknown	unknown	unknown	unknown	unknown
Pedicel					
Pubescence					
Pistillate Corolla					
Styles					
Max Fruit Width	7mm	6mm	immature fruits	4mm	immature fruits
Max Fruit Length	10mm	8mm		11mm	
notes				in swamp	

MO number	McPherson 14130	McPherson 14235	Ratovoson 1838	Ramananjanahary 412	Dumetz 1128
Other locations	TAN	TAN	P, TAN	P, TAN	TAN
Height	7m	12m	10m	4m	20m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	2-4mm	2-5mm	2-5mm	2-4mm	2-4mm
Leaf Scars	absent	absent	absent	absent	absent
Leaf Shape	obovate	obovate	obovate	obovate	obovate
Widest Point	just below apex	just below apex	just below apex	just below apex	just below apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	1.5cm	2.5cm	3cm	3cm	3.5cm
Max. Leaf Length	5cm	6cm	7.5cm	10cm	8cm
Leaf Apex	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate
Leaf margin	strongly revolute	strongly revolute	strongly revolute	strongly revolute	strongly revolute
Secondary Veins	4-5	4-5	4-5	5-6	4-5mm
Tertiary Venation	ramified	ramified	ramified	ramified	ramified
4+ Venation	reduced	reduced	reduced	reduced	reduced
Petioles	5-6mm	6-7mm	5-9mm	8-11mm	5-9mm
Stipules	3-4mm	6mm	6-7mm	4-6mm	4-5mm
Inflorescence width	5-6mm	unknown	unknown	unknown	unknown
Pedicel	sessile				
Pubescence	absent				
Pistillate Corolla	white				
Styles	2				
Max Fruit Width		immature fruits	8mm	10mm	immature fruits
Max Fruit Length			20mm	17mm	
notes					

MO number	Faliniaina 90	Rabenantoandro 1825	Randrianaivo 1982	Rabevohitra 4708	Rabenantoandro 1171
Other locations	TEF		P, TAN	P, TEF	
Height	12m	18m	12m	10m	10m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	2-3mm	2-5mm	2-4mm	2-6mm	2-4mm
Leaf Scars	persistent	persistent	absent	absent	persistent
Leaf Shape	obovate	obovate	obovate	obovate	obovate
Widest Point	just below apex	just below apex	just below apex	just below apex	just below apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	3.5cm	3cm	2cm	2.5cm	1.5cm
Max. Leaf Length	10cm	7.5cm	6.5cm	6.5cm	6.5cm
Leaf Apex	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate	rounded or mucronulate
Leaf margin	strongly revolute	strongly revolute	strongly revolute	strongly revolute	strongly revolute
Secondary Veins	4-6	4	4-5	4-5	4-5
Tertiary Venation	ramified	ramified	ramified	ramified	ramified
4+ Venation	reduced	reduced	reduced	reduced	reduced
Petioles	6-9mm	8-9mm	5-9mm	5-8mm	5-7mm
Stipules	5-7mm	3-4mm	3-4mm	5-6mm	4-7mm
Inflorescence width	unknown	unknown	unknown	unknown	unknown
Pedicel					
Pubescence					
Pistillate Corolla					
Styles					
Max Fruit Width	9mm	immature fruit	12mm	8mm	8mm
Max Fruit Length	15mm		18mm	18mm	12mm
notes		Beronono	Lipaty	Beronono	

Table 3: Specimen Data for *T. vohibensis*

MO number	Rakotoarivelo 627	Andriatsiferana 2560
Other locations	P, TAN	P, TAN
Height	10m	16m
twigs	glabrous	glabrous
twig diameter	2-3mm	3-4mm
Leaf Scars	absent	absent
Leaf Shape	obovate	obovate
Widest Point	at apex	at apex
Leaf Texture	coriaceous	coriaceous
Max. Leaf Width	2cm	1.5cm
Max. Leaf Length	4cm	3cm
Leaf Apex	truncate	truncate
Leaf margin	slightly revolute	slightly revolute
Secondary Veins	3-4(-5)	3-4
Tertiary Venation	ramified	ramified
4+ Venation	reduced	reduced
Petioles	2-4(-6)	2-4
Stipules	1-3mm	absent
Inflorescence width	flowers unknown	flowers unknown
Pedicel	unknown	unknown
Pubescence	unknown	unknown
Pistillate Corolla	unknown	unknown
Styles	unknown	unknown
Max Fruit Width	15mm	10mm
Max Fruit Length	20mm	15mm
notes		

Table 4: Specimen Data for *T. andapensis*

MO number	Rakotovao 2770	Antilahimena 683	Antilahimena 497	Razakamalala 3282	Ravelonarivo 1623	Rakotovao 3495
Other locations	P, TAN			P, TAN	P, TAN	P, TAN
Height	16m	17m	20m	12m	9m	14m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	2-5mm	2-3mm	2-4mm	2-5mm	2-4mm	2-5mm
Leaf Scars	absent	absent	persistent	absent	persistent	persistent
Leaf Shape	Obovate	obovate	obovate	obovate	obovate	obovate
Widest Point	¼ from apex	¼ from apex	¼ from apex	¼ from apex	¼ from apex	¼ from apex
Leaf Texture	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous
Max. Leaf Width	3.5cm	3.7cm	2.5cm	4.5cm	3.5cm	2.5cm
Max. Leaf Length	7.5cm	10cm	6cm	9.5m	7cm	9cm
Leaf Apex	acuminate, 5mm	acuminate, 8mm	acuminate, 3-4mm	acuminate, 4-5mm	acuminate, 5-6mm	acuminate, 3-5mm
Leaf margin	entire, slightly revolute	entire, slightly revolute	entire, flat	entire, slightly revolute	entire, flat	entire, slightly revolute
Secondary Veins	5-6	5-6	5	5-6	5	5-6
Tertiary Venation	ramified	ramified	ramified	ramified	ramified	ramified
4+ Venation	ramified	ramified	ramified	ramified	ramified	ramified
Petioles	7-10mm	8-10mm	7-9mm	6-10mm	7-9mm	8-10mm
Stipules	5mm	5-8mm	4-5mm	5mm	4mm	5mm
Inflorescence width	unknown	unknown	immature, emerging	unknown	unknown	unknown
Pedicel			sessile			
Pubescence			present, hairs >0.5mm			
Pistillate Corolla			present			
Styles			2			
Max Fruit Width	18mm	immature fruit	not present	15mm	20mm	immature fruit
Max Fruit Length	25mm			29mm	35mm	
notes			dark red calyx			

MO number	Rakotovao 3450	Razafitsalma 206
Other locations	G, P, TAN	P, TAN, TEF
Height	13m	
twigs	glabrous	glabrous
twig diameter	3-5mm	2-5mm
Leaf Scars	persistnet	absent
Leaf Shape	obovate	obovate
Widest Point	¼ from apex	¼ from apex
Leaf Texture	coriaceous	coriaceous
Max. Leaf Width	4cm	6.5cm
Max. Leaf Length	8cm	14cm
Leaf Apex	acuminate, 5-9mm	
Leaf margin	entire, slightly revolute	entire, slightly revolute
Secondary Veins	5-6	5-6
Tertiary Venation	ramified	ramified
4+ Venation	ramified	ramified
Petioles	9-10mm	10-13mm
Stipules	5mm	7mm
Inflorescence width	unknown	unknown
Pedicel		
Pubescence		
Pistillate Corolla		
Styles		
Max Fruit Width	19mm	18mm
Max Fruit Length	30mm	23mm
notes		

Table 5: Specimen Data for *T. borealis*

MO number	Ratovoson 1352	Ramananjanahary 6	Manjakahery 78	Rakotonandrasana 895	Guittou 410	Andrianantoanina 941
Other locations	CNARP, P, TAN	CNARP, P, TAN	P, TEF	CNARP, P, TAN	CNARP, P, TAN	
Height	14m	7m	unknown	10m	10m	12m
twigs	glabrous	glabrous	glabrous	glabrous	glabrous	glabrous
twig diameter	3-4mm	1-4mm	3-5mm	1-3mm	1-4mm	
Leaf Scars	persistent	persistent	persistent	persistent	persistent	persistent
Leaf Shape	elliptic	elliptic	elliptic	elliptic	elliptic	elliptic
Widest Point	midpoint	midpoint	midpoint	midpoint	midpoint	midpoint
Leaf Texture	chartaceous	chartaceous	chartaceous	chartaceous	chartaceous	chartaceous
Max. Leaf Width	3cm	3cm	2.5cm	3cm	3.5cm	3cm
Max. Leaf Length	6.5cm	4.5cm	3.5cm	5cm	4.5cm	5cm
Leaf Apex	acuminate, 4-5mm	acuminate, 2-4mm	acuminate, >5mm	acuminate, >5mm	acuminate, 4-7mm	
Leaf margin	entire, flat	entire, flat	entire, flat	entire, flat	entire, flat	entire, flat
Secondary Veins	4-5	4-6	4-7	4-8	4-9	4-10
Tertiary Venation	reticulate	reticulate	reticulate	reticulate	reticulate	reticulate
4+ Venation	reticulate	reticulate	reticulate	reticulate	reticulate	reticulate
Petioles	5-6mm	5-7mm	5-6mm	6-10mm	6-10mm	6-8mm
Stipules	3mm	3-5mm	3-4mm	unknown	3mm	3-5mm
Inflorescence width	6-9mm	unknown	unknown	unknown	unknown	unknown
Pedicel	5mm					
Pubescence	present, hairs >0.1mm					
Pistillate Corolla	color unknown					
Styles	2					
Max Fruit Width	unknown				immature fruit	immature fruit
Max Fruit Length	unknown					
notes						