A PRELIMINARY MONOGRAPH OF THE FAMILY TRIGONIACEAE

by

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Abstract

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by

Eduardo Lleras

Advisor: Professor Ghillean T. Prance

The Angiosperm family Trigoniaceae is Amphi-Pacific Tropical in distribution. It is found principally in riverine and gallery forests in the Neotropics where it is represented by the genus Trigonia with 24 species. In the Paleotropics, it is found in primary forest, and is represented by the monotypic genera Trigoniastrum in Malaysia, and Humbertodendron in Madagascar.

The history of the family is surveyed and its taxonomic position is discussed both historically and in light of present evidence.

Anatomical and palynological information is included, and the anatomy of Humbertodendron is interpreted for the first time.

Geography and Ecology are discussed, and for Trigonia, interpreted according to the current views on Pleistocene forest refuges.

Possible evolutionary trends within the family are proposed.

Twenty four species are treated in Trigonia and the following new species are described: Trigonia bracteata, T. candelabra, T. prancei, T. reticulata and T. rotundifolia.

Keys to the genera, species and varieties are provided. The study is documented by representative collections of more than 2000 herbarium specimens

borrowed from 22 herbaria.

The genus Euphronia is removed from the family and returned to the Vochysiaceae.

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The new taxa and new combinations included in the following pages indicate my intent for future publication; their appearance in this thesis is not intended to constitute formal publication under the International Code of Botanical Nomenclature.

INTRODUCTION

The present study includes all the known Trigoniaceae, both Neotropical and Paleotropical. Although the family is primarily Neotropical, it is represented by two monotypic genera found in Malaysia (Trigoniastrum) and Madagascar (Hunbertodendron). The Neotropical genus, Trigonia is represented by 24 species of treelets, shrubs, or scandent shrubs, and ranges from the southernmost portion of Mexico to the south of Brazil and eastern Paraguay.

As will be seen in the chapter on taxonomic history, no comprehensive treatment has been undertaken for the family in the past hundred years; Warming's treatment for Flora Brasiliensis was published in 1875. In his monograph on the Trigoniaceae, Warming recognized only two genera, one of which is here returned to the Vochysiaceae. In the time since 1875, two new genera have been recognized as belonging in the family, and several new species have been published.

This paper was undertaken in an attempt to delimit the family, and to determine taxonomically the number of species known at present. Although Warming had a good working knowledge of the group, the small amount of material available at the time of his publication led to errors that can now be corrected. His incomplete knowledge of type material has also led to a duplication of names for taxa that are morpholigically indistinguishable. This treatment is a preliminary survey of the Trigoniaceae, and is necessarily the first step in any comprehensive study of this family.

The taxonomic position of the genus Euphronia has been reconsidered during the course of this study, as is explained in detail later. Although it has been excluded from the Trigoniaceae and returned to the Vochysiaceae, it is treated as part of this dissertation.

TAXONOMIC HISTORY

In his Histoire des Plantes (1775), Aublet described the genus Trigonia in which he included two species, Trigonia villosa and T. laevis. He placed these species in Decandria Monogynia (10 stamens, 1 ovary) based on the Linnean system of classification. Lamarck (1786), erroneously described a species of Trigonia as Croton eriospermum, based on fruit characters.

De Jussieu (1789) placed Trigonia near Malpighia in the Malpighiaceae. The only subsequent treatments worthy of note until 1824 were the publications of two illegitimate generic names for Trigonia: Hoeffnagelia, published by Necker (1790) in Elementa Botanica, and Sprengel's publication of Nuttallia in 1821.

De Candolle (1824) in his treatment for the Prodromus placed Trigonia in the Hippocrateaceae. This position was accepted by Cambessèdes in 1829. In 1825 Martius and Zuccarini proposed Euphronia, a genus which was placed in Kunth's family Spiraeaceae; this assignment was ignored by later authors, or at least by those who have undertaken systematic treatments of the Trigoniaceae. Vellozo, in 1829, published the last superfluous name for Trigonia, Mainea.

The first application of the familial name, Trigoniaceae, was by Martius (1835), who published the name without a description in his Conspectus. The name was taken up, and again published without a description by Endlicher in 1840 in his Genera Plantarum, and was validated the following year when he provided a description of the family in his Enchiridion Botanicum.

Robert Schomburgk (1847) published the genus Lightia, based on material from his own collections. Lightia proved to be a synonym for Euphronia. His name was not only unnecessary, but was also invalidated by his prior use of the

name Lightia (1844) as a generic epithet for what is now known as Herrania in the Sterculiaceae. Schomburgk placed his second Lightia in the Vochysiaceae. Although illegitimate, Lightia has persisted to the present day in the literature in spite of occasional references to the correct name.

The only author to treat the Trigoniaceae as a separate family in literature appearing between 1841 and 1875 was Grisebach (1849) in a partial revision of Trigonia. Agardh (1858) placed Trigonia in the Polygalaceae, a view that was followed by Miquel when he published the Malaysian genus Trigoniastrum in 1862 and thus showed that Trigoniaceae is represented on more than one continent. Wallich, in 1832, listed a specimen of Trigoniastrum under the name Isopteris penangiana, but this name was never validly published.

Bentham and Hooker (1867) and Baillon (1874) placed both Trigonia and Lightia in the Vochysiaceae, and retained Trigoniastrum in the Polygalaceae.

The Trigoniaceae were finally established as a family with Warming's monographic treatment for Flora Brasiliensis (1875). He treated two genera in the family, Trigonia and Lightia, and provided a detailed discussion of the reasons for regarding the group as a separate family. Warming's treatment was the most comprehensive study of the family until then, and has remained so until the present. Although he studied in detail only the Brazilian species, he listed all those known until then, recognizing 26 species in Trigonia, of which 10 were then new, and 2 species in Lightia, one of which was new. He also established three sections within Trigonia, based on the ultimate arrangement of the flowers: Racemosae, Cymosae and Cincinnatae. He recognized that these sections were purely artificial, and did not reflect relationships within the genus. In the present treatment these sections are considered unnecessary and are not given taxonomic recognition.

In 1895 and 1896 there were two important publications on the Trigoniaceae. Chodat (1895) tranferred Trigoniastrum into the family, and suggested that Lightia did not belong there. In the following year, Barth, one of Chodat's students, gave anatomical support to Chodat's suggestions.

Chodat's conclusions were only partially followed in later treatments; thus Trigoniastrum was definitely recognized as trigoniaceous (although not in time to be considered so by Petersen in the first edition of Engler & Prantl, 1896), but Lightia remained a member of the family, and has remained so until the present treatment.

Chodat also established three tribes within the Trigoniaceae, to accommodate the three known genera. The tribes were Trigoniae, Trigoniastrae, and Lightiae (sic). The first two are considered unnecessary in the present work, and Lightia (i.e. Euphronia) is tranferred to Vochysiaceae.

No detailed study of the family has been made in the present century, although it has been treated in several local revisions, in all cases including only one genus. Thús the ónly important occurrence between 1897 and the present was Leandri's (1949) description of Humbertiodendron (Humbertodendron) for the Flora of Madagascar, which added another continent to the known distribution range of the family.

Trigonia was treated by Standley (1924) for North American Flora, by Stafleu (1951) for the Flora of Suriname, by Reitz (1967) for Flora Ilustrada Catarinense, and most recently by Austin (1968) for the Flora of Panama.

Trigoniastrum was revised by Van Steenis (1949) for Flora Malesiana and by NG (1972) in Tree Flora of Malaya. Apart from the original publication in 1949, Humbertiodendron was studied by Perrier and Leandri (1955) for the Flora de Madagascar, in which they changed the orthography to Humbertodendron. This

second name is accepted here as the correct orthographic variation, based on the recommendation for botanical nomenclature according to the International Code of Botanical Nomenclature (Stafleu, 1972).

GEOGRAPHY AND ECOLOGY

The Trigoniaceae are found in the Neotropics and in the Paleotropics of Malaysia and Madagascar, with one genus occurring in each of these three geographical areas. (Fig. 1). The family is found in tropical lowlands, usually at altitudes below 500 meters above sea level. The Paleotropical genera, Trigoniastrum (Malaysia) and Humbertodendron (Madagascar) are found as elements of the tropical wet forest. Trigonia, the Neotropical genus, is known from periodically flooded riverine forests (called varzeas in Brazil), gallery forests, the edges of primary and secondary wet forests (in the ecotone with adjacent open areas) and along roadsides. Thus we have two main modes of adaptation within the family; in the Paleotropics the Trigoniaceae are actual elements of the forests, while in the Neotropics they are found in open but protected habitats.

This dual mode of adaptation is correlated with important differences in habit and dispersal mechanisms that separate the Paleotropical genera from Trigonia. Trigoniastrum and Humbertodendron are tall trees (ca 25 meters), while Trigonia spp. are treelets, shrubs, or scandent shrubs. In the Paleotropical genera the seed is dispersed with the fruit, an indehiscent tri-winged samara. This type of dispersal mechanism is fairly effective for tall trees, and permits the seeds to be dispersed a fair (but not very long) distance from the parent plant. The fruit effectively acts as a parachute, and a moderate breeze will insure adequate dispersal. In Trigonia, the fruit is a trilocular capsule that opens with progressive drying of the fruit. In the only species I have observed in fruit in the field (T. spruceana), the capsule opens at the top, so that the seeds cannot fall out. A moderate wind is

probably required to carry the seeds away from the fruit. Of the 24 species treated here in Trigonia, two have echinate trichomes on the seed and are probably limited to dispersal by water (or animals?). The other 22 species have long silky trichomes that are adequate for both wind and water dispersal. The dispersal mechanism of Trigonia can probably account for dispersal over much greater distances than that of the Paleotropical genera.

The original trigoniaceous stock was probably formed of elements that share more characters in common with present day Trigonia than with Trigoniastrum or Humbertodendron. A large number of connate stamens were probably present, the fruits were probably capsules with several villous seeds. (The seeds of Trigoniastrum and Humbertodendron are relictually villous, but these trichomes serve no apparent function, for in Trigoniastrum the seeds are reported as germinating in situ by Ng, 1972). It is probable that the pubescence on the seeds of the ancestral stock was not as functional for wind dispersal as that found in present Trigonia; it could have been much shorter and still have provided adequate dispersal for tall trees (acting as a parachute in the same manner as the fruit of the Paleotropical genera). With a progressive change in habit from tall trees to lower shrubs, a more effective dispersal mechanism was probably selected for in the ancestry of Trigonia. The leaves of the ancestral stock were probably opposite, with the alternate leaves of Trigoniastrum representing the derived condition. This can be postulated based on the presence of opposite leaves in Trigonia and Humbertodendron, and suggests an ancestral stock for these genera with opposite leaves, as the Neotropical and Paleotropical Trigoniaceae were probably separated before the ancestors of Trigoniastrum and Humbertodendron. The arborescent condition in Trigoniastrum and Humbertodendron is probably relictual, and the shrubby, vining habit of Trigonia derived.

Although the Trigoniaceae, and especially Trigonia are fairly common in some areas, the group is, with some exceptions, a poorly collected one. There is probably no one reason for this; Trigonia as a whole is found close to river banks in periodically flooded forests, and in drier areas along gallery forests. In general, species represented in gallery forests are collected more often than those found along periodically flooded river edges. These collecting practices could be due to several causes. First, gallery forests are usually botanically diverse, while there is a certain tendency to ignore riverside collections as repositories of common (probably often collected) species and therefore less worth bothering with in areas where these periodically flooded forests are found along well-travelled waterways. Thus, in many ways, the ease of access to the localities where this family is represented may account for the scarcity of material represented in herbaria. This has been recognized by present collectors, and areas that have been ignored in the past are now being sampled with very rewarding results.

Other causes may be responsible for the scarcity of collections in the family. Some species probably have very low densities. In the course of my field work in Brazil (1973), I had the opportunity to observe individuals of four species in the field. Of the four species, only one had more than one individual at any given locality.

Also during my field work, I was able to obtain seeds of one species (T. spruceana). The seeds were subjected to several different types of treatment at the research greenhouse of the New York Botanical Garden. Some seeds were cold- or heat-treated; others were placed in water at different pH (5.6, 6.0); others were planted in snad or different types of soil at different $_{p}H$ to simulate the natural conditions present at the site where they were collected. To the present, it has been impossible to break dormancy and induce germination.

The Trigoniaceae are regarded by Thorne (1972) as having an Amphi-Pacific tropical distribution. Together with Elaeocarpaceae, Chloranthaceae, and sixteen genera in other families, Trigoniaceae are what Thorne calls a group with tropical Amphi-Pacific-Madagascar distribution. The modes by which these and other families have achieved their present disjunct distribution have been the subject of much speculation. Van Steenis (1962) has postulated the existence of land-bridges across the Pacific. Others (Wolfe, 1969; Thorne, 1972) have favored the Beringian land-bridge as a more probable path for the dispersal of disjuncts. Thorne (1972) also indicates that a similar land-bridge could have existed in Antarctica that would account for groups with austral dispersal patterns. Continental Drift has also been suggested as a possible cause (eg. Raven and Axelrod, 1972, 1974), a possibility which Thorne (1972) considers as improbable.

In spite of the lack of fossil evidence, I find it possible to hypothesize a possible explanation for the disjunct distribution of the Trigoniaceae based on the current views on Continental Drift. The present views on the origin of the Angiosperms place the date for this event (or series of events) in the lower Cretaceous ca 125 million years ago (Axelrod, 1970; Raven & Axelrod, 1974). By the Middle Cretaceous (ca 110 million years) many genera and several extant families were already present. (Raven & Axelrod; 1974). Africa, South America, Antarctica, Madagascar and India were in close contact at that time, and they remained in contact until 90 to 100 million years ago, according to the current views on continental drift (Green, 1972; Raven & Axelrod, 1972; Raven & Axelrod, 1974). By the end of the mid-cretaceous, Africa and South America started to drift apart, and Madagascar and India became separated from the African main-land. Madagascar and India either started to drift apart from each other

(Raven & Axelrod, 1974) or might have remained in contact for a longer period of time (Cracraft, 1973 in Raven & Axelrod, 1974). Direct migration between Africa and South America (West Gondwanaland) was last possible between 90 and 110 million years ago, and between Africa and Madagascar (and thus India) about 100 million years ago (Raven & Axelrod, 1974).

Raven & Axelrod (1974) note that the families for which a relationship with the Trigoniaceae is suggested in this paper, Polygalaceae, Sapindaceae, Malpighiaceae, Dichapetalaceae and Vochysiaceae, all presumably migrated between Africa and South America during or prior to the Paleocene (before 54 million years ago). Of these, Dichapetalaceae more closely resemble Trigoniaceae; the basic difference in distribution is the absence of Trigoniaceae from Africa at present. A similar situation to that postulated for the above-cited families can be hypothesized for the Trigoniaceae.

If the Trigoniaceae originated in West Gondwanaland (Africa-South America), and if the initial migration occurred while the continents were still together, the ancestral stock giving origin to the extant Trigoniaceae was already present in the Upper Cretaceous. Subsequent migration into Madagascar-India probably occurred before these two areas were separated. This migration probably occurred via Africa, where the Trigoniaceae were probably present in the past. The series of climatic changes that have affected African flora, with conditions becoming progressively more arid, probably account for the extinction of the family in that continent. This case is not unique, and has been reported for many groups for which there is adequate paleobotanical evidence (Thorne, 1972; Raven & Axelrod, 1974). The climate in Africa is characterized by having severe dry periods, even in the tropical wet forests. Present day Trigoniaceae are characteristic of humid environments in which

there is no extreme dry period. If this characteristic was inherent in the family from the beginning, it would help explain their limited success and disappearance from the African mainland.

When Madagascar-India became separated from the African mainland, the Trigoniaceae that migrated into this land mass became isolated from those present in the African mainland. After a period of uncertain duration during which Madagascar and India were isolated together, and during which a certain degree of evolution probably occurred, the ancestral stocks for Humbertodendron and Trigoniastrum were separated with the separation of India from Madagascar. The hypothetical common ancestral stock that was to give rise to these two genera were trees, with (probably) opposite leaves, a few (5-6) connate stamens, and fruit in tri-winged samaras. Whether this ancestral stock had evolved most of these characters while still on the African mainland, or whether these characters were evolved on the Madagascar-India land mass is uncertain. When the Indian subcontinent came into contact with Asia, the floras of these two areas came in contact with each other, with the subsequent migration of elements (including Trigoniaceae) from one area to the other. Subsequent extinction of Trigoniaceae from the Indian subcontinent must be hypothesized.

The above hypothesis, based on Continental Drift, is not the only possible explanation for the present distribution of disjuncts in the family. Long distance dispersal may have accounted for some or all of the disjuncts. Thorne (1972) notes that of the 89 genera known to be Amphi-Pacific, 25 are known to have migrated successfully over the great distances of water. The dispersal mechanism of Trigonia, if present in the ancestral stock, makes it possible to envision long-distance dispersal by either wind or water. When I was trying to induce seeds of Trigonia spruceana to germinate, I floated some

seeds in water, in hope of breaking their dormancy. I got no such results. After three months most of the seeds used were still floating, and had absorbed little or no water, as the trichomes retained air and kept water from reaching the seed coat.

It is now believed that a series of drastic climatic changes similar to those reported for Africa took place in South America during the Pleistocene. Vuillemier-Simpson (1971), Haffer (1969) and Vanzolini (1970), using palynological and climatological data have postulated the existence of a series of alternating dry and wet periods. Palynological data obtained be van der Hammen (1966, 1974 in press, cited by Haffer, 1974) indicate that several arid conditions prevailed during the peaks of the glaciation periods. Haffer notes that the fluctuation of the temperature between glacial and interglacial periods was of 3 to 4° C in the tropical lowlands, and of 7 to 8° or more at high altitudes. This suggests that at high altitudes glacial periods caused a greater impact on the environment in regard to the temperature than at lower elevations. It can be hypothesized that in the lowlands the critical factor that was affected by glacial periods was humidity and not (to any large extent) temperature. This led to a reduction of the rainforests and a gradual invasion by more xerophytic types of vegetation (Haffer 1969; Vanzolini 1970; Vuillemier-Simpson 1971).

Studies on distribution pattern in birds (Haffer, 1969 & 1974), Anolis lizards (Vanzolini, 1970 & 1973) and angiosperms (Prance, 1973) have led these authors to postulate the existence of forest refuges in the Amazon Basin during the Pleistocene. These refuges were restricted areas of forest that were isolated with the invasion of the savannas. The species of forest taxa that survived in the refuges were isolated until the more humid interglacial periods, when the forests re-invaded the areas that had been claimed by the savannas.

Geological and palynological data for Andean South America indicate that at least three major glaciations occurred during the pleistocene (van der Hammen, 1966; Haffer, 1974). This would suggest that refuges have existed at least three times in the past 1.2 million years. The present-day refuges as postulated by Haffer (1969 & 1974), Vanzolini (1970 & 1973) and Prance (1973) probably only reflect the refuges formed during the last dry-glacial period (10,000-15,000 years ago), and are not necessarily the same as those formed in previous glaciations.

The present distribution of Trigonia is further evidence in support of the theory of Pleistocene forest refuges for the Amazon basin. I have obtained similar results to those reported by Prance (1973) for Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. For the purpose of this paper, I have adopted the concepts and nomenclature used by Prance (1973) to delimit the refuges (Fig 2). With further paleobotanical work in the Amazon Basin, a somewhat different distribution of refuges may have to be postulated.

Although little work has been done on the ecology of Trigonia, my observations in the field, as well as the examination of herbarium specimens provide enough data to infer some of the possible reasons for the distribution pattern in the genus. It is difficult here to refer to populations, as it has proven to be very hard to determine what constitutes a population for any species in Trigonia. In most cases, I have been unable to observe more than one individual, or to find more than one or two individuals that are apparently part of the same population. The data presented in this treatment reflect data collected on individuals only, and from these data one must extrapolate the possible impact of the environment on Trigonia spp.

The papilionaceous flower of Trigonia (and all Trigoniaceae) is suggestive of pollination by insects. The presentation mechanism of the stamens and the stigma to the pollinator is essentially the same as that found in the Fabaceae, and I believe it works in a similar manner. Whether the attractant is nectar produced by the glands or not is not known at present, as I have been unable to find any traces of nectar on either dry or the few fresh flowers available. Although the flowers are described as white for all species, a careful examination of the standard in fresh material shows the presence of tenuous purple or yellow nectar guides. Although I have not been able to observe pollination in the field, the label on one herbarium specimen of Trigonia paniculata indicates that it "was visited by a large bee".

A distribution pattern with few, widely separated individuals can be correlated with pollination by large bees; Janzen's (1971) work on flight patterns and range of euglossine bees indicates that those bees are capable of covering long distances on their normal forage flights. It is improbable that Trigonia is self-pollinated; the small number of fruits in contrast with the large number of flowers produced suggests that this is not the case.

The presence of buds, flowers and fruits at various stages of development on the same herbarium specimen for most of the species of Trigonia suggests a lack of seasonality in flowering and fruiting. This is suggestive of a more or less homogeneous environment throughout the year. Further evidence for the above statement is provided by the types of environment where Trigonia spp. have been collected, as is indicated at the beginning of this chapter.

The above-noted ecological observations may help in understanding why Trigonia spp. are useful indicators of the refuge theory. The genus is adapted to a humid environment, and seems to have a specialized pollination mechanism. These two factors would help explain why there has not been significant migration of the different elements here cited when the savannas were reclaimed by the rainforests, and also help explain the large number of endemic taxa.

The present distribution of Trigonia in South America shows a phytogeographical dichotomy. There is a southeastern group with several species found in the vicinity of Rio de Janeiro, and with distributions extending towards the north in the eastern coastal forests, and toward the northwest of Brazil along gallery and edges of forests. These species probably survived the dry period of the last pleistocene recession of the forests in the eastern coastal forests, or in the gallery forests, and only the northernmost populations were influenced and in some cases survived in refuges, as has been shown by Prance (1973) for other families. A second, north-central group, presents a large number of species in the coastal forests of the Guianas and Venezuela, and also along the riverine forests of central and northern Amazonia. This group was the most strongly affected by the Pleistocene dry periods, and the species were isolated in refuges (Prance 1973). Several species were isolated throughout their ranges in different refuges. Some have distributions in eastern coastal and gallery forests in the south, and in refuges in the northern part of their ranges.

At present it is impossible to determine the extent to which gallery forests were destroyed or survived with the invasion of the forests by savannas during the Pleistocene. There are no data to indicate what the succession pattern was in the reclamation of grasslands by the forests once

conditions became more humid.

With few exceptions, the species in Trigonia are not widespread, even in the same river basins. This could indicate that a great destruction of gallery forests occurred, or that the genus cannot adequately compete with other plants found in the same habitat. This could also explain the difficulties encountered in attempting germination.

Several species are found in the eastern coastal forests: Trigonia rotundifolia (Fig. 6), T. rytidocarpa (Fig. 6), and T. paniculata. Trigonia nivea var fasciculata (Fig. 7) is also endemic to this area, while var nivea is also found in Paria and Guiana refuges and var pubescens is found in the Manaus refuges. Trigonia eriosperma subsp eriosperma and subsp simplex are endemic to the eastern coastal forests, while T. membranacea (Fig. 3) is found only in northern S. America and C. America and was probably associated with the Nechi and Santa Marta refuges. Trigonia villosa (Fig. 5) var macrocarpa is endemic to the eastern coastal forest, while var villosa is also a component of the Guiana refuge.

Three species are endemic to the forests protected by the rainshadow of the eastern limit of the Andes: Trigonia boliviana (Fig. 4), T. floccosa (Fig. 4) and T. echiteifolia.

The Guiana refuge harbors the largest number of species of Trigonia. Four species are endemic to this area: T. hypoleuca (Fig. 5), T. coppenamensis (Fig. 6), T. subcymosa (Fig. 4) and T. candelabra (Fig. 4). Several other species are represented there, although they are not endemic, notably T. nivea, T. villosa and T. laevis (Fig. 6).

The Napo refuge is also important in number of species. Two species are endemic there, Trigonia macrantha (Fig. 5) and T. prancei (Fig. 4) (this

species could also be from the East Peru refuge; it is a borderline case). Two others are represented: T. sericea (Fig. 5), which is also found in the Napo and Nechi refuges, and T. virens (Fig. 5), which is also found in the Rondônia-Aripuanã refuge.

Trigonia spruceana (Fig. 5), a moderately widespread species, is found in the Manaus refuge, and possibly in the Imerí. Trigonia costanensis (Fig. 5) is found in the Rancho Grande refuge.

The Nechi refuge contains Trigonia rugosa (Fig. 3), T. sericea, and T. eriosperma subsp membranacea; the Santa Marta refuge contains T. rugosa and possibly T. eriosperma var membranacea. Trigonia bracteata (Fig. 4) is found close to the Rancho Grande refuge. The Catatumbo refuge contains T. rugosa and T. reticulata (Fig. 6), and T. killipii (Fig. 5) is found in the East Peru refuge.

FIG. 1. Geographic distribution of Trigoniaceae. 1, Range of the genus Trigonia. 2, Range of the genus Humbertodendron (Humbertodendron saboureaui). 3, Range of the genus Trigoniastrum (Trigoniastrum hypoleucum).

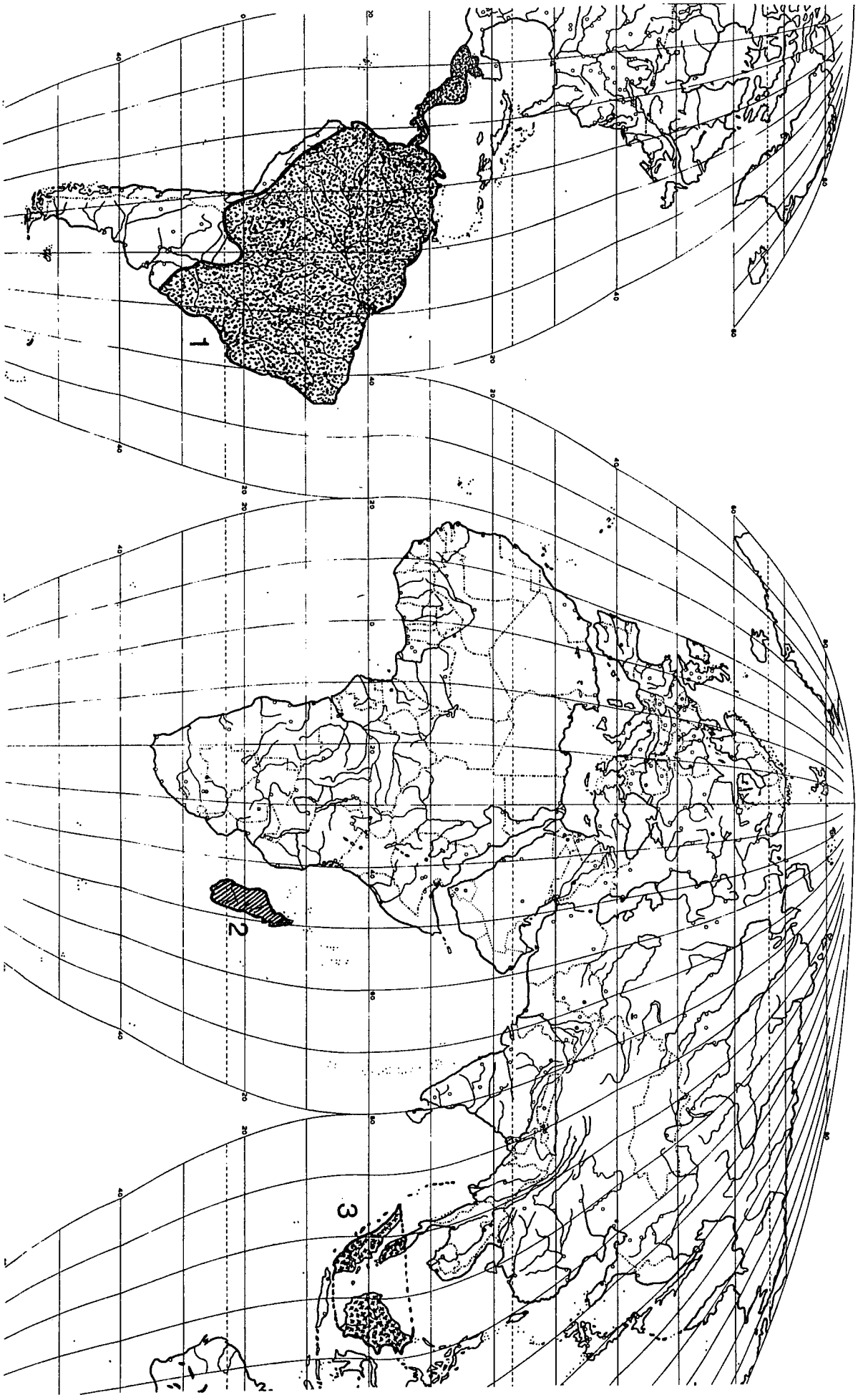


FIG. 1

FIG. 2. Forest refuges proposed by Prance (1973). 1. Chocó; 2. Nechi; 3. Santa Marta; 4. Catatumbo; 5. Rancho Grande; 6. Paria; 7. Imataca; 8. Guiana; 9. Imerí; 10. Napo; 11. Olivença; 12. Tefé; 13. Manaus; 14. East Peru; 15. Rondônia-Aripuanã; 16. Belem-Xingu. The areas surrounded by a heavy black line correspond to areas flooded during the pleistocene.

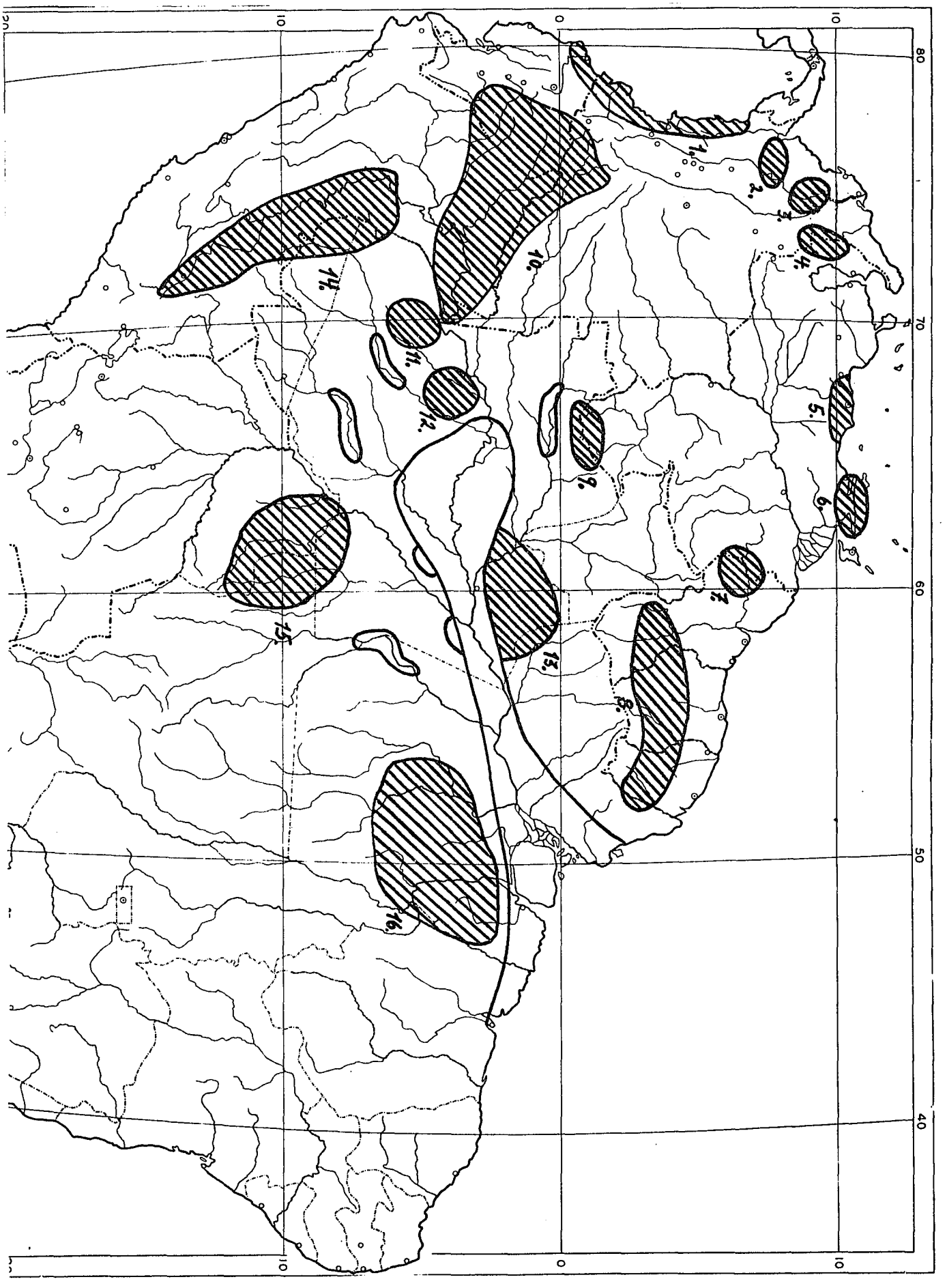


FIG. 2

FIG. 3. Known distribution of species of *Trigonia*. ● *T. rugosa*; ▽ *T. eriosperma* subsp. *membranacea*.

FIG. 4. Known distribution of species of Trigonia. ● T. prancei; ☆ T. boliviana; ⊠ T. floccosa; ▲ T. candelabra; ✪ T. eriosperma subsp eriosperma; ★ T. eriosperma subsp simplex; ▲ T. subcymosa; □ T. bracteata.

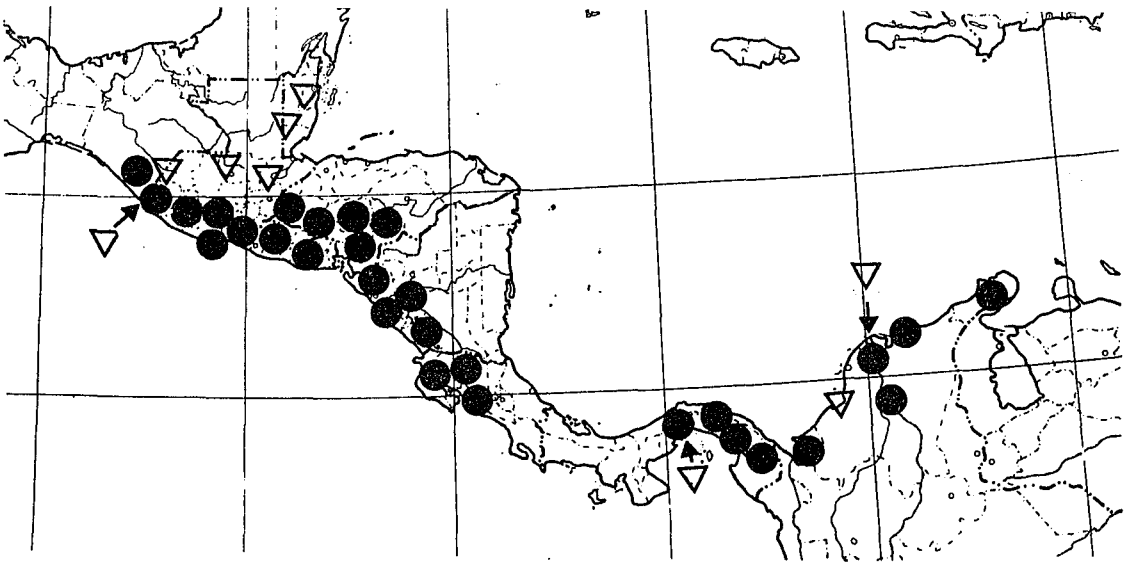


FIG. 3

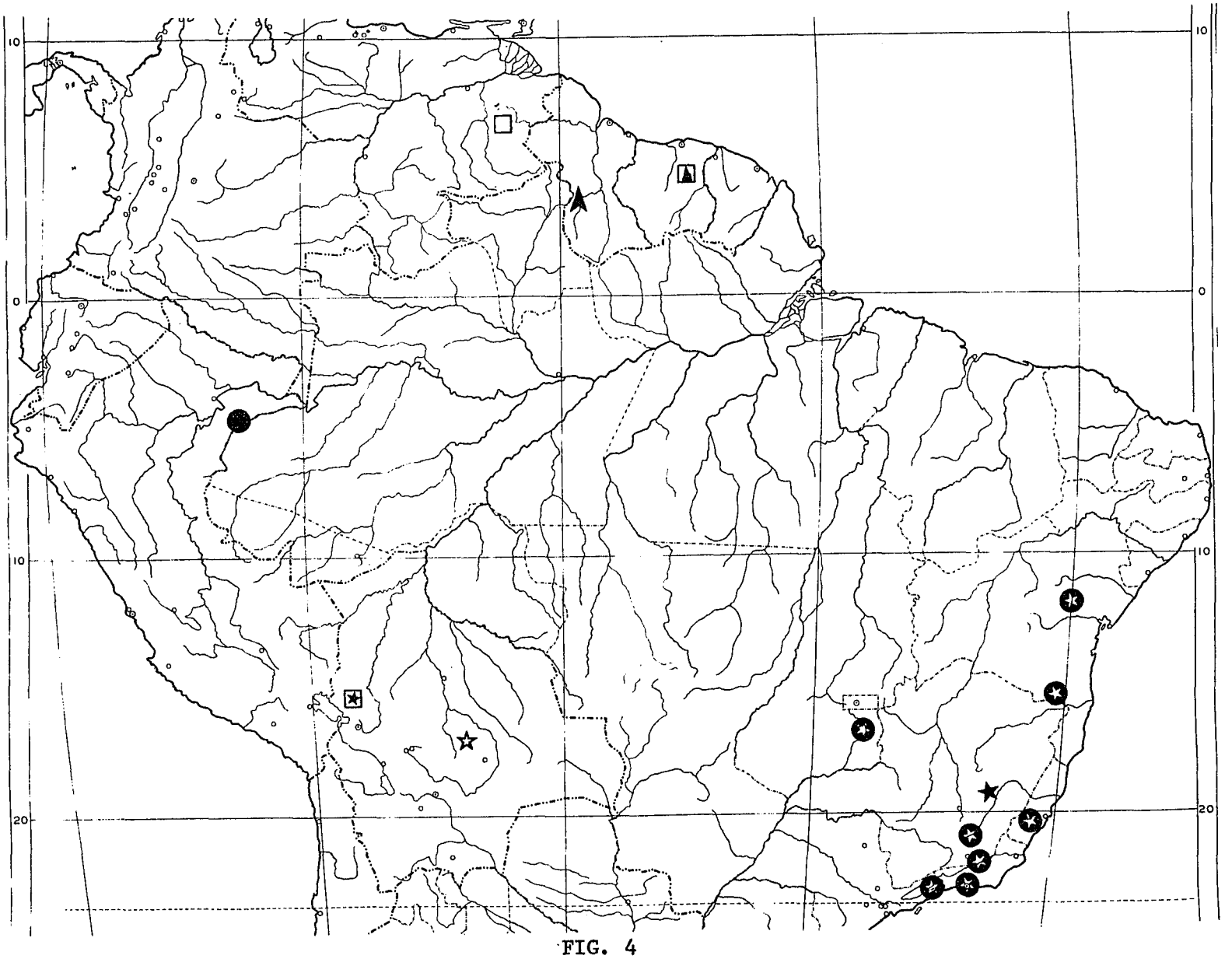


FIG. 4

FIG. 5. Known distribution of species of Trigonia. ■ T. macrantha; ○ T. killipii; ◆ T. virens; △ T. sericea; ◇ T. hypoleuca; □ T. echiteifolia; ▲ T. spruceana; ● T. villosa var. villosa; ◙ T. villosa var. macrocarpa; ✶ T. paniculata; ✪ T. costanensis.

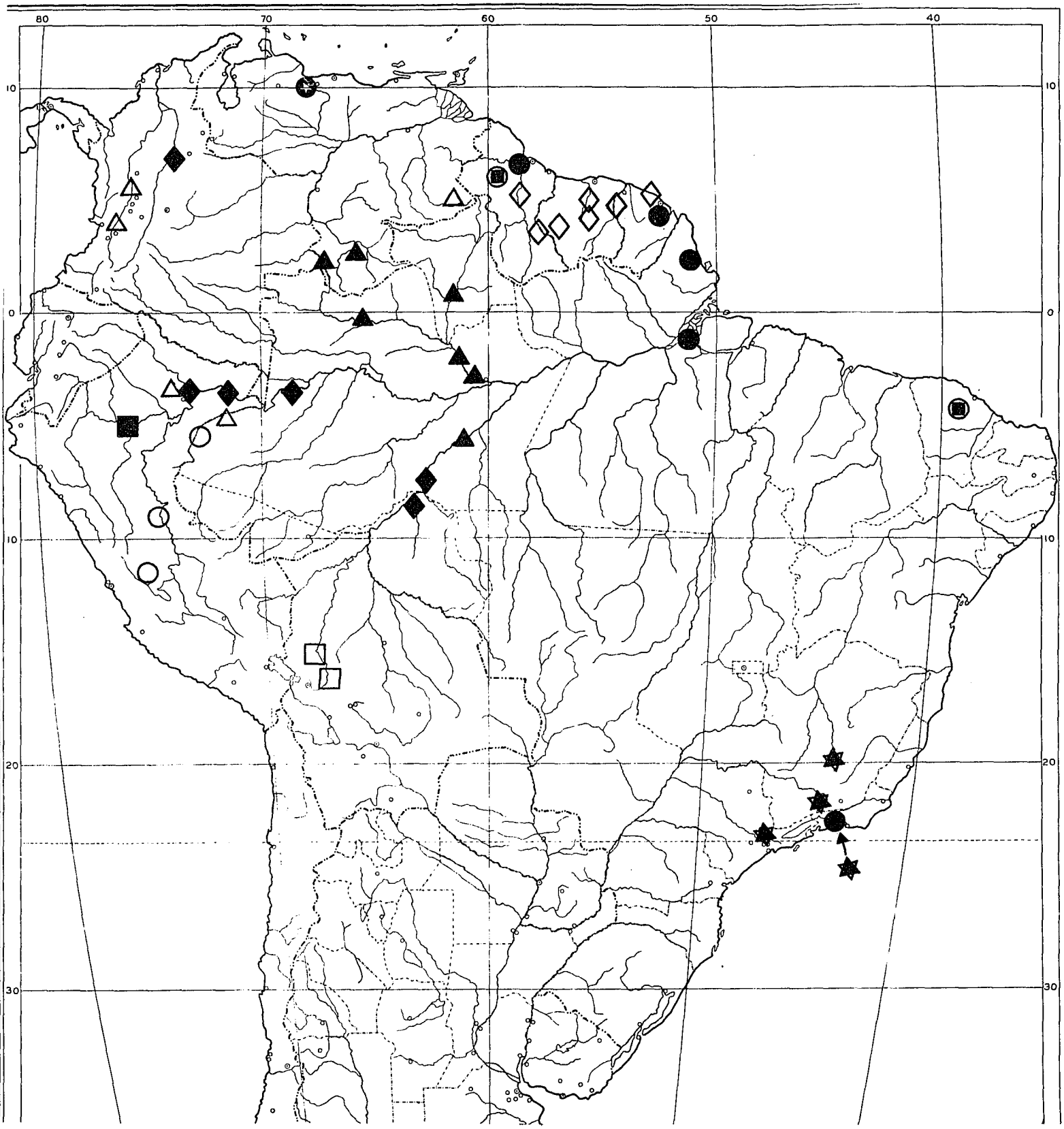
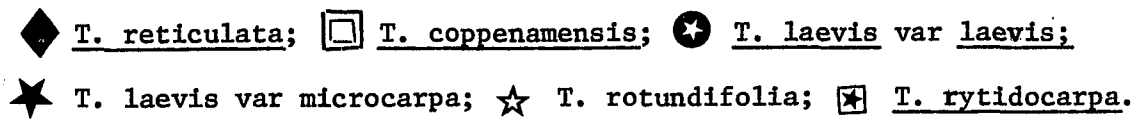


FIG. 5

FIG. 6. Known distribution of species of Trigonia.



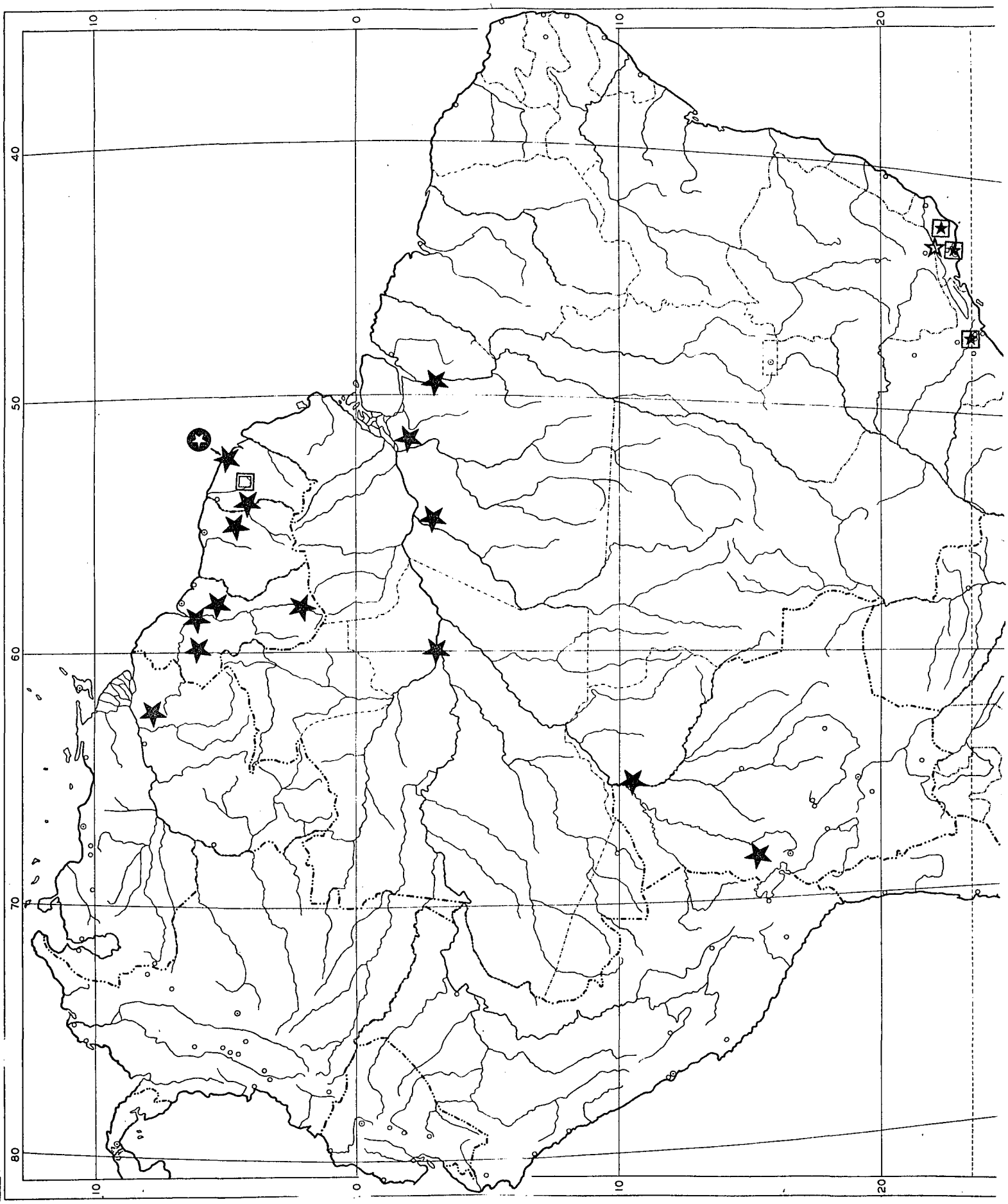


FIG. 6

FIG. 7. Known Distribution of species of Trigonia. ● *T. nivea* var. *nivea*; ◭ *T. nivea* var. *pubescens*; ◯ *T. nivea* var. *fasciculata*.

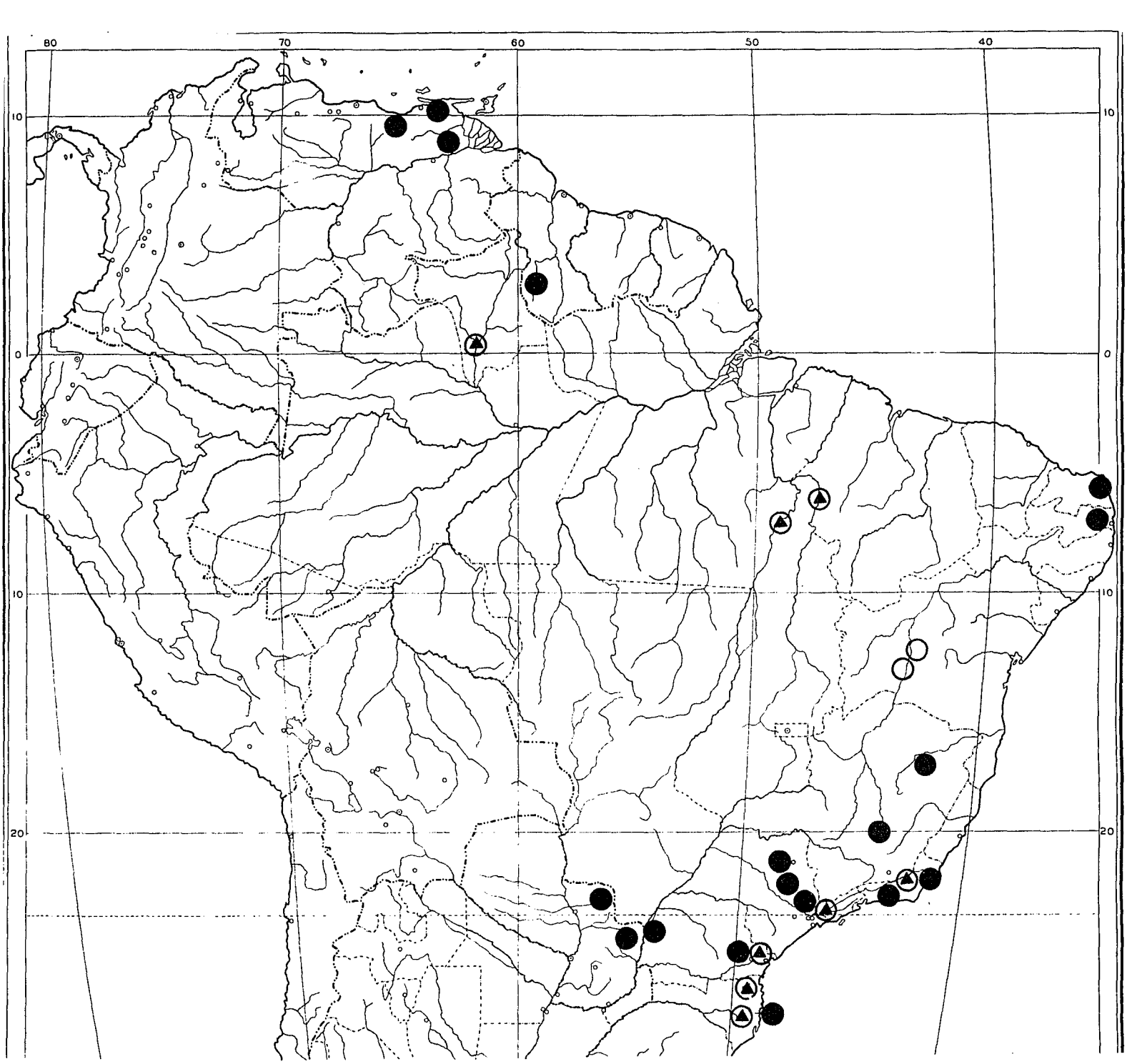


FIG. 7

ANATOMICAL CONSIDERATIONS

The anatomy of the Trigoniaceae was studied thoroughly by Barth (1896), who treated most of the known species of Trigonia as well as Trigoniastrum and Euphronia. The secondary xylem was also treated by Heimsch (1942) and the Trigoniaceae were studied by Metcalfe and Chalk (1951).

In the present study five randomly selected specimens of each of the more commonly collected species and one specimen each of those poorly known from collection were surveyed for anatomical study. Small stem segments, petioles, and leaf blades were sectioned using different techniques. Most were sectioned with the aid of a freezing microtome, but some sections were made by the freehand method, and a small number were treated using paraffin technique. The dyes used in all cases were saffranin and fast green.

I examined enough material to confirm the data given by Barth (1896), Heimsch (1942) and Metcalfe and Chalk (1950). I also studied Humbertodendron, a genus that previously had not been treated anatomically, (Fig 8). In the leaf, I found trichomes to be simple and unicellular; the epidermis often with mucilaginous cells, is uniseriate in Trigonia (except T. rugosa) and 2-layered in Trigoniastrum and Humbertodendron. Stomata are paracytic, and confined to the lower surface. Mesophyll is with branched sclereids in Trigoniastrum and Humbertodendron; palisade parenchyma is usually 1-layered but sometimes 2-layered in Trigoniastrum and Humbertodendron; rhomboid or irregularly chambered crystals of calcium is present in Trigoniastrum, Humbertodendron and several species of Trigonia.

The petiole has a simple epidermis in all three genera; the trichomes, when present, are simple and unicellular. The phloem completely surrounds the xylem in Humbertodendron and some species of Trigonia, or is open at the top

as in Trigoniastrum and other Trigonia species. In the stem, the epidermis is simple and often has tannins. The cork is derived from subepidermal phellogen, and the cork cells often have tannins, and the region just below the peridermis is often subcollenchymatous. Cortical sclereids are often present and are especially common in Trigoniastrum and Humbertodendron. Calcium oxalate crystals are frequent in all three genera (lacking in some species of Trigonia). The secondary phloem has sclereids. Intraxylary phloem is absent, and the vessels are solitary (although Heimsch 1942, reports pore multiples in some Trigonia spp.). The perforations are simple and elliptic (sometimes double in T. eriosperma, fide Barth). The parenchyma is apotracheal in all three genera (1 specimen of Trigoniastrum reported as having paratracheal parenchyma by Metcalfe & Chalk). The rays are 1-5-seriate, heterogeneous (Kribs' type IIa and IIb). The wood is diffuse-porous. The pith often has tannins, with or without crystals; in Humbertodendron, rhomboid crystals are very common.

Cross sections and dissections of the flower of Trigonia spruceana and T. prancei were made in order to determine the nature of the floral glands. The vascularization of the glands is the same as that found in the staminal ring, with 2-3 vascular strands attached to (i.e. entering) each gland. This supports my views based on morphology considering the glands are actually modified stamens.

Anatomically, the family is fairly uniform, with no single character facilitating differentiation among the genera, although there are trends that are more noticeable in some groups than in others.

Humbertodendron is anatomically very close to Trigoniastrum; in fact, the anatomy of the leaf blade is so similar in the two genera that laminar material of the two genera easily can be confused in the laboratory. The petioles are somewhat different, however, especially in the position of the

vascular bundles. As was indicated in the anatomical description the phloem in Humbertodendron totally surrounds the xylem, but is open in Trigoniastrum. In Humbertodendron sclereids are present only along the rays, while they are randomly distributed in Trigoniastrum. Although rhomboid crystals occur in the pith in both genera, they are much more abundant in Humbertodendron.

Barth (1896) considered the Trigoniaceae as related to the Dichapetalaceae on anatomical grounds. Heimsch (1942), based on his work on secondary xylem, considered the Trigoniaceae close to the Polygalaceae, the Tremandraceae, the Zygophyllaceae, the Malpighiaceae and the Vochysiaceae. Metcalfe and Chalk (1951) considered the family closest to the Vochysiaceae.

The Trigoniaceae differs from the Vochysiaceae in the absence of intraxylary phloem, the absence of libriform fibers, and in having apotracheal (vs. paratracheal) parenchyma.

Anatomically, the Trigoniaceae have undoubtedly close affinity to the Vochysiaceae as well as the Polygalaceae. The suggested relationships with Dichapetalaceae may also be correct. The taxonomic positions and familial relationships of the families in both Cronquist's (1968) Sapindales and Polygalales, as well as the relationship of these families with the ancestral Rosales, remain rather unclear at present.

On the basis of anatomy, which corroborates the morphological observations, I agree with Barth that Euphronia should be removed from the Trigoniaceae. Anatomically, there is no serious objection to returning Euphronia to the Vochysiaceae, with which it has many characters in common. The data used to support this decision are discussed in the Appendix under Euphronia.

FIG. 8. Anatomy of Humbertodendron saboureaui (Perrier & Louvel 14896bis). A, young stem, longitudinal section X 14; B, young stem, longitudinal section showing rhomboid crystals X 52; C, young stem, cross section X 14; D, petiole, cross section X 28; E, lamina, cross section X 100; F, lamina central nerves X 28.

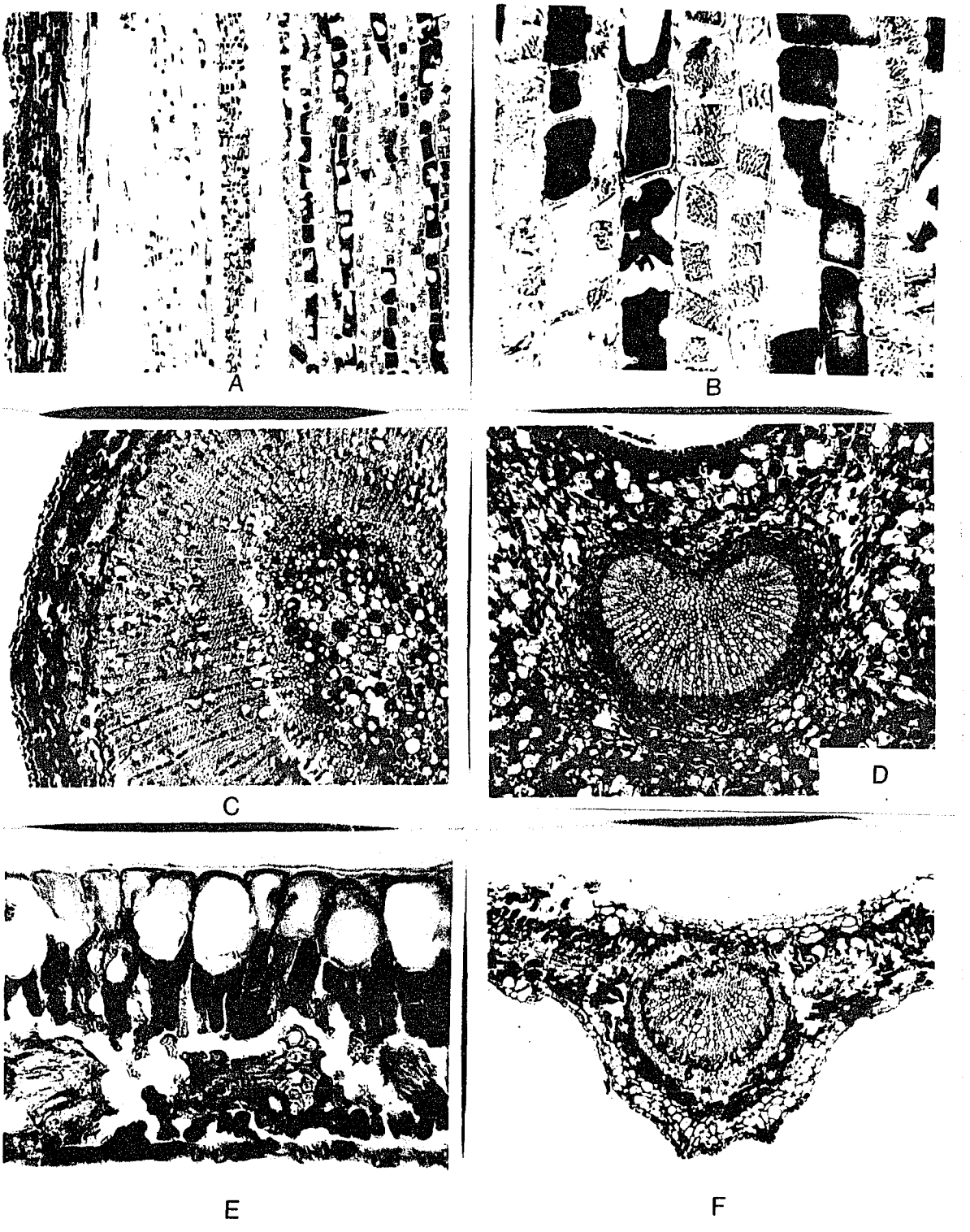


FIG. 8

POLLEN

The terminology and format used here to describe the pollen of the Trigoniaceae are taken from Erdtman (1952) and Walker (1971).

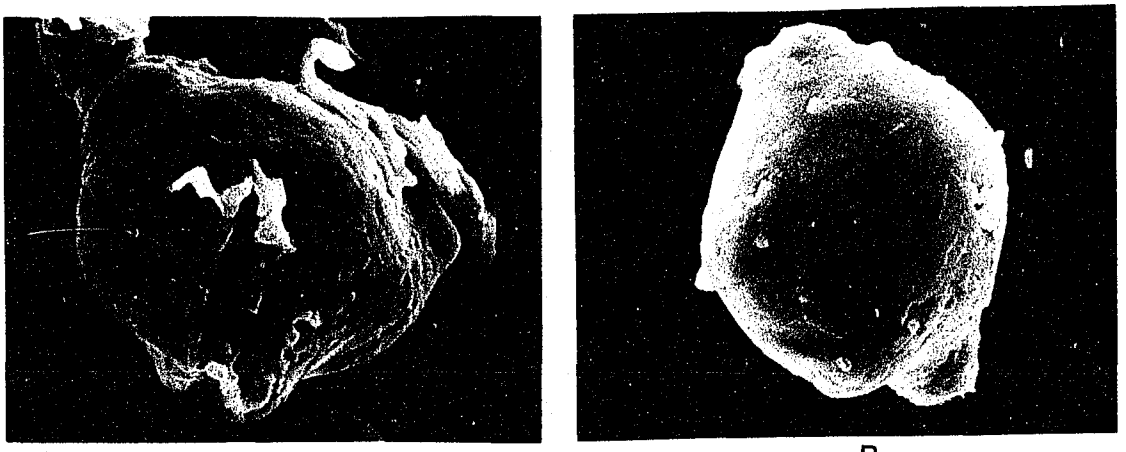
Pollen Morphology: (Fig. 9) The grains are solitary, square or sub-oblate, sometimes oblong; 3-4 (rarely 5)-porate; 25-60 u on the longest axis (highly variable within the same species). The exine stratification is obscure, and the surface, when observed with the Scanning Electron Microscope, is tenui-exinous and psilate. The sexine is probably thicker than the nexine, which has (fide Erdtman, 1952) small projections directed towards the interior of the grain.

In Trigonia, T. spruceana (42-60 μ) and T. nivea (40-55 μ) have the largest grains. Trigonia rugosa (28-40 μ) and T. prancei (25-38 μ) present the samllest grains. The majority of the species have grains ranging between 35 and 45 μ (eg T. villosa, T. virens, T. rotundifolia, T. echiteifolia, T. laevis and T. reticulata). The pollen of Humbertodendron (only one specimen available for sampling) has a size of ca 55 μ; Trigoniastrum has grains ranging between 35-43 μ. The high degree of overlap in grain size in Trigonia makes it impossible to separate the pollen into discrete size groups. Without such discrete groups it is impossible to suggest polyploids within the genus based on pollen evidence.

Although pollen characters have not proved useful taxonomically within the family due to the high degree of overlap in size and to the very similar morphology (practically identical for all three genera), pollen has proved to be of great value in distinguishing the Trigoniaceae from other families, and has been useful in establishing this family's relationship with the

Sapindaceae. Erdtman (1952) noted a similarity of pollen in the Trigoniaceae with the pollen of Paullinia (Sapindaceae), an observation with which I concur. There is a slight tendency in the Trigoniaceae towards multiporate pollen, as can be seen in the progression from 3-porate to 5-porate grains (as in Trigonia prancei, Fig. 9-E), and this might indicate a relationship with the Polygalaceae, which have multiporate pollen. One might consider Trigoniaceous pollen as somewhat intermediate between that of the Sapindaceae and the Polygalaceae, but this does not mean that I consider the Trigoniaceae as an intermediate family.

FIG. 9. Pollen of Trigoniaceae. A-C, Scanning Electron Micrographs, X 660. D-F, with light microscope, X 260. A, Humbertodendron saboureaui (Perrier & Louvel 14896 bis); B, Trigonia villosa (Pires & Cavalcante 52283); C, Trigonia rugosa (Burger 7841); D, Trigonia prancei (Lleras, Steward et al 17115); E, Trigonia prancei (Lleras, Steward et al 17115); F, Trigonia rugosa (Haught 4227).



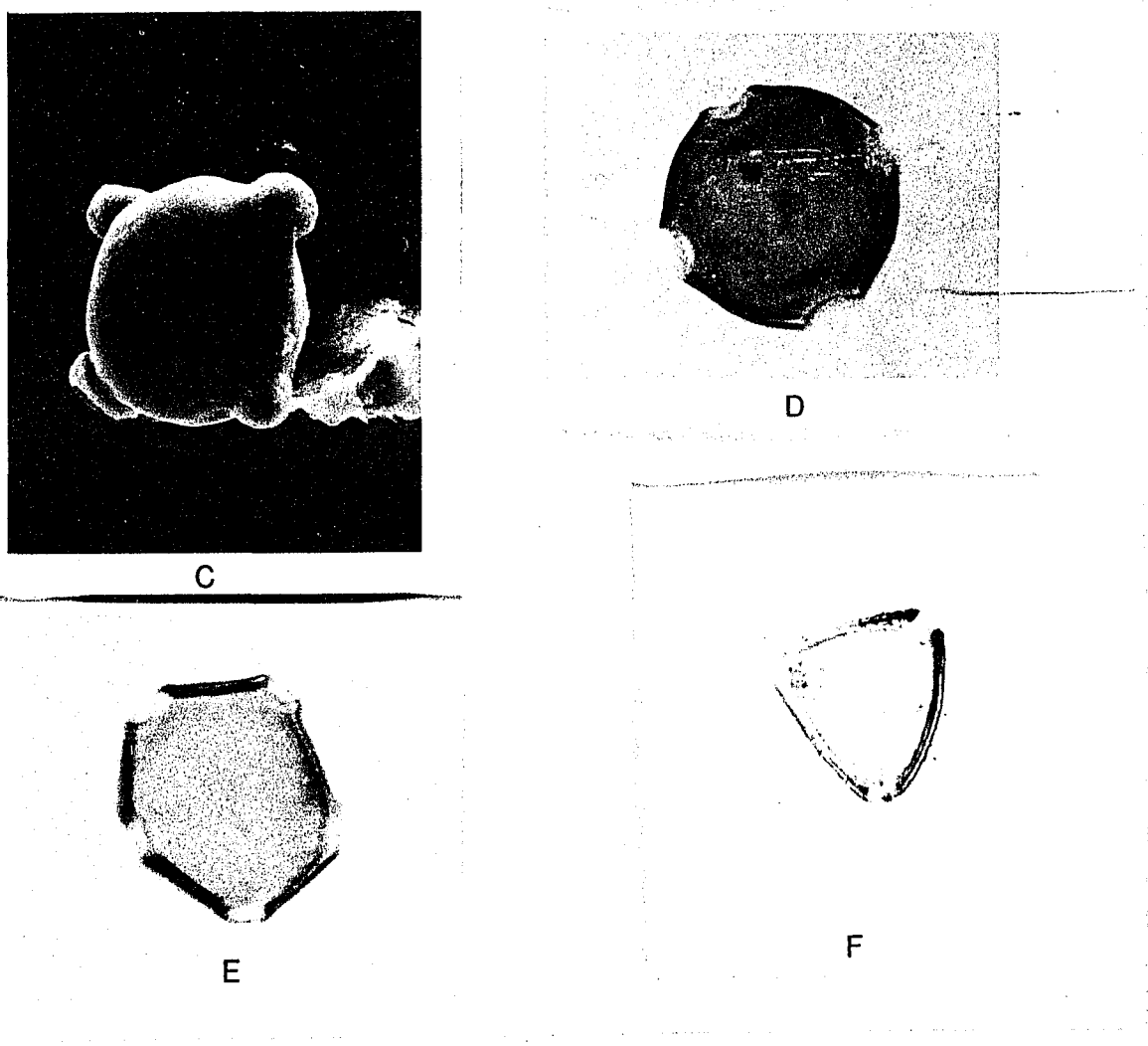


FIG. 9

EVOLUTION OF CHARACTERS WITHIN THE FAMILY

Although it is difficult at present to discern generalized trends of evolution within the Trigoniaceae, the possible evolution of individual characters can be discussed. It is accepted here that the major trends in Angiosperm floral evolution have involved progressive reduction and simplification, as postulated by Bessey (1915), Tajktajan (1959, 1969) and Cronquist (1968).

One of the most interesting features is the change from a basically trilocular ovary (4-locular in Trigonia rotundifolia) to a unilocular ovary. The unilocular ovary occurs in T. virens and T. hypoleuca. This reduction can also be observed in Humbertodendron and several other species of Trigonia, although in a less advanced state, with the septa present but not fused at the center. This process has apparently occurred by a gradual reduction of the lateral septa of the locules: first, as in Humbertodendron and T. sericea, the septa are complete but fail to fuse at the center; then, as both T. virens and T. hypoleuca, a gradual shortening of the septa occurs. Although several of the intermediate steps can be observed in the ovaries of the last two species, by the time the fruit reaches maturity no trace of the lateral septa remains.

Evidence of a gradual reduction of the androecium can be seen in living species of the Trigoniaceae. The most primitive existing condition occurs in Trigonia macrantha and T. nivea, whose flowers have fairly large numbers of stamens (ca 12), some of which are reduced to staminodes. The intermediate condition is found in species in which the staminodes have been lost, and all of the stamens are fertile, as in T. virens. The condition which I consider

to be the most evolved, where there are no staminodes and a relatively small number of stamens (ca 6), is present in both Trigoniastrum and Humbertodendron.

If we accept an ancestor in the Rosales (as discussed in Chapter 7) as the precursor for Trigoniaceae, it was probably a group of plants with a large number of indefinite or definite stamens disposed in a staminal ring. The reduction process probably occurred as follows: first, a complete reduction of a whole section of the staminal ring, with a subsequent evolution of the disc glands. I interpret these glands as reduced and modified stamens, based on the laciniae which are morphologically vestigial filaments; anatomical evidence for this is discussed in Chapter 4 . Next there was a loss of anthers on some of the remaining (outer) stamens of the portion that remained; and finally, a loss of staminodes, giving rise to the extant taxa displaying few fertile stamens and no staminodes.

The obvious difference in the dispersal mechanism between the Neotropical and Paleotropical Trigoniaceae represents an important evolutionary change. In both Humbertodendron and Trigoniastrum, the seeds remain in the winged fruit, and are dispersed with it. In Trigonia, however, the fruits are dehiscent, and the seeds are adapted to wind and water dispersal. This transference of function for seed protection and dispersal from the seed to the ovary and vice-versa is common in the Angiosperms (Stebbins, 1974).

As is discussed in Chapter 3 on geography and ecology, and based on geographical and ecological evidence, the plants of the ancestral trigoniaceous stock were probably trees, with many-seeded capsules. The seeds were probably villous, although the trichomes were probably shorter than those found on present-day Trigonia spp.

Figure 10 is a schematic representation of my opinion of similarities and differences in Trigonia. The distances do not represent closeness of relationship and only serve to separate taxa of dubious position. It is not my intention to suggest phylogeny, as I believed that present evidence is insufficient to do so. It is also difficult to determine which species are primitive or advanced, as in almost every case a species that presents a character that I consider primitive also presents characters that I consider advanced.

FIG. 10. Schematic representation of similarities and differences within Trigonia.

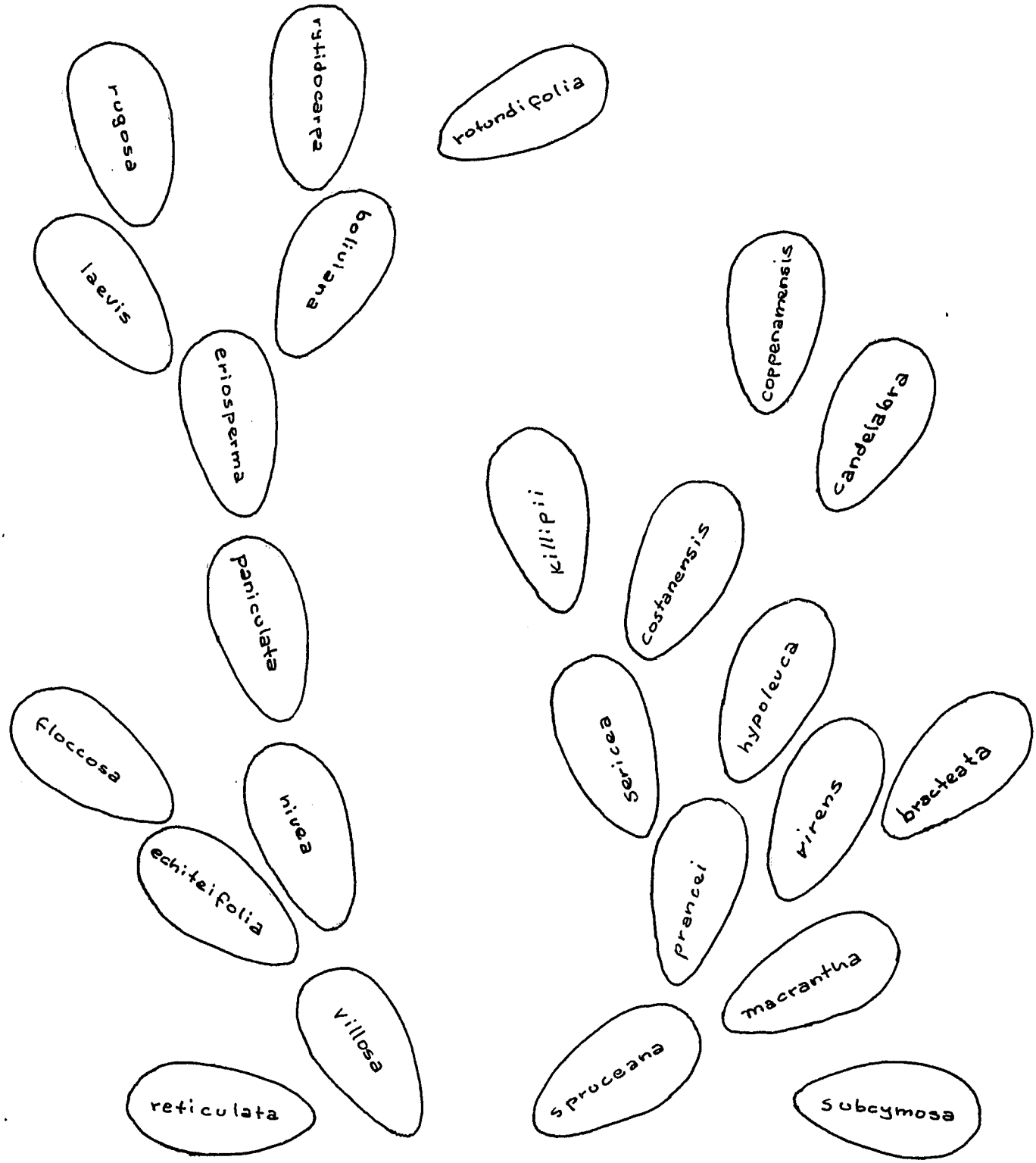

rugosa
ruthidocarpa
rotundifolia
laevis
bollviana
eriosperma
paniculata
floccosa
nivea
echiteifolia
villosa
reticulata
coppenamensis
candelabra
killipii
costanensis
sericea
hypoleuca
virens
bracteata
prancei
macrantha
spruceana
subcymosa

FIG 10

SYSTEMATIC POSITION OF THE TRIGONIACEAE

Chapter 2 presents the taxonomic positions previously suggested for the family and in some cases for individual genera. As can be seen from this account, there has been considerable divergence of opinion as to the systematic position of the Trigoniaceae. A summary of the most important relationships suggested for the family follows:

Aublet (1775)	Decandria Monogynia
De Jussieu (1789)	aff. *Malpighia*
De Candolle (1824)	*in* Hippocrateaceae
Cambessèdes (1829)	*in* Hippocrateaceae
Martius (1835)	fam. *in* Malpighinae
Grisebach (1849)	*with* Polygalaceae & Euphorbiaceae
Agardh (1858)	*in* Polygalaceae
Bentham & Hooker (1867)	*in* Vochysiaceae
Baillon (1874)	*in* Vochysiaceae
Petersen in Engler & Prantl (1896)	Polygalales
Hallier (1921)	*with* Dichapetalaceae & Chrysobalanaceae *in* Linales
Leandri (1949)	*Humbertodendron* close to Sapindaceae
Cronquist (1968)	Polygalales
Tahktajan (1969)	Polygalales
Hutchinson (1973)	Polygalales
Breteler (1973)	with Dichapetalaceae & Malpighiaceae

Most frequently the Trigoniaceae have been associated with the Vochysiaceae and the Polygalaceae (Polygalales); alternatively the family has been linked with the Dichapetalaceae and Malpighiaceae. These two suggested relationships

are less contradictory than may be supposed. Evidence is presented here suggesting a closer relationship for these families than is commonly assumed.

Anatomical and morphological evidence has been cited to support both points of view; for example, Barth (1896), on anatomical grounds, suggested the relationship between Trigoniaceae and Dichapetalaceae. He considered Euphronia (placed in the Vochysiaceae in the present work) as anatomically intermediate between the two families. Heimsch (1942), who based his decision on anatomy of the secondary xylem, placed Trigoniaceae with the Polygalaceae and Malpighiaceae, as well as with the Tremandraceae and Zygophllaceae, all families included in Cronquist's (1968) Sapindales or Polygalales. Metcalfe & Chalk (1950) considered Vochysiaceae to be anatomically the family closest to the Trigoniaceae. These opinions based on anatomy perhaps demonstrate that the family is not clearly defined anatomically. It also suggests that several of the families suggested as relatives for the Trigoniaceae have about the same level of anatomical specialization.

Palynological evidence cited by Erdtman (1952), and with which I agree, indicates a relationship with the Sapindaceae; the smooth, 3-5-porate pollen in the Trigoniaceae is very similar to that of Paullinia. It is also somewhat similar to the pollen of the Polygalaceae, although this family is characterized by a multiporate type of pollen grain.

Morphologically, the Trigoniaceae bear a striking similarity to several families; Breteler (1973) and Prance (1972) have both indicated possible relationships of the Trigoniaceae and the Dichapetalaceae, based on both anatomical and morphological data. Prance has cited the tendency towards zygomorphy, the lack of endosperm, and the polygamous flowers of the Dichapetalaceae as possible evidence of relationships of this family with the

Polygalales; Breteler has interpreted the apparent corolla of both the Trigoniaceae and the Dichapetalaceae as not being a true corolla but as a structure derived from modified stamens. He felt this to be further evidence for considering these two families as closely allied. This may be true for the Dichapetalaceae, but I find no evidence to support this hypothesis for the Trigoniaceae. Nevertheless, the reduction of the disc glands, and the presence of connate stamens (if they can be regarded as such in Stephanopodium), seem to me to be significant characters in considering these two families as closely allied, as they suggest similar evolutionary trends.

The relationships of Trigoniaceae with both Sapindaceae and Polygalaceae are probably more evident at first sight. Both the Trigoniaceae and the Polygalaceae have the papilionaceous corolla that makes them distinct. The Sapindaceae, although not papilionaceous, have several characters that have probably evolved in the same direction; the stamens are in many cases very much like those of Trigoniaceae, and some petals are very similar (almost identical) to those of the Old World genera of the latter family. Another significant character is the occurrence of winged samaras in all three families.

Table 1 present a comparison of morphological characters of the Trigoniaceae, the Vochysiaceae, the Polygalaceae, the Sapindaceae and the Malpighiaceae. A comparison of characters in the table is indicative of the difficulties encountered when trying to establish relationships based on morphological data.

The evidence cited above supports Cronquist (1968) who accepted a general relationship among these families, which he believes are derived from the common Rosalean stock, but I am not entirely convinced that the degree of relationship among the families is altogether clear at present. There is no doubt that the families included in the Polygalales are related, and are close to the Sapindales

(Cronquist, 1968) and possibly the Celastrales (Prance, 1972). However, the relationships among the families in these three orders are complex. Indications for this have been given by Prance (1972), and Breteler (1973) on morphological grounds, and anatomical evidence has been provided by Barth (1896) and Heimsch (1942).

The evidence presented above supports a common origin in the Rosales for the Polygalales, Celastrales and Sapindales as has been suggested by Prance (1972). This would explain a number of families that seem to have affinities in all three orders. Thus, the Trigoniaceae together with the Vochysiaceae and the Dichapetalaceae and probably the Malpighiaceae (fide Breteler, 1973) would occupy positions close to the point of divergence of the three orders.

The Trigoniaceae have (as have the other three families) evolved in a direction of their own, and probably arrived at the papilionaceous type of flower independently. This suggests that this distinctive flower type has evolved at least three times in response to insect pollinators (the Fabaceae, the Polygalaceae and the Trigoniaceae). At present it is difficult to establish the closest relatives of the Trigoniaceae, but it would be misleading to give undue emphasis to the papilionaceous corolla.

It is significant that the relatives suggested for the Trigoniaceae all belong to families that have significantly modified corollas (Breteler, 1973). This suggests a highly adaptable group in relation to the corolla, another factor that would suggest a common ancestry.

Taxonomically, I am maintaining Trigoniaceae in the Polygalales as defined by Cronquist (1968), as most of the possible relatives suggested in this paper are included in that order.

Table 1. Comparison of characters between the Trigoniaceae, the Dichapetalaceae, the Malpighiaceae, the Sapindaceae, the Vochysiaceae and the Polygalaceae.

TABLE 1

	Trigoniaceae	Dichapetalaceae	Malpighiaceae	Sapindaceae	Vochysiaceae	Polygalaceae
position of leaves	opposite or alternate	alternate	opposite (u)	alternate, opposite	opposite, alternate verticellate	alternate or (R) opposite
type of leaves	simple	simple	simple	simple or compound	simple	simple
stipules	+	+	+ (-)	+ (R)	- + (or glands)	-
floral symmetry	zygomorphic	actino (-zygo)	actinomorphic	actino, zygo	zygomorphic	zygomorphic
number of sepals	5	5	5	5	5	5
arrangement of sepals	imbricate	imbricate	imbricate	imbricate or valvate	imbricate	imbricate
number of petals	5 (papil.)	5	5	3 - 5	1 - 5	5 (papil.)
arrangement of petals	convolute	imbricate	convolute	imbricate	convolute	not applicable
number of stamens (total)	5 - 13	5	10	Ca 8	1 - 5	8(4-5)
staminodes	+ (-)	+	-	-	+	-
filaments	connate	free or connate	connate (u)	free	free	connate
number of locules on anthers	2	2	2	2	2	1 - 2
type of dehiscence of anther	introrse	introrse	introrse	introrse	introrse	introrse (apical)
glands	+	+	+ (ext)	+	+	+
position of ovary	superior	superior-inferior	superior	superior	superior	superior
number of locules	3(1-4)	2 - 3	3	3(1-4)	1 - 3	(1)2-3-4-5
type of style	simple	simple	divided	simple or divided	simple	simple
number of ovules per locule	1 - many	2	1	1 - 2 (many)	2 - many (1)	1
orientation of ovules	epitropous	epitropous	epitropous	epitropous	apotropous	epitropous
placentation	on intruded placentas	axile-pendulous	ascending-pendulous	axile or parietal	axile	axile-pendulous
type of fruit	capsules or samaras	drupes	samaras or drupes	various	capsules or samaras	capsules or drupes
endosperm	-	-	-	-	- (rare)	+
embryo	straight	straight	straight or curved	plicate or twisted	straight	straight

TAXONOMIC POSITION OF *EUPHRONIA*

As is discussed in Chapter 2, *Euphronia* was placed in the Trigoniaceae by Warming (1875), a decision later questioned on morphological grounds by Chodat (1895) and on anatomical grounds by Barth (1896). Nevertheless, until now *Euphronia* has remained in the Trigoniaceae of all authors. There are, however, many marked anatomical and morphological differences between *Euphronia* and Trigoniaceae sens. str. A comparison of some characters in Trigoniaceae, *Euphronia* and Vochysiaceae is given below:

Trigoniaceae	*Euphronia*	Vochysiaceae
Pollen 3-5 porate	Pollen tricolporate	Pollen tricolporate
Petals 5	Petals 3	Petals 1-5
Stamens all connate in one structure	Stamens in 2 or 3 groups	Stamens in 1-several groups
Staminodes 0-several	Staminode 1	Staminodes several
Disc glands present	Disc glands absent	Disc glands absent
Ovary lacking a central column	Ovary with a central column	Ovary with a central column
Placentation on inner ends of the lateral septa	Placentation axile	Placentation axile
Fibers not libriform	Fibers libriform	Fibers libriform
Parenchyma apotracheal	Parenchyma paratracheal	Parenchyma paratracheal
Pith lacking sclereids	Pith with sclereids	No data
Foliar bundles immediately fused with the stele	Foliar bundles extending some distance (down the stem) before fusing with the stele	Foliar bundles extending some distance (down the stem) before fusing with the stele
Petiole epidermis simple	Petiole epidermis multiple and collenchymatous	No data
Hypodermis absent in leaf	Hypodermis present in leaf	Hypodermis present in some leaves
Palisade parenchyma of 1-2 stratified layers	Palisade parenchyma of 2-several irregularly disposed layers	No data

Using anatomical evidence, Barth considered Euphronia a possible intermediate between Trigoniaceae and Dichapetalaceae, but at the same time noted that anatomically it could be accommodated in either family. Metcalfe & Chalk (1950) observed the anatomical similarity between Trigoniaceae and Vochysiaceae; several important anatomical characters are shared by Euphronia (considered by Metcalfe & Chalk as Trigoniaceae) and Vochysiaceae but are not found in Trigoniaceae. For example, both Euphronia and Vochysiaceae have libriform fibers, paratracheal parenchyma, and very small cells on the upper epidermis of the leaf. Intraxylary phloem, the character given most emphasis by Metcalfe and Chalk to distinguish Trigoniaceae and Vochysiaceae, is not found in Euphronia (Heimsch, 1942). Although intraxylary phloem is very common in Vochysiaceae, it is not present in all of that family (Metcalfe and Chalk, 1950). This holds true for many families in which this character occurs; that is, usually occurs in a large number of species or genera of a family, but not in all.

Morphological comparison between Euphronia and Vochysiaceae shows that the only major difference is in the number and arrangement of stamens and staminodes; the Vochysiaceae, as currently delimited, usually has only 1 fertile stamen and several staminodes, while Euphronia has several fertile stamens and one staminode. The staminode in Euphronia occupies the position of the fertile stamen in Vochysiaceae. This comparatively small difference in stamen number and arrangement does not seem to me to be sufficient evidence to maintain Euphronia apart from Vochysiaceae. It is a relatively easy evolutionary step to change the stamen number in response to selective pressure. It is highly possible that Euphronia and Vochysiaceae have diverged from a

common ancestor all of whose stamens were fertile, but have diverged in degrees of reduction in the number of stamens.

During the course of my research on the Trigoniaceae, I have come to agree with Chodat (1895) and Barth (1896) that Euphronia does not belong in the Trigoniaceae. I believe that the relationships of Euphronia are with the Vochysiaceae, and consider that it is superfluous to create a new family to accommodate this unusual genus. I propose to return Euphronia to the Vochysiaceae, with which its affinities are closest.

SPECIFIC CONCEPTS

The concepts used to delimit species in the Trigoniaceae, especially in Trigonia, have been determined by the data available for the family. As is noted in the chapter on Geography and Ecology, it has proven difficult to determine populations in Trigonia (as is true for many other tropical taxa). The scarcity of collections noted above, as well as the lack of success in obtaining live material for work in the laboratory have made it very difficult to obtain data that would provide clues to the biology of Trigonia. Most of the evidence cited here and elsewhere in this treatment about the ecology and biology of Trigonia has been obtained from label data and personal observations on a few individuals of four species.

Biological species as defined by Mayr (1963), Simpson (1953) and others may be best exemplified by Mayr's (1963) definition as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." However, plant taxonomists find this concept difficult to accept in its totality. Hybridization between species with production of viable hybrids that are capable of successful reproduction is not an uncommon phenomenon in the plant kingdom (Grant, 1963, and 1971; Anderson, 1968). The heterotrophic mode of obtaining energy and the importance of locomotion have placed heavy restrictions on hybridization in animals, as they are in most cases highly adapted (Cronquist, 1968). Plants are for the most part nonmotile, and share similar mechanisms for obtaining energy. Hybrids are usually present in disturbed or intermediate habitats to which neither parent is fully adapted, if capable of living there at all (Grant, 1963; Anderson, 1968).

Thus, we encounter a series of problems with the concept of biological species as defined above. Essentially, it does not allow the existence of hybrids in that the basic requirements is reproductive isolation. The term "potentially" implies that if conditions were appropriate (such as the elimination of an ecological barrier, or a "catastrophic" disruption of the environment) any two populations that are capable of interbreeding must constitute elements of the same species. Cronquist (1968) has defined the species in its biological sense as "the smallest population which is permanently (in terms of human time) distinct and distinguishable from all others." This definition makes it possible to accept hybridization, while recognizing that a degree (reasonable, according to Cronquist, 1968) of reproductive isolation must always exist. Although I question the use of population (which I define as a group of organisms sharing a common gene pool, and consider that gene flow should be an actual process, and not "actual and potential" as can be inferred in Cronquist's definition), and would replace it with "population or group of populations", I find Cronquist's definition to reflect my own point of view on species.

I choose here to consider the species recognized in Trigonia as taxonomic species, a concept proposed by Grant (1963), primarily on morphological evidence. The data available at present is insufficient to establish all of the biological taxa in the genus. However, I am inferring that the species proposed here do (for the most part) represent self-perpetuating populations or groups of populations reproductively isolated from other such groups.

I have recognized both subspecies and varieties as infraspecific categories in Trigonia. Although these two terms have been the objects of continued discussions (eg Grant, 1963; Cronquist, 1968) no agreement has been reached as to the usage of these terms. I have used the term subspecies

to separate taxa that are allopatric and almost completely distinct morphologically, but that I believe are elements of the same species. The term variety has been used here to separate taxa that are geographically sympatric (but presumably not occupying the same niche) or allopatric, and in which a morphological distinction is not always possible.

INTRODUCTORY COMMENTS TO THE SYSTEMATIC TREATMENT

The following brief comments are given to aid the user of the key and to clarify the descriptions.

Since sterile material is not adequately represented in collections, and sterile shoots and vegetative branches often have much larger leaves, leaf size measurements are taken from fertile branches only.

In the species descriptions and keys, the surface of the venation is treated separetely from the description of the intercostal pubescence; thus, "leaf glabrous" will refer to intercostal surfaces, but not to the venation unless otherwise stated.

The petals are treated using nomenclature applicable to papilionaceous flowers, thus the terms standard, keel, and wings; when the throat is mentioned in relation to the standard, this indicates all of the area surrounding the mouth of the pouch.

The term peduncle refers to the primary axis from which the pedicels of the flowers arise. The term panicle is here used to describe elongate mixed panicles, often leafy-bracteate below. These inflorescences have the primary branches and the terminal part of the main axis well spaced, elongate, narrow and raceme-like. Thyrse is used to describe inflorescences having the primary branches and the terminal part of the main axis with evident ramified secondary branches. These thyrsoid inflorescences are more compact or dense than the panicles.

Dichasium here describes ultimate inflorescences (or flower groups) having what has traditionally been considered a complete or a compound

dichasium. Cymule is here used to describe modified or reduced dichasia in which some of the flowers have been lost. The term cincinnus is here applied to helicoid cymes (or flower groups) in which a spiral or helicoid arrangement of the flowers can be inferred even when only 2 or 3 flowers are present.

The descriptive terminology for inflorescences here used is not wholly in agreement with the usage of other authors (Lawrence, 1951; Rickett, 1944; Gray, 1875), as the inflorescences of the Trigoniaceae do not fit any standard definition. The terms used are therefore the closest descriptive terms found in the literature, slightly modified as to their interpretation and usage in order to meet the needs for the family.

Laciniae, when used in respect to the floral glands, refer to the fairly short, often solitary, filamentous structures found at the apex.

In species with few collections, all herbarium material examined has been cited; in common species, only selected specimens are cited in the text.

Abbreviations used.

fl = flowering

fr = fruiting

st = sterile

bds = buds

Herbaria abbreviations are those of Index Herbariorum (Holmgren & Keuken, 1974).

Table 2. Comparison of characters between species of Trigonia.

BEL = Broadly elliptic

CHA = Chartaceous

CIN = Cincinnus

DI = Dichasium

ECH = Echinate

EL = Elliptic

EN = Entire

ER = Erect

GLO = Globose

L = Large

M = Medium (size)

MEM = Membranaceous

NA = Not applicable

NAS = Nasiform

OBL = Oblong

OBLEL = Oblong-elliptic

OBO = Obovate

OV = Ovate

OVEL = Ovate-elliptic

PA = Panicle

R = rotund

RA = Raceme

RV = Revolute

S = Small

Sb = Shrub

SCO = Subcoriaceous

SS = Scandent shrub

TH = Thyrse

Tr = Treelet

V = Villous

VA = Variable

\+ = present

\- = absent

Characters / Species	LEAF										INFLORESCENCES			
											Principal		Ultimate	
	Petiole L/mm	Lamina shape	length cm	width cm	L/w ratio	Consistency	Margin	pubescence above	pubescence below	No. of secondary veins	Type	Length cm	Type	
Coppenamensis	10-22	EL-OBO -R	5.5-15	2.5-12	VA	SCO	EN	+	+	6-9	TH	to 12	DIC	4
Rotundifolia	7-30	R	6-15	5-11	6:5	CHA	EN	-	+	6-9	PA	5-15	CIN	1-
Hypoleuca	5-12	OBLEL -OBO	8-18(20)	4-10	2:1	SCO	EN	-	+	7-8	PA	to 30	CIN	1-
Candelabra	8-15	EL-OBO	8-21	4-10	2:1	SCO	EN	-	+-	6-9	TH	5-9	COMP DIC	se
Bracteata	12-14	EL-OBO	12-18	4.5-9	2:1	SCO	EN	-	+	6-8	PA	8-17	CIN	1
Virens	5-8(10)	EL-BEL	8-16	4-9	2:1	CHA	EN	-	+	6-9	PA	2-15	DIC	1
Macrantha	12-18	EL-OVEL	9-13	3.7-7	2:1	CHA	EN	-	+	6-9	PA; RA	to 20	DIC	1
Prancei	8-15	EL-OBO	6-11	3-6	2:1	SCO	EN	-	-	5-6	TH	5-15	DIC	1
Rytidocarpa	5-10(15)	OBLEL-EL-BEL	5-11	2.5-5 (-7)	2:1	SCO	EN-SRV	-	+	6-8	PA	5-15	CIN	1-
Laevis	4-8	BEL-OVEL	4-9	2.2-4.5	2:1	SCO	EN	-	-	4-6(7)	PA(TH)	to 30	CIN	1
Echiteifolia	6-10	OV-OB-OBL	5-12	2-6	2:1	SCO	EN-RV	-(+)	+	10-12	PA	to 10	DIC	1
Flocossa	5-15	OV-OBO	4-13	2-6	2:1	SCO	EN	+	+		TH	to 12	DIC	1
Rugosa	5-25	OBLEL-OBO	5-15	4-8	2:1	SCO -CHA	EN	-	+	6-9	TH	7-25	DIC	1
Sericea		EL-BEL	6-19	4-11	2:1	SCO	EN	-	+-	8-11	PA	to 10	DIC	C
Sprueceana	5-13	EL-OVEL	7-14	2.5-5	2:1	SCO	EN	-	+-	9-11	PA	to 25	CIN	1
Reticulata	9-18	OV-EL	4.5-11	3-6.5	1.9-1	SCO	RV	-	+	(9) 9-11 (12)	TH	4-15	DIC	S
Subcymosa	3-4	EL-OBO	3-8	2-4	2:1	CHA	EN	+	+	8-10	PA	to 15	DIC	
Villosa	3-10	EL-OBO	6-14	2-8.5	1.7:1	SCO	EN	+	+	6-9	PA	to 25	CIN	
Nivea	2-8	EL-OBLEL	5-13	2-4.5	VA	SCO	EN-RV	-	+	10-16	PA, RA	5-10	CIN	
Paniculata	5-8	OBL-EL	5-10	2.5-5	2:1	CHA	RV	+(-)	+	8-9	PA	6-15	CIN	
Eriosperma	2-5	OBLOV -OBLEL	1.5-9	1-3.5	2.5:1	MEM -CHA	EN	+	+	4-7	TH, PA, RA	1.5-10	DIC	
Boliviana	5-8	EL-OBLEL	4-7	2-3.5	2:1	CHA	EN	+	+	7-8(9)	RA	4-8	CIN	
Killipi	6-8	OBLEL-EL	6-13	3-7.5	2:1	SCO	EN	+	+	14-16	PA, RA	to 10	DIC	
Costanensis	15-20	OBLEL-OBL	8-15	4-8	2:1	CHA	EN	-	+	6-8	TH	10-15	DIC	

No. of	INFLORESCENCES Principal Type	Principal Length cm	Ultimate Type	Ultimate No. of flowers	FLOWER Relative Size	Peduncles L/mm	Pedicels L/mm	bracts L/mm	bracteoles L/mm	shape standard pouch	standard apex	wing pubescence	Stamens Number	Stamens No. fertile	Stamens No. of staminodes	Appendages on staminode	Anthers length/mm
7	TH	to 12	DIC	4-6	NA	4-8	2.5-5.5	3-6	3-6	GLO	NA	+	9-10	6	3-4	—	NA
7	PA	5-15	CIN	1-2 (3)	L	0-1.5	1-2.5	2.5-3	1-2	GLO	RV	+	9-10	6-7	3-4	+	0.8-1.
8	PA	to 30	CIN	1-4	L	2-2.5	2-4.5	1-2.5	1-2.5	GLO	RV	+	10-11	6-7	3-4	+	0.5-0
7	TH	5-9	COMP DIC	several	L	0.2-2	1-2.5	1.5-2.5	0.8-1.5	GLO	sRV	—	8-10	6	2-4	—	0.8-1
8	PA	8-17	CIN	1-4	M	0.1-1	2-3	2-5(7)	1.5-3	GLO	RV	—	8-10	6	2(4)	—	0.5-
9	PA	2-15	DIC	1-3	L	2-4	2-4	1.5-3	1-2.5	GLO	ER	+	8	8	0	—	0.6-
9	PA, RA	to 20	DIC	1-4	L	0-1	to 1	3-4	1.2-2.3	GLO	ER	+	10-12	6-7	4-5	—	0.8-
6	TH	5-15	DIC	1-2	L	0.5-2	1.5-2	1.5-2	0.8-1.3	GLO	ER	—	8-10	6	2-4	—	0.5-
8	PA	5-15	CIN	1-4	S	0.4-1.5	0.4-1.5	1-2.5	1-2.5	NAS	ER	+	9-10	6	3-4	—	0.2-
(7)	PA(TH)	to 30	CIN	1-7	S	0.2-0.5	0.8-2	1-3	0.3-1	NAS	sRV	+	8-9	5-7	1-3	—	0.4-
12	PA	to 10	DIC	1-4	L	0.5-1	0.5-1	2.5-3.5	1.5-2	GLO	ER-RV	+	8-10	5-7	2-3	—	0.5-
	TH	to 12	DIC	1-2	L	NA	1-1.5	2.5-10	2.5-10	GLO	sRV	+	8-9	6-7	2	—	0.8-
9	TH	7-25	DIC	1-3	M	0.7-2	1-2	0.8-1.5	0.8-1.5	GLO	RV	+	8-10	6	2-4	+(-)	0.4-
11	PA	to 10	DIC	(3) 6-7 (10)	L	2.5-4	0.9-1.2	1.5-2	1.5-2	GLO	ER-RV	+	10	6	4	—	0.6-
11	PA	to 25	CIN	1-4	L	0.1-2.5	1.5-2.5	2-3	0.7-1.4	GLO	RV	+	6-7	6-7	0	—	0.8
9-(12)	TH	4-15	DIC	several	L	0.3-1	1-2.5	1-2.5	1-1.5	GLO	sRV	+	8-10	6	2-4	+(-)	0.5-
10	PA	to 15	DIC	2-4	S	1-8	1-2	2-3	2-3	GLO	ER	—	8	5-6	2-3	—	0.4-
9	PA	to 25	CIN	1-3	L	0.5-3	1.8-2.8	2-3	1-2	GLO	RV	+	10-11(12)	6-7	3-4	—	0.5
16	PA, RA	5-10	CIN	1-4	L	0-5	1-5	2-6	1-4	GLO	sRV	+	10-11	6-7	3-4	—	0.4
9	PA	6-15	CIN	1-2	M	0-0.4	1-1.8	1.5-2.5	1.5-2.5	NAS	ER	+	9-10	6-7	3-4	—	0.2
7	TH, PA, RA	1.5-10	DIC	1-3	S	1-6	3-4	0.7-4	0.2-1	GLO	ER	+	9-10	6	3-4	+	0.2
8(9)	RA	4-8	CIN	1-2	S	0.1-1	1-2	3-5	1-2	GLO	ER	+	8-9	6-7	2	—	ca
16	PA, RA	to 10	DIC	1-3(4)	L	0.1-0.5	0.5-1	4-4.5	4-4.5	GLO	ER-RV	+	8	6-7	1-2	—	0.6
8	TH	10-15	DIC	1-3	L	2-4	1-2	3-5	2-3.5	GLO	ER	+	8-9	6	2-3	—	0.8

Stamens										FRUIT						Seed pubescence	HABIT
No. fertile	No. of staminodes	Appendages on staminode	Anthers length/mm	Anthers width/mm	Anthers L/w ratio	Glands laciniae	No. of locules in ovary	style length/mm	style pubescence	shape	length/cm	width/cm	exocarp pubescence	endocarp pubescence	No. seeds locule		
6	3-4	—	NA	NA	NA	—	3	NA	—	NA	NA	NA	NA	NA	NA	NA	SS
5-7	3-4	+	0.8-1.1	0.4-0.5	2:1	—	4	1.8-2.1	+	NA	NA	NA	NA	NA	NA	NA	NA
5-7	3-4	+	0.5-0.7	0.3-0.4	2-1	+	1	1.5-1.8	—(+)	OBL	5-7	2.5-3	—	—	20	ECH	Sb SS
6	2-4	—	0.8-1.5	0.6-0.9	1.5-1	+	3	1.3-1.6	+	OBL-OV	6.5-8	0.8-1	+	—	-10	V	SS
6	2(4)	—	0.5-1	0.3-0.4	2.5-1	—	3	1.8-2	+	NA	NA	NA	NA	NA	NA	NA	Sb
8	0	—	0.6-0.8	0.4-0.5	2:1	—	1	1.8-2	—	OBL	7-8	0.8-1	—	—	NA	NA	SS
5-7	4-5	—	0.8-1	0.4-0.5	2:1	—	3	1.5-1.8	—	OBL	7-9	0.8-1	+	—	-20	V	Sb Tr
6	2-4	—	0.5-0.7	0.2-0.3	2.5:1	+	3	1.5-1.8	+	OBL	8.5-9	1-1.2	+	—	-20	V	Sb
6	3-4	—	0.2-0.3	0.2-0.3	1:1	—	3	1.5-1.8	+	OBL	2.8-3	0.8-1	—	+	-5	V	SS
5-7	1-3	—	0.4-0.5	0.4-0.5	1:1	—	3	1-1.3	+	OBL-OBO	0.6-3	0.6-1	—	—	1-4	V	SS
5-7	2-3	—	0.5-0.8	0.3-0.4	2:1	—	3	1.8-2	+	NA	NA	NA	NA	NA	NA	NA	NA
5-7	2	—	0.8-1	0.4-0.5	2:1	—	3	1.8-2	+	OBL	5-6	1-1.2	+	—	8-10	V	SS
6	2-4	+(-)	0.4-0.5	0.2-0.3	2:1	—	3	1.2-1.3	—+	OBL	2-3.2	1-2	—	—	6-9	V	SS
6	4	—	0.6-0.8	0.3-0.4	2:1	+	3	1.5-1.7	—(+)	OBL	3-7	0.5-1.5	+	—	-20	V	Sb Tr
5-7	0	—	0.8-1	0.5-0.8	1.5:1	—	3	2.8-3	+	OBL	7-9	1.4-2	+	—	-20	ECH	SS
6	2-4	+(-)	0.5-0.7	0.3-0.4	1.6:1	—	3	1.0-1.2	+	NA	NA	NA	NA	NA	NA	NA	SS
5-6	2-3	—	0.4-0.5	0.2-0.3	2:1	—	3	0.8-1.1	+—	NA	NA	NA	NA	NA	NA	NA	Sb
6-7	3-4	—	0.5-0.7	0.4-0.5	1.7:1	—	3	2.5-2.8	—+	OBL	4.5-11	0.6-2	+	+	-20	V	Sb
5-7	3-4	—	0.4-0.7	0.3	1:1-2:1	+—	3	1-2	—	OBL	3-7	1-1.5	+	+	-10	V	SS
5-7	3-4	—	0.2-0.3	0.2-0.3	1:1	—	3	0.9-1.1	—	OBL	1.5-2	0.8-1	—	—	1-2(3)	V	Sb, SS
6	3-4	+	0.2-0.3	0.2-0.3	1:1	—	3	0.9-1.2	—	OBL	0.8-2.5	0.6-0.7	—	—	1-4	V	Sb Tr
5-7	2	—	ca 0.3	ca 0.3	1:1	—	3	1.9-2.1	—	OBL	2-2.5	0.8-1	—	—	3-5	V	Sb
5-7	1-2	—	0.6-1.1	0.6-0.7	2:1	—	3	2.6-3	+	OBL	10-11	0.9-1	+	—	NA	V	SS
6	2-3	—	0.8-1.0	0.4-0.5	2:1	—	3	1.8-2	—	NA	NA	NA	NA	NA	NA	NA	SS

SYSTEMATIC TREATMENT

TRIGONIACEAE Endlicher, Enchir. Bot. 570. 1841; Martius, Conspec. 51. 1835 (nomen nudum); Endlicher, Gen. Pl. n. 5659. 1840 (nomen nudum); Grisebach, in Linnaea 22: 27. 1849; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 122. 1875; Chodat, Bull. Herb. Boiss. 3: 136. 1895; Barth, Bull. Herb. Boiss. 4: 481. 1896; Petersen, (Trigoniaceae) Engler & Prantl, Nat. Pflanzenfam. 3 (4): 309. 1896; Standley, (Trigoniaceae) North Am. Fl. 25 (4): 297. 1924; Van Steenis, (Trigoniaceae), Fl. Malesiana 1 (4): 58. 1949; Stafleu, (Trigoniaceae) Pulle Fl. Suriname 3 (2): 174. 1951; Perrier & Leandri, (Trigoniaceae) Fl. de Madagascar 108bis: 1. 1955; Reitz, Fl. Ilustr. Catarinense 1 (13) 3: 1967; Austin, (Trigoniaceae) Fl. Panama, Ann. Missouri Bot. Gard. 54 (3): 207. 1967; Ng, (Trigoniaceae) Tree Fl. Malaya 1: 448. 1972.

Trigoniaceae tribe Trigoniae Chodat, Bull. Herb. Boiss. 3: 138. 1895.

Trigoniaceae tribe Trigoniastrae Chodat, Bull. Herb. Boiss. 3: 138. 1895.

Trigoniaceae tribe Lightiae (sic) Chodat, Bull. Herb. Boiss. 3: 138. 1895.

Flowers obliquely zygomorphic, hypogynous to subperigymous, plane of symmetry through the third sepal, receptacle of varied shape and size, slightly gibbous at base. Calyx gamosepalous, quincuncial, the base cupulate; sepals imbricate in bud, unequal. Corolla papilionacious; petals 5, contorted in bud; the two anterior petals forming a keel, often saccate, the posterior or standard petal saccate, the two lateral petals or wings spathulate. Stamens 5-8, monadelphous and 0-4 staminodes, unilateral, opposite the keel petals; filamental tube subperigynous; anthers introrse, 2-locular, longitudinally dehiscent. Pollen 3-4-porate, the exine smooth or slightly verrucose. Disc glands opposite the standard, sometimes laciniate. Ovary superior, basically trilocular, seldom 4-locular, if 1-locular, then by reduction of the parietal septa; central column absent. Ovules 1-numerous, biseriate, anatropous, attached

to the interior ends of the lateral septa. Style terminal, simple; stigma capitate. Fruit a septicidal capsule or 3-winged samara. Seed exalbuminous; embryo straight, longitudinal or transverse to the length of the seed, cotyledons plane, thin, the radicle very short.

Trees, treelets, shrubs, or scandent shrubs. Branches terete, lenticellate. Leaves simple, entire, alternate or opposite, often subcoriaceous, glabrous or pubescent, pinnately veined. Stipules present, interpetiolar, often connate, deciduous or caducous. Inflorescences thyrses, panicles or racemes, sometimes reduced to cymes; flowers bibracteolate.

Twenty six species in three genera found in lowland wet forests or humid riverine forests or forest edges in the Neotropics and Paleotropics.

TYPE.GENUS.. Trigonia Aublet. The name is derived from the Greek words Trias- (three) and Gonos- (angles), and refers to the three-sided or angular fruit.

Key to the Genera of Trigoniaceae

1. Leaves opposite; New World and Madagascar.
   2. Fruit a loculicidal capsule; ovary lacking lateral ridges; ovules more than one per locule; tropical and subtropical America. 1. Trigonia.
   2. Fruit a three-winged samara; ovary with lateral ridges; ovules one per locule; Madagascar. 2. Humbertodendron.
1. Leaves alternate; Malaysia. 3. Trigoniastrum.

1. Trigonia Aublet, Hist. Pl. Guian. Fr. 387. 1775; H.B.K., Nov. Gen. 5: 141. 1821; De Candolle, Prod. 1: 571. 1824; Cambessèdes, in St. Hil. Fl. Bras. Mer. 2: 112. 1829; Endlicher, Gen. Pl. n. 5659. supl. 4 (3): 82. 1840; Grisebach,

in Linnaea 22: 27. 1849; Bentham and Hooker, Gen. Pl. 1: 977. 1867; Baillon, Hist. Pl. 5: 103. 1874; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 122. 1875; Barth, Bull. Herb. Boiss. 4: 481. 1896; Petersen, (Trigoniaceae) Engler & Prantl, Nat. Pflanzenfam. 3 (4): 309. 1896; Standley, (Trigoniaceae) North Am. Fl. 25 (4): 297. 1924; Stafleu, (Trigoniaceae) Pulle Fl. Surin. 3 (2): 174. 1951; Reitz, (Trigoniaceae) Fl. Ilust. Catar. 1 (13): 3. 1967; Austin, (Trigoniaceae) Fl. Panama, Ann. Missouri Bot. Gard. 54 (3): 207. 1967.

Hoeffnagelia Necker, Elem. Bot. 3: 68. 1790

Nuttalia Sprengel, Neue Entdeck. 2: 158. 1821.

Mainea, Vellozo, Fl. Flum. 275. 1829.

Treelets, shrubs, or scandent shrubs, the branches terete, and conspicuously lenticellate. Leaves simple, opposite, petiolate, the margins entire; stipules interpetiolar, deciduous or caducous, often connate, simple or bifid at the apex. Inflorescences thyrses, panicles or racemes. Flowers ultimately disposed in dichasia (simple or compound), cymes or cincinni; bracts glandular or eglandular at the margins; sepals 5, quincuncial; unequal; petals 5, contorted, unequal, papilionaceous, fertile stamens 5-8, staminodes present or absent, when present to 4, the filaments connate at base, the anthers basifixed, bilocular, introrse, dehiscing along a central slit; pollen 3-4-porate, smooth; glands usually 2, lobed, sometimes laciniate; ovary 1-, 3- or 4-locular, when 1-locular by reduction of the lateral septa, these when present fused or open at the center; central column absent; ovules numerous to few in each locule, biseriate, anatropous, attached to the interior ends of the lateral septa. Fruit a septicidal capsule, dehiscing (in situ) from the apex towards the base. Seeds 2 to several per locule, pubescent.

TYPE SPECIES. Trigonia villosa Aublet

DISTRIBUTION. Southern Mexico to northern Paraguay, usually in low-altitude forests. The pubescent seeds, suggestive of wind dispersal, as well as collection data and personal observations, seem to indicate that this genus is restricted to open forest edges or gallery forests. It is usually recorded from river margins, edges of clearings, and along roadsides and other disturbed areas.

Key to the Species of *Trigonia*

1. Leaves rotund or subrotund, length/breadth ratio ca 6:5-6:4.
   2. Branches densely golden-strigose; inflorescence a thyrse; flowers disposed in dichasia; peduncles 4-8 mm long; bracts and bracteoles navicular. 1. *T. coppenamensis.*
   2. Branches white-lanate, becoming glabrous; inflorescence a panicle; flowers disposed in cincinni; peduncles 0-1.5 mm long; bracts and bracteoles subulate or linear. 2. *T. rotundifolia.*
1. Leaves ovate to obovate, elliptic or oblong-elliptic, length/breadth ratio ca 2:1.
   3. Leaves glabrous beneath.
      4. Ultimate inflorescences dichotomous dichasia; wing petals glabrous at base; glands laciniate. 3. *T. prancei.*
      4. Ultimate inflorescences cymules or cincinni; wing petals barbate at base; glands not laciniate.
         5. Flowers disposed in cymules; standard erect; style glabrous.
            6. Petioles 5-8 (-10) mm long; bracts 1.5-3 mm long; peduncles 2-4 mm long; stamens 8, staminodes absent; ovary unilocular. 4. *T. virens.*
            6. Petioles (10-) 12-18 mm long; bracts 3-4 mm long; peduncles 0-1 mm long; stamens 10-12; staminodes present; ovary trilocular. 5. *T. macrantha.*
         5. Flowers disposed in cincinni; standard revolute; style villous.
            7. Secondary leaf veins 4-7 pairs; standard pouch nasiform; stamens 8-9, staminodes present; fruit 0.6-3 cm long; seeds villous. 6. *T. laevis.*

7. Secondary leaf veins 9-11 pairs; standard pouch globose; stamens 6-7, staminodes absent; fruit 7-9 cm long; seeds echinate. 7. T. spruceana.

3. Leaves pubescent beneath.

8. Inflorescence of thyrses.

9. Flowers in dichasia.

10. Leaf margins revolute; tertiary and quaternary leaf venation very evident; bracts, bracteoles and sepals papillose-glandular. 8. T. reticulata.

10. Leaf margins plane; tertiary and quaternary venation not especially evident; bracts, bracteoles and sepals not papillose-glandular.

11. Leaf pubescence tomentellous (sometimes almost glabrous); wing petals glabrous at base; staminodes lacking appendages, anthers 0.8-1.5 mm long, glands laciniate; fruit 6.5-8 cm long, velutinous-tomentose. 9. T. candelabara.

11. Leaf pubescence appressed-lanate (sericeous) sometimes almost glabrous; wing petals barbate at base; staminodes often appendiculate; anthers 0.4-0.5 mm long; glands not laciniate; fruit 2-3.2 cm long, glabrous. 10. T. rugosa.

9. Flowers disposed in cymules or cincinni.

12. Branches densely golden-strigose, lenticels never visible; bracts and bracteoles navicular. 1. T. coppenamensis.

12. Branches not densely golden-strigose, becoming glabrous with age, lenticels visible; bracts and bracteoles not navicular.

13. Standard pouch nasiform; anthers subglobose, 0.2-0.3 mm long, staminodes appendiculate; petiole 2-5 mm long; (thyrses often reduced to panicles or racemes). 11. T. eriosperma.

13. Standard pouch globose; anthers elliptic, 0.8-1 mm long; staminodes not appendiculate; petioles 5-10 mm long; (thyrses never reduced to panicles or racemes).

14. Leaves with mixed intercostal pubescence beneath, lanate & strigose; peduncles absent or nearly so; bracts and bracteoles 5-10 mm long; sepals papillose-glandular at the margins; style villous. 12. T. floccosa.

14. Leaves lanate, with only 1 type of pubescence; peduncles 2-4 mm long; bracts and bracteoles less than 5 mm long; sepals not glandular; style glabrous. 13. T. costanensis.

8. Inflorescences panicles or racemes.

15. Leaves pubescent above.

16. Flowers disposed in cymules.

17. Inflorescences terminal pyramidal panicles; wing petals glabrous at base; stamens 8. 14. T. subcymosa.

17. Inflorescences terminal and axillary panicles and racemes, not pyramidal; wing petals barbate at base; stamens 9-11.

18. Secondary leaf veins 4-7 pairs; staminodes appendiculate; glands lacking laciniae. 11. T. eriosperma.

18. Secondary leaf veins 10-16 pairs; staminodes not appendiculate; glands laciniate. 15. T. nivea.

16. Flowers disposed in cincinni.

19. Secondary leaf veins 14-16 pairs. 16. T. killipii.

19. Secondary leaf veins 4-12 pairs.

20. Leaves oblong to elliptic, the leaf pubescence dark olive-green beneath (or seemingly so) in exsiccatae, distinctly white-lanate at the margins; fruit truncate at base. 17. T. paniculata.

20. Leaves broadly elliptic to obovate, the leaf pubescence light yellowish-green or white beneath in exsiccatae, glabrous at the margins; fruit not truncate at base.

21. Bracts 2-3 mm long; standard revolute; stamens 10-11; style 2.5-2.8 mm long; fruit 4.5-11 cm long; the valves not cornate at apex. 18. T. villosa.

21. Bracts 3-5 mm long; standard erect; stamens 8-9; style 1.9-2.1 mm long; fruit 2-2.5 cm long, the valves distinctly cornate at the apex. 19. T. boliviana.

15. Leaves glabrous above.

22. Staminodes absent; inflorescences, when terminal, borne on short axillary branches; when axillary 1 per node, unilateral. 4. T. virens.

22. Staminodes present; inflorescences, when terminal, not borne on short axillary branches; when axillary 2 per node, bilateral.

23. Flowers noticeably caducous, the bracts and bracteoles then forming rosettes on the axes; bracts and bracteoles papillose-glandular; the wing petals glabrous at base. 20. T. bracteata.

23. Flowers not noticeably caducous, bracts and bracteoles not forming rosettes on the axes; bracts and bracteoles not papillose-glandular; wing petals barbate at base.

24. Leaves sparsely arachnoid-pubescent beneath.

25. Petioles 12-18 mm long; flowers disposed in cymules, bracts never laciniate, 3-4 mm long, not sheathing the peduncles or pedicels; anthers 0.8-1 mm long; fruit 7-9 cm long; exocarp velutinous-tomentose. 5. T. macrantha.

25. Petioles 5-10 (-12) mm long; flowers disposed in cincinni; bracts often laciniate; 1-2.5 mm long, sheathing the peduncles and pedicels; anthers 0.2-0.3 mm long; fruit 2.8-3 cm long; exocarp glabrous. 21. T. rytidocarpa.

24. Leaves lanate or appressed lanate (sericeous) beneath.

26. Ovary 1-locular; staminodes appendiculate; fruit with the exocarp flush with the endocarp. 22. T. hypoleuca.

26. Ovary imperfectly 3-locular; staminodes not appendiculate; fruit with the exocarp shorter than the endocarp.

27. Flowers disposed in cymules.

28. Leaves densely brownish yellow-lanate beneath; peduncles 0.5-1 mm long; bracts subulate or linear, 2.5-3.5 mm long; glands not laciniate; ovary with septa not fused at center. 23. T. echiteifolia.

28. Leaves white appressed-lanate beneath; peduncles 2.5-4 mm long; bracts ovate, 1.5-2 mm long; glands laciniate; ovary with septa fused at center. 24. T. sericea.

27. Flowers disposed in cincinni.

29. Stamens 6-7, all fertile; glands never laciniate; style 2.8-3 mm long, villous; fruit 7-9 cm long; seeds echinate pubescent; leaves sometimes becoming glabrous. 7. T. spruceana.

29. Stamens 10-11; staminodes present; glands often laciniate; style 1-2 mm long, glabrous; fruit 3-7 cm long, seeds villous. 15. T. nivea.

1. Trigonia coppenamensis Stafleu, Rec. Trav. Bot. Neerl. 42: 70. 1950; Stafleu, Med. Bot. Mus. Utr. 105: 70. 1950; Stafleu, in Pulle Fl. Surin. 3 (2): 176. 1951.

Scandent shrub, the branches striate, (almost angular), not conspicuously lenticellate, ferruginous-strigose. Stipules 4.0-7.0 mm long, 2.0-3.0 mm wide, triangular, strigose; petioles 10.0-22.0 mm long, ca 1.0 thick, striate to terete, strigose; lamina elliptic to obovate, sometimes almost circular, 5.5-15.0 cm long, 2.5-12.0 mm wide, subcoriaceous, the margins entire, the apex acute to acuminate, the base subrotund; venation eucamptodromous, densely golden strigose (including tertiary veins beneath), the midrib prominulous above, prominent beneath, secondary veins 6-9 pairs, plane above, prominulous beneath, the tertiary nervation impressed above, prominulous beneath. Inflorescences terminal and subterminal axillary thyrses, to 12 cm long. Flowers in dichasia of 4-6; peduncles 4.0-8.0 mm long, ca 0.5 mm thick, strigose; pedicels 2.5-5.5 mm long, ca 0.5 mm thick, strigose, the bracts and bracteoles of equal size, 3.0-6.0 mm long, 1.0-2.0 mm wide, linear-ovate (almost navicular), revolute at the margins, curved upwards towards the apex of the flower, strigose. Flower buds to 6.0 mm long; sepals ovate to oblong, ca 5.0 mm long, thickened at the nerves (appearing striate), strigose; standard with the pouch extending to 1/2 of the length, barbate at the throat, the wings spathulate, barbate at the base, the keel petals saccate; stamens 9-10, 6 fertile, staminodes 3-4, the anthers with a short knob-like projection at the apex; glands 2, 2-3-lobed; style glabrous; the stigma trilobate; ovary subglobose, densely villous, the ovules numerous. Fruit unknown.

TYPE. Maguire 24857, Suriname, Coppename River Headwaters, Mt. Schmidt, buds (holotype U; isotypes F, NY).

DISTRIBUTION. Known only from the type gathering.

This very distinct species can be recognized easily by its striate stems, petioles and sepals, as well as by its very large navicular bracts and bracteoles.

There is insufficient data to indicate the relationships for this species. Stafleu has suggested an affinity with Trigonia subcymosa based on the inflorescence and bracts, but without knowledge of the structure of the fruits, which are still unknown for the two species, it is premature to assign relationships.

2. Trigonia rotundifolia Lleras, sp nov

Rami juvenili adpressi-lanati, glabrescenti, lenticellati. Stipulae caducae (nv). Folia opposita, petiolo 0.7-3.0 mm long, ca 1.0 mm crasso, adpresso-lanato, glabrescenti; laminae rotundae, 6.0-15.0 cm longae, 5.0-11.0 cm latae, chartaceae, margine integre, apice rotundato usque emarginato varianti, basi obtusa, supra glabrae, infra adpresso-lanatae; costa media supra plana, glabra, infra prominula, adpressa-lanata, costis secundariis 6-9 jugis, eucamptodromis. Inflorescentiae in paniculis terminalibus vel axillaribus dispositae, 5.0-15.0 cm longae. Flores in cincinnos 1-2 (raro 3) dispositi; pedunculi 0.0-1.5 mm longi, 0.5-0.7 mm crassi, strigoso-tomentosi, bracteis 2.5-3.0 mm longis, ca 0.4 mm latis, strigosis; pedicelli 1.0-2.5 mm longi, 0.4-0.6 mm crassi, strigoso-tomentosi, bracteolis subulatis, 1.0-2.0 mm longis, strigosis; sepala ovata vel leviter oblonga, 3.5-4.2 mm longa, 1.5-2.0 mm lata, strigoso-tomentosa; vexillum 5.0-5.5 mm longum, 2.0-2.8 latum, usque ad medium longitudinaliter saccatum, apice revolute, intus barbato-tomentosum, alis petalis concavi-spathulatis, 5.0-5.2 longis, 1.0-1.5 mm latis, ad basem barbatis, carinae petala saccata, 3.5-4.0 mm longa, 2.0-2.2 mm lata, apice cristato; stamina 9-10, fertilia 6-7, sterilia 3-4, appendiculata, filamentis ad medium connatis, 1.8-2.2 mm longis, antheris oblongis, 0.8-1.1 mm longis, (0.3-) 0.4-0.4 mm latis, castaneis; glandulae 2, bilobae, reniformes, ca 0.5 mm longae, 0.8 mm latae, lanatae; stylus erectus, strigosus, 1.8-2.1 mm longus, stigma circulari, alba, ca 0.4 mm lata; ovarium subglobosum, ca 1.0 mm in diametro, 4-loculare, ovulis in quoque loculo numerosis. Fructus mihi ignotus.

TYPE. L.B. Smith & McWilliams 15441, Brazil, Rio de Janeiro, Mangaratiba, fl (holotype MO; isotype US).

DISTRIBUTION. Known only from the type gathering.

This distinctive species is characterized by its almost round leaves, and especially by the 4-locular ovary. At present it is impossible to establish its relationships within the genus, as no fruiting material is available for comparison.

FIG. 11. Trigonia rotundifolia Lleras sp nov. A, habit X 0.5; B, cross section of ovary X 20; C, flower X 5; D, sepals X 5; E, ovary X 5; F, stamens X 5; G, anthers X 10; H, glands X 10; J, keel petal X 5; K, wing petal X 5; L, standard X 5.

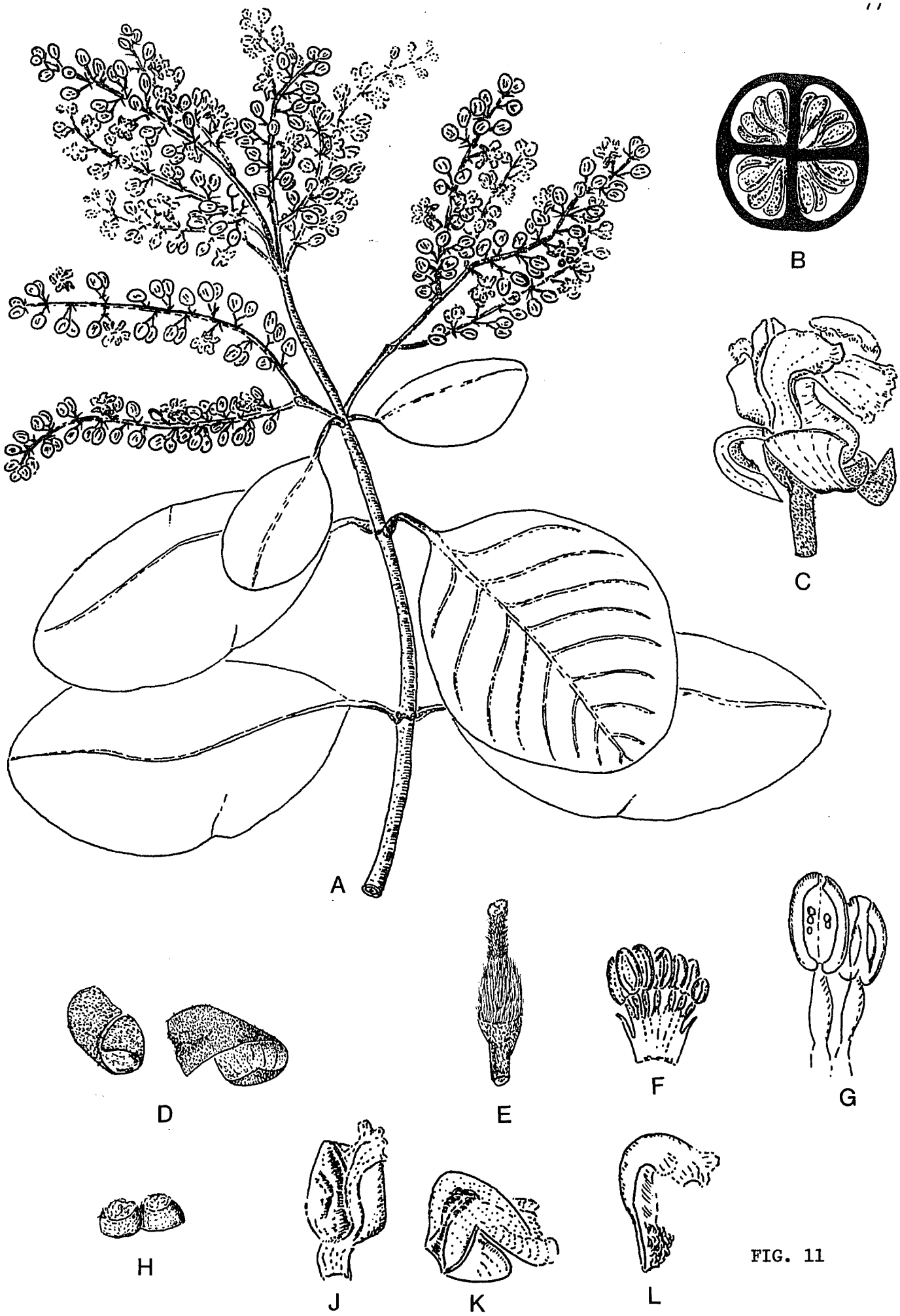


FIG. 11

3. Trigonia prancei Lleras, sp nov

Frutex, ramulis juvenilibus tomentellis, glabrescentibus, lenticellatis. Stipulae caducae, ca 5.0 mm longae, ad basem connatae. Folia opposita, petiolo 8.0-15.0 mm longo, 0.8-15.0 mm crasso, leviter tomentello; laminae ellipticae vel obovatae, 6.0-11.0 cm longae, 3.0-5.8 cm latae, subcoriaceae, margine integre, apice acuto usque acuminato varianti, basi obtusa vel obliqua, glabrae; costa media supra plana, infra prominentia, strigulosa, costis secundariis 5-6 jugis, eucamptodromis. Inflorescentiae in thyrsos terminalibus vel axillaribus dispositae, 5.0-15.0 cm longae. Flores in cymis 1-bifloris; ad extremum in inflorescentias secundarias dispositi, ab dichasiis dichotomis usque cymis solitariis variantes; axibus inflorescentiarum secundariarum 1.5-4.0 (-7.0) mm longi, 1.0-3.0 mm crassis, tomentellis; pedunculi 0.5-2.0 mm longi, 0.2-0.3 mm crassi, tomentelli, bracteis ovatis, 1.5-2.0 mm longis, tomentellis, caducis; pedicelli 1.5-2.0 mm longi, 0.2-3.0 mm crassi, tomentelli, bracteolis ovatis, 0.8-1.3 mm longis, tomentelli, bracteolis ovatis, 0.8-1.3 mm longis, tomentellis; sepala ovata vel leviter oblonga, 3.4-4.0 mm longa, 1.3-2.2 mm lata, tomentella vel strigulosa; vexillum 4.0-4.8 mm longum, 2.0-2.5 mm latum, usque ad medio longitudinaliter saccatum, apice erectus, intus barbatum, alis petalis spathulatis, 3.5-4.3 mm longis, 1.0-1.8 mm latis, glabris, carinae petala saccata, 3.2-3.5 mm longa, 1.1-2.0 mm lata; stamina 8-10, sterilia 2-4, fertilia 6, filamentis usque ad 2/3 longitudinorum connatis, 1.2-1.5 mm longis, antheris oblongis, 0.5-0.7 mm longis, 0.2-0.3 mm latis; glandulae 2, bilobae, reniformes, laciniatae, ca 0.3 mm longae, 0.4 mm latae; stylus erectus, 1.5-1.8 mm longus, villosus usque glaber varianti, stigma circulari, alba, ca 0.3 mm lata; ovarium subglobosum, ca 1.0 mm in diametro, 3-loculare, ovulis

in quoque loculo numerosis. Fructus 8.5-9.0 cm longus, ca 1.2 cm latus, extus velutino-tomentosus, intus cartilaginaceous, glaber. Semina ca 20 in quoque loculo, subglobosa, ca 3.0 mm in diametro, pilis ca 7.0 mm longis.

TYPE. Lleras, Steward et al P17115, Peru, Loreto, Río Javari, Angamo Garrison, fl, fr (holotype INPA; isotypes COL, F, K, MG, MO, NY, US).

DISTRIBUTION. Known only from type collection, which was from non-flooded ground in an open disturbed area at the edge of the forest.

This species is probably closely related to Trigonia sericea from which it differs in the type of inflorescence (thyrses, rather than panicles in T. sericea), the shorter peduncles, smaller bracts and bracteoles, and the larger fruit, the glabrous leaves, as well as other minor characters.

I am dedicating this species to Dr. Ghillean T. Prance, under whose auspices the type material was collected and whose help and guidance in this study have been invaluable.

FIG. 12. Trigonia prancei Lleras sp nov. A, habit X 0.5; B. flower X 5; C, ovary X 5; D, keel petal X 5; E, wing petal X 5; F, standard X 5; G, stamens X 5; H, anthers X 10; J, cross section of ovary X 20.

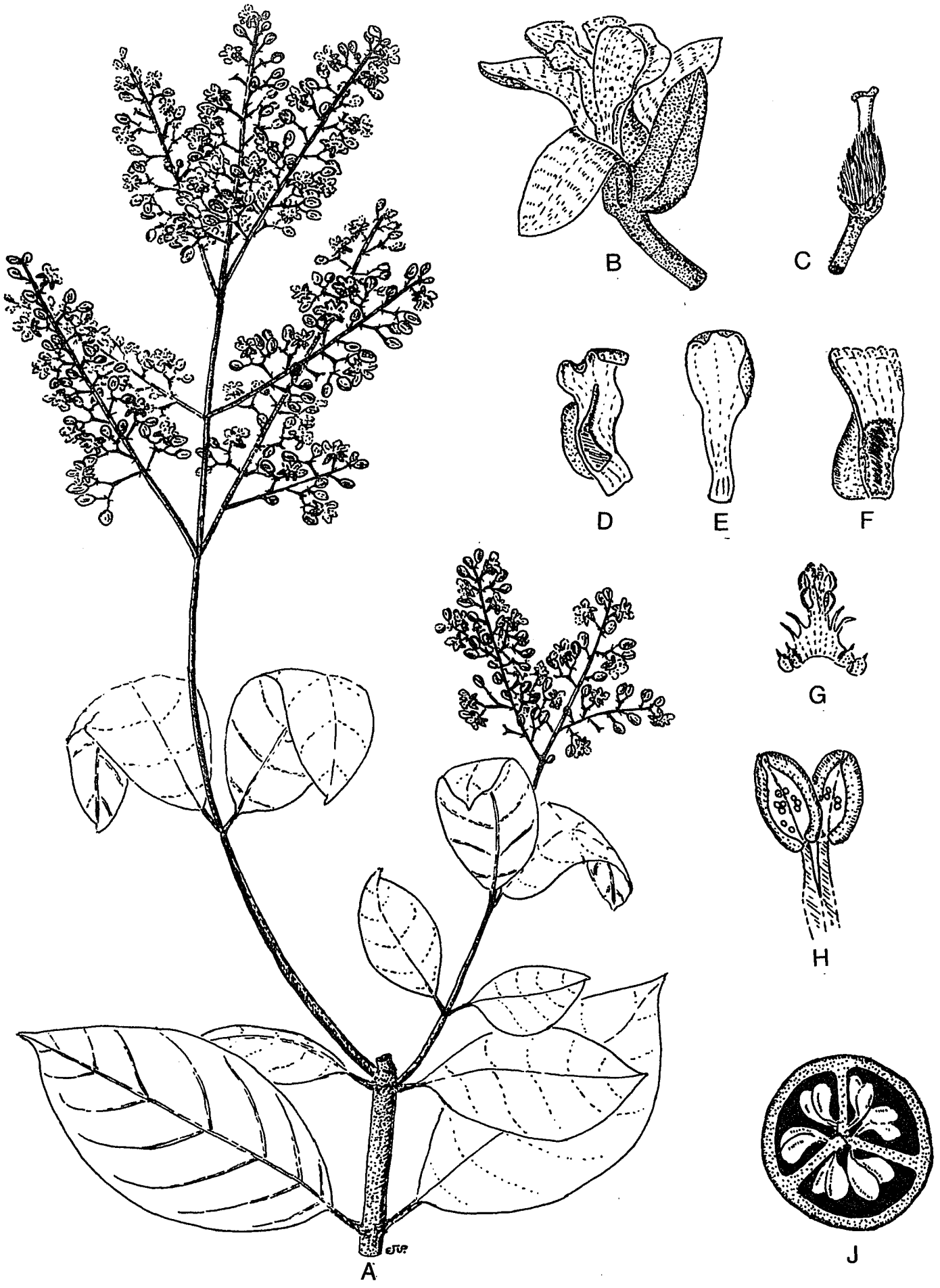


FIG. 12

4. Trigonia virens Macbride, Publ. Field Mus. Nat. Hist. Bot. 11 (2): 68. 1931; Smith, Phytologia 3: 130. 1935.

Trigonia crassiflora A.C. Smith, Phytologia 3: 129. 1935.

Scandent shrub, the branches terete, lenticellate. Stipules caducous (n.v.); petioles 5.0-8.0 (-10.0) mm long, 1.0-2.0 mm thick, densely strigose; lamina elliptic to broadly elliptic, 8.0-16.0 cm long, 4.0-9.0 cm wide, chartaceous, smooth, the margins entire, the apex acute to acuminate, the base acute to obtuse; venation eucamptodromus, slightly strigose-pubescent, the midrib plane above, prominulous beneath, the secondary nerves 6-10 pairs; intercostal pubescence absent on both surfaces, rarely with arachnoid pubescence beneath. Inflorescences condensed terminal and axillary panicles, when axillary, present only associated with one of the leaves of a pair, 2.0-15.0 cm long. Flowers in groups of 1-3 (usually 2); peduncles and pedicels of equal length, 2.0-4.0 mm long, 0.7-0.9 mm thick, densely strigose, the bracts 1.5-3.0 mm long, ovate, strigose, the bracteoles 1.0-2.5 mm long, narrowly ovate, strigose; sepals ovate to deltoid, the inner ones usually narrower, 4.0-5.5 mm long, 2.5-5.0 mm wide, the exposed portions strigose, the protected portions white-lanate-pubescent; standard 5.0-6.0 mm long, 4.0-5.0 mm wide, the pouch extending 2/3 of the length, the upper portion erect, the apex irregular, barbate-pubescent on the inside of the throat, the wings spathulate, 4.0-5.0 mm long, 3.0-3.5 mm wide, barbate at the inside of the base, the keel petals 4.0-5.0 mm long, 3.0-4.0 mm wide, the pouch extending down, the apex irregular; stamens 8, all fertile, the filaments 1.5-2.0 mm long, free at apex, the anthers ovate-elliptic,

0.6-0.8 mm long, 0.4-0.5 mm wide, adhering 4 on each side of the style; glands 2, 3-lobate, ca 0.9 mm high, 2.0 mm long, glabrous; style clavate, 1.8-2.0 mm long, ca 0.5 mm thick at the apex, the stigma trilobate, white; ovary ovoid, 1.0-1.2 mm high, ca 1.5 mm wide at base, barbate-pubescent, 1-locular, the ovules numerous. Fruit 7.0-8.0 cm long, the valves ca 10.0 mm per side; exocarp thin, coriaceous, glabrous; endocarp cartilaginous. Seeds not seen.

TYPE. Killip & Smith 29539. Peru, Loreto, fl (holotype US; isotypes F, G, NY).

DISTRIBUTION. Growing at low altitude, in humid periodically flooded forests in Colombia, Peru and Brazil. PERU. Loreto: Asplund 14281 fl (G, K, NY, P, US); Williams 2395 fl (F, G). BRAZIL. Amazonas: Krukoff 6149 fl (BR, F, G, K, M, NY, U, US, W); Krukoff 8424 fr (A, BR, G, MICH, MO, NY, P, U, US). Pará: Black & Ledoux 501680 fl (IPEAN); Santander: Haught 1800 fl (COL); Haught 1907 fl (US); Haught 2211 fl (F, US).

This species is easily distinguished by its large, glabrous leaves, its unilateral, condensed inflorescences, the presence of a clavate style, and the unilocular ovary. Trigonia crassiflora A.C. Smith is not taxonomically distinct and thus is here treated as a later synonym.

5. Trigonia macrantha Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 129. 1875.

Shrub or small tree, the branches terete, lenticellate. Stipules lorate, 6.0-8.0 mm long, 0.6-0.9 mm wide, tomentose, caducous; petioles 12.0-18.0 mm long, 0.6-0.8 mm wide, slightly tomentose or sometimes glabrous, lamina elliptic to ovate-elliptic, 9.0-13.0 cm long, 3.5-7.0 cm wide, chartaceous, slightly rugulose, the margins entire, the apex acuminate, the base obtuse; venation eucamptodromous, slightly strigose pubescent, the midrib plane to sunken above, prominulous beneath, the secondary nerves 6-9 pairs; intercostal areas arachnoid-pubescent on both surfaces, sometimes becoming entirely glabrous. Inflorescences terminal and subterminal axillary panicles, sometimes reduced to racemes, the subterminal ones 3-4 pairs. Flowers in cymules of 1-4 (usually 2-3); peduncles and pedicels of equal length, to 1.0 mm long, tomentose, the bracts lorate or subulate, 3.0-4.0 mm long, 0.6-1.3 mm wide, the bracteoles narrowly obovate to subulate, 1.2-2.3 mm long, 0.3-0.6 mm wide, tomentose; sepals ovate to deltoid, 3.0-5.5 mm long, 2.0-4.0 mm wide, tomentose, the apex rounded or acute, the base truncate; standard 5.0-6.0 mm long, 4.0-5.0 mm wide, the pouch extending to 1/2 the length, the upper portion erect, the apex slightly irregular, barbate-pubescent at the inside of the throat, the wings spathulate, the upper portion slightly convex, 3.0-4.5 mm long, 1.3-1.6 mm wide, barbate-pubescent on the inside of the base, the keel petals 3.0-4.0 mm long, the pouch extending along 1/3 of the length, the apex slightly irregular, barbate pubescent at base; stamens 10-12, 6-7 fertile, with 4-5 staminodes, the filaments to 1.5 mm long, free along 1/2 of their length, the anthers elliptic,

0.8-1.0 mm long, 0.4-0.5 mm wide; glands 2, 1-lobed, slightly trapezoid, ca 1.0 mm high, 1.0 mm long, fused to the staminodes; style 1.5-1.8 mm long, glabrous, the stigma trilobate, white, ca 0.4 mm in diameter, ca 0.3 mm high; ovary subglobose, 1.0-1.4 mm in diameter, barbate-pubescent, the ovules numerous. Fruit 7.0-9.0 cm long, the valves ca 10.0 mm per side; exocarp thin (ca 0.5 mm), fleshy, with a greenish-gray velutinous-tomentose pubescence; endocarp cartilaginous. Seeds ca 20 per locule, ovoid, 2.0-3.0 mm in diameter, barbate-pubescent, the trichomes to 10.0 mm long.

TYPE. Spruce 3871. Peru, Loreto, "Yurimaguas ad flumen Huallaga", fl (lectotype W; isotypes BR, CGE, G, NY, OXF).

DISTRIBUTION. An endemic species known only from the vicinity of the type locality; found in rainforest at low elevation between Yurimaguas and Balsapuerto on the Huallaga river basin. PERU. Loreto: Killip & Smith 28136 fr (NY, US); Klug 2954 fl (A, F, G, GH, MO, NY, US); Klug 3028 fl (A, F, G, GH, MO, NY, US).

I am designating the Vienna (W) specimen as lectotype, as there is no specimen deposited at Copenhagen and the W material was seen by Warming.

6. Trigonia laevis Aublet, Hist. Pl. Guian. Fr. 1: 390, pl. 150. 1775; De Candolle, Prod. 1: 571. 1824; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2) : 131. 1875.

Trigonia kaieteurensis Maguire, in Bull. Torr. Bot. Club. 75: 399. 1948. Type. Maguire & Fanshawe 23192, Kaieteur Plateau, Guyana, fr (holotype NY; isotypes A, BR, F, MO, NY, P, US, VEN).

Scandent shrub, the branches terete, lenticellate, the young ones strigulose, becoming glabrous with age. Stipules 1.5-2.0 mm long, subulate, strigulose; petioles 4.0-8.0 mm long, terete to canaliculate, strigose or glabrous; lamina broadly elliptic to oblong-elliptic, sometimes laterally unequal, 4.0-9.0 cm long, 2.2-4.5 cm wide, chartaceous to subcoriaceous, the margins entire, the apex acute to acuminate, the base oblique to obtuse; venation eucamptodromous, glabrous or slightly pilose, the midrib prominulous above, prominent beneath, the secondary veins 4-6 (-7) pairs, prominulous on both surfaces; intercostal pubescence absent. Inflorescences terminal and subterminal panicles (sometimes thyrses), to 30 cm long. Flowers in groups cincinni of 1-7; peduncles 0.2-0.5 mm long, strigose, the bracts 1.0-3.0 mm long, subulate to linear, strigose; pedicels 0.8-2.0 mm long, strigose, the bracteoles 0.3-1.0 mm long, subulate to linear, strigose; sepals deltoid to oblong, 2.0-3.0 mm long, 0.8-1.5 mm wide, strigose; standard 2.5-5.0 mm long, 2.0-3.0 mm wide, the pouch extending along 2/3 of the length, barbate at the throat, the wings 2.5-5.0 mm long, spathulate, 0.5-1.0 mm wide, barbate at the base, the keel petals 2.0-3.5 mm long, 1.5-2.0 mm wide, sometimes lanate at the apex; stamens 8-9, 5-7 fertile, staminodes 1-3, the filaments 0.7-1.2 mm long, connate for 2/3 of the length, the anthers subglobose, 0.4-0.5 mm long,

ca 0.4 mm wide, the staminodes sometimes with a small, terminal, laciniate appendage; glands 2, 2-3 lobed, irregular, ca 0.3 mm per side, glabrous; style slightly villous, 1.0-1.3 mm long, the stigma trilobate, ca 0.2 mm in diameter; ovary subglobose, 0.6-0.8 mm in diameter, villous, the ovules numerous. Fruit oblong or obovate, 0.6-3.0 cm long, 0.6-1.0 cm per side; exocarp thin, yellow-velutinous when young, becoming glabrous with age; endocarp woody, glabrous. Seeds 1-4 per capsule, subglobose, ca 0.3 mm in diameter, barbate villous, the trichomes ca 10.0 mm long.

This species is separated into two varieties.

Key to the varieties of Trigonia laevis

1. Flowers in groups (cincinni) of 1-2 (-3); fruit oblong, 1.5-3.0 cm long. a. var. laevis.

1. Flowers in groups (cincinni) of (2-) 3-6; fruit obovate, 0.6-1.0 cm long. b. var. microcarpa.

6a. Trigonia laevis var laevis

Flowers in groups of 1-3; petals 2.5-3.5 mm long. Fruit oblong, 1.5-3.0 cm long, ca 1.0 cm wide; seeds usually 3-4 per locule.

TYPE. Aublet sn, French Guiana, Cayenne, fl, fr (holotype BM, isotypes F, P).

DISTRIBUTION. Known only from a few collections in French Guiana, and one collection (type of Trigonia kaieteurensis) from Guyana. FRENCH GUIANA. Gabriel 1802 fl, fr (G); Soubirou sn fl, fr (P).

Without fruiting material, it is practically impossible to separate this variety from var microcarpa. It is quite possible that some material placed by me in var microcarpa might actually be var laevis.

6b. Trigonia laevis var microcarpa Sagot, Ann. Sci. Nat. 6 (2): 176. 1881

Trigonia parviflora Bentham, Hook. Jour. Bot. 3: 163. 1851. Type. Spruce sn, Brazil, Pará, Santarém, fl, (holotype K; isotypes C, CGE, F, G, GH, GOET, M, NY, P, W), nomen illegit.

Trigonia microcarpa Sagot et Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 131. 1875; Stafleu, (Trigoniaceae) Pulle Fl. Surin. 3 (2): 174. 1951. Type. Sagot 36, French Guiana, Karouany, fl, fr (holotype P; isotypes BR, F GH, GOET, P, W).

Trigonia bicolor Suessenguth & Overkott, Fedde Rep. Sp. Nov. Regni Veg. 51: 204. 1942. Type. Buchtien 1631, Bolivia, Mapiri, fl (lectotype F; isotype nv US).

Flowers in groups of 3-6; petals usually 3.5-5.0 mm long. Fruit obovate, 0.6-1.0 cm long, as wide as it is long; seeds usually 1-2 (-3) per locule.

TYPE. Sagot 36, French Guiana, Karouany, fl, fr (holotype P; isotypes BR, F, GH, GOET, P, W).

DISTRIBUTION. A rainforest variety found from French Guiana to Bolivia, but not yet reported from Colombia. VENEZUELA. Delta Amacuro: Blanco 426 fr (NY, VEN); Steyermark 87550 fl (M, NY, VEN, W); Wurdack & Monachino 39697 fr (F, NY, U, US). GUYANA. Fanshawe 4573 fl (U); Sandwith 563 fl, fr (G, NY, P, U, US); A.C. Smith 2752 fl (A, G, MO, NY, U, US); Schomburgk 953 fl (G). SURINAME. Lanjouw & Lindeman 2416 fr (IPEAN, NY, US); Lindeman 5785 fl (U); Stahel & Gonggrÿp 631 fl (U); van Donselaar 2894 fr (U). FRENCH GUIANA. Geay 1890 fl (P); Lambert sn fl (BR); Martin sn fl (P); Mélinon 230 fr (P); Poiteau sn fl, fr (G, US). PERU. Spruce 4944 fl (BR, C, CGE, F, G, GOET, K OXF, W). BRAZIL. Amazonas: Ducke 1208 fl (GH, IPEAN, MG, MO, NY, US); Ducke 1282 fl (F, GH, IPEAN, MG, NY, US). Pará: Black 47-932 fl (IPEAN, U); Fróes 32914 fl (IPEAN, U). Rondônia: N.T. Silva 439 fl (IPEAN, U). BOLIVIA. La Paz: Krukoff 10338 fr

(A, F, G, MICH, MO, NY, U, US); Krukoff 10956 fr (A, F, G, MICH, MO, NY U); Rusby 1220 fr (MICH, NY); Rusby 2449 fl (E, G, GH, MO, NY, P, US).

This widespread variety includes the taxa formerly known as Trigonia microcarpa, T. parviflora Bentham, and T. bicolor which are later synonyms. Although there is a tendency for an increase of size of the inflorescence going from East to West, I do not consider this significant enough to merit taxonomic recognition.

Trigonia parviflora Bentham was, when published, an illegitimate name, as this name had been published by Schott in 1827; the name T. bicolor is clearly superfluous, but must be used if T. parviflora is recognized as a separate taxon.

7. Trigonia spruceana Bentham ex Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 130. 1875.

Scandent shrub, the branches terete, glabrous, lenticellate. Stipules deltoid or subulate, 0.8-2.0 mm long, 0.7-1.0 mm wide, pilose, caducous; petioles (5.0-) 6.0-12.0 (-13.0) mm long, 0.9-2.1 mm thick, sparsely strigose; lamina elliptic to ovate-elliptic, sometimes ovate, 5.0-14.0 cm long, 2.0-5.0 cm wide, subcoriaceous, the margins entire, the apex acute or acuminate, the base oblique; venation brochidodromous or seemingly so, sparsely strigose; the midrib prominulous above, prominent beneath, the secondary veins 9-13 pairs; intercostal pubescence absent above, frequently caducous beneath, sometimes becoming entirely glabrous. Inflorescences terminal and subterminal axillary panicles to 15 cm long. Flowers in groups (cincinni) of 1-4 (usually 1-2), solitary on the axes of the ultimate inflorescences, the axes 0.0-4.0 mm long, 0.6-0.8 mm long, decreasing in length towards the apices of the primary inflorescences; peduncles 0.2-2.5 mm long, 0.6-0.8 mm thick, strigose, often resembling an articulated peduncle with the axes of the ultimate inflorescences, the bracts 2.0-3.0 mm long, 0.2-0.3 mm wide, subulate to linear, strigose, caducous; pedicels 1.5-2.5 mm long, 0.6-0.8 mm thick, strigose, the bracteoles 0.7-1.4 mm long, 0.2-0.6 mm wide, deltoid or subulate, strigose; sepals ovate or oblong, (4.0-) 4.5-5.1 (-5.8) mm long, 1.8-3.0 mm wide, tomentellous or lanate standard 6.0-7.5 mm long, 2.0-3.5 mm wide, the pouch globose, extending to 2/3 of the length, revolute at the apical portion, barbate at the throat; the wings spathulate, 5.8-6.2 mm long, 3.4-4.0 mm wide, barbate at the base, keel petals 5.0-6.0 mm long, 3.0-4.0 mm wide, the pouch excentric, barbate at the base; stamens 6-7, all fertile, the filaments connate for 1/2-2/3 of their length,

3.0-3.5 mm long, the anthers subglobose, 0.8-1.0 mm long, 0.5-0.8 mm wide; glands 2, 2-3-lobed, ca 0.3 mm long, 0.4 mm wide, glabrous; style 2.8-3.0 mm long, the stigma ca 1.0 mm in diameter; ovary subglobose, 1.0-2.0 mm in diameter, villous, the ovules numerous. Fruit 7.0-9.0 cm long, 1.4-2.0 per side; exocarp fleshy, thin (ca 0.5 mm), with a whitish golden-brown velutinous-tomentose pubescence; endocarp cartilaginous, glabrous. Seeds ca 20 per locule, ovoid to globose, 5.0-6.0 mm long, ca 4.0 mm wide, equinate pubescent, the trichomes ca 2.0 mm long.

TYPE. Spruce 1501, Brazil, Amazonas, Manaus, fl (holotype C; isotypes CGE, F, G, GH, GOET, M, NY, P, W).

DISTRIBUTION. A common but poorly collected riverine species from the basin of the Rio Negro. It grows in periodically flooded riverside forests, especially along black-water rivers, although it has once been collected along the Rio Madeira, and is known to have been in cultivation in a garden in Rio de Janeiro. Known from Venezuela and Brazil, probably also found in Colombia.

VENEZUELA. Territorio Amazonas: Gaillard 164 fl (P); Bunting, Akkermans & Rooden 4067 fl (U); Level 101 fl (NY, VEN); Wurdack & Adderley 43194 fl (NY, VEN); Wurdack & Adderley 43283 fl (NY, VEN); Wurdack & Adderley 43747 fl (NY, VEN). BRAZIL. Amazonas: Cavalcante 552 fr (MG); Coêlho, L. 1139 fl (INPA, IPEAN); Ducke 179 fl (A, F, MO, NY, US); Frões 21293a fl (F, IPEAN, NY, US); Frões 22588 fr (IPEAN, U); Frões 25056 bds (IPEAN); Labroy sn fl (P); Prance et al 2657 fl (COL, F, INPA, MG, NY, US); Prance et al 4945 fl (COL, INPA, NY); Prance et al 15200 fl (COL, MG, NY); Prance et al 17700 fr (COL, INPA, MG, NY, US); Rodriguez, W. 726 fr (IPEAN); Silva, M. 950 fl, fr (MG, NY); Spruce 2416 fl (CGE, F, FHO, G, GH, GOET, P, W); Ule 6074 fl (G, L, MG); Ule 6140 fl (GOET, MG, W).

8. Trigonia reticulata Lleras, sp nov

8. Trigonia reticulata Lleras, sp nov

Frutex scandens, ramulis juvenilibus tomentellis, glabrescentibus, lenticellatis. Stipulae caducae, haud visae. Folia opposita; petiolo 9.0-18.0 mm longo, 1.0-3.0 mm crasso, tomentello; laminae ovate vel ellipticae, interdum obovatae, 4.5-11.0 cm longae, 3.0-6.5 mm latae, subcoriaceae, margine leviter revolute, apice acuto usque acuminato variante, basi obliqua vel subrotundata, supra glabrae, infra lanato-tomentellae; costa media supra plana, infra prominentia, strigulosa; costis secundariis (8-) 9-11 (-12) jugis, costis tertiariis quaternariisque reticulatis, evidentibus infra. Inflorescentiae in thyrsis terminalibus vel axillaribus dispositae, 4.0-15.0 cm longae. Flores in dichasios simplices usque compositos dispositi; axibus dichasiorum 0.5-2.0 mm longis, 0.5-0.8 mm crassis, tomentellis; pedunculi 0.3-1.0 mm longi, 0.5-0.8 mm crassi, tomentelli, bracteis subulatis, 1.0-2.5 mm longis, margine glanduloso-papillatis, tomentellis; pedicelli 1.0-2.5 mm longi, 0.3-0.5 mm crassi, tomentelli, bracteolis subulatis, 1.0-1.5 mm longis, margine ut in bracteis, tomentellis; sepala ovata vel oblonga, 2.8-4.0 mm longa, 1.7-2.2 mm lata, nonnumquam glandulosa, tomentella; vexillum 4.3-4.6 mm longum, 2.5-2.8 mm latus, usque ad medium longitudinaliter saccatum, apice leviter revolute, intus barbatum, alis petalis spathulatis, 3.3-3.8 mm longis, 1.3-1.6 mm latis, ad basem barbatis, carinae petala saccata, 2.8-3.0 mm longa, 1.0-1.8 mm lata; stamina 8-10, sterilia 2-4, fertilia 6, staminodiis interdum appendiculatis, filamentis ad medium connatis, 1.0-1.4 mm longis, antheris oblongis vel ellipticis, 0.5-0.7 mm longis, 0.3-0.4 mm latis; glandulae 2, unilobae, a fronte visae labiatae, lanato-villosae; stylus erectus, 1.0-1.2 mm longus, villosus, stigma circulari, ca 0.3 mm in diametro,

alba; ovarium subglobosum usque pyramidale varians, ca 0.6 mm latum, 3-loculare, villosum, ovulis in quoque loculo numerosis. Fructus juvenilibus oblongus, dense villoso-tomentosus.

TYPE. Tillett & Tillett 45524, Guyana, Upper Mazaruni River Basin, Kako River, fl (holotype NY; isotypes F, GH, P, US).

DISTRIBUTION. At edge of forest in open areas along roads or rivers.

VENEZUELA. Bolivar: Steyermark & Aristeguieta 77 fl, imm fr (VEN, U). GUYANA. Forest Department 7992, Kuku River, fl (NY).

Due to lack of adequate fruiting material, the relationships of this species are impossible to determine. It has been confused with Trigonia villosa var macrocarpa (T. macrocarpa Bentham) and somewhat resembles this taxon, from which it differs in the reticulation of the leaves, the more complex inflorescence, and several other minor characters. It is unique in Trigonia in having glandular papillae on the margins of the bracts, bracteoles and sometimes the sepals, characters shared with T. bracteata.

9. Trigonia candelabra Lleras, sp nov

Frutex scandens, ramulis juvenilibus tomentellis, glabrescentibus, lenticellatis. Stipulae caducae, non vidae. Folia opposita; petiolo 8.0-15.0 mm longo, 1.0-3.0 mm crasso, tomentello, postea glabro; laminae ellipticae vel obovatae, 8.0-21.0 cm longae, 4.0-10.0 cm latae, subcoriaceae, margine integre, apice acuto usque acuminato variante, basi obtusa vel obliqua, supra glabrae, infra minute tomentellae postea glabra; costa media supra plana, infra prominentia, strigulosa, costis secundariis 6-9 jugis. Inflorescentiae in thyrsis terminalibus vel axillaribus dispositae, 5.0-9.0 cm longae. Flores in dichasios compositos dispositi; axibus dichasiorum 1.0-7.0 mm longis, 0.4-0.9 mm crassis, tomentellis; pedunculi 0.8-2.0 mm longi, 0.5-1.0 mm crassi, tomentelli, bracteis subulatis, 1.5-2.5 mm longis, tomentellis; pedicelli 1.0-2.5 mm longi, 0.3-0.5 mm crassi, tomentelli, bracteolis subulatis vel ovatis, 0.8-1.5 mm longis, tomentellis; sepala ovata vel oblonga, 4.3-4.6 mm longa, 1.0-2.0 mm lata, tomentella; vexillum 4.5-5.0 mm longum, 2.0-3.0 mm latum, usque ad medium longitudinaliter saccatum, apice leviter revolute, intus barbatum, alis petalis spathulatis, 4.0-4.5 mm longis, 1.3-1.6 mm latis, glabris, carinae petala saccata, 3.0-3.5 mm longa, 1.0-1.3 mm lata; stamina 8-10, sterilia 2-4, fertilia 6, filamentis ad medium connatis, 1.5-1.8 mm longis, antheris oblongis vel ovatis, 0.8 mm longis, 0.6-0.9 mm latis, apice acuminatis; glandulae 2, 2-3 lobae, rectangulatae, ca 0.5 mm latae, laciniatae; stylus erectus, 1.3-1.6 mm longus, villosus usque glaber varianti; stigma circulari, ca 0.3 mm in diametro, alba; ovarium subglosum, ca 1.0 mm in diametro, 3-loculare, villosum, ovulis in quoque loculo numerosis. Fructus 6.5-8.0 cm longus, ca 1.0 cm latus, oblongo-obovatus, extus velutino-tomentosus, intus

cartilagineus, glaber. Seminae ca 10 in quoque loculo, subglobosae, ca 4.0 mm in diametro, pilis ca 7.0 mm longis.

TYPE. Van Donselaar 2812, Suriname, Brokopondo, village of Brokopondo, at edge of secondary forest, fl (holotype U).

DISTRIBUTION. Known only from the type locality, and 3 three collections in Brazil. Suriname. Brokopondo: Van Donselaar 2891, fr (paratpye U). BRAZIL. Pará: Fróes 32897 fl (IPEAN); Pires & Silva 4734 fl (IPEAN).

This very distinct species shows affinities with Trigonia hypoleuca, in the leaf (shape, pubescence, color, etc) and the fruit. However, the inflorescence is very distinct. It is the only species in the genus in which the flowers are arranged in perfect compound dichasia. The sterile (vegetative) branches bear some of the largest leaves in the genus, another character that separates it from T. hypoleuca. The pubescence in the younger leaves cannot be seen with the naked eye, or even with a dissecting microscope (100K).

I have selected flowering material as the holotype for the species. It is quite possible that the fruiting material designated as paratype is from the same plant, gathered at a later date.

The specific epithet, candelabra, refers to the arrangement of the ultimate inflorescences.

FIG. 13. Trigonia candelabra Lleras sp nov. A, Habit, vegetative branch; B, Habit, flowering branch; C, Habit, fruiting branch, x 0.5.

FIG. 13

FIG. 14. Trigonia candelabra Lleras sp nov. A, flower X 10; B, ovary X 10; C, anthers X 20; D, Keel petal X 10; E, Wing Petal X 10; F, Standard X 10; G, compound dichasium in bud X 10.

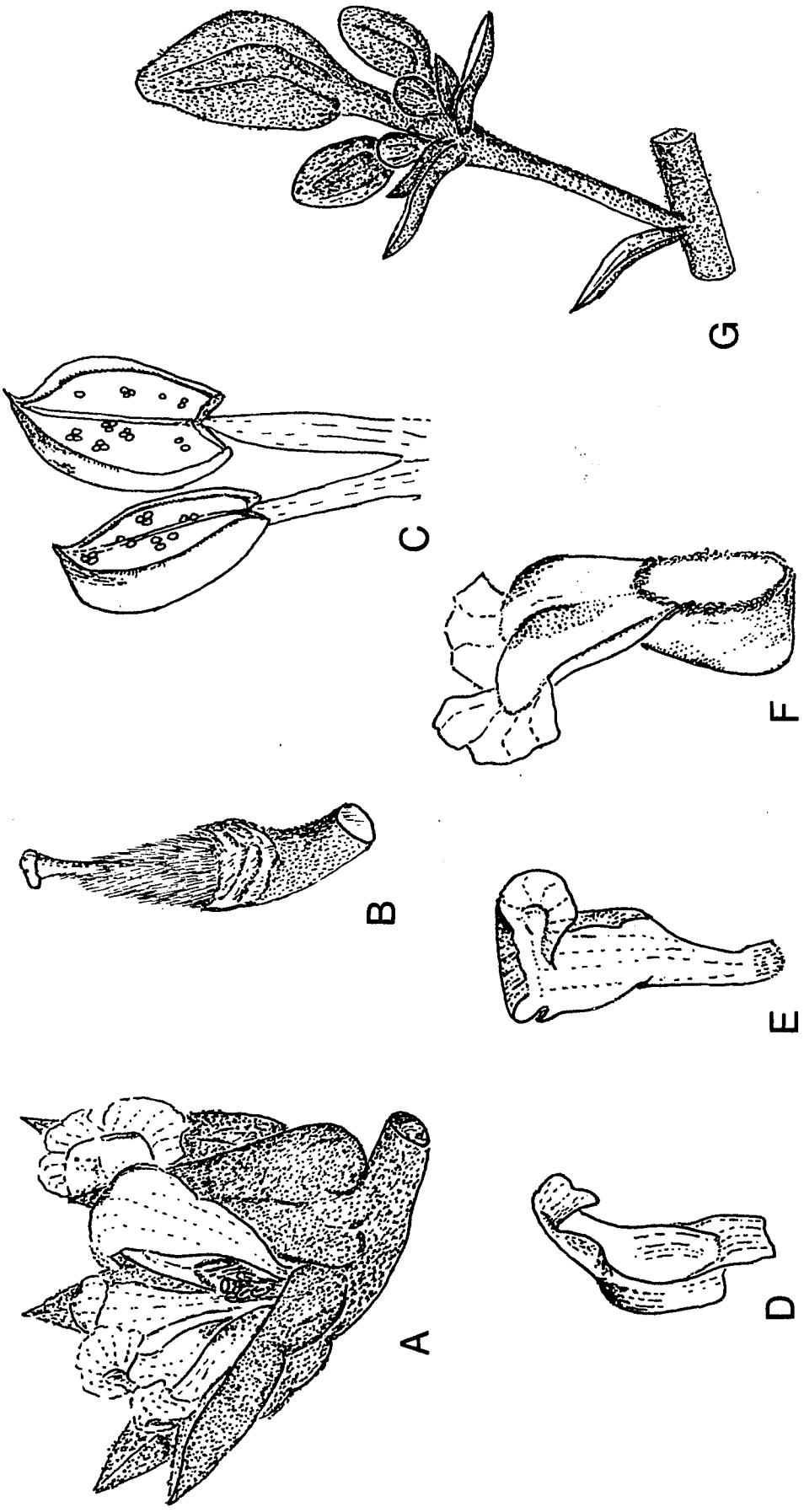


FIG. 14

10. Trigonia rugosa Bentham, Bot. Voy. Sulph. 74. 1844.

10. Trigonia rugosa Bentham, Bot. Voy. Sulph. 74. 1844.

Trigonia floribunda Orsted, Dansk Naturh. Foren., Copenh. Vide. Meddel. 38. 1856; Standley, N. Am. Fl. 25: 297. 1924; Austin, Fl. of Panama, Ann. Missouri Bot. Gard. 54 (3): 208. 1967. Type. Orsted 3721 Nicaragua, Granada, fl (holotype C; isotypes F).

Trigonia rigida Orsted, Dansk Naturh. Foren., Copenh. Vide. Meddel. 38. 1856. Type. Orsted 3722 Nicaragua, Granada, fl (holotype C).

Trigonia thyrsifera Donnell Smith, Bot. Gaz. 23: 3. 1897. Type. Biolley 2638 Costa Rica, Alajuela, San Mateo, fl (holotype US; isotype CR).

Trigonia euryphylla Standley, N. Am. Fl. 25: 297. 1924. Type. Baker 2554 Nicaragua, Granada, fr (holotype US; isotypes A, G, GH, K, MO).

Trigonia panamensis Standley, Publ. Field Mus. Nat. Hist. Bot. 22: 346. 1940. Type. Aviles 961 Panama, Canal Zone, Barro Colorado, fl (holotype F).

Scandent or subscandent shrub, the branches terete, lenticellate, the young ones densely tomentose, becoming glabrous with age. Stipules caducous (nv); petioles 5.0-25.0 mm long, 0.8-1.2 mm thick, subcanaliculate, tomentose or glabrous; lamina oblong-elliptic to obovate, (3.5-) 5.0-15.0 cm long, (2.5-) 4.0-8.0 cm wide, chartaceous or subcoriaceous, the margins entire, the apex rounded or acute, the base obtuse to acute; venation eucamptodromous, tomentose to strigose on both surfaces, the midrib prominulous above, prominent beneath, the secondary veins 6-9 pairs; intercostal pubescence absent above, lanate-adpressed to arachnoid when young, frequently becoming glabrous with age. Inflorescences terminal and subterminal thyrses, 7.0-25.0 cm long. Flowers in dichasia of 1-3, arranged ultimately in secondary inflorescences varying from dichotomous dichasia to individual cymules; axes of secondary inflorescences 4.0-7.0 mm long, ca 0.8 mm thick, tomentose, the bracts ovate, 2.0-3.5 mm long,

tomentose; peduncles 0.7-2.0 mm long, ca 0.4 mm thick, tomentose; pedicels 1.0-2.0 mm long, ca 0.4 mm thick, tomentose, the pedunclar bracts and bracteoles of equal size, 0.8-1.5 mm long, tomentose; sepals ovate or oblong, 2.2-3.5 mm long, 1.2-1.8 mm wide, lanate; standard 3.2-4.0 mm long, 1.2-2.2 mm wide, the pouch globose, extending to 1/2 of the length, the apex revolute, barbate at the throat, the wings broadly spathulate, 2.8-3.2 mm long, 1.0-1.5 mm wide, barbate at the base, the keel petals 2.7-2.9 mm long, 0.6-1.5 mm wide, sometimes lacking a pouch, glabrous; stamens 8-10, with 6 fertile, staminodes 2-4, sometimes with knob-like appendages, the filaments 1.0-1.2 mm long, connate to the middle, the anthers oblong, 0.4-0.5 mm long, ca 0.2 mm wide; glands 2, 2-3 lobed, irregular, ca 0.5 mm per side, villous or glabrous; style 1.2-1.3 mm long, slightly villous or glabrous, the stigma trilobate, ca 0.2 mm in diameter; ovary subglobose, ca 0.6 mm in diameter, short-villous, the ovules numerous. Fruit oblong to elliptic, 2.0-3.2 cm long, 1.0-2.0 cm wide; exocarp yellow velutinous-tomentose when young, glabrous when mature. Seeds 6-9 per locule, ovate, ca 4.0 mm long, villous-barbate, the trichomes ca 10.0 mm long.

TYPE. Sinclair sn, Central America, fl, fr (holotype, K).

DISTRIBUTION. A well collected species known from S. Mexico to N. Colombia, from the tropical and subtropical deciduous forests along the Pacific coast of Central America, and the Atlantic coast of northern South America. MEXICO. Chiapas: Matuda 2517 fl (F, G, K, MICH, NY); Matuda 16548 fl (F, MICH, NY). GUATEMALA. Retalheu: Standley 87755 st (F); Standley 88330 st (F); Standley 88718 st (F). Suchitepéquez: Standley 62205 st (F). Escuintla: Molina & Molina 12477 fl (NY). Santa Rosa: Standley 78860 st (F); Standley 79927 st (F). Zacapa: Standley 73760 fl (F); Standley 73850 st (F). Chiquimula:

Standley 32044 st (F); Standley 74348 st (F). Jutiapa: Standley 95137 st (F); Standley 75475 st (F). EL SALVADOR: Santa Ana: Standley & Padilla 3068 st (F). Salvador: Standley 20596 fr (GH, NY, US); San Vicente: Standley 21340 fr (GH, NY, US); Standley & Padilla 3411 st (F). San Miguel: Calderón 2124 fr (GH, NY, US). HONDURAS: Octepeque: Molina 22436 fr (F, NY). Morazán: Glassman 1723 fl (F, NY); Molina 131 fl (F, GH, MO, US); Webster, Miller & Miller 12040 fl (GH, MO, U); Williams & Molina 11262 fr (F, US). El Paraiso: Molina 7494 fl (F). Choluteca: Molina 14206 fl (F, NY). NICARAGUA: Managua: Chaves 213 fl (US); Garnier A1283 fr (A, F). Masaya: Maxon 7675 fl (US); Maxon 7686 fl (US). Granada: Lévy 192 fl (C, G, P, US); Lévy 1073 fl (G, P); Orsted 3723 fl (C, F). COSTA RICA. Guanacaste: Burger & Burger 7841 fl (F, NY); Jiménez 1575 fr (F); Quiróz 848 fr (F); Tonduz 13486a fr (NY, US); Webster, Miller & Miller 12479 fl (GH, MO, U). Alajuela: Standley 40045 st (US). PANAMA. Canal Zone, Barro Colorado: Croat 16581 fl (NY); Standley 40949 st (US). Darien: Stern et al 163 fl (MO); Stern et al 224 fl (GH, MO, U, US); Stern et al 993 fl (GH, U, US). COLOMBIA. Antioquia: Haught 4866 fl (COL, US). Atlantico: Bro. Elias 258 fl (NY, US); Bro. Elias 357 fl (US). Magdalena: H.H. Smith 884 fl (K); H.H. Smith 886 fl (F, G, MICH, P, US); H.H. Smith 888 fl (F, MICH, MO, US). Cesár: Haught 4186 fl (COL, F, US). Guajira: Haught 4227 fl (COL, NY, U, US).

Trigonia rugosa has been commonly known as T. floribunda, but the former is the older, valid name. The name T. rugosa has been used only for the material collected in the type gathering and although this material is very poor, it belongs together with what has been known as T. floribunda. Both the specimens used to typify T. rugosa and T. euryphylla have thicker leaves than most of of the material representing the rest of the species, but I consider this to be

a local variation of no taxonomic significance.

As the high variability of the species makes it impossible to recognize subspecific categories, I agree with Austin in considering the other epithets cited under this species as being synonyms.

11. Trigonia eriosperma (Lamarck) Fromm & Santos, Bol. Mus. Rio de Janeiro 42: 2. 1971.

Croton eriospermum Lamarck, Encycl. 2: 211. 1786. Type. Commerson sn Brazil, Rio de Janeiro, fr (holotype P -Herb. Lamarck; isotype P).

Mainea racemosa Vellozo, Fl. Flum. 275. 1829; Vellozo, Iconog. 7: pl. 8. 1831; Netto, Arch. Mus. Rio de Janeiro 5: 260. 1881.

Trigonia crotonoides Cambessèdes, (Hippocrateaceae) St. Hilaire Fl. Bras. Merid. 2: 83. pl. 105. 1829; Grisebach, in Linnaea 22: 31. 1849; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 127. 1875. Type. St. Hilaire c102, Brazil, Rio de Janeiro, fl, fr (holotype MPU; isotype P).

Trigonia crotonoides var incana Cambessèdes, (Hippocrateaceae) St. Hilaire Fl. Bras. Merid. 2:83. 1829; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 127. 1875. Type. St. Hilaire sn, Brazil, Rio de Janeiro, fr (holotype MPU).

Trigonia crotonoides var oblongifolia Cambessèdes, (Hippocrateaceae) St. Hilaire Fl. Bras, Merid. 2: 83. 1829; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 127. 1875. Type. St. Hilaire Bl-385, Brazil, Minas Gerais, fl (holotype MPU; isotype P).

Trigonia micrantha Martius, Flora 20 (2): 102. 1837. Nomen nudum.

Trigonia crotonoides Cambessèdes var elliptica Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 128. 1875. Type. Glaziou 2114, Brazil, Rio de Janeiro, fl (lectotype C; isotypes BR, P).

Trigonia racemosa (Vellozo) Hoehne, Ind. Bibliog. Num. 256. 1951.

Shrubs or scandent shrubs, sometimes treelets, the branches terete, lenticellate, strigose, becoming glabrous with age. Stipules linear, 1.5-4.0 mm long, strigose to almost glabrous, caducous; petioles 2.0-5.0 mm long, 0.3-0.5 mm thick, strigose; lamina oblong-ovate to oblong-elliptic, 1.5-9.0 cm long,

1.0-3.5 cm wide, membranaceous to chartaceous, the margins entire, the apex acuminate, the base obtuse; venation eucamptodromous to brochidodromous, strigose to very densely strigose on both surfaces, the midrib plane above, prominent beneath, secondary veins 4-7 pairs, impressed on both surfaces. Inflorescences terminal panicles, thyrses or racemes, 1.5-10.0 cm long. Flowers in cymules of 1-3; peduncles 1.0-6.0 mm long, ca 0.2 mm thick, tomentellous or strigose, the bracts linear, 0.7-4.0 mm long, strigose; pedicels 1.0-3.0 mm long, ca 0.2 mm thick, tomentellous or strigose, the bracteoles deltoid to linear, 0.2-1.0 mm long; sepals ovate to oblong, 2.0-3.0 mm long, 0.8-1.0 mm wide, membranaceous, tomentellous or strigose; standard 4.0-5.0 mm long, ca 1.5 mm wide, the pouch extending along 1/4 of the length, spurred, barbate at the throat, the wings spathulate, 2.5-3.5 mm long, 0.8-1.0 mm wide, barbate at the base, the keel petals 2.8-3.5 mm long, ca 1.0 mm wide, the pouch centered on the petal, nasiform; stamens 9-10, 6 fertile, 3-4 staminodes, the filaments 0.9-1.2 mm long, connate for 4/5 of the length, the staminodes with a small, knob-like terminal appendage, the anthers subglobose, 0.2-0.3 mm in diameter; glands 2, 2-lobed, irregular, ca 0.3 mm per side, villous; style glabrous, 0.9-1.2 mm long, the stigma trilobate, ca 0.1 mm in diameter; ovary subglobose, ca 0.6 mm in diameter, densely villous, the ovules ca 4 per locule. Fruit oblong, 0.8-2.5 cm long, the valves ca 0.7 cm per side, exocarp velutinous when immature, becoming glabrous with maturity; endocarp woody, glabrous. Seeds subglobose, ca 1.0 mm in diameter, villous, the trichomes ca 6 mm long.

This species is separated into 3 subspecies.

Key to the subspecies of Trigonia eriosperma

1. Inflorescences usually longer than 4.0 cm, in panicles or thyrses; cymes usually 2-3-flowered.
   2. Inflorescences panicles; cymules usually 3-flowered (sometimes 1); leaves villous or lanate; from S. Brazil. a. subsp. eriosperma.
   2. Inflorescences thyrses; cymules 2-flowered; leaves glabrous or nearly so; from Central & N. South America. c. subsp. membranacea.
1. Inflorescences shorter than 3.5 cm, racemes cymules 1-flowered; from S. Brazil. b. subsp. simplex.

11a. Trigonia eriosperma subsp. eriosperma

Leaves 1.5-7.0 cm long, 1.0-3.0 cm wide, villous-strigose to lanate. Inflorescences terminal panicles, 4.0-8.0 cm long. Flowers in 3-florate cymes (sometimes 1-florate). Fruit 0.8-1.5 cm long.

TYPE. Commerson sn Brazil, Rio de Janeiro, fr (holotype P-Herb. Lamarck; isotype P).

DISTRIBUTION. Known from forests in southern Brazil. BRAZIL. Bahia: Belém 1185 fr (NY); Blanchet 3593 fl (F, G, MO, P). Minas Gerais: Claussen 1096 fl (G, P); Glaziou 13480 fl (MPU, P); Glaziou 13811 fl (B, C, F, G, IPEAN, MG, P, US); Glaziou 14689 fl (BR, C, G, IPEAN, MPU, US); Mexia 4120 fl (F, G, NY, US). Espírito Santo: Duarte 4011 fl (NY); Pereira 9835 fl (F, M). Rio de Janeiro: Brade 11215 fl (GH); Glaziou 9417 fl (BR, E, P); Langsdorff sn fl, fr (P, US); Martius 122 fl (BR, F, G, GH, MO, NY, P, US); Pereira & Duarte 1246 fl (NY); Vauthier 522 fl (G, GH); Weddell 684 fl (G). Guanabara: Lindley 749 fr (BR); Luschnath sn fl, fr (BR, GH); Schenk 1589 fr (C); Schenk 3061 fr (C).

This species is one of the most collected taxa in the genus. Because of the high variability of characters, it has been treated as several

species, or at best, as several varieties. I agree with Fromm and Santos (1971) in considering it as only one taxon, as it is impossible to separate morphologically the taxa as delimited by other authors.

The affinities of the species as a whole indicate close relationships with both Trigonia laevis and T. paniculata.

Trigonia eriosperma subspecies eriosperma can be separated from T. paniculata by its shorter panicles, the panicles being terminal (vs terminal and axillary in T. paniculata), by its more glabrous stems and flowering branches, by the lack of a white "border" on the margins of the leaves, and by the sparser pubescence of the leaves in general.

11b. Trigonia eriosperma subsp. simplex (Warming) Lleras, stat nov
Trigonia simplex Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 125. 1875.

Leaves 3.5-5.0 cm long, 1.5-2.5 cm wide, strigose. Inflorescences terminal racemes, 1.5-3.5 cm long. Flowers in 1-florate cymules. Fruit (immature) ca 2.5 cm long.

TYPE. Warming 596, Brazil, Minas Gerais, Lagoa Santa, fl, fr (holotype C, on 2 sheets as indicated by Warming).

DISTRIBUTION. Known only from the type locality. BRAZIL. Minas Gerais: Warming sn fl, fr (topotypes collected at different times, C, US).

11c. Trigonia eriosperma subsp. membranacea (A.C. Smith)Lleras, stat nov
Trigonia membranacea A.C. Smith, in Phytologia 3: 128. 1935.
Trigonia rasa Standley & Steyermark, in Publ. Field Mus. Nat. Hist. 23 (2): 59. 1944. Type. Standley 78584 Guatemala, Santa Rosa, Rio Panal, fr (holotype F; isotype F).

Leaves 4.0-9.0 cm long, 2.5-3.5 cm wide, very slightly strigose to glabrous. Inflorescences terminal thyrses 3.0-10.0 cm long. Flowers in 2-florate cymes. Fruit oblong, 1.5-2.0 cm long, glabrous.

TYPE. Killip & Smith 14396, Colombia, Bolívar, Turbaco, fr (holotype NY; isotypes A, GH, US).

DISTRIBUTION. Reported from fairly open areas or edges of forest from the Atlantic Coast to Central America, and Northern South America, from the South of Mexico to Northern Colombia. MEXICO. Chiapas: Matuda 17630 fl (F, NY). GUATEMALA. Bernoulli & Cario 3139 fl (C, K); Standley 87416 sterile (F); Snedaker C-24 fl (F); Snedaker C-25 fl (F). BELIZE. Gentle 5251 fr (MICH, U); Lundell 7021 fr (MICH, U). PANAMA. Hayes 720 fl, fr (BR, E, K, M). COLOMBIA. Atlantico: Bro. Elias 1202 fr (US); Bro. Elias 1651 fr (F, US); Bro. Elias 1105 fr (F, US).

Both subspecies membranacea and subspecies simplex have larger fruits than subspecies eriosperma. Subspecies membranacea is in general the most glabrous of the three subspecies in the species, and subspecies simplex is probably more xerophytic than the other two.

12. Trigonia floccosa Rusby, Bull. N.Y. Bot. Gard. 4: 325. 1907.

Scandent shrub, the branches terete, lenticellate, strigose or adpressed-lanate, becoming glabrous with age. Stipules subulate to lanceolate, 10.0-12.0 mm long, tomentellous, caducous; petioles 5.0-15.0 mm long, ca 1.5 mm wide, strigulose; lamina ovate to obovate, inequilateral, 4.0-13.0 cm long, 2.0-6.0 cm wide, subcoriaceous, the margins entire, the apex acute to acuminate, the base subcordate; venation eucamptodromous, lanate to glabrous along the midrib above, strigose beneath, the midrib plane above, prominent beneath, secondary veins impressed above, prominulous beneath; intercostal pubescence arachnoid-lanate to glabrous above, adpressed white-lanate and golden-strigose beneath. Inflorescences terminal and subterminal axillary thyrses, to 12 cm long. Flowers in cymules of 1-2, peduncles absent or nearly so; pedicels 1.0-1.5 mm long, ca 0.4 mm thick, tomentellous, bracts and bracteoles of equal size, 2.5-10.0 mm long, subulate, tomentellous; sepals ovate to oblong, sometimes deltoid, 3.5-5.2 mm long, 2.0-2.5 mm wide, papillate at the margins, lanate or strigose; standard 5.0-5.5 mm long, 2.5-3.0 mm wide, the pouch extending along 1/3 of the length, slightly revolute at the apex, barbate at the throat, the wings spathulate, 5.0-5.5 mm long, ca 1.5 mm wide, densely barbate at the base, the keel petals 4.0-4.5 mm long, ca 3.0 mm wide, the pouch nasiform; stamens 8-9, fertile ones 6-7, staminodes 2, the filaments 1.8-2.0 mm long, connate for 1/2 of the length, anthers oblong, 0.8-1.0 mm long, ca 0.4 mm wide; glands 2, 2-3 lobed, 0.5-0.8 mm per side, acute at the apex, fused to the staminal tube; style 1.8-2.0 mm long, villous, the stigma trilobate, ca 0.3 mm in diameter; ovary subglobose, ca 0.6 mm in diameter,

villous, the ovules numerous. Fruit (immature) 5.0-6.0 cm long, ca 1.2 mm per side; exocarp velutinous-tomentose; endocarp woody, glabrous. Seeds 8-10 per locule, subglobose, ca 3.0 mm in diameter, barbate pubescent, the trichomes ca 12 mm long.

TYPE. Bang 2191, Bolivia, Yungas, Coripati, fl (holotype NY; isotypes E, G, GH, M, MICH, MO, NY, US, W).

DISTRIBUTION. Known only from two localities in Bolivia. BOLIVIA. Santa Cruz: Rusby 2450 fl (GH, MICH, NY, US); Rusby 2596 fr (MICH, NY).

This species can easily be recognized by the dual pubescence on the underside of the leaf, by the large glands fused to the staminal tube, and especially by the papillae on the sepals.

13. Trigonia costanensis Steyermark & Badillo, Acta Bot. Ven. 6 (1-4): 77. 1971.

Scandent shrub, the branches terete, lenticellate, slightly yellow-puberulent-tomentose when young, becoming glabrous with age. Stipules caducous (nv); petioles 15.0-20.0 mm long, ca 1.0 mm thick, puberulent-tomentose, sometimes glabrous; lamina oblong-elliptic to oblong, 8.0-15.0 cm long, 4.0-8.0 cm wide, coriaceous, the margins entire, the apex obtuse or rounded, sometimes mucronate, the base obtuse; venation eucamptodromous, glabrous above, slightly villous beneath, the midrib plane above, prominulous beneath, the secondary nerves 6-8 pairs; intercostal pubescence absent above, adpressed-lanate (sericeous) beneath. Inflorescences axillary thyrses 10.0-15.0 cm long. Flowers in groups of 1-3; peduncles 2.0-4.0 mm long, ca 0.4 mm thick, densely yellow-puberulent tomentose; the bracts 3.5-5.0 mm long, linear to subulate, puberulent-tomentose; pedicels 1.0-2.0 mm long, ca 0.4 mm thick, puberulent-tomentose, the bracteoles 2.0-3.5 mm long, 1.0-2.0 mm wide, linear to ovate, puberulent-tomentose; sepals ovate or oblong, 4.5-6.0 mm long, 2.0-3.0 mm wide, puberulent-tomentose on exposed portions, adpressed-lanate on covered portions; standard 4.5-5.0 mm long, ca 3.0 mm wide, the pouch extending to 2/3 of the length, the apex rounded, barbate at the throat, the wings spathulate, 4.5-5.0 mm long, 1.5-1.8 mm wide, barbate at base, the keel petals 4.0-4.5 mm long, 2.0-2.5 mm wide, ovate-oblong, not saccate, ciliate (fide Steyermark & Badillo) at the apex; stamens 8-9, with 6 fertile, staminodes 2-3, the filaments 1.8-2.0 mm long, connate for most of their length, the anthers oblong, 0.8-1.0 mm long, ca 0.4 mm wide; glands 2, 2-3-lobed, deltoid or trapezoid, ca 0.3 mm long per side, glabrous; style 1.8-2.0 mm

long, glabrous, the stigma trilobate, ca 0.1 mm in diameter; ovary subglobose, ca 1.5 mm in diameter, densely villous, the ovules numerous. Fruit unknown.

TYPE. Madriz 37, Venezuela, Yaracuy, north of Nirgua, fl (holotype NY).

DISTRIBUTION. Confined to the cloud forests of the coastal Cordillera of the states of Yaracuy and Carabobo. VENEZUELA. Yaracuy: Steyermark, Bunting & Wessels-Boer 100290 fl (paratypes NY, VEN): Carabobo: Steyermark & Steyermark 95234 fl (paratypes NY, VEN).

This species is closely related to Trigonia sericea, from which it differs in having shorter and less ramified inflorescences, slightly longer petioles, and specially in the much longer bracts and bracteoles, as well as several other minor characters.

14. Trigonia subcymosa Bentham, Hook. Lond. Jour. Bot. 2: 373. 1843; Grisebach, in Linnaea 22: 31. 1849; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 127. 1875; Stafleu, in Pulle Fl. Surin. 3 (2): 176. 1951.

Large shrub, the branches terete, densely lenticellate, strigose when young, becoming glabrous with age. Stipules subulate, 4.0-5.0 mm long, ca 2 mm wide, caducous; petioles 3.0-4.0 mm long, ca 0.5 mm thick, densely golden-brown strigose; lamina elliptic to obovate, or oblong, 3.0-8.0 cm long, 2.0-4.0 cm wide, chartaceous, the margins entire, the apex obtuse, acute or mucronate, the base cuneate to obtuse; venation eucamptodromous, sparsely golden-strigose pubescent, the midrib plane above, prominulous beneath, the secondary nerves 8-10 pairs; intercostal pubescence very sparsely strigose above, depressed-lanate beneath, the indumentum cream or yellowish in most cases. Inflorescences terminal pyramidal panicles to 15 cm long. Flowers in cymules of 2-4; peduncles 1.0-8.0 mm long, diminishing in length towards the apex of the inflorescence; pedicels 1.0-2.0 mm long, villous-strigose, the bracts and bracteoles of equal size, 2.0-3.0 mm long, 0.5-0.7 mm wide, ovate, curved upwards, villous-strigose; sepals ovate or oblong, 2.5-3.5 mm long, 0.7-1.5 mm wide, strigose or villous-strigose along exposed portions, lanate along protected portions; standard 3.0-3.5 cm long, ca 2.0 mm wide, the pouch extending to 1/2 of the length, erect along the upper portion or nearly so, the apex revolute, barbate at the throat, the wings spathulate, 2.5-3.1 mm long, 0.8-1.0 mm wide, glabrous at base, the keel petals 2.5-2.8 mm long, ca 2.0 mm wide, with the pouch extending from 1/3 of the length up, the apex revolute, glabrous; stamens 8, fertile ones 5-6, staminodes 2-3, the filaments 1.0-1.5 mm long, free for 1/3 of the length, the anthers ovate

or oblong, 0.4-0.5 mm long, ca 0.2 wide; glands 2, 2-3 lobed; deltoid or trapezoid, ca 0.4 mm per side, glabrous; style 0.8-1.1 mm long, glabrous or villous, the stigma trilobate ca 0.1 mm in diameter; ovary subglobose, ca 0.4 mm in diameter, villous-barbate, the ovules numerous. Fruit not known.

TYPE. Schomburgk 56 Guyana, fl (lectotype K - Bentham Herb.; isotypes CGE, G, NY, W).

DISTRIBUTION. The exact range of this species is unknown, as it is only known from Schomburgk collections made in Guyana. No precise data as to localities is reported. GUYANA. Schomburgk 63 fl (paratypes BR, CGE, G, OXF, U, W); Schomburgk 249 fl (F, W); Schomburgk 373 fl (GOET, K).

Trigonia subcymosa is easily recognized by its short, pyramidal panicles, the long peduncles, the typically curved bracts and bracteoles, and its fairly small leaves and flowers.

Bentham cited both Schomburgk 56 and 63 in his description of this species. These specimens are very similar and either one could be selected to typify the taxon. I have selected Schomburgk 56 as the lectotype. There are elements labeled as 63 and 56 that are not referable to this species but Trigonia villosa, and this mixture has led to confusion in the past. The specimen from Bentham's herbarium at Kew has Schomburgk collections 56, 63, and 373 mounted on the same sheet. This could well mean that they constitute elements of the same gathering that were numbered differently, as the specimens are extremely similar, but there is not enough evidence to allow me to assume that this is the case.

The lack of fruit makes it extremely difficult to determine the relationships of this species.

15. Trigonia nivea Cambessèdes, (Hippocrateaceae) St. Hil. Fl. Bras. Mer. 2: 81. 1829; Grisebach, in Linnaea 22: 29. 1849; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 134. 1875; Reitz, in Fl. Ill. Catar. 1 (13): 10. 1967.

Trigonia candida Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 139. 1875. Type. Glaziou 2505, Brazil, Rio de Janeiro, fl, fr (holotype C; isotypes A, BR, C, F, GH, IPEAN, NY, US).

Trigonia ovalifolia Glaziou, Bull. Soc. Bot. Fr. 3 (52): 34 . 1905. Type. Glaziou 14690, Brazil, Minas Gerais, fl (holotype P; isotypes C, F, G, P).

Trigonia nivea forma paniculata Chodat & Hassler, Bull. Herb. Boiss. 2 (8): 801. 1903. Type. Hassler 8416, Paraguay, Apa River Headwaters, fl, fr (holotype G; isotypes BM, G, MO, NY).

Scandent shrub, the branches terete, lenticellate, lanate when young, becoming glabrous with age. Stipules triangular, 6.0-10.0 mm long, strigulose, caducous; petioles 2.0-8.0 mm long, 0.5-1.0 mm wide, strigose or lanate, sometimes becoming glabrous; lamina elliptic to oblong-elliptic, sometimes ovate or obovate, 5.0-13.0 cm long, 1.0-4.5 cm wide, subcoriaceous, the margins entire or revolute, the apex acute to acuminate, sometimes mucronate, the base obtuse; venation eucamptodromous, slightly strigulose or glabrous above, lanate or strigose beneath, the midrib plane above, prominent beneath, the secondary nerves 10-16 pairs; intercostal pubescence absent above, lanate to appressed lanate (almost sericeous) beneath. Inflorescences terminal and axillary racemes, or panicles 5.0-10.0 cm long, varying from highly

congested to very open (sometimes on the same plant). Flowers in groups (cincinni) of 1-4; peduncles 0.0-5.0 mm long, ca 0.5 mm thick, strigose, the bracts 2.0-6.0 mm long, subulate or triangular, strigose; pedicels 1.0-5.0 mm long, ca 0.5 mm thick, strigose, the bracteoles 1.0-4.0 mm long, subulate, strigose; sepals ovate or oblong, 3.0-5.0 mm long, 1.5-3.0 mm wide, lanate on protected portions, strigose on exposed areas; 4.5-6.5 mm long, ca 3.0 mm wide, the pouch extending along 1/2 of the length, barbate at the throat, the keel petals 3.5-5.0 mm long, ca 3.0 mm wide, the pouch extending along 2/3 of the length; stamens 10-11, fertile ones 6-7, staminodes 3-4, the filaments 1.0-2.0 mm long, free for 1/2 the length, the anthers oblong, 0.4-0.7 mm long, ca 0.3 mm wide; glands 2-3-lobed, trapezoid or rounded, ca 0.4 mm per side, in some cases with short laciniae on the lobes, glabrous; style 1.0-2.0 mm long, glabrous, the stigma trilobate, 0.2-0.3 mm in diameter; ovary subglobose, 1.0-1.5 mm in diameter, densely villous, the ovules numerous. Fruits 3.0-7.0 cm long, 1.0-1.5 cm per side; exocarp thin, velutinous-tomentose or slightly strigose; the endocarp separable from the mesocarp, velutinous-tomentose or partially so, sometimes glabrous. Seeds ovate, barbate pubescent, the trichomes ca 10.0 mm long.

This species is separated into 3 varieties.

Key to the varieties of Trigonia nivea

1. Petioles shorter than 3 mm; glands laciniate. b. var fasciculata.
1. Petioles 4-8 mm long; glands not laciniate.
   2. Peduncles, when present, to 1.5 mm long; leaves usually oblong to oblong-elliptic with dense, white pubescence; bracts usually as long as the pedicels. a. var nivea.

2. Peduncles 2-5 mm long; leaves usually elliptic or ovate-elliptic; bracts shorter than the pedicels. c. var pubescens.

15a. Trigonia nivea var nivea

Leaves oblong to oblong-elliptic, densely lanate to adpressed-lanate beneath, the margins entire to revolute; petioles 4.0-8.0 mm long. Flower buds ca 5 mm long; peduncles 0.0-1.5 mm long, the bracts 4.0-5.0 mm long. Fruit 5.0-7.0 mm long; endocarp usually pubescent.

TYPE. St Hilaire 226 Brazil, fl, fr (holotype MPU).

DISTRIBUTION. Extending in a coastal and mediterranean belt from Venezuela to Santa Catarina in south Brazil and adjacent eastern Paraguay; the habitats most frequently occupied by this variety seem to be coastal forests and mesophilic grasslands and forests, with some populations found in drier, more xerophytic areas. VENEZUELA. Sucre: Aristeguieta 3988 fl (US, VEN). Anzoategui: Aristeguieta & Agostini 5554 fl (VEN); F.D. Smith 32 fl (US). Monaguas: Pursell et al 8911 fl (NY, US). GUYANA. Rupununi: Irwin 679 fl (US). Quelch & McDonnell 222 fl (K). BRAZIL. Pará: Black 49-7957 fl (IPEAN); Fróes & Black 24606 fl (IPEAN). Maranhão: Pires & Black 2481 fl (IPEAN). Piauí: Ducke HG 814 fr (MG); Lisbôa 2388 fr (MG); Ceará: Frá Allemão 602 fl (P); Ducke 2453 fl, fr (IPEAN); Guedes 483 fl (IPEAN, MG); Lisbôa 2433 fl (MG). Pernambuco: Gardner 943 fl (W); Schenk 425 fl (C); Pickel 133 fl (F, IPEAN, US). Bahia: Belem 1170 fl (IPEAN, NY); Belem 3632 fl (IPEAN); Belem 3652 fl, fr (IPEAN); Blanchet 2029 buds (F, G, M, NY); Guillot sn fl (U). Minas Gerais: Barreto 7154 fl (A, F); Pires & Black 3314 fl (IPEAN, NY); Sampaio 7163 fl, fr (F). Rio de Janeiro: Glaziou 10730 fl (C, G, P); Glaziou 8670 fl, fr (G, P); Pereira 4250 fl (F). Guanabara: Aparício & Rizzini 59 fl (NY); Trinta 511 & Fromm 1587 fl (M). São Paulo: Humboldt & Bonpland 1870 fl (NY); Hoehne sn, São Paulo Botanical

Garden, fl (NY); Novães 1108 fl (US). Paraná: Dusén 8696 fl (L); Dusén 12168 fl (GH); Hatschbach 6861 fl (L, W); Hatschbach 19042 & Guimarães 131 fl (C). PARAGUAY. Amambay: Fiebrig 5133 fl, fr (A, G, GH, GOET, L, M, US, W); Hassler 5588 fl (G, NY). Alto Paraná: Hassler 5362 fl, fr (BM, G).

Common name: Cipó de Paína (Santa Catarina, São Paulo).

This highly variable variety includes the taxa formerly known as Trigonia candida and T. ovalifolia, as well as T. nivea var paniculata. Warming proposed T. candida based primarily on leaf characters, and a more open inflorescence. An examination and a comparison of the types of T. candida and T. nivea yield information which makes it impossible to maintain them as separate taxa. Furthermore, had Warming been able to examine more sheets of the same material that he used as a basis for T. candida, he would have found his specific characters to be variable even within the same specimen. The sheets examined by Warming have fairly open inflorescence, while material of the same collections deposited in other herbaria was almost identical to the St. Hilaire collection of T. nivea.

This high variability is present throughout the whole species, but is especially noticeable in this variety. Although I have established 3 varieties within the species, this solution is not perfect. There is some overlap in characters between the three. On the other hand, I have retained material in var nivea that might possibly be distinct, if there were consistency in the characters.

15b. Trigonia nivea var fasciculata (Grisebach) Lleras, stat nov_v

Trigonia fasciculata Grisebach, in Linnaea 22: 29. 1849; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 139. 1875.

Leaves oblong to oblong-elliptic, sometimes elliptic, densely lanate beneath, the margins entire; petioles 1.5-3.0 mm long. Flower buds ca 5.0 mm long, the bracts 3.0-6.0 mm long. Glands laciniate. Fruit ca 4.0 cm long; endocarp with very short velutinous-tomentose pubescence.

TYPE. Blanchet 2921, Brazil, Bahia, Rio São Francisco, fl (lectotype G, isotypes BR, E, F, G, MG, P, W).

DISTRIBUTION. Reported only from Bahia and Minas Gerais. BRAZIL. Bahia: Dialer 618 fl (M); Rose & Russell 19950 fl, fr (NY, US); Rose & Russell 19968 fl, fr (GH, NY). Minas Gerais: G. Mendes Magalhães 5343 bds (IPEAN).

This variety, corresponding to what has previously been known as Trigonia fasciculata, can easily be distinguished by its short petioles, the lanate pubescence on the nervation of the underside of the leaf, and by the presence of laciniae on the glands. Although it merits taxonomical recognition, I do not consider it to be distinct enough to justify maintaining it as a separate species.

15c. Trigonia nivea var pubescens (Cambessèdes) Lleras, stat nov.

Trigonia pubescens Cambessèdes, (Hippocrateaceae) St. Hilaire Fl. Bras. Mer. 2: 114. 1829; Grisebach, in Linnaea 22: 28. 1849; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 135. 1875; Reitz, Fl. Ill. Catar. 1 (Trigoniaceae): 4. 1967.

Leaves elliptic to ovate-elliptic, thinly lanate-pubescent beneath (having a grayish or brownish aspect), the margins entire; petioles 5-8 mm long. Flower buds ca 3.0 mm long; pedicels 2.0-5.0 mm long, the bracts 1.0-3.0 mm long. Fruit 3.0-4.0 mm long; the endocarp velutinous-tomentose.

TYPE. St. Hilaire 2205 Brazil, Minas Gerais, fl (holotype MPU; isotype P).

DISTRIBUTION. Found in coastal forests from Pará to Santa Catarina; absent or not known from Ceará, south to Bahia. BRAZIL. Pará: Froes 29747 fl (IPEAN). Maranhão: Prance 58579 fl (F, MO, NY, U, US). Minas Gerais: Mendes Magalhães 765 fl (IPEAN, US); Hatschbach 26974 fl (NY); St. Hilaire 27 fl (P). Rio de Janeiro: Schott 5982 fr (F, US, W). São Paulo: St. Hilaire 1234 fl (F, P). Paraná: Hatschbach 3722 fl (US); Hatschbach 6782 fl, fr (US). Santa Catarina: Gevieski 62 fl (NY, US); Reitz 1748 fl (GH); Reitz 2016 fl (US); Reitz & Klein 2549 fl (US); Smith 5795 fr (US); Ule 1029 fl (G, US).

This variety can be recognized by its broader leaves, the typical gray or brown aspect of the leaf pubescence, and by the relatively long peduncles. Although I agree with Cambessèdes in recognizing it as taxonomically distinct, I consider that the distinctions are not enough to merit specific status. This variety includes all the material previously known as Trigonia pubescens.

16. Trigonia killipii Macbride, (Trigoniaceae) Fl. of Peru, Publ. Field Mus. Nat. Hist. 13 (3) : 95. 1950.

Shrub or scandent shrub, the branches terete, lenticellate, when young lanate to strigose, becoming glabrous with age. Stipules narrowly triangular, membranaceous, 15.0-25.0 mm long, 1.5-2.5 mm wide, slightly strigose, persistent; petioles 6.0-8.0 mm long, ca 1.5 mm thick, densely strigose; lamina elliptic to obovate-elliptic, 6.0-13.0 cm long, 3.0-7.5 cm wide, subcoriaceous, smooth, the margins entire, the apex acute to acuminate, the base obtuse; venation eucamptodromous, the midrib plane above, prominulous beneath, strigose on both surfaces, the secondary nerves 14-16 pairs, usually opposite to subopposite, usually less than 10.0 mm from one another; intercostal pubescence very slightly villous above, lanate beneath. Inflorescences terminal and subterminal axillary panicles, sometimes reduced to racemes, to 10.0 cm long. Flowers in groups (cincinni) of 1-3 (usually 1); peduncles, when present, 0.1-0.5 mm long, strigose, the bracts ovate, 4.0-4.5 mm long, 1.5-2.5 mm wide, the pedicels 0.5-1.0 mm long, ca 0.5 mm thick, strigose; sepals oblong to deltoid, 4.0-6.0 mm long, 2.0-4.0 mm wide, strigose on the exposed portions, lanate on the protected areas, acute to rounded at the apex; standard 6.0-6.5 mm long, 4.5-5.0 mm wide, the pouch extending 1/3 of the length, the upper portion erect to revolute, barbate at the throat, the wings spathulate, 5.5-6.0 mm long, 2.5-3.0 mm wide, the apex rounded, densely barbate at the base, the keel petals 4.5-5.0 mm long, 2.5-2.8 mm wide, the pouch extending along most of the length, the apex revolute; stamens 8, 6-7 fertile, 1-2 staminodes, the filaments 2.5-3.0 mm long, free along 1/2 of the length,

the anthers oblong to obovate, 0.6-1.1 mm long, ca 0.6 mm wide, one of them smaller; glands 2, 2-lobed, more or less rectangular to trapezoid, ca 0.6 mm high, 1.0 mm long, glabrous to slightly pilose; style 2.5-3.0 mm long, barbate, the stigma trilobate, approximately triangular, 0.5-0.6 mm per side; ovary subglobose, 1.0-1.5 mm in diameter, barbate-pubescent, the ovules numerous. Fruit 10.5-11.0 cm long, the valves 9.0-10.0 mm wide; exocarp thin, fleshy, velutinous-tomentose; endocarp cartilaginous. Seeds not seen.

TYPE. Macbride 5513, Peru, Junin, La Merced, fl (holotype F, isotype G).

DISTRIBUTION. Tropical rainforests in western Amazonia. PERU. Killip & Smith 23846 fl (F, NY, US); Schunke 2299 fr (MO, NY). BRAZIL. Amazonas: Lleras, Steward et al 16995 fl (INPA, MG, NY). Rondônia: Prance et al 5195 fl (INPA, MG, NY); Prance et al 6711 fl (INPA, MG, NY).

This species is a close relative of Trigonia echiteifolia Rusby, from which it differs in its larger flowers, broader bracts and bracteoles, larger number of secondary nerves on the leaves, and in the shorter peduncles.

17. Trigonia paniculata Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 132. 1875.

Trigonia schottiana Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 133. 1875. Type. Schott 1677, Brazil, Rio de Janeiro, fl (lectotype W; isotypes F, W).

Shrub or treelet, the branches terete, lenticellate, densely tomentellous, becoming glabrous with age. Stipules caducous (nv); petioles 5.0-8.0 mm long, ca 0.3 mm thick, densely tomentellous; lamina oblong to elliptic, 5.0-10.0 cm long, 2.5-5.0 cm wide, the margins revolute, the apex acuminate, the base rounded to slightly cordate; venation eucamptodromous, densely tomentellous along the midrib above, densely tomentellous beneath, the midrib prominent above, prominulous beneath, secondary veins 8-9 pairs, tertiary venation reticulate, visible beneath; intercostal pubescence sparsely lanate or arachnoid on the upper surface of the young leaves, becoming glabrous with age, villous beneath, imparting a typical olive-green coloration, white-lanate along the revolute margins, in exsiccatae. Inflorescences terminal and subterminal axillary pyramidal panicles, 5.0-15.0 cm long. Flowers in groups (cincinni) of 1-2; peduncles short or absent, to 0.4 mm long; pedicels 1.0-1.9 mm long, ca 0.2 mm thick, densely tomentellous, the bracts and bracteoles of equal size, linear, 1.5-2.5 mm long, tomentellous; sepals oblong or ovate, 1.5-2.5 mm long, 0.5-0.8 mm wide, tomentellous; standard 3.5-4.0 mm long, ca 2.0 mm wide, the pouch extending along 1/4 of the length, nasiform, barbate at the throat, the wings narrowly spathulate, 2.5-3.0 mm long, ca 0.5 mm wide, barbate at

the base, the keel petals 2.0-2.5 mm long, ca 2.0 mm wide, the pouch centered on the petal; stamens 9-10, 6-7 fertile, 3-4 staminodes, the filaments 0.9-1.2 mm long, connate for most of the length, the anthers subglobose, 0.2-0.3 mm in diameter; glands 2, 2-3-lobed, irregular, ca 0.3 mm per side, glabrous; style glabrous, 0.9-1.1 mm long, stigma trilobate, ca 0.2 mm in diameter; ovary subglobose, ca 0.5 mm in diameter, villous, the ovules numerous. Fruit oblong, truncate at base, 1.5-2.0 cm long, the valves ca 1.0 cm wide; exocarp yellow-villous when immature, turning glabrous with age; endocarp woody. Seeds 1-2 (-3) per locule, subglobose, ca 0.5 mm in diameter, reddish-brown pubescent, the trichomes ca 5.0 mm long.

TYPE. Glaziou 2938, Brazil, Rio de Janeiro, Larangeiras, fl (lectotype C; isotypes BM, BR, P).

DISTRIBUTION. Known from forest edges and gallery forests from eastern central Brazil. BRAZIL. Minas Gerais: Irwin 2195 fl (F, NY, US); Irwin 2713 fl buds (F, NY); Mexia 4516 fl (G, GH, MO, NY, P, US); Mexia 4705 fr imm (F, G, GH, MICH, MO, NY, P). Rio de Janeiro: Barth P2 fl (US); Glaziou 3882 fl (C, P); Glaziou 5793 fl (P. US); Glaziou 10728 fl (C, P); Pereira 4256 fl (F); Vauthier 168 fl (G, P). Guanabara: Houllet sn fl (BR); Luschnath sn fl (BR). São Paulo: Burchell 4029 fl buds (BR, G); Burchell 4608 fr imm (BR, G, P); Hoehne 28821 fl (A, NY, US).

This species is closer to Trigonia eriosperma than to any other. It can be separated from T. eriosperma by the presence of axillary panicles,

the larger inflorescences, and especially by the typical white-lanate border on the leaf margins, a character which is found in no other species of the genus.

Of the material listed by Warming, I have selected Glaziou 2938 as the lectotype for this species. I cannot find the difference between Trigonia paniculata and T. schottiana as indicated by Warming; the two cannot be distinguished. Schott 1677 is considered as the lectotype of the name T. schottiana.

18. Trigonia villosa Aublet, Hist. Pl. Guian. Fr. 1: 338. pl. 149. 1775; Poiret, Encyc. Meth. Bot. 8: 98. 1808; De Candolle, Prod. 1: 571. 1824; Grisebach, in Linnaea 22: 28. 1849; Warming, in Mart. Fl. Bras. 13 (2): 137. 1875; Stafleu, in Pulle Fl. Surin. 3(2): 176. 1951.

Trigonia villosa var. obtusata De Candolle, Prod. 1: 571. 1824. Type. Perrottet 261, French Guiana, fl (holotype G; isotype G).

Trigonia villosa var. cuneata De Candolle, Prod. 1: 571. 1824. Type. Perrottet 259, French Guiana, fl (holotype G; isotype G).

Trigonia villosa var. oblonga De Candolle, Prod. 1: 571. 1824. Type. Perrottet 260, French Guiana, fl (holotype G; isotype G).

Trigonia mollis De Candolle, Prod. 1. 571. 1824. Type Martius 179 Brazil, Guanabara, Rio de Janeiro, Corcovado, fl (holotype G, isotype M).

Trigonia cepo Cambessèdes, (Hippocrateaceae) St. Hilaire Fl. Bras. Merid. 2: 115. 1829. Type. St. Hilaire 125, Brazil, Guanabara, Rio de Janeiro, fl (holotype MPU; isotypes F,G,P,US).

Shrub, the branches terete, slightly lenticellate, densely golden-brown strigose when young, becoming glabrous with age. Stipules subulate, 3.0-6.0 mm long, 1.5-2.0 mm wide, coriaceous, caducous; petioles 3.0-10.0 mm long, ca 1.0 mm thick, very densely golden-brown strigose; lamina broadly elliptic to obovate, sometimes oblong, inequilateral, 5.0-14.0 cm long, 2.0-8.5 cm wide, subcoriaceous, the margins entire, the apex acute to acuminate, the base cuneate to obtuse; venation eucamptodromous, densely golden-strigose pubescent, the midrib plane above, prominulous to prominent beneath, the secondary nerves 6-9 pairs, inserted at angles of ca 70° to midrib; intercostal pubescence very sparsely strigose above, yellowish or greenish-white lanate beneath. Inflorescences terminal and subterminal axillary panicles to 25.0 cm long. Flowers in groups of 1-3, commonly 1-2; peduncles

0.5-3.0 mm long, 0.7-0.9 mm thick, strigose, the bracts subulate to linear, sometimes ovate, 2.0-3.0 mm long, 0.5-1.5 mm wide, strigose, the pedicels 1.8-2.8 mm long, 0.5-1.5 mm thick, strigose, the bracteoles subulate to linear, 1.0-2.0 mm long, 0.4-0.7 mm wide, strigose; sepals ovate or oblong, 4.0-5.5 mm long, 2.0-3.5 mm wide, acute or rounded at apex, lanate along protected portions, strigose along exposed areas; standard 5.0-7.0 mm long, the pouch extending to 1/2 of the length, with the upper half revolute, irregular at apex, barbate at the throat, the wings spathulate, 6.0-6.5 mm long, 2.0-3.0 mm wide, barbate at the base, the keel petals 4.0-5.0 mm long, 3.0-4.0 mm wide, the pouch extending along 2/3 of the length, barbate at the base; stamens 10-11 (-12) 6-7 fertile, staminodes 3-4, the filaments 2.5-3.0 mm long, free for 1/3 of the length, the anthers obovate or oblong, 0.5-0.7 mm long, ca 0.4 mm wide; glands 2, 2-3 lobed, the lobes deltoid, 0.2-0.3 mm per side, glabrous; style 2.5-2.8 mm long, glabrous or slightly villous, the stigma trilobate, ca 0.2 mm in diameter; ovary subglobose, ca 1.0 mm in diameter, barbate pubescent, the ovules numerous. Fruit 4.5-11.0 cm long, the valves 6.0-20.0 mm per side; exocarp thin (ca 0.7 mm) fleshy, with reddish-brown or yellowish-brown velutinous-tomentose pubescence; mesocarp woody, separable from the endocarp; endocarp thin, sometimes densely covered with long, brown velutinous-tomentose pubescence, to glabrous or nearly so. Seeds ca 20 per locule, ovoid, barbate pubescent, the trichomes to 20.0 mm long, spirally disposed around the seed.

This species is divided into two varieties.

Key to the varieties of Trigonia villosa

1. Petioles over 5.0 mm long; fruits under 7.5 cm long; endocarp densely pubescent. a. var villosa

1. Petioles 3.0-4.0 mm long; fruits over 9.0 cm long; endocarp glabrous or nearly so. b. var macrocarpa

18a. Trigonia villosa var villosa

Leaves with petioles 5.0-10.0 mm long. Fruit 4.5-7.5 cm long; exocarp usually reddish-brown; endocarp densely velutinous-tomentose pubescent.

TYPE. Aublet sn, French Guiana, "Cayenne 1775", fl, fr (lectotype BM).

DISTRIBUTION. Known from coastal areas in Guyana, French Guiana, the states of Amapá and Pará, Brazil, and as a significant range disjunction, from the vicinity of Rio de Janeiro. GUYANA. Jenman 1083 fl (U); Jenman 6736 fl (NY, U). FRENCH GUIANA. Leblond 36 fr (G); Poiteau 1826 fr (P); Herb. Moquin-Tandon "Fragment d'Aublet" fl (P); Broadway 662 fr (GH, NY, US); Lemée sn fl, fr (P). BRAZIL. Amapá: Pires & Cavalcante 52283 fl (IPEAN, MG NY, U, US), Pires & Cavalcante 52522 fl (IPEAN, MG); Pará: Fróes 20368 fl (IPEAN, NY, US), Pires & Silva 4570 fl (IPEAN); Prance & Silva 58711 fl (IPEAN); Silva, N. 3016 fl (IPEAN). Guanabara: Guillemin 696 fl, fr (F, G, P); Dominguez 239 fl (NY); Dusén 108 fl (GH).

This variety includes all of the material formerly known as Trigonia mollis and T. cepo, as well as the three varieties recognized by De Candolle.

De Candolle's varieties based on leaf characters are untenable, as it is possible to assign varietal epithets to portions of the same collection following his usage. Trigonia cepo has long been known to be a synonym for T. mollis. Although there is a very significant range disjunction between those elements formerly referred to as T. mollis (Rio de Janeiro), and T. villosa (the Guianas and northern Brazil), I find no taxonomically significant distinction.

After careful evaluation of the material, I can find no justification for

maintaining so many varieties within the species, or for splitting this taxon into several species, as it has been done in the past.

I have designated the material deposited at the British Museum as the lectotype, as there is no collection of Trigonia villosa in Aublet's herbarium, nor, to my knowledge, in the general collection of Paris. Two specimens, one from the Poiret Herbarium, and the other from the Moquin-Tandon Herbarium, are annotated in pencil as "Fragments d'Aublet". Although they match the lectotype fairly well, I hesitate to designate them as isotypes.

18b. Trigonia villosa var macrocarpa (Bentham) Lleras, stat. nov.

Trigonia macrocarpa Bentham, in London Jour. Bot. 2: 373. 1843.

TYPE. Schomburgk 54, Guyana, Essequibo River, fl, fr (holotype K, isotypes C, CGE, F, G, NY, US, W).

DISTRIBUTION. Along riverbanks in periodically flooded forests. GUYANA. Schomburgk 54 (Type). BRAZIL. Amazonas: Chagas INPA 971 fr (INPA). Ceará: Schery 417 fl (GH, MO), Ducke 216 fl, fr (NY, US).

This variety corresponds to Bentham's Trigonia macrocarpa. I do not consider that it merits specific status, as morphologically it is very close to var. villosa, from which it differs in the shape of the leaf, and the size and pubescence of the fruit.

19. Trigonia boliviana Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 134. 1875.

Trigonia simplex Warming var pilosula Kuntze, Rev. Gen. 3 (2): 18. 1898.

Type. Kuntze sn Bolivia, Yapagani, fl (holotype NY; isotype US).

Shrub, the branches terete, slightly striate, lenticellate, tomentellous when young, becoming glabrous with age. Stipules connate at base, triangular to subulate, slightly tomentellous; petioles 5.0-8.0 mm long, 0.4-0.8 mm thick, strigose; lamina elliptic to obovate-elliptic, 4.0-7.0 cm long, 2.0-3.5 cm wide, chartaceous, the margins entire, the apex acuminate, the base obtuse to subrotund; venation eucamptodromous, glabrous above, slightly villous beneath, the midrib plane above, prominulous beneath, secondary veins 7-8 (-9) pairs, plane above, prominulous beneath, tertiary venation not visible; intercostal pubescence sparsely strigulose above, lanate beneath. Inflorescences terminal and axillary racemes, 4.0-8.0 cm long. Flowers in groups (cincinni) of 1-2; peduncles 0.1-1.0 mm long, villous, the bracts linear, 3.0-5.0 mm long, curved upwards, villous; peduncles 1.0-2.0 mm long, villous, the bracteoles linear, 1.0-2.0 mm long; sepals oblong or ovate, 3.0-4.0 mm long, 1.0-1.5 mm wide, strigose; standard 4.6-5.0 mm long, 2.5-2.8 mm wide, the pouch extending along 1/4 of the length, barbate at the throat, the wings spathulate, 3.0-4.0 mm long, 1.2-1.5 mm wide, barbate at the base, the keel petals 3.0-3.5 mm long, 3.5-4.0 mm wide, the pouch covering most of the petal; stamens 8-9, with 6-7 fertile, staminodes 2, the filaments 2.0-2.2 mm long, connate along 2/3 of the length, the anthers subglobose, ca 0.3 mm in diameter; glands 2, 2-3-lobed, irregular, ca 0.4 mm per side; style slender, 1.9-2.1 mm long, glabrous, the stigma trilobate, ca 0.2 mm in diameter; ovary subglobose, ca 0.4 mm in diameter, villous, the ovules numerous. Fruit oblong, 2.0-2.5 cm long,

the valves ca 1.0 cm per side, connate at the apex, the horn ca 4.0 mm long; exocarp rugose, glabrous when mature; endocarp woody, reddish-brown. Seeds 3-4 (-5) per locule, subglobose, ca 2.0 mm long, barbate-villous, the trichomes ca 5.0 mm long.

TYPE. Cuming 214, Bolivia, fl (holotype W; isotype F).

DISTRIBUTION. Known only from Bolivia, thus far only from the Department of Santa Cruz. BOLIVIA. Santa Cruz: Bridges sn fl (CGE, G); Herzog 1417 fl, fr (G, U); Steinbach 8132 fl, fr (F, GH, NY, U, US).

This species is very close to Trigonia eriosperma, especially to subsp. simplex, with which it has been associated in the past. As with other species associated with T. eriosperma, it is possible that with more data it will be impossible to maintain them as separate species. I am recognizing T. boliviana as a separate species based on the differences in the morphology of the fruit which has cornate valves, a character found in no other Trigonia. In addition to the fruit character, T. boliviana differs from T. eriosperma in the longer bracts and bracteoles, and the shorter peduncles.

20. Trigonia bracteata Lleras, sp nov

Frutex, ramulis juvenilibus strigosis, glabrescentibus, lenticellatis. Stipulae connatae, triangularae, 6.0-8.0 mm longae, 4.0-5.0 mm latae, chartaceae, strigulosae. Folia opposita, petiolo 12.0-14.0 mm longo, 1.0-2.0 mm crasso, strigoso; laminae ellipticae vel obovatae, 12.0-18.0 cm longae, 4.5-9.0 cm latae, subcoriaceae, margine integre, apice acuto vel acuminato variante, basi obtusa, supra leviter strigosae, infra strigosae; costa media supra plana infra prominentia, strigosa, costis secundariis 6-8 jugis. Inflorescentiae in paniculis terminalibus vel axillaribus dispositae, 8.0-17.0 cm longae. Flores saepe cadentes, in cincinnos 1-4 floratis; axibus cincinnorum ad 3.0 mm longis, ca 0.8 mm crassis, strigosis; pedunculi 0.1-1.0 mm longi, 0.7-0.9 mm crassi, strigosi, bracteis persistentis, triangularis, 2.0-5.0 (-7.0) mm longis, 0.8-2.0 mm latis, margine saepe glanduloso-papillatis, strigosis; pedicelli 2.0-3.0 mm longi, 0.4-0.5 mm crassi, strigosi, bracteolis persistentis, subulatis vel triangularis, 1.5-3.0 mm longis, 0.5-1.0 mm latis, margine ut in bracteis, strigosis; sepala ovata vel oblonga, 3.5-4.5 mm longa, 1.5-2.2 mm lata, lanata vel strigosa; vexillum 3.5-4.0 mm longum, 2.8-3.2 mm latum, usque ad 1/3-1/4 partes longitudinaliter saccatum, apice revolute, intus barbatum, alis petalis late spathulatis, 3.2-3.5 mm longis, 2.0-2.3 mm latis, concavis, glabris, carinae petala saccata, 2.4-2.6 mm longa, ca. 1.0 mm lata; stamina 8 (-10?), sterilia 2 (-4?), fertilia 6, filamentis ad medium connatis, 1.6-1.8 mm longis, antheris oblongis vel ellipticis, 0.5-1.0 mm longis, 0.3-0.4 mm latis, glandulae 2, bilobae, 0.5-0.7 mm latae, a fronte visae leviter labiatae, intus villosae; stylus erectus, 1.8-2.0 mm longus, villosus, stigma circulare, ca 0.5 mm in diametro, alba; ovarium subglobosum, 0.8-1.0 mm in diametro, 3-loculare,

villosum, ovulis in quoque loculo numerosis. Fructus juvenilibus oblongus, dense villoso-tomentosus.

TYPE. Steyermark & Rabe 96588, Venezuela, Barinas, 35 km SW of Santa Barbara, fl, imm fr (holotype U; isotypes US, VEN).

DISTRIBUTION. Known only from type gathering.

This species can easily be distinguished by its large bracts and bracteoles, that persist after the flowers have fallen. In some cases, rosettes of bracts and bracteoles can be seen on the flowering axes, even when there are no longer any flowers, hence the specific epithet for the species.

Superfically, Trigonia bracteata appears similar to T. virens; however, it differs in enough significant characters to be treated as a separate species. T. bracteata has staminodes while T. virens has only fertile stamens; T. virens has a unilocular ovary, but in T. bracteata it is 3-locular. The lack of fruiting material makes it difficult to establish the relationships of these two species to other species of the genus.

21. Trigonia rytidocarpa Casaretto, Nov. Stirp. Decand. 76. 1845.

Trigonia glazioviana Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2). 129. 1875. Type. Glaziou 733 Brazil, Rio de Janeiro, fl (holotype C; isotypes BR, P).

Subscandent shrub (fide Casaretto), the branches terete, lenticellate, tomentellous, becoming glabrous with age. Stipules subulate, bifid, to 2.0 mm long, tomentellous; petioles 5.0-10.0 (-13.0) mm long, 0.8-1.5 mm thick, glabrous or nearly so; lamina oblong-elliptic to elliptic, sometimes broadly elliptic, 5.0-11.0 cm long, 2.5-5.0 (-7.0) cm wide, the margins entire to very slightly revolute, the apex abruptly acuminate, the base acute to obtuse; venation eucamptodromous, glabrous above, very slightly lanate beneath, the midrib depressed to plane above, prominent beneath, secondary veins 6-8 (-9) pairs, tertiary venation reticulate, visible beneath; intercostal pubescence absent above, sparsely arachnoid to lanate beneath. Inflorescence terminal and subterminal axillary panicles, 5.0-15.0 cm long. Flowers in groups (cincinni) of 1-4, usually grouped dichotomously in racemose ultimate inflorescences; peduncles and pedicels of variable length, 0.4-1.5 mm long, diminishing towards the apex of the inflorescence, tomentellous, the bracts and bracteoles of equal size, triangular, 1.0-2.5 mm long, tomentellous, sometimes sheathing the peduncles and pedicels; sepals ovate or oblong, 2.5-3.0 mm long, 1.0-1.5 mm wide, tomentellous, sometimes laciniate at the margins; standard 3.4-3.8 mm long, the pouch extending to 3/4 of the length, barbate at the throat, the wings narrowly spathulate (to almost linear), 2.8-3.0 mm long, 0.4-0.5 mm wide, barbate at the base, the keel petals 2.5-2.8 mm long, 0.9-1.5 mm wide, the pouch along the upper portion; stamens 9-10, with 6 fertile, staminodes 3-4, the

filaments 1.5-2.0 mm long, connate for 2/3 of the length, the anthers 0.2-0.3 mm long, ca 0.2 mm wide; glands 2, 2-3-lobed, irregular, ca 0.2 mm per side, barbate or glabrous; style 1.5-1.8 mm long, villous, the stigma trilobate, ca 0.2 mm in diameter; ovary subglobose, ca 0.5 mm in diameter, the lateral septae not fused at the center, the ovules numerous. Fruit 2.8-3.0 cm long, broadly oblong; the exocarp rugose, yellow-velutinous when young, becoming glabrous when mature; endocarp very slightly tomentellous. Seeds ovate, ca 0.4 mm in diameter, the trichomes ca 5.0 mm long.

TYPE. Casaretto 1956, Brazil, Rio de Janeiro, fl fr (holotype TO; isotype G).

DISTRIBUTION. A species probably endemic only to coastal forests in Rio de Janeiro, Guanabara and northern São Paulo. BRAZIL. Rio de Janeiro: Glaziou 2506 fl (BR, C, P); Glaziou 3670 sterile (BR, C, P); Glaziou 12499 fl (BR, C, G, P); Luschnath sn imm fr (BR); Riedel 660 fl, fr (G); Schott 5980 fr (F, US, W). Guanabara: Glaziou 10729 fl (IPEAN, K); Glaziou 6877 fl (C, F, P); Luschnath sn fr (BR). São Paulo: Martius sn fl (M).

Trigonia rytidocarpa can be separated from T. eriosperma by its larger, more complex inflorescences, its generally larger leaves, and by its unique rugose, crested fruit, as well as several other minor characters.

The relationships of this species are closer to Trigonia eriosperma than to any other. Warming interpreted T. crotonoides (T. eriosperma var eriosperma) as an intermediate between this species and T. simplex (T. eriosperma var simplex); although in a sense, this may be true, I find that

T. rytidocarpa is distinct enough to merit specific status, while considering that T. simplex is just a variety under T. eriosperma.

This species has been commonly known as Trigonia glazioviana, name that is now being rejected for the earlier T. rytidocarpa.

22. Trigonia hypoleuca Grisebach, Linnaea 22: 30. 1849; Warming, (Trigoniaceae)

22. Trigonia hypoleuca Grisebach, Linnaea 22: 30. 1849; Warming, (Trigoniaceae)

Mart. Fl. Bras. 13 (2): 140. 1875; Macbride, Publ. Field Mus. Hist. Bot. 11 (2): 69. 1931; Stafleu, (Trigoniaceae) Pulle Fl. Surin. 3 (2): 175. 1951.

Trigonia hypoleuca var. pubescens Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 140. 1875. Type. Wullschlaegel 8161 Suriname, fl, fr (holotype BR, isotypes IPEAN, NY, VEN).

Trigonia xanthopila Garke, Linnaea 22: 51. 1849. Kegel 1177 Suriname, fl (holotype on 2 sheets as indicated by Garke, GOET).

Shrub or scandent shrub, the branches terete, densely lenticellate, the young ones strigose, becoming glabrous with age. Stipules subulate, 2.0-3.0 mm long, caducous; petioles 5.0-12.0 mm long, ca 1.0 mm thick, rugulose, almost glabrous; lamina oblong elliptic or obovate, sometimes laterally unequal, 8.0-18.0 (-20.0) mm long, 4.0-10.0 mm wide, subcoriaceous, the margins entire, the apex acute to acuminate, the base cuneate to obtuse; venation eucamptodromous, strigose-pubescent, the midrib plane above, prominulous beneath, the secondary nerves 7-8 pairs; intercostal pubescence absent above, lanate beneath. Inflorescence terminal and subterminal axillary panicles, to 30.0 cm long. Flowers in groups of 1-4; peduncles and pedicels of equal length, 2.0-4.5 mm long, strigose, the bracts and bracteoles linear, 1.0-2.5 mm long, densely strigose; sepals ovate to oblong, 4.8-6.0 mm long, 1.5-3.0 mm wide, strigose along exposed portions, lanate on protected areas; standard 5.5-8.5 mm long, 4.0-5.0 mm wide, the pouch extending along 1/2 of the length, the upper portion revolute, barbate at the throat, the wings broadly spathulate, 5.5-8.5 mm long, 2.8-5.0 mm wide, barbate at the base, the keel petals 5.0-7.0 mm long, 2.2-3.5 mm wide,

the pouch extending along 1/2 of the length, barbate at the base; stamens 10-11, 6-7 fertile, 3-4 staminodes, the staminodes with terminal globose knobs, the filaments 1.5-1.8 mm long, free along the upper 1/2, the anthers obovate, 0.5-0.7 mm long, 0.3-0.4 mm wide; glands 2, 2-3-lobate, the lobes 2.0-3.0 mm high, the upper 1/2 formed by subulate, pointed, strigose laciniae; style clavate, 1.5-1.8 mm long, glabrous; the stigma ca 0.3 mm in diameter; ovary subglobose, 1.0-1.5 mm indiameter, barbate-pilose, 1-locular, the ovules numerous. Fruit 5.0-7.0 cm long, the valves 2.5-3.0 cm wide; exocarp coriaceous, the nerves prominulous, glabrous; endocarp ending flush with the exocarp, cartilaginous. Seeds 6.0-8.0 mm long, elliptic, flattened, equinate-pubescent.

TYPE. Schomburgk 315, Guyana, fl (holotype GOET; isotype K).

DISTRIBUTION. This species is found mainly along forested, periodically flooded riverbanks in Guyana, Suriname, and French Guiana and northeastern Brazil. GUYANA. Schomburgk 224 fl (CGE, G, K, P, W); Gleason 516 fl (G, K, NY, US); Gleason 549 fr (GH, NY, US); Jenman 1155 fl (K, NY); Jenman 1296 fl (K). SURINAME. B.W. 2161 fl (U); Florschutz & Maas 2741 fl (NY,U,US); Splitgerber 1136 fl (L); Mennega 371 fl (A, C, U). FRENCH GUIANA. Herb. Sagot s.n. "Ile Portal Bar". fl (F, G, GH, NY, US); Service des Aux & Forets 4204 fl (U). BRAZIL. Ducke 8955 fl, fr (MG); Prance et al 22982 fl (COL, F, INPA, MG, NY, US).

Trigonia hypoleuca is probably closer to Trigonia virens than to any other species. The presence of unilocular ovaries in both species suggests similar trends in evolution. Trigonia hypoleuca can be distinguished from Trigonia virens by the lanate pubescence on the leaves, the presence of laciniae on the glands, and the presence of staminodes, as well as other minor characters.

Warming's recognition of varieties in this species appears untenable at present; no clear distinctions can be made within the species that would merit formal recognition.

Grisebach's citation of the type as "Schomburgk 313" is erroneous. He was misled by a not altogether clear 5 that could easily be interpreted as a 3; the situation is clarified on examination of the Kew isotype on which the collection number is unmistakeably Schomburgk 315.

The material used by Garke to typify T. xanthopila, and labelled as Kegel 1177, is according to the label data, constituted by two different collections: one made on the Saramacca River in May 1846, and an earlier one gathered on the Cassepocreek River in November 1845; it is impossible to determine whether one of the two sheets deposited at Goettingen is a mixed collection, or if both are mixed collections, or if one sheet corresponds to each locality. The specimens were treated by Garke as one specimen on two sheets, and I consider that for all practical purposes it would be convenient to treat the holotype as such. This name is obviously a later synonym of T. hypoleuca.

23. Trigonia echiteifolia Rusby, Bull. N.Y. Bot. Gard. 4: 324. 1907; Macbride, Publ. Field Nat. Hist. 13 (3): 96. 1950.

Shrub, the branches lenticellate, strigose pubescent, turning glabrous with age. Stipules subulate, 6.0-8.0 mm long, ca 2.0 mm wide, strigose-lanate; caducous; petioles 6.0-10.0 mm long, 0.8-1.0 mm thick, strigose to glabrous; lamina inequilaterally ovate to obovate or oblong, 5.0-12.0 cm long, 2.0-6.0 cm wide, subcoriaceous, the margins entire to slightly revolute, the apex acuminate, the base obtuse to slightly cordate; venation eucamptodromous, strigose pubescent, the midrib plane above, prominulous beneath, the secondary nerves 10-12 pairs; intercostal areas arachnoid-pubescent or glabrous above, lanate beneath. Inflorescences terminal and subterminal axillary panicles, to 10.0 cm long. Flowers in groups of 1-4 (usually 3); peduncles and pedicels of equal length, 0.5-1.0 mm long, 0.4-0.5 mm thick, strigose; the bracts subulate to linear, 2.5-3.5 mm long, ca 0.2 mm wide, strigose, the bracteoles linear, 1.5-2.0 mm long, strigose; sepals ovate to deltoid, 4.0-5.0 (-6.0) mm long, 1.5-2.5 mm wide, strigose externally, the interior lanate; standard 4.5-5.0 mm long, 4.0-5.0 mm wide, the pouch extending to 2/5 of the length, the upper portion erect or revolute, the apex rounded, barbate-pubescent at the inside of the throat, the wings spathulate 4.0-4.5 mm long, 1.5-2.0 mm wide, barbate at the base, the keel petals 3.8-4.0 mm long, 3.0-4.0 mm wide, the pouch extending along 2/3 of the length; stamens 8-10, fertile ones 5-7, staminodes 2-3, the filaments 1.8-2.0 mm long, connate to the middle, the anthers obovate, 0.5-0.8 mm long, 0.3-0.4 mm wide; glands 2, 3-lobed, the lobes deltoid, ca 0.2 mm per side, strigose; style 1.8-2.0 mm long, barbate, the stigma trilobate, ca

0.2 mm in diameter; ovary subglobose, the locules not always totally fused at the center, barbate-villous, the ovules numerous. Fruit not seen.

TYPE. Bang 2812. Bolivia, La Paz, fl (holotype NY; isotypes F, GH, MICH, MO, NY, US).

DISTRIBUTION. Known only from 3 collections. BOLIVIA. La Paz: Krukoff 10466 fl (A, F, NY). BRAZIL. Rondônia: Black & Cordeiro 52-14678 fl (IPEAN).

The relationships of this species are impossible to determine at present, due to the lack of fruiting material.

24. Trigonia sericea H.B.K., (Hippocrateaceae) Nov. Gen. et Sp. Pl. 5: (4). 1821.

Trigonia najadum Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 126. 1875. Type. Martius s.n., Brazil, Rio Solimões, fl (holotype M; isotype M).

Shrub or treelet, the branches terete, lenticellate. Stipules narrowly triangular, membranaceous, 20.0-25.0 mm long, ca 5.0 mm wide, glabrous, caducous; petioles 9.0-15.0 (-20.0) mm long, 1.0-2.0 mm thick, slightly strigose; lamina elliptic to broadly elliptic, 6.0-19.0 cm long, 4.0-11.0 cm wide, subcoriaceous, smooth, the margins entire, the apex acuminate, the base obtuse; venation eucamptodromous, the midrib plane above, prominulous beneath, glabrous above, tomentose beneath, the secondary nerves 8-11 pairs, plane above, prominulous beneath; intercostal pubescence absent above, white-lanate beneath. Inflorescence loose terminal and subterminal axillary panicles, to 10 cm long. Flowers in groups of 3-10, (commonly 6-7); peduncles 2.5-4.0 mm long, 0.5-0.7 mm thick, tomentose, the bracts ovate, 1.5-2.0 mm long, 0.3-0.5 mm wide; tomentose, the pedicels 0.9-1.2 mm long, ca 0.6 mm thick, tomentose; sepals ovate, 3.5-5.0 mm long, 1.5-2.5 mm wide, strigose; standard 4.0-5.0 mm long, 3.5-4.0 mm wide, the pouch extending 1/2 of the length, the upper portion erect or revolute, the apex irregular, barbate pubescent at the inside of the throat, the wings spathulate, 3.5-4.0 mm long, 2.0-3.0 mm wide, the apex irregular, barbate at the inside of the base, the keel petals 2.5-3.5 mm long, 3.0-3.5 mm wide, the pouch extending along 2/3 of the length, the apex irregular; stamens 10, 6 fertile, 4 staminodes, the filaments 1.4-1.8 mm long, free for 1/2 the length, the anthers elliptic to oblong, 0.6-0.8 mm long, 0.3-0.4 mm wide,

adhering 3 on each side of the style and completely surrounding it; glands 2, 2-3-lobate, ca 1.0 mm high, 1.5 mm long, with a knob-like projection at the apex of each lobe, glabrous; style 1.5-1.7 mm long, slightly pilose or glabrous, the stigma trilobate, ca 0.2 mm in diameter, ca 0.2 mm high; ovary subglobose, 1.0-1.2 mm in diameter, barbate-pubescent, the ovules numeorus. Fruit 3.0-7.0 cm long, the valves 0.5-1.5 mm wide; exocarp thin, fleshy, velutinous-tomentose; endocarp cartilaginous. Seeds numerous, subglobose, ca 2.0 mm in diameter, barbate-pubescent, the trichomes ca 10.0 mm long.

TYPE. Humboldt 1859, Colombia, "Andes de Quindie", fl (holotype P, (n.v.; isotype P).

DISTRIBUTION. Known only from periodically flooded rainforests in the Amazon basin of Colombia, Venezuela, Peru and Brazil.

COLOMBIA. Antioquia: Romero C. 2423 fr (COL). Caldas: Bro. Daniel 2317 fl (US). Valle: Hutchinson & Wright 3293 fl (COL, F, US); Uribe 1550 fr (COL, US). VENEZUELA. Bolívar: Steyermark 74649 fl (F, NY, VEN). PERU. Loreto: Killip & Smith 29542 fl, fr (F, NY, US); Schunke 50 fl (A, F, NY, US). BRAZIL. Amazonas: Lleras, Steward et al. P16897 fl (INPA, MG, NY).

Trigonia sericea is probably related to T. prancei, from which it differs in the simpler inflorescence, larger flower parts (in general), and the pubescent leaves, as well as other minor characters.

2. Humbertodendron Leandri, in Heim; Compt. Rend. Acad. Paris. 229: 847. 1949; Perrier & Leandri (Trigoniaceae) Humbert, Fl. de Madagascar. 108 bis: 1-4. 1955.

Small tree, branches terete. Leaves simple, opposite, petiolate, with connate stipules. Inflorescences axillary triflorate cymes. Flowers zygomorphic, sharing a common peduncle; bracts 2, eglandulate; sepals 5 quincuncial, unequal; petals 5, contorted, unequal, papilionaceous; fertile stamens 6, staminodes absent, the filaments connate at base, free above, the anthers basifixed, bilocular, introrse, dehiscing along two lateral slits; pollen triporate, deltoid in equatorial view. Gland one, strongly adpressed to the ovary. Ovary superior, 3-winged, 3-sulcate, trilocular, the locules incompletely closed, lacking a central column; ovules 1 per locule, attached to the interior ends of the lateral septae. Fruit (fide Leandri) a 3-winged samara; seed lacking endosperm; embryo with an inferior radicle.

TYPE SPECIES. Humbertodendron saboureaui Leandri

DISTRIBUTION. Monotypic endemic genus known only from the eastern coastal forests in Malagasy.

1. Humbertodendron saboureaui Leandri, in Heim, Compt. Rend. Acad. Paris. 229: 847. 1949; Perrier & Leandri, (Trigoniaceae) Humbert, Fl. de Madagascar. 108 bis: 2. 1955.

Tree, branches terete, lenticellate, glabrous. Stipules oblong, 2.5-3.0 mm long, strigose; petioles 4.5-6.0 mm long, ca 1.0 mm thick, strigose; lamina elliptic to obovate, 2.5-5.0 cm long, 1.0-3.0 cm wide, chartaceous,

the margins entire, the apex obtuse to emarginate, the base acute to obtuse; venation brochidodromous, glabrous, the midrib prominulous above, prominent beneath, secondary veins 4-6 pairs. Flowers in trifloral axillary cymes; peduncles 6.0-18.0 mm long, strigose; pedicels 4.0-7.0 mm long, strigose, the bracts and bracteoles subulate, 1.5-2.0 mm long, strigose; sepals ovate to oblong, 4.0-5.0 mm long, 2.0-2.5 mm wide, strigose; standard 3.5-5.0 mm long, 3.0-4.0 mm wide, the pouch extending along 2/3 of the length, revolute at the apex, slightly strigose externally, barbate at the throat, the wings sublinear to obovate, 3.5-4.5 mm long, 0.5-1.5 mm wide, slightly strigose, the keel petals deltoid to ovate, 3.5-4.5 mm long, 2.5-3.5 mm wide, strigose externally; stamens ca 4.5 mm long, the filaments connate to the middle, 1.5-3.5 mm long, the anthers ovate to elliptic, 1.0-1.4 mm long, ca 0.5 mm wide; gland reniform, ca 1.0 mm long, 1.5 mm wide, strigose or pilose; style 1.5-3.0 mm long, glabrous, the stigma triangular, ca 0.4 mm wide; ovary ovate to subpyramidal, strigose or pilose, 1.0-1.5 mm high, 0.9-1.3 mm per side. Fruit (fide Leandri) 2.0-2.5 cm long, 1.5-1.8 mm per side; wings narrowly semi-elliptic. Seeds glabrous, narrowly ovate.

TYPE. Ramarokoto 1522 RN, Malagasy, Ambodivila, near Ambila, fl (holotype P; photograph NY).

DISTRIBUTION. Eastern coastal forests of Malagasy. Flowering in February, fruiting in October (?).

MALAGASY. Ambila: Louvel & Perrier 14896 fl (P); Tamatave: Louvel & Perrier 14896 bis fl (P); Service Forestier 44 fl, fr (P).

LOCAL NAMES. Hazombaroranalahy (Ambila), Fandrianakanga (Tamatave).

3. Trigoniastrum Miquel, Fl. Ind. Bat. Suppl. 394. 1862; Bentham & Hooker, Gen. Pl. 1: 139. 1862; Baillon, Hist. Pl. 5: 91. 1873; Chodat, Bull. Herb. Boiss. 3: 1895; Barth, Bull. Herb. Boiss. 4: 481. 1896; Engler & Prantl, Nat. Pflanzenfam. 209. 1897; Van Steenis, Fl. Malesiana 1, (4): 58. 1948; Ng, in Tree Fl. Malaya. 1: 449. 1972.

Isopteris Wall. Cat. 7261. 1832, nom. nud.

Small to medium tree, branches terete, lenticellate. Leaves simple, alternate, petiolate, the margins and acumen sometimes glandular; stipules caducous. Inflorescences terminal and subterminal axillary panicles. Flowers zygomorphic, the bracts glandular on the margins; sepals 5, quincuncial, unequal; petals 5, contorted, unequal, papilionaceous; fertile stamens 6, staminodes absent; the filaments connate at base, free above, the anthers basifixed, bilocular, introrse, dehiscing along a central slit; pollen 3-4 porate; glands 1-2; ovary 3-locular, lacking a central column; ovules 2 per locule, pendulous, attached to the interior ends of the lateral septae. Fruit a 3-winged samara; seeds one per locule, lacking endosperm.

TYPE SPECIES. Trigoniastrum hypoleucum Miquel

DISTRIBUTION. Monotypic endemic genus known from tropical rainforests in the Malay Peninsula, Sumatra and Borneo.

1. Trigoniastrum hypoleucum Miquel, Fl. Ind. Bat. Suppl. 394. 1862; Chodat Bull. Herb. Boiss. 3: 136. 1895; Barth, Bull. Herb. Boiss. 4: 481. 1896; Van Steenis, Fl. Malesiana I, (4):58. 1948; Ng in Tree Fl. Malaya 1: 449. 1972.

Isopteris penangiana Wallich ex Benn., Hooker f. Fl. Br. Ind. 1: 208. 1872.

Trigoniastrum hypoleucum var. oliganthum Airy Shaw, Kew Bull. 1940: 253. 1940. Type. Native collector, Richards 1921, Malaysia, Sarawak, fl (holotype A; isotype A).

Trigoniastrum hypoleucum var. viride Airy Shaw, Kew Bull. 1940: 253. 1940. Type. Elmer 21302, Malaysia, Sabah, Tawao, fl, fr (holotype A; isotypes BR, F, GH, M, MO, U, US).

Tree, to 30 m. Petioles 4.0-8.0 mm long, 2.0-4.0 mm wide, sulcate, sometimes sparsely strigose, the stipules caducous (n.v.); lamina oblong, 7.0-20.0 cm long, 2.5-6.0 cm wide, glabrous above, thinly lanate beneath, the margins entire, with small impressed glands, the apex acuminate, the acumen cuneate, to 30.0 mm, glandular thickened, the midrib plane to depressed above, prominulous beneath, slightly strigose, the secondary nerves 4-6 pairs, brochidodromous. Inflorescences 15.0-40.0 cm long, the bracts foliolate on lower panicles, becoming fusiform towards the upper ones, the glands circular, fleshy. Flowers (fide Van Steenis) white; sepals 2.0-3.5 mm long, 1.0-2.0 mm wide, ovate, the apex acute, strigose; standard 4.0-5.0 mm long, the pouch extending to 1/2 the length, 2.0-3.0 mm wide, slightly pilose externally, the wings 3.0-4.0 mm long, 1.0-2.0 mm wide, spathulate, the keel petals 3.5-5.0 mm long, oblique to oblong; filaments 1.0-2.0 mm long, connate for 2/3 of the length, the anthers 0.5-1.0 mm long, ovate; glands ca 0.7 mm wide, 0.6 mm high, reniform, puberulous; style 1.0-1.5 mm long, sparsely strigose, the stigma ca 0.2 mm diameter; puberulous; ovary 0.5-0.8 mm in diameter, subglobose, strigose to lanate pubescent. Fruit 3.0-5.0 cm long, the locules semi-elliptic, extending to 2.5 cm, the wings to 2.5 mm long, 10.0 mm wide, extending upwards, oblong, the inner side straight, rounded on the external margin, nervation prominulous. Seeds obovate, flattened, ca 20.0 mm long, 5.0 mm wide, velutinous. Seedlings (fide Van Steenis) with epigeal cotyledons, first pair of leaves opposite.

TYPE. Teysmann, Herb. Bogor. # 4548, Sumatra, "Mangala Lamp." fl, fr (lectotype U; isotypes GH, US).

DISTRIBUTION. Forests of Indonesia, Malaysia, Singapore and Brunei. INDONESIA. Sumatra: Forbes sn fr (A); Forbes 3039 fl, fr (A, GH, MO, NY, US); Forbes 3187 fr (A, NY, US); Soepadmo 136 fl (A); Teysmann sub. n. Herb. Bogor. 4411 fl, fr (Syntype U). MALAYSIA: Penang: Dr. King's coll. 1680 fl (A). Perak: Dr. King's coll. (Soping) 6002 fr (US); Dr. King's coll. 6768 fl (U, US) Dr. King's coll. (Thaiping) 8467 fl (F, US); Wray 3253 fr (US). Kelantan: Henderson 2482A fl (A). Selangor: Kochummen 94447 fl (A). Trengganu: Cockburn 8259 fr (A). Sarawak: Ashton 22620 fl (A); Haron 21332 fl (A); Hou 410 fl, fr (A); Jacobs 6264 fr (US); Richards 2324 fl (A); Richards 2448 fl (A); Wee-lek 621 fl (A); Sabah: Gibot 33034 fl (A); Sinanggul 30548 fl, fr (A); Singh 21020 fl (A, US); Tikun 39342 fl, fr (A); Wood 16258 fr (A). SINGAPORE. Ngadiman 34965 fl (A); Ngadiman 36148 fl (A). BRUNEI. S.W. sub. n. Kepong 80176 st (A).

COMMON NAME. SE Borneo: Kikir: mangkudor; Asanan: tinga Catu; Malaya: marasali, mata pasak, suginara.

Trigoniastrum hypoleucum is the only species in the genus. Airy Shaw, 1940, established two varieties under this species: var. oliganthum, and var. viride based on leaf characters. I can find no justification to maintain varieties under this species, as the leaves are very variable. The typification of the species has been somewhat problematic, as Miquel's treatment is obscure as to the type. He indicated it as "Mangala prope Lampong". Several Teysmann specimens seen on loan are annotated as "Mangala Lamp", and probably represent syntypes. Other treatments in the literature have ignored this problem by not citing the type. I am annotating the Utrecht specimen labeled as Herb. Bogor. # 4548, as the lectotype.

APPENDIX

TAXONOMY OF EUPHRONIA

Euphronia Martius ex Martius & Zuccarini, Nov. Gen. Sp. Pl. Flora 7 (1): 32. 1825; Martius & Zuccarini, Nov. Gen. Sp. 121. 1826.

Lightia Rob. Schomburgk, in Linnaea 20: 753. 1847; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 121. 1875.

Tree or shrub, branches terete. Leaves simple, alternate, petiolate, the margins revolute. Inflorescences terminal and subterminal racemes. Sepals 5, quincuncial, unequal; petals 3, imbricate, adnate to the staminal tube; stamens 5 (-7), fertile 4 (-6), staminode 1, connate into a tube surrounding the ovary, the tube divided to the base opposite the staminode; fertile stamens of two lengths, and divided into two groups separated by the staminode; anthers basifixed, bilocular, introrse, dehiscing along central slit; ovary trilocular, the ovules anatropous, two per locule; placentation axial. Fruit a trivalvate capsule, dehiscing from the apex towards the base. Seed one per locule.

TYPE SPECIES. Euphronia hirtelloides Martius ex Martius & Zuccarini.

DISTRIBUTION. A monotypic tropical genus known only from the Guiana crystalline shield of northern South America.

1. Euphronia hirtelloides Martius ex Martius & Zuccarini, Nov. Gen. et Sp., Pl. Flora 7(1): 32. 1825; Martius & Zuccarini, Nov. Gen. et Sp. 122. 1826.

Lightia guianensis Rob. Schomburgk, in Linnaea 20: 754. 1847; Warming, (Trigoniaceae) Mart. Fl. Bras. 13 (2): 121. 1875. Type. No specimen.

Lightia licanoides Warming (Trigoniaceae) Mart. Fl. Bras. 13 (2) : 122. Type. Spruce 3413, Venezuela, Amazonas, Casiquiare, fl (holotype W; isotypes F, G, GH, GOET, NY, W).

Tree or shrub, branches terete, lanate pubescent when young, becoming

glabrous with age. Leaves with petioles (2.0-) 3.0-6.0 (-7.0) mm long, 1.1-2.0 mm thick, lanate pubescent or glabrous; lamina elliptic to obovate, sometimes ovate, 1.0-5.5 cm long, 3.0-3.6 cm wide, subcoriaceous to coriaceous, the abaxial surface glabrous intercostally, the adaxial surface lanate; midrib plane above, prominulous beneath, lanate pubescent on both surfaces, the secondary nervation inconspicuous, the margins entire to revolute, the revolute portion of variable width, the apex acute or acuminate, the base obtuse. Inflorescences terminal and subterminal racemes 2.0-13.0 cm long, 1-15-flowered, the subterminal ones subtended by leaves, the axis lanate pubescent. Flowers subtended by subulate bracts, 0.3-1.7 mm long, 0.1-0.8 mm wide, barbate pubescent, caducous; pedicels 2.5-5.0 mm long, 0.9-1.2 mm thick, lanate or strigose pubescent; sepals unequal, the outer ones ovate to subtriangular, 4.0-6.0 mm long, 1.8-3.0 mm wide, the margins entire, sometimes with papillae, the apex acute, the base truncate, strigose-pubescent on both surfaces, the inner ones broadly oblong, the margins entire, the apex acute, the base truncate, strigose-pubescent along exposed portions, lanate-pubescent on protected areas; petals unequal, spathulate, lilac to purple, 9.0-16.0 mm long, 4.0-7.0 mm wide, apex rounded, irregular, base truncate, slightly strigose pubescent on both surfaces; stamens of 2 lengths, the longer with filaments 7.0-13.0 mm, exceeding the shorter ones by ca 2.0 mm, and united with them for the basal 2.0-4.5 mm, the anthers reddish-brown, ovate or oblong, 1.5-2.5 mm long, 1.0-1.4 mm wide; style 9.0-13.0 mm long, geniculate 2.0-3.0 mm from the apex, pilose or lanate pubescent, the stigma trilobate, 0.5-0.8 mm in diameter, ca 0.6 thick, cream; ovary subglobose to globose, 1.0-3.0 mm in diameter, lanate pubescent, the ovules 2 per locule. Fruit with valves 1.2-1.6 cm long, 3.5-5.0 (-5.5) mm wide per side; exocarp

thin (ca 0.3 mm), fleshy, lanate pubescent, attached to the persistent style; endocarp cartilaginous, tan. Seeds subtrullate, slightly winged, 9-11 mm long, 3-5 mm wide, glabrous, reddish-brown.

TYPE. Martius sn, Colombia, Putumayo, fr (lectotype M; isotype M). The type locality was given by Martius as "Inter Coari et Ega". This locality is phytogeographically improbable as this species is otherwise only known from the Guiana crystalline shield where it is widespread. The only place within the Guiana crystalline shield visited by Martius was the Araracuara Hills near the Putumayo river, and more recent collections from this area are morphol gically similar to the type. It is probable that the locality for the type is erroneous.

DISTRIBUTION. Known only from savannas on the Guyana crystalline shield. COLOMBIA. Amazonas: Maguire, Maguire & Fernandez 44153 fl (COL, NY). VENEZUELA. Territorio Amazonas: Maguire & Wurdack 34525 fl (COL, NY, VEN); Maguire & Wurdack 34546 fl (NY, VEN); Maguire, Wurdack & Keith 41813 fl (NY, VEN); Medina 83975 fl (VEN); Vareschi & Jaffe 74033 fl (VEN). Bolivar: Agostini 258 fl (NY, VEN); Bernardi 2626 fl (NY); Cardona 2443 fl (VEN); Cardona 2726 fl (NY); Cardona 2872 fl (US); Lasser 1273 fl (NY, VEN); Maguire 32283 fl (COL, NY, VEN); Maguire 33717 fl (COL, NY, VEN); Rutkis & Foldats 504 fl (VEN); Steyermark 60274 fl (F, MO, US, VEN); Steyermark 75330 fl (F, NY, VEN); Tamayo 2699 fl (F, US, VEN). BRAZIL. Amazonas: Ducke 159a fl (NY); Fróes 22753 fl, fr (COL, GH, IPEAN, M, MO, NY, U, US, VEN). Roraima: Ducke 1407 fl (F, GH, MG, NY, US); Pires, Cavalcante & Magnano 14021 fl (MG); Ule 8628 fl (G, L).

This species is highly variable in respect to leaf morphology, the character that was used previously to separate it into two species. No consistency, geographical or otherwise, can be noted in respect to leaf shape, size or pubescence, thus making it impossible to delimit varieties.

FIG. 15. Scanning electron micrographs of pollen of Euphronia hirtelloides. A-B, Maguire et al. 33293, X 660; C-D, Maguire et al. 34546, C X 660, D X 2000; E-F, Vareschi & Jaffe 8016, E X 660, F X 600.

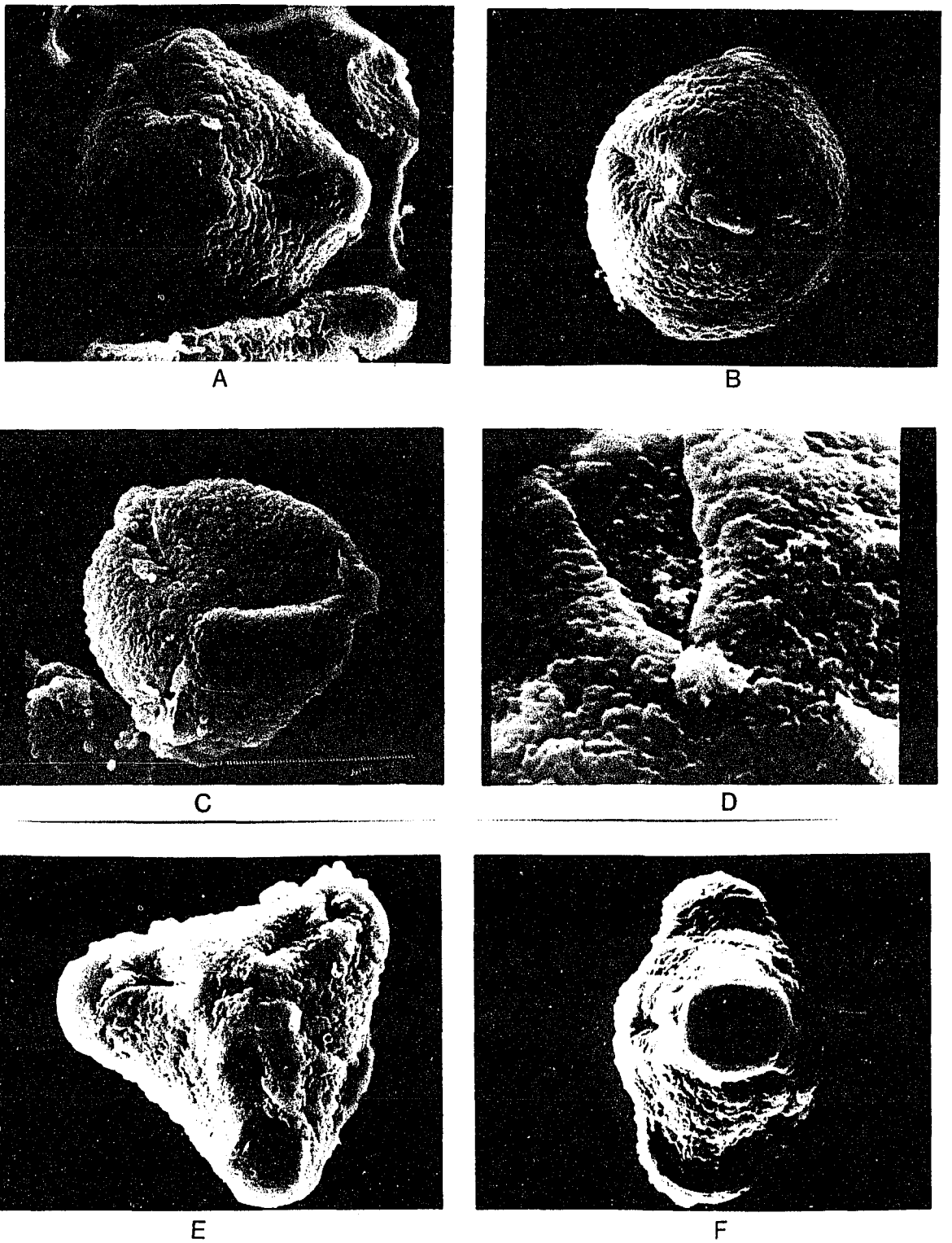


Fig. 15

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