# SYSTEMATIC STUDIES IN 'GOMIDESIA' O. BERG (MYRTACEAE)

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# Systematic studies in *Gomidesia* O.Berg (Myrtaceae)

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To my parents, Jimmy and Kate

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Eimear Nic Lughadha
October 1997

# STATEMENT

I was admitted as a research student in October, 1990, and as a part-time candidate for the degree of Doctor of Philosophy in October 1991; the higher study for which this is a record was carried out in the University of St. Andrews (and at the Royal Botanic Gardens, Kew) between 1991 and 1997.

Eimear Nic Lughadha
October 1997

# CERTIFICATE

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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October 1997

'Seeing then that truth consisteth in
the right ordering of names in our
affirmations, a man that seeketh
precise truth hath need to remember
what every name he uses stands for;
and to place it accordingly; or else he
will find himself entangled in words,
as a bird in lime twiggs; the more he
struggles, the more belimed.'

**Hobbes**, Leviathan: [15].

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# Abstract

*Gomidesia* is a neotropical genus with a distribution centred on the Atlantic rain forest biome of southeastern Brazil. Most species of *Gomidesia* are confined to Brazil but a single species extends to the Antilles and another is known only from Bolivia and Argentina. Forty species are delimited and described in the present study. For each species, notes are provided on distribution, ecology, nomenclature and typification. A century of nomenclatural malpractice has resulted in much confusion in the application of names. In some cases conservation action is required to preserve existing usage of long-established binomials.

The genus is distinguished from other genera of the Myrciinae by virtue of its relatively long anthers in which the thecal arcs retain some degree of curvature after dehiscence and the ventral pollen sacs are vertically displaced on the connective relative to the dorsal pollen sacs . Unlike the situation in other genera of the Myrciinae, in *Gomidesia* stamen number is not correlated with disk size. These features of the androecium may represent an adaptive response to buzz-pollination. Other characters observed in some species of *Gomidesia* and unknown elsewhere in the Myrtoideae include a sterile connective stub which separates the pollen sacs from the filament and a pubescent hypocotyl. Species of *Gomidesia* tend to flower later than other sympatric Myrtaceae and the fruit maturation period may extend over six months or more.

Field observations indicate that pre-dawn anthesis and buzz-pollination are prevalent but not ubiquitous in *Gomidesia* and that populations of a single species may vary considerably in pollination ecology. Breeding system studies demonstrate that most species of *Gomidesia* are outcrossers but that there is no evidence of pre-zygotic discrimination against flowers hand-pollinated with self pollen. Preferential outcrossing in *Gomidesia* is maintained by a post-zygotic mechanism, the precise functioning of which remains to be elucidated.

# Introduction

The Myrtaceae is a large and mostly tropical family which includes an estimated 3500 to 4600 species (Schmid, 1980; Mabberley, 1997) of which 1300 or more are neotropical. Members of the family are an important component of a number tropical ecosystems (Mori et al., 1983; Gentry, 1988). Problems of generic and specific circumscription are characteristic of both neo- and paleotropical taxa but the situation in the neotropics is particularly acute. This is reflected in numerous Floras and checklists from which the Myrtaceae are omitted or only cursorily treated as numbered morphospecies, and in herbaria where it is usual to find large proportions of the neotropical Myrtaceae collections (often 50% or more) unidentified even to generic level. In their notoriety as a taxonomically difficult group the neotropical Myrtaceae are rivalled only by the Lauraceae.

Proença (1991) discussed the biological and historical factors which have contributed to the reputation that the neotropical Myrtaceae have acquired as a 'difficult' group. Biological factors include genuinely high α-diversity, cryptic generic characters which often require dissection and an experienced eye, strikingly uniform flowers and fruits, vegetative characters which change over time in an individual and complex variation patterns with much homoplasy. Historical factors include domination of the group by a single taxonomist, Otto Berg, who published more than 1000 new species and 30 new genera over a seven year period, and the subsequent destruction during the second World War of much of Berg's original material.

The sheer volume of Berg's output was daunting for subsequent workers and a century passed before another taxonomist emerged who was sufficiently familiar with Berg's work to judge it. McVaugh's 1968 review of generic limits in the American Myrtaceae heralded a small scale revival of interest in the family in the neotropics. In the past three decades the family has been treated for a number of Brazilian states and in florulas of smaller areas and several of the less speciose genera have been revised for Flora Neotropica. However no genus of more than 40 species has been monographed this century and taxonomic understanding of the large genera *Eugenia* (c. 1000 spp., mostly neotropical), *Myrcia* (> 250 spp., neotropical), and *Calyptranthes* (>120 spp., neotropical) has scarcely advanced, though *Psidium* (> 100 spp., neotropical) is currently being monographed by Landrum (ASU) and collaborators.

All but one species of the neotropical Myrtaceae belong to the subfamily Myrtoideae, which includes most of the fleshy-fruited members of the family. The Myrtoideae comprises a single tribe, the Myrteae, which is traditionally divided into three subtribes. The Eugeniinae, with bean-like embryos and the Myrtinae (Pimentinae) with C-shaped embryos are found both in the Old and New Worlds while the Myrciinae, with foliaceous embryos are confined to the New World. The Myrciinae contribute more than half the species diversity of Myrtaceae in eastern and central Brazil, the focal area for neotropical fieldwork by staff of the Royal Botanic Gardens, Kew, for the past 20 years. The accumulation of unidentified myrtaceous material from this region provided the initial impetus for this study. *Gomidesia* was chosen to be monographed on the basis of its relatively manageable size (*Myrceugenia* with 38 species had already been monographed (Landrum, 1981) and the remaining genera of the Myrciinae are estimated to contain in excess of one hundred species) and because the unusual anther morphology offered scope for field investigations of pollination ecology.

The aims of the study presented here were:

- To study the breeding biology of a representative sample of species of *Gomidesia* in their various natural habitats.
- To investigate the potential contribution of characters derived from pollination and breeding system studies to the taxonomy of the Myrtaceae.
- To re-examine the anther character on the basis of which the genus *Gomidesia* was first distinguished and evaluate its taxonomic and functional significance.
- To analyse the distribution patterns of species and infrageneric groups of *Gomidesia* and discuss the ecological and historical factors which may underpin them.
- To produce a modern revision of the genus incorporating anatomical and micromorphological data and field observations where available.
- To develop the first identification key for species in the genus.

The remainder of the thesis takes the following form. A review of the taxonomic history of *Gomidesia* and the Myrciinae is followed by a general survey of the morphology, anatomy etc. of *Gomidesia*. Where possible, these data are presented in the context of the Myrciinae, as are observations on the ecology and biogeography of *Gomidesia*. Discussion then moves to species level, the species concept employed in this study is described and justified, and some informal infrageneric groupings are presented. In the systematic treatment 40 species of *Gomidesia* are recognised and more than 180 binomials and trinomials are treated. Data on the pollination and breeding systems of the Myrciinae proved to be very scarce indeed and so a review of the reproductive biology of the Myrtoideae (Nic Lughadha & Proença, 1996) was prepared in order to provide a background for field and laboratory studies on *Gomidesia*. Considerations of length precluded the inclusion of the review as part of the present work but a reprint of the paper is provided for cross-reference. Finally, the results of field studies on pollination ecology and breeding systems in *Gomidesia* are presented and interpreted, followed by a discussion of their wider implications.

## Taxonomic History

The Myrciinae were first distinguished as a group by Alphonse de Candolle (1828). He focused attention on the morphology of the myrtaceous embryo and used the characters he discovered to divide the Myrteae into three principal groups which were later treated by Berg (1857 - 59) as subtribes. The embryo of the Myrciinae comprises two broad, thin, foliaceous, much folded or contortuplicate cotyledons which are encircled by the elongate, curved hypocotyl. Of the genera now treated in the Myrciinae only *Calyptranthes*, with its distinctive calyptrate calyx, had been recognised before the work of de Candolle. De Candolle (1828) described *Myrcia* in which he treated more than one hundred species with free calyx lobes and (presumed to have) foliaceous embryos. Approximately a quarter of these species had previously been described in *Eugenia* or *Myrtus*. Cambessedes (1833) described a third American genus with a myrcioid embryo: *Marlierea* was distinguished on the basis of its closed calyx which splits open irregularly at anthesis.

By the mid-nineteenth century vast quantities of collections made by the early botanical explorers in South America were available for study by European botanists. Otto Berg, Professor of Pharmacy at the University of Berlin, produced a monumental revision of the American Myrtaceae (1855-56, 1857-59) in which he described some 30 new genera and more than 1000 new species. He treated some 500 species in what de Candolle would have called *Myrcia* and recognised a total of eleven genera in his subtribe Myrciinae. All but one of these genera had biovulate locules, the exception being *Myrceugenia* with multi-ovulate locules and, apart from the characteristic embryo, rather little in common with the other myrcioid genera. In distinguishing the genera with biovulate locules, Berg placed great emphasis on the mode of opening of the calyx and on the degree of prolongation of the hypanthium above the top of the ovary. Five new genera were described on the basis of such characters only to be relegated to synonymy by most subsequent authors (*Rubachia* and *Eugeniopsis* to *Marlierea*, and *Aulomyrcia*, *Calycampe* and *Calyptromyrcia* to *Myrcia,* see Table 1). The other two new genera in Berg's Myrciinae were based on characters of the anther: the monotypic *Cerqueiria* was described as having quadrilocular anthers opening by four apical pores while *Gomidesia* was characterised by *either* quadrilocular, oval anthers in which pairs of locules are

Table 1. Historical treatments of the genera of the Myrciinae.

| Berg (1855-59) | Niedenzu (1893) | Kiaerskou (1893) | Kausel (1948, 1966) | McVaugh (1968) | Landrum (1981) |
|---|---|---|---|---|---|
| Subtribe Myrcioideae | Myrciinae | Myrcioideae | Myrcioideae | 'Myrcioid' genera | Myrciinae |
| **Cerqueiria** | = Gomidesia | | | = Gomidesia | |
| **Gomidesia** | **Gomidesia** | = Myrcia | **Gomidesia** | **Gomidesia** | **Gomidesia** |
| **Rubachia** | = Marlierea | = Marlierea | | = Marlierea | |
| **Marlierea** | **Marlierea** | **Marlierea** | | **Marlierea** | **Marlierea** |
| **Calyptranthes** | **Calyptranthes** | **Calyptranthes** | **Calyptranthes** | **Calyptranthes** | **Calyptranthes** |
| **Calyptromyrcia** | = Myrcia | | | = Myrcia | |
| **Aulomyrcia** | = Myrcia | = Myrcia | **Aulomyrcia** | = Myrcia | |
| **Eugeniopsis** | = Marlierea | = Marlierea | | = Marlierea | |
| **Myrcia** | **Myrcia** | **Myrcia** | **Myrcia** | **Myrcia** | **Myrcia** |
| **Myrceugenia** | **Myrceugenia** | = Myrcia | **Myrceugenia** | **Myrceugenia** | **Myrceugenia** |
| **Calycampe** | = Myrcia | | | | |
| | | | **Nothomyrcia** | **Nothomyrcia** | = Myrceugenia |
| | | | **Myrceugenella** | | **Luma** |
| | | | | **Mitranthes** | **Mitranthes** |
| | | | **Feijoa** | | = **Acca (Myrtinae)** |

superposed, the lower locules being longer and introrsely dehiscent and the upper extrorsely dehiscent with explanate margins *or* oblong or linear, subquadrilocular anthers, dehiscent by means of a sigmoid-flexuose fissure, gaping extrorsely above and introrsely below, with margins not at all explanate.

Berg appears to have expected that his treatment of the Brazilian Myrtaceae as a chapter in Martius' Flora Brasiliensis would be published before his broader Revisio Myrtacearum Americae (hereafter Revisio). Thus the species treated in Flora Brasiliensis are not described in the Revisio but merely mentioned there with a reference to their serial number in Flora Brasilensis. However, contrary to his expectations, the Revisio was published in Linnaea in November 1855 and January and February 1856 while the Flora Brasiliensis treatment did not appear until May 1857 with a supplement in January 1859. McVaugh (1956a) discussed in some detail the sequence of events leading to the publication of Berg's Myrtaceae treatment and outlined the complex nomenclatural consequences. For the purpose of the present study the implications can be summarised as follows: Berg's new genera and new combinations date from Linnaea but the new species based on Brazilian material were only validly published in Flora Brasiliensis. Thus at the time of publication *Gomidesia* comprised a dozen species but this figure rose to 38 when the Flora Brasiliensis treatment appeared in print. In supplements to the Flora Brasiliensis treatment Berg published a further 9 species of *Gomidesia*, mostly based on the collections by Riedel and Langsdorff not available to him at the time of preparation of the original treatment. He indicated where they should be included in his numbered series. A single Antillean species brought the total number of species of *Gomidesia* recognised by Berg to 48.

The Revisio and the complementary Flora Brasiliensis account remain the most comprehensive treatment of the neotropical Myrtaceae to the present day. Few of the larger genera have been monographed since then and no genus of more than 40 species has been monographed this century. For most species of Myrciinae Berg's text remains the only published description. It is fortunate therefore that his descriptions are of very high quality. They are entirely in Latin and include many measurements and detailed descriptions of the nature and distribution of the indumentum, the venation, locule and ovule numbers. Most are based on a single collection and, even where no number is cited, the description is often sufficient to allow one to be certain that the specimen in hand is the one which is described. Since no keys are provided, identification of material not cited involves the rather laborious process of comparing the material in hand with the lengthy descriptions. Occasionally a species treatment is followed by a brief note comparing it to other species to which Berg considered it similar. In *Gomidesia* identification is facilitated by the fact that the species are treated in five groups. (See under Infrageneric Relationships).

The fact that most species were described on the basis of a single collection reflects the limited material available and also the rather narrow specific concepts employed by Berg. Both factors were normal for the time since the early botanical explorers tended to make collections in which a species would usually be represented only by a single gathering from a particular area. Thus Berg would not have been in a position to assess spatial patterns of variation within species and distinguish narrow endemics from widespread species with considerable variation in characters such as leaf shape. Where more than one collection is cited under a single species these were often treated as distinct varieties. The differences between Berg's varieties were usually very minor and they generally do not merit taxonomic recognition.

While Berg's species concepts were fairly normal for his time his nomenclatural practices would have been considered unorthodox, even by his contemporaries. Where he divided existing species he regularly failed to take up the original epithet for any of the resulting species and would not hesitate to use that epithet instead for an entirely unrelated new species of his own. In some instances such practices are acceptable under present nomenclatural rules because Berg cited synonyms with expressions of doubt. However, in other cases Berg's cavalier approach to nomenclature and the attempts of subsequent myrtologists to correct his worst excesses have resulted in long-standing confusion. In this respect it is perhaps quite fortunate that most of the species treated by Berg were new to science, since those based on previously described species, in genera as diverse as *Eugenia*, *Plinia* and *Myrcia,* tend to be the most problematic (see, for example, discussion under *G. cordiifolia*, *G. crocea*, *G. nitida* in Systematic Treatment).

Another difficulty is presented by Berg's practice of citing the collector and locality of the material on which his species were based, and the herbaria from which he had studied material, but often without a collection number. The absence of a collection number in the protologue does not necessarily imply an unnumbered collection: many of the presumptive types, which bear Berg's distinctive handwriting, also bear numbers not cited by him. Finally, the loss of the myrtaceous types from Berlin, where Berg was based, represents a further obstacle to any myrtologist endeavouring to understand Berg's treatment.

Many of Berg's new genera, among them *Gomidesia* and *Cerqueiria*, were reduced to synonymy by Bentham (1869) in a treatment that McVaugh (1968) later dismissed as 'somewhat superficial'. Having studied the Australian Myrtaceae in some detail for his Flora of Australia account Bentham appears to have taken a rather theoretical approach to the

American species, basing his comments on an analysis of Berg's published work rather than on the original material. He advocated treating *Aulomyrcia*, *Calyptromyrcia*, *Gomidesia*, *Cerqueiria* and *Calycampe* as synonymous with *Myrcia*, commenting that 'the division of this overgrown genus into good sections must be the work of renewed and patient investigation.' He maintained *Calyptranthes* and *Marlieria* as separate genera. In general he did not comment on individual species nor make the new combinations necessitated by merging these genera. With regard to *Cerqueiria*, however, he noted a similarity with several *Gomidesia* species of Berg's group *Magnifoliae*. He noted that the anthers (of *Cerqueiria*) were said to be 4-celled, opening in as many terminal pores but he considered this to be 'a delusion, arising from the anthers having opened already in bud, and the margins of the slits being closely involute, so as to apparently divide the cells.'

Many other taxonomists followed Bentham's lead in reducing the number of genera recognised in the Myrtaceae. Two such works appeared in swift succession in 1893. In April of that year Niedenzu (1893) treated *Aulomyrcia* and *Calyptromyrcia* as sections of *Myrcia* but maintained *Gomidesia* as a distinct genus. *Cerqueiria* was treated within *Gomidesia* under the new name *Gomidesia cerqueiria* and an attempt was made to correct some of Berg's idiosyncratic nomenclature. October of the same year saw the publication of Kiaerskou's Enumeratio Myrtacearum Brasiliensum. Although the title might lead one to expect a rather comprehensive work building on Berg's impressive foundation, Kiaerskou's treatment is basically a determination list of specimens collected by Glaziou, Lund, Mendonça, Raben, Reinhardt, Schenck, Warming and others. The distributions listed are based only on these specimens and descriptions are provided only in the case of new species, or where the material available includes inflorescences or fruits not described by Berg. *Gomidesia* was treated as one of four subgenera in a rather broadly circumscribed *Myrcia*, the other subgenera being *Eumyrcia* (*Myrcia sensu* Berg), *Aulomyrcia* (*Aulomyrcia sensu* Berg, now generally acknowledged to belong in *Myrcia*) and, curiously, *Myrceugenia* (now considered to be rather distantly related to the other genera of the Myrciinae). *Calyptranthes* and *Marlierea*, which most modern workers consider to be rather closer to *Myrcia* than is *Myrceugenia*, were recognised as separate genera. The merging of *Aulomyrcia* and *Gomidesia* with *Myrcia* necessitated the creation of a number of new names as Berg had used the same epithets repeatedly in these genera. In all, 29 species were recognised in *Myrcia* subgenus *Gomidesia,* including six new species. No mention was made of *Calycampe*, *Calyptromyrcia* or *Cerqueiria* but there can be little doubt that Kiaerskou would have included these genera within his broad concept of *Myrcia* had he been familiar with the material.

Kausel (1948, 1949, 1966) chose to recognise *Aulomyrcia*, *Gomidesia* and *Myrceugenia* at generic level in his broadly circumscribed Myrcioideae. Thus he recognised a rather narrowly defined *Myrcia* along with *Calyptranthes*. No mention was made of *Marlierea* but, given his narrow generic concepts, it is likely that he would have considered this a good genus too. Also included were *Luma* (treated under the illegitimate name *Myrceugenella* and discussed further below) and, rather surprisingly, *Acca sellowiana* (as *Feijoa*.) The other two species now treated in *Acca* (*A. lanuginosa* and *A. macrostema*) were placed here with some doubt. Kausel's decision to treat *Acca* in the Myrcioideae appears to have been prompted by the slightly leafy cotyledons of *Acca sellowiana* which bear a superficial resemblance to the embryos of *Myrcia* and other members of the Myrciinae (Landrum 1986).

Legrand (1959) published a synopsis entitled 'Las especies tropicales del genero *Gomidesia*'. This paper is dated 1958 on the title page and often cited by Legrand and others as 1957. However, since it is was printed on December 31 1958 it is unlikely to have been in circulation until 1959. Despite the title, the paper treats all the species of *Gomidesia* recognised by Legrand, both tropical and subtropical. These number 43 in total. Legrand placed in synonymy 19 of the species recognised by Berg, and listed a further four as 'incertae sedis' though he commented that they appeared to be good species. He made new combinations in *Gomidesia* for five of the species which Kiaerskou had treated as new in his *Myrcia* subgenus *Gomidesia* and four species originally described by Cambessedes in *Myrcia*. He mentioned six new taxa by name but none were validly published in the synopsis, as they lack Latin diagnoses and clear indications as to type material. Most of these names were eventually validated, maintaining the tradition established by Berg a century earlier! The main body of the synopsis is an enumeration of the species with synonymy, distribution by state within Brazil and specimen citations. For a number of species Legrand saw only a photograph of the type or no type material whatsoever. No keys or species descriptions are provided but the enumeration is preceded by a short introduction and a systematic table in which four new sections were proposed (see under Infrageneric Relationships).

Since Legrand's synopsis, the most substantial contribution to knowledge of *Gomidesia* was Legrand and Klein's (1967) account of the genus for the Flora Ilustrada Catarinense, a Flora of the state of Santa Catarina produced in fascicles. Nine species were treated, including *G. flagellaris* which had been described in a precursor paper (Legrand, 1961) and a new variety, *G. affinis* var. *catharinensis*, first proposed in Legrand's synopsis, invalidly published for the second time in the precursor paper and the first of the new taxa from the synopsis to be validated, eight years after the name first appeared in print. This taxon is here treated at species level. A new combination, *Gomidesia palustris* (DC.) D.Legrand was proposed for *Myrcia palustris* but this appears to have been predated by Kausel (1966). New names are attributed to Legrand only and it is clear from the text that the taxonomic treatment is his work.

A further three of the new names invalidly published by Legrand (1959) in his synopsis were validated sixteen years after they were originally published in a paper authored jointly with J.R. Mattos (Legrand & Mattos, 1975). Only one of these three is recognised in the present treatment (*G. velutiflora*) while the other two are treated under Doubtful Names and Excluded Taxa (*G. minutiflora* and *G. myrcioides*). A further new species, *G. squamata* from Paraná, was also described in this paper. There remain two new names invalidly published in Legrand's synopsis and never subsequently validated. *Gomidesia acuminatissima* Legrand was based on *Occhioni 254*, and this collection was subsequently cited as the type of *G. tijucensis* var. *flexuosa* (Legrand & Mattos, 1975), indicating a change of mind on Legrand's part concerning the status of his new taxon. *Gomidesia rotundifolia* is more problematic. I have not seen the collection *Reitz & Klein 2314* on which this name was based. Legrand (1959) compared the leaves of *G. rotundifolia* to those of *G. beyrichiana* (= *G. eriocalyx*) but commented that the anthers were more like those of *G. sellowiana* and that the overall aspect of the plant was that of a small-leaved *G. pubescens*. From these comments I infer that the material may be referrable to *G. sellowiana* but it is not cited under that species in Legrand and Klein's (1967) account for Santa Catarina. Curiously, in the introduction to their paper, Legrand and Mattos (1975) state that seven taxonomic novelties are presented in *Gomidesia* (along with dozens of novelties in other genera of the Myrtaceae). However, in the main body of the paper only six novelties are presented in *Gomidesia*. This discrepancy could be attributed to a counting error were it not for the fact that each taxon in the paper is allocated a running number. The four new names mentioned above appear with the running numbers 32 - 35, while numbers 37 and 38 are allocated to *G. grandifolia* (Cambess.) Mattos and Legrand and *G. tijucensis* var. *flexuosa* respectively. Taxon 36 does not appear, suggesting an accidental omission when the manuscript was being prepared for publication. I suspect that the missing taxon may be *G. rotundifolia*.

*Gomidesia barituensis*, described by Legname in 1978 is the most recently published species in the genus and the only one with an exclusively extra-Brazilian distribution.

McVaugh (1968) re-examined Berg's treatment in the light of modern work on the family. He arranged the genera of the American Myrtaceae in informal groups and described his Group 1, the 'myrcioid genera', as the most readily comprehensible of the groups of the Myrteae. *Gomidesia* was maintained as a distinct genus within this group with the comment that 'although the anther character is the only thoroughly consistent one distinguishing the genus from *Myrcia*, most of the species are recognizable by the tawny or reddish brown silky, somewhat appressed pubescence that covers the inflorescence and the flowers'. McVaugh's Group 1 differs from Niedenzu's Myrciinae only in the inclusion of *Nothomyrcia*, a monotypic genus which had been described by Kausel (1948) in the interim. McVaugh considered that *Myrceugenia* and *Nothomyrcia* did not form part of the main line of evolution of the myrcioid genera but were derived directly from ancient myrtaceous stocks. In his list of imperfectly known genera he included the Antillean *Mitranthes* which he regarded as 'a relatively unspecialised member of the myrcioid alliance.'

Landrum (1981) monographed *Myrceugenia*, which he circumscribed as including *Nothomyrcia*. He emphasized that although *Myrceugenia* shares the myrcioid embryo with *Calyptranthes*, *Gomidesia*, *Marlierea* and *Myrcia*, in other charcteristics it is quite different from them. He considered *Myrceugenia* to be primitive within the Myrciinae, perhaps similar to the ancestor of the Myrciinae and also similar to the ancestor that would link the three subtribes of the Myrteae together. In his diagram to show the postulated position of *Myrceugenia* in the tribe Myrteae *Luma* is not placed in a subtribe but subsequently Landrum (1986) stated that 'if *Luma* is to be assigned to a subtribe it should be placed in the Myrciinae.' Landrum (1984) confirmed McVaugh's (1968) opinion that *Mitranthes* should be treated in the Myrciinae and deemed it 'most closely allied to *Calyptranthes* because of its overall similarity to that genus.' Thus Landrum's view of relationships in the Myrciinae differs from that of McVaugh only in the disposition of *Luma*, which McVaugh treated in the same informal grouping as *Myrcianthes* although he concluded that *Luma* evolved 'independently of *Myrcianthes*, and quite apart from any other major evolutionary line.'

Grifo (1992) revised *Myrcianthes* (Eugeniinae) and her treatment included a cladistic analysis of the Myrteae at subtribal level. *Luma* was included as a separate terminal taxon and emerged as sister to the Eugeniinae and the Myrciinae in an unresolved trichotomy.

Thus most modern myrtologists would delimit the Myrciinae as comprising *Calyptranthes*, *Gomidesia (*including *Cerqueiria*), *Marlierea* (including *Eugeniopsis* and *Rubachia*), *Mitranthes*, *Myrceugenia (*including *Nothomyrcia)* and *Myrcia* (including *Aulomyrcia*, *Calycampe* and *Calyptromyrcia*), with *Luma* being included or treated as a sister group. Judging by determination slips, some myrtologists now treat *Gomidesia* as synonymous with *Myrcia* but most Flora treatments published over the past two decades have followed McVaugh (1968) and continued to recognise it as a distinct genus.

## Morphology

### Habit

The species of *Gomidesia* are usually trees but many of them can also grow as shrubs, depending on the habitat in which they occur. Some species occur as apparently mature shrubs of one metre or less while others reach heights of 25 to 30 m. The most common habit, however, is that of a small tree or treelet and most species do not exceed 10 m in height.

### Bark

Most species have fairly smooth, fine-grained, pale grey bark but occasionally the bark may be darker and in some species scaly or exfoliating outer layers have been observed.

### Twigs

Young twigs may be terete or flattened and slightly channelled. They usually bear a dense indumentum which is lost with age. In many species the nodes are ringed by a pair of straight or inverted V-shaped scars which run between the petiole bases. In the taxonomic treatment this feature is referred to as the inter-petiolar ridge. In other species the interpetiolar ridge is faint or entirely absent. Minute stipule lobes are detectable at the youngest nodes in many species. These are generally subulate, dark-coloured and caducous.

### Leaves

The leaves are invariably entire and usually petiolate, though the petiole may be very short, or occasionally absent. Their arrangement is almost always opposite, but subopposite leaf pairs are occasional in some species. Most leaves are elliptic, oblong or lanceolate in outline, while obovate or orbicular leaves are rarer. Acute or acuminate leaf apices are most common, but rounded, truncate or emarginate leaves are also frequent. The leaf base is often cuneate but other shapes occur and are often of taxonomic use. The posture of the leaf margin is also variable, ranging from flat to revolute. In the taxonomic treatment, I follow Rohwer (1993) in describing as 'bent down' any leaf margin which curves to the lower surface, ending not more than perpendicular to the lamina (turned by 90 degrees or less). The margin is described as recurved if it ends between perpendicular and parallel to the lamina (turned by 90 - 180 degrees, i.e. upside down). Where the margin is curved further (by more than 180 degrees), approaching the lamina again, then it was termed revolute. Leaf size is enormously variable both between and, to a lesser extent, within, *Gomidesia* species. The lamina of *G. montana* rarely reaches 30 mm in length while leaves of *G. magnifolia* often exceed 600 mm. Leaves of some of the species intermediate between these two extremes are depicted in Figures 1-3 to illustrate some of the variation in leaf size and shape within the genus. The leaves described in the taxonomic treatment are, wherever possible, the pairs immediately below the inflorescence or infructescence. These are often significantly smaller than those on vegetative shoots but have the advantage of being almost always represented on herbarium sheets. Data on the consistency of mature leaves are supplied where available. Mature leaves are generally flat (apart from their margins) and more or less concolorous unless otherwise stated.

**Leaf venation.** Klucking's (1988) extensive survey of Myrtaceae leaf venation included 85 species of *Myrcia* s.l. Among these are ten species of *Gomidesia* which Klucking apparently considered to span most of the spectrum of variation detected in the genus *Myrcia* (Fig, 2 & 3). His treatment is difficult to interpret: typographical errors abound and internal inconsistencies are frequent. The following attempt to summarise his analyses reflects these limitations. In some of the *Gomidesia* leaves examined by Klucking the marginal veins were interpreted as acrodromal secondary veins and the pinnate venation which extends over most of the leaf lamina was described as 'secondary-like'. In other cases however, the pinnate venation was considered to be truly secondary in origin and the marginal vein, where present, to be composed at least in part of the coalescent branches of the secondary veins. Even where the pinnate venation was considered secondary-like rather than secondary, the term intersecondary was applied to the intervening lateral veins. This application of the term differs from that of Hickey (1973) whose intersecondary veins are parallel to, thinner than and shorter than the true secondary veins.

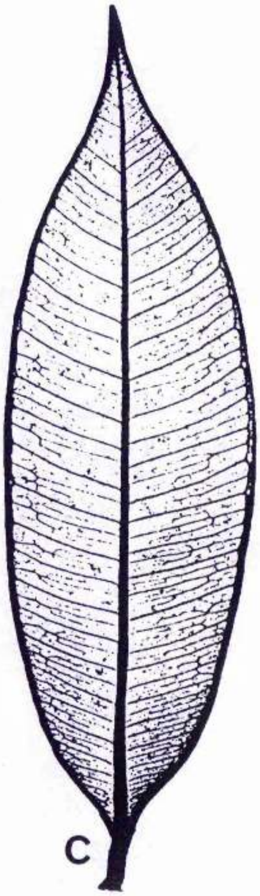
Hickey's system of classification of leaf architecture is widely cited and accepted. There are, however, considerable practical and philosophical difficulties inherent in its application to the venation patterns encountered in the Myrtaceae. In particular, Hickey's system does not distinguish between different orders of lateral veins, nor does it allow distinctions to be drawn between non-homologous marginal veins. Carr and Carr (1985) addressed the latter problem and adopted the term paramarginal for a marginal vein formed from brochidodromous arches while reserving the term intramarginal for truly acrodromous marginal veins. Carr et al. (1986) advocated the use of the term sub-marginal for the small longitudinal vein which lies between the leaf-margin and the intramarginal or paramarginal vein. Carr and Carr (1985) also highlighted the pitfalls associated with any attempt to interpret leaf venation on the basis of the course and relative sizes of venation in mature leaves only. They stressed the fact that

FIG. 1. Nature prints of leaves of species of *Gomidesia*. **A** *G. blanchetiana*; **B** *G. sellowiana*; **C** *G. nitida* (as *G. chamissoeana*); **D** *G. reticulata*; **E** *G. affinis* (as *G. hookeriana*); **F** *G. fenzliana*; **G** *G. cambessedeana*; **H** *G. palustris* (as *Myrcia palustris*).

(Reproduced from Berg, 1857).

A

B



C

D

E

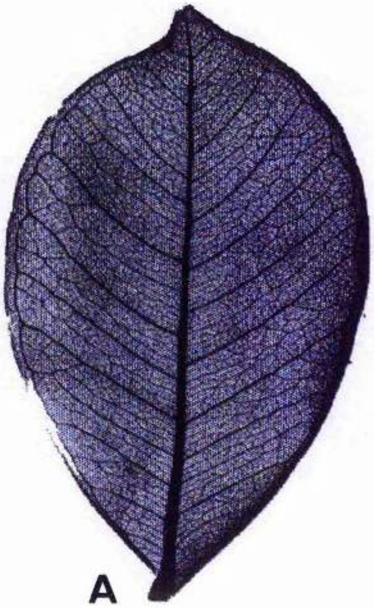
F

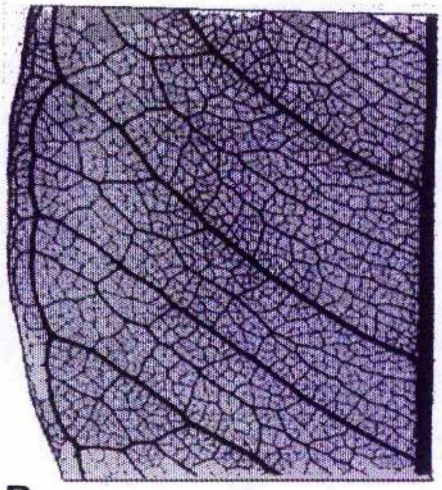
G

H

FIG. 2. Cleared leaves of species of *Gomidesia.* **A, B** *G. lindeniana*; **C, D** *G. flagellaris*; **E** *G. sellowiana;* **F** *G. schaueriana*; **G** *G. tijucensis*. (Reproduced from Klucking, 1988).

[Vouchers and determinations listed by Klucking: A, B *Duke 7024, Myrcia lindeniana;* C, D *Hatschbach 26266, M. flagellaris*; E *Hatschbach 26307, M. splendens*; F *Reitz & Klein 9583, M. fenzliana*; G *Reitz 6093, M. seriviflora*.]


A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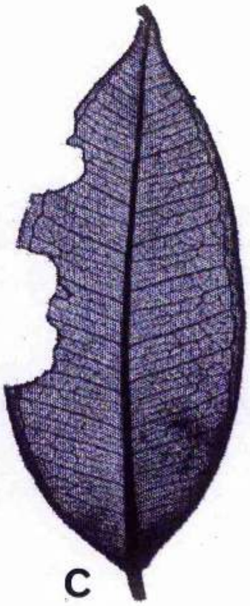
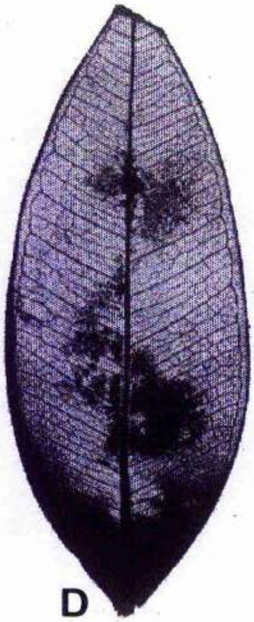
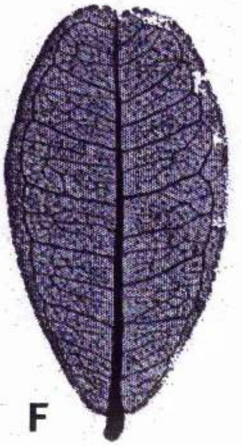

C


D


E


F

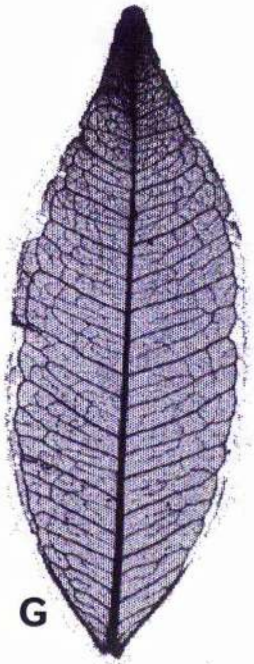
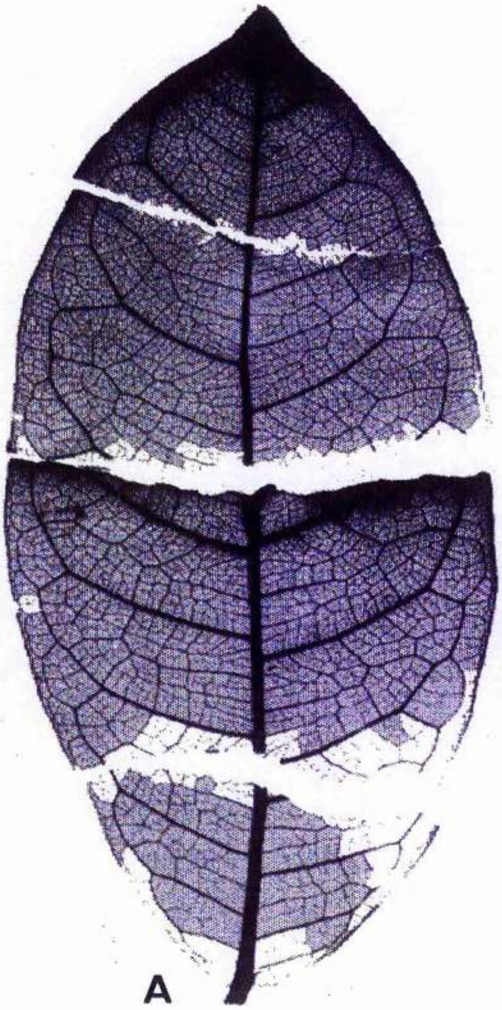
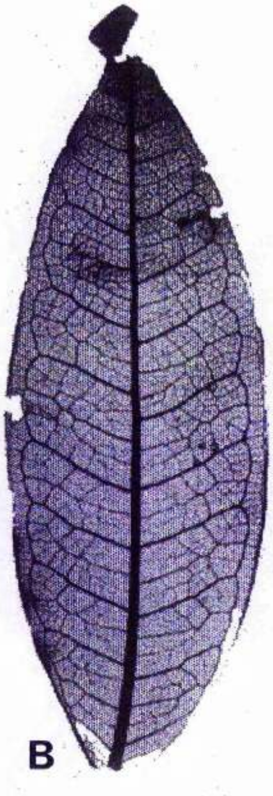

G

FIG. 3. Cleared leaves of species of *Gomidesia.* **A** *G. anacardiifolia;* **B** *G. barituensis;* **C** *G. palustris;* **D** *G. fenzliana;* **E** *G. tijucensis;* **F** *G. catharinensis.* (Reproduced from Klucking, 1988).

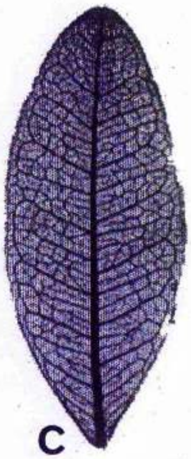
[Vouchers and determinations listed by Klucking: A *Hatschbach 18170, Myrcia anacardiaefolia*; B *Legname 9737, M. barituensis*; C *Pedersen 4415, M. bergiana*; D *Hatschbach 18169, M. schaueriana*; E *Hatschbach 13573, M. tijucensis*; F *Reitz & Klein 1987, M. reticulata.*]



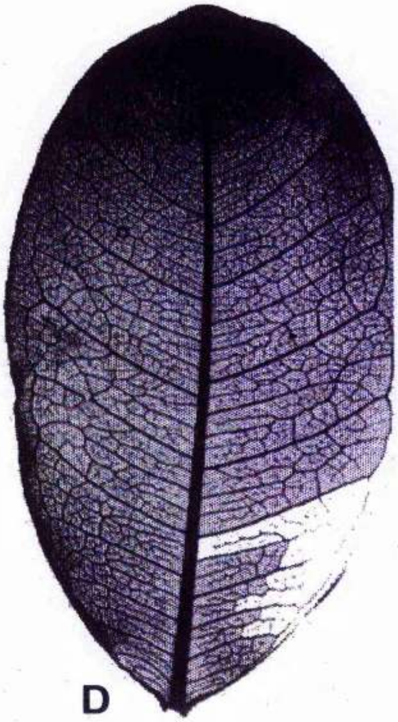
A



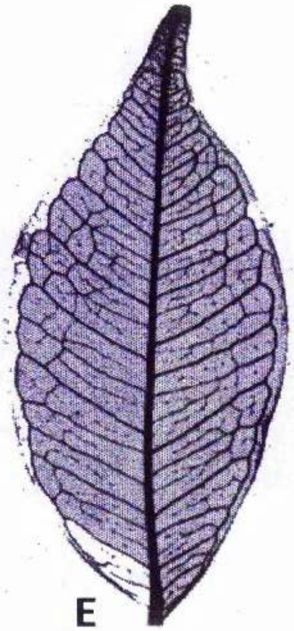
B



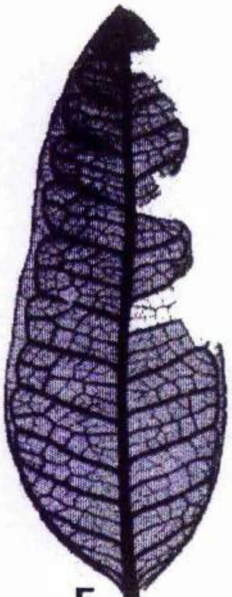
C



D



E



F

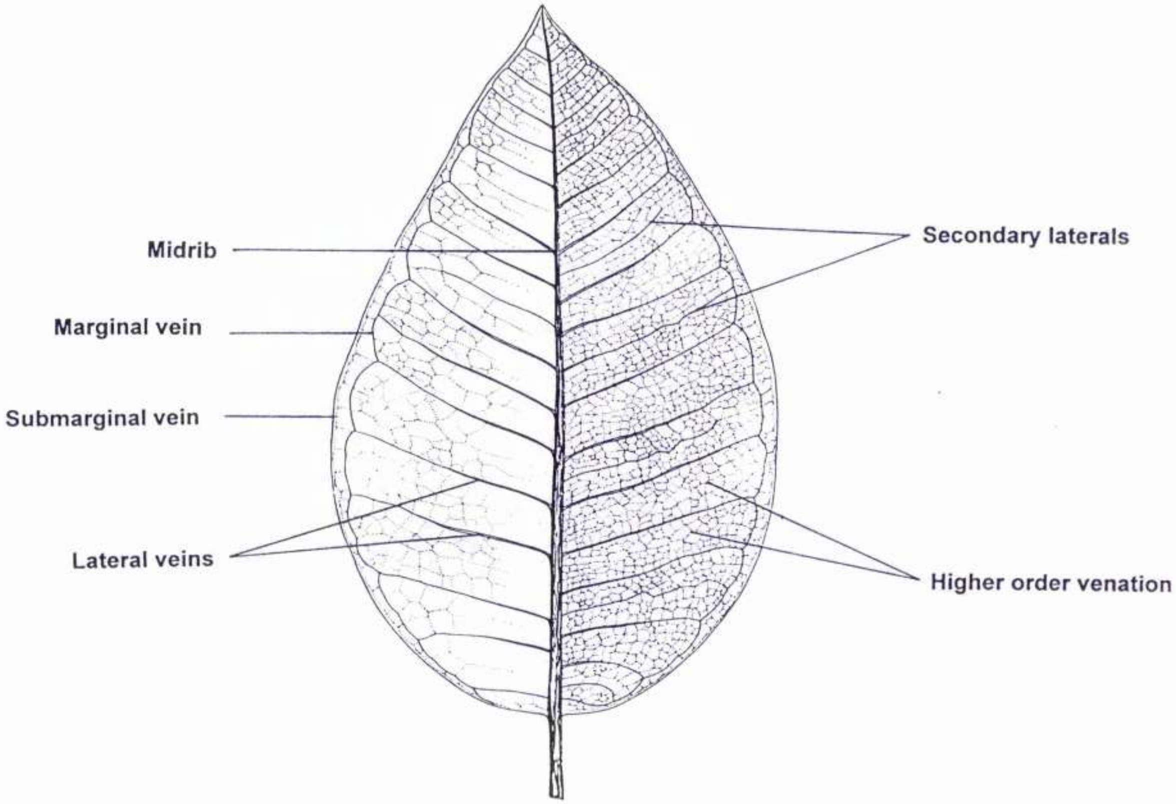
differential growth of the lamina may distort the course of an acrodromous vein so that it imitates the pattern of a paramarginal (brochidodromous) system.

The descriptions of venation patterns in *Gomidesia* leaves presented here are, of necessity, open to this latter criticism. It is hoped however, that careful choice of descriptors will enable the avoidance of both the internal inconsistencies of Klucking's scheme and the 'uncomparable intransigents' of Hickey's system. I have chosen to apply the (relatively theory-free) terms midrib, laterals (of various orders), marginal, submarginal and higher order venation (Fig. 4). In the absence of ontogenetic studies I have not presumed to classify the venation as acrodromous, brochidodromous or otherwise but have simply commented on the course and relative prominence of the various orders of venation. Also of importance in *Gomidesia* is the degree to which the veins of various orders are elevated above or sunken below the plane of the leaf lamina. In this treatment a vein is called raised if it is somewhat elevated above the lamina with a gradual transition between vein and lamina. A vein is called prominent if it is abruptly and markedly elevated above the lamina. Similarly, the surface of an impressed vein is slightly below the surface of the lamina with a gradual transition while in the case of a sulcate vein the transition is abrupt and the surface of the vein may be obscured by the lamina which rises above it at right angles or overhangs it.

### Indumentum

Since the myriad technical terms for the description of indumentum are subject to significant differences in interpretation by different botanists I prefer to describe the density, posture, morphology, colour and length of the hairs on the organs where the nature of the indumentum appears to differ between species. A dense indumentum is one where the hairs are so close together that they completely obscure from view the surface on which they are borne. The term moderately dense is applied to an indumentum where the hairs are close enough together to touch each other when laid flat but not so dense as to render the surface on which they are borne invisible. A sparse indument is one in which the hairs are fairly regularly spaced but at intervals such that the hairs would not touch each other if laid flat. Where there are very few hairs distributed in an apparently irregular fashion over the surface in question the indumentum is described as scattered. The posture of the hairs is recorded as follows: hairs described as appressed form an angle of 30° or less with the surface on which they are inserted. Erect hairs stand at an angle of approximately 90° to the surface while ascending hairs are intermediate between these two extremes.

FIG. 4. Terms used in the description of leaf venation in this study. (Leaf outline reproduced from Kawasaki, 1989).


Midrib
Marginal vein
Submarginal vein
Lateral veins
Secondary laterals
Higher order venation

**Inflorescence structure**

Bentham (1869) was one of the first students of the Myrtaceae to recognize the importance of inflorescence architecture, observing that 'Inflorescence, although it can scarcely be taken as an absolute character, is often one of the best indications of generic affinity'. His synopsis of the genera of the Myrtaceae includes brief comments on inflorescence morphology. He included *Gomidesia* in *Myrcia* and cited the inflorescence 'which is usually more compound' (than in *Myrtus*) among his reasons for maintaining *Myrcia* as a genus. Subsequent workers paid little attention to characters of the inflorescence until McVaugh (1956b) once again drew attention to their taxonomic significance. He distinguished three principal inflorescence types associated with the three subtribes of the Myrteae: 1. The raceme, characteristic of the subtribe Eugeniinae; 2. The myrcioid panicle, found in the principal genera of the Myrciinae; and 3. The dichasium, characteristic of the Pimentinae (Myrtinae) and also found in some genera of the Eugeniinae. The myrcioid panicle was described as follows:

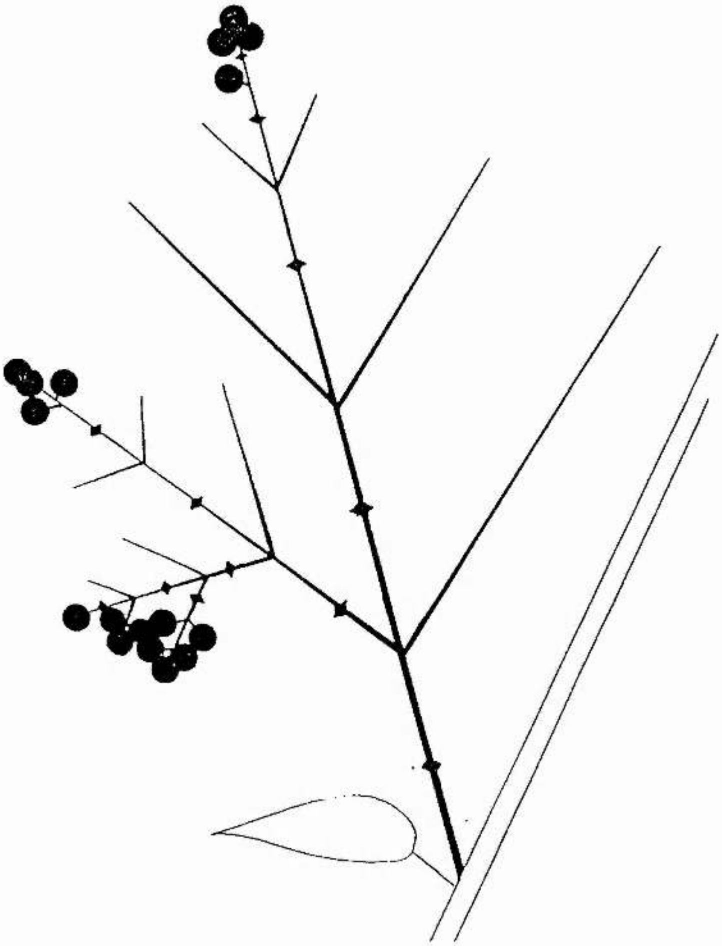
> "The axillary panicle is compound or decompound, with the primary axis and each of the subsidiary branches terminating in a flower. The principal branches are opposite and decussate, the lower ones elongate and usually themselves compound and many-flowered, and the ultimate branchlets of the panicle usually with the flowers aggregated in threes (i.e. in simple dichasia) near the tips. The transition between elongate basal branches and simple dichasia at the tips is accomplished by gradual reduction, in successive branches, of the number of nodes and the length of the internodes. Branching towards the tips of the panicle may be irregular because of abortion of one or both buds at a given node, or because of the dehiscence (at the point of origin) of one or both branchlets after the initiation of growth; either of these processes may result in, or be accompanied by, distortion or zigzag growth of the axis which remains." (See Fig. 5).

Among the myrcioid genera McVaugh recognised two tendencies in the branching of the inflorescence:

> "In the genus *Myrcia*, and in the segregate genera *Aulomyrcia* and *Gomidesia*, the principal axis of the inflorescence is as long as, or a little longer than, the primary lateral branches; the panicle, as a result of this, is about as long as wide. In *Marlierea* and *Calyptranthes* the principal axis may abort at the node where the lowest lateral branches emerge, so that the inflorescence as a whole appears to consist of paired spikes or panicles arising from the same axil. This condition is found regularly in some species, occasionally in others, and rarely or never in a third group. It is thus by no means consistent in the genera in which it occurs, but as far as I am aware it never occurs in *Myrcia*."

McVaugh also discussed the difficulties encountered in recognizing the proper limits of a single inflorescence, citing *Myrcia* as an example of a genus in which almost any new branch arising from the axil of a foliage leaf may represent a potential inflorescence. He concluded that leaf size was useful in the resolution of this issue, leaves often being reduced in size when

FIG. 5. Diagram of the myrcioid panicle. Position of flowers and branches indicated to the extent that it is necessary to make clear the pattern of branching which is repeated in each part of the panicle. Branches in one plane are shown; those at right angles to this plane are omitted but their positions are indicated by diamonds. (Reproduced from McVaugh, 1956b).



occurring on temporary (inflorescence) branches. In fact, he interpreted the myrcioid panicle as arising from the reduction of leaves to bracts in whole branch systems. McVaugh's study was based on an overview of much South American material and his pragmatic approach resulted in an eminently workable system. Combining inflorescence morphology and calyx characters he was able to produce keys to genera for which it was not always necessary to have flowering and fruiting material. Although the theoretical bases of his work were undermined by subsequent workers his contribution to our understanding of inflorescence structure in the Myrtaceae was nevertheless critically important.

Chief among these subsequent workers were Briggs and Johnson (1979). Their detailed, non-typological analysis of inflorescence structure in the Myrtaceae is a model of its kind and is often cited by students of other families, Myrtalean and otherwise (Daly, 1987; Todzia & Almeda, 1991; Conn, 1995). For the genus *Gomidesia* Briggs and Johnson reported panicles, metabotryoids, botryoids and triads. Exactly the same spectrum of variation was reported for *Marlierea,* and the other myrcioid genera *Myrcia* and *Calyptranthes* were found to exhibit a very similar range of inflorescence types, though these latter genera include species with monads, and thyrsoids are also occasional in *Myrcia*.

Briggs and Johnson used the term panicle to describe an anthotelic (ending in a flower) inflorescence in which (a) the main and at least some of the lateral axes have nodes distal to the prophyllar node(s) and (b) the lateral branch systems are not themselves thyrsoids (or aggregates of thyrsoids). The term thyrsoid was used as a noun and defined as an anthotelic inflorescence with a multinodate main axis that bears lateral cymes of order of branching > 1. In practice then, the difference between a panicle and a complex thyrsoid is that 'in the *panicle* each multinodate lateral branch (of whatever order) must *either* itself bear single flowers at two (or more) successive nodes (i.e. be botryoidal in the distal portion at least) *or* ultimately bear branches that show this condition, whereas in the *complex thyrsoid* no axes have such botryoidal portions'.

The authors themselves admitted that this distinction is somewhat artificial and other workers have apparently encountered some difficulties in applying it. Daly (1987), for instance, complained that it was not clear from Briggs' and Johnson's discussion whether the single flowers referred to can be the terminal flowers of cymules, the laterals unexpressed in the axils of bracts (and the bracts thus termed metaxyphylls), or whether they must be truly solitary. This problem was in fact addressed, albeit rather casually, by Briggs and Johnson in the legend to their table of inflorescence conditions in the Myrtaceae: uniflorescences that resemble thyrsoids but have metaxyphylls were recorded as panicles. Elsewhere they made the point that all gradations from panicle to thyrsoid occur in Myrtaceae and that the artificial distinction is not of much importance.

Briggs and Johnson (1979) also addressed the problem of defining the limits of the inflorescence. They distinguished two different levels of organization within inflorescence systems in the Myrtaceae. The uniflorescence is an anthotelic branch system that is lateral to a blastotelic (ending in a vegetative bud or sprout) axis. A conflorescence is a floriferous branch system of which the main axis bears uniflorescences. The terms anthotelic and blastotelic are adopted as theory-free alternatives to monotelic or determinate and polytelic or indeterminate. Blastotelic inflorescences may be auxotelic (continuing growth beyond the flowering region) or anauxotelic (terminating in an abortive vegetative axis). Briggs' and Johnson's criticism of McVaugh's work is based on his failure to relate blastotelic and anthotelic inflorescence types, an essential step in deriving the 'myrcioid panicle' from a branching system of solitary flowers in the axils of ordinary leaves on indeterminate branches.

Landrum (1981) concurred with McVaugh in describing the sort of panicle found in *Myrcia* as derived from a whole branching system whose leaves have been reduced to bracts. He commented that such panicles, which may include bracteate shoots and dichasia as subunits, are also found in the other genera of the Myrciinae, but not in *Myrceugenia*. Some species of *Myrceugenia* exhibit solitary flowers, each subtended by a normal leaf. Landrum described this as the simplest myrtaceous inflorescence but not necessarily the most primitive. He distinguished three kinds of elaboration of this simple inflorescence which are found in *Myrceugenia*, the most common being the vertical superimposition of several peduncles between the shoot and the petiole or bract. This pattern is uncommon outside the genus.

Weberling (1988) reviewed the architecture of inflorescences in the Myrtales. He considered that in Myrtaceae the "central type" and perhaps the phylogenetically primitive form of inflorescence is a monotelic thyrsoid or panicle terminating a leafy shoot. He described *Gomidesia hookeriana* (here treated in the synonymy of *G. affinis*) as bearing a proliferating inflorescence in which the partial inflorescences that originate from the axils of foliage leaves are highly ramified and present themselves as thyrsoid-paniculate systems. Thus he applied the term partial inflorescence to what Briggs and Johnson would consider an inflorescence and reserved the term inflorescence for what they considered to be a conflorescence. The inflorescences (*sensu* Briggs and Johnson) of some species of *Marlierea* and *Myrcia* are described by Weberling as 'more or less ramified thyrsoid-paniculate paracladia'.

Landrum (1981) considered the largely unknown terminology introduced by Briggs and Johnson to be excessively specific at times and preferred to use more traditional descriptive language in his monographs. However, I have found the non-typological approach advocated by Briggs and Johnson most helpful in the analysis of inflorescences in the Myrciinae and have therefore chosen to employ their terminology where appropriate.

The conflorescences of most species of *Gomidesia* consist of a series of paired inflorescences in the axils of distal foliage leaves. The individual inflorescences (hereafter termed uniflorescences) may be complex thyrsoids, panicles, metabotryoids or dichasia. Sequences of reduction from a panicle to these other inflorescence types are illustrated in Fig. 6. Accessory branching at the base of the inflorescence is occasional (e.g. seen in *G. cordiifolia*, *G. lindeniana*, *G. reticulata*, *G. springiana*) and where it occurs it is always phylloscopic. Briggs and Johnson consider this type of elaboration to be a primitive feature within the family. I have found it to be associated with many-flowered inflorescences in which the degree of branching tends to be more variable within species than is the case with few-flowered inflorescences.

**Flowers**

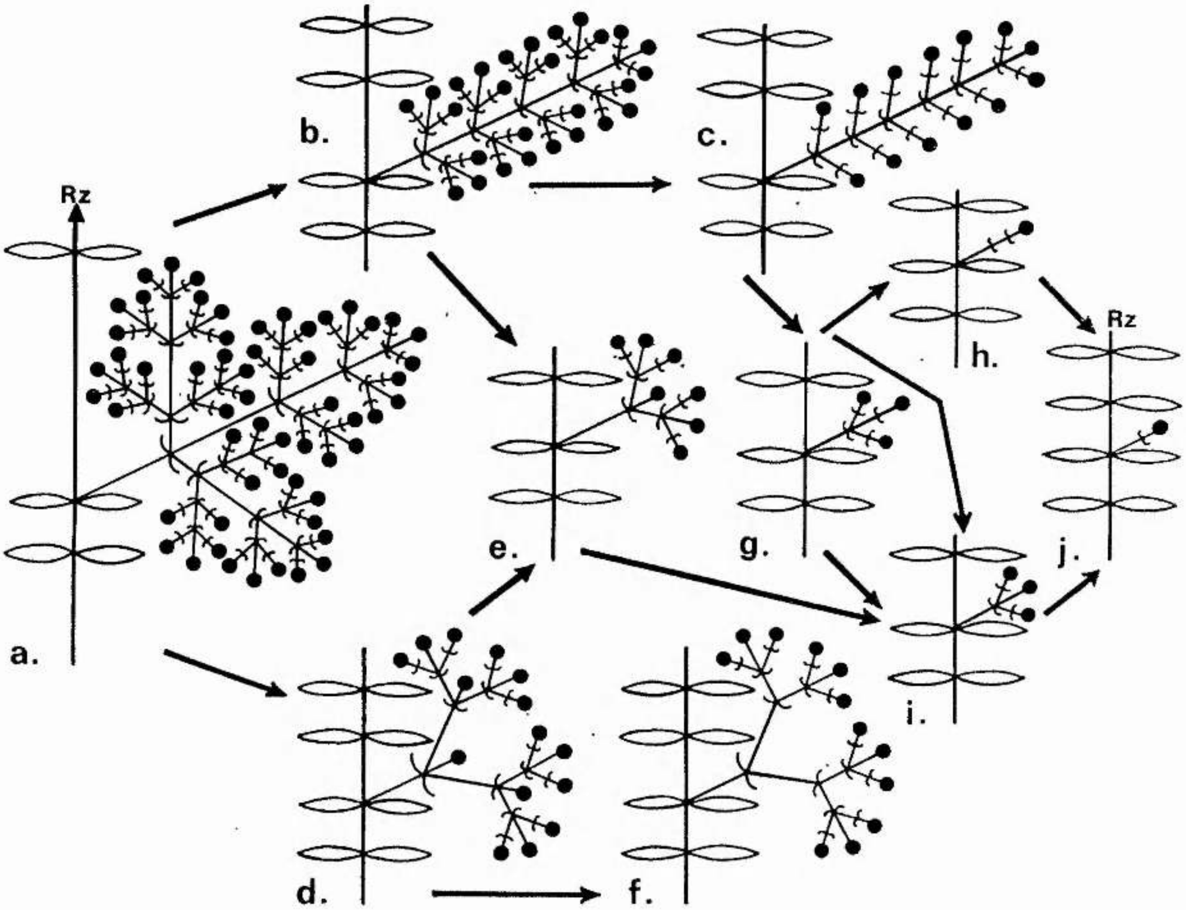
**Calyx lobes.** The shape of the calyx lobes and the density and distribution of indumentum thereon have proved very useful taxonomically at infrageneric level. The calyx lobes described in the species accounts are the outer lobes of a mature flower bud or open flower. These are usually triangular or depressed ovate with a moderately dense or dense indumentum externally and internally. The indumentum on the inner surface tends to be composed of shorter hairs than those observed externally. The inner calyx lobes are often broader than the outer ones with membranous margins.

**Petals.** The petals are white or creamy white and may be tinged with deep pink in bud. The external surface is generally densely pubescent while the internal surface is glabrous. After anthesis the petals appear translucent and they become strongly reflexed and rather inconspicuous relative to the stamens.

**Stamens.** The stamens are numerous and their puffball-like arrangement forms the most conspicuous part of the flower. Inclusion of stamen numbers in species descriptions of Myrtaceae is a relatively recent phenomenon which appears to have been initiated by McVaugh (1956b, 1958). He identified reduction trends in stamen numbers in certain lineages and included stamen counts in his descriptions of new species. Subsequently stamen number proved useful for delimiting species in *Myrcianthes* (Grifo, 1992) and was used in hybrid studies of *Myrceugenia* by Landrum (1981). Landrum (1981) and Proença (1991)

FIG. 6. Sequences of reduction from **a** panicle to **b** metabotryoid, **c** botryoid, **d** dichasium, **e** small dichasium, **f** dichasium with abortion of median flowers, **g** metaxytriad, **h** metaxymonad, **i** triad, and **j** monad.

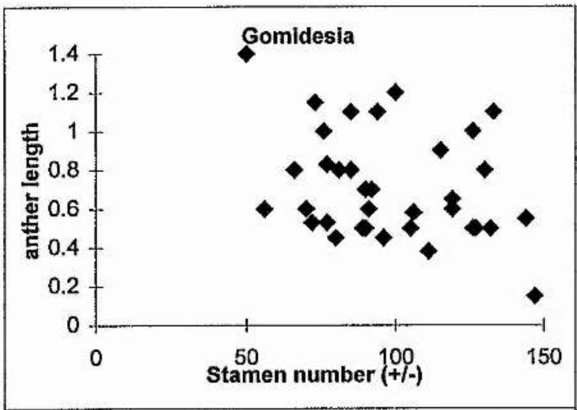
(Reproduced from Briggs and Johnson, 1979).

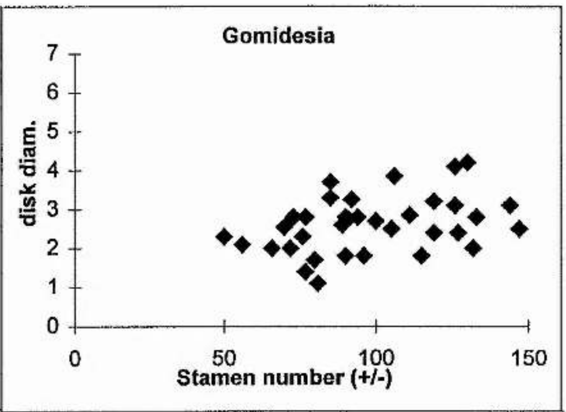

Rz
a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
Rz

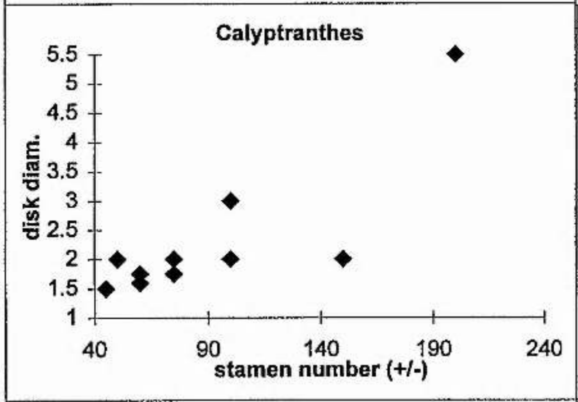
commented on the tedious and time-consuming work required to evaluate this character but argued that the data generated were worthwhile. Curiously, none of these authors discussed the relationship beween stamen number and overall flower size although McVaugh commented that within the Myrciinae smaller stamen number seemed to be correlated with lesser development of accessory structures (the "staminal disk") and with thinner and more prolonged hypanthial margins. Analysis of measurements from descriptions in recent monographs indicates that disk diameter and median stamen number are strongly correlated in *Myrceugenia* ($r = 0.817$, $p < .01$, $v = 38$, Fig. 7) and *Myrcia* ($r = 0.477$, $p < .01$, $v = 39$, Fig. 7). Similarly there is a statistically significant correlation between median stamen number and hypanthium/calyptra diameter in *Calyptranthes* ($r = .803$, $p < .01$, $v = 16$). In the case of *Marlierea*, I considered style length more likely to provide an accurate reflection of flower size than disk or hypanthium diameter because measurements of these latter may vary with the age of the flower and the degree of tearing of the hypanthium. Median stamen number and style length are positively correlated in *Marlierea* ($r = .606$, $p < .01$, $v = 19$) and also in *Myrcia* ($r = .616$, $p < .01$, $v = 39$), *Calyptranthes* ($r = .579$, $p < .05$, $v = 16$) and *Myrceugenia* ($r = 0.379$, $p < .05$, $v = 36$) (See Fig. 8). Hence it may be concluded that median stamen number is strongly correlated with disk diameter and style length (and therefore with overall flower size) in the Myrciinae in general. This correlation can also be demonstrated in the Eugeniinae (e.g. in *Myrcianthes* for median stamen number vs. disk diameter $r = 0.491$, $p < .01$, $v = 30$, Fig. 7, but there is no significant correlation with style length: $r = 0.3$, $p = > .05$, $v = 28$, Fig. 8) and in the Myrtinae (in *Pimenta* for median stamen number vs. disk diameter $r = 0.869$, $p < .01$, $v = 10$ and for median stamen number vs. style length $r = 0.782$, $p < .01$, $v = 10$; in *Campomanesia* for median stamen number vs. disk diameter $r = 0.681$, $p < .01$, $v = 25$ and for median stamen number vs. style length $r = 0 .614$, $p < .01$, $v = 25$). These data represent a strong case for the consideration of stamen number as a taxonomic character in the context of flower size, rather than in isolation.

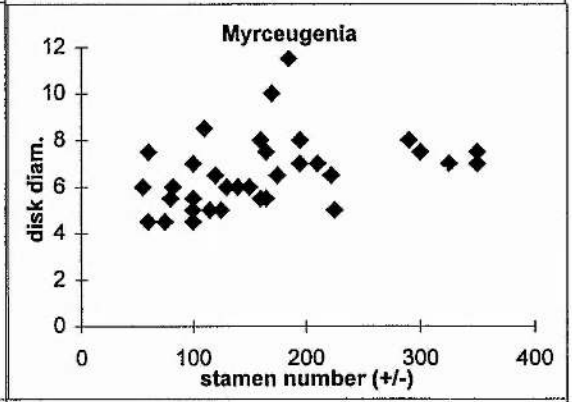
McVaugh (1969) considered the Myrciinae to exhibit a tendency towards reduction in stamen number from 200 or more to 25 - 30. In the partial data sets compiled for the stamen number/flower size discussion above, this trend can be detected at generic level within the Myrciinae (Fig. 9). Most species of *Calyptranthes* recorded had median stamen numbers of 100 or less (outliers up to 200). Most *Marlierea* species recorded had median stamen numbers of 140 or less (one outlier to 200). *Myrcia* had higher median values with most species at 200 or less (and outliers up to 300). *Myrceugenia*, the putatively primitive genus of the subtribe, had most species with median values of 240 or less and outliers to 360. Given these trends it is tempting to postulate a link between extent of calyx fusion and reduction in

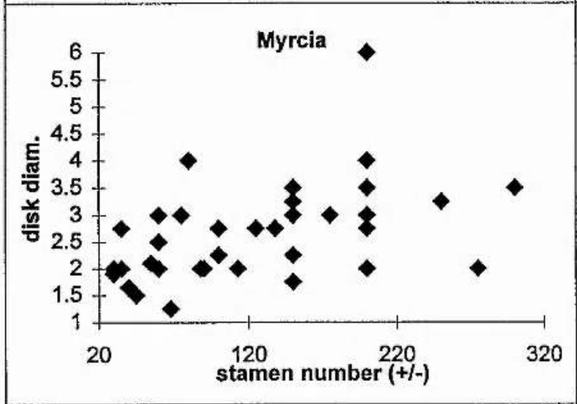
FIG. 7. Plots of stamen number and disk diameter in selected genera of the Myrtaceae, and of stamen number and anther length in *Gomidesia* (top left).

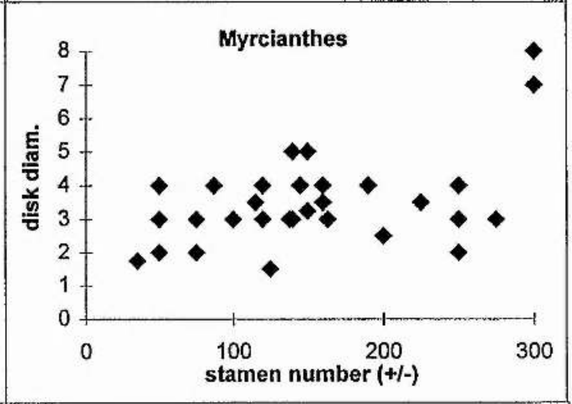

Gomidesia
anther length
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
50
100
150
Stamen number (+/-)

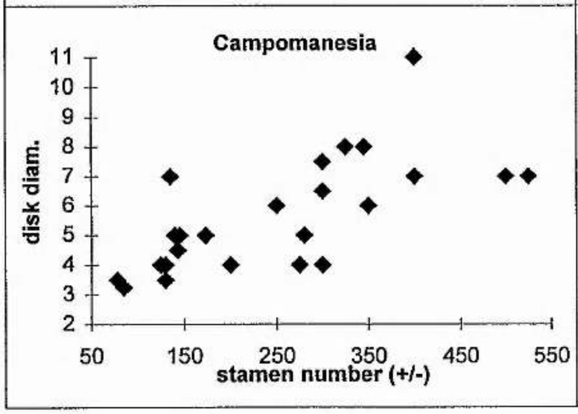

Gomidesia
disk diam.
7
6
5
4
3
2
1
0
0
50
100
150
Stamen number (+/-)


Calyptranthes
disk diam.
5.5
5
4.5
4
3.5
3
2.5
2
1.5
1
40
90
140
190
240
stamen number (+/-)


Myrceugenia
disk diam.
12
10
8
6
4
2
0
0
100
200
300
400
stamen number (+/-)


Myrcia
disk diam.
6
5.5
5
4.5
4
3.5
3
2.5
2
1.5
1
20
120
220
320
stamen number (+/-)


Myrcianthes
disk diam.
8
7
6
5
4
3
2
1
0
0
100
200
300
stamen number (+/-)


Campomanesia
disk diam.
11
10
9
8
7
6
5
4
3
2
50
150
250
350
450
550
stamen number (+/-)

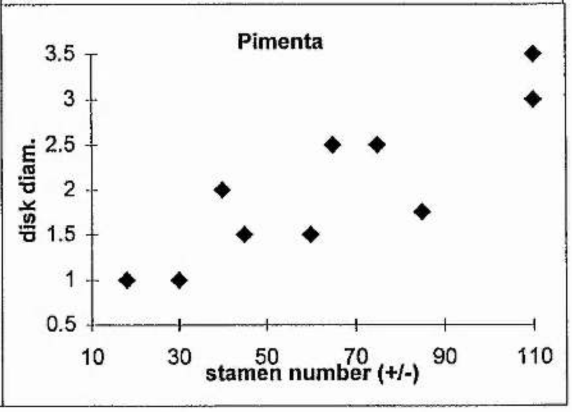
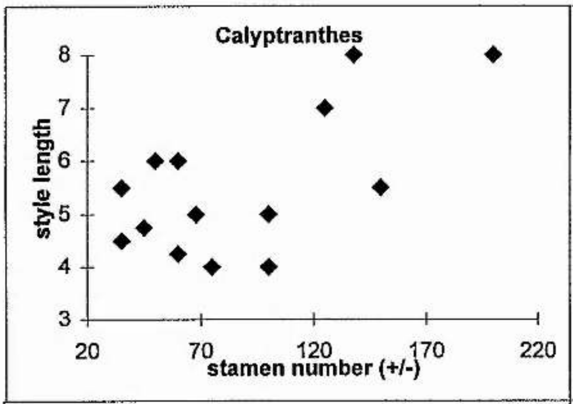
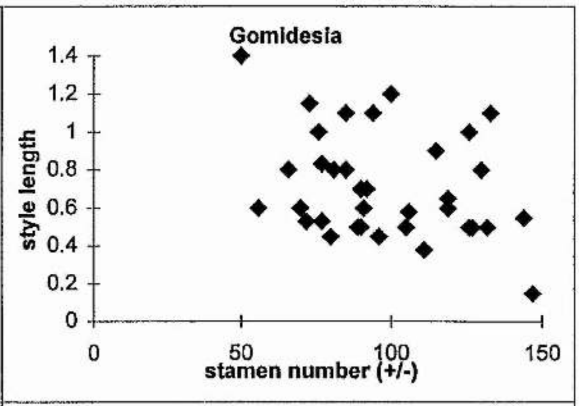
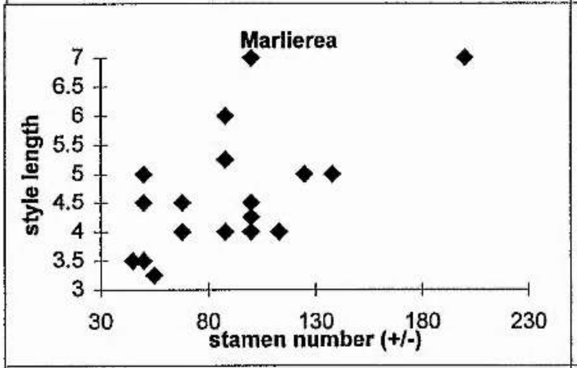
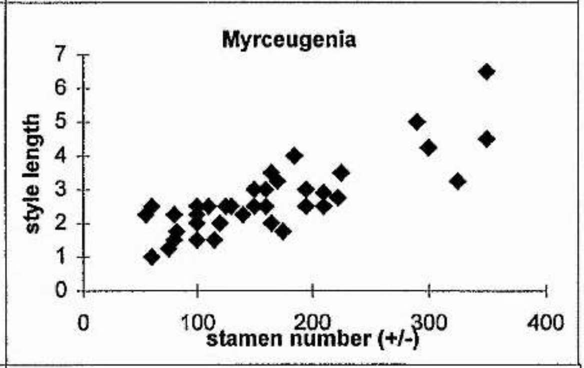

Pimenta
disk diam.
3.5
3
2.5
2
1.5
1
0.5
10
30
50
70
90
110
stamen number (+/-)

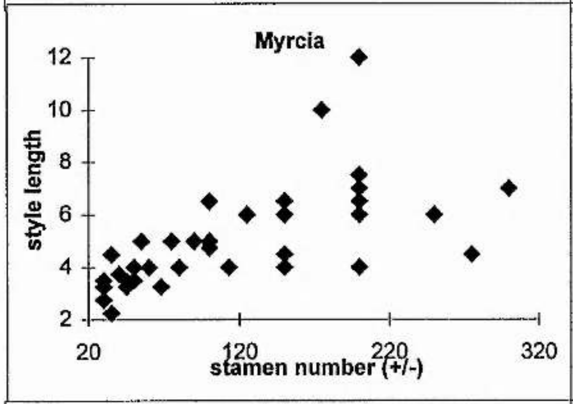
FIG. 8. Plots of stamen number and style length in selected genera of the Myrtaceae.

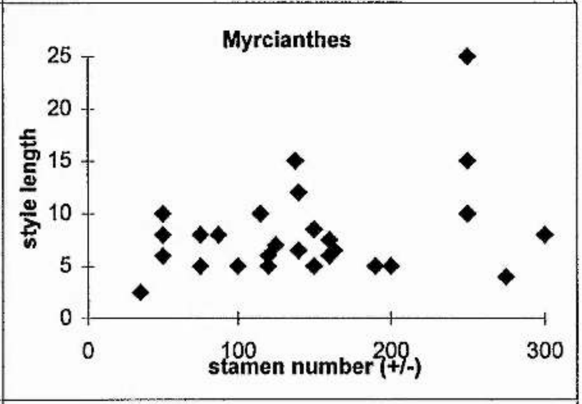

Calyptranthes
style length
8
7
6
5
4
3
20
70
120
170
220
stamen number (+/-)

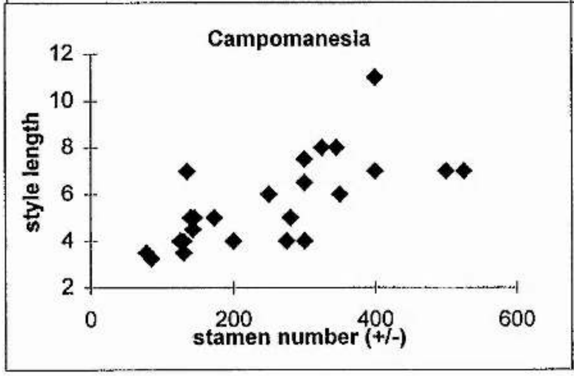

Gomidesia
style length
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
50
100
150
stamen number (+/-)


Marlierea
style length
7
6.5
6
5.5
5
4.5
4
3.5
3
30
80
130
180
230
stamen number (+/-)


Myrceugenia
style length
7
6
5
4
3
2
1
0
0
100
200
300
400
stamen number (+/-)


Myrcia
style length
12
10
8
6
4
2
20
120
220
320
stamen number (+/-)


Myrcianthes
style length
25
20
15
10
5
0
0
100
200
300
stamen number (+/-)


Campomanesia
style length
12
10
8
6
4
2
0
200
400
600
stamen number (+/-)

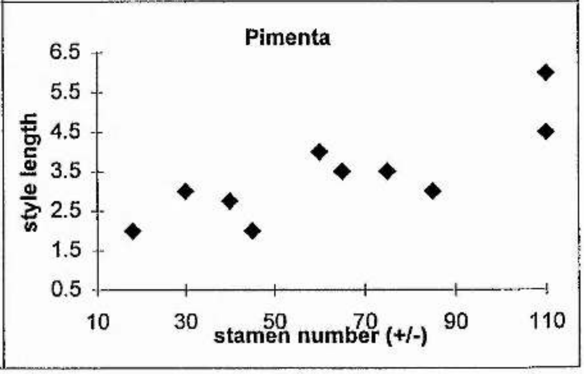
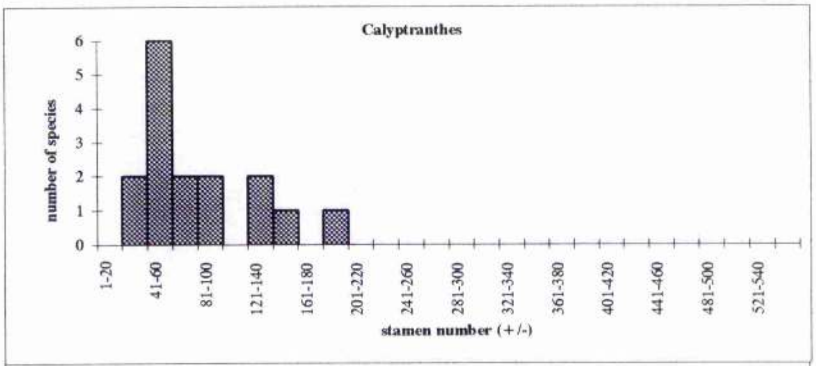
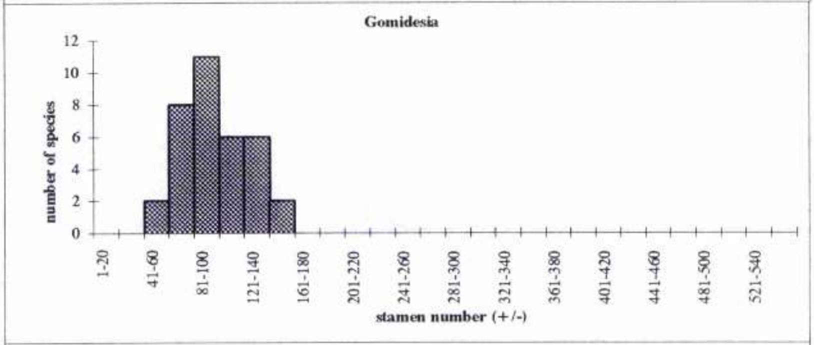
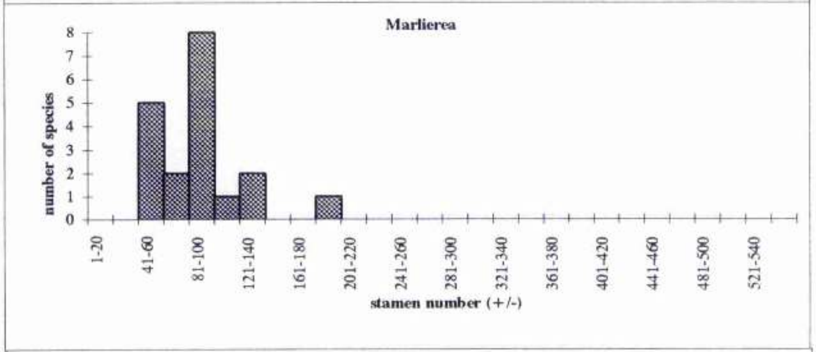
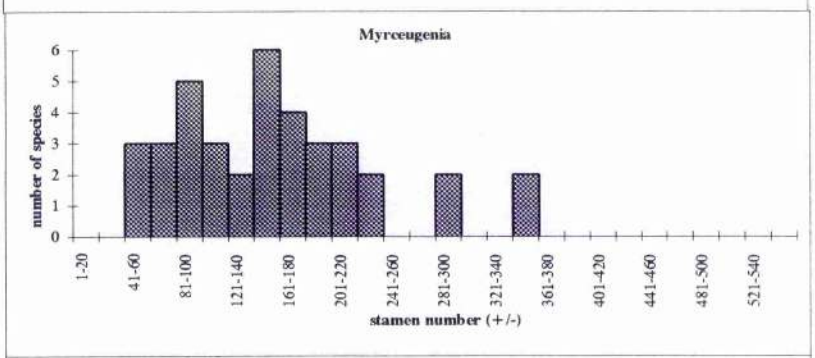

Pimenta
style length
6.5
5.5
4.5
3.5
2.5
1.5
0.5
10
30
50
70
90
110
stamen number (+/-)

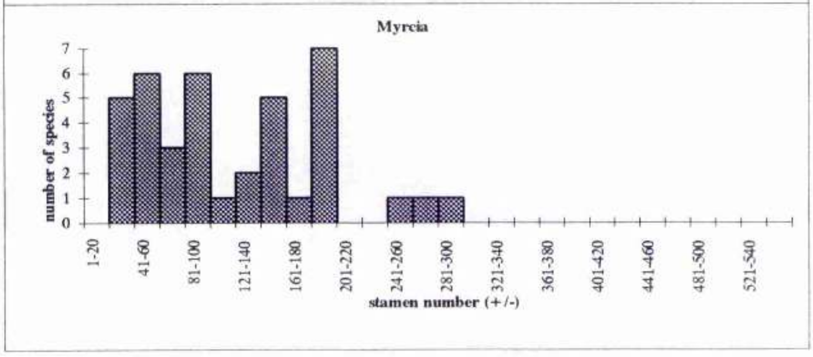
FIG. 9. Median stamen numbers of species in five genera of the Myrciinae.


Calyptranthes
number of species
0
1
2
3
4
5
6
1-20
41-60
81-100
121-140
161-180
201-220
241-260
281-300
321-340
361-380
401-420
441-460
481-500
521-540
stamen number (+/-)


Gomidesia
number of species
0
2
4
6
8
10
12
1-20
41-60
81-100
121-140
161-180
201-220
241-260
281-300
321-340
361-380
401-420
441-460
481-500
521-540
stamen number (+/-)


Marlierea
number of species
0
1
2
3
4
5
6
7
8
1-20
41-60
81-100
121-140
161-180
201-220
241-260
281-300
321-340
361-380
401-420
441-460
481-500
521-540
stamen number (+/-)


Myrceugenia
number of species
0
1
2
3
4
5
6
1-20
41-60
81-100
121-140
161-180
201-220
241-260
281-300
321-340
361-380
401-420
441-460
481-500
521-540
stamen number (+/-)


Myrcia
number of species
0
1
2
3
4
5
6
7
1-20
41-60
81-100
121-140
161-180
201-220
241-260
281-300
321-340
361-380
401-420
441-460
481-500
521-540
stamen number (+/-)

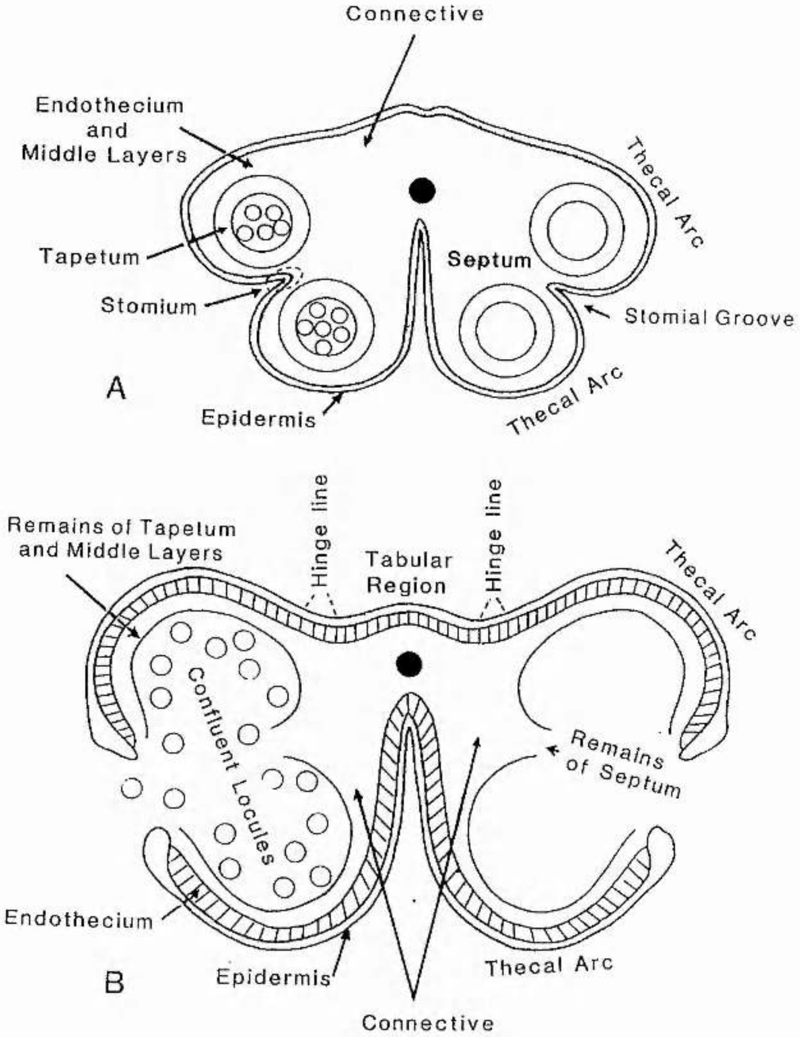
stamen number since *Calyptranthes* represents the extreme case of both these processes and *Marlierea* is intermediate with respect to both characters while *Myrceugenia* and *Myrcia* have free calyx lobes and higher stamen numbers. However, it should be noted that each of the two calyptrate species transferred by Landrum (1984) to *Myrceugenia* has a rather greater stamen number than its non-calyptrate putative sister species.

In the present study stamen counts for *Gomidesia* species were found to range from ca. 50 to ca. 200, only rarely exceeding 175. Counts of different flowers from the same collection (generally from the same tree) were usually very similar (differing by ten or less) while variation within species was much greater. I found no significant correlation between stamen number and disk diameter or style length in *Gomidesia* ($r = 0.37$, $v = 35$ and $r = 0.37$, $v = 33$ respectively, $p > .05$ in each case). Rather, stamen number appeared to be inversely related to anther length. Although this correlation was not statistically significant ($r = - 0.32$, $v = 35$, $p > .05$) the data suggest that in *Gomidesia* stamen number has been decoupled from flower size and has decreased in parallel with an increase in anther size. Since larger anthers are associated with buzz-pollination, both the reduced stamen numbers and the larger anther size may represent adaptive responses to selection for a more specialised pollination mechanism.

In most of the Myrciinae (as indeed in most Myrtoideae) the anthers are tetrasporangiate and bilocular at anthesis and bear a strong resemblance to the 'typical' anther so often depicted in text books (e.g. D'Arcy & Keating,1996) (Fig. 10). Each anther comprises four parallel sporangia, separated into two pairs, each pair being called a theca. Thus each theca has two sporangia/pollen sacs/locules which are initially separated by a septum of connective tissue. Before dehiscence, the septum between the two pollen sacs usually dissolves, at least in part, so that the two pollen sacs merge into one. At maturity each theca normally opens along a preformed dehiscence line, the stomium, through which the contents of both its pollen sacs are liberated. Upon dehiscence the thecal arcs/halves generally open wide and their curvature is lost or reversed so that the interior of the thecal arcs is exposed. Often the thecal arcs diverge to the extent that they end up back to back with the thecal arcs of the opposite theca, thus standing rigid in a plane of 90 degrees to the plane of the septum. Vestiges of the septum may persist as a vertical flap of tissue or the position of the septum may simply be marked by a furrow between the open thecal halves. The anthers of most species of *Myrcia* conform to this general pattern and usually measure up to 0.45 mm in length. In ventral view the interior of the thecal halves is exposed as convex surfaces (Fig. 15 v & w).

In *Gomidesia*, however, the thecal halves retain more or less their original curvature (Fig. 12) or are, at most, somewhat flattened after dehiscence (Fig. 11) but their curvature is never reversed. In addition the thecal halves tend not to open so widely but retain their original

FIG. 10. Terminology used in the description of anther morphology in this study. (Reproduced from D'Arcy and Keating, 1996. Note: anther shown is of *Lilium*, not of *Gomidesia*).


Connective
Endothecium and Middle Layers
Thecal Arc
Tapetum
Septum
Stomium
Stomial Groove
A
Epidermis
Thecal Arc
Hinge line
Hinge line
Remains of Tapetum and Middle Layers
Tabular Region
Thecal Arc
Confluent Locules
Remains of Septum
Endothecium
B
Epidermis
Thecal Arc
Connective

position or are held parallel to each other or slightly divergent. The combined effect of these differences is that in the anthers of many species of *Gomidesia* the interior surfaces of the thecal halves remain largely hidden from view or, where the interior surface of the thecal halves is exposed, it appears as a concave surface rather than a convex one (Fig. 15 f & j). Furthermore, in many species of *Gomidesia* there is some degree of vertical displacement between the pollen sacs of an individual theca, the ventral sac of each pair appearing to be inserted on the connective slightly distal to the dorsal sac. Thus, in dorsal view the interior of the distal region of the ventral sac of each theca is visible (e.g. Fig. 12 a, c, e, g, m) while in ventral view the interior of the proximal part of the dorsal sacs may be exposed or remain closed. Where the thecal halves retain curvature and have margins which remain connivent or overlapping after dehiscence the overall effect is that of a poricidal anther (e.g. Fig. 14 p & q). In other species where the degree of divergence of the thecal halves is greater, in lateral view the concave interior of the thecal halves is exposed over most of their length (e.g. Fig. 15 f, j, m). The vertical displacement of the pollen sacs has been emphasized in recent keys to the genera of the American Myrtaceae (McVaugh, 1968; Kawasaki 1989) but the curvature characters have been overlooked. Another taxonomically useful character is anther length. Though most published descriptions do not include this character my observations indicate that anthers of *Myrcia* species rarely exceed 0.45 mm in length while anthers of most species of *Gomidesia* are at least 0.5 mm long.

In their recent survey of anther glandularity in the American Myrtinae, Landrum and Bonilla (1996) reported a single 'gland' per anther in most species of Myrciinae studied. Anther glands were not observed in the anomalous genus *Luma* (basal in or sister to the Myrciinae). The genera *Calyptranthes* and *Myrceugenia* were found to include species with and without anther glands while all species of *Myrcia* sampled had glandular anthers, though *Myrcia cuprea* was variable in this respect. Landrum and Bonilla's (1996) findings confirm the present author's observation that many (most?) Myrciinae exhibit a secretory cavity at the apex of the anther connective. The functional significance of the apical secretory cavity in the anther connective was discussed by Nic Lughadha and Proença (1996). All species of *Gomidesia* studied exhibit an apical connective gland though this varies in size and is rather inconspicuous in some species.

The degree to which the connective is exposed at the base of the anther also differs between species of *Gomidesia*. In *G. spectabilis* and related species (Fig. 11) the bases of the thecae are separated from the point of insertion of the filament by a length of sterile connective tissue, hereafter termed a connective stub. The filaments are bent down in bud so that the developing anthers are densely packed around the base of the style in the hypanthial cup. The filament

FIG. 11. Anther morphology in *Gomidesia.* All images ~ x 42. *G. crocea*: **a**, **c**, dorsal views; **b**, lateral view. *G. martiana*: **d**, lateral view; **e**, dorsal view. *G. spectabilis*: **f**, **h**, dorsal views; **g**, obliquely lateral view.

(Material prepared for SEM and photographed by Elizabeth Woodgyer. For methods see Appendix 1).

[Vouchers: a-c from *Glaziou 7641*, d & e from *Harley 17947*, f-g from *Lindeman 13550.*]

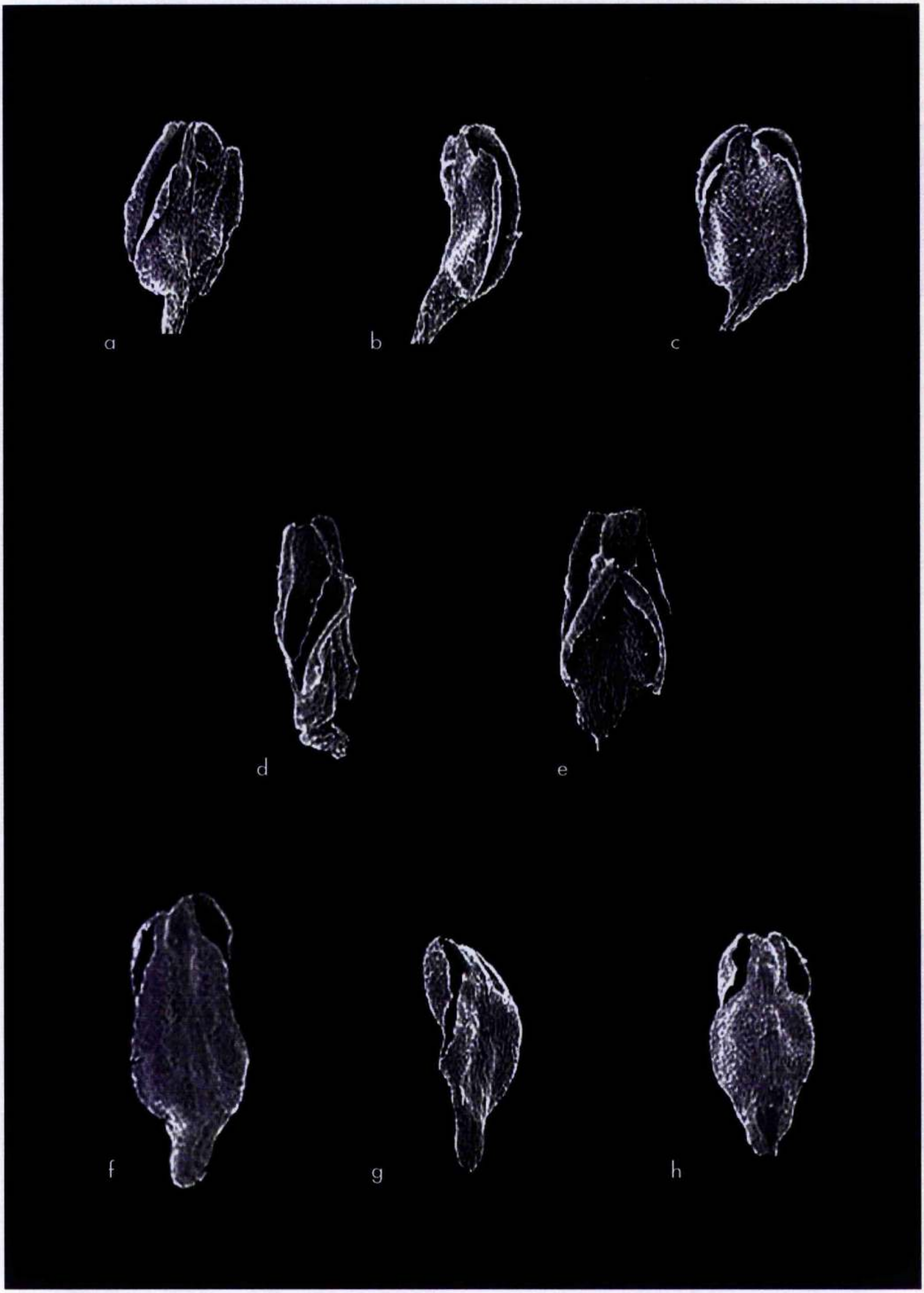

a
b
c
d
e
f
g
h

FIG. 12. Anther morphology in *Gomidesia.* All images ~ x 42. *G. anacardiifolia*: **a, c, e,** dorsal views; **b, d, e**, lateral views. *G. reticulata*: **g,** dorsal view; **h,** obliquely dorsal view; **j,** obliquely lateral view. *G. catharinensis*: **k, m,** dorsal views; **n, p,** lateral views.

(Material prepared for SEM and photographed by Elizabeth Woodgyer. For methods see Appendix 1).

[Vouchers: a & b from *Reitz & Klein 6270,* c-f from *Glaziou 17670*, g-j from *Glaziou 6546*, k-p from *Reitz & Klein 8360.*]

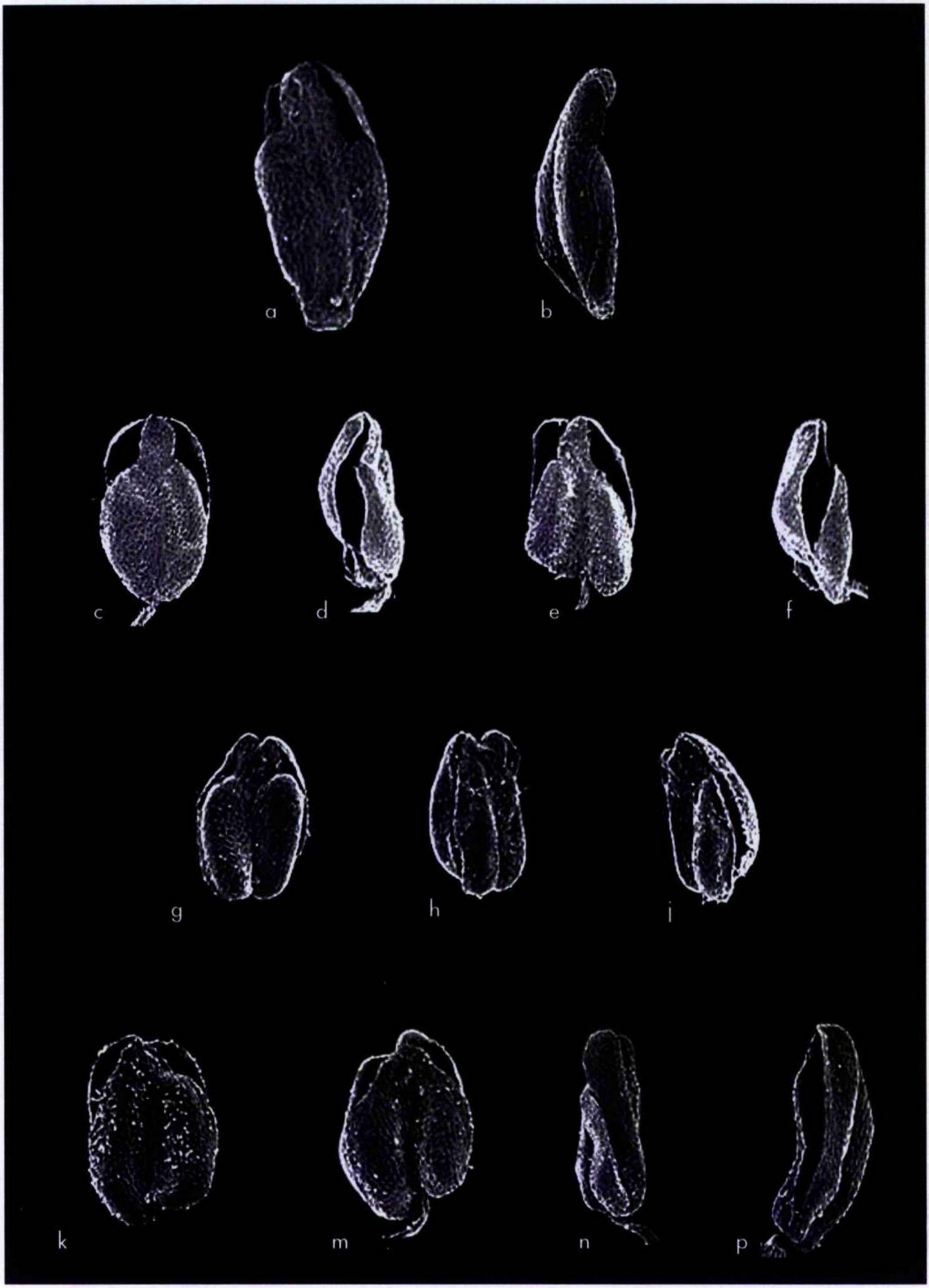

a
b
c
d
e
f
g
h
j
k
m
n
p

FIG. 13. Anther morphology in *Gomidesia.* All images ~ x 42. *G. flagellaris*: **a**, **b**, **d**, dorsal views; **c**, lateral view. *G. nitida*: **e**, dorsal view; **f**, lateral view. *G. eriocalyx*: **g**, **n**, dorsal views; **h**, **p**, lateral views. *G. cerqueiria*: **k**, **m**, dorsal views. (Material prepared for SEM and photographed by Elizabeth Woodgyer. For methods see Appendix 1).

[Vouchers: a-d from *Hatschbach 13552,* e & f from *Mikan/Pohl 1047*, g & h from *Claussen s.n.*, n & p from *Irwin 20460.*]


a
b
c
d
e
f
g
h
k
m
n
p

FIG. 14. Anther morphology in *Gomidesia.* All images ~ x 42. *G. lindeniana* (Brasília population): **a**, **d**, dorsal views; **b**, **c**, lateral views. *G. lindeniana* (Catolés population): **e**, **g**, dorsal views; **f**, **h**, obliquely lateral views. *G. fenzliana* (Catolés population): **j**, **n**, obliquely lateral views; **k**, viewed from above; **m**, dorsal view. *G. cerqueiria*: **p**, **q**, dorsal views. *G. fenzliana* (Catolés population): **r**, dorsal view; **s**, lateral view; **t**, obliquely lateral view.

(Material prepared for SEM and photographed by Elizabeth Woodgyer. For methods see Appendix 1).

[Vouchers: a-d and j-n from *Nic Lughadha s.n.* (liquid-preserved material for breeding system studies), e-h from *Harley 53344;* p-q from *Nic Lughadha 154,* r-t from *Harley 52001*]

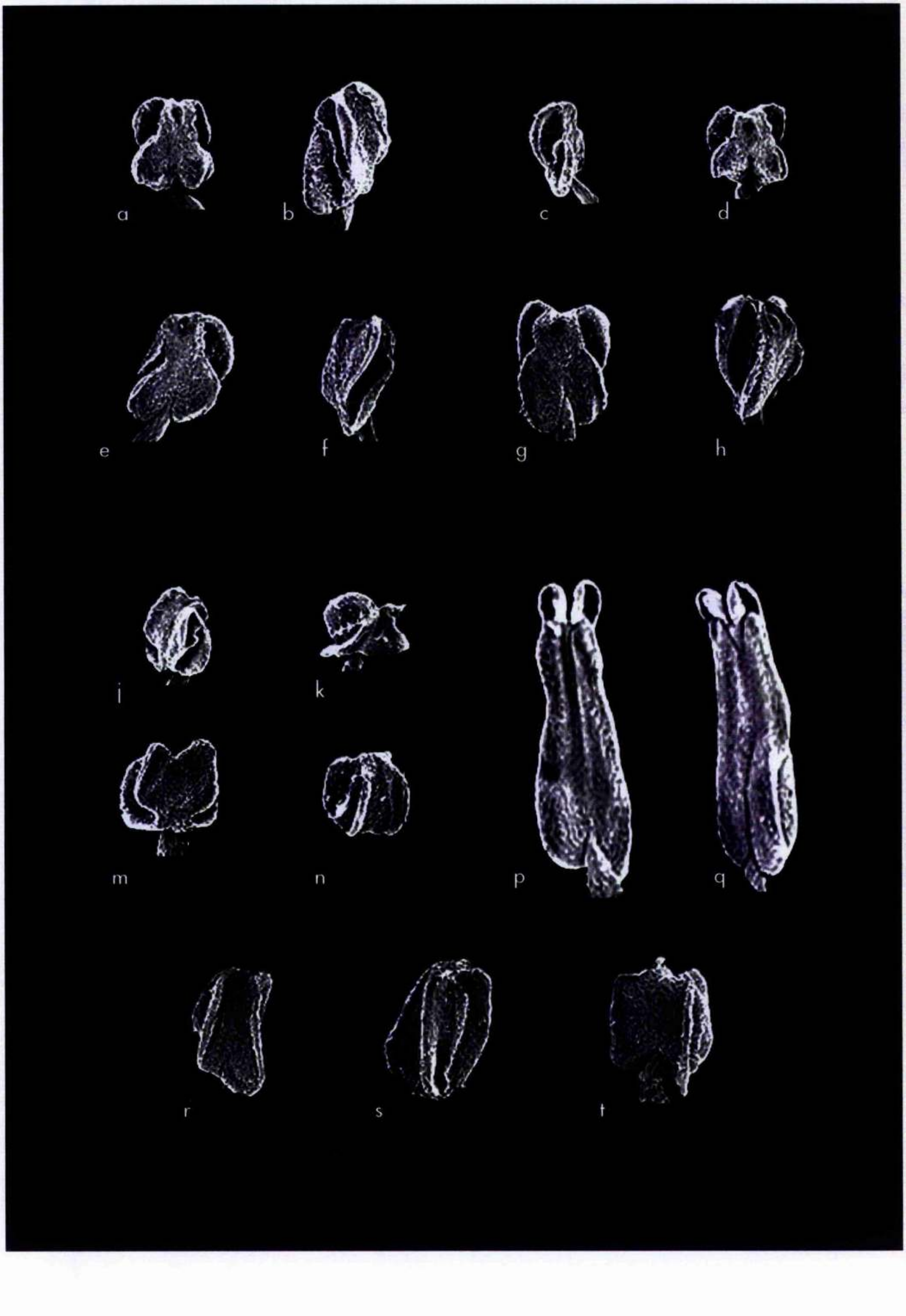
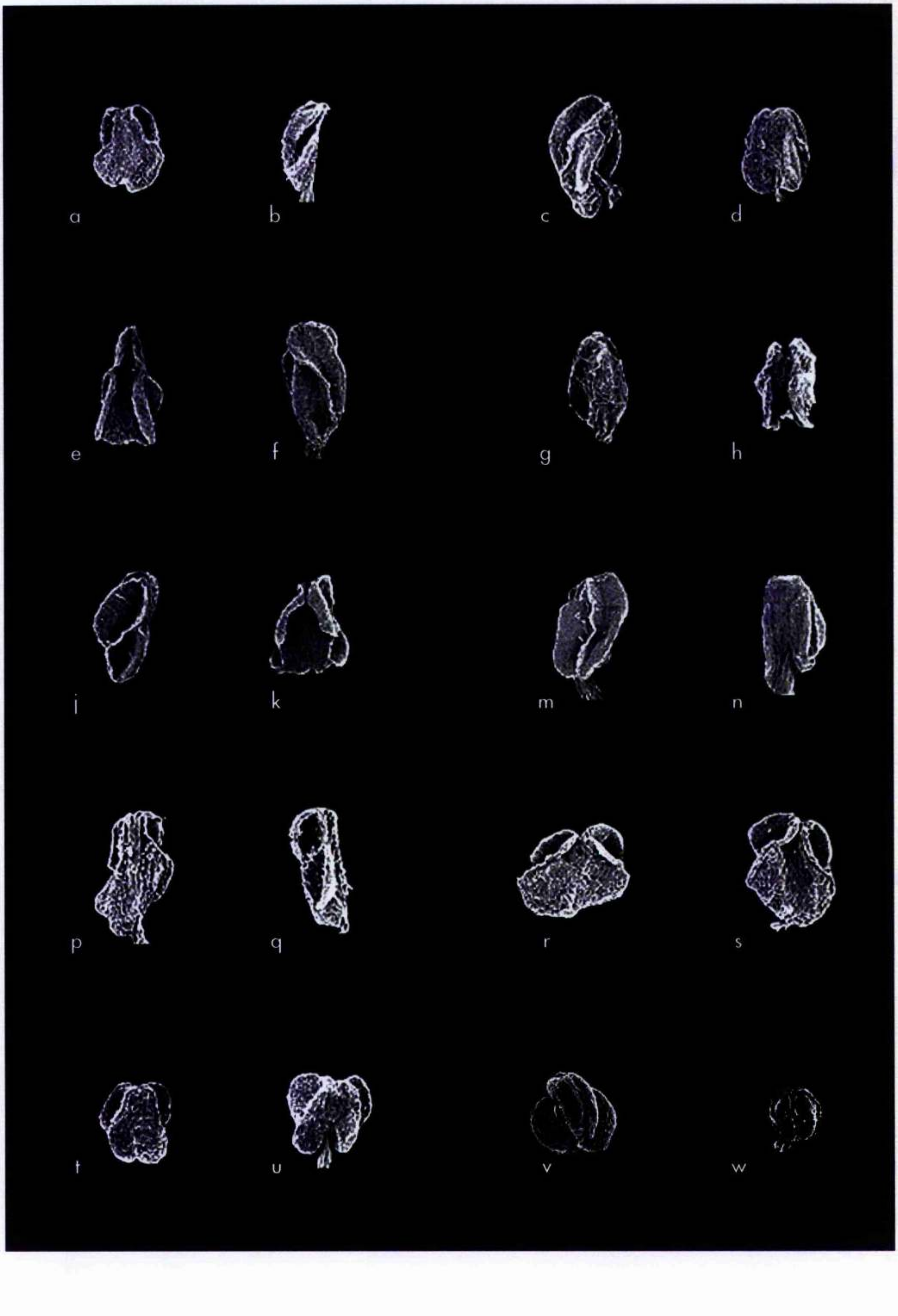

a
b
c
d
e
f
g
h
j
k
m
n
p
q
r
s
t

FIG. 15. Anther morphology in *Gomidesia.* All images ~ x 42. *G. affinis*: **a**, dorsal view; **b**, lateral view. *G. fenzliana*: **c,** lateral view; **d,** dorsal view. *G. montana*: **e,** dorsal view; **f,** lateral view. *G. palustris*: **g,** lateral view; **h,** dorsal view. *G. pubescens*: **j,** lateral view; **k,** dorsal view. *G. schaueriana*: **m,** lateral view; **n,** obliquely dorsal view. *G. sellowiana*: **p,** dorsal view; **q,** lateral view. *G. tijucensis*: **r,** **s**, dorsal views. *G velutiflora*: **t, v**, dorsal views. *Myrcia gardneriana*: **v,** ventral view. *M. decrescens*: **w**, lateral view.

(Material prepared for SEM and photographed by Elizabeth Woodgyer. For methods see Appendix 1).

[Vouchers: a & b *Glaziou 19738*, c & d *Harley 18045*, e & f *Brade 17015*, g & h *Legrand 4415*, j & k *Lindeman 4706*, m & n *Hatschbach 23438*, p & q *Brade 20895*, r & s *Reitz & Klein 8296*, t & u *Duarte 6265*, v *Richards 6893*, w *Ratter 3597.*]


a
b
c
d
e
f
g
h
j
k
m
n
p
q
r
s
t
u
v
w

may be uniform in diameter along its length but is often abruptly or gradually tapered apically, being narrowest at the point of insertion on the connective. The functional significance of variation in these structures remains to be investigated but it seems likely that these modifications affect stamen rigidity and the 'buzzability' of the anther. I have not observed such extensions of the connective in any other genus of Myrtaceae but connective extensions occur in many genera of the Melastomataceae, a Myrtalean family in which buzz pollination is prevalent (Renner, 1989).

**Hypanthium.** In *Gomidesia* the hypanthium is usually obconic, and rounded in cross-section, but cylindrical or infundibuliform hypanthia also occur and in some species the hypanthium is pentagonal or hexagonal in cross-section due to vertical ridges on its surface. The hypanthium is usually prolonged above the top of the ovary forming a cup which may be relatively shallow or up to twice the height of the ovary itself. Externally, the indumentum on this free part of the hypanthium may differ in density from that on the part which is fused to the ovary. Internally, the free portion of the hypanthium is almost invariably densely pubescent, and the indumentum is sometimes so copious as to completely fill the cavity, so that to the casual observer the disk may appear to be flat.

Berg (1855-56, 1857-59) attached great importance to the character of the prolonged hypanthium, distinguishing the genus *Aulomyrcia* in which the hypanthium is 'valde productum' and usually glabrous internally from *Myrcia* in which the hypanthium is 'vix productum' and the disk often bears a dense indumentum. Most subsequent authors relegated *Aulomyrcia* to the synonymy of *Myrcia* (McVaugh, 1958). McVaugh discussed the difficulties associated with over-reliance on the character of the prolonged hypanthium, concluding that it 'may often provide a convenient means for contrasting limited numbers of species in the flora of a given area, but its evolutionary significance, as shown by its correlation with other characters or sets of characters, remains to be demonstrated'. McVaugh (1969) distinguished three sections of *Myrcia*: *Myrcia* sect. *Myrcia*, sect. *Aulomyrcia* and sect. *Armeriela*. The latter section included species considered by McVaugh to resemble *Marlierea* in having more or less deciduous calyx lobes but to differ from members of that genus in that the margins of the hypanthium do not split between the calyx lobes. Species referred by McVaugh to *Myrcia* sect. *Armeriela* have a cup-like prolongation of the hypanthium which is usually glabrous within. This section included many species originally described by Berg in *Aulomyrcia*. Thus McVaugh, while questioning the taxonomic significance of the prolonged hypanthium, continued to recognise groups of species with *either* a prolonged hypanthium which is glabrous internally *or* an internally pubescent hypanthium which is scarcely prolonged vertically above the pubescent summit of the ovary. Clearly the presence of a prolonged hypanthium which is densely pubescent internally, as reported here for most species of *Gomidesia,* represents a combination of characters which differs from either of those described as prevalent in *Myrcia.* However, it should be noted that a number of Peruvian species of *Myrcia* were described by McVaugh (1958) as presenting sunken hirsute disks and at that time he considered that 'depending on the species selected one can demonstrate almost any desired stage of the transition between the glabrous and prolonged hypanthium and calyx of *Aulomyrcia* proper on the one hand and the hairy ovary and short calyx of *Myrcia* proper' (McVaugh, 1956b). It would appear that a detailed re-examination of this Peruvian material is needed.

**Top of the ovary.** The top of the ovary is always pubescent and may be more or less flat or form a shallow dome topped by the style (or by the base of the style in fruit). This latter tendency is most marked in *Gomidesia martiana.*

**Stigma and style.** The style usually just exceeds the stamens in length and is folded over the folded stamens in bud. Even when it has straightened upon anthesis, the style often retains a kink or notch at its midpoint. The lower third or half of the style is often clothed more or less densely with long white hairs but the upper portion is always glabrous and sometimes conspicuously glandular. The stigma is often so small as to be indistinguishable even at a magnification of x 50, but some species have well-defined, minutely capitate stigmas on which papillae can be observed at this magnification.

**Ovary.** The ovary is usually inferior as in most Myrtoideae but in *G. martiana* the upper part of the ovary is free (Fig. 38 G). The ovary is usually bilocular but may be 3-, 4- or 5-locular in some species. Placentation is basal and there are two ovules per locule.

### Fruit and seed

**Fruit.** Mature fruits of *Gomidesia* vary in diameter from c. 5 mm (*G. glazioviana*) to more than 20 mm (*G. grazielae* and *G. magnifolia*). The fruit are usually more or less globose and round in cross-section but a few species have fruits with deep vertical ridges. In some cases these are species in which the hypanthium is ridged in bud (*G. crocea* and *G. warmingiana*) but in other cases ridged fruit develop from hypanthia which are terete in bud (e.g. *G. cerqueiria*). The functional significance of such deeply sulcate fruit is unclear at present but the character would appear to have arisen on a number of occasions in the evolution of the Myrtoideae since deeply ridged fruit occur elsewhere in the Myrciinae (e.g. in *Marlierea velutina*) and in the Eugeniinae (e.g. in *Eugenia uniflora*). In *Gomidesia* the calyx lobes are usually persistent in fruit and are held erect or closely connivent so that they often partially or entirely obscure the disk from view. In contrast, in *Myrcia* the calyx lobes are often divergent or patent so that the disk is easily visible. In a few species of *Gomidesia* the calyx lobes fall as the fruit develops and the free part of the hypanthium persists as a ring which crowns the mature fruit (*G. montana*, *G. nitida* and *G. sonderiana*). The fruits are often one-seeded, and in some species the number seems to be fixed at one. However in other species the number of developing seeds is variable and may be as many as six.

**Seeds.** In one-seeded fruits the seed is often more or less globose but where there is more than one developing seed the seeds may be hemi-orbicular or with two flat surfaces and one convex one. The testa is chartaceous and usually pale, yellowish-brown. The embryo conforms to the general type characteristic of the Myrciinae in that the cotyledons are green, foliaceous, very slightly fleshy and contortuplicate with the long hypocotyl wrapped around them and partially embedded in them. A number of species exhibit a feature not reported elsewhere in the Myrtoideae in that the hypocotyl bears a dense indumentum over some or all of its length. The functional significance of this pubescence is unknown but it is tempting to speculate that it may serve to protect the hypocotyl from fungal growth when it emerges through the testa and begins to penetrate the leaf litter and soil of the forest floor. Whatever its adaptive role this character has proved useful in grouping species in the present study. First reported by Berg (1857) in *Gomidesia spectabilis*, pubescent hypocotyls are here shown to occur in approximately one quarter of species of *Gomidesia* and their occurrence is correlated with anther morphology, supporting one of the more robust informal groupings within the genus. The only report I have found of pubescent embryos elsewhere in the Myrtaceae is that of Grifo (1992) who described the plumule of *Myrcianthes* as silkily hairy.

## Anatomy

### Wood

When work began on the present revision there were virtually no data available on the wood anatomy of *Gomidesia*. The only detailed description purporting to be of *Gomidesia* wood anatomy (Barbosa et al. 1977/1978) appears to have been based on a collection of *Myrcia pubipetala* Miq. erroneously identified as *Gomidesia crocea* (Vell.) Berg. In fact Landrum (1981) commented that there had been only cursory investigations of the wood anatomy of the American Myrtaceae as a whole. Elsewhere in the Myrtaceae studies of wood anatomy have proved very useful to taxonomists, revealing many consistent clear-cut anatomical features that are of value at the generic level. (e.g. Ingle & Dadswell 1953). For these reasons a wood-anatomical survey of the Myrciinae was undertaken in parallel to the present study. Four genera were sampled viz. *Calyptranthes*, *Gomidesia*, *Marlierea* and *Myrcia*, and a total of 31 species were studied (Table 2). Thus all the South American genera of the Myrciinae were represented except *Myrceugenia* which was studied by Landrum (1981) and which is in any case rather different from the other myrcioid genera, resembling them chiefly in embryo-type. The results of this survey have been published elsewhere (Dias-Leme, Gasson & Nic Lughadha, 1995) and are presented here in summary form only, followed by a more detailed discussion of the observations on *Gomidesia*.

**General wood anatomical description of the subtribe Myrciinae (excluding *Myrceugenia*)**

Wood: diffuse porous.

Vessels: typically solitary, perforations simple, intervessel pits alternate, vestured; vessel to ray pitting of same type as the intervascular pitting.

Fibres: mostly thick-walled with bordered pits in both tangential and radial walls, some of which are vestured in most species.

Parenchyma: scanty paratracheal, diffuse and/or diffuse-in-aggregates forming complete or interrupted bands, in strands of 4 - 8 (3 - 10) cells.

Rays: 1 - 3 (-4) seriate, body ray cells procumbent with over 4 rows of square and/or upright marginal cells, some chambered. Disjunctive ray parenchyma cell walls present.

The observations on which this general description is based are presented in Table 2. As can be seen from this table the four genera cannot be reliably separated on the basis of wood anatomy alone. However, some variation in character distribution between genera could be detected and seemed worthy of note.

**Axial parenchyma distribution.** *Calyptranthes* has parenchyma that is scanty paratracheal and diffuse-in-aggregates and in continuous tangential bands up to three cells wide. The parenchyma of *Marlierea* is very similar to that of *Calyptranthes* but one species (*Marlierea umbraticola*) had wider bands. *Gomidesia* parenchyma is also scanty paratracheal and diffuse-in-aggregates but is rarely banded and *G. affinis* has only diffuse parenchyma.

Table 2. Wood anatomical characters in four genera of the Myrciinae.
(Reproduced from Dias-Leme, Gasson & Nic Lughadha, 1995).

| Species Character (see key below): | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calyptranthes fasciculata* Berg | – | + | – | – | + | + | + | – | – | + | – | – | > 5 |
| *grandifolia* Berg | – | + | – | – | + | + | + | – | – | – | – | – | > 8 |
| *lucida* Mart. ex DC. | + | + | – | – | + | + | + | – | – | – | – | – | > 8 |
| *pileata* D. Legrand | + | + | – | – | + | + | – | – | + | + | – | – | 4–8 |
| *pulchella* DC. | – | + | – | – | + | + | + | – | + | – | – | – | > 8 |
| *speciosa* Sagot | – | + | – | – | + | + | + | – | – | + | – | – | > 8 |
| *widgreniana* Berg | – | + | – | – | + | + | + | – | – | – | – | – | > 8 |
| *Gomidesia affinis* (Cambess.) D. Legrand | + | – | + | + | – | – | – | – | – | – | – | – | 5–8 |
| *anacardiifolia* Berg | + | + | + | – | + | + | – | – | – | + | + | – | 4–8 |
| *sellowiana* Berg | + | + | + | – | + | + | – | – | – | + | – | – | 4–8 |
| *tijucensis* (Kiaersk.) D. Legrand | + | + | + | – | + | + | – | – | – | + | + | – | 4–8 |
| *Marlierea montana* (Aubl.) Amshoff | – | + | – | – | + | + | – | – | + | + | – | – | > 8 |
| *parviflora* Berg | – | + | – | – | + | + | – | – | + | + | – | – | > 8 |
| *scytophylla* Diels | – | + | – | – | + | + | + | – | – | + | – | – | > 8 |
| *spruceana* Berg | – | + | – | – | + | + | + | – | + | + | – | – | > 5 |
| *sylvatica* (Gardner) Kiaersk. | – | + | – | – | + | + | + | – | – | – | + | – | 5–8 |
| *umbraticola* (Kunth) Berg | – | + | – | – | + | + | + | + | + | – | – | – | > 8 |
| *Myrcia amazonica* DC. | – | + | – | +/– | +/– | + | + | +/– | – | +/– | – | – | > 8 |
| *bracteata* (Rich.) DC. | + | + | – | + | – | + | – | – | – | + | – | + | 3–8 |
| *deflexa* DC. | + | + | – | +/– | +/– | + | – | – | – | + | – | – | 3–8 |
| *fallax* DC. | + | + | – | +/– | +/– | + | – | – | + | + | +/– | – | 3–8 |
| *grandis* McVaugh | – | + | – | – | – | + | + | + | + | + | – | – | > 5 |
| *guianensis* DC. | – | + | – | + | – | + | – | – | + | + | – | – | > 5 |
| *inaequiloba* (DC.) D. Legrand | – | + | – | – | – | + | + | + | + | + | – | – | > 5 |
| *multiflora* (Lam.) DC. | – | + | – | + | – | – | + | + | + | + | – | – | 3–8 |
| *pyrifolia* (Desv. ex Ham.) Nied. | + | + | – | – | + | + | + | – | + | + | – | – | > 5 |
| *servata* McVaugh | – | + | – | – | + | + | – | – | – | + | – | – | 3–8 |
| *splendens* (Swartz) DC. | + | + | – | + | – | + | – | – | + | + | – | – | 3–8 |
| *subobliqua* (Benth.) Nied. | – | + | – | – | + | – | + | – | + | + | – | – | > 5 |
| *sylvatica* (G. Meyer) DC. | – | + | – | + | – | + | – | – | + | + | – | – | > 5 |
| *tomentosa* (Aubl.) DC. | + | + | – | – | + | + | – | – | + | – | – | – | 4–10 |

1. Growth rings
2. Fibres thick-walled
3. Fibres thin-walled
4. Axial parenchyma diffuse
5. Axial parenchyma diffuse in aggregates
6. Axial parenchyma scanty paratracheal
7. Axial parenchyma in bands up to three cells wide
8. Axial parenchyma in bands more than three cells wide
9. Axial parenchyma with crystals
10. Dark contents
11. Pith flecks
12. Helical wall thickenings in fibres
13. Axial parenchyma strand length (number of cells)

*Myrcia* exhibits the whole range of parenchyma types from diffuse, diffuse-in-aggregates, and discontinuous to continuous bands of various widths.

**Crystal presence and distribution.** *Gomidesia* was the only genus in which no crystals were recorded in any species. There were several crystals of different sizes per non-chambered axial parenchyma cell in two *Calyptranthes* species and of the same size in some *Marlierea* species. Single prismatic crystals were found in chambered axial parenchyma cells in many *Myrcia* species and were sometimes also found in chambered ray cells in *Myrcia*, confirming Metcalfe and Chalk's (1950) observation but contradicting Van Vliet and Baas's (1984) implied assumption that crystals are always absent from the genus.

**Helical wall thickenings.** Helical wall thickenings were found only in *Myrcia bracteata* and in this species they appeared to be confined to the fibres as they were not found in any vessels. Such thickenings have been reported in vessels and/or fibres of eight genera of Myrtaceae including four species of *Myrcia* (Schmid & Baas, 1984). Landrum (1981) found spiral thickenings in nine out of fifteen species of *Myrceugenia* studied by him and interpreted this result as supporting his opinion 'that *Myrceugenia* is one of the more primitive genera of the Myrteae'. However, Schmid and Baas (1984) found correlations between the strength of helical wall thickenings and tropical, subtropical and temperate distributions of taxa of Myrtaceae. They suggest that the high incidence of scalariform perforation plates in cool mesic floras could be explained by a lack of strong selective pressures in these ecological conditions to eliminate this primitive feature. Thus, the temperate to subtropical distribution of *Myrceugenia* may account for the prevalence of spiral thickenings in the species studied by Landrum.

**Septate fibres and vestured pits.** Metcalfe and Chalk (1950) reported occasional septate fibres in *Marlierea* but only non-septate fibres were observed in our study. Another discrepancy between the results of our survey and the literature is in the occurrence of vestured pits. These are generally thought to be ubiquitous in the Myrtaceae (Bailey, 1933; Metcalfe & Chalk, 1950) but in some species studied, e.g. *Marlierea sylvatica*, the bordered pits in fibre-tracheids are not vestured. Van Wyk et al. (1983) noted the occasional occurrence of unvestured pits in the wood of southern African *Eugenia* and commented that the bordered pit chambers of fibre tracheids were conspicuously less vestured than those of vessel elements.

**Wood anatomical description of *Gomidesia***

(based on observations in *G. affinis*, *G. anacardiifolia, G sellowiana* and *G. tijucensis*).

Growth rings: distinct in *G. anacardiifolia*, *G. sellowiana* and *G. tijucensis*, marked by thick-walled and radially flattened fibres.

Fibres: thin-walled.

Parenchyma: scanty paratracheal and diffuse in aggregates in most species. *G. affinis* has only diffuse parenchyma. Parenchyma strands of 4 - 8 cells.

Prismatic crystals not observed in any species.

Dark contents: present in radial and axial parenchyma of *G. anacardiifolia*, *G. sellowiana* and *G. tijucensis*.

Pith flecks: present in *G. anacardiifolia* and *G. tijucensis*

Metcalfe and Chalk (1950) reported rays up to eight cells thick in some species of *Gomidesia* but none of the specimens included in our study exhibit rays more than four cells wide. These authors also described the vessels of *Gomidesia* as typically solitary with occasional to numerous multiples of two to three cells in some species. No vessel multiples were observed in the four species of *Gomidesia* included in our survey.

**Leaves**

The leaf anatomy of *Gomidesia*, and indeed of many other species of Brazilian Myrtaceae, has been the subject of a long-term study by a research team at the Universidade Federal do Rio de Janeiro (UFRJ). Fontenelle et al. (1993) published a detailed description of the leaf anatomical features of two *restinga* (coastal woodland) species, *G. fenzliana* and *G. martiana*. Two forest species *G. nitida* and *G. spectabilis* were the subject of a Masters thesis by Gomes (1992). The following descriptions are largely based on these two studies and have been prepared following discussions with Doria Gomes at UFRJ. Her perceptive insights and generosity with regard to time and data are acknowledged with gratitude.

**Epidermis.** The epidermis is composed of cells of various dimensions which generally have sinuous anticlinal walls. In *G. spectabilis* the cells over the vascular traces are straight-walled. In *G. fenzliana* the sinuosity of cells in the adaxial epidermis is only visible in rather shallow focus, the cells appearing straight-walled at deeper levels. In *G. nitida* the abaxial epidermis is composed of straight-walled cells while the adaxial epidermis has cells with sinuous anticlinal walls except for the cells covering the secretory cavities which are less sinuous in outline, and stain less intensely with safranin. These latter generally occur in pairs (occasionally singly), and are more or less reniform in outline with the wall which separates the pair being straight or slightly sinuous. The cells surrounding these pairs are radially disposed. Such cells covering the secretory cavities were also observed singly or in pairs on both faces of leaves of *G. fenzliana* and *G. martiana*. In *G. spectabilis* however, the epidermal cells covering the secretory cavities did not appear to be differentiated from the other epidermal cells in any way. In all four species studied the small clear areas visible near the anticlinal walls of adaxial and abaxial epidermal cells are due to differences in the thickness of the periclinal walls in these cells.

**Stomata.** The stomata are confined to the abaxial surface and are predominantly paracytic, rarely staurocytic in *G. fenzliana* or anisocytic in *G. spectabilis*. Mean stomatal densities range from 244 $mm^{-2}$ in *G. nitida* through 438 $mm^{-2}$ in *G. martiana* and 538 $mm^{-2}$ in *G. fenzliana* to 945 $mm^{-2}$ in *G. spectabilis*. The stomatal cells typically are characterized by a cutinized thickening of the periclinal walls which is confined to the area adjacent to the osteole except in the case of *G. nitida* where the thickening extends to the poles of the stomatal cells. In all species studied the stomata are slightly raised above the level of the other epidermal cells.

**Trichomes.** Trichomes are present on the abaxial and adaxial surfaces of the epidermis except in the case of *G. nitida* where they are largely confined to the abaxial surface though they may occur in small numbers on the midrib adaxially. The cells surrounding the trichomes are radially arranged (in *G. fenzliana*, *G. martiana* and *G. spectabilis*) and their anticlinal walls may be thickened adjacent to the point of insertion of the trichome (in *G. nitida*).

Only unicellular trichomes have been encountered in *Gomidesia* to date. The most common type is straight or slightly curved, broader towards the base and variable in length. The colour is also variable and depends to some extent on the degree to which the protoplasm extends into the lumen of the trichome. Where the protoplasm extends the entire length of the lumen the trichome is often brownish in colour. Often however, the protoplasm is confined to the basal portion of the trichome and a new cell wall may be observed giving the trichome a biseriate appearance. In this case the upper part of the trichome may fall, leaving the remnants of its wall at the base and giving a cup-shaped appearance to the abscission region. In *G. fenzliana* the protoplasm is often retracted to the part of the trichome that is embedded in the epidermis and after the formation of an inner parietal coat, the outer coat is shed like the finger of a glove. The contents of the lumen are rich in tannins. The walls of these hairs are thick and lignified. Undulations in the walls of hairs of this type can result in the formation of small mamillate projections. These trichomes are often anvil-shaped in *G. spectabilis* and exceptionally one of the horns of the anvil may be lacking. Fontenelle et al. (1993) referred to this trichome class as Type I. This is equivalent to what Briggs and Johnson (1979) termed the 'standard' myrtaceous trichome type, the only type of trichome reported by them for the Myrciinae (and indeed for all neotropical Myrtoideae). Their description leaves no doubt that this is the type of trichome in question: acute, rather thick-walled and unicellular. Curled, bent, basally saccate and two-armed ('biramous') hairs are mentioned as variations of the basic type. Briggs and Johnson also explain that the formation of a 'membrane' across the lumen near the cell base, enclosing the shrunken protoplast, often gives a misleading impression that the hair consists of more than one cell.

Gomes (1992) and Fontenelle et al. (1993) report the occurrence in *G. spectabilis* and *G. martiana* of a second class of unicellular trichome, unknown elsewhere in the Myrtoideae. These trichomes (referred to by Gomes (1992) and hereafter as type II trichomes) are short, thick-walled and lignified, with apparently random mamilloid projections which confer a very distinctive aspect. The extremity of the type II trichome is often pointed and the wall is particularly thick towards the base. This type of trichome has to date been found only on the abaxial surface and petioles of leaves of *G. martiana* and on the abaxial surface of leaves of *G. spectabilis*, conferring on these surfaces an arenaceous aspect when viewed with a dissecting microscope.

**Leaf waxes.** In *G. martiana*, *G. nitida* and *G. spectabilis* epicuticular wax was distributed over the abaxial leaf surface in granular form. In *G. spectabilis* the wax on the adaxial surface was granular also while in *G. martiana* and *G. nitida* the wax on the adaxial surface took the form of platelets. Epicuticular waxes were not observed on the leaves of *G. fenzliana*. However, this does not exclude the possibility that wax is present as a smooth layer not detectable by the scanning electron microscopy techniques employed.

**Intercostal region.** The leaf is dorsiventral and the epidermis is one-layered (as in all Myrtoideae?). The palisade is one-layered in all species studied except in *G. fenzliana* where it consists of two layers of cells, the first layer being interrupted at times by the occurrence of a discontinuous, achlorophyllous, subepidermal layer. The lacunose parenchyma is columnar in *G. fenzliana* and *G. martiana* and loosely arranged in *G. nitida* and *G. spectabilis*. In *G. fenzliana* the small to medium-sized veins have sclerenchymatic bundle sheath extensions which extend to the adaxial epidermis. Collenchymatic bundle sheath extensions were observed in *G. spectabilis* while no such feature is reported for *G. martiana* or *G. nitida*.

**Secretory cavities.** Subepidermal secretory cavities, spherical in shape and lined internally with thin-walled lipid-rich epithelial cells are characteristic of the Myrtaceae and were observed in all species of *Gomidesia* studied. In *G. fenzliana* and *G. martiana* these cavities were observed on both faces of the leaf lamina while in *G. spectabilis* and *G. nitida* they were confined to the adaxial surface. The position of the cavities relative to the epidermis may also vary between species. In *G. fenzliana* and *G. martiana* the cavities are described as being in direct contact with the epidermis or separated from it by one or, rarely, two cells. The position of the cavities in *G. nitida* appears to be similar to those of *G. fenzliana* and *G. martiana* as they are described as being immersed in the palisade parenchyma (which is only one layer thick in this species) and are illustrated in contact with the epidermis. In *G. spectabilis* however, the secretory cavities appear to be more deeply immersed, being located in the lacunose parenchyma and occasionally invading the palisade parenchyma.

**Vascular system.** The vascular system is organized in a single trace, consisting of xylem surrounded by phloem except in the distal region of the leaf lamina where the phloem is laterally interrupted. The phloem is more abundant on the adaxial surface and the elements are arranged in well developed groups separated by parenchyma cells. The vascular system is surrounded by a supporting tissue which has two types of cells: cellulosic fibres and typical lignified fibres. Both cell types occur along the whole length of the petiole in *G. martiana* but the cellulosic fibre is more abundant. In the midrib of *G. martiana* the supporting tissue consists only of lignified fibres arranged in a layer on the abaxial face. The two types of fibre also co-occur in the petiole of *G. fenzliana* except in the proximal region where the vascular trace is surrounded only by cellulosic fibres. In the midrib of *G. fenzliana* the lignified fibres surround the vascular trace in the median and distal portions of the leaf while in the proximal portion they co-occur with cellulosic fibres which are situated in the abaxial region. In *G. nitida* and *G. spectabilis* the vascular trace is enveloped in cellulosic tissue along the whole length of the petiole. Some lignified tissue was observed in *G. nitida*, especially in the median and distal regions of the petiole. In *G. spectabilis* the basal portion of the midrib is clothed in a sheath which is largely cellulosic with scattered lignified cells. In the median and distal regions the sheath is lignified. In *G. nitida* the sheath appears to be lignified along the whole length of the midrib. Clearly there is much between-species variation in these characters but whether it is of taxonomic utility or merely environmentally influenced remains to be established.

Gomes (1992) and Fontenelle et al. (1993) highlighted suites of characters which they considered particularly useful in distinguishing between species of *Gomidesia*. Less emphasis was placed on shared characters which might reflect relationships within the genus. Below selected characters are discussed in the context of the Myrtaceae as whole.

Type I hairs are abundant on the abaxial leaf surfaces of *G. nitida* and *G. fenzliana*. This is the most common trichome type found in most alliances of the Myrtaceae, including all the neotropical Myrtoideae (Briggs and Johnson 1979).

A variant of Type I hairs is the biramous hair type reported by Gomes (1992) as frequent in *G. spectabilis* and rare in *G. nitida*. McVaugh (1969) remarked on the tendency demonstrated by the Myrciinae towards the development of dibrachiate hairs and noted that they may occur intermixed with basifixed hairs. Nearly all species of *Myrceugenia* have dibrachiate hairs (Landrum 1981) and they occur frequently in species of *Calyptranthes* and often in *Marlierea* (McVaugh 1958). Dibrachiate hairs are also reported from genera of the Eugeniinae, occurring in some species of *Eugenia* (McVaugh 1958) and in a single species of *Myrcianthes* (Grifo 1992). They are absent from *Acca, Accara* and *Myrteola* and perhaps from the Myrtinae as a whole.

Type II hairs are reported from *G. martiana* and *G. spectabilis* and unknown elsewhere in the Myrtaceae. The balance of evidence from other characters also suggests that these are sister species (see Systematic Treatment) and they have frequently been confused and/or treated as synonymous.

*Gomidesia nitida* is unique among the species studied at UFRJ by virtue of its completely glabrous adaxial surface. However, completely glabrous leaves occur frequently elsewhere in the Myrtaceae and the mere absence of indumentum is not likely to prove helpful in indicating affinities.

A sclerenchymatic bundle sheath extension was observed in *G. fenzliana* while a similar structure in *G. spectabilis* was collenchymatic in origin. Intrageneric variation in the structure of the bundle sheath has been reported elsewhere in the Myrtaceae (e.g. *Eugenia*) and it has been suggested that these may be of taxonomic importance (Costa, 1995 and references cited therein).

### Floral anatomy

Floral anatomy has contributed to the resolution of a number of taxonomic problems in the Myrtaceae, most notably the clarification of the generic circumscription of *Eugenia* and

*Syzygium* (Schmid 1972). With the exception of *Eugenia,* however, no detailed studies of this kind have been published for the neotropical Myrtoideae. Grifo (1992) found details of the floral vasculature, especially the nature of the supply to the ovaries and the androecium, useful in generic circumscription in *Myrcianthes.*

## Embryo and Seed Development

Given the importance of features of the mature embryo in the higher level classification of the Myrtoideae surprisingly little attention has been paid to embryo and seed development. The dearth of information in this area is acute, even in the context of our rudimentary knowledge of Myrtaceae biology in general, and may be attributable to the extreme difficulties experienced in fixation for histological studies in the family (Mauritzon, 1939; Davis, 1968; Beardsell et al. 1989, 1993a). There are no published data available for the Myrciinae, but those for the Myrtoideae were summarised and discussed by Nic Lughadha and Proença (1996). (See also under Case Studies in the Reproductive Biology of *Gomidesia*).

## Cytology

No chromosome counts are available for *Gomidesia.* The only Myrciinae so far investigated are species of the genus *Myrceugenia.* Landrum (1981) stated that n = 11 or 2n = 22 appear to be probable numbers for 8 species in this genus and Sanders et al. (1983) provided counts of n = 11 for a further 2 species. These results are consistent with reports for other genera of Myrtaceae: all major divisions of the family and a great majority of the genera are based on n = 11 (Rye, 1979). This striking stability of chromosome number was highlighted by Atchison (1947) who considered the lack of chromosome number variation in the Myrtaceae "perhaps more pronounced than in any other dicotyledonous family of its size". As a result of this lack of variation, cytological information has proven to be of relatively little systematic value within the family (Landrum, 1981). A further disincentive to the inclusion of a cytological survey within the present study was the small size of the chromosomes which are generally described as being difficult to handle (Rye, 1979) and difficult to count (Landrum, 1981).

## Pollen morphology

Pollen morphology has not proved a particularly useful taxonomic tool in the Myrtaceae to date. Erdtman (1952) described the family as stenopalynous on the basis of his investigation of about 45 species from 30 genera. These findings were confirmed by Pike (1956) who surveyed 300 species in 71 genera. Pike concluded that Myrtaceae pollen is essentially uniform, that grains of different species of the same genus are usually indistinguishable and that there appears to be no particular feature that separates pollen of the Myrtoideae from that of the Leptospermoideae.

While Pike's study still represents the most comprehensive palynological review of the family to date, its South West Pacific focus resulted in an emphasis on the genera of the Leptospermoideae, with only a few representatives of the Myrtoideae being included for comparison. Barth and Barbosa (1972) sought to offset this imbalance with their survey of the pollen of 140 species from 19 genera of Myrtoideae from Santa Catarina, southern Brazil. They considered the Myrtoideae to be stenopalynous but distinguished 8 different pollen types on the basis of 'secondary features' such as aperture morphology and exine structure. They concluded that, in general, neither species nor genera could be differentiated according to pollen grain morphology: the morphological groupings discerned cut across generic boundaries and ecological/phytogeographical patterns.

### Re-analysis of published pollen data

In fact, examination of the data published by Barth and Barbosa suggests that pollen may be more taxonomically informative than their conclusions indicated. Among the 28 species of *Eugenia* studied there were representatives from each of the eight different pollen groupings. However, a comparable number of species of *Myrcia* sampled represented only five of the pollen groupings but spanned the full range of variation found in the other genera of the Myrciinae. Thus the Myrciinae sampled did not include any species with consistently syncolpate or regularly parasyncolpate grains.

Since Barth and Barbosa listed all the material on which their observations were made, and since much of that material has been widely distributed and sometimes redetermined in the intervening years some reworking of their data was judged worthwhile. This seemed particularly appropriate in the case of the recently monographed *Myrceugenia* for which an extensive exsiccatae list was available (Landrum, 1981). Pollen morphology was not treated in this monograph but the taxa sampled by Barth and Barbosa included approximately one third of the species recognised by Landrum. Applying Landrum's nomenclature it may be stated that pollen of *Myrceugenia* is almost exclusively irregularly parasyncoplate with the exception of *M. campestris,* which consistently exhibits brevicolpate pollen with psilate tectum (three collections), and *M. myrcioides*, one collection of which was found to have brevicoplate pollen with an undulate surface while two other collections were irregularly parasyncoplate and with psilate and undulate tectum respectively. Among the remaining irregularly parasyncolpate taxa the undulate condition is prevalent (eight taxa) but species with psilate tectum also occur (four taxa).

Elsewhere in the Myrciinae the irregularly parasyncolpate condition is occasional in *Myrcia* (6/28 taxa), rare in *Calyptranthes* and *Marlierea* (1/15 and 1/6 taxa respectively) and absent in *Gomidesia*. Barth and Barbosa drew attention to the fact that the brevicolpate condition is the most common one in *Calyptranthes*. This is also true of *Myrcia* and in both these genera species with undulate pollen surfaces are much more numerous than those with psilate pollen. The brevicolpate condition is also prevalent in *Gomidesia* and *Marlierea* but psilate (or almost psilate) tectum is by far the most frequent in the species sampled in these genera. *Marlierea* was rather poorly represented in this study (as it is in the state of Santa Catarina) with only about 5% of the genus being included; thus the generalisations above must be regarded as tentative in relation to this genus. *Gomidesia*, in contrast, was rather well represented with some 15 - 20 % of currently recognised species being sampled, and as these include species from several different informal groups the conclusions drawn seem more likely to be fairly robust.

Of the eight species of *Gomidesia* included in Barth and Barbosa's study, all but one were assigned to the same morphological group. These seven species (*Gomidesia affinis* var. *catharinensis, G. anacardiaefolia, G. palustris, G. schaueriana, G. sellowiana, G. spectabilis* and *G. tijucensis*) were considered elements of Barth and Barbosa's group 1a by virtue of their simply tricolporate grains whose surfaces are psilate or nearly so. The grains are generally oblate (peroblate in *G. sellowiana* and *G. tijucensis*) and brevicolpate and the tectum is usually finely undulate (psilate in *G. spectabilis*). The eighth species, *G. fenzliana,* was assigned to group 3, characterised by grains which are tricolporate-longicolpate and tricolporate syncolpate or sometimes parasyncolporate, this variation occurring within a single species. This latter mixed pollen type was also seen in a few species of *Myrcia* (5/28) and of *Calyptranthes* (2/15) but was not reported for any species of *Marlierea* or *Myrceugenia.*

### Infraspecific variation and discrepancies

It is important to note that in Barth and Barbosa's survey the vast majority of pollen descriptions were based on a sample of pollen from a single specimen of each species. Thus any within-species variation is likely to be greatly under-represented. In the few instances where more than one sample of a species was studied or where data from other studies was available for comparison considerable within-species variation was detected. In the case of *Gomidesia sellowiana* a subsequent study (Lieu & Melhem, 1973) of material from São Paulo produced data which differed considerably from those of Barth and Barbosa for this species. Lieu and Melhem (1973) described pollen of *G. sellowiana* as oblate (rather than peroblate), with mean P/E values of 0.65 (rather than 0.46) and psilate (rather than finely undulate) tectum. The grains were considered to be a mixture of longicolpate and syncolpate. On the basis of this description the pollen sample of *G. sellowiana* studied by Lieu and Melhem would be referrable to Barth and Barbosa's pollen type 3 whereas the pollen of this species studied by Barth and Barbosa was referred by them to pollen group 1. Lieu and Melhem (1973) published data on a further two species of *Gomidesia* (*G. lindeniana* and *G. martiana*) which were reported to have oblate grains with a high P/E ratio (0.6 and 0.57 respectively) and long colpi. Thus there are ten species of *Gomidesia* for which detailed palynological data have been published. These data are summarized in Table 3.

The discordance between the findings of Lieu and Melhem and those of Barth and Barbosa is by no means confined to the genus *Gomidesia*. In fact the predominance of the brevicolpate condition among the Myrciinae as a whole inferred from Barth and Barbosa's study is contradicted by the data of Lieu and Melhem. Among the seven species of *Myrcia* studied by these latter authors no brevicolpate grains were reported. One species exhibited parasyncolpate grains and the other species were reported to have longicolpate and/or syncolpate grains. Lieu and Melhem highlighted some of the discrepancies between their data and those of Barth and Barbosa. They commented that the exine in the polar region is very delicate and therefore subject to much variation. Whether the differing results of these studies are indeed due to inherent variation in the material studied or merely to differences in preparation or interpretation cannot be definitively resolved without further study. However, circumstantial evidence provided by a third study strongly suggests that the latter explanation is the most likely; Pike (1956) treated only three species of Myrciinae in her survey: *Calyptranthes fastigiata*, *C. lucida* and *Myrceugenia myrtoides* (as *Luma myrtoides*). All three were described as being longicolpate and the latter two were illustrated. Pike's drawing of pollen of *C. lucida* in polar view clearly shows a grain with colpi as short as, if not shorter than, those shown by Barth and Barbosa (1972) in their diagrammatic representation of brevicolpate pollen in *Calyptranthes*, including *C. lucida* (Fig. 16 A & B respectively). Similarly Pike's illustration of *Myrceugenia myrtoides* (as *Luma myrtoides*) bears a strong resemblance to Barth and Barbosa's diagrammatic representation of their pollen type 4 to

Table 3. Morphological characteristics of pollen grains of *Gomidesia.*

Morphological characteristics of pollen grains of *Gomidesia*

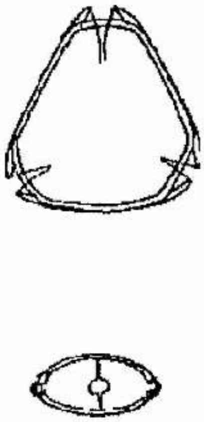
| Species | Collection | Ref. | Axes |  | P/E | Shape | Exine |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | Polar | Equatorial |  |  | exine | sexine | nexine | sculpturing |
| *G. affinis* | *Klein 1872* | 1 | 15 | 30.5 | 0.49 | oblate |  | 0.7 | 0.5 | small undulations |
| *G. anacardiaefolia* | *Reitz & Klein 6325* | 1 | 15 | 29 | 0.52 | oblate |  | 0.6 | 0.4 | small undulations |
| *G. fenzliana* | *Reitz & Klein 1516* | 1 | 12 | 24.5 | 0.49 | oblate |  | 1.1 | 0.5 | small undulations |
| *G. lindeniana* | *Brade 18750* | 2 | 12.4 | 20.7 | 0.60 | oblate | 1.4 | 0.7 | 0.7 | psilate |
| *G. martiana* | *Brade s.n. RB 139516* | 2 | 13.5 | 23.6 | 0.57 | oblate | 0.9 |  |  | psilate |
| *G. palustris* | *Reitz 4851* | 1 | 14.5 | 27 | 0.54 | oblate |  | 0.9 | 0.5 | small undulations |
| *G. schaueriana* | *Reitz 5015* | 1 | 13.5 | 27.5 | 0.49 | oblate |  | 0.7 | 0.4 | small undulations |
| *G.sellowiana* | *Brade 20827* | 2 | 12.9 | 19.8 | 0.65 | oblate | 1.4 | 0.6 | 0.7 | psilate |
| *G. sellowiana* | *Smith & Klein 11235* | 1 | 11 | 24.5 | 0.45 | peroblate |  | 0.8 | 0.5 | small undulations |
| *G. spectabilis* | *Reitz & Klein 2561* | 1 | 14 | 26.5 | 0.53 | oblate |  | 0.6 | 0.4 | psilate |
| *G. tijucensis* | *Reitz & Klein 2594* | 1 | 13 | 27 | 0.48 | peroblate |  | 0.6 | 0.5 | small unduations |

References: 1. Barth & Barbosa, 1972; 2. Lieu & Melhem, 1973. All measurements are in $\mu$m.

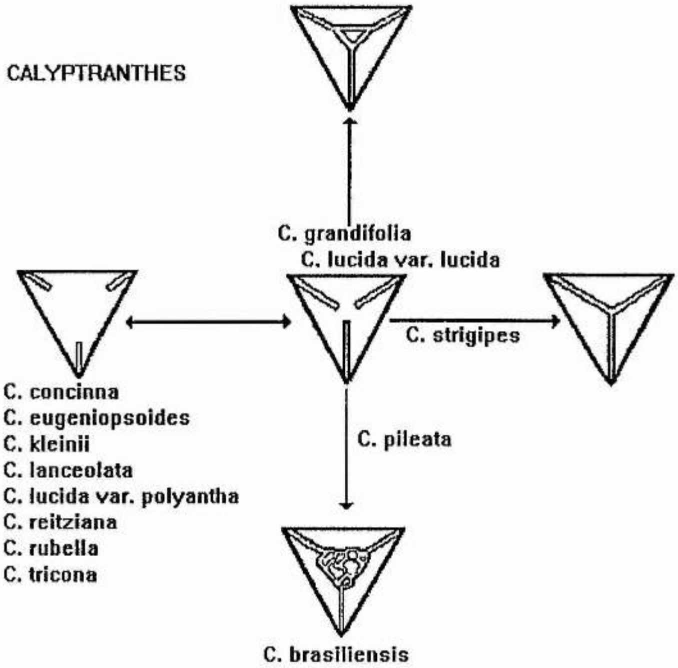
FIG. 16. Diagrammatic representations of pollen of the Myrciinae - see text for discussion.

**A** Drawing of pollen grain of *Calyptranthes lucida* in polar view (above) and equatorial view (below); **B** Diagrammatic representation of pollen types in species of *Calyptranthes*; **C** Drawing of pollen grain of *Myrceugenia mytoides* (as *Luma myrtoides)* in polar view (above) and equatorial view (below); **D** Diagrammatic representation of irregularly parasyncolpate pollen grain, the type to which most species of *Myrceugenia* studied by Barth and Barbosa (1972) were assigned. (A & C reproduced from Barth & Barbosa, 1972; B & D reproduced from Pike, 1956).

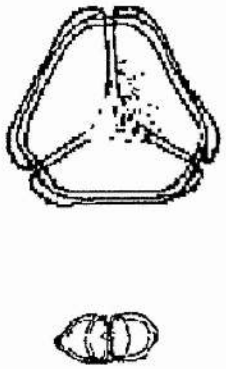
A



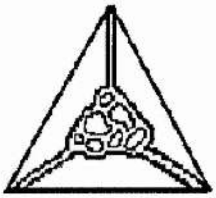
B


CALYPTRANTHES
C. grandifolia
C. lucida var. lucida
C. strigipes
C. pileata
C. concinna
C. eugeniopsoides
C. kleinii
C. lanceolata
C. lucida var. polyantha
C. reitziana
C. rubella
C. tricona
C. brasiliensis

C



D



which most of the species of *Myrceugenia* studied by them were assigned (Fig. 16 C & D respectively). These examples suggest that, in some instances at least, the differences in pollen descriptions between authors owe more to variation in application of terminology than to variation in pollen morphology. Pike (1956) commented that the longitudinal furrow (colpus) "narrows at the polar extremities and often extensions from it continue over the polar surfaces in the form of narrow grooves. In the following descriptions these grooves are regarded as parts of the colpi and are included in that term."

Given the levels of uncertainty attached to the data available it seems best to err on the side of conservatism and conclude that in the pollen of the Myrciinae a tendency toward the apocolporate condition (including brevicolpate and longicolpate) may be observed in all genera except *Myrceugenia* which tends to exhibit irregularly parasyncolpate pollen.

More recently Lourenço-Esteves et al. (1991) reported a pollen survey of restinga plants, including 12 species of *Gomidesia: G. affinis, G. anacardiaefolia, G. cambessedeana, G. crocea, G. eriocalix* (sic), *G. fenzliana, G. kunthiana, G. nitida, G. pubescens, G. riedeliana, G. schaueriana, G. spectabilis,* and a further eight Myrtaceous species from the genera *Calyptranthes*, *Eugenia* and *Myrrhinium*. This publication is a conference abstract in which no voucher specimens were cited. The fact that most of the species of *Gomidesia* listed are far from typical of *restinga* vegetation raises some doubts as to whether the material may have been incorrectly identified. In any case, the pollen of individual species is not described. The authors sum up all the Myrtaceae taxa studied as stenopalynous with pollen grains which tend to rest in polar view and are tricolporate, with a triangular amb and goniotremate. The sexine is micro-reticulate.

In total therefore the pollen of some eighteen species of *Gomidesia* has been studied and very little between-species variation has been reported. Pollen studies were not included in the research programme for the present revision as, at the outset, they seemed unlikely to yield results of use in species delimitation. The question of whether slight differences in pollen morphology may prove informative in relation to generic limits remains open, a resolution requiring more data on the pollen morphology of the other genera of the Myrciinae. One trend that may merit investigation in any such future survey is the apparent tendency of *Gomidesia* species to have pollen with a higher P/E than that of the other Myrciinae. I am indebted to C. Proença for drawing my attention to this pattern and for her suggestion that this phenomenon may be linked to buzz-pollination (Proença in litt. 1995). Another potentially interesting area of study is the association between apocolporate (including brevicolpate and longicolpate) grains and poricidal dehiscence. Johnson and Briggs (1984) considered that 'a more or less oblate syncolporate or parasyncolporate condition is fundamental in the Myrtacean line.'

Within the Myrtaceae they saw apocolporate grains as 'a secondary development' occurring in 'genera scattered through several alliances'. They emphasized that this condition was highly homoplastic within the *Chamelaucium* alliance and 'therefore irrelevant to its phylogenetic recognition'. To the reproductive biologist, however, their conclusion that more or less brevicolpate grains have arisen on more than one occasion in the evolution of the Australian Myrtaceae provides much food for thought: brevicolpate pollen is reported from a number of genera which exhibit poricidally dehiscent anthers. Although it is tempting to draw some parallels between the co-occurrence of poricidal dehiscence and brevicolpate pollen in *Gomidesia* and in these members of the *Chamelaucium* alliance the underlying explanation could well have more to do with hydration effects than with buzz-pollination.

## Phytochemistry

Although the secondary metabolites of many Myrtaceae are of considerable economic importance the phytochemistry of the Myrciinae has scarcely been studied. Nonetheless the schizogenous secretory cavities found in most unlignified tissues of the shoot can be presumed to contain the ethereal oils (variously monoterpenes, sesquiterpenes, triterpenes, other terpenoids or polyphenols) so characteristic of the family as a whole. Fragmentary phytochemical data are available for a handful of species of *Calyptranthes* and *Myrcia*. Gottlieb et al. (1972) isolated eucalyptin and β-amyrin from *Myrcia citrifolia* (Aubl.) Urb. Craveiro et al. (1979) studied the essential oils of various species of Myrtaceae from northeastern Brazil and reported 40% neral and 57% geranial from *Myrcia polyantha*. Neral and geranial are also important consitituents of the essential oils of *Calyptranthes spruceana,* though Silva et al. (1984) found that the proportions of these and other essential oils varied between samples. On the basis of their results they distinguished two chemical races within the species: one containing limonene, geranial and perillaldehyde as the main constituents of its essential oil and the other with α-pinene, β-pinene, neral and geranial as its major oil components. Landrum (1986) described a similar situation in *Pimenta* where a species may have more than one common odour. Clearly chemistry is of great potential systematic value but extensive sampling will be required before the data can be interpreted with any confidence. There appear to be no published phytochemical data for *Gomidesia*, *Marlierea* or *Myrceugenia*.

## Distribution

The Myrciinae are exclusively neotropical. *Calyptranthes* is a widespread genus which is particularly well represented in the West Indies and in Central America though it also occurs in Brazil (Amazon and SE Brazil) and in the Guayana Highlands and just reaches the Andes. *Myrcia* has a similar overall distribution pattern but its stronghold is further south, being particularly speciose in the Guayana Highlands and in Brazil south of the Amazon. *Marlierea* is also well represented in Brazil south of the Amazon and in the Guianas and just reaches Central America (1 species) and the West Indies (3 species). It does not extend to the Andes. *Myrceugenia* is a temperate to subtropical genus whose widely disjunct distribution is well documented (Landrum, 1981). There are 2 species on the Juan Fernandez Islands off Chile, 12 in central and southern Chile and adjacent Argentina and 25 in eastern South America, mostly along the eastern edge of the planalto and along the coast from Porto Alegre to Rio de Janeiro, with outlying populations extending as far north as Brasilia and central Bahia.

At generic level the Myrciinae are approximately evenly distributed but they are depauperate at specific level in the Andes (Grifo, 1992). In this respect they differ from the Myrtinae and Eugeniinae which both show high diversity in two areas, the Andes and southeastern Brazil. This latter region has long been considered a centre of diversity for the family as a whole and boasts more genera (21) than any other neotropical region.

At specific level, both in terms of species numbers and as a proportion of total Myrtaceae species, the Myrciinae are very important in the Guayana Highlands (95/206 = 46%) and in the states of Santa Catarina and Rio Grande do Sul in southern Brazil (81/190 = 43% and 48/130 = 37% respectively). South of these states diversity of Myrtaceae falls off quite sharply and Myrciinae also decline as a proportion of total Myrtaceae e.g. Myrciinae contribute 15 of a total of 61 Argentinian species (= 24.6%). Values for the area to the north of Santa Catarina (the southeastern region of Brazil) are almost certainly higher but the sheer diversity of Myrtaceae in these areas and the lack of regional treatments for the family makes it difficult to estimate total species numbers, let alone the proportion represented by the Myrciinae. Local Flora accounts and vegetation descriptions give some indication of levels of diversity however. Numbers of species of Myrciinae as a proportion of total Myrtaceae are presented in Fig. 17. On the Ilha do Cardoso in the state of São Paulo Myrtaceae are second only to Orchidaceae in terms of species numbers with 71 species representing some 7% of the total known flora (Barros, 1991). Of these 58% are Myrciinae. In cerrado areas in the interior of São Paulo Myrtaceae is the most speciose family accounting for 9.8% of the tree

FIG. 17. Numbers of species of Myrciinae as a proportion of total number of species of Myrtaceae in regional or local Floras or checklists.


20
10
0
10
20
30
70
60

flora (exceeding 2m in height) and of these 48% (14/29) are Myrciinae (Leitão Filho, 1992). In the Ecological Reserve at Macaé de Cima in the Atlantic Forest of Rio de Janeiro some 60% (28/47) of the Myrtaceae species reported belong to the Myrciinae (Barroso & Peron, 1994). Remarkably similar values have been obtained for montane areas (of *campo rupestre* and associated habitats) further north and inland: in the Serra do Cipó of Minas Gerais, Myrciinae account for 57% (26/46) of the Myrtaceae species collected (Kawasaki, 1989) and towards the northern extreme of the same mountain range in the Pico das Almas, Bahia, the corresponding value is 60% (18/30) (Nic Lughadha, 1995). Berg reported 192 species of Myrciinae out of a total of 389 Myrteae known to him from states of Minas Gerais and Goyaz (49%) and Myrciinae comprise 55% (36/65) of the Myrtaceae of the Distrito Federal (Proença, pers. comm.).

East of the cerrado domain Myrtaceae are even more important. In terms of tree species numbers, Myrtaceae are second only to Leguminosae in plots in Mata Atlantica in the north of Espirito Santo, accounting for 14.4% (31/216) of the tree species sampled (Peixoto & Gentry, 1990) while further north in the southern Bahian moist forests Myrtaceae are the most important family both in terms of individuals and species numbers representing 15 - 30% of total species in some areas (Mori et al, 1983; Carvalho & Thomas, pers. comm.). The myrtaceous flora of this region is rather poorly understood as yet so the proportion of these totals represented by the Myrciinae cannot be estimated with any degree of precision but, if it is assumed to be similar to those in adjacent areas, these wet forests seem likely to represent one of the strongholds of the Myrciinae. Further north in the caatinga and in Brazilian Amazonia Myrtaceae are rarely such an important element of the natural vegetation as they are in south and central Brazil. The relict high altitude *brejo* forests of Paraiba and Pernambuco may represent an exception to this generalisation (M. Sales, pers. comm.) but their Myrtaceae have yet to be studied critically. Myrtaceae appear occasionally among the top ten families in lowland tropical forest in Peru but in Brazilian Amazonia the family tends to be much less important e.g. 20th in importance in Amazonian forest near Manaus (Prance et al., 1976) and 26th in importance in Balée's Amazonian study area (Balée, 1994). Thus while Myrciinae may contribute a significant proportion of the species of Myrtaceae occurring in these areas (57% and 29.6% respectively in these studies) they can hardly be said to represent an important element of the vegetation.

Numbers of species of *Gomidesia* recorded per degree square are presented in Fig. 18 and distribution data is summarised in Table 4. South of the equator the areas of high diversity of *Gomidesia* mirror those for the Myrciinae as a whole. However, *Gomidesia* is under-represented north of the equator in northern South America and the Caribbean. The main

FIG. 18. Distribution and species density of *Gomidesia.* Symbols indicate number of species found within degree squares. Based on counts of numbers of species per grid square from herbarium studies, probably an underestimate of actual diversity.

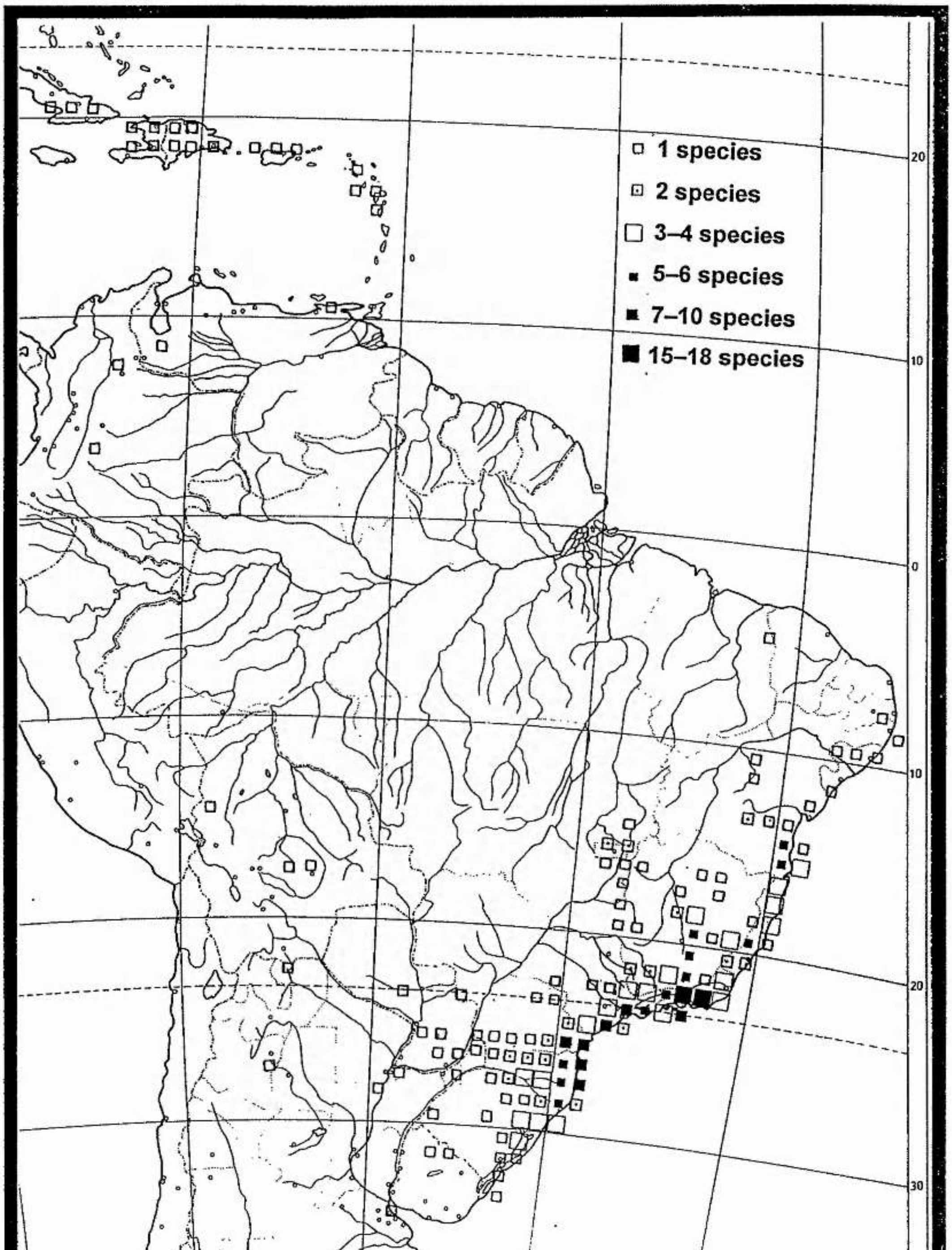

□ 1 species
⊡ 2 species
☐ 3–4 species
▪ 5–6 species
■ 7–10 species
■ 15–18 species
20
10
0
10
20
30
80
70
60
50
40

Table 4. Distribution patterns in *Gomidesia*.

+ present in state

# endemic to state

Two letter codes for Brazilian states: **AL,** Alagoas; **BA,** Bahia; **CE,** Ceará; **ES,** Espírito Santo; **DF,** Distrito Federal; **GO,** Goiás; **MG,** Minas Gerais; **PE,** Pernambuco; **PR,** Paraná; **RJ,** Rio de Janeiro; **RS,** Rio Grande do Sul; **SC,** Santa Catarina; **SE,** Sergipe; **SP,** São Paulo.

| | BRAZILIAN REGIONS AND STATES | | | | | | | | | | | | | | EXTRA-BRAZILIAN NEOTROPICS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nordeste | | | | | Centro Oeste | | Sudeste | | | | Sul | | | |
| | CE | PE | AL | SE | BA | GO | DF | MG | ES | RJ | SP | PR | SC | RS | |
| Gomidesia | | | | | | | | | | | | | | | |
| aff | | | | | | | | + | | ? | + | ? | | | |
| ana | | | | | | | | | | + | + | + | + | ? | |
| bar | | | | | | | | | | | | | | | Bolivia, Argentina |
| blan | | | | | # | | | | | | | | | | |
| bru | | | | | | | | # | | | | | | | |
| camb | | | | | | | | | | # | | | | | |
| carv | | | | | # | | | | | | | | | | |
| cath | | | | | | | | | | | | + | + | | |
| cerq | | | | | + | | | | + | | | | | | |
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| croc | | + | | | + | | | + | + | + | + | | | | |
| erio | | | | | | | | + | | + | | | | | |
| fenz | | | | | + | | | | + | + | + | + | + | | |
| flag | | | | | | | | | | | + | + | + | | |
| frey | | | | | + | | | | + | + | | | | | |
| gest | | | | | | | | | | # | | | | | |
| glaz | | | | | | | | | | # | | | | | |
| gran | | | | | | | | + | | + | + | | | | |
| graz | | | | | + | | | | | | | | | | |
| inn | | | | | | | | | | # | | | | | |
| lind | | | | | + | + | + | + | | | + | | | | Bolivia, Columbia, Venezuela and the Antilles |
| lut | | | | | | | | # | | | | | | | |
| mag | | | | | | | | | | + | | | | | |
| mart | | + | | | + | | | | + | + | + | | | | |
| mont | | | | | | | | + | | + | + | | | | |
| nit | | | | | | | | | + | + | | | | | |
| pal | | | | | | | | | | + | + | + | + | + | Argentina, Paruguay, Uruguay |
| pub | + | | | | | + | + | + | + | + | + | | | | Bolivia |
| ret | | | | | | | | + | | + | | | | | |
| ros | | | + | + | + | | | | | | | | | | |
| scha | | | | | | | | | | + | + | + | + | + | |
| sell | | | | | | | | + | | + | + | + | + | + | |
| sond | | | | | | | | | | # | | | | | |
| spec | | | | | | | | + | | + | + | + | + | | |
| spri | | | | | # | | | | | | | | | | |
| spru | | | | | | | | # | | | | | | | |
| squa | | | | | | | | | | | | # | | | |
| tij | | | | | | | | | | + | + | + | + | + | |
| vel | | | | | | | | | | # | | | | | |
| warm | | | | | | | | | | # | | | | | |
| Endemics | | | | | 3 | | | 3 | | 7 | | 1 | | | |
| Total | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 7 | 2 | 1 | 1 | 9 | 4 | 4 |
| | | | | | 1 | | | 3 | | 4 | 6 | 0 | | | |

centre of diversity for *Gomidesia* is in Rio de Janeiro state. Half of the species of the genus are represented in this area and six species are endemic to the state of Rio de Janeiro. Most of these endemic species have very narrow distributions, being known from only a single grid square, and usually from a single locality within that square (Fig. 19). *Gomidesia gestasiana*, *G. sonderiana* and *G. velutiflora* are known only from the Tijuca forest within the city of Rio de Janeiro while *G. glazioviana* and *G. warmingiana* have only been collected in Macaé, near Nova Friburgo. These are all species of the Atlantic rain forest. Similarly narrow distributions are seen for *G. brunnea* and *G. lutescens* in Minas Gerais and for *G. squamata* in Paraná, all species of high altitude forest. Individual distribution maps for these species and for most other species in the genus are presented at the end of the Systematic Treatment in a separate numbered series for ease of reference (Maps 1-37).

The other species of *Gomidesia* endemic to Rio de Janeiro have slightly broader distributions within the state. *Gomidesia innovans* (Map 18) and *G. magnifolia* (Map 21) are each known from both the Tijuca square and the Macaé square mentioned above and from one additional adjoining square. Similar patterns are seen in *G. grandifolia* (Map 16), *G. nitida* (Map 24) and *G. reticulata* (Map 27), all with distributions centred in Rio de Janeiro but extending beyond the borders of that state into neighbouring São Paulo, Minas Gerais and/or Espirito Santo. All of these species are known from 2 - 6 grid squares and the greatest distance between known populations does not exceed 500 km. Similar range sizes are seen in a number of species of the coastal plain, with distributions not centred on Rio de Janeiro e.g. (from north to south) *G. rosangelae* (Map 28), *G. grazielae* (Map 17), *G. carvalhoi* (Map 5), *G. springiana* (Map 33), *G. cerqueiria* (Map 7), *G. freyreissiana* (Map 13) and *G. flagellaris* (Map 12). These are species of the Atlantic rain forest for the most part with distributions which follow the coast and rarely extend as much as 200 km inland.

Another group comprises species more or less confined to the coastal plain but having more extensive ranges, with the greatest distance between known populations 1000 to 2000 km. In this category I include *G. crocea* (Map 9) and *G. martiana* (Map 22), with a northern limit in Pernambuco and a southern limit near the Tropic of Capricorn (north of the city of São Paulo), along with *G. spectabilis* (Map 32) and *G. tijucensis* (Map 35) whose distributions are more southern. Thus most of the species of *Gomidesia* have distributions confined to the eastern seaboard of Brazil. The remaining species which extend far inland are largely subtropical or montane. Apart from the montane narrow endemics mentioned above, *G. eriocalyx* (Map 10) and *G. montana* (Map 23) occur near the coast in Rio de Janeiro and extend inland into the mountains of Minas Gerais. *Gomidesia cordiifolia* has a curious disjunct distribution, occurring in a single grid square at each extremity of the Serra da

FIG. 19. Point endemism in *Gomidesia*.

Species of *Gomidesia* with distributions confined to a single degree square.

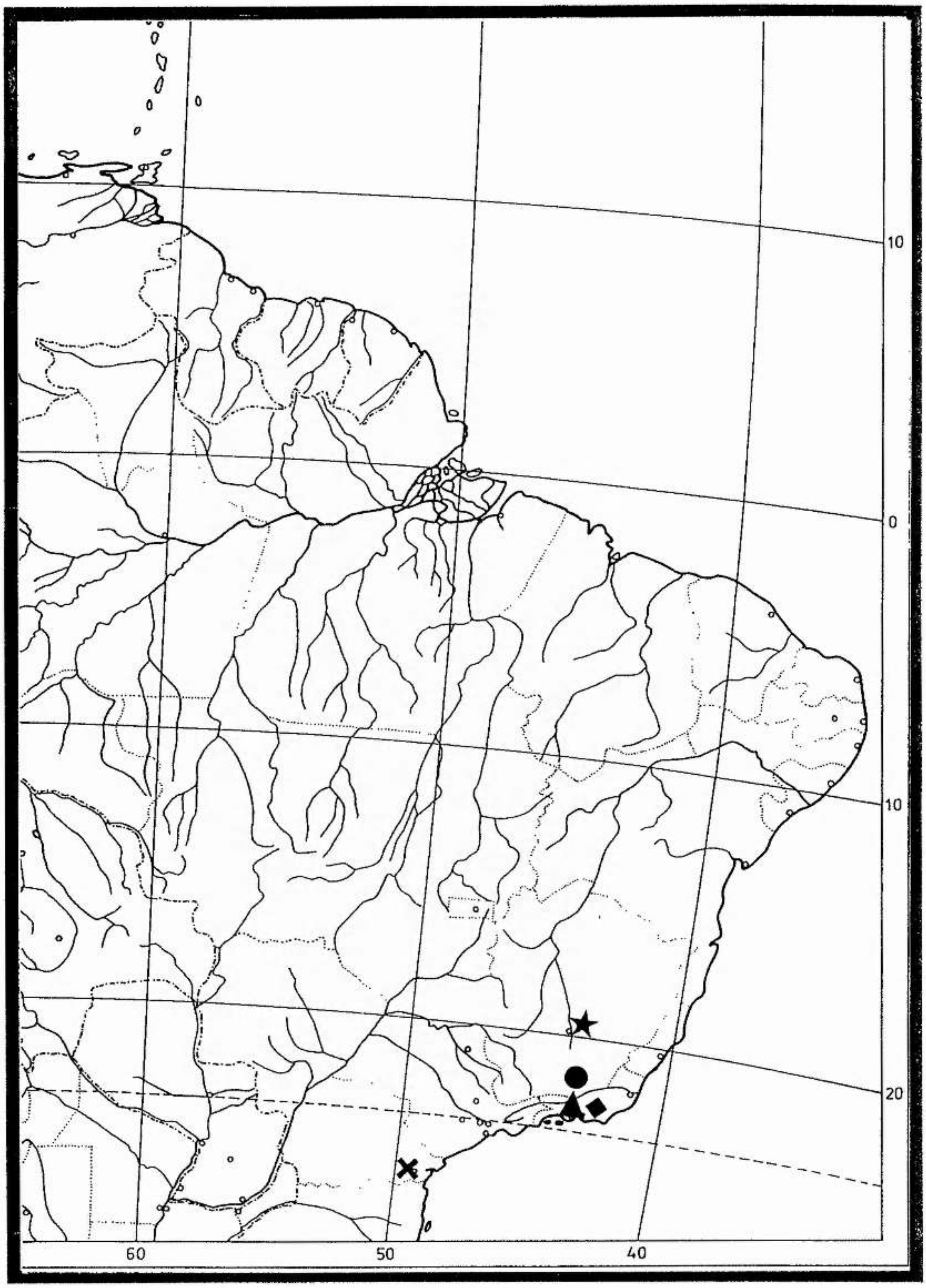
★ *G. lutescens* known only from this square

● *G. brunnea* known only from this square

▲ *G. gestasiana, G. sonderiana* and *G. velutiflora* known only from this square

◆ *G. glazioviana* and *G. warmingiana* known only from this square

✕ *G. squamata* known only from this square


10
0
10
20
60
50
40

Mantiqueira. The northern part of the distribution of G. *affinis* (Map 1) resembles that of G. *eriocalyx* (Map 10), following the Serra do Espinhaço while further south it extends into the cerrado of São Paulo and the southern limit of its range remains unclear (see under G. *affinis* in Systematic Treatment).

The subtropical species of *Gomidesia* which extend inland tend on the whole to have rather broad distributions, being recorded from at least 12 grid squares and often many more, with maximum distances between known populations ranging from 500 to 1300 km. Included in this category are *G. catharinensis* (Map 6), *G. palustris* (Map 25), *G. schaueriana* (Map 29) and *G. sellowiana* (Map 30). All but the first of these actually extend into Rio de Janeiro but are here treated as subtropical because the major part of their range is further to the south. Despite extending inland, all these species have significant representation along the southern Brazilian seaboard. Indeed, *G. schaueriana* could equally be treated with the coastal plain group since inland records for this species are rather few. *Gomidesia palustris* (Map 25) has a largely subtropical distribution extending into Uruguay, Paraguay, and Argentina and is one of only four species of *Gomidesia* with a distribution known to extend outside Brazil. The remaining three are discussed individually below.

*Gomidesia barituensis* (Map 3) is the only species of the genus with an exclusively extra-Brazilian distribution. It occurs at altitudes of 950 to 1250 m in northern Argentina and southern Bolivia (the eastern cordillera of the Andes?) where it is reported from moist subtropical forest and montane forest. Grifo (1992) described apparently similar distributions for *Myrcianthes mato* and *M. pseudomato*. She considered them to be relict species from the Oligocene-Miocene period when their ranges and a wetter climate extended further inland.

*Gomidesia pubescens* (Map 26) has a rather puzzling distribution, occurring in upland areas (600 - 1700 m) in southeastern and central Brazil with disjunct populations in central and western Bolivia and in Ceará. (NE Brazil). Again, this pattern is suggestive of a species which was formerly more widely distributed and which, with climatic warming, has suffered a contraction in its distribution and is now confined to cool upland areas or islands of relatively cool temperatures such as is found in Brasília. If the disjunct populations are disregarded, the distribution of *G. pubescens* is comparable to that of *Myrceugenia alpigena* (DC.) Landrum, though this latter species extends into southern Brazil whereas *G. pubescens* is exclusively tropical.

*Gomidesia lindeniana* (Map 19) is the most widespread species of the genus and the only one with a distribution extending beyond continental South America. The distribution is somewhat reminiscent of the pleistocene arc pattern discussed by Prado and Gibbs (1993) but *G. lindeniana* is a species of humid forest, rather than the dry seasonal forests treated by those authors. Similarly the distribution of *G. barituensis* closely resembles the Piedmont node delimited by Prado and Gibbs but, again, habitat data indicate that this species tends to occur in more upland, humid areas than do the seasonal forest species of which the pleistocene arc distribution is characteristic.

## Ecology

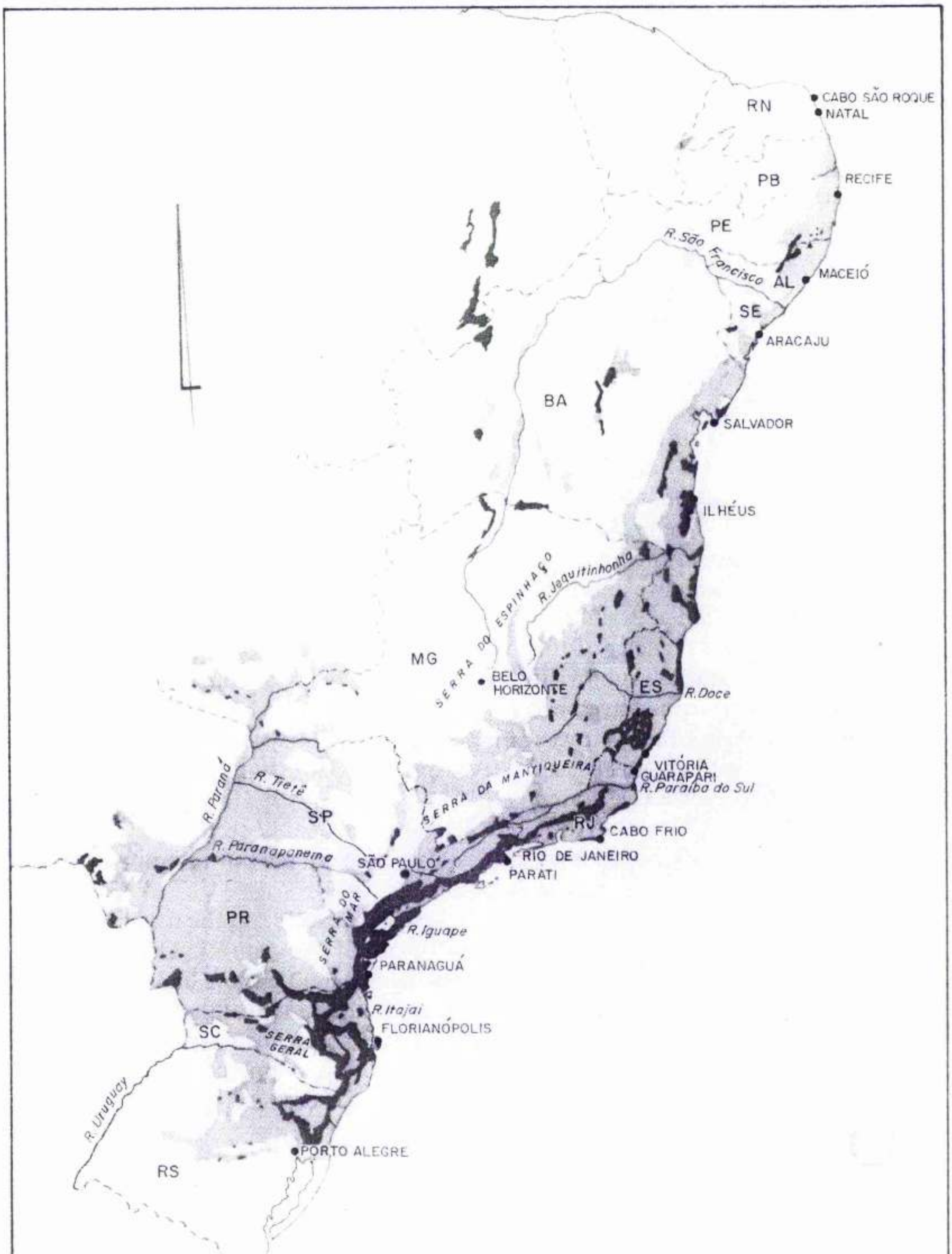
### Habitat

The fact that 90 % of the species of *Gomidesia* are confined to Brazil is largely attributable to the distribution of what survives of the Atlantic rain forest. This is the vegetation province which Martius named Dryades (after the nymph of the oak forests) and which, at the time of his sojourn in Brazil extended over 4000 km from Cape São Roque at 5° S, in the state of Rio Grande do Norte to 30° S in the state of Rio Grande do Sul (Por, 1992). This continuous belt of forest along the Atlantic shore is estimated to have been 150 - 160 km wide on average and was broken only from Cabo Frio (Rio de Janeiro) to Guarapari (Espirito Santo). The present day remnants of this forest represent at best 5% of the original area and these are now considered one of the most endangered vegetation types on earth (Mori, 1988). Fig. 20 shows the original extent of the Atlantic rain forest and the areas still under native forest (both primary and secondary) in the early 1990s. Comparison with the individual distribution maps, or with Fig. 18, indicates that the vast majority of the species of *Gomidesia* are known only from the area currently or formerly covered by forest. Thus *Gomidesia* can be said to be primarily an Atlantic rain forest genus.

This generalistion does not, however, do justice to the diversity of habitats within the Atlantic forest biome in which species of *Gomidesia* can be found. The following survey of habitat types is based on label data and to a lesser extent on my own field observations which include only a third of the species in the genus. The habitat which boasts the greatest diversity of *Gomidesia* species is the classical Atlantic rain forest, with a canopy 20-30 m high and rich in epiphytes. Species of *Gomidesia* occupy niches in all layers within this habitat, occurring as understorey shrubs or treelets (e.g. *G. cerqueiria*) as small trees of the middle layer (e.g. *G. spectabilis*) or components of the canopy (e.g. *G. tijucensis*). This forest type is often divided into altitudinal zones (with the main division occurring at 800 - 1000 m depending on the author and the area under study) and some species of *Gomidesia* are confined to the lower zone e.g. *G. tijucensis* and *G. schaueriana*.

FIG. 20. Original extension of the Atlantic rain forest and the present day remnants. Presumed original extension of the Atlantic rain forest is shaded in light grey. Surviving remnants (both primary and secondary forest, as of 1991) are shaded in dark grey.

(Reproduced from Por, 1992).


CABO SÃO ROQUE
NATAL
RN
PB
RECIFE
PE
R. São Francisco
AL
MACEIÓ
SE
ARACAJU
BA
SALVADOR
ILHÉUS
SERRA DO ESPINHAÇO
R. Jequitinhonha
MG
BELO HORIZONTE
ES
R. Doce
VITÓRIA
GUARAPARI
R. Paraíba do Sul
SERRA DA MANTIQUEIRA
R. Paraná
R. Tietê
SP
R. Paranapanema
SÃO PAULO
RJ
CABO FRIO
RIO DE JANEIRO
PARATI
SERRA DO MAR
PR
R. Iguape
PARANAGUÁ
R. Itajaí
FLORIANÓPOLIS
SC
SERRA GERAL
R. Uruguay
PORTO ALEGRE
RS
0
500 km

An even more restricted altitudinal range is shown by the species characteristic of the *restinga*. This is a general term applied to diverse vegetation types ocurring on sandy soil along the coastline, ranging from dunes to low forest communities. *Gomidesia fenzliana*, *G. martiana* and *G. palustris* often represent an important component of these communities, and most records for these species are from 0 - 50 m above sea level.

At the other altitudinal extreme are the species occurring only in the upper reaches of the Atlantic rain forest (above about 1000 m) and in the alpine-meadow-like vegetation termed *campos de altitude* (in Rio de Janeiro) or *campos rupestres* (in Minas Gerais and Bahia). These communities are mosaics of low vegetation on rocky soils, bare rocks, marshy areas (*brejos*) and gallery forest (*mata ciliar*) (See also Case Study 2).

The gallery forests form a link with the *cerrado* biome and the few species of *Gomidesia* which occur in *cerrado* are largely restricted to the gallery forest therein, rarely extending into the more open savanna vegetation of which the greater part of this biome is comprised. (See also Case Study 4.) Returning to the Atlantic forest biome, inland in the southern states of Brazil the uplands are dominated by *Araucaria* forests (*pinheiral*) interspersed with steppe/prairie open vegetation (*campos*) and though *Gomidesia* diversity is relatively low in these areas it is one of the few habitats where individual species of *Gomidesia* achieve dominance. According to Legrand and Klein (1967) *Gomidesia sellowiana* is an important pioneer species in the early stages of the development of patches of *pinheiral* and is also frequent near the margins of established copses.

Where *Gomidesia* species occur outwith the Atlantic forest biome they are either in *cerrado* (as discussed above) or in moist subtropical, submontane or montane forest (e.g. *G. barituensis*, or the Antillean populations of *G. lindeniana*). In general, it seems that most species of the genus have rather narrow ecological amplitude and tend to occur on well-drained soils (often on slopes) in areas with fairly high rainfall and relatively low temperatures. Exceptions include *G. freyreissiana* and *G. pubescens* which appear to be tolerant of flooding.

### Phenology and pollination

Most tropical species of the Myrciinae seem to follow the flowering pattern prevalent in the neotropical Myrtoideae as a whole (Nic Lughadha & Proença, 1996) generally flowering at the dry-rainy season transition (spring) and fruiting two months later, with fruits maturing during the summer months (Kawasaki, 1984). The genera *Myrceugenia* and *Gomidesia* represent notable exceptions to this generalisation. Landrum (1981) noted that there are species of *Myrceugenia* flowering in every month of the year, but that most flower during the summer and autumn from December to May, generally maturing their fruits 9 to 12 months later in the summer or fall of the following growing season. Thus in the majority of the species of this temperate and sub-tropical genus the incipient fruits overwinter as fertilised ovaries. Species of *Gomidesia* tend to flower rather later than sympatric Myrtaceae of other genera, with flowering typically commencing in January or February at the rainy-dry season transition and fruits maturing two to seven month later. In some species two flowering periods within the year have been recorded (C. Proença, pers. comm.) but data from herbarium specimens suggest that most species have a single major flowering period during the year.

One-day flowers are the norm in *Gomidesia* and in the Myrciinae, and indeed in the Myrtoideae as a whole. Little information is available on flowering strategies. *Myrcia rhodosepala* is reported as exhibiting a pulsed-bang strategy (Proença & Gibbs 1994) while the flowering pattern of *Myrcia linearifolia* was described as intermediate, starting with a few flowers, peaking and falling off abruptly. Similar pulsed bang patterns were observed in *Gomidesia fenzliana* and *G. pubescens*, while *G. cerqueiria* exhibits more or less continuous flowering and between population variation in flowering strategy is reported for *G. lindeniana* (See Case Studies in the Reproductive Biology of *Gomidesia*, hereafter Case Studies).

The existence of cryptic dioecy is postulated but unconfirmed in three species of *Calyptranthes* and four species of *Myrcia* (Nic Lughadha & Proença, 1996). No reduced styles or abortive ovaries suggestive of dioecy have been observed in any species of *Gomidesia* to date.

Breeding systems have been studied in three species of *Myrcia* to date (Proença & Gibbs, 1994). Results ranged from complete self-compatibility in *M. rhodosepala*, through *M. fallax* which shows significantly diminished fruit set after self-pollination as compared to cross-pollination but nonetheless is technically self-compatible, to *M. linearifolia* which exhibits partial self-incompatibility. In this latter species self-pollen tubes were observed to penetrate ovules and no differences were observed between self- and cross-pollinations with respect to mean number of penetrated ovules per flower at 24 or 72 hours after pollination. Young fruit abortion was concentrated in the first three weeks after anthesis, dropped off sharply in the fourth and fifth week, increased in the sixth week and dropped off again as the fruit started to swell. No ovary enlargement was detected in crossed or selfed pistils up to the time of abscission of the latter. The authors infer some kind of late acting mechanism operating against selfed flowers after ovule penetration has taken place.

Field studies carried out as part of the current study of *Gomidesia* were planned in the light of the above information. The results of this research are presented and discussed under Case

Studies. Much of this material is now in press as under the title 'Preferential Outcrossing in *Gomidesia* is maintained by a Post-zygotic Mechanism' (Nic Lughadha, 1998).

Stamens are the main visual attractant in flowers of *Gomidesia,* as in the flowers of most Myrciinae. Petals are often translucent and/or strongly reflexed after anthesis and therefore relatively inconspicuous. This trend is even more evident in *Calyptranthes* and *Marlierea* where petals may be absent or rudimentary.

All species of Myrciinae studied to date are bee-pollinated and offer pollen as a reward. Buzz-pollination has been reported for two species of *Myrcia* (Proença, 1992; Proença and Gibbs, 1994). *Myrcia rhodosepala* is buzz-pollinated by *Bombus* species and *M. dictiophylla* by *Augochloropsis* spp. *Bombus* species were also considered the principal pollinators of *Myrcia linearifolia* but no buzzing behaviour was noted during observation of this species. In the present study buzz-pollination is reported in three species of *Gomidesia* (see Case Studies).

### Dispersal

No fruit dispersal events were observed in the course of this study and a literature search revealed no published observations for *Gomidesia*. Nic Lughadha and Proença (1996) summarised the scanty data on fruit dispersal for the Myrtoideae as a whole. *Myrcia* was the only genus of the Myrciinae represented in their survey. Snow (1981) listed *Acmena, Eugenia*, *Myrcia* and *Syzygium* as forming part of the diet of specialized frugivorous birds, while fruits of *Eugenia* and *Myrcia* are also exploited by non-specialized birds. Fruits of *Myrcia torta* DC. are eaten by *Neothraups fasciata* (Emberizidae), a generalist, low-foraging tanager (Alves, 1992). Bird dispersal seems the most probable mechanism for most fruits of *Gomidesia* but field observations are required.

## Conservation

Given the massive losses of Atlantic forest habitat and the extremely narrow distribution of many species of *Gomidesia* it could be argued that more than half the species in the genus qualify as threatened or endangered. The situation is not quite as bleak as it might seem as many of the richest forest fragments are within state, federal or non-governmental nature reserves. However, more specialist fieldwork is required to assess the status of known populations and to ascertain whether some of the more restricted distribution patterns are artefacts of undercollecting. Where available, conservation information on individual species is discussed in the Systematic Treatment.

## Intergeneric relationships

Any natural system will group *Calyptranthes*, *Gomidesia*, *Marlierea* and *Myrcia* on the basis of inflorescence type, ovule and locule number and embryo type. Within this group *Calyptranthes* was the first genus to be described and is arguably the most distinct by virtue of its closed circumscissile calyx. *Marlierea* was distinguished on the basis of its closed calyx that splits open irregularly at anthesis. In these two genera the paniculate inflorescence is often more highly specialised than in the other Myrciinae as indicated by the abortion of the terminal bud at the first node, and the consequent development of a pair of panicles that are morphologically equivalent to the lower branches of the panicle in *Myrcia* (or *Gomidesia*). This tendency links *Calyptranthes* and *Marlierea*, as do some intermediate species, arbitrarily assigned to *Marlierea*, in which the 'closed (floral) bud opens irregularly, but one of the divisions is somewhat or much larger than the others, simulating a calyptra.' Similarly a number of intermediate species blur the distinction between *Marlierea* and *Myrcia*, this latter being characterised by its 'well-formed separate and usually markedly imbricate calyx lobes which are persistent and do not split irregularly in the sinuses'.

McVaugh (1968) conceded that 'if it were possible to erase from mind all knowledge of the taxonomy and nomenclature of the Myrtaceae and then to begin again, I suppose that *Calyptranthes*, *Marlierea* and *Myrcia* should be combined into one vast genus' However, he argued against such a move to 'lump' on the grounds that 'these 'genera' are after all recognizable units; they are taxa; they are assemblages of species in which correlations of evolutionary tendencies can be demonstrated'.

It is in this context that I have chosen to maintain *Gomidesia* as a genus. The combination of specialised anthers, prolonged hypanthium which is densely pubescent internally and calyx lobes erect or connivent in fruit (rather than spreading) renders *Gomidesia* at least as distinct from *Myrcia* as *Marlierea* is from *Calyptranthes* (or indeed from *Myrcia*). There can be little doubt that the ancestors of present day *Gomidesia* would be classified as *Myrcia* but this is equally true of the ancestors of *Calyptranthes* and *Marlierea*. The recognition of these genera leaves *Myrcia* paraphyletic, a situation which cannot be rectified merely by treating them all as a single genus. For even within such a large and amorphous genus (of more than 600 species) coherent groups such as these would demand recognition at some level (Subgenus? Section?) and this would render Section *Myrcia*/Subgenus *Myrcia* paraphyletic. A resolution of this dilemma must await a greatly improved understanding of *Myrcia*. Until such time as this is achieved there is little to be gained by merging these genera and much to be gained in terms of nomenclatural stability by maintaining them. It may be noted in passing that, in spite of the opprobium of the strict cladists, pragmatic approaches of this kind are still deemed the only acceptable course by many (most?) taxonomists working on intractable groups: a multi-disciplinary study (Grifo, 1992) failed to reveal any autapomorphies for *Myrcianthes* (Myrtaceae) which is nonetheless recognised as a genus; recognition of *Nectandra* (Lauraceae) leaves *Ocotea* paraphyletic (Rohwer, 1993). Most taxonomists active at a practical level in these two families would consider the merging of these genera with their respective (enormous) sister genera to be a retrograde step. Brummitt (1995) presented an impassioned case in defence of paraphyly, and a number of points made by him have yet to be refuted effectively by the advocates of strict monophyly.

## Infrageneric relationships

Overly narrow specific and generic concepts are often cited as one of the historical factors contributing to the fraught taxonomic situation in the Myrtaceae (McVaugh, 1968). Such sweeping criticism of the treatments by earlier workers would seem to imply that their successors consider themselves significantly better placed to decide what species concept should be applied within the group. Nothing could be further from the truth. While few systematists today would defend the pre-Darwinian view of species prevalent among Berg's contemporaries (e.g. 'thoughts of the creator which are real' (Agassiz 1857)), viewpoints on the numerous theoretical alternatives proposed in the intervening century and a half are many and disparate.

Recent reviews of the subject have surveyed some dozen species concepts regarded as current but have failed to reach any consenus as to which is ideal or best. It is not the intention of the present treatment to debate or review the relative merits of the diverse concepts currently in vogue. While the desirability of continuous reassessment of the tenets on which taxonomic procedure is based is obvious, for the practising systematist such discussion has become increasingly remote from reality. In practice, for the vast majority of taxa under study, the only species concept which it is feasible to apply is the morphological species concept. A modified version of the morphological species concept is expounded by

Mallet (1995). His model allows for polytypic species and the incorporation of new knowledge from genetics but is fundamentally the same concept which many (most?) practising taxonomists have long been applying, for want of a better alternative, whatever creed they may profess in theory. Crisp and Weston (1993) defended this long-established practice of drawing a distinction between theoretical concepts and operational definitions of species. They argued that species can be recognised as clusters in phenetic space because their distinctions must be due to some underlying factor such as infraspecific polymorphism (e.g. sex differentiation or ontogenetic stages), pleiotropic effects of a single gene difference (an unlikely explanation) or phylogenetic divergence (most plausible explanation and therefore the working hypothesis). To relate this operational definition of a species to a conceptual definition proves difficult. Crisp and Weston's solution was to compromise: they took the view that species are ambivalent - some appear to be monophyletic taxa but some lack autapomorphies and are metataxa (an idea which is discussed further below).

While many taxonomists agree that a morphological (phenetic) species concept is the only one that is applicable in practice, they diverge widely on the issue of how distinct the phenetic cluster should be in order to merit treatment as different species. These discrepancies reflect not only differences in attitude between systematists but also, and perhaps more importantly, differences in the nature of the groups in which they specialize. Thus systematists in Orchidaceae, Labiatae and Leguminosae may expect and require actual discontinuities in the spectrum of phenetic variation (phenetic gaps) for the recognition of species while taxonomists brave enough (or foolish enough) to work on groups such as Lauraceae or Myrtaceae may consider mere troughs in the curve of distribution of phenotypes as sufficient bases for species (or even genera!!). This difference in criteria is by no means always attributable to excessive 'splittiness' on the part of the taxonomists working on these 'difficult' groups. As Cronquist (1988) explains:

> "One cannot escape the problem simply by expanding the specific concept, because the expansion must proceed beyond the point of absurdity."

In the same work he cited the problem of *Senecio* where

> " The species that one would arrive at ... if he/she insisted on really sharp interspecific distinctions, would be so large, amorphous and internally diversified as to be completely useless."

Rohwer (1993) came to a similar conclusion in his study of *Nectandra*. Initially he had followed the previous monographer (Bernardi, 1962) in advocating the use of rather wide specific concepts. However, he came to realize that in some instances narrow concepts were inevitable in order to maintain any boundaries at all. His practice was to assign specific rank to

'.. any consistently recognisable assemblage of individuals that is separated from other such assemblages by a relative gap i.e., in practice the number of collections intermediate between related species must be far smaller than the number of collections typical for each species'.

Rohwer fully acknowledged that such a definition implies a species concept which is very dependent on thorough collecting. Some may consider this collection-dependency a serious deficiency. However, to me it seems no less acceptable and far more easily ameliorated than the dependency on inferred breeding patterns which is implicit in other species concepts currently advocated.

Another problem arising from such an approach, and one not discussed by Rohwer, is how to interpret the (not insignificant) number of collections which floor the phenetic valleys between the peaks recognised as species. Should such material be regarded as being of hybrid origin? And is hybridisation therefore a much more widespread phenomenon than has been acknowledged by monographers to date? Landrum (1981, 1986) has documented several hybrid or putatively hybrid populations in various genera of Myrtaceae. His interpretations appear to be based on implicit assumptions of allopatric or parapatric speciation with subsequent migration resulting in contact between distinct but cross-compatible species and the formation of hybrid populations. However, Grifo (1992) suggested an important role for sympatric speciation in the diversification of *Myrcianthes*. Where sympatric or parapatric speciation is significant, intermediates may be interpreted as representatives of a relictual hybrid zone, which Mallet (1995) suggested should be a common feature of ongoing sympatric or parapatric divergence.

The approach to species recognition followed in the present treatment is, of necessity, a very pragmatic one, not unlike that of Rohwer. Delimitations of species are based on phenetic troughs or, where they exist, phenetic discontinuities. The species so recognised are often, but by no means always, supported by autapomorphies. Obviously, a situation where all species recognised are diagnosable by autapomorphies would be preferable - theoretical considerations aside, this would greatly facilitate key construction. However, I do not share the viewpoint of the strict cladist to whom paraphyletic species are anathema. Within the framework of speciation processes as we understand them today it is perfectly possible to envisage situations where geographically local models of speciation will produce a paraphyletic progenitor and monophyletic derivative species (Rieseberg & Brouillet, 1994). Several authors have advocated the use of the term metataxon for groups lacking a synapomorphy, thus recognising that such groups may turn out to be monophyletic either after further investigation (discovery of hitherto unobserved apomorphies) or time (to evolve a synapomorphy), (Donoghue, 1985; Queiroz & Donoghue, 1988; Crisp & Weston, 1993). It is a relatively small step from acknowledging the existence of demonstrably paraphyletic ancestral populations or species (Donoghue & Cantino, 1988) to recognising, as many practising taxonomists do, that such taxa are far from rare. Indeed if local speciation is as common as Levin (1993) argues, then paraphyletic species are very much to be expected, particularly in groups characterized by low levels of gene flow and significant geographic differentiation.

The decision to apply this pragmatic but theoretically defensible species concept in the present revision was not reached without difficulty. Interestingly, other monographers in the neotropical Myrtaceae seem to have reached the same compromise situation via differing routes. Grifo (1992) stated that species delimitations in her monograph of *Myrcianthes* are based on phenetic concepts, supported by autapomorphies but she also commented that the quantitative nature of the boundaries between species impeded her attempts at species-level cladistic analyses. Landrum (1981, 1986), currently the most active monographer of the neotropical Myrtaceae, does not explicitly describe the species concept he employs. Nonetheless a careful reading of the discussion which follows critical species in his treatments indicates that by no means all the species recognised are diagnosable by autapomorphies and that, on occasion, species clearly considered to be paraphyletic are accepted.

The application of a rather conservative morphological species approach resulted in the recognition of 40 species in *Gomidesia.* Table 5 illustrates how these species correlate with those recognised by Berg (1857-59) and how these were treated by Kiaerskou (1893) and Legrand (1959) in the intervening years. Also shown in this table are infra-generic groupings proposed by Berg and Legrand. None of these are nomenclaturally valid but since they represent an important insight into the authors' views of relationships between the species the alternative schemes are discussed in turn below.

Berg (1855) divided *Gomidesia* into five unnamed sections. Subsequently (1857) he named the first section *Magnifoliae*, but since this section contains the type species of the genus, *G. spectabilis*, it should correctly be named Sect. *Gomidesia.* The other sections remained unnamed. Their distinguishing characters as listed by Berg are outlined below and the species included in each group are shown in Table 5. For convenience these groups are hereafter termed 'Berg's first section' and so on.

**First Section** (Magnifoliae). Branchlets with transverse interpetiolar ridges, very often/nearly always provided with excurrent, fleshy, stipular setae. Leaves large. Sepals broad, truncate or obtuse. Anthers linear or oblong, dehiscent on either side by means by means of sigmoid fissures, margins not at all flattened/outspread.

**Second section.** Branchlets with transverse interpetiolar ridges, sometimes/occasionally provided with excurrent, fleshy, stipular setae. Leaves larger, sepals truncate or obtuse. Anthers oval, compressed, subquadrilocular, locules dehiscent by a spiral fissure extrorse at the apex and introse at the base, margins flattened/outspread.

**Third Section.** Branchlets lacking interpetiolar ridges. Leaves smaller. Sepals obtuse. Anthers oval, compressed, subquadrilocular, locules dehiscent by a spiral fissure extrorse at the apex and introse at the base, margins flattened/outspread.

**Fourth Section.** Branchlets lacking interpetiolar ridges. Leaves smaller. Sepals obtuse. Anthers oval, compressed, subquadrilocular, locules dehiscent by a spiral fissure extrorse at the apex and introse at the base, margins flattened/outspread.

**Fifth Section.** Branchlets lacking interpetiolar ridges. Leaves with cordate base. Sepals acute. Anthers oval, compressed, subquadrilocular, locules dehiscent by a spiral fissure extrorse at the apex and introse at the base, margins flattened/outspread.

Kiaerskou's (1893) major subdivisions of his subgenus *Gomidesia* were based on the presence or absence of interpetiolar ridges. Thus his informal group A is equivalent to Berg's First and Second Section. Within group A further subdivisions were made purely on the basis of indumentum type. Within group B (those lacking interpetiolar ridges and therefore equivalent to Berg's Third, Fourth and Fifth Section) further subdivisions were made on the basis of sepal shape, and leaf size and shape. Many species treated by Berg were not listed by Kiaerskou, presumably because he did not receive material of these taxa. It is not clear which, if any of the groups outlined below the level of subgenus he considered to be natural entities or whether the subdivisions were provided merely as an aid to identification. I consider the latter most likely to be the case.

**A.** Branchlets with a thickened transverse line between the petioles, often bearing fleshy stipular setae at either end.

**I** Indumentum, where present, minutely furfuraceous
*M. innovans, M. spectabilis, M. vittoriana*

**II** Indumentum, where present, shortly sericeous
*M. nitida, M. springiana*

**III** Indumentum, where present, adressed pilose or adpressed pubescent
*M. brasiliensis, M. freyreissiana, M. tijucensis, M. warmingiana*

**IV** Indumentum, where present, villose or pilose-villose, flowers often sericeous villose
*M. anacardiifolia, M. candolleana, M. crocea, M. dolichopetala*
*M. estrellensis, M. hookeriana, M. magnifolia, M. reticulata*
*M. ticuensis*

**B.** Branchlets without a thickened transversal interpetiolar line

**I** Leaf base not cordate

(a) Sepals obtuse: *M. hartwegiana, M. ilheosensis*

(b) Sepals acute or acuminate

1. Larger leaves: *M. minensis, M. sintenisii*
2. Smaller leaves: *M. eriocalyx, M. glazioviana,*
   *M. kunthiana, M. ouropretoensis*

**II** Leaf base cordate

*M. alpina, M. schenckiana, M. sessilifolia*

Legrand's (1959) sections and subsections are based entirely on anther characters, though the larger subsections are further subdivided into informal groupings on the basis of a combination of other floral features and vegetative features. Legrand's sectional and subsectional placements of the species recognised by Berg are indicated in Table 5 by means of abbreviations of the sectional and subsectional epithets. In total four new Sections were proposed by Legrand (1959) but three were invalidated by Legrand's failure to indicate the type of each name ( as required by Art. 37.1 of the International Code for Botanical Nomenclature, Greuter et al. 1994). Only the monotypic Section *Tetraspora* based on *Gomidesia cerqueiria* is validly published (Art. 37.2). The distinguishing features of the other sections and subsections are summarised below.

**Section *Elytroteca*.** Anthers with thecal margins incurved, closed or sometimes a little open laterally. The most apparent dehiscence occurs towards the apex by means of lateral-extrorse or completely extrorse fissures.

**Subsection *Subaequales*.** Anthers oblong, with pollen sacs at scarcely differing levels and with apical or lateral extrorse dehiscence or with foraminal extrorse dehiscence when the vertical displacement of the thecae is more marked.

**Subsection *Oppositae*.** Anthers with pollen sacs at markedly different levels, from almost to completely superposed

**Section *Platyteca*.** Anthers with thecal margins open (almost always showing the interior of the locules) and differentiated in a more or less auriculate fashion at diagonally opposite extremes. The pollen sacs may be diagonally opposite or completely superposed

**Subsection *Auriculatae*.** Pollen sacs obliquely opposite to completely superposed (with residual septum oblique to almost transverse); thecal margins broadened towards opposite extremes, with lateral extrorse dehiscence.

**Subsection *Collaterales*.** Vertical displacement of the thecae slight, margins scarcely obliquely broadened, never auriculate.

**Section *Micranthera*.** Flowers small. Anthers minute, with thecal margins differentiated as in Subsection Auriculatae, but attenuate. Lateral valvate dehiscence.

Table 5. Berg's species of *Gomidesia* and their placement by subsequent authors. Sheet one of three, continued overleaf. Alternate columns in bold for ease of examination, except in the final column, where the names of taxa appearing in bold are those which have remained unchanged since Berg's treatment.

| **BERG (1855-59)** | KIAERSKOU (1893) | **LEGRAND (1959)** | | | NIC LUGHADHA (1997) |
|---|---|---|---|---|---|
| *Gomidesia* | *Myrcia* subgenus *Gomidesia* | *Gomidesia* | Sect. | Sub sect. | *Gomidesia* |
| **First Section** | | | | | |
| **1. G. chamissoeana** | M. nitida | **= G. nitida** | plat | aur | = G. nitida |
| **2. G. martiana** | M. vittoriana | **G. martiana** | ely | sub | **G. martiana** |
| **3. G. spectabilis** | M. spectabilis | **G. spectabilis** | ely | sub | **G. spectabilis** |
| **4. G. ? browniana** | not treated | **= G. spectabilis** | ely | sub | = G. spectabilis |
| **4b. G. magnifolia** | M. magnifolia | **G. magnifolia** | ely | sub | **G. magnifolia** |
| **5. G. amplexicaulis** | not treated | **= G. crocea** | ely | sub | = G. ? crocea |
| **5b. G. langsdorffii** | M. crocea | **= G. crocea** | ely | sub | = G. crocea |
| **6. G. springiana** | M. springiana | **G. springiana** | ely | sub | **G. ? springiana** |
| **7. G. blanchetiana** | M. crocea var. blanchetiana | **G. blanchetiana** | ely | sub | **G. blanchetiana** |
| **7b. G. riedeliana** | M. estrellensis | **G. riedeliana** | ely | sub | = G. anacardiifolia |
| **8. G. poeppigiana** | not treated | **incertae sedis** | | | incertae sedis |
| **8b G. sonderiana** | M. dolichopetala | **incertae sedis** | | | **G. sonderiana** |
| **9. G. anacardiaefolia** | M. anacardiaefolia | **G. anacardiifolia** | ely | sub | **G. anacardiifolia** |
| **10. G. reticulata** | M. reticulata | **G. reticulata** | ely | sub | **G. reticulata** |
| **11. G. linkiana** | not treated | **G. linkiana** | ely | sub | = G. cordiifolia |
| **12. G. pohliana** | not treated | **= G. affinis var. pohliana** | ely | sub | = G. affinis |
| **13. G. jacquiniana** | M. crocea | **= G. crocea** | ely | sub | = G. crocea |
| **13b. G. crocea** | ? M. crocea | **G. crocea** | ely | sub | **G. crocea** |

Table 5 continues overleaf > > >

plat = Section *Platyteca*
aur = Subsection *Auriculatae*
ely = Section *Elytroteca*
sub = Subsection *Subaequales*

Table 5. Berg's species of *Gomidesia* and their placement by subsequent authors.

Sheet two of three, continued overleaf.

Continued from previous page.

| **BERG**<br>**(1855-59)** | KIAERSKOU<br>(1893) | **LEGRAND**<br>**(1959)** | | | NIC LUGHADHA<br>(1997) |
|---|---|---|---|---|---|
| *Gomidesia* | *Myrcia*<br>subgenus *Gomidesia* | *Gomidesia* | Sect. | Sub sect. | *Gomidesia* |
| **Second Section** | | | | | |
| **14. G. candolleana** | M. candolleana | **= G. affinis var. pohliana** | ely | sub | = G. affinis |
| **15. G. hebepetala** | not treated | **G. hebepetala** | ely | sub | = G. affinis |
| **16. G. hookeriana** | M. hookeriana | **= G. affinis var. affinis** | ely | sub | = G. affinis |
| **17. G. schaueriana** | M. brasiliensis | **G. schaueriana** | platy | coll | **G. schaueriana** |
| **18. G. freyreissiana** | M. freyreissiana | **G. freyreissiana** | platy | coll | **G. freyreissiana** |
| **19. G. willdenowiana** | not treated | **incertae sedis** | | | incertae sedis |
| **Third Section** | | | | | |
| **20. G. fenzliana** | M. ilheosensis | **G. fenzliana** | platy | coll | **G. fenzliana** |
| **21. G. casaretteana** | not treated | **= G. pubescens var. casaretteana** | platy | aur | = G. pubescens |
| **22. G. mikaniana** | not treated | **= G. pubescens var. pubescens** | platy | aur | = G. pubescens |
| **23. G. sprengeliana** | not treated | **G. sprengeliana** | platy | aur | = G. sellowiana |
| **24. G. sellowiana** | M. hartwegiana | **G. sellowiana** | platy | aur | **G. sellowiana** |
| **25. G. hartwegiana** | M. hartwegiana | **G. hartwegiana** | platy | aur | = G. sellowiana |
| **26. G. gardneriana** | not treated | **omitted** | | | incertae sedis |
| **27. G. banisteriaefolia** | not treated | **G. banisteriaefolia** | platy | aur | = G. palustris |

Table 5 continues overleaf > > >

plat = Section *Platyteca*

aur = Subsection *Auriculatae*

coll - Subsection *Collaterales*

ely = Section *Elytroteca*

sub = Subsection *Subaequales*

Table 5. Berg's species of *Gomidesia* and their placement by subsequent authors. Sheet three of three, continued from previous page.

Continued from previous page.

| **BERG** **(1855-59)** | KIAERSKOU (1893) | **LEGRAND** **(1959)** | | | NIC LUGHADHA (1997) |
|---|---|---|---|---|---|
| *Gomidesia* | *Myrcia* subgenus *Gomidesia* | *Gomidesia* | Sect. | Sub sect. | *Gomidesia* |
| **Fourth Section** | | | | | |
| **28. G. kunthiana** | M. kunthiana | **G. kunthiana** | platy | aur | = G. montana |
| **29. G. clausseniana** | M. ouropretoensis | **29. G. clausseniana** | platy | aur | = G. montana |
| **29b G. klotzschiana** | not treated | **= ? G. clausseniana** | platy | aur | = G. ? montana |
| **30. G. cambessedeana** | not treated | **incertae sedis** | | | **G. cambessedeana** |
| **31. G. miqueliana** | M. eriocalyx var. miqueliana | **= G. eriocalyx var. eriocalyx** | ely | opp | = G. eriocalyx |
| **32. G. eriocalyx** | M. eriocalyx | **17. G. eriocalyx** | ely | opp | **G. eriocalyx** |
| **33. G. beyrichiana** | M. eriocalyx var. beyrichiana | **= 17. G. eriocalyx** | ely | opp | = G. eriocalyx |
| **34. G. widgreniana** | M. minensis | **= 24. G. pubescens var. widgreniana** | platy | aur | = G. pubescens |
| **34b. G. haenkeana** | not treated | **= ? G. pubescens var. casaretteana** | platy | aur | = G. pubescens |
| **35. G. raddiana** | not treated | **= G. pubescens var. pubescens** | platy | aur | = G. pubescens |
| **36. G. hilariana** | M. eriocalyx var. miqueliana | **= G. elliptica** | ely | opp | = G. eriocalyx |
| **Fifth Section** | | | | | |
| **37. G. aubletiana** | not treated | **= G. aubletiana** | ely | opp | = G. pubescens |
| **37b G. spruceana** | not treated | **= G. gaudichaudiana** | ely | opp | **G. spruceana** |
| **37c. G. regeliana** | M. sessilifolia | **= G. gaudichaudiana** | ely | opp | = G. eriocalyx |
| **38. G. gaudichaudiana** | M. alpina | **G. gaudichaudiana** | ely | opp | = G. eriocalyx |

plat = Section *Platyteca*

aur = Subsection *Auriculatae*

coll - Subsection *Collaterales*

ely = Section *Elytroteca*

opp = Subsection *Oppositae*

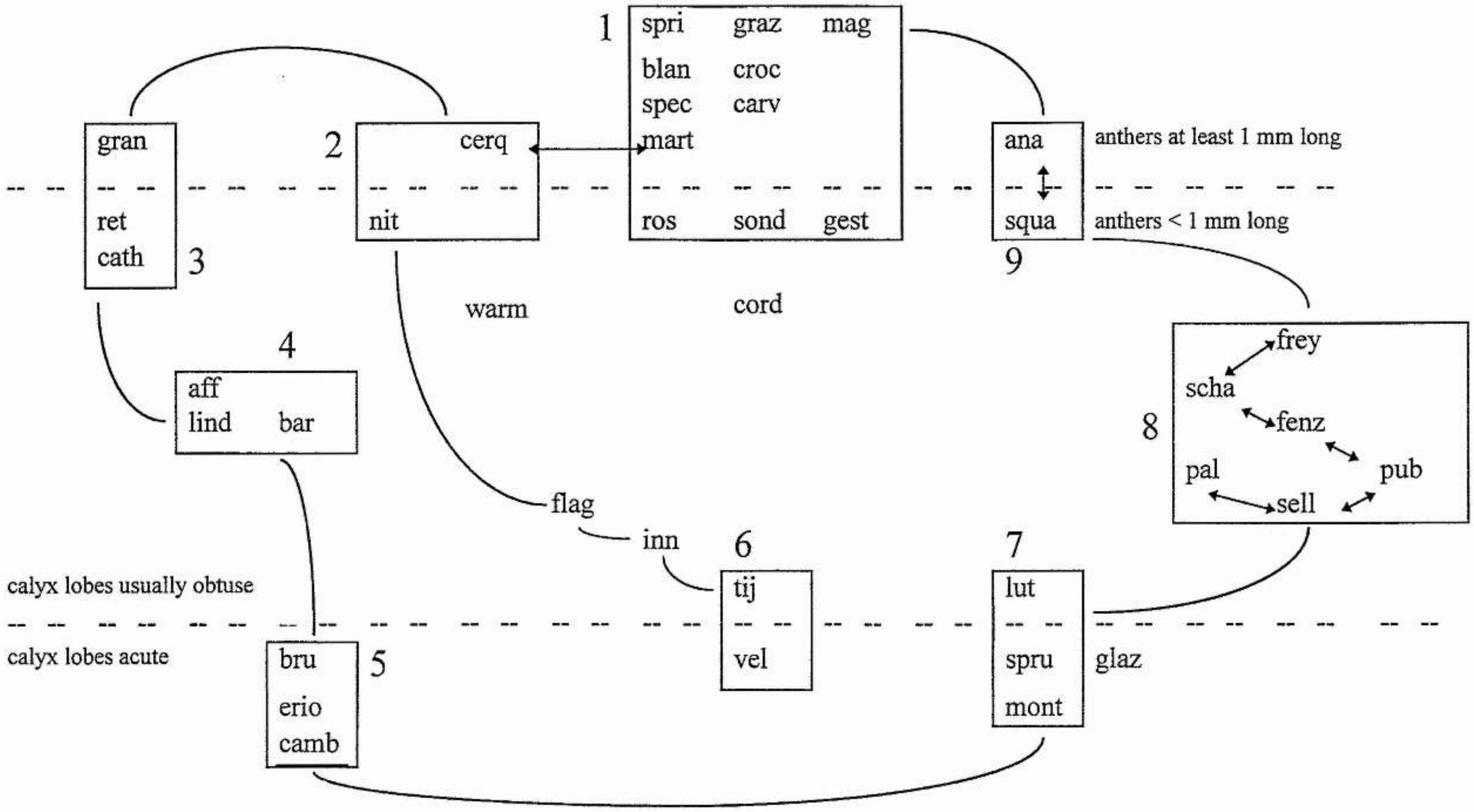
The degree of congruence between Legrand's classification and Berg's is striking (Table 5). All but one of the species which Berg included in his first section are referred by Legrand to Section *Elytroteca* Subsection *Subaequales*. The single exception is Berg's *G. chamissoeana* which is referred by Legrand to the synonymy of *G. nitida* and placed in Section *Platyteca* Subsection *Auriculatae*. As defined by Legrand this subsection embraces all but one of Berg's third section (the exception being *G. fenzliana*) and most of Berg's fourth section. The remainder of Berg's fourth section (four species all treated as synonyms of *G. eriocalyx* in the present treatment) and all of Berg's fifth section are placed in Legrand's Section *Elytroteca* Subsection *Oppositae*. Finally Legrand placed two of the species from Berg's second section along with *G. fenzliana* (from Berg's third section) in his Section *Platyteca* Subsection *Collaterales*. A further two species unknown to Berg form the basis of Legrand's Section *Micranthera*.

The degree of congruence appears even more marked when Berg's system and Legrand's are compared using the species concepts employed in the present revision. For example Berg's first section differs from Legrand's Section *Elytroteca* Subsection *Subaequales* only by the inclusion of *G. nitida* and the exclusion of three taxa now considered synonyms of *G. affinis*, though other elements of *G. affinis* were included in this section by Berg. Berg's second section differs from Legrand's Section *Platyteca* Subsection *Collaterales* only by the inclusion of *G. affinis* and the exclusion of *G. fenzliana*. Berg's fifth section differs from Legrand's Section Elytroteca Subsection Oppositate only by the exclusion of *G. eriocalyx* as circumscribed in the present treatment. Thus, changes in the placement of only four species (*G. affinis*, *G. eriocalyx*, *G. fenzliana* and *G. nitida)* are sufficient to reconcile the differences between Berg's groupings and those of Legrand.

In the present revision no formal categories between generic and specific rank are proposed. A putative grouping of the species as currently understood is presented in Fig. 21. The groups outlined here are based on overall similarity of the constituent species and on the occurrence of intermediate forms between some species. I have not attempted to include every species in one of the groups since the placement of some species is as yet uncertain.

Group 1 comprises the type species, *Gomidesia spectabilis,* along with a number of large-leaved species of the Atlantic rain forest and three new species from northeastern Brazil. These species have rather long anthers in which the thecal halves usually retain curvature and remain connivent after anthesis. Where mature fruit are known the hypocotyl is usually densely sericeous, though the indumentum may be confined to the inner surface (as in *G. magnifolia*) or to a small area near the point of insertion of the hypocotyl on the cotyledons

FIG. 21. Putative groupings of species in *Gomidesia.* For explanation and discussion, see text.

1
spri
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vel
7
lut
spru
mont
glaz
8
frey
scha
fenz
pub
pal
sell
9
ana
squa
warm
cord
flag
inn
anthers at least 1 mm long
anthers < 1 mm long
calyx lobes usually obtuse
calyx lobes acute

(as in *G. martiana* and *G. rosangelae*). As delimited here Group 1 is equivalent to the intersection of Berg's First Section and Legrand's Section *Elytroteca* Subsection *Subauriculatae.* I concur with Legrand in excluding *G. nitida* from this grouping. The species limits in this group are reasonably well-defined, with few intermediate specimens not readily determined to species.

One such intermediate links this group to *Gomidesia cerqueiria* which has such distinctive anthers that it was originally described in its own, monotypic genus. *Gomidesia cerqueiria* is very close to *G. nitida* (Group 2). Both species have a short, stout much compressed peduncle and leaves with rather obscure venation in which the secondary laterals more or less equal the lateral veins in prominence. These characters are also shared by a probable third species (as yet undescribed) known only from two fruiting specimens from Rio de Janeiro. The long, closed, pseudo-poricidal anthers of *G. cerqueiria* are unmatched elsewhere in the genus but *G. nitida* has a less unusual anther morphology which closely resembles that seen in *G. catharinensis*, *G. flagellaris*, *G. grandifolia*, and *G. reticulata*. Of these, only *G. flagellaris* can be said to bear a vegetative resemblance to *G. nitida*, having a similar venation pattern and indumentum type. However, since *G. flagellaris* also appears to have affinities with other species groups its correct placement is still in doubt.

As well as resembling each other (and *G. nitida*) in anther morphology *Gomidesia catharinensis, G. grandifolia* and *G. reticulata* (Group 3) share rather large (for the genus) flowers, and leaves with deeply impressed venation producing a distinctive bullate leaf surface. Strikingly similar leaves are seen in *G. affinis* (so much so that *G. catharinensis* was originally described as a variety of this variable species) but *G. affinis* has quite a different anther type which it shares with *G. lindeniana* and which resembles that seen in *G. tijucensis*, *G. velutiflora*, *G. sellowiana.* These anthers are among the smallest in the genus and have thecal halves which generally lose curvature on dehiscence but are still held parallel to each other (or at most slightly divergent). *Gomidesia affinis* is here placed with *G. lindeniana* which it resembles in anther morphology and in leaf characters and fruit shape, and *G. barituensis* is included in this group on the basis of vegetative and fruit characters. The anthers of this latter species are as yet poorly understood and require further study.

*Gomidesia brunnea* is vegetatively very close to *G. lindeniana* but its acute calyx lobes and deeply emarginate anthers suggest that it is best placed with *G. cambessedeana* and *G. eriocalyx.* (Group 5). These species exhibit highly reduced inflorescences and *G. eriocalyx* shows a tendency to flexuous peduncles while the peduncle of *G. cambessedeana* is extremely flexuous and, probably, pendulous. Flexuous peduncles are also characteristic of *G. flagellaris* (unplaced in Fig. 21). Also unplaced nearby is *G. innovans* which resembles *G.*

*flagellaris* in anther morphology but also shows a striking affinity with *G. tijucensis*, with which it shares strongly bicolorous, glabrescent leaves and reduced inflorescence with bicolorous buds. These similarities seem likely to be attributable to parallel evolution since anther morphology indicates that *G. tijucensis* is only distantly related to *G. innovans* and has closer affinities with *G. velutiflora* with which is grouped in Fig. 21 (Group 6). These are tall trees of the Atlantic rain forest with anthers which are among the smallest in the genus and as broad or broader than long after dehiscence.

The species in Group 7 share a rather open anther type (close to that seen in *G. pubescens*) and coriaceous leaves with (often) raised venation on the adaxial surface. *G. spruceana* and *G. montana* share acute calyx lobes while *G. lutescens* and *G. spruceana* resemble each other in their matted indumentum which is also seen in *G. glazioviana*. I have seen insufficient material of *G. glazioviana* to allow its placement with any degree of confidence. The species in this group are all montane.

Group 8 includes a number of taxa which have proved problematic with respect to species delimitation. Though intermediate specimens are troublesome when attempting to establish species boundaries they are of great utility in indicating probable relationships. Species linked by intermediate specimens are connected by doubleheaded arrows on Fig. 21. All the members of this rather tightly knit group have rather small anthers with thecal halves losing curvature on dehiscence, and held parallel or divergent with margins recurved, so that in lateral view the pollen is usually exposed along the whole length of the anther. Species in this group tend to have rather small, relatively broad leaves, often with obtuse or rounded apices. As here delimited Group 7 is equivalent to Berg's Second and Third Sections if *G. affinis* (treated by Berg as three distinct species) is excluded from the Second Section. *Gomidesia fenzliana*, *G. freyreissiana* and *G. schaueriana* are unusual in the genus in having ovaries which are regularly 3–5-locular. This character is also seen in *G. anacardiifolia* (Group 9) though this species is rather variable as currently delimited and requires further study. Some specimens of *G. anacardiifolia* have anthers resembling those of members of Group 1 in that they have distinct connective stubs and long, closed thecae.

There remain two little known species of *Gomidesia* whose placement within Fig. 21 is as yet unclear. With its large leaves, marked inter-petiolar ridges and fairly long, closed anthers *Gomidesia cordiifolia* is reminiscent of a number of species in Group 1. However because of the glabrous hypocotyl and the rather small fruit I am reluctant to suggest a definitive placement for this species. *Gomidesia warmingiana* resembles *G. cerqueiria* in venation pattern and in having ridged fruit but the acute calyx lobes and unusual fruit shape set it apart from the rather narrowly circumscribed Group 2.

## Systematic Treatment

**Gomidesia** O.Berg, Linnaea **27:** 6. 1855. Type. *Gomidesia spectabilis* (DC.) O.Berg.
*Cerqueiria* O.Berg, Linnaea **27:** 5. 1855. Type. *Cerqueiria sellowiana* O.Berg.
*Myrcia* subgen. *Gomidesia* Kiaersk., Enum. Myrt. bras. 100. 1893.

*Trees* or *shrubs* with opposite branches; foliage, flowers, fruits and often branchlets more or less densely beset with resinous glands and/or brownish indumentum. Leaves opposite or rarely subopposite, simple, entire, pinnately veined, midvein usually prominent on abaxial leaf surface, principal lateral veins usually united distally into a well-defined marginal vein extending nearly the length of the blade, pellucid dotted but not aromatic, usually with a moderately dense to dense indumentum on the abaxial surface. Flowers borne on axillary branches in bracteate inflorescences with opposite branching, these arranged in opposite pairs in the axils of distal foliage nodes forming conflorescences of 2–6(–8) inflorescences (uniflorescences). Uniflorescence a panicle, complex thyrsoid, metabotryoid, triad or monad. *Flowers* regular, perfect; hypanthium ('calyx tube' of some authors) adnate to ovary and prolonged beyond it so that stamens, petals and calyx lobes appear to arise from distal margin of a small tube surrounding the summit of the ovary; calyx lobes 5, distinct and imbricate; petals 5, densely pubescent abaxially, glabrous adaxially, strongly reflexed at anthesis; stamens 'indefinitely many' c. 50–175(–200), arising at margin of elongate tubular hypanthium (summit of ovary and surrounding staminal ring forming so-called floral disk), filaments filiform and distinct, of constant diameter or tapering distally to the point of insertion on the connective, connective equalling the pollen sacs in length or exceeding them and exposed below their point of insertion forming a sterile connective stub, anthers (0.3–)0.5–1.3(–1.5) mm long, pollen sacs four per anther, arranged in two pairs with the ventral sac of each pair more or less overtopping the dorsal sac, pollen sacs merging on dehiscence due to partial breakdown of septum, residual septum usually persistent, vertical, oblique or transverse, often obscured by the connivent thecal arcs, thecal arcs retaining or losing curvature on dehiscence but never reversing curvature so that the interior of the sac is exposed as a convex surface; ovary inferior or, rarely, semi-inferior (*G. martiana*), 2(–5)-locular with placentae affixed to central dissepiment or central axis near base, ovules 2 per locule, style simple, more or less equalling or slightly exceeding stamens in length, stigma small, punctiform or minutely capitate, simple. *Fruit* a fleshy to semi-dry berry with one or more seeds, globose or, rarely, pyriform, or ovoid or deeply sulcate, crowned by the connivent, erect or, rarely, spreading calyx lobes or by a ring formed by the free part of the hypanthium, the calyx lobes having fallen; embryo myrcioid, green in fresh material, with cotyledons foliaceous, crumpled and folded (contortuplicate), encircled by elongate, glabrous or more or less densely sericeous hypocotyl.

## Synoptical Key to the Species

This key has been prepared according to the methodology recommended by Leenhouts (1966). Each numbered entry outlines the distribution of the states of a single character. A synoptic key has the advantage of allowing the user to start with any number and choose the characters which are most evident in the material available for identification. However, since the sequence is arranged roughly in order of difficulty, with the characters which can easily be assessed from most material appearing before those for which a microscope and/or more expertise is required, the user is strongly advised to work from the beginnning.

The species are represented by the first three or four letters of the specific epithet - for explanation see the numerical list of accepted taxa. Species mentioned in more than one lead appear in italics. Where the character states are unknown for a particular species the abbreviated epithet appears in square brackets in each of the leads for that character. Where there is a marked difference between the frequency ratio of the character states, only the lead for the less frequent character state is printed in full. The alternative character state seen in most species is then described in parentheses.

### 1. Leaf ratio

a. less than 3 times as long as wide: *aff*-ana-bar-blan-bru-*carv*-cath-cord-*croc*-erio-*flag*-fenz-frey-*gest*-glaz-graz-*gran-inn-lind*-mag-*mart-mont-pal*-pub-ros-scha-sell-*sond-spri*-spru-squa-*tij-vel-warm*

b. at least 3 times as long as wide: *aff*-camb-*carv*-cerq-*croc-flag-gest-gran-inn-lind-mart-mont*-nit-*pal*-ret-*sond*-spect-*spri-tij-vel-warm*

### 2. Leaf length (measured from leaves subtending lowest uniflorescence).

a. up to 119 mm long: aff-*ana*-bar-bru-camb-*carv-cath-cerq-croc*-erio-fenz-*flag*-frey-*gest*-glaz-inn-*lind-mart*-mont-pal-pub-*ret*-ros-scha-sell-*sond-spri*-spru-squa-tij-*vel*-warm

b. at least 120 mm long: *ana*-blan-*carv-cath-cerq*-cord-*croc-flag-gest*-gran-graz-*lind*-mag-*mart*-nit-*ret-sond*-spec-*spri-vel*

### 3. Leaf apex

a. acute or acuminate: *aff*-ana-bar-blan-bru-camb-carv-cath-cerq-*cord*-croc-*erio*-flag-*frey*-gest-*glaz*-gran-graz-inn-lind-*mag*-mart-*mont*-nit-*pal*-ret-*ros-scha*-sond-spec-spri-spru, squa-tij-vel-warm

b. obtuse or rounded: *aff-cord-erio*-fenz-*frey-glaz-mag-mont-pal*-pub-*ros-scha*-sell-*spru*

### 4. Indument of lower leaf surface

a. conspicuous, with individual hairs easily distinguishable: aff-*ana*-bar-bru-camb-carv-cath-cord-croc-erio-fenz-glaz-gran-graz-lind-mag-*mont-pal-pub*-ret-*ros-sond*-spru-squa

b. inconspicuous or absent or individual hairs so short and/or closely appressed as to be indistinguishable: *ana*-blan-cerq- flag-frey-gest-inn-mart-*mont*-nit-*pal-pub-ros*-scha-sell-*sond*-spec-spri-tij-vel-warm

### 5. Leaf colour

a. markedly bicolorous (upper surface drying much darker than the lower surface): blan-bru-flag-glaz-graz-inn-lut-mont-nit-*ros*-spec-spri

### 6. Leaf texture

a. coriaceous (versus chartaceous or membranaceous): aff-*cord-croc-erio*-fenz-graz-*inn*-lind-lut-*mart*-mont-*pub*-ros-*scha*-sell-*spri*-spru

### 7. Leaf surface

a. markedly bullate, with lateral and/or higher order venation sunken below the level of the rest of the upper leaf surface (versus more or less smooth above): aff-cath-gran-graz-ret

### 8. Leaf lamina

a. Markedly convex, often splitting along midrib when pressed (versus more or less flat): *erio*-graz-lind-*mont-pub-sell*

### 9. Apex of calyx lobes

a. acute (versus obtuse or rounded): *bar*-bru-camb-*cath*-erio-gest-glaz-*gran-lind-mag*-mont-*pub-sell-sond-spec-spru-tij*-vel-*warm*.

### 10. Calyx lobe ratio

a. calyx lobes at least as long as broad (versus broader than long): bru-camb-*erio*-mont-spruc-warm.

### 11. Calyx lobe colour

a. much darker than the hypanthium due to less dense covering of indumentum (versus not contrasting markedly with colour of hypanthium): *ana*-frey-*mont-pal*-scha-spri-*pub-sell*-warm

### 12. Number of flowers per inflorescence

a. no more than 15: ana-*blan-bru*-camb-carv-cath-cerq-*croc-erio*-flag-*frey*-gest-glaz-*inn*-[mag]-mont-*nit-pal-scha-sell-sond-spec*-spru-squa-*tij-vel*-warm

b. 15 - 35:bar-*blan-bru-croc-erio-fenz-frey-inn-lind*-[mag]-*mart-nit-pal-pub*-ret-*ros-scha-sell-sond-spec-spri-tij-vel*

c. more than 35: aff-cord-*croc-erio-fenz*-gran-graz-*lind*-[mag]-*mart-pal-pub-ros-sell-spec-spri*

### 13. Peduncle posture

a. flexuous or pendulous (vs. more or less straight and erect): camb-*erio*-flag

### 14. Mature flower bud size

a. at least 4 mm in diameter: *ana*-[bar]-blan-[bru]-*camb*-carv-*cath*-croc-erio-*fenz*-flag-*frey*-gest-gran-graz-inn-[mag]-*mart*-nit-*ret*-ros-scha-sond-*spec*-spri-[spru]

b. 3-3.9 mm in diameter: *aff-ana*-[bar]-[bru]-*camb-cath*-cerq-cord-*fenz-frey*-glaz-lut-[mag]-*mart-mont-pal-ret-sell-spec*-[spru]-squa-*tij*-warm

c. less than 3mm in diameter: *aff*-[bar]-[bru]-lind-[mag]-*mont-pal*-pub-*sell*-[spru]-*tij*-vel

### 15. Anther length

a. at least 1 mm long: ana-blan-carv-cerq-croc-*gran*-graz-mag-mart-spec-spri spru-*squa*

b. less than 1 mm long: aff-bar-bru-camb-cath-cord-erio-fenz-flag-frey-gest-glaz-*gran*-inn-lind-lut-mont-nit-pal-pub-ret-ros-scha-sell-sond-spru-*squa*-tij-vel-warm

### 16. Locule number

a. ovary 3-, 4- or 5-locular (versus ovary bilocular): *ana-cath*-fenz-frey-*glaz-mart*-scha

### 17. Fruit size

a. less than 10 mm in diameter: aff-ana-[blan]-[bru]-[camb]-*carv*-[cerq]-cord-erio-fenz-*flag*-[frey]-[gest]-glaz-*lind*-lut-mont-pal-pub-*ret*-sell-[spru]-[squa]-[vel]-warm.

b. at least 10 mm in diameter: bar-[blan]-[bru]-[camb]-*carv*-cath-[cerq]-croc-*flag*-[frey]-[gest]-gran-graz-inn-*lind*-mag-mart-nit-*ret*-ros-scha-sond-spec-spri-[spru]-[squa]-tij-[vel]

### 18. Fruit shape

Fruit more or less deeply longitudinally ridged (versus round in cross-section): [blan]-[bru]-[camb]-*cerq*-croc-[frey]-[gest]-*mag*-[spru]-[squa]-[vel]-warm

### 19. Calyx lobe persistence

a. falling as fruit matures (versus crowning mature fruit): [blan]-[bru]-[camb]-*cerq*-[frey]-[gest]-glaz-mont-nit-sond-[spru]-[squa]-[vel]

### 20. Hypocotyl indument

a. hypocotyl pubescent, at least in part: [blan]-[bru]-[camb]-carv-croc-[frey]-[gest]-graz-mag-mart-ros-sond-spec-spri-[spru]-[squa]-[vel]

b. hypocotyl glabrous: aff-ana-bar-[blan]-[bru]-[camb]-cath-cerq-cord-erio-fenz-flag-[frey]-[gest]-glaz-gran-inn-lind-lut-mont-nit-pal-pub-ret-scha-sell-[spru]-[squa]-tij-[vel]-warm

### 21. Distribution

NE Brazil: blan-carv-*cerq-croc-fenz-frey*-graz-*lind-mag*-ros-spri

GO and DF: *lind-pub*

MG: *aff*-bru-*cord-croc-erio-gran-lind*-lut-mont-*ret-spec*-spru

BA: blan, carv-cath-*cerq-croc-fenz-frey*-graz-*lind-mart-ros*-spri.

ES: *cerq-croc-fenz-frey-mart-nit-pub*

RJ: [*aff*]-*ana*-camb-*croc-erio-fenz*-frey-*gest-glaz*-gran-*inn-mag-mart-mont-nit-pal-pub-ret-scha-sell*-sond-spec-tij-*vel-warm*

SP: *aff-ana-cord-croc-fenz-flag-gran-lind-mart-mont-pal-pub-scha-sell-spec-tij*

PR: [*aff*]-*ana-cath-fenz-flag-pal-scha-sell-spec*-squa-*tij*

SC: *ana-cath-fenz-flag-pal-scha-sell-spec-tij*

RS: [*ana*]-*pal-scha-sell-tij*

Extra-Brazilian: bar-*lind-pal-pub*

**1. Gomidesia affinis** (Cambess.) D.Legrand, Notul. Syst. (Paris) **15:** 260. 1958.

*Myrcia affinis* Cambess., *in* Saint-Hilaire, Fl. Bras. merid. **2:** 307. 1832. Type. Brazil. São Paulo: "in campis prope urbem Mugy das Cruzes," *Saint-Hilaire C1 655* (holotype, P!).

Fig. 22 (also 1E & 15a&b)

*Myrcia cordiaefolia* var. *minor* DC., Prodr. **3:** 248. 1828. Type. Brazil. São Paulo: "Habitat in campis taboleiro ad Taubaté," *Martius s.n.* (holotype, M!).

*Myrcia hebepetala* DC., Prodr. **3:** 246. 1828. Type. Brazil. "Rio S. Francisco," *Martius s.n.* (holotype, M!).

*Myrcia itajuruensis* Cambess., *in* Saint-Hilaire, Fl. Bras. merid. **2:** 307. 1832. Type. Brazil. Minas Gerais: "Prope praedium Itajuru de S. Miguel de Mato dentro," *Saint-Hilaire s.n.* (lectotype, P!; isolectotypes, P! (2 sheets)).

*Gomidesia hebepetala* (DC.) O.Berg, Linnaea **27:** 8. 1855.

*Gomidesia pohliana* O.Berg, Linnaea **27:** 8. 1855. based on *Myrcia cordiifolia ('cordiaefolia')* var. *minor* DC.

*Gomidesia candolleana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 17. 1857. Type. Brazil. São Paulo: *Sellow 748* (holotype, B, presumed destroyed; lectotype, K!, here designated).

*Gomidesia hookeriana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 18. 1857. Type. Brazil. Rio de Janeiro: *Schott 1077* (lectotype, W!, here designated; isolectotypes, K! (2 sheets), W!).

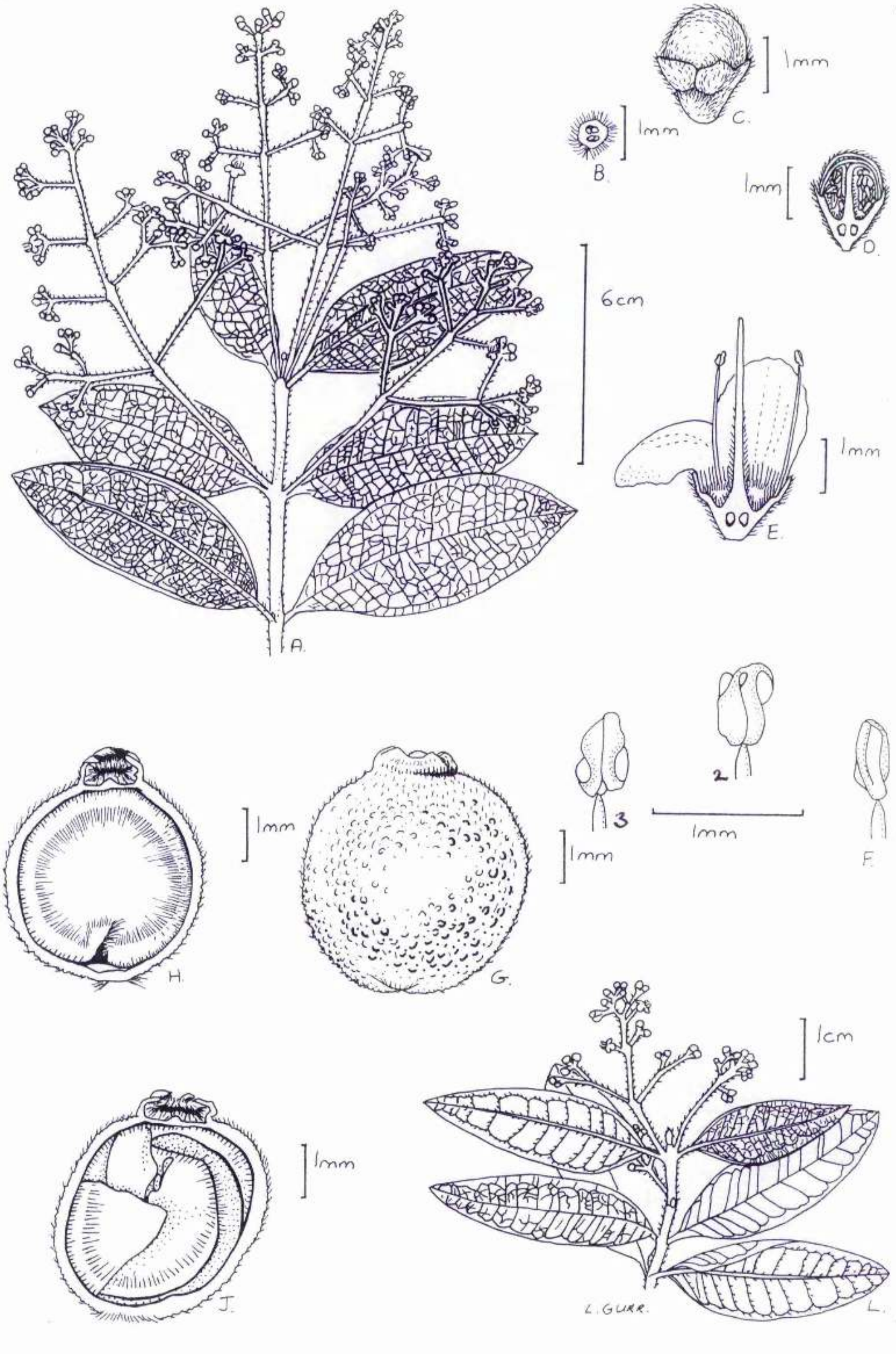
*Myrcia candolleana* (O.Berg) Kiaersk., Enum. Myrt. bras. 105. 1893.

*Myrcia hookeriana* (O.Berg) Kiaersk., Enum. Myrt. bras. 107. 1893.

*Gomidesia affinis* var. *pohliana* (O.Berg) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 14. 1959.

*Tree, treelet* or *shrub* 1.5–10 m tall. Branchlets 10 cm below the terminal bud 3 mm in diameter, more or less rounded, with a moderately dense indumentum of erect or ascending, straight or curved, straw-coloured or brownish hairs to 0.9 mm long; terminal bud 5–6 mm long, with dense indumentum. Stipule lobes to 1.6 mm long. Inter-petiolar ridge absent. Petioles 3–6 mm long, 1.5–2 mm wide, channeled. *Lamina* elliptic or oblong, sometimes narrowly so, 51–112 mm long, 21–38 mm wide, (2–)2.3–3.2 times as long as wide; apex obtuse or acute to acuminate; base cuneate or obtuse; margin bent down or recurved; midrib sulcate above, prominent below; lateral veins more or less straight, sulcate or impressed above, raised or prominent below, diverging at c. 55–70° from the midrib; secondary laterals irregularly composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping between them; higher order

FIG. 22. *Gomidesia affinis.* **A** Conflorescence and foliage; **B** Transverse section of ovary; **C** Flower bud; **D** Longitudinal section of flower bud; **E** Longitudinal section of flower; **F** Anthers in lateral (1), dorsal (2) and ventral (3) view; **G** Fruit; **H** Longitudinal section of fruit showing seed with testa intact; **J** Longitudinal section of fruit showing seed with testa removed; **L** Conflorescence and foliage. A - F from *Silva 1403/1404*, G - J from *Cesar s.n.*, L from *Gaudichaud 730*. Drawn by L. Gurr.


1mm
C.
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1cm
1mm
J.
L. GURR.
L.

venation impressed or faintly impressed above, raised below; venation between marginal vein and margin conspicuous. Indumentum absent or scattered to sparse above, consisting of fine, white, appressed hairs, moderately dense below, consisting of erect, straight, pale, straw-coloured or brownish hairs to 0.6 mm long. Gland dots indistinct above and below. Mature leaves coriaceous. *Conflorescence* comprising 1–3 pairs of uniflorescences in the axils of distal leaves or occasionally with pairs of uniflorescences borne at otherwise bare nodes below the distal leaves. Uniflorescence an erect complex thyrsoid or panicle of c. 70–100 flowers, c. 52–102 mm long, reaching c. 4/5–4/3 the length of the subtending leaf (i.e. almost equalling or exceeding it); peduncle 15–38 mm long i.e., c. 1/3–2/5 the length of the inflorescence, 0.7–1.2 mm wide, flattened; lateral branches 4–6 opposite or subopposite pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 2.7–3.5 mm long x 2.5–3.5 mm wide. Calyx lobes hemi-orbicular, c. 0.8 mm long x 1.5 mm wide, apex rounded, with a moderately dense indumentum of appressed, curved, pale hairs up to 0.6 mm long externally, indumentum shorter internally; hypanthium 1.3–1.7 mm long, prolonged c. 0.6–0.8 mm above the ovary with a dense indumentum of appressed, straight or curved, whitish hairs internally and externally; disk c. 1.5–2.1 mm diameter, indumentum dense. Stamens 80–100 per flower; filament not markedly tapered to point of insertion; anthers c. 0.7 mm long, apex truncate, vertical displacement of thecae marked, thecal halves losing curvature on dehiscence, held more or less parallel with margins recurved, effective dorsal opening c. 1/2 the length of the anther, residual septum visible, oblique. Style c. 6 mm, with moderately dense indumentum in lower 1/3; stigma minutely capitate. Ovary 0.7–0.8 mm long, bilocular, ovules 2 per locule. *Fruit* globose, up to 9 mm diameter, crowned with the connivent to erect calyx lobes. Mature seeds two per fruit, c. 6 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 1) and ecology.** Most collections of *Gomidesia affinis* are from Minas Gerais and São Paulo but the distribution may extend into the north of the state of Paraná. There are dubious records for Rio de Janeiro (see discussion). Occurring at altitudes from 600–1300 m above sea level, *G. affinis* is reported from gallery forest, low montane rain forest and secondary scrub vegetation.

**Phenology.** *Gomidesia affinis* has been collected in flower from January to April and rarely in May. Peak flowering is in March. Mature fruit have been collected from September to November.

**Representative specimens examined. BRAZIL.** MINAS GERAIS: locality not indicated, *Glaziou 19378* (C!, LE!, P!); Serra do Itacolumi, 1250 m, 21 Apr 1957, *Pereira 3045* (RB!); Mun. Ouro Preto, Estação Ecológica do Tripui, 17 Nov 1987, *Peron 469* (RB!); Caldas, 13 Apr 1868, *Regnell*

*552 III* (C!, LE!, P!); In mont. Itacolumi sylv. umbr, Aug 1824, *Riedel 350a* (LE!); Três Pontas, 18 Mar 1983, *Santos & Yano s.n.* (K!); Inter Taquarassu et Serrinha, 3 May 1892, *Schwacke Herb. 8245* (RB!); Lagoa Santa, 835 m, 3 Sep 1863, *Warming 229* (C!, W!); Sandstone area, Serra da Bocaina, 10 km. northwest of Serro, Mun. of Serro, 4 May 1945, *Williams & Assis 6880* (C!, K!, MO!, R!, U!). **SÃO PAULO:** Serra da Cantareira, Pedra Grande, 20 Feb 1981, *Aguiar SPSF6214* (SPF!); Mun. Itanhaém, Km 118 da Rodovia SP 55, 19 Jan 1985, *Araújo 6546* (NY!); Campinas, Faz. Sta Genebra, 14 Mar 1986, *Arruda 19857* (UEC!); São Paulo, Capital, Feb 1947, *Brade 18750* (RB!); Praça da Alegria, by Aroucheis, west towards Água Branca about 2 m from Tanque de Zunica, 24 Mar 1827, *Burchell 4681-26* (K!); Praça da Alegria, 17 Jun 1827, *Burchell 4772-2* (K!); Campinas, *Campos Novaes 321* (K!, NY!); Mun. Anhembi, Fazenda Barreiro Rico, 12 Dec 1980, *Cesar s.n.* (UEC!); Mun. Anhembi. Fazenda Barreiro Rico, 21 Nov 1983, *Cesar s.n.* (UEC!); São Paulo Capital, 26 Oct 1945, *Coelho 2351* (US!); Moji-Guaçu, Pádua Sales, Fazenda Campininha, 600 m, 24 Sep 1980, *Forero 8372* (K!, SP!); S. Paul, Jan 1839, *Guillemin s.n.* (P!); São Paulo, Capital, Cidade Jardim, 8 Apr 1935, *Hoehne 359* (K!); Habitat in campis taboleiro ad Taubaté, *Martius s.n.* (M!); Cananéia, junto à Balsa, 29 Sep 1961, *Mattos 9183* (SP!); Rio Claro, Fazenda São José, 1 Apr 1980, *Pagano 230* (UEC!); Ytú, Mar 1834, *Riedel 2060* (F!, K!, LE!, NY!, P!, R!, S!, US! (photo), W!); Cotia, Cemucam, 22 Nov 1984, *Rossi 431* (SPF!); São José dos Campos, estrada Turvo, depois do Horto, 20 Mar 1986, *Silva & L. Capellari Jr. 1403* (UEC!); São José dos Campos, 20 Mar 1986, *Silva 1404* (RB!); São José dos Campos, Reserva Florestal da Boa Vista, 4 Oct 1986, *Silva & L. Capellari Jr. 1473* (UEC!); Serra do Japi, 22 Sep 1983, *Sugiyama & S. Correa Chiea 15519* (UEC!); Mun. Campinas, distrito de Cabras, mata próximo ao Observatório de Capricórnio, 30 Apr 1986, *Taroda 18593* (UEC!). **STATE UNCERTAIN:** Minas Gerais or Rio de Janeiro: *Glaziou 16077* (C!, F!, K!, LE!, P!, R!, RB!). **STATE NOT INDICATED:** *Sello s.n.* (LE!); *Sellow 5726* (LE!, W!);

**Local name.** Guamirim (São Paulo). This name is applied to a number of species of *Gomidesia* in southern Brazil including *G. anacardiifolia*, *G. fenzliana*, *G. palustris*, and *G. sellowiana.*

As circumscribed here *G. affinis* is a rather variable species with respect to leaf shape and indumentum. Apart from the distinctive anthers (Fig. 15a&b) most collections can be distinguished by their coriaceous leaves with veins deeply impressed above and well-developed inflorescences with numerous flowers. The present broad circumscription embraces material treated by Berg as five different species which were distinguished on the basis of characters such as leaf shape and degree of branching of the inflorescence. I have found these traits to vary continuously among the material cited above. Legrand (1959) also treated most of these taxa in the synonymy of *G. affinis*. Two exceptions are *Myrcia itajuruensis*, not mentioned by Legrand though he appears to have studied the types of many of Cambessedes' *Myrcia* species, and *G. hebepetala* which Legrand (1959) treated as a distinct species having examined only a photograph of the type. Subsequently Legrand and Klein (1967) suggested that *G. hebepetala* should be included 'in the circle of *G. affinis*'. This remark was made in a note under *G. affinis* var. *catharinensis,* without discussion of the nomenclatural implications of such an action. Applying strict priority, the name *G. hebepetala* should be taken up for this species. However, I am reluctant to do this since this name has never been generally applied. Apart from the type I have seen no material annotated as *G. hebepetala* and the name has appeared in print on only two occasions since Berg's original publications. In contrast, the name *G. affinis* is well-established, appearing on numerous herbarium specimens and in local Flora treatments and vegetation studies. The International Code for Botanical Nomenclature (Greuter et al. 1994) now permits the conservation of established names over earlier names where this is in the interests of nomenclatural stability. Pending submission of a proposal on this subject to the Committee for Spermatophyta I here continue to apply the name in current use, following ICBN Rec. 14A.

In discussing *G. hebepetala,* Legrand compared it to his new variety *G. affinis* var. *catharinensis*. However I consider this material to represent a distinct species with rather long closed anthers more comparable to those of *G. reticulata* than to *G. affinis* (Fig. 12 & 15). At the time of my herbarium visits to the USA I had not yet decided to treat *Gomidesia catharinensis* as distinct from *G. affinis*. For this reason I am unsure of the southern limit of the latter species, as I have records of collections of *G. affinis* from Paraná which might now be referrable to *G. catharinensis*. Records of *G. affinis* from Rio de Janeiro are based on *Glaziou* collections for which different localities are cited by different authors. As the locality data associated with *Glaziou* collections are often unreliable these records of *G. affinis* are not plotted.

*Gomidesia candolleana* was based on a Sellow collection at Berlin for which no number was cited. The K sheet here designated lectotype was annotated by Berg as *G. candolleana* and distributed from B in 1859. Also in Berg's hand is the annotation *Sellow 748.*

When describing *Gomidesia hookeriana*, Berg mentioned *Schott 1077* and a *Sello* collection for which no number was cited. Some sheets of the Sello syntype may have been distributed with the number 5858 but, as this cannot now be demonstrated with certainty, the collection *Schott 1077* was the preferred choice for lectotype.

**2. Gomidesia anacardiifolia** (Gardner) O.Berg, Linnaea **27:** 8. 1855. 'anacardiaefolia'

*Myrcia anacardiifolia* Gardner, Hooker's London Journal of Botany **2:** 354. 1843. 'anacardiaefolia' Type. Brazil. Rio de Janeiro: Organ Mountains, *Gardner 422* (lectotype, K!, here designated; isolectotypes, F!, K!, P!, W!).

(Fig. 3A and 12a-e)

*? Gomidesia anacardiifolia* var. *oblongata* O.Berg, *in* Martius, Fl. Bras. **14(1):** 15. Type. Brazil. São Paulo: *Sello s.n.* (holotype, B, n.v., presumed destroyed).

*? Gomidesia anacardiifolia* var. *ovalis* O.Berg, *in* Martius, Fl. Bras. **14(1):** 15. 1857. Type. Brazil. São Paulo: *Sello s.n.* (holotype, B, n.v., presumed destroyed; probable isotype, K!).

*Gomidesia anacardiifolia* var. *opaca* O.Berg, *in* Martius, Fl. bras. **14(1):** 15. 1857. Based on *Myrcia anacardiifolia* Gardner. Inadmissible name to be replaced by *Gomidesia anacardiifolia* var. *anacardiifolia*.

*Gomidesia riedeliana* O.Berg, *in* Martius, Fl. bras. **14(1):** 532. 1859. Type. Brazil. Rio de Janeiro: "in montibus S. d'Estrella," *Riedel s.n.* (lectotype, LE!, here designated; isolectotypes, K!, LE! (2 sheets), P!, U!).

*Myrcia estrellensis* Kiaersk., Enum. Myrt. bras. 107. 1893. *Nom. nov.* based on *G. riedeliana* O.Berg non *M. riedeliana* O.Berg.

*Tree, treelet* or *shrub* 3–5(–8) m tall. Branchlets 10 cm below the terminal bud 2–3.5 mm in diameter, rounded or flattened and channeled or slightly quadrangular, glabrous or with a moderately dense to dense indumentum of erect or ascending, straight or curved, whitish hairs to 1.2 mm long; terminal bud 5–7 mm long or proliferating, with a dense indumentum of appressed, straight, pale brown hairs to c. 1 mm. Stipule lobes c. 0.8–1 mm long. Interpetiolar ridge distinct, horizontal or apparently absent. Petioles 2–5 mm long, 1–2.5 mm wide, channeled, glabrous or with a moderately dense indumentum of erect or appressed, straight or curved, pale or brown hairs to 1 mm. *Lamina* wide elliptic to elliptic or suborbiculate, 52–141 mm long, 23–70 mm wide, 1.4–2.3(–2.7) times as long as wide; apex obtuse or rounded or acute or shortly and abruptly acuminate, rounded at very tip; base cuneate or truncate or obtuse or rounded, rarely auriculate; margin flat or bent down; midrib sulcate above, prominent below; lateral veins straight or curved, sulcate or deeply impressed or flat above, prominent below, diverging at c. 60–80° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping markedly between them; higher order venation inconspicuous or conspicuous above, pale and slightly raised, raised or slightly raised below;

venation between marginal vein and margin distinct or conspicuous, often including secondary arches and/or submarginal vein. Indumentum absent above or scattered to moderately dense, consisting of erect or appressed, pale or brown, straight or curved hairs to 1 mm, moderately dense to sparse or scattered below, consisting of erect, straight or curved, white or brownish hairs of variable length but most c. 0.1–0.4 mm long. Gland dots indistinct above, or distinct, impressed, dark, indistinct or more or less distinct below, slightly raised. Mature leaves chartaceous, flat or undulate. *Conflorescence* comprising a single pair of uniflorescences in the axils of distal leaves. Uniflorescence an erect triad or thyrsoid (or rarely a monad?) of c. (1–)3–13 flowers, 33–65 mm long, reaching c. 1/2–9/10 the length of the subtending leaf; peduncle 23–53 mm long i.e., c. 1/3–4/5 the length of the inflorescence, 1.5–2.5 mm wide, more or less flattened; lateral branches 0–2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 4–6.5 mm long x 3–6.5 mm wide. Calyx lobes hemi-orbicular, 1–2.7 mm long x 2–4 mm wide, apex rounded or obtuse, indumentum moderately dense externally, dense internally near base, sparse towards apex, or uniformly moderately dense; hypanthium 2–3.3 mm long, prolonged c. 1–1.6 mm above the ovary, indumentum dense internally and externally; disk c. 2.5–3.7 mm diameter, indumentum dense. Stamens 53–199 per flower; filament abruptly narrowed to point of insertion on connective (or rarely on connective stub), anthers c. 1 mm long, apex truncate or shallowly emarginate, rarely apiculate, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent or gaping, thecal margins flat after dehiscence, effective dorsal opening 1/3–1/2 the length of the anther, residual septum not visible or visible and vertical. Style c. 8–13 mm, with moderately dense to dense indumentum in basal 1/3 to 2/3, glabrous in upper 1/3; stigma minutely capitate or indistinct. Ovary c. 1–1.7 mm long, bilocular or trilocular, ovules 2 per locule. *Fruit* globose, to 13 mm diameter, crowned with the erect, imbricate calyx lobes. Mature seed c. 2–3 per fruit, c. 8–9 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 2) and ecology.** *Gomidesia anacardiifolia* occurs from Rio de Janeiro south to Santa Catarina (and perhaps into Rio Grande do Sul) at altitudes of 10 to 1900 m above sea level. In Santa Catarina it is considered characteristic of the Atlantic coastal rain forest while at the northern end of its range it appears to be restricted to rain forest at altitudes above 800 m.

**Phenology.** Flowering collections have been made as early as November and as late as April but the main flowering peak is in January. Mature fruit have been collected from April to October.

**Specimens examined. BRAZIL.** **PARANÁ:** Mun. S. José dos Pinhais, Col. S. Andrade, 12 Oct 1966, *Hatschbach 14851* (C!, US!); Mun. S. José dos Pinhais, Col. S. Andrade, 3 Feb 1967, *Hatschbach 15960* (US!); Mun. Guaratuba, Serra de Araraquara, 21 Dec 1967, *Hatschbach 18170* (C!); Mun. Paranaguá, Rio Cambará 50 m, 28 May 1968, *Hatschbach 19252* (C!, K!, MO!, NY!, US!); Mun. Guaratuba, Rio S. João, Porto Miranda, 24 Jun 1968, *Hatschbach 19421* (C!, K!); Mun. Guaratuba, Garuva, 4 Nov 1957, *Hatschbach 3584* (PACA!); Mun. S. José dos Pinhais, Rio Arraia, 26 Jan 1983, *Hatschbach 46066* (F!, IBGE!, MU!, NY!, UB!); Mun. S. José dos Pinhais, Rio Castelhanos, 6 Apr 1983, *Hatschbach 46265* (BR!, UB!, US!); Mun. S. José dos Pinhais, Sto. Andrade, 10 Jul 1984, *Hatschbach 48381* (MO!); Mun. S. José dos Pinhais, Col. S. Andrade, 17 Sep 1985, *Oliveira 933* (HUCS!, MU!). **RIO DE JANEIRO:** Alto Macahé et Serra da Estrella, Nov 1879, *Glaziou 10780* (C!, K!, P!); Serra da Estrella, 17 Feb 1879, *Glaziou 10790* (R!); Alto Macahé, *Glaziou 17670* (C!, K!, LE!, P!); Petrópolis, Quitandinha, 790 m, 18 Jan 1940, *Lutz 1556* (R!); Mun. Nova Friburgo, Morro da Caledônia, 1500 m, 8 Jun 1977, *Martinelli 2492* (RB!); Theresópolis, Montanha do Lonzada. 16 Jan 1883, *Palma 6834* (R!). **SANTA CATARINA:** Estação Florestal I.N.P., Ibirama, 300 m, 6 Mar 1956, *Klein 1894* (UB!, US!); Ribeirão do Areado, Ibirama, 100 m, 21 May 1956, *Klein 2018* (NY!, PACA!); Horto Florestal, I.N.P., Ibirama, 300 m, 13 Apr 1956, *Reitz 3121* (B!, NY!, PACA!, US!); Rio Mirador - Opleães, 200 m, 18 Jan 1950, *Reitz 3375* (S!); Ribeirão do Ouro, Brusque, 600 m, 8 May 1950, *Reitz 3550* (PACA!, S!, US!); Três Barras, Garuva, S. Francisco do Sul, 100 m, 19 Dec 1957, *Reitz 5467* (US!); Sabiá, Vidal Ramos, 750 m, 7 Oct 1956, *Reitz 5906* (B!, BR!, NY!, U!, US!); Mina Velha, Garuva, S. Francisco do Sul, 10 m, 21 Jan 1958, *Reitz 6270* (B!, BR!, K!, NY!, U!, US!); Sabiá, Vidal Ramos, 750 m, 28 Jan 1958, *Reitz 6325* (NY!, US!); Alto Matador, Rio do Sul, 800 m, 2 Aug 1958, *Reitz 6921* (PACA!); Sanga da Areia, Jacinto Machado, 200 m, 13 Jul 1959, *Reitz 8934* (M!); Arar., Turvo, 50 m, 3 May 1944, *Reitz c573* (RB!). **SÃO PAULO:** Estrada de Ibiúna para Vargedo, 700 m, 24 Apr 1980, *Barreto 131* (HRB!); Mun. Sete Barras, Parque Est. Carlos Botelho. 500 m, 22 Dec 1979, *Benson 10895* (UEC!); without locality 1833, *Gaudichaud 767* (P!); Registro, rod. p/Sete Barras, 70 m, 10 May 1983, *Hatschbach 46286* (C!, MO!, MU!); Serra da Cantareira, Jul 1933, *Koscinski 120* (SP!); sylvis St. paulo, Jan 1834, *Lund s.n.* (C! (5 sheets)); without locality *Lund s.n.* (F!); Circa Tieté, *Riedel s.n.* (NY!, S!); Brasilia: Tieté, St. Paulo, Jan 1834, *Riedel 1834* (K!, LE!, P! (2 sheets), U!); Estr. de Ibiúna para Vargedo, 700 m, Aug 1982, *Rubens 131* (RB!); without locality, *Sellow s.n.* (BR!); without locality, *Serviço Florestal do Estado 15* (RB! 33064). **STATE NOT INDICATED:** *Sello s.n.* (LE!, P! (2 sheets)); *Ule 1641* (P!).

**Local names.** Guamirim (Santa Catarina), Guamirim vermelho (Santa Catarina), Marmelinho (São Paulo), Rapa Guela (Santa Catarina). The name Rapa Guela is also applied to *Gomidesia catharinensis* in Santa Catarina. For other species of *Gomidesia* known as Guamirim see under *G. affinis*.

There may be a case for distinguishing more than one species among the material cited above. Collections from Santa Catarina typically have few-flowered inflorescences of large flowers with numerous (> 150) anthers and tri-locular ovaries while collections from Rio de Janeiro often exhibit more branched inflorescences of smaller flowers with lower anther numbers (< 100) and bilocular ovaries. These latter collections typically have fairly copious brown indumentum while the paler indumentum of the southern collections tends to be shed rather early in development. In addition, in the Santa Catarina material the leaves are usually narower, the lateral veins are generally deeply impressed above and prominent below, giving an undulate appearance to the dry leaf, and the marginal vein loops markedly between the laterals. In the Rio de Janeiro collections the leaves are often orbicular to suborbicular, the lateral venation is not so conspicuous and the marginal vein merely curves between the laterals. Unfortunately none of these characters appear to be consistently correlated when all of the material available is studied. Furthermore, examination of duplicates of the same collection suggests that leaf shape and inflorescence size can vary considerably within populations. My current understanding of this complex is that the 'tendencies' described above represent responses to differing environmental conditions and, in particular, to different altitudes. Between the two geographical extremes, in Paraná, the extreme forms and intermediates appear to occur in close proximity. Intensive collecting in this area followed by multivariate analysis could help to resolve this problem.

It should be noted that the two extreme forms described above do not correspond to the two species distinguished by Berg and here treated as synonymous. The type material of *Gomidesia riedeliana* is fairly representative of the northern extreme while that of *G. anacardiifolia* is similar but shows considerable variation in leaf form and degree of branching of the inflorescence. In current usage such material is generally determined as *G. riedeliana*. The name *G. anacardiifolia* has consistently been applied to the southern material. Thus, should further study lead to the conclusion that two or more species should be distinguished within this complex, conservation action would be required to conserve current usage of the name *G. anacardiifolia* for a taxon which does not include the type of that name.

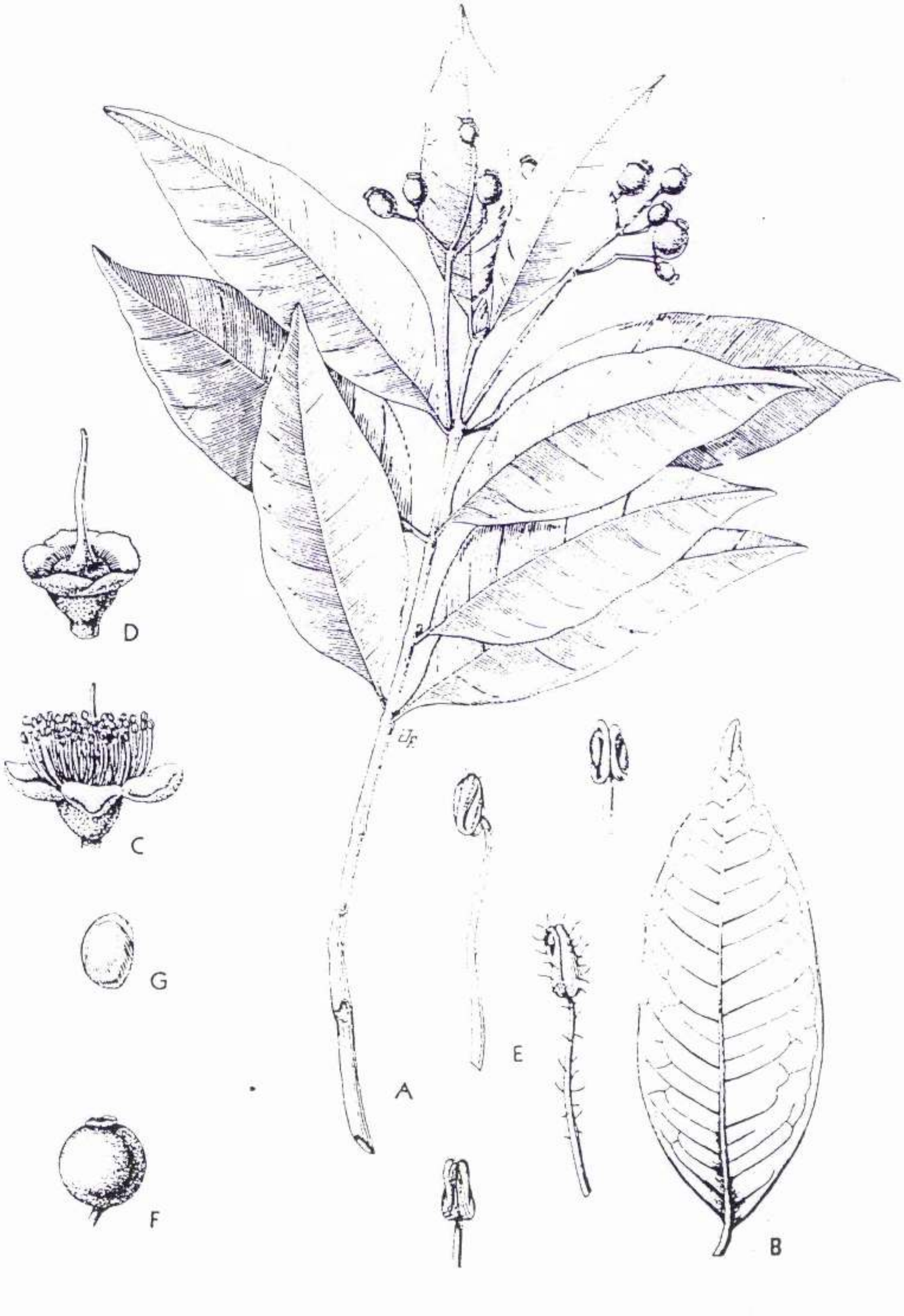
Berg distinguished three varieties within *Gomidesia anacardiifolia*. Two of these were based on Sellow material seen at Berlin. The holotypes must therefore be presumed to have been destroyed and, since no numbers were cited, isotypes cannot be identified with certainty. However, Sellow material at K, LE and W is consistent with the unusually brief description provided by Berg and is close to the southern extreme of the spectrum of variation described above. These names are therefore tentatively treated in the synonymy above.

**3. Gomidesia barituensis** Legname, Lilloa 35: 79. 1978. Type. Argentina. Salta: Salta, Dep. Santa Victoria, Camino de Los Toldos a Lipeo, a más o menos 2 km de Lipeo, por senda de herradura, 1250 m, 4 Oct 1973, *Legname 9737* (holotype, MVM, n.v.).

Fig. 23 (also 3B).

*Tree* (3–)7–15 m tall. Branchlets 10 cm below the terminal bud 2–3 mm in diameter, rounded or subquadrangular, more or less glabrous, terminal bud c. 6 mm long with a dense indumentum of erect or ascending, straight, pale brown hairs to c. 1 mm. Stipule lobes not seen. Inter-petiolar ridge absent. Petioles c. 8 mm long, 2 mm wide, channeled, with a moderately dense indumentum of straight or crisped, pale brown hairs to 0.5 mm. *Lamina* oblong to narrowly ovate, 48–106 mm long, 20–38 mm wide, (2.4–)2.7–2.8 times as long as wide; apex acuminate, sometimes abruptly so; base obtuse; margin flat, undulate; midrib sulcate near base, flat near apex above, prominent below; lateral veins straight or curved, more or less flat above, raised below, diverging at c. 70° from the midrib; secondary laterals simple, sometimes almost equalling the laterals in prominence; marginal equalling the laterals in prominence and curving between them; higher order venation inconspicuous above, slightly raised below; venation between marginal vein and margin inconspicuous. Indumentum absent above, sparse to moderately dense below, consisting of appressed, straight or curved, whitish hairs to 0.7 mm long. Gland dots indistinct above and below. Mature leaves chartaceous. *Conflorescence* comprising a single pair of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 30 flowers, 50–92 mm long, reaching c. 3/4–4/5 the length of the subtending leaf; peduncle 32–52 mm long i.e., c. 1/2–2/3 the length of the inflorescence, 1.5–2 mm wide, flattened; lateral branches 2 or 3 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* not seen. Calyx lobes shallowly triangular or hemiorbicular, c. 1.2 mm long x 2.3 mm wide, apex acute or rounded, with a dense indumentum externally and internally; hypanthium 2.5 mm long, prolonged c. 1.2 mm above the ovary, indumentum dense externally and internally; disk c. 2.7–3 mm diameter, indumentum dense. Stamens not counted; anthers c. 0.5–0.6 mm long, filament tapering gradually to point of insertion on connective, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves retain curvature after dehiscence, connivent or held parallel or slightly divergent, thecal margins reflexed, effective dorsal opening 1/3–1/2 the length of the anther, residual septum sometimes visible, more or less vertical. Style c. 5 mm long, with moderately dense indumentum in lower 2/3; stigma inconspsicuous. Ovary 1.2 mm long,

FIG. 23. *Gomidesia barituensis*. **A** Fruiting branches; **B** underside of the leaf; **C** Flower; **D** calyx and gynoecium; **E** stamens in different positions to show dehiscence; **F** Fruit; **G** Seed. A - G from *Legname-Cuezzo 9737*. Reproduced from Legname, 1978.



D
C
G
F
A
E
B

bilocular, ovules 2 per locule. *Fruit* globose, 11 mm diameter, crowned with the connivent to erect, imbricate calyx lobes. Mature seed 2 per fruit, c. 9 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 3) and ecology.** *Gomidesia barituensis* occurs in northern Argentina and southern Bolivia in moist subtropical forest and cloud forest at altitudes of 950–1250 m.

**Phenology.** *Gomidesia barituensis* appears to have a phenology closely comparable to the majority of the Brazilian species of the genus, flowering early in the year (between January and March?) and fruiting from June onwards. Mature fruit have been collected in September and October.

**Specimens examined. ARGENTINA.** SALTA: Dep. Santa Victoria, camino de Los Toldos a Lipeo, a 10 km del Lipeo, 9 Dec 1973, *Legname & Cuezzo 9832* (K!); Dep. Santa Victoria, camino de Baritu a Porongal, a 12 km +/- de Baritu, 1500 m, 30 Oct 1971, *Marmol & P.R. Legname and A.R. Cuezzo 8834 C* (BM!, C!); Dep. Santa Victoria, camino de Baritu a Porongal (Loma Quemada), 1530 m, 19 Sep 1972, *Marmol & A.R. Cuezzo 9269C* (NY!); Oran, pena colorada del Celibar, Aug 1937, *Tortorelli 343* (K!).

**BOLIVIA.** Santa Cruz, Caballero Province. Entre 15 y 25 km al norte de San Juan de Portrero hacia Cerro Bravo, 2250 m, 6 Jun 1992, *Killeen 4097* (K!); Dpto. Tarija, Prov. Arce, ca. 2 hours by trail N of Sidras (trail to Tariquia), 950 m, Apr 1983, *Solomon 10118* (MO!, NY!); Dpto. Tarija, Prov. Arce. Hillsides vicinity of Sidras, (5.5 km N. of Emborozu), 950 m, Oct 1983, *Solomon 11121* (MO!, NY!, US!); Cuyambuyo, Aug 1937, *Tortorelli 1159* (K!).

**Local names.** Guayabo negro (Salta, Argentina).

I have not seen the type material of this, the most recently described species of *Gomidesia* and the only member of the genus with an entirely extra-Brazilian distribution. However, the paratypes coincide closely with the description in the protologue, the only discrepancy being that the anthers were reported and depicted as bearing hairs, a character unknown elsewhere in the genus. I have not been able to observe such hairs in any of the material available to me. Rotman (1986) appears to have examined the type and she noted that she had failed to find the staminal hairs described. I therefore conclude that the original observation was erroneous and may have been due to fungal growth (common in many Myrtaceae) or to stray hairs which had fallen from other organs and adhered to the stamens.

**4. Gomidesia blanchetiana** O.Berg, *in* Martius, Fl. bras. **14(1):** 14. 1857. Type. Brazil. Bahia: "Igreja Velha," *Blanchet 3415* (lectotype, W!, here designated; isotypes, BM!, BR!, C!, F!, LE!, NY!, P!, W!).

? *Aulomyrcia bullata* O.Berg, *in* Martius, Fl. bras. **14 (1):** 96. 1857. Type. Brazil. Bahia: *Blanchet 3112* (syntype, P!); *Luschnath 110* (syntype, W, *n.v.*).

*Myrcia crocea* var. *blanchetiana* (O.Berg) Kiaersk., Enum. Myrt. bras. 106. 1893.

(Fig. 1A).

*Habit* unknown. Branchlets 10 cm below the terminal bud c. 3 mm in diameter, flattened, with a moderately dense to dense indumentum of appressed, straight, golden brown hairs to 0.3 long; terminal bud 8–18 mm long, with a dense indumentum of appressed, straight, straw-coloured hairs to 1 mm long. Stipule lobes c. 1–1.4 mm long. Inter-petiolar ridge distinct, inverted V-shaped. Petioles c. 8 mm long, 1.5–2 mm wide, channeled. *Lamina* narrowly ovate, c. 150 mm long, 54 mm wide, c. 2.8 times as long as wide; apex acuminate, rounded at very tip; base acute or obtuse; margin flat or bent down; midrib sulcate near base, flat towards apex above, prominent below; lateral veins more or less straight, slightly raised above, prominent below, diverging at c. 70° from the midrib; secondary laterals simple or composite, sometimes equalling the laterals in prominence and then difficult to distinguish from them; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation distinct, slightly raised above, raised below; venation between marginal vein and margin distinct, including submarginal vein. Indumentum sparse to scattered above, consisting of appressed, straight, white hairs to 0.8 mm, sparse below, consisting of appressed, straight, straw-coloured hairs to 0.8 mm intermixed with ascending to erect, straight, whitish hairs to c. 0.2 mm long. Gland dots indistinct above and below. Mature leaves chartaceous, markedly bicolorous. *Conflorescence* comprising 1 or 2 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 15–27 flowers, c. 76–80 mm long, reaching c. 3/5 the length of the subtending leaf; peduncle c. 48 mm long i.e., c. 2/3 the length of the inflorescence, 2 mm wide, flattened; lateral branches 2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 6.5 mm long x 5.5 mm wide. Calyx lobes hemi-orbicular, c. 1.5 mm long x 3.3 mm wide, apex rounded, with a moderately dense to dense indumentum of appressed, straight, straw-coloured hairs up to 0.4 mm long externally, indumentum dense internally; hypanthium c. 4.2 mm long, prolonged c. 1.7 mm above the ovary with a dense indumentum of appressed, straight or curved, straw-coloured hairs of mixed length to 0.5 mm externally, indumentum dense internally; disk c. 2.8 mm diameter with dense indumentum. Stamens c. 94 per flower; filament tapered to point of insertion above short connective stub; anthers c. 1.1 mm long, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves retain curvature after dehiscence, connivent, with margins remaining in plane of curvature and overlapping, effective dorsal opening 1/4 the length of the anther, residual septum not usually visible. Style c. 10 mm, with dense indumentum in lower 3/4; stigma punctiform. Ovary c. 2.7 mm long, bilocular, ovules 2 per locule. *Fruit* unknown.

**Distribution (not mapped) and ecology.** Known only from Bahia. See discussion.

**Phenology.** Known only from flowering material for which the month of collection is unknown.

**Specimens examined. BRAZIL.** BAHIA: Locality not stated, *Blanchet 3112* (P!); Igreja Velha (or Jacobim?), 1841, *Blanchet 3415* (lectotype, W!, here designated; isotypes, BM!, BR!, C!, F!, LE!, NY!, P! (2 sheets but see discussion), W!).

In the protologue the type locality is given as 'Igreja Velha' by Berg. I have been unable to trace any locality in Bahia known by this name. However, the LE isotype bears the locality 'Jacobim', referring to Jacobina in the north of the Chapada Diamantina in the interior of Bahia. Blanchet is known to have received collections made by Brazilian collectors in this area.

Kiaerskou (1893) treated *G. blanchetiana* and *G. crocea* as conspecific, basing his *Myrcia crocea* var. *blanchetiana* on *Blanchet 3415*. Legrand reinstated *G. blanchetiana* and published a nom. nud. *G. blanchetiana* var. *alagoensis* for what is here treated as a separate species, *G. rosangelae*. I consider *G. blanchetiana* to have marked affinities with both *G. crocea* and *G. springiana* but to treat it with either of these would blur the distinction between them. I have therefore chosen to treat *G. blanchetiana* as a distinct species although, apart from the type I have seen only one collection, *Blanchet 3112*. This latter collection is cited by Berg as a syntype of *Aulomyrica bullata* based on material seen by him at B and W. However, the sheet of *Blanchet 3112* which I examined at P is a near perfect match for *G. blanchetiana* and bears little or no relation to Berg's description of *A. bullata*. The most likely explanation for this discrepancy is that the P sheet in question is incorrectly labelled. Study of the Blanchet collections at G or W may resolve this problem and permit the lectotypification of this name. *Gomidesia blanchetiana* is also based on material seen by Berg at B and W. The material at B is presumed to have been destroyed so one of the W sheets of *Blanchet 3415* is here designated lectotype. This collection was rather widely distributed but appears to have been subject to some confusion concerning numbering. Of the three sheets of *Blanchet 3415* which I received on loan from P only two bear material comparable to that described above. The third sheet bears a specimen of *Eugenia sp.*

**5. Gomidesia brunnea** (Cambess.) D.Legrand, Notul. Syst. (Paris) **15:** 261. 1958.
*Myrcia brunnea* Cambess., *in* Saint-Hilaire, Fl. Bras. merid. **2:** 306. 1832. Type. Brazil. Minas Gerais: "in sabulosis montis Serra Negra," *Saint-Hilaire s.n.* (lectotype, P!, here designated; isotypes, F! (fragment), P! (2 sheets)).

*Shrub* 1–3 m tall. Branchlets 10 cm below the terminal bud 3 mm in diameter, terete, with a moderately dense indumentum of more or less erect, straight or curved or crisped, brownish hairs to 0.4 mm long; terminal bud 10–12 mm long with a dense indumentum of appressed, straight hairs to 0.6 mm long. Stipule lobes to 1.4 mm long, purplish black, fleshy. Interpetiolar ridge absent. Petioles c. 9 mm long, 1.5–2 mm wide, channeled. *Lamina* ovate, 63–99 mm long, 34–50 mm wide, 1.6–2 times as long as wide; apex acute; base obtusely cuneate; margin flat or bent down; midrib sulcate to impressed above, prominent below; lateral veins straight, more or less flat or slightly raised above, prominent below, diverging at c. 70–80° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein slightly less prominent than the laterals and curving between them; higher order venation inconspicuous, very slightly raised above, raised below; venation between marginal vein and margin conspicuous. Indumentum moderately dense above, consisting of straggling white hairs of diverse orientation to 0.8 mm, moderately dense below, consisting of erect, straight, brownish hairs to 0.6 mm. Gland dots indistinct above and below. Mature leaves chartaceous, bicolorous. *Conflorescence* comprising 1–2 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 15 flowers, 3.9–7 mm long, reaching c. 2/3–9/ 10 the length of the subtending leaf; peduncle 1.9–4 mm long i.e., c.1/2–3/5 the length of the inflorescence, c. 2 mm wide, more or less rounded; lateral branches 2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* not seen. Calyx lobes triangular, 2.5 mm long x 2 mm wide, apex acute, with a dense indumentum externally consisting of appressed, straight, brownish hairs up to 0.5 mm long, indumentum shorter but dense internally; hypanthium 2.5 mm long, prolonged c. 1 mm above the ovary, indumentum dense; disk c. 2.5 mm diameter, indumentum dense. Stamens not counted; anthers to 0.5 mm long, filament tapering slightly immediately below point of insertion on connective, apex deeply emarginate, vertical displacement of thecae marked, thecal halves retain curvature after dehiscence, connivent, thecal margins flat or slightly reflexed after dehiscence, effective dorsal opening 1/3–1/2 the length of the anther, residual septum not usually visible. Style c. 7 mm, with moderately dense indumentum in lower 1/2; stigma indistinct. Ovary 1.7 mm long, bilocular, ovules 2 per locule. *Fruit* not known.

**Distribution (Map 4) and ecology.** *Gomidesia brunnea* is known only from the type collection from the Serra Negra, Minas Gerais.

**Phenology.** Flowering material was collected in February.

**Specimens examined. BRAZIL.** **MINAS GERAIS:** Serra Negra, *Saint-Hilaire s.n.* (F! (fragment), P! (3 sheets)).

Vegetatively *G. brunnea* is very close to acute leaved collections of *G. anacardiifolia* but flowering material is easily distinguished since the calyx lobes of *G. brunnea* are acutely triangular and slightly longer than wide while those of *G. anacardiifolia* are broad and obtuse. *Gomidesia brunnea* also bears a marked resemblance to *G. lindeniana* and the two names have been used interchangeably by some myrtologists. With the exception of the type collection, all the material I have seen identified as *G. brunnea* is actually referrable to *G. lindeniana*, the commonest species of *Gomidesia* in the Brazilian interior. *Gomidesia brunnea* can be distinguished vegetatively from most collections of *G. lindeniana* as the latter species usually exhibits markedly convex, coriaceous leaves which split upon drying and pressing. *Gomidesia lindeniana* also has a larger inflorescence with anthers whose thecal halves lose curvature upon dehiscence. In contrast *G. brunnea* has a rather reduced inflorescence and anthers whose thecal halves retain curvature after dehiscence. These latter characters are suggestive of a relationship with *G. eriocalyx* which also occurs in Serra Negra. The possibility of a hybrid origin for *G. brunnea* might repay investigation.

Cambessedes' eptithet *brunea* was clearly intended to refer to the brown indumentum of this species (described as *bruneo-tomentosa/ae/i/us* throughout the description) and so should be corrected to *brunnea*. Cambessedes noted that he had found the ovary to be bilocular but Saint-Hilaire's notes reported it as trilocular. My dissections confirmed Cambessedes' description: Saint-Hilaire's observation may have been based on a single aberrant flower or may simply represent an error.

Not having had the opportunity to examine Saint-Hilaire's material, Berg treated *G. brunnea* under *Myrcia* with an expression of doubt. His description is rather shorter than that provided for other species and is clearly based on Cambessedes' original description. Legrand (1958) studied some of the Saint-Hilaire collections held at P and transferred half a dozen of

Cambessedes' *Myrcia* species to *Gomidesia*, making new combinations where required. One of the three Saint-Hilaire sheets of *G. brunnea* at P bears Legrand's annotation with his new combination and an isotype label, while the other two sheets lack any annotation by Legrand and are labelled isotype and type respectively. The latter is here designated lectotype.

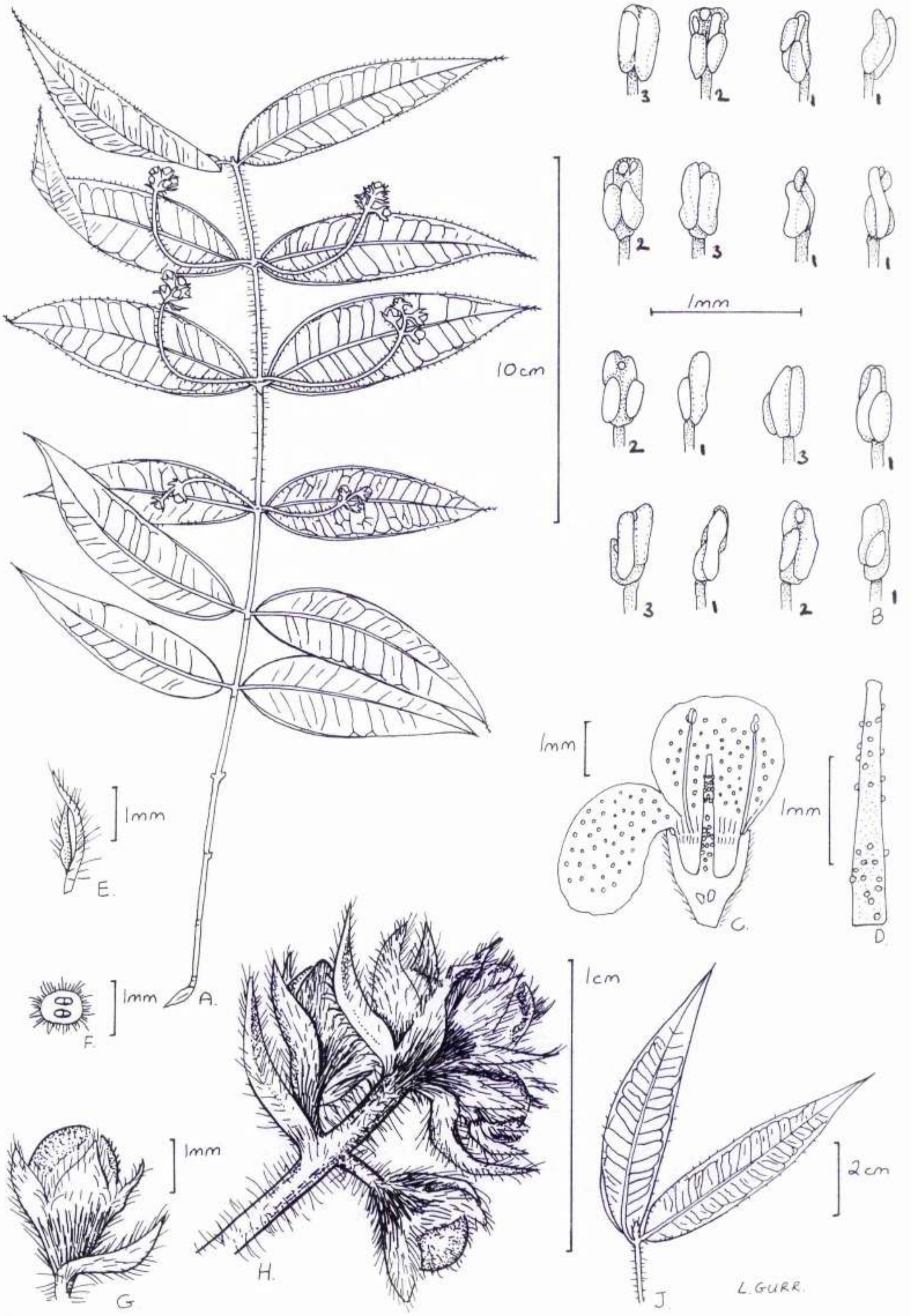
In the course of his travels Saint-Hilaire (1974a, 1974b) visited at least two different localities named Serra Negra, Minas Gerais: one in the north of the state near Minas Novas and the other in the south near the border with Rio de Janeiro. The latter locality, an outlier of the Serra da Mantiqueira, where he collected at the beginning of his second journey through Minas Gerais, seems the more probable locality for *Gomidesia brunnea*.

**6. Gomidesia cambessedeana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 24. 1857. Type. Brazil. Rio de Janeiro: "in nemorosis pr. Santa Anna," *Beyrich s.n.* (holotype, B, n.v., presumed destroyed; probable isotype, P!, here designated lectotype).

Fig. 24 (also 1G).

*Habit unknown.* Branchlets 10 cm below the terminal bud 1-1.2 mm in diameter, rounded, with a moderately dense indument of erect or slightly deflexed, straight, brown, simple hairs up to 2 mm long; terminal bud 6–8 mm long with a very dense indument of appressed hairs. Stipule lobes 0.8–2.5 mm long. Inter-petiolar ridge distinct. Petioles (1–)1.5–2.5(–3) mm long, 1 mm wide, flat or slightly channeled. *Lamina* lanceolate (to narrowly elliptic), 55–74 mm long, 15–23 mm wide, 3.2–4.2 times as long as wide; apex long acuminate; base rounded or obtuse and minutely auriculate; margin flat or bent down in apical portion of leaf, strongly recurved to revolute near leaf base; midrib sulcate above, raised to prominent below; lateral veins more or less straight, slightly raised above and below, diverging at c. 70–80° from the midrib; secondary laterals composite, rarely equalling the laterals in prominence and somtimes indistinct; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation inconspicuous above and below; venation between marginal vein and margin inconspicuous or obscured by revolute margin. Indumentum sparse or absent above except along midrib where it is dense, sparse to moderately dense below, consisting of erect, straight or slightly curved, brown hairs up to 1.2 mm long. Gland dots indistinct above, occasionally distinct below. Mature leaves membranaceous to chartaceous. *Conflorescence* comprising 2–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence a pendulous botryoid (??) of c. 5 flowers, c. 3.5–6 mm long, reaching c. 2/3 to 3/4 the length of

FIG. 24. *Gomidesia cambessedeana.* **A** Conflorescence and foliage; **B** Anthers in lateral (1), dorsal (2) and ventral (3) view; **C** Longitudinal section of flower; **D** Style; **E** Bract; **F** Transverse section of ovary; **G** Flower bud; **H** Inflorescence; **J** Branch apex showing terminal vegetative bud. L from *Beyrich s.n.*, the rest from *Sellow s.n.* Drawn by L. Gurr.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the subtending leaf; peduncle c. 2.5–4.5 mm long i.e., c. 2/3 to 3/4 or more of the length of the inflorescence, curved, 1 mm wide, lateral branches a single pair below the terminal cyme or cluster of cymes. *Mature flower buds* 4–5.5 mm long x 3.5–5 mm wide. Calyx lobes triangular, 2–2.5 mm long x c. 1.5 mm wide, apex long-acuminate (terete?), with a moderately dense indumentum externally, glabrous internally, at least towards the base; hypanthium c. 2.1 mm long, prolonged c. 1.2 mm above the ovary with a moderately dense indument internally, except in the area immediately surrounding the base of the style where it is glabrous; disk c. 2–3.7 mm diameter densely pubescent. Stamens c. 111 per flower; anthers 0.3–0.45 mm long, apex truncate with conspicuous gland, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, margins in the plane of curvature, connivent, effective dorsal opening c. 1/3 the length of the anther, residual septum occasionally visible. Style c.10 mm, with conspicuous glands conferring a knobbly appearance, especially in the upper 1/3; stigma capitate. Ovary 1.6 mm long, bilocular, ovules 2 per locule. *Fruit* not seen.

**Distribution (not mapped) and ecology.** Apparently confined to the Atlantic rain forest of Rio de Janeiro though none of the old localities cited can be pinpointed with certainty.

**Conservation.** A decade ago this distinctive species was thought likely to be extinct, as it had not been collected for more than 50 years. However, recent collections from Poço das Antas may be referrable to this species (G.M.Barroso, in litt.).

**Phenology.** Flowering material has been collected in February.

**Specimens examined. BRAZIL. RIO DE JANEIRO:** In nemorosis pr. St. Anna, Dec, *Beyrich s.n.* (P!); Tocovão (Socovão?), perto do Bananal, 17 Feb 1833, *Palma 7130* (R!). **LOCALITY NOT STATED**: *Sellow s.n.* (K! (ex. B), LE!).

*Gomidesia cambessedeana* is easily distinguished from all other members of the genus by the combination of its few-flowered inflorescence with a curved (presumably pendulous) peduncle, its triangular calyx lobes with a distinct acumen and its erect indumentum of brown hairs. The inflorescence of *G. flagellaris* is similar in structure to that of *G. cambessedeana* but the former species has obtuse, depressed-obovate calyx lobes and a pale appressed indument. I have not yet had the opportunity to examine the Poço das Antas material mentioned above; should it prove to be referrable to *G. cambessedeana* it will represent the first fruiting material of the species, allowing the completion of the description. A single collection from Espírito Santo, *Santos 229* from near Conceição da Barra, is strongly reminiscent of *G. cambessedeana*, resembling the material cited above in leaf shape, indument and in having few-flowered inflorescences (in bud). However, in view of the relatively stout peduncles which are only very slightly curved (suggesting an erect inflorescence), the broad bracts and the depressed-obovate calyx-lobes observed in this material I prefer not to place it in *G. cambessedeana* at present but to reserve judgement until flowering material can be studied. I consider *G. cambessedeana* to be a rather isolated species within the genus. It may have affinities with *G. eriocalyx* which also has flexuous peduncles, few-flowered inflorescences, acute calyx lobes and similar anthers.

7. **Gomidesa carvalhoi** Nic Lughadha sp. nov. ined. Type. Brazil. Bahia: Mun. Una, Ribeirão da Caveira, Serra Javo. Ramal com entrada no km 11 da Rodovia São José/Una, 425 m, 25 Feb 1986, *Santos 3996* (holotype, CEPEC!; isotypes, K!, US!).

*Treelet* or *shrub* 0.5–5 m tall. Branchlets 10 cm below the terminal bud 3 mm in diameter, rounded, with a dense indumentum of erect, straight, pale hairs to 1 mm long; terminal bud c. 11 mm long with a dense indumentum of appressed or ascending, straight, brown hairs to 0.6 mm. Stipule lobes not seen. Inter-petiolar ridge distinct, transverse. Petioles 7 mm long, 2 mm wide, channeled. *Lamina* oblanceolate, (85–)187–200 mm long, (36–)57–64 mm wide, (2.4–)3.1–3.3 times as long as wide; apex abruptly acuminate; base truncate, minutely auriculate; margin flat or bent down; midrib sulcate or impressed above, prominent below; lateral veins curved, flat above, prominent below, diverging at c. 70–80° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein almost equalling the laterals in prominence and curving between them or running more or less parallel to the margin; higher order venation conspicuous, flat and pale above, raised below; venation between marginal vein and margin distinct, including submarginal vein. Indumentum moderately dense above, consisting of erect, straight or curved, whitish hairs to 0.6 mm, moderately dense below, consisting of erect, straight or curved, pale brown hairs to 1 mm long. Gland dots indistinct above and below. *Conflorescence* comprising a single pair of uniflorescences in the axils of distal leaves. Uniflorescence an erect metabotryoid of c. 13 flowers, c. 32 mm long, reaching c. 1/6 the length of the subtending leaf; peduncle c. 12 mm long i.e., c. 2/5 the length of the inflorescence, 2 mm wide, more or less rounded; lateral branches 3 below the terminal cyme or cluster of cymes. *Mature flower buds* 7 mm long x 5.5 mm wide. Calyx lobes hemi-orbicular, c. 1.7 mm long x 3.6 mm wide, apex rounded, with a dense indumentum of curved straw coloured hairs to 0.8 mm above, internally glabrous towards base, elsewhere with a moderately dense indumentum of appressed, straight, pale hairs to 0.3 mm; hypanthium 3.5 mm long, prolonged c. 1.7 mm above the ovary, with a dense indumentum of ascending, straight, straw-coloured hairs to 1.2 mm long externally, dense internally; disk c. 3.3 mm diameter, indumentum dense. Stamens 85 per flower; filament narrowing abruptly to the point of insertion on connective, anthers 1.1 mm long, apex deeply emarginate, vertical displacement of thecae marked, thecal halves retain curvature after dehiscence, connivent or held parallel with margins inrolled, effective dorsal opening c. 1/8 the length of the anther, residual septum occasionally visible, vertical. Style c. 8.5 mm, with dense indumentum in lower 2/3; stigma indistinct or minutely capitate. Ovary c. 1.7 mm long, bilocular, ovules 2 per locule. *Fruit* globose, 9–14 mm diameter, crowned with the erect, imbricate calyx lobes. Mature seed one per fruit, c. 7 mm long, testa mid-brown, hypocotyl densely sericeous.

**Distribution (Map 5) and ecology.** *Gomidesia carvalhoi* is endemic to the Atlantic rain forest of Bahia between Ilhéus and Una.

**Phenology.** I have seen only two flowering collections of *Gomidesia carvalhoi,* made in October and February respectively. Fruiting material is much more commonly collected from February to June.

**Specimens examined. BRAZIL. BAHIA:** Mun. Ilhéus. Ca. 7 km na estrada de Olivença para Vila Brasil, 30 May 1991, *Carvalho 3288* (CEPEC!, K!); Mun. Una, Estrada Olivença/Vila Brasil, 33 km a SW de Olivença. Maruim, fazenda 2 de Julho, 26 Apr 1981, *Carvalho 648* (CEPEC!, K!, NY!); Mun. Ilhéus. Ramal novo para o povoada de Vila Brasil, com entrada no Km 28 do rodovia Ilhéus/Una, 27 Feb 1985, *Mattos Silva & Plowman 1830* (CEPEC!, F!); Mun. Una. Km 19 da Rod. São José de Buerarema/Una, 1 Apr 1980, *Mattos Silva 718* (CEPEC!); Mun. Una. Km 17 de estrada que liga a Rod. BR-101 (São José) a Rod. BA-215, 29 Oct 1978, *Mori 11024* (CEPEC!, K!); Mun. of Ilhéus, road from Olivença to Una, 18 km S of Olivença, 0 m, 21 Apr 1981, *Mori 13702* (CEPEC!); Mun. Una. Rodovia BA-265. a 19 km de Una, 60 m, 25 Feb 1978, *Mori 9281* (CEPEC!, K!); Mun. Una. Ramal que liga a BA 265 (Rod. Una Rio Branco) a BR 101 (São José) a 8 km SW do cruzamento e a 20 km NW de Una, em linha reta, 50 m, 27 Feb 1978, *Mori 9326* (CEPEC!, K!, MO!, NY!); Una, Faz. S. Rafael Mata solo para Seringa, 18 Jun 1971, *Pinheiro 1407* (CEPEC!); Mun. Una. Estação Experimental Lemos Maia. CEPLAC. Ao lado W da sede da estação, 11 Oct 1980, *Rylands 39/1980* (CEPEC!); Mun. Una, Riberão da Caveira, Serra Javo. Ramal com entrada no km 11 da Rodovia São José/Una, 425 m, 25 Feb 1986, *Santos 3996* (CEPEC!, K!, US!); Mun. Una, Serra da Luzia. Ramal com entrada no km 5.7 da rodovia São José/Una, lado N, 1.8 km. Fazenda "Conjunto Santa Rosa", 7 km por ar ENE São José, 550 m, 27 Feb 1986, *Santos 4048* (CEPEC!, K!, US!); Mun. Una, Km 20, rodovia São José a Una, 100 m, 22 Feb 1986, *Santos & Judiewicz 4114* (CEPEC!, US!).

**Local names.** Pitanga (Bahia). This name is also applied to diverse species of *Eugenia*.

*Gomidesia carvalhoi* is clearly related to *G. crocea* with which it shares characters such as the scutate leaf base (truncate and minutely auriculate) and the densely sericeous hypocotyl. However it lacks the deeply ridged ovary and fruit so characteristic of *G. crocea* and also differs in having rather few-flowered inflorescences and less rigid leaves.

This species is dedicated to Dr. André Carvalho who, with his team at CEPEC, has added so much to our knowledge of the biodiversity of the southern Bahian moist forest.

**8. Gomidesia catharinensis** (D.Legrand) Nic Lughadha comb. et stat. nov. ined.

*Gomidesia affinis* (Cambess.) D.Legrand var. *catharinensis* D.Legrand [Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 14. 1959; Sellowia 13; 278. 1961. *nom. nud.*] Flora Ilustr. Catar. [MIRT]: 13. Type. Brazil. Santa Catarina: Garapuvu, Vista Alegre, Sombrio, 29 Jan 1960, *Reitz & Klein 9485* (holotype, MVM? n.v.; isotype, HBR, n.v.).

(Fig. 3F and 12k-p).

*Treelet* or *tree* 2–8(–15) m tall. Branchlets 10 cm below the terminal bud 1.5–2 mm in diameter, slightly flattened or rounded, with a moderately dense or dense indumentum of erect or ascending, straight or curved or crisped brown hairs to c. 0.5–1.2 mm long; terminal bud 5–12 mm long. Stipule lobes to 1.6 mm long. Inter-petiolar ridge absent. Petioles 5–8 mm long, 1–2 mm wide, channeled. *Lamina* oblong to narrowly oblong, 67–139 mm long, 16–27 mm wide, (2.8–)3–5.4 times as long as wide; apex acuminate or apiculate; base acutely or obtusely cuneate; margin recurved to revolute; midrib sulcate above, prominent below; lateral veins more or less straight, impressed above, prominent below, diverging at c. 55–90 ° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping between them; higher order venation conspicuous, impressed above, raised below; venation between marginal vein and margin conspicuous or hidden by recurved margin. Indumentum sparse to moderately dense above, consisting of appressed or erect, curved or straight, white hairs c. 0.4 mm long, moderately dense to dense below, consisting of erect, straight, brownish hairs, c. 0.5 mm long. Gland dots indistinct above and below. Mature leaves chartaceous to coriaceous. *Conflorescence* comprising 1–2 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect triad or metabotryoid of c. 3–13 flowers, 26–60 mm long, reaching c. 3/10–3/5 the length of the subtending leaf; peduncle 14–25 mm long i.e., c. 1/3–3/4 the length of the inflorescence, 1–1.5 mm wide, flattened; lateral branches none or 1–3 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 5.5 mm long x 5 mm wide. Calyx lobes depressed ovate, 1.4–1.8 mm long x 3–4.1 mm wide, apex asymmetrically apiculate, with a dense indumentum of appressed, curved, pale brown hairs to 1.2 mm long externally, dense internally, consisting of appressed, straight pale hairs of mixed lengths; hypanthium 3.6–4.2 mm long, prolonged c. 2.3–2.5 mm above the ovary with dense indument internally and externally; disk c. 4.2 mm diameter, indumentum dense. Stamens 110–149 per flower; anthers c. 0.8 mm long, filament tapering to point of insertion on connective, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves retain curvature on dehiscence, connivent or held parallel or gaping, with margins flat or recurved, effective dorsal opening 1/6–1/4 the length of the anther, residual septum often visible, vertical. Style c. 8–9 mm, with moderately dense indumentum in lower 1/3; stigma minutely capitate. Ovary 1.3–1.7 mm long, bilocular (or rarely trilocular), ovules 2 per locule. *Fruit* globose, 10–12 mm diameter, crowned with the erect, imbricate calyx lobes. Mature seed 1 per fruit, c. 8 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 6) and ecology.** *Gomidesia catharinensis* is confined to the states of Paraná and Santa Catarina at altitudes from 4 to 1200 m above sea level. Most of the collections studied provide little information on habitat (Reitz and Klein often described the collection area simply as 'mata') and Legrand and Klein (1967) describe this species as being without pronounced affinities for particular habitats. It appears to be most frequent in Araucaria forest formations (*pinheiral*) but is also reported from secondary forest and from the Atlantic rain forest.

**Phenology.** *Gomidesia catharinensis* flowers from January to March with a distinct flowering peak in February. Mature fruit have been collected from May to October.

**Specimens examined. BRAZIL.** PARANÁ: locality not stated, *Dusen s.n.* (S!); Serrinha, 10 Oct 1908, *Dusen 6853* (S!); Mun. S. José dos Pinhais, Purgatório, 19 Jul 1967, *Hatschbach 16705* (C!, MO!, NY!, SPF!, UEC!, US!); Mun. Piraquara, Mananciais da Serra, 21 Feb 1968, *Hatschbach 18625* (C!, F!, MO!, P!); Mun. S. Mateus do Sul. Tezoura, 25 Jun 1969, *Hatschbach 21669* (MO!, MU!); Mun. S. Jerônimo da Serra, Fda. Nho Ó 27 Sep 1970, *Hatschbach 24808* (NY!, C!); Barracão, 17 May 1977, *Hatschbach 39917* (MO!, MU!, NY!, UB!, UEC!); Mun. Tijucas do Sul, Araçatuba, 900 m, 15 Mar 1962, *Hatschbach 9047* (U!); Col. Roseira (mun. S. José dos Pinhais), 22 Feb 1968, *Koczicki 89* (MU!); Brandalize, 20 km N of Clevelândia, 700 m, 3 May 1966, *Lindeman 1187* (RB!, U!, US!); near Campo Novo, N. of Bocaiúva do Sul, 32 km N of Curitiba, 1000 m, 17 Aug 1966, *Lindeman & Haas 2364* (K!, NY!, RB!, U!); SANTA CATARINA: Vargem Grande, Ilha de S. Catarina. Florianópolis, 50 m, 20 Feb 1974, *Bresolin 1118* (PACA!); Morro da Ressacada, Itajaí, 150 m, 20 Feb 1956, *Klein 1872* (PACA!, US!); Estação Florestal I. N. P., Ibirama, 300 m, 6 Mar

1956, *Klein 1902* (B!, BR!, K!, NY!, US!); Horto Florestal I.N.P., Ibirama, 300 m, 19 May 1956, *Klein 2008* (NY!, PACA!, US!); Mata da companhia hering, Bom Retiro, Blumenau, 250 m, 10 Mar 1960, *Klein 2389* (NY!, US!); Mata da companhia hering, Bom Retiro, Blumenau, 300 m, 3 Jun 1960, *Klein 2452* (BR!); entre Anchieta e Campo erê, 17 Jan 1983, *Pirani 459* (SP!); Nova Teutônia, 27 Jan 1944, *Plaumann 360* (RB!); Serra do Espigão, Papanduva, 1000 m, 10 Jul 1962, *Reitz 13064* (NY!); Horto Florestal, I.N.P., Ibirama, 300 m, 1 Mar 1954, *Reitz & Klein 1593* (NY!, PACA!, S!, U!, US!); Braço Joaquim, Luís Alves, Itajaí, 4 m, 19 Jul 1954, *Reitz & Klein 1987* (NY!, US!); Braço Joaquim, Luís Alves, Itajaí, 4 m, 16 Feb 1956, *Reitz & Klein 2714* (NY!, US!); Pilões, Palhoça, 4 m, 24 Feb 1956, *Reitz & Klein 2803* (NY!, US!); Rio Mirodor - Oleães, 250 m, 18 Jan 1950, *Reitz 3392* (S!); Pilões, Palhoça 300 m, 7 Sep 1957, *Reitz & Klein 3671* (US!); Campo Alegre, 900 m, 6 Sep 1957, *Reitz 4840* (US!); Morro do Iquererim, Campo Alegre, 1200 m, 5 Feb 1958, *Reitz 6462* (S!, US!); Serra do Matador, Rio do Sul, 700 m, 26 Jan 1959, *Reitz & Klein 8360* (K!); Mun. Lajes: Pinheiral, 8 km east of Encruzilhada, 950 m, 13 Feb 1957, *Smith & Klein 11358* (R!, US!); Mun. Lajes. Residual forest between the crest of the Serra Geral and Encruzilhada, 950 m, 2 Dec 1956, *Smith 8025* (S!, US!); Mun. Dionísio Cerqueira: Pinheiral and ruderal, Tracotinga, 20 km west of the Rio Capetinga on the road to Dionísio Cerqueira, 950 m, 30 Dec 1956, *Smith & Reitz 9638* (K!, NY!, RB!, US!).

**Local names.** Batinga (Santa Catarina), Batito (Paraná), Liga-boca (Santa Catarina), Rapa Guela (Santa Catarina). The name batinga is applied to a number of different species of *Gomidesia*, including *G. cerqueiria*, *G. fenzliana* and *G. freyreissiana*. The name rapa guela is applied to *G. anacardiifolia* in Santa Catarina. Liga-boca probably refers to the astringent nature of the fruit; this name is only reported on fruiting specimens of this species. The name Rapa Guela (scratch throat) may have similar origins.

*Gomidesia catharinensis* is recognised by its rather narrow leaves with impressed venation and its few-flowered inflorescences. Legrand (1967) distinguished this taxon as a variety of *G. affinis* but noted that there was no convergence between his *G. affinis* var. *catharinensis* and the other species of the *G. affinis* complex. Despite the striking resemblance of the leaves, I consider *G. catharinensis* quite distinct from *G. affinis* which has much smaller flowers and more open anthers. *Gomidesia catharinensis* appears to be closely related to *G. reticulata* which it resembles in flower size and anther morphology. The similarity between these species is reflected in the fact that material of *G. catharinensis* has been mis-identified as *G. reticulata* on a number of occasions (see under *G. reticulata*).

Although I have not seen the type of *G. affinis* var. *catharinensis* I have seen many of the paratypes cited in the protologue and am confident of the application of the name.

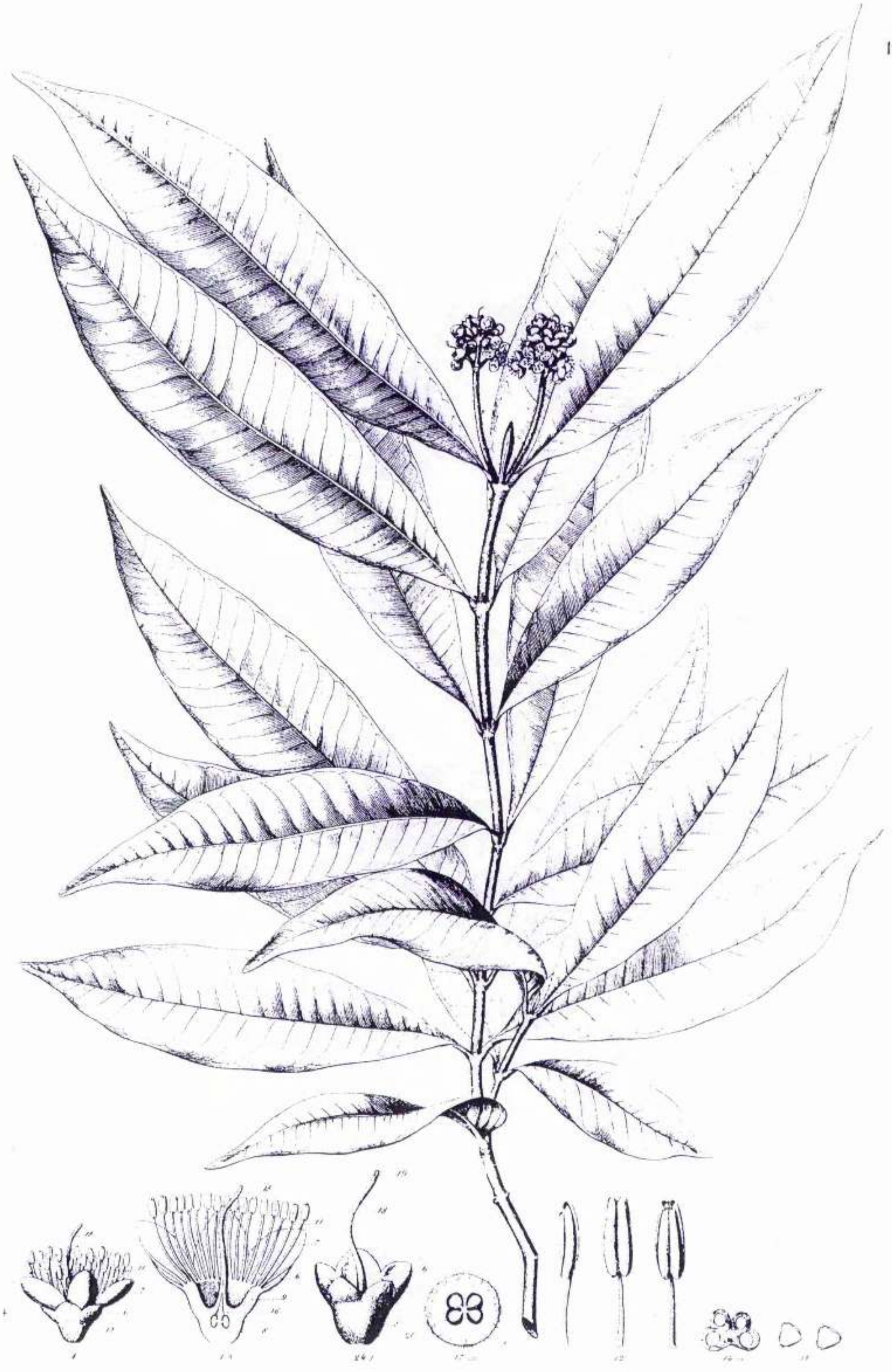
**9. Gomidesia cerqueiria** Nied., *in* Engl. & Prantl, Nat. Pflanzenfam. **3 (7):** 78. 1893, based on *Cerqueiria sellowiana*.

*Cerqueiria sellowiana* O.Berg, Linnaea **27:** 6. 1855. Type. Brazil. Bahia. *Sellow s.n.* (holotype, B!, presumed destroyed; probable isotype, K!, here designated lectotype).

Fig. 25 & 26 (also 13k&m and 14p&q)

*Shrub* or *small tree* 2–3 m tall. Branchlets 10 cm below the terminal bud 3.5 mm in diameter, rounded, with a moderately dense indumentum of appressed, straight, white hairs to 0.3 mm long; terminal bud c. 6 mm long with a dense indumentum of appressed, straight, white hairs to 0.4–0.5 mm. Stipule lobes 0.6–0.8 mm long, stout. Inter-petiolar ridge distinct. Petioles 4–6(–7) mm long, 1.5–2 mm wide, flat or channeled, with a dense indumentum of appressed, straight, white hairs, c. 0.3–0.5 mm long. *Lamina* lanceolate, 89–230 mm long, 21–55 mm wide, 4.2–4.5(–5.4) times as long as wide; apex acuminate; base acutely cuneate; margin flat or bent down; midrib raised and channeled above, prominent below; lateral veins straight, slightly raised above and below, diverging at c. 80 ° from the midrib; secondary laterals composite, almost equalling the laterals in prominence and often difficult to distinguish from these latter; marginal vein more or less equalling the laterals in prominence and scarcely curving between them, almost parallel to the margin; higher order venation inconspicuous above and below; venation between marginal vein and margin inconspicuous. Indumentum absent above, moderately dense below, consisting of appressed, straight, white hairs of variable length, most c. 0.1–0.2 mm but a few up to 0.4–0.6 mm long. Gland dots indistinct above, distinct below, dark and slightly raised. Mature leaves chartaceous. *Conflorescence* comprising a single pair of uniflorescences in the axils of distal leaves. Uniflorescence an erect triad or crowded thyrsoid of c. 15 flowers, 15–45 mm long, reaching c. 1/10 the length of the subtending leaf; peduncle 11–32 mm long i.e., c. 3/4 the length of the inflorescence, 2–3 mm wide, flattened; lateral branches a single pair or none below the terminal cyme or cluster of cymes. *Mature flower buds* 5 mm long x 3.5 mm wide. Calyx lobes hemi-orbicular, c. 1–1.1 mm long x 2–2.1 mm wide, apex rounded, with a moderately dense or dense indumentum of appressed, straight, white or silvery hairs up to 0.2 mm long externally, indumentum shorter and less dense internally, moderately dense towards base, absent towards apex; hypanthium more or less deeply ridged vertically, c. 2.2–2.4 mm long, prolonged c. 1.4–1.9 mm above the ovary with a dense indumentum of appressed, straight, white or silvery hairs to 0.3 mm long; disk c. 2.1–2.5 mm diameter, indumentum dense. Stamens 44–56 per flower; filament

FIG. 25. *Gomidesia cerqueiria*. Plate 10 from Martius' Flora Brasiliensis **14 (1)** which appeared as "*Cerqueiria sellowiana*."



CERQUEIRIA Sellowiana.

narrowed abruptly at point of insertion on connective, anthers c. 1.3–1.5 mm long, apex deeply emarginate or bifid, vertical displacement of thecae marked, thecal margins inrolled after dehiscence, thecal halves retaining curvature, connivent, effective dorsal opening c. 1/8 the length of the anther, residual septum not visible. Style c. 8 mm, indumentum moderately dense in lower 1/3, sparse or absent in middle third, absent in upper third; stigma minutely capitate, distinctly papillate. Ovary c. 0.7–1.2 mm long, bilocular, ovules 2 per locule. *Mature fruit* not seen, developing fruit more or less globose, with or without deep vertical ridges, crowned with the erect, imbricate calyx lobes. Developing seed one per fruit.

**Distribution (Map 7) and ecology**. *Gomidesia cerqueiria* is known from only three sites in the Atlantic rain forest of Espírito Santo and southern Bahia. Most of the collections cited are from the most southerly of these sites where *G. cerqueiria* frequently forms an important element of the understorey in *nativo* and *tabuleiro* forest.

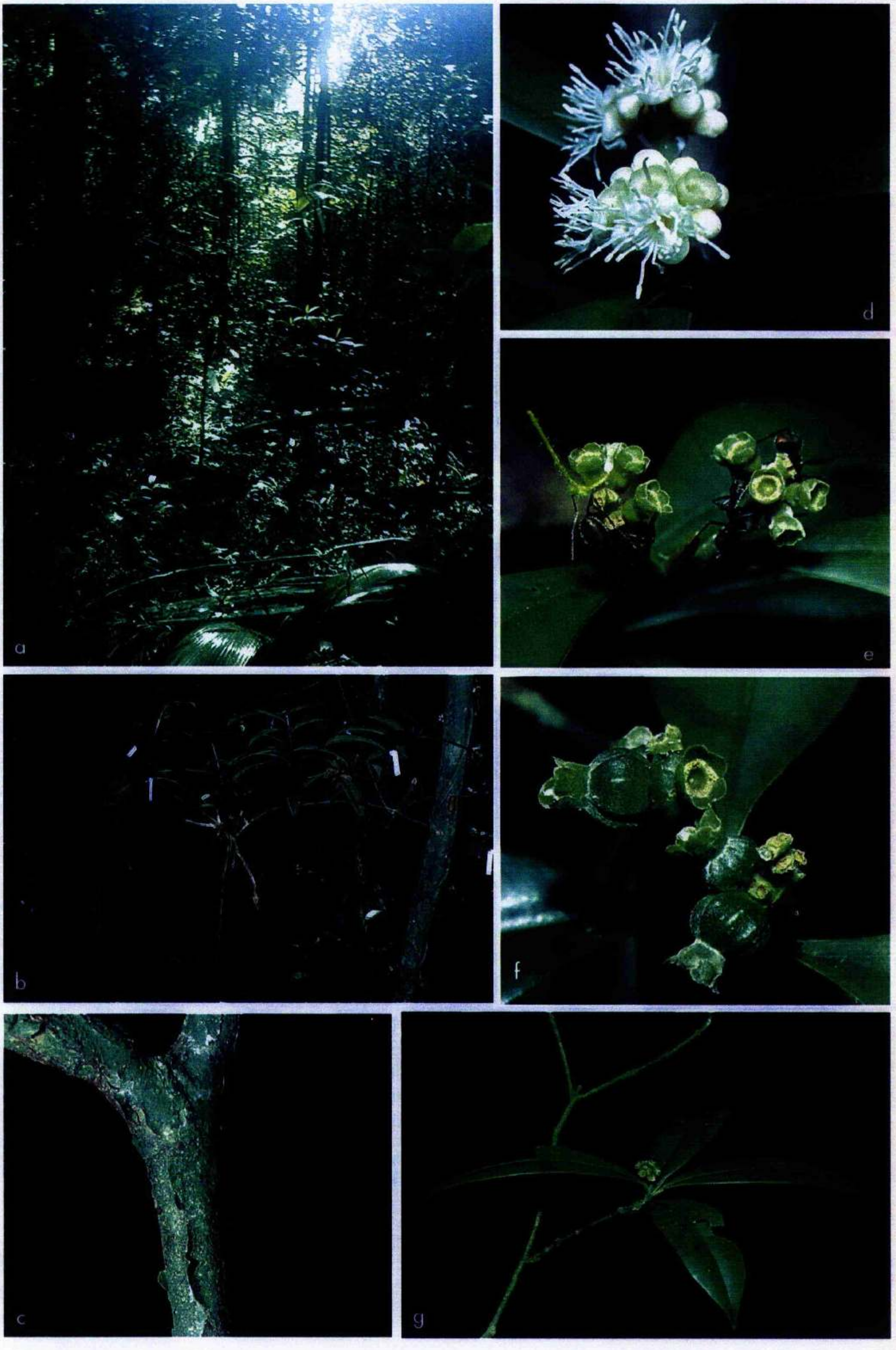
**Phenology**. Flowering collections have been made in January and February while immature fruits are reported in July. Results of detailed phenological observations on *G. cerqueiria* are presented under Case Studies.

**Specimens examined. BRAZIL. BAHIA:** Alcobaça, ramal para S. Antônio. Mata, 24 Jan 1972, *Pinheiro 1762* (CEPEC!); without locality, *Sello s.n.* (K!). **ESPÍRITO SANTO:** Reserva Florestal da CVRD, Linhares. Próximo ao viveiro de mudas, 17 Feb 1993, *Nic Lughadha 154* (CVRD!, K!); Reserva Florestal da CVRD. Linhares. Estrada Parajú a 0.5 km da estrada da Gávea, 17 Mar 1993, *Nic Lughadha 155* (CVRD!, K!); Mun. Linhares, Reserva Florestal da CVRD. Vegetação de 'Nativo', 17 Jan 1975, *Peixoto 417* (NY!, RB!); Reserva Florestal da Companhia Vale do Rio Doce, 23 Mar 1986, *Sobral 4660* (CVRD!); Reserva de Linhares. DOCEMADE. crescendo em mata de tabuleiro, 31 Jan 1972, *Sucre 8344* (NY!, RB!, US!); São Mateus, Reserva Biológica de Sooretama, Mun. Linhares. Mata de Tabuleiro, Jul 1969, *Sucre 9659* (RB!).

**Local names.** Batinga da mata (Espírito Santo) The name batinga is applied to a number of species of *Gomidesia* in this area e.g. *G. fenzliana* and *G. freyreissiana*.

*Gomidesia cerqueiria* is vegetatively very similar to *G. nitida* but differs in having only moderately dense indumentum on the abaxial surface of the leaf and thus lacking the metallic appearance so characteristic of *G. nitida*. The two species also resemble each other in their inflorescence structure but differ markedly in their anther morphology, the anthers of *G. cerqueiria* being more than twice as long as those of *G. nitida* with inrolled thecal margins and closely connivent thecal halves quite unlike the more open anthers of *G. nitida* which have reflexed thecal margins and residual septa normally visible. Two fruiting collections from Rio

FIG. 26. *Gomidesia cerqueiria* near Linhares, Espírito Santo. **a** habitat; **b** habit; **c** bark; **d** flower, **e** developing fruits; **f** older fruits with marked longitudinal ridges; **g** infructescence and leaves.


a
b
c
d
e
f
g

de Janeiro resemble *G. cerqueiria* in their leaf venation and stout compressed peduncle and may represent an undescribed species.

Berg (1855) published the monotypic genus *Cerqueiria* to accommodate the only species of Brazilian Myrtaceae to exhibit what he considered to be truly poricidal anthers. The generic name was intended to commemorate one Ignácio Acciolo de Cerqueira e Silva of Pará, Brazil author of '*Corografia Paraense ou descripam fisica histórica e politica da Provincia do Gram-Pará*' and '*Memórias históricas e politicas da Prov. da Bahia*'. Niedenzu's (1893) transfer of *Cerqueiria sellowiana* to *Gomidesia* necessitated a new name since the epithet *sellowiana* was no longer available in that genus. Niedenzu coined the new binomial *Gomidesia cerqueiria*. I have interpreted his use of the epithet *cerqueiria* in this context as a noun in apposition; thus the spelling does not require correction.

**10. Gomidesia cordiifolia** (DC.) Nic Lughadha comb. nov. ined.

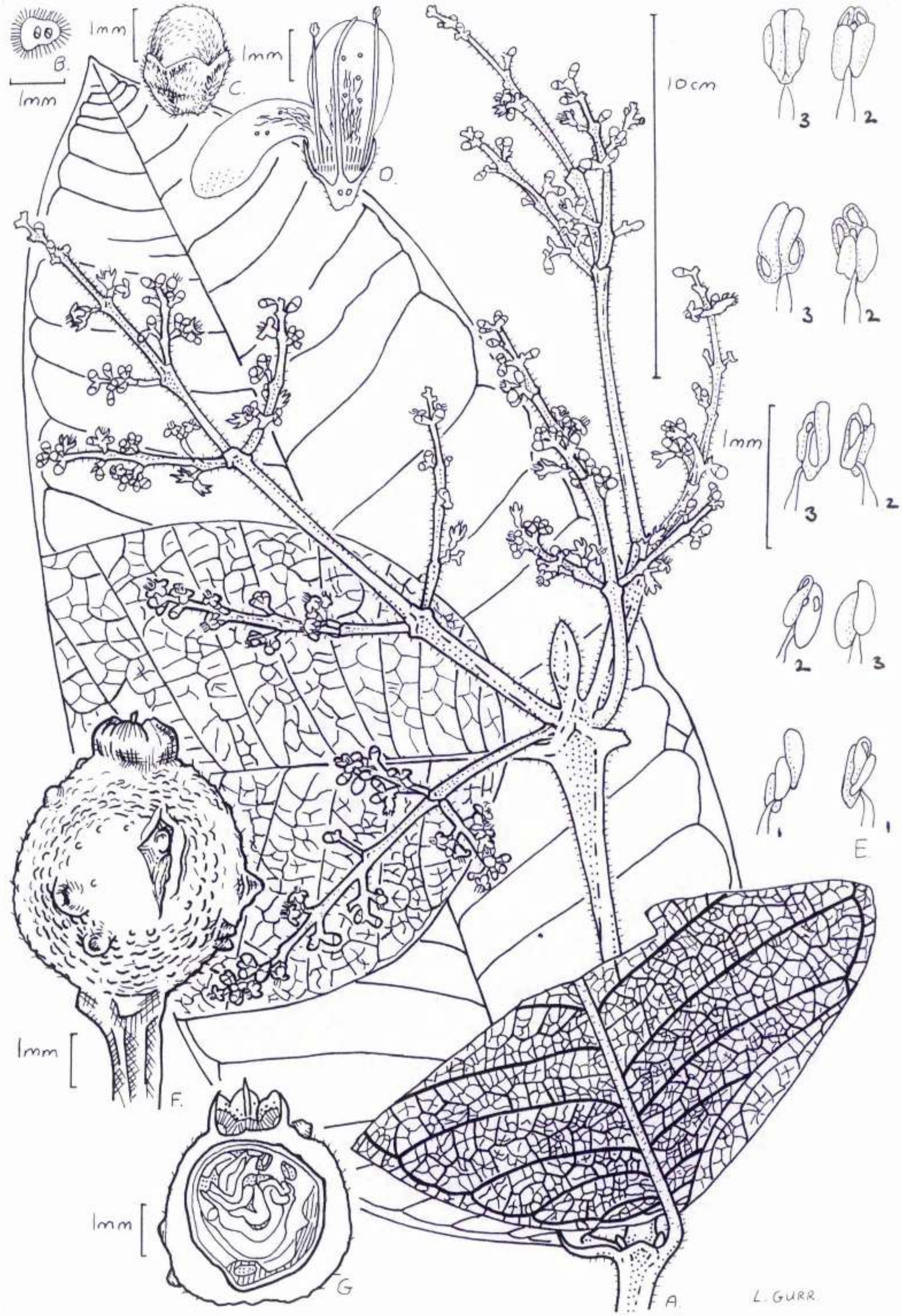
*Myrcia cordiifolia* DC., Prodr. **3:** 248. 1828. "cordiaefolia". Type: Brazil, São Paulo: "in silvis, vulgo Capões, udis ad Taubaté et Aldea da Escada (Epada?)," *Martius s.n.* (lectotype, M!, here designated; isolectotype, M!).

Fig. 27.

*Gomidesia linkiana* O.Berg in Martius, Fl. bras. **14 (1):** 16. 1857. *nom. illeg.* based on *Myrcia cordiifolia* DC.

*Tree* 4–5 m tall. Branchlets 10 cm below the terminal bud c. 6 mm in diameter, slightly flattened, with a dense indumentum of mostly erect, straight, brown hairs to 0.5 mm long (but many significantly shorter); terminal bud to 27 mm long. Stipule lobes not seen. Inter-petiolar ridge prominent, inverted V-shaped. Petioles c. 10–15 mm long, 5 mm wide, deeply channeled. *Lamina* oblong or ovate, 230–340 mm long, 120–160 mm wide, 1.5–2.2 times as long as wide; apex abruptly acuminate or rounded and minutely apiculate; base truncate; margin bent down; midrib sulcate above, prominent below; lateral veins more or less straight, sulcate to impressed above, prominent below, diverging at c. 60–70° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping between them; higher order venation conspicuous, deeply impressed above, raised below; venation between marginal vein and margin conspicuous. Indumentum sparse above, consisting of appressed, straight or curved, pale hairs to 0.8 mm, moderately dense below, consisting of mostly erect, straight, reddish-brown hairs to 0.5 mm

FIG. 27. *Gomidesia cordiifolia*. **A** Conflorescence and foliage; **B** Transverse section of ovary; **C** Flower bud; **D** Longitudinal section of flower; **E** Anthers in lateral (1), dorsal (2) and ventral (3) view; **F** Fruit; **G** Longitudinal section of fruit and seed. **A** - **E** from *Emygdio Filho 3766*, **F** & **G** from *Eiten 15078*. Drawn by L. Gurr.


B.
1mm
1mm
C.
1mm
D.
10cm
3
2
3
2
1mm
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2
3
1
1
E.
1mm
F.
1mm
G
A.
L. GURR

long, dense on veins. Gland dots indistinct above and below. Mature leaves chartaceous to coriaceous. *Conflorescence* comprising 1–2 pairs of uniflorescences in the axils of distal leaves; phylloscopic accessory inflorescences frequent. Uniflorescence an erect complex thyrsoid of > 250 flowers, c. 210 mm long, reaching c. 1/2 or 3/5 the length of the subtending leaf; peduncle curved towards the axis, c. 50 mm long i.e., c. 1/4 the length of the inflorescence, 6 mm wide, terete or slightly flattened; lateral branches 6–7 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 4 mm long x 3 mm wide. Calyx lobes depressed ovate, c. 1 mm long x 1.7 mm wide, apex rounded, with a dense indumentum of straight hairs up to 1 mm long externally, indumentum shorter and paler internally; hypanthium c. 1.4 mm long, prolonged c. 0.5 mm above the ovary, densely pubescent externally and internally; disk c. 2 mm diameter, densely pubescent. Stamens c. 66 per flower; filaments tapering to a very fine point at apex, anthers 0.8 mm long, apex deeply emarginate, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent or gaping slightly, thecal margins flat, effective dorsal opening 1/4–1/3 the length of the anther, residual septum sometimes visible, vertical. Style c. 7 mm, with dense indumentum in lower 1/6; stigma minutely capitate, distinctly papillate. Ovary c. 1 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 9 mm diameter, crowned with the connivent to erect, imbricate calyx lobes. Mature seed one per fruit, c. 7 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 8) and ecology.** Known only from two localities at the northern and southern extremities of the Serra da Mantiqueira. Collected in primary and secondary forest as an understorey treelet and in forest islands (presumably in *cerrado* vegetation).

**Phenology.** Collected in flower in December and with apparently mature fruit in September.

**Specimens examined. BRAZIL. MINAS GERAIS:** Mun. Marlierea, Parque Estadual do Rio Doce, 400 m, 18 Sep 1975, *Heringer & Eiten 15078* (MO!, UB!, US!); Parque Florestal do Rio Doce, *Mello Filho & Duarte 3766* (R!). **SÃO PAULO:** " sylvis capões udis ad Taubaté et Aldea da Epada"(Espada?), Dec, *Martius s.n.* (lectotype, M!, isolectotype, M!).

The combination of extremely large, bullate leaves and rather small flowers serves to distinguish *G. cordiifolia* from most other species of *Gomidesia*. Most (all?) other large-leaved species with which *G. cordiifolia* might be confused can be distinguished in flower by virtue of their more closed, tube-like anthers and in fruit by their hypocotyl which is pubescent, at least towards the base. One of the sheets of *Heringer 15078* was previously determined as *G. anacardiifolia* but this species differs in its few-flowered inflorescences and smaller leaves which may be flat or undulate but never bullate.

Berg (1857) recognised two species of *Gomidesia* among the material previously treated by de Candolle (1828) as two varieties of *Myrcia cordiaefolia*. On transferring the taxa to *Gomidesia* Berg gave new names at species level to each of the varieties and failed to take up de Candolle's original epithet. Thus *M. cordiaefolia* var. *minor* was renamed *G. pohliana* while the typical variety, which should have retained the original epithet, was given the superfluous new name *G. linkiana*. The large-leaved taxon which de Candolle treated as the typical variety is actually a rather rare species (known from only a handful of collections) and therefore the illegitimate name has scarcely become established in the literature. The only subsequent reference I can find to this species is by Legrand (1959) who commented that he had not seen material of *G. linkiana* but that its affinities with *G. affinis* (Cambess.) Legrand and allies were clear. As there is no case for conservation of this little known name the required new combination is in press in preparation for a treatment of *Gomidesia* for the Flora of São Paulo (Nic Lughadha, 1997).

De Candolle cited the Martius herbarium as the location of the type material. I have examined two 'Martius iter Brasil.' sheets of this species at M, both annotated as *Myrcia cordiaefolia* and subsequently, by Berg, as *Gomidesia linkiana*. In choosing between these I designated as lectotype the sheet which was also annotated by de Candolle and which bears the more complete specimen.

Since the epithet employed by de Candolle was clearly intended to convey the fact that the leaves resemble those of a *Cordia*, the correct spelling is *cordiifolia*. This correction, obligatory under article 60.8, renders the name extremely similar to *Myrcia cordifolia* a quite different species described by Berg at the same time as he remodelled *Myrcia cordiaefolia* DC. As the names differ only by a single vowel I consider them to be so similar that they are likely to be confused, though this case has yet to be referred to the General Committee for examination. If the two names are deemed to be confusingly similar then they must be treated as homonyms, the later of which is illegitimate. Unfortunately the species described by Berg under the later homonym *Myrcia cordifolia* is more widespread and better known than the earlier *Myrcia cordiifolia* DC. On these grounds it could conceivably be argued that there is a case for conserving the later name in the interests of nomenclatural stability. However, I consider that further study is likely to lend support to Kiaerskou's (1893) suggestion that *Myrcia cordifolia* Berg is merely a variety of *Myrcia lasiantha* DC. Since this latter name dates from 1828 and is also in current use (Kawasaki 1989), the merging of *Myrcia cordifolia* O.Berg and *Myrcia lasiantha* DC. would circumvent the problem of homonymy. There is an additional reason for my decision not to attempt to conserve *Myrcia cordifolia* O.Berg against *Myrcia cordiifolia* DC. Recognition of *Gomidesia* as a genus probably renders the genus *Myrcia* paraphyletic. There is therefore a distinct possibility that some future student will decide to sink *Gomidesia* into *Myrcia* - in which case the name *Myrcia cordiifolia* DC would be required.

**11. Gomidesia crocea** O.Berg, *in* Martius, Fl. bras. **14(1):** 533. 1859. Type. Brazil. *Riedel s.n.* (holotype, LE!).

Fig. 28 (also 11a-c)

*?Eugenia amplexicaulis* Vell., Fl. flumin. 210. 1829, non Lindley 1826/27. Type. Brazil. Rio de Janeiro: "Silvis maritimis ad S. Crucem," (lectotype, Fl. flumin. Icones **5:** Tab. 44, here designated).

*Plinia crocea* sensu Vell. as to plate only, Fl. flumin. Icones 5: Tab. 47. 1831, non Fl. flumin. 210. 1829 (= *Plinia crocea* L. 1771.).

*Gomidesia amplexicaulis* (Vell.) O.Berg, Linnaea **27:** 7. 1855. *Nom. illeg.*

*Gomidesia langsdorffii* O.Berg, *in* Martius, Fl. bras. **14 (1):** 531. 1859. Type. Brazil. Rio de Janeiro. *Riedel s.n.* (lectotype, LE!, here designated; isolectotypes, K!, LE! (2 sheets), P!, US! (photo)).

*Myrcia amplexicaulis* (Vell.) Hook. f., Curtis's Bot. Mag. sub t. 5790. 1869. *nom. illeg.*

*Tree, treelet* or *shrub* (2–)4–10 m tall. Branchlets 10 cm below the terminal bud 3–4 mm in diameter, rounded or slightly flattened and channeled, with a dense indumentum of erect, straight or slightly curved, brown hairs up to 1 mm long; terminal bud up to 24 mm long. Stipule lobes to 0.9 mm long. Inter-petiolar ridge prominent. Petioles 4–8(–10) mm long, c. 3 mm wide, flat or slightly channeled. *Lamina* oblong, elliptic, broadly elliptic or lanceolate, 110–270 mm long, 60–105 mm wide, 1.9–3.6 times as long as wide; apex short acuminate to long acuminate; base rounded or truncate and minutely auriculate; margin flat to bent down or recurved; midrib flat, slightly impressed or sulcate above, prominent below; lateral veins more or less straight or slightly curved, raised above, sometimes only very slightly so, usually slightly more conspicuous than the secondary laterals, especially below, diverging at c. 60–75° from the midrib; secondary laterals markedly composite, straight or curved; marginal vein equalling the laterals in prominence and curving between them; higher order venation distinct, raised above and below; venation between marginal vein and margin conspicuous; submarginal

FIG. 28. *Gomidesia crocea.* Plate 47, from Vellozo's Florae Fluminensis **5** which appeared as "*Plinia crocea.*"

Icos. Mónog.

PLINIA CROCEA

(Tab. 47.)

vein distinct. Indumentum of appressed, straight, pale hairs, dense on midrib and sparse to scattered elsewhere above, sparse to moderately dense below, consisting of erect, straight, brownish hairs to 1 mm long, intermixed with Type II trichomes. Gland dots indistinct above, distinct below. Mature leaves chartaceous to coriaceous. *Conflorescence* comprising one (or more) pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. (12–)25–100 flowers, c. 60–90 mm long, reaching c. 2/3 the length of the subtending leaf; peduncle c. 30 mm long i.e., c. 1/3 the length of the inflorescence, 2.5–3 mm wide, compressed; lateral branches 2–4 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 4.5–7 mm long x 4–5.5 mm wide. Calyx lobes depressed ovate to narrowly transversely oblong, 1.8–2.3 mm long x 3.5–4(–5.6) mm wide, apex rounded, with a dense indumentum of straight hairs up to 1 mm long externally, indumentum shorter internally; hypanthium usually longitudinally ridged, 3–3.3 mm long, prolonged c. 1–1.3 mm above the ovary, densely pubescent internally and externally ; disk c. 2.8 mm diameter, indumentum dense. Stamens 100–165 per flower; anthers 1.1 mm long, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves more or less losing curvature after dehiscence, held parallel with thecal margins recurved, effective dorsal opening 1/5–1/4 the length of the anther, residual septum not visible or visible and vertical. Style c. 8 mm, with moderately dense to dense indumentum in lower 1/3 to 2/3, glabrous in upper 1/3; stigma punctiform. Ovary c. 2 mm long, bilocular, ovules 2 per locule. *Fruit* globose to depressed globose or obconic with 9–10 deep longitudinal ridges, 11–16 mm diameter (including ridges up to 2.5 mm deep), crowned with the connivent to erect, imbricate calyx lobes so that the disk is scarcely visible. Mature seed usually one per fruit, c. 10 mm long, testa pale, hypocotyl densely sericeous.

**Distribution (Map 9) and ecology.** Occurs from Pernambuco south to Rio de Janeiro and just over the border into the north of São Paulo state. Occasional in Atlantic rain forest and tall coastal forest (*restinga arbórea*).

**Phenology.** The main flowering peak is in January but flowering can be as late as March. Most fruiting collections are from April through to August but there is a single fruiting collection from February.

**Specimens examined. BRAZIL. BAHIA:** Fazenda S. Rafael, Una, 16 Feb 1966, *Pinheiro 60* (CEPEC!). **ESPÍRITO SANTO:** Santa Teresa, Valgusana Velha, Estação Biológica de Santa Lúcia. Mata alterada à beira do rio Timbuí, 24 Mar 1988, *Fernandes & L. Kollmann 2429* (NY!, RB!, US!); Derrubada dos Paulistas - Córrego Dourado, *Magnanimi & Mattos 24* (RB!); Santa Teresa, Santa Lúcia, 12 Jun 1984, *Vimercat 179* (NY!, RB!, US!). **MINAS GERAIS:** E(stação).

B(iológica).C(aratinga)., Mata do Rafael, 26 Apr 1984, *Lopes 367* (RB!); Atlantic forest, Caratinga. Estação Biológica de Caratinga, 10 Nov 1983, *Strier 618* (NY!). **PERNAMBUCO:** Vicência. Mata úmida da Serra da Mascarenhas. Margem da estrada do Engenho Chichá à Fazenda Rochedo, 28 Nov 1957, *Andrade-Lima 57-2816* (K!). **RIO DE JANEIRO:** Mun. Campos, Mata Bom Jesus, 25 Jan 1984, *Araújo 5985* (GUA!); Represa S. Pedro, Rio d'Ouro, 10 May 1931, *Brade 10823* (R!); Leblon, Apr 1946, *Duarte 104* (RB!); *Glaziou 1121* (BR! P!); Environs de Rio de Janeiro, *Glaziou 12003* (C!, K!, P!, R!); *Glaziou 1281* (BR!, C!, P!, S); Porto das Caixas, Morro da Babylônia, Serra da Estrella, *Glaziou 7641* (BR!, C!, K!, P!, S!); Restinga da Tijuca, 23 Aug 1947, *Machado s.n. RB75174* (RB!); Ilha Grande, 27 Jul 1862, *Nadeaud s.n.* (P!); Serra da Estrella, Jan 1881, *Palma 5516* (R!); Villa de Itaguahy, 6 Feb 1928, *Pessoal do Horto Florestal 764* (RB!); *Riedel 370* (R!, US!); *Riedel 635* (R!); Serra da Estrela, *Schwacke Herb. 3257* (RB!); Restinga da Gávea, Aug 1897, *Ule s.n.* (R!); in silvis ad montem "dois irmãos" prope Rio de Janeiro, Jun 1866, *Warming s.n.* (C!); Serra da Estrella, 1844, *Weddell 768* (P!). **SÃO PAULO:** Fazenda do Cruzeiro, Serra da Mantiqueira, Jan 1884, *Palma s.n.* (R!); *Riedel 631* (R!). **STATE NOT INDICATED:** Gruta da Imprensa, 4 Nov 1945, *Duarte s.n.* (R45790!); locality not indicated, 1927, *Humberto de Almeida 9* (RB!); locality not indicated, *Pohl & Schott s.n.* (W!).

The earliest treatment of this species in the literature appears to be a plate and accompanying text in Florae Fluminensis (Vellozo, 1829) presented as *Plinia crocea*. The name *P. crocea* has been attributed to Vellozo by authors such as Berg (1857-59), Kiaerskou (1893), Niedenzu (1893) and Legrand (1959). These later authors made no mention of the earlier *Plinia crocea* of Linnaeus. Linnaeus (1771) proposed the name *P. crocea* to replace his earlier name *P. pinnata*, perhaps because he had realised that the species of *Plinia* in question did not in fact have pinnate leaves. Thus *P. crocea* L. was nomenclaturally superfluous when published and is illegitimate. Linnaeus also expressed some doubt as to whether *P. crocea* should be recognised as a species distinct from *P. rubra* or merely as a variety.

Vellozo's observations on *P. crocea* leave no doubt that he was aware of Linnaeus' earlier use of the name. Although his comments are open to differing interpretations, I take them to intend a comparison of his material to that of Linnaeus and an affirmation to the effect that if Linnaeus had had the Vellozo material at his disposal he would not have hesitated in recognising *P. crocea* as a species distinct from *P. rubra*. Thus it would seem that Vellozo's intention was merely to amplify the description and confirm the status of the species described by Linnaeus rather than to describe a new species. Vellozo's use of *P. crocea* does not constitute publication of a new name. All combinations based on *P. crocea* Vell. must be treated as if they are based on *P. crocea* L. unless the latter species is explicitly excluded.

However, applying modern taxonomic concepts, it is clear that the material illustrated by Vellozo can by no means be conspecific, nor even congeneric, with that described by Linnaeus. The pentamerous flowers mentioned by Vellozo and the paniculate inflorescence depicted in his plate indicate a member of the Myrciinae while the bean-like embryo of the Linnaean material is typical of the Eugeniinae. Vellozo commented that the sulcate fruit 'enticed' him to place his material among the *Plinias*; in this instance his undue emphasis on this single fruit character led him into error. Thus the material depicted by Vellozo represented a previously undescribed species for which no legitimate name was available until Berg (1857-59) produced his monographic treatment.

Berg (1857) cited *P. crocea* Vell. in the synonymy of *Gomidesia jacquiniana* with an expression of doubt (see under *G. jacquiniana* for further discussion). Subsequently, in the supplement which forms an integral part of this work (1859), Berg described what he considered to be two distinct new species, *G. crocea* and *G. langsdorffii,* both based on Riedel collections. *P. crocea* was explicitly excluded from *G. crocea* with the comment that *G. crocea* was very similar to *P. crocea* in appearance but differed in its leaves which were obtuse and and very shortly acuminate rather than gradually long-acuminate. As circumscribed in the present revision, *G. crocea* varies in the shape of the leaf apex from short-acuminate to long-acuminate and this variation can often be seen between leaves on a single flowering shoot. The plant depicted by Vellozo as *P. crocea* falls within this broader interpretation of *G. crocea*. So too does the type of *G. langsdorffii*. Thus Berg published simultaneously two legitimate names for what I consider to be a single taxon. In such situations, where a choice is possible between legitimate names of equal priority, following article 11.5, the first such choice to be effectively published establishes the priority of the chosen name. Although the name *G. langsdorffii* has never been taken up since its publication, appearing in print only in synonymy, I can find no instance where *G. crocea* was explicitly chosen over *G. langsdorffii.*

Subsequent authors appear to have misinterpreted the intentions of Vellozo and/or Berg in various ways. Niedenzu (1893) judged that Berg should have taken up the epithet *crocea* for the species he named *G. jacquiniana*, so he made the combination *G. crocea* (Vell.) Niedenzu which should be interpreted as *G. crocea* (L.) Niedenzu. This name is illegitimate on two counts: both because it is a later homonym of *G. crocea* O.Berg and because the basionym *P. crocea* L. is superfluous. No mention is made of Berg's species *G. crocea* or *G. langsdorffii* in Niedenzu's treatment.

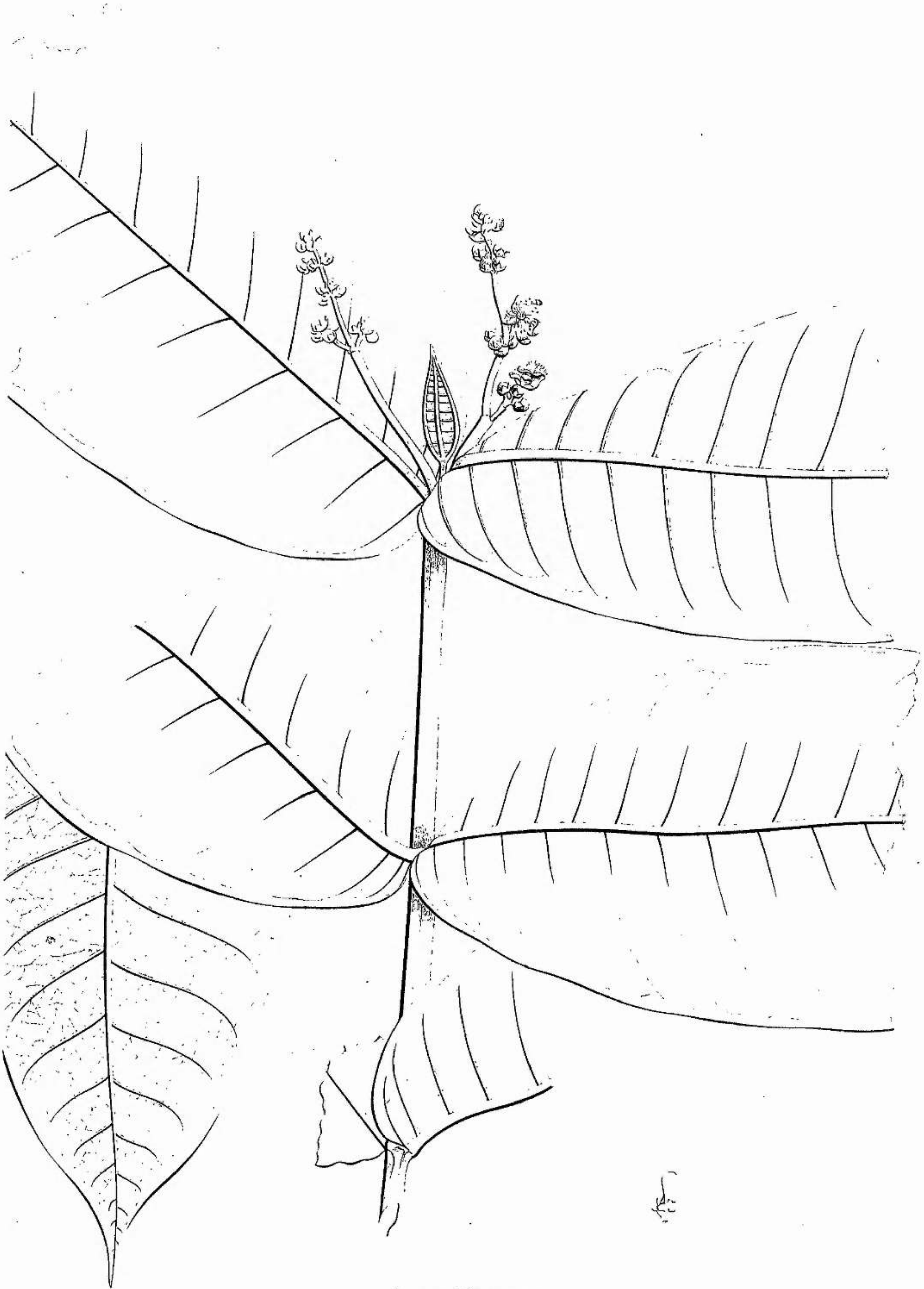
Similarly Kiaerskou (1893), who recognised *Gomidesia* only at subgeneric level within *Myrcia*, made the new combination *M. crocea* (Vell.) Kiaersk. which should be interpreted as

*M. crocea* (L.) Kiaersk. Again, this name is illegitimate because it is based on the superfluous *P. crocea*. Kiaersk. included *G. langsdorffii* under the synonymy of *M. crocea* and expressed the opinion that *G. crocea* O.Berg undoubtedly belonged there too, though he had not seen a specimen determined by Berg. As neither *G. crocea* O.Berg nor *G. langsdorffii* O.Berg was accepted in this treatment no choice was made between them.

Legrand's (1959) citation of *G. crocea* (Vell.) O.Berg is based on another misapprehension, namely that Berg's *G. crocea* was based on *P. crocea* Vell. Thus while Legrand's relegation of *G. langsdorffii* to the synonymy of *G. crocea* could be construed as a choice of the latter name over the former, it was actually done on the assumption that *G. crocea* automatically had priority. In the interests of nomenclatural stability I here maintain *G. crocea* O.Berg and treat *G. langsdorffii* as a synonym thereof, thus establishing the priority of *G. crocea* over *G. langsdorffii*.

With some misgivings I have placed the illegitimate *Eugenia amplexicaulis* Vell. and combinations based thereon in the synonymy of *G. crocea*. The Florae Fluminensis plate here selected as lectotype of *E. amplexicaulis* Vell. (reproduced here as Fig. 29) does not show the flower in sufficient detail to allow a positive identification. Furthermore, as Hooker (1869) emphasized, the drawing is inaccurate with respect to detail e.g, the calyx lobes are drawn as acute on the plant of natural size but truncate in the enlarged analysis. Berg considered that the anthers are figured by Vellozo as those of a *Gomidesia* and made the combination *G. ? amplexicaulis* although he had not seen the flowers. Hooker found no evidence of gomidesioid anthers in the Florae Fluminensis plate, nor in fresh material of what he took to be the same species and therefore made the new combination *Myrcia amplexicaulis* (Vell.) Hooker. I concur with Hooker's view that the anthers illustrated by Vellozo are by no means clearly those of a *Gomidesia*. However, I interpret this as typical of the general lack of detail in the Florae Fluminensis plates rather than as an indication that the plant depicted is referrrable to *Myrcia*. The general aspect of the plant illustrated, the inflorescence, the leaf venation and the hint of an interpetiolar ridge at the lowest node are all strongly suggestive of *Gomidesia crocea*. The fact that Vellozo's phrase describing the habitat and locality of *E. amplexicaulis*, 'habitat silvis maritimis Regii Praedii Sanctae Crucis', is almost identical to that cited for his plate of the plant now known as *G. crocea* (presented as *P. crocea*) adds further support to this idea. The major discrepancy between the material illustrated by Vellozo as *E. amplexicaulis* and what I consider to be typical *G. crocea* is that the latter has a distinct petiole. This character is somewhat variable however, as is demonstrated by occasional specimens with sessile, slightly amplexicaul leaves e.g., *Andrade-Lima 57-2816*. Legrand (1959) noted a tendency in this species to a scutate leaf base and a shortening of the petiole on

FIG. 29. *Gomidesia crocea?* Plate 44, from Vellozo's Florae Fluminensis **5** which appeared as "*Eugenia amplexicaulis.*"



Icos. Monog.

EUGENIA AMPLEXICAULIS

(Tab. 44.)

account of which he considered *G. amplexicaulis* to be a form of *G. crocea* though he did not include it in the synonymy of this latter species. Since *E. amplexicaulis* Vell. is an illegitimate later homonym of *E. amplexicaulis* Lindley its inclusion in synonymy here does not pose a threat to the priority of *G. crocea*. However, when further material becomes available for study, should the amplexicaul leaved specimens prove to be distinct from *G. crocea* at species level a new name will be required for them.

The various forms of citation mentioned above can be seen on herbarium specimens of the distinctive sulcate-fruited species whose correct name is here established as *G. crocea* O.Berg. Unfortunately the situation is further complicated by the fact that the name *G. crocea* has been frequently misapplied to a completely different species, *Myrcia pubipetala* Miq. Perhaps the most unfortunate example of this is the study by Barbosa et al. (1977/78) on the wood anatomy of several tree species from the Serra da Cantareira, São Paulo, in which *M. pubipetala* is clearly depicted in a plate labelled *G. crocea*. The origin of this misapplication is unclear but in my experience many (perhaps even most?) records of *G. crocea* from São Paulo state are referrable to *M. pubipetala* Miq. The name *G. crocea* has also been misapplied to two species of *Gomidesia* with hypanthia markedly ridged in bud: *G. gestasiana*, which differs in having smaller leaves, shorter anthers lacking a connective stub and thecal halves retaining curvature after dehiscence, and *G. grazielae* which differs in its bullate leaves and smooth unridged fruit.

Flowering material of *G. crocea* is frequently determined in error as *G. spectabilis*. The scutate leaf-base and different indumentum are sufficient to distinguish these species in the vegetative state while fruiting specimens are practically unmistakeable. Nonetheless the overall resemblance of these species is also borne out by characters such as the distinct connective stub, the prominent interpetiolar ridge and the densely sericeous hypocotyl which probably reflect a close affinity.

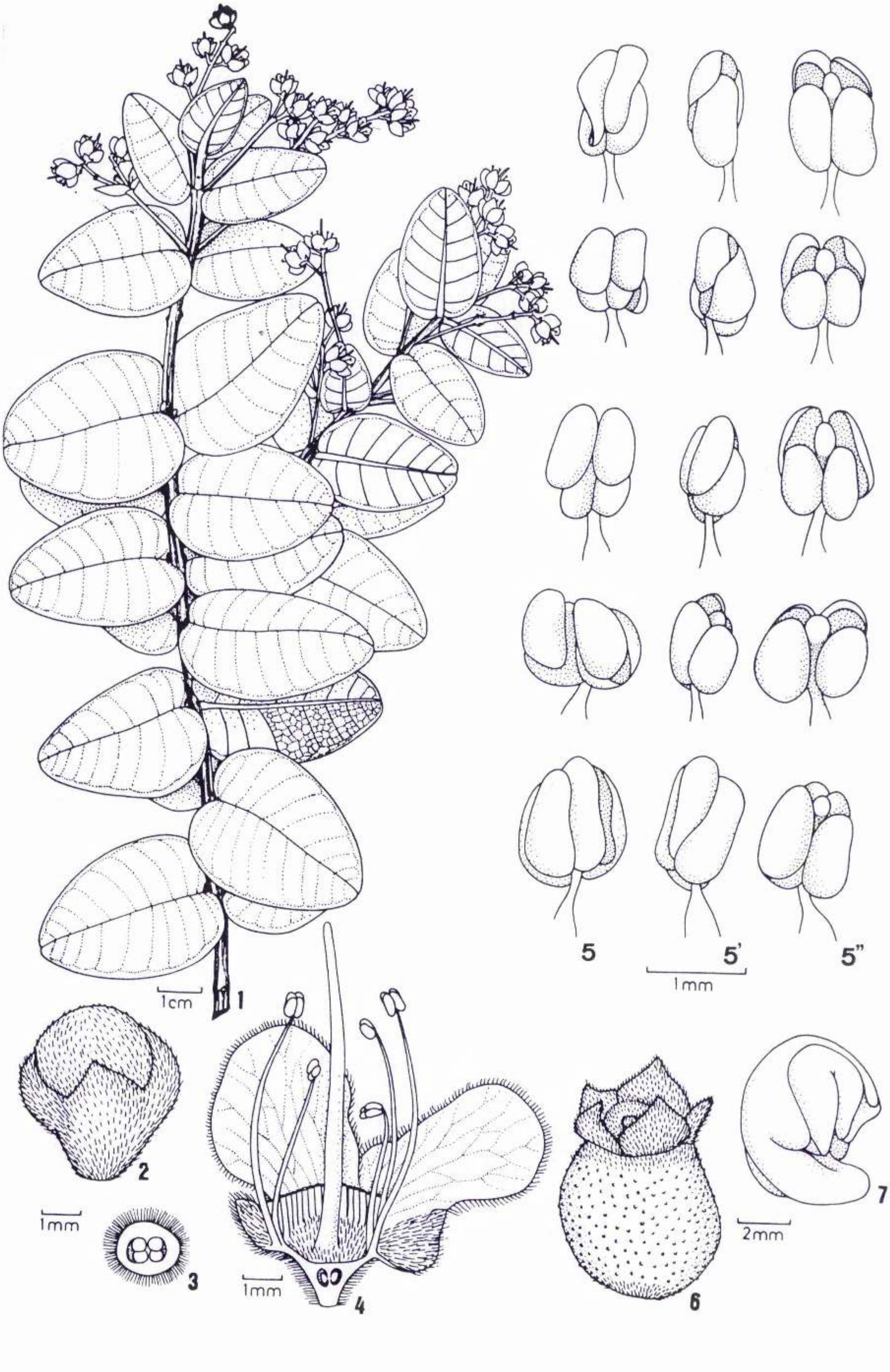
**12. Gomidesia eriocalyx** (DC.) O.Berg, Linnaea **27:** 10. 1855.

*Myrcia eriocalyx* DC. Prod. **3:** 247. 1828. Type. Brazil. Minas Gerais: 'Habitat in silvis Capões, territorii Adamantium' *Martius s.n.* (holotype, M!).

Fig. 30 (also 13g,h,n&p).

*Myrcia pauciflora* Cambess., *in* Saint-Hilaire, Fl. Bras. merid. **2:** 321. 1832. Type. Brazil. Minas Gerais: "Ad basim montis Serra Negra," *Saint-Hilaire D 140* (lectotype, P!; isotypes, P! (2 sheets)).

FIG. 30. *Gomidesia eriocalyx*. Figs. 1 - 7 from Kawasaki's Flora da Serra do Cipó, Minas Gerais, Myrtaceae which appeared as '*Gomidesia gaudichaudiana* Berg'. **1** - Habit, **2** - Floral bud, **3** - Ovary in cross-section, **4** - Flower in long-section, **5-5"** - Anthers, frontal view, lateral view and dorsal view, **6** - Fruit, **7** - Myrcioid embryo.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7

*Myrcia elliptica* Gardner, Hooker's London Journal of Botany **2:** 352. 1843. Type. Brazil. Rio de Janeiro: Organ Mountains, Brazil, Feb 1837, *Gardner 415* (lectotype, K!, here designated; isotypes, F!, K!, NY!, (2 sheets), US!, W! (2 sheets)).

*Gomidesia gaudichaudiana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 27. 1857. Type. Brazil. Minas Gerais: "in montibus Serra do Caraça," *Sellow s.n., hb. Fl. Br. Mart. 1236* (lectotype, M!, here designated).

? *Gomidesia beyrichiana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 25. 1857. Type. Brazil. Rio de Janeiro: "ad flumen Rio Paquaquer prope villam Cantagallo," *Beyrich s.n.* (holotype, B, n.v., presumed destroyed).

*Gomidesia hilariana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 26. 1857. Type. Brazil. Rio de Janeiro: *Schuch s.n.* (lectotype, W!, here designated).

*Gomidesia miqueliana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 24. 1857. Type. Brazil: *Sello 1608/1054* (holotype, B, presumed destroyed; lectotype, P!, here designated; isolectotype, K!).

*Gomidesia miqueliana* var. *brunnea* O.Berg, *in* Martius, Fl. bras. **14 (1):** 25. 1857. Type. Brazil. Minas Gerais: "prope Cachoeira do Campo," 1840, *Claussen 529* (holotype, BR!; isotype, S!).

*Gomidesia miqueliana* var. *ferruginea* O.Berg, *in* Martius, Fl. bras. **14 (1):** 24. 1857. Inadmissible name to be replaced by *G. miqueliana* var. *miqueliana*.

*Myrcia pauciflora* var. *brunnea* O.Berg, *in* Martius, Fl. bras. **14 (1):** 201. 1857. based on *Myrcia pauciflora* Cambess. var. *B*

*Gomidesia beyrichiana* var. *acutata* O.Berg, *in* Martius, Fl. bras. **14 (1):** 534. 1859. Type. Brazil. Rio de Janeiro: *Riedel & Langsdorff 842* (holotype, LE!).

*Gomidesia miqueliana* var. *angustifolia* O.Berg, *in* Martius, Fl. bras. **14 (1):** 534. 1859. Type. Brazil. Minas Gerais: *Langsdorff s.n.* (Probable holotype, LE!).

*Gomidesia miqueliana* var. *obtusata* O.Berg, *in* Martius, Fl. bras. **14 (1):** 534. 1859. Type. Brazil. Minas Gerais: Ouro Preto, *Riedel 2577* (holotype, LE!; isotypes, K!, P!).

*Gomidesia regeliana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 535. 1859. Type. Brazil. Minas Gerais: *Langsdorff s.n.* (probable holotype, LE!).

*Myrcia alpina* Kiaersk., Enum. Myrt. bras. 113. 1893, *nom. superfl.* based on *G. gaudichaudiana* O.Berg, to be replaced by *M. gaudichaudiana*.

*Myrcia eriocalyx* var. *beyrichiana* (O.Berg) Kiaersk., Enum. Myrt. bras. 110. 1893.

*Myrcia eriocalyx* var. *miqueliana* (O.Berg) Kiaersk., Enum. Myrt. bras. 111. 1893.

*Myrcia sessilifolia* Kiaersk., Enum. Myrt. bras. 115. 1893, *nom. nov.* based on *G. regeliana* O.Berg non *M. regeliana* O.Berg.

*Gomidesia eriocalyx* var. *acuminata* D.Legrand, Notul. Syst. (Paris) **15:** 262. 1958. Based on *Myrcia pauciflora* Cambess. 'eryocalyx'.

*Gomidesia elliptica* (Gardner) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 17. 1959. (This new combination erroneously attributed to Berg by Legrand.).

*Treelet* or *shrub* 0.5–4 m tall or rarely a *tree* 6–10 m tall. Branchlets 10 cm below the terminal bud 2–2.5 mm in diameter, rounded, glabrous or with a dense indumentum of erect, straight or crisped, greyish or straw-coloured hairs to 0.6 mm long; terminal bud 5 mm long or proliferating, with a dense indumentum of erect, straight or crisped, straw-coloured hairs to 0.6 mm long. Stipule lobes stout, c. 0.7–1.4 mm long. Inter-petiolar ridge absent. Petioles 2–2.5 mm long, 0.8–1.5 mm wide, channeled, with a dense indumentum of appressed hairs to 0.2 mm. *Lamina* ovate to wide-ovate or elliptic to wide-elliptic or suborbiculate to wide-oblong, 9–33 mm long, 7.5–22 mm wide, 1.2–2 times as long as wide; apex obtuse or rounded, sometimes appearing apiculate due to dense indumentum on midrib below which overtops lamina; base obtuse or rounded or truncate or subcordate or cuneate; margin bent down or recurved or revolute; midrib sulcate or impressed or flat above, prominent below; lateral veins straight or curved, impressed or flat or very slightly raised above, prominent below, diverging at c. 60–80° from the midrib; secondary laterals simple or composite, rarely equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them, or obscured by the revolute margin; higher order venation raised or slightly raised above, raised or prominent below; venation between marginal vein and margin distinct or obscured by indumentum and recurved margin. Indumentum absent or moderately dense to dense above, consisting of ascending, straight, white hairs to 0.6 mm long, moderately dense to dense below, consisting of erect or ascending, straight or curved or crisped, straw-coloured hairs to 1 mm long. Gland dots distinct above, impressed, indistinct below. Mature leaves coriaceous (or rarely chartaceous), flat or markedly convex. *Conflorescence* comprising 1–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. (3–)5–15(–35) flowers, 23–41 mm long, reaching c. 3/4–5/2 times the length of the subtending leaf; peduncle 16–22 mm long i.e., c. 1/2–2/3 the length of the inflorescence, 0.5–2 mm wide, terete, flexuous; lateral branches one or two below the terminal cyme or cluster of cymes. *Mature flower buds* c. 5.5 mm long x 4.5 mm wide. Calyx lobes shallowly triangular to deltate, 1.2–3.3 mm long x 1.9–2.9 mm wide, apex acuminate or long acuminate, with a dense indumentum of appressed or ascending, straight or curved, pale brown or whitish hairs c. 0.8–1 mm long externally, indumentum dense or moderately dense internally; hypanthium 1.3–2.5 mm long, prolonged c. 0.8–1.5 mm above the ovary, indumentum dense externally, consisting of erect or ascending, straight or curved, pale brown hairs c. 0.7–0.9 mm, induementum dense internally; disk c. 2.1–3.4 mm diameter, indumentum dense. Stamens 67–114 per flower; anthers 0.5–0.7 mm long, filament tapered to a fine point or thread-like portion at the point of insertion on the connective, apex deeply emarginate, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent, with margins in the plane of curvature, effective dorsal opening 1/3–1/2 the length of the anther, residual septum not visible. Style c. 7 mm with moderately dense to dense indumentum in lower 1/2 to 2/3, prominently glandular in distal portion, stigma indistinct. Ovary c. 0.75–1.3 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 6 mm diameter, crowned with the spreading calyx lobes. Mature seed one or two per fruit, c. 4 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 10) and ecology.** *Gomidesia eriocalyx* occurs in Minas Gerais and Rio de Janeiro in a wide variety of habitats including gallery forest, *campo rupestre*, *cerrado* and secondary vegetation at altitudes of 1000–1800 m.

**Phenology.** *Gomidesia eriocalyx* has a very clear flowering peak in January and, especially, February. However occasional flowering collections have been made as early as December and as late as May. Fruiting collections have been made from May to October, with mature fruit being reported from July on.

**Representative specimens examined. BRAZIL. MINAS GERAIS:** Mun. Diamantina, ca. 14 km SW of Diamantina on road to Gouveia, 1330 m, 5 Feb 1972, *Anderson 35492* (MO!, NY!, UB!); Serra do Cipó, 1225 m, 18 Feb 1972, *Anderson & Stieber 36188* (MO!, NY!, R!, UB!, US!); Serra do Espinhaço, Serra do Cipó, 1200 m, 20 Feb 1972, *Anderson & Stieber 36360* (MO!, NY!, UB!, US!); Tiradentes, subida da Cachoeira da Serra, 24 Feb 1987, *CFCR & D.C.Zappi 10333* (SPF!); São Thomé das Letras. Serra de São Thomé, 30 Oct 1984, *CFCR & J.R.Pirani 5660* (SPF!); Trinta Réis. Estrada Serro-Diamantina, 27 Jan 1986, *CFCR 9261* (K!); Santana do Riacho, Serra do Cipó, Rodovia Belo Horizonte - Conceição do Mato Dentro: km 132, 23 May 1980, *CFSC & Furlan 6102* (SP! SPF!); Santana do Riacho, Serra do Cipó, Rodovia Belo Horizonte - Conceição do Mato Dentro: km 109, 7 Feb 1972, *CFSC & Semir 697* (E!, SP!, SPF!); Serra da Bocaina / Ingaí - Itumirim, 1100 m, 27 Feb 1987, *Carvalho s.n.* (UEC!); 'Caxoeira' do campo, Feb 1839, *Claussen 126* (BR!); locality not stated, 1840, *Claussen 145A* (LE!, NY!); prope Cachoeira do Campo, 1840, *Claussen 529* (BR!, S!); Mun. Itabira, Cauê, 12 Feb 1934, *Collector unknown 12395-D* (R!); Diamantina, 13 Jan 1947, *Egler 110* (RB!); Mun. Itabirito, Serra de Itabirito, Campos Rupestres próximos do Belvedere da Estrada Itabirito/Ouro Preto, 1250 m, 23 Jan 1986, *Farney 1045* (RB!); Santana do Riacho, Serra do Cipó, km 107 caminho para Usina Dr. Pacífico Mascarenhas, 7 Sep

1980, *Forero 8002* (NY!); Mun. Santana do Riacho: km 134 ao longo da rodovia Belo Horizonte-Conceição do Mato Dentro, 23 May 1980, *Furlan & Pirani CFSC 6102* (K!); Sabará, au Morro do Ramão, *Glaziou 20325* (C!, K!, LE!); Mun. Diamantina: Biri-biri, 20 Jan 1972, *Hatschbach 29026* (SPF!); Serra do Espinhaço: Serra do Itabirito, ca. 48 km SE of Belo Horizonte, 1750 m, 9 Feb 1968, *Irwin & Maxwell 19629* (NY!, UB!); Serra do Espinhaço. Pico de Itabirito, ca. 50 km SE of Belo Horizonte, 1750 m, 11 Feb 1968, *Irwin & Maxwell 19863* (F!, NY!, UB!, US!, W!); Wooded seep in gallery forest, Serra do Itabirito, ca. 45 km S.E. of Belo Horizonte, 1500 m, 12 Feb 1968, *Irwin & Maxwell 19972* (F!, MO!, NY!, RB!, UB!, US!); Serra do Espinhaço. Serra do Cipó, km. 115 (ca. 140 km N. of Belo Horizonte), 1250 m, 19 Feb 1968, *Irwin & Maxwell 20460* (F!, K!, MO!, NY!, RB!, UB!, US!); Serra do Espinhaço, 30 km N of Serro on road (MG 2) to Diamantina, 1200 m, 26 Feb 1968, *Irwin 20900* (MO!, NY!, R!, UB!); Serra do Espinhaço, ca. 12 km SW of Diamantina, 1350 m, 23 Jan 1969, *Irwin & Reis dos Santos 22464* (MO!, NY!, R!, UB!, US!); Middle and upper slopes, south side of Serra da Piedade, 5 km N. of Caeté, 1800 m, 19 Jan 1971, *Irwin 28731* (MO!, NY!, UB!, UEC!); Serra do Espinhaço, ca. 3 km N of Mariana, road to Santa Bárbara, 1500 m, 2 Feb 1971, *Irwin & Harley 29665* (F!, NY!, UB!); Mun. Lavras, 10 Dec 1980, *Leitão Filho 11930* (UEC!); Mun. Tiradentes. campo rupestre próximo a cidade, 6 Dec 1983, *Leitão Filho 15185* (UEC!); Serra do Caraca prov. Minas Geraes, *Mart. Fl. Bras. Hb 1236* (M!); Habitat in silvis Capões, territorii Adamantium, *Martius s.n.* (M!); Mun. Ouro Preto, formações rupestres, Cachoeira das Andorinhas, 1250 m, 15 Jul 1978, *Martinelli 4728* (RB!); Mun. Santana do Riacho. Serra do Cipó. Estrada para Conceição do Mato Dentro. Km 116. ramal para Cachoeira, 1100 m, 26 Jan 1986, *Martinelli 11368* (RB!, SPF!); Bucão, Mun. Marianna, 3 Dec 1933, *Mello Barreto 7346* (F!); Mun. Tiradentes. Serra de São José, 1350 m, 3 Oct 1987, *Peron 322* (RB!); Mun. Ouro Preto, Camarinhas, 1450 m, 14 Oct 1987, *Peron 399* (RB!); Mun. Caeté. Serra da Piedade, 1350 m, 13 Jan 1988, *Peron 605* (RB!); Mun. Belo Horizonte, Serra da Moeda, Reserva da MBR, 16 Jan 1988, *Peron 627* (RB!); Ouro Preto, *Riedel 2577* (K!, LE!, P!); locality not indicated, *Riedel & Langsdorff 842* (LE!); Serra do Curral, Belo Horizonte, 15 Jan 1957, *Roth 2470* (SPF!); Ad Ganelea prope Ouro Preto, 1 Jan 1892, *Schwacke Herb. 7524* (RB!); locality not indicated, *Sello 1608/1054* (K!, LE!, P!); locality not indicated, *Sellow t6* (LE!); Mun. Jaboticatubas, km 114 ao longo da rodovia Lagoa Santa - Conceição do Mato Dentro - Diamantina, 7 Feb 1972, *Semir & M. Sazima 697* (RB!, UEC!); locality not indicated, *Saint-Hilaire B1 155* (P!); locality not indicated, *Saint-Hilaire B1 729* (P!); locality not indicated, *Saint-Hilaire D 140* (P!); Tiradentes, Estrada entre Tiradentes e São João del Rey, 6 Dec 1983, *Sugiyama 404* (K!); Sabará, Nov 1843, *Weddell 1551* (P!). **Rio de Janeiro:** Serra dos Órgãos, 1600 m, 19 Mar 1932, *Brade 11491* (R!); 1.5 miles S. of Mr. March's house. Near Teresópolis, 15 Feb 1826, *Burchell 2317* (K!, P!); Mun. Macaé, Pico de Frade. Matas de altitude, 1200 m, 7 Feb 1985, *Farney & Martinelli 595* (F!, RB!); Organ Mountains, Brazil, Feb 1837, *Gardner 415* (F!, K!, NY!, P!, US!, W!); Alto Macahé de Nova Friburgo, *Glaziou 13890* (BR!, C!, K!, LE!, P!, R!); Teresópolis, Posse section of Teresópolis, 27 Jan 1982, *Landrum 4201* (NY!); Teresópolis. Posse section of Teresópolis. Hills with secondary vegetation, 27 Jan 1982, *Landrum 4202* (NY!); Vale das Videiras, Mun. Petrópolis, 1800 m, 7 Jan 1973, *Martinelli 168* (RB!); Theresópolis. Montanha do Ricardo, 14 Jan 1883, *Palma 6839* (R!); Serra Estrella, *Riedel s.n.* (K!, NY!, U!); Teresópolis, Feb 1888, *Schwacke Herb. 6028* (RB!); Teresópolis Posse, Morro das Antenas de Televisão, 10 Feb 68, *Sucre & Braga 2334* (K!, LE!, RB!); locality not indicated, *Wilkes s.n.* (LE!, US!). STATE NOT INDICATED OR UNCERTAIN: Environs de Rio de Janeiro et d'Ouro Preto, *Glaziou 14827* (C!, K!, LE!); locality not indicated, *Langsdorff 11* (LE!);

Berg compared *G. eriocalyx* to *G. miqueliana*, observing that the species resembled each other with regard to inflorescence but differed in habit and leaves. He considered *G. eriocalyx* distinct from *G. beyrichiana* by virtue of its more robust habit, its ferrugineous indumentum and its ovate-oblong leaves with obtuse apices and bases. *Gomidesia gaudichaudiana* was treated in a separate section because of its cordate leaves. *Gomidesia eriocalyx* is here delimited as a rather inclusive taxon which spans the range of variation shown by the types of all these species as well as the other taxa listed in the synonymy above. However, two elements which have hitherto been included in this complex are here excluded from it. The first element is *G. spruceana* which was referred by Legrand to the synonymy of *G. gaudichaudiana* without discussion. *Gomidesia gaudichaudiana* is here relegated to the synonymy of *G. eriocalyx* but examination of the anthers of the type of *G. spruceana* revealed a morphology quite distinct from that seen in the *eriocalyx* complex. *Gomidesia spruceana* is therefore reinstated as a distinct species which is probably more closely related to *G. montana* than to *G. eriocalyx*. The second element to be excluded does not appear to have a name. It is comprised of half a dozen collections from the São Thomé - Baependi area of Minas Gerais which have been variously determined as *G. eriocalyx* or synonyms thereof by various myrtologists, myself included. These collections appear to fall outside the range of variation shown in the *eriocalyx* complex by virtue of their markedly coriaceous folded leaves, large floral buds and anther with thecal halves losing curvature on dehiscence. Further study is required to establish whether these collections represent a distinct species or merely an aberrant or hybrid population.

**13. Gomidesia fenzliana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 20. 1857. Type. Brazil. Rio de Janeiro: *Mart. hb. Fl. Bras. 683* (lectotype, BR!, here designated; isolectotypes BR!, F!, K!, LE!, NY!, P!, US! (photo), W!).

Fig. 31-33 (also 1F, 3D, 14j-n&r-t and 15c&d).

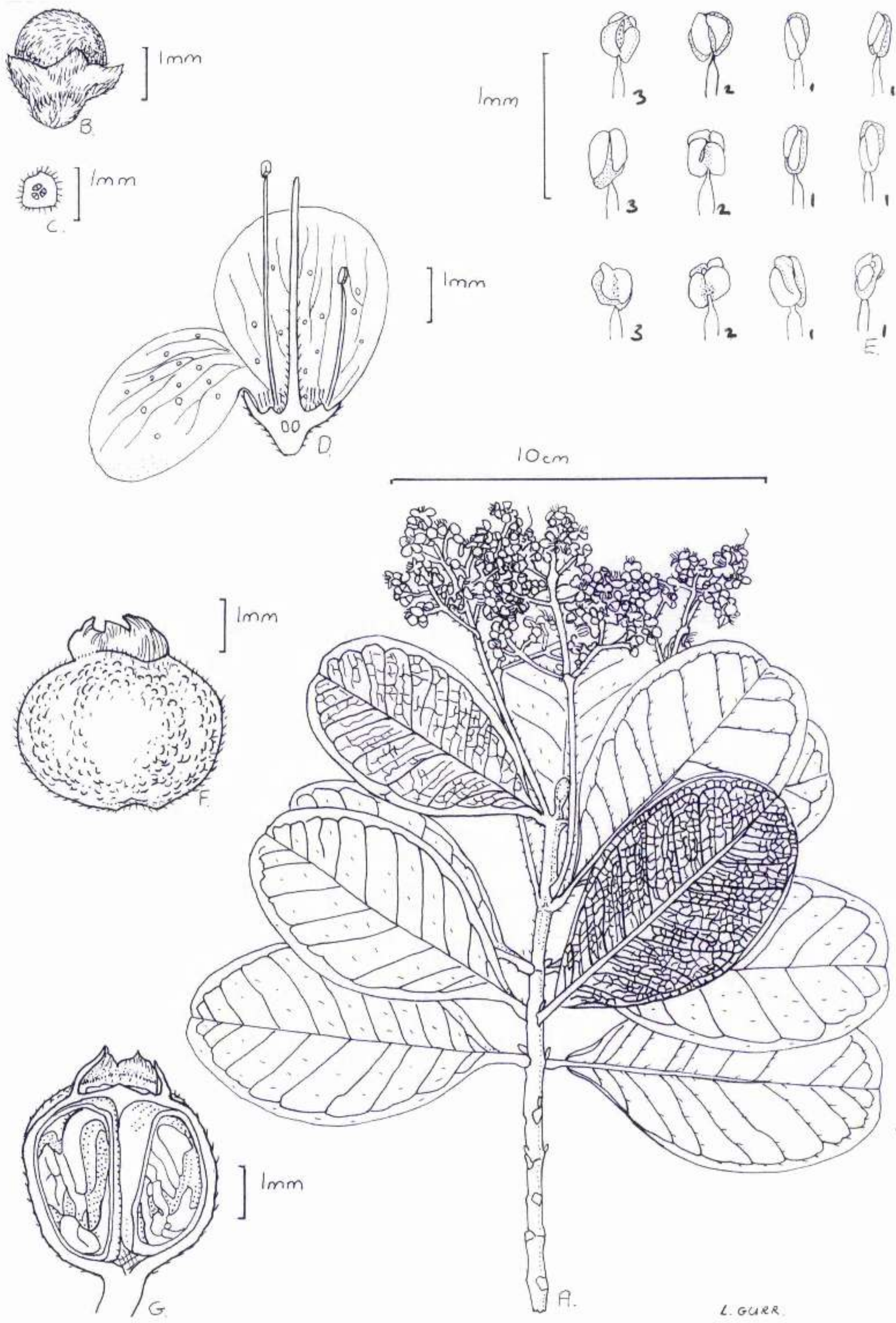
*Gomidesia fenzliana* var. *obovata* O.Berg, *in* Martius, Fl. bras. **14(1):** 20. 1857. Inadmissible name to be replaced by *G. fenzliana* var. *fenzliana.*

*Gomidesia fenzliana* var. *spathulata* O.Berg, *in* Martius, Fl. bras. **14(1):** 20. 1857. Type. Brazil. Rio de Janeiro: *Luschnath s.n.* (lectotype, BR!, here designated; isolectotypes BR!, W!).

*Myrcia ilheosensis* Kiaersk., Enum. Myrt. bras. 109. 1893. *Nom. nov.* for *G. fenzliana* O.Berg non *M. fenzliana* O.Berg nec *Aulomyrica fenzliana* O.Berg.

*Shrub, treelet* or *tree* (0.5–)1.5–10(–15) m tall. Branchlets 10 cm below the terminal bud 2.5–4 mm in diameter, slightly flattened or subquadrangular, with a dense indumentum of erect, straight, pale or dark brown hairs to 0.2 mm long; terminal bud 5–12 mm long. Stipule lobes to 1 mm long. Inter-petiolar ridge absent to distinct. Petioles 3–6 mm long, 2 mm wide, channeled, with a dense indumentum of ascending, straight, pale hairs to 0.5 mm. *Lamina* wide elliptic, suborbiculate, ovate, oblong, wide oblong, wide obovate or narrowly obovate, 36–116 mm long, 23–69 mm wide, 1.4–2.3(–2.8) times as long as wide; apex rounded or obtuse or shallowly emarginate; base acutely cuneate or acuminate or rounded; margin bent down to recurved or flat; midrib sulcate to impressed above, prominent below; lateral veins more or less straight, flat or very slightly raised or very slightly impressed above, raised below, diverging at c. 70° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation indistinct or very slightly raised above, raised or slightly raised below; venation between marginal vein and margin indistinct, or distinct below, paramarginal vein sometimes visible. Indumentum sparse to moderately dense above, consisting of appressed, straight, pale hairs to 0.4 mm, moderately dense below, consisting of erect, straight, pale or dark hairs of varying lengths to 0.7 mm long. Gland dots indistinct or distinct and impressed above, indistinct below. *Conflorescence* comprising one or two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 50–150 flowers, 76–158 mm long, reaching c. 3/4–4/3 the length of the subtending leaf; peduncle 44–76 mm long i.e., c. 1/2–7/4 the length of the inflorescence, c. 2 mm wide, flattened or subquadrangular; lateral branches 4–6 below the terminal cyme or cluster of cymes. *Mature*

FIG. 31. *Gomidesia fenzliana.* **A** Conflorescence and foliage; **B** Flower bud; **C** Transverse section of ovary; **D** Longitudinal section of flower; **E** Anthers in lateral (1), dorsal (2) and ventral (3) view; **F** Fruit; **G** Longitudinal section of fruit and two seeds. **A** - **E** from *Dusen 16093*, **F** & **G** from *Hatschbach 14397*. Drawn by L. Gurr.


B.
1mm
C.
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L. GURR.

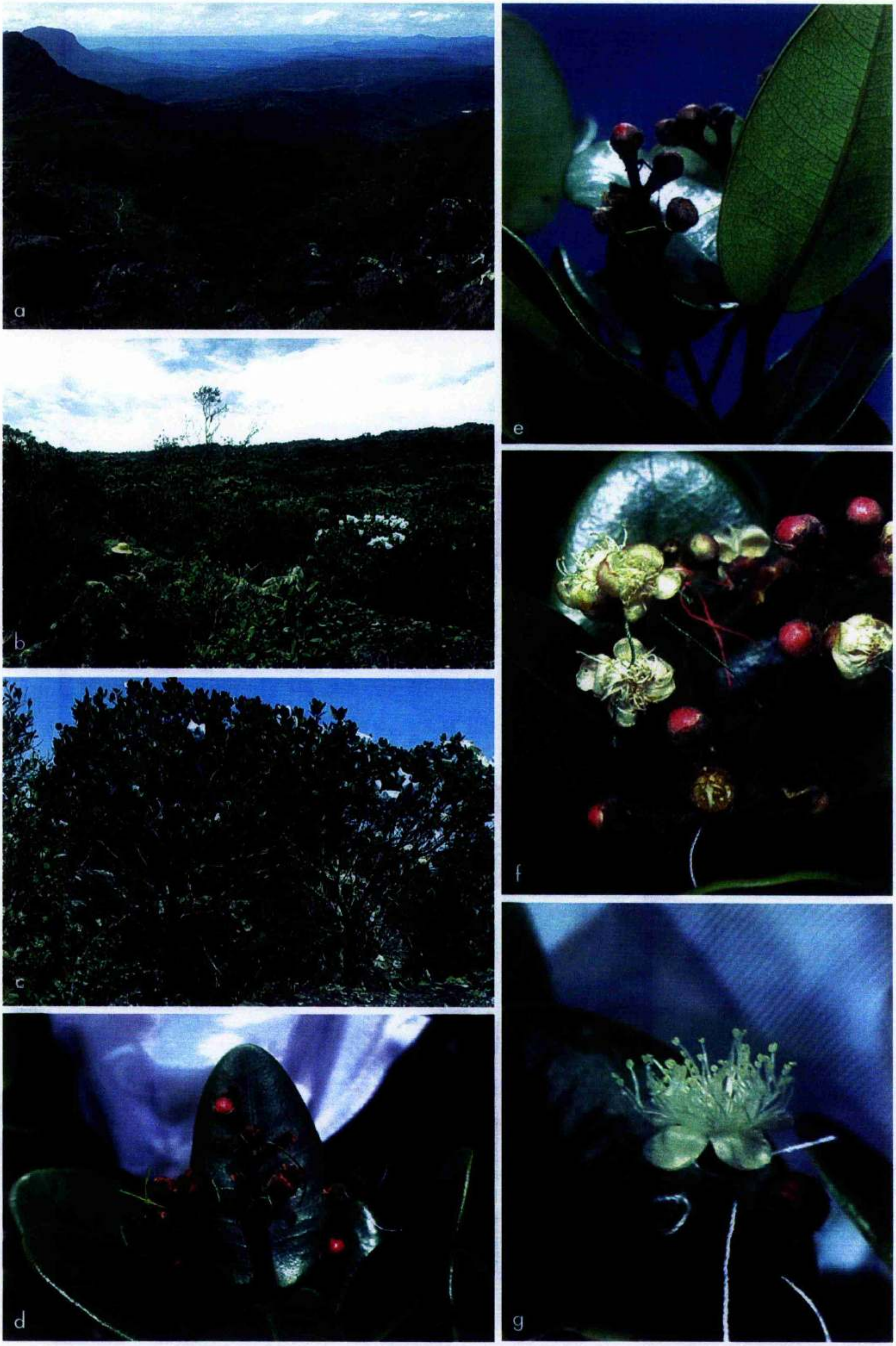
*flower buds* 3–4.3 mm long x 3–4.7 mm wide. Calyx lobes triangular to shallowly triangular, 1.2–1.5 mm long x 1.7–2.8 mm wide, apex obtuse or rounded, with a moderately dense to dense indumentum externally, moderately dense internally; hypanthium 1.2–1.5 mm long, prolonged c. 0.5 mm above the ovary, with dense indumentum externally and internally; disk c. 1.8–2.2 mm diameter, indumentum dense. Stamens 110–154 per flower; filament narrowed abruptly towards point of insertion on connective, anthers c. 0.5 mm long, apex more or less truncate, vertical displacement of thecae slight, thecal halves lose curvature on dehiscence, parallel or slightly divergent, thecal margins recurved after dehiscence, residual septum usually visible, sometimes very faint, oblique. Style c. 6.5 mm, with moderately dense indumentum in lower 1/2; stigma minutely punctiform. Ovary 0.8–1.2 mm long, 3- or 4-locular, ovules 2 per locule. *Fruit* globose, 7–8 mm diameter, crowned with the connivent, imbricate calyx lobes. Mature seed 2–6 per fruit, c. 6 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 11) and ecology.** *Gomidesia fenzliana* has a mainly coastal distribution extending from Bahia south to Santa Catarina (and perhaps into the northern part of Rio Grande do Sul). Most records are from *restinga* vegetation where *Gomidesia fenzliana* often forms an important element of the plant communities on secondary dunes. In addition there are inland populations in upland areas of Bahia in copses and gallery forest within the *campo rupestre* vegetation mosaic. Thus while the altitudinal range for the species as a whole is 0–1500 m, most collections are from 0–30 m above sea level with a small number from altitudes above 300 m.

**Phenology.** Flowering collections of *Gomidesia fenzliana* have been made from December to March, with the peak flowering season being in January and February.

**Representative specimens examined. BRAZIL.** BAHIA: Santa Cruz Cabrália, 31 Oct 1966, *Belém & Pinheiro 2806* (CEPEC!, F!, UB!); Maraú, 17 Jan 1967, *Belém & Pinheiro 3143* (CEPEC!, F!, UB!); Santa Cruz Cabrália, 8 Feb 1967, *Belém & Pinheiro 3321* (CEPEC!, F!, UB!); 1834, *Blanchet 1903* (F!, P!); Mucugê, Estrada Mucugê-Guiné, a 5 km de Mucugê, 7 Sep 1981, *CFCR 1924* (K!); Mucugê. Estrada Mucugê–Guiné, a 7 km de Mucugê, 7 Sep 1981, *Pirani et al. in CFCR 2009* (K!); Mun. Ilhéus, Litoral Norte, a 9 km NE de Ilhéus, 3 Aug 1980, *Carvalho 300* (CEPEC!, NY!, RB!); Ponta Grande, Porto Seguro, 7 Jun 1962, *Duarte 6682* (F!, NY!, RB!); Mun. Valença. Rodovia que liga Valença a Guaibim (litoral), km 14, 13 Aug 1980, *Hage 397* (CEPEC!, NY!); 5 km south of Santa Cruz Cabrália, 0 m, 18 Mar 1974, *Harley 17137* (K!); Between Alcobaça and Caravelas on BA 001 highway. 20 km S. of Alcobaça, 0 m, 17 Jan 1977, *Harley & Mayo 18045* (CEPEC!, K!, MO!, NY!, SPF!, U!); 19.5 km SE of the town of Morro do Chapéu on the BA052 road to Mundo Novo, by the Rio Ferro Doido, 900 m, 2 Mar 1977, *Harley 19236* (CEPEC!); Nova Viçosa, arredores, Bahia, 9 Dec 1984, *Hatschbach & Silva 48745* (C!, CEPEC!, K!, MO!, US!);

FIG. 32. *Gomidesia fenzliana* near Catolés, Bahia. **a** habitat; **b** habitat (B.Stannard, the best of field companions, for scale); **c** habit (trunks extend for c. 2 m in cleft between rocks); **d**, **e** buds and flowers several days after pollination; **f**, buds and flowers one day after anthesis; **g**, flowers c. 2 hours after anthesis, petals not yet fully reflexed.


a
b
c
d
e
f
g

Mun. Ilhéus, Fazenda Barra do Manquinho. Ramal com entrada no km 10 da Rod. Pontal Olivença, lado direito. 3 km a Oeste da Rod, 5 Feb 1982, *Mattos Silva & T.S. dos Santos 1407* (CEPEC!, NY!); Mun. Ilhéus. Estrada que liga Olivença ao povoado de Vila Brasil, km 3, entrada de ramal a esquerda (próx. à Fazenda Cururupitanga), 70 m, 24 Feb 1984, *Mattos Silva 1717* (ALCB!, CEPEC!, HUEFS!); Mun. Una. Ramal que liga o Povoado de Comandatuba (localizado a 17 km ao sul de Una) a Pedras, com 8 km de extensão, 13 Jan 1985, *Mattos Silva 1811* (CEPEC!, HUEFS!, NY!, RB!); Mun. Alcobaça. Rodovia Alcobaça/Prado (BA 001), km 3, 3 m, 29 Mar 1989, *Mattos Silva 2634* (CEPEC!, K!); Mun. Belmonte. Km 26 da Rod. Belmonte/Itapebi, 18 May 1979, *Mattos Silva 388* (CEPEC!, NY!); Mun. Santa Cruz Cabrália. Estrada que liga S.C. Cabrália ao Povoado de Santo Andre, numa extensão de aprox 3 km, 0 m, 17 Jun 1980, *Mattos Silva & Brito 865* (CEPEC!, HUEFS!, NY!); Mun. Santa Cruz Cabrália, estrada que liga S.C. Cabrália ao povoado de Santo Andre. Numa extensão de aprox. 3 km, 17 Jun 1980, *Mattos Silva 875* (CEPEC!, NY!); Mun. Santa Cruz Cabrália. Estrada que liga S.C. Cabrália ao Povoado de Santo Andre, numa extensão de approx 3 km, 0 m, 17 Jun 1980, *Mattos Silva & Brito 880* (CEPEC!, US!); Mun. Santa Cruz Cabrália. Km 4 da rodovia que liga S.C. Cabrália a Estação Ecológica do Pau-Brasil (antiga rodovia Sta. Cruz/Porto Seguro), 19 Jun 1980, *Mattos Silva & H.S. Brito 918* (CEPEC!, NY!); Mun. Maraú. Rod. BR 030, a 3 km ao S de Maraú, 7 Feb 1979, *Mori & Mattos Silva 11452* (CEPEC!, K!, NY!); Mun. Santa Cruz Cabrália. A 2-3 km a W de Santa Cruz Cabrália, 6 Apr 1979, *Mori & Santos 11695* (CEPEC!, K!, NY!); Mun. Santa Cruz Cabrália, Entre Santa Cruz e Porto Seguro, a 15 km ao norte da segunda, 27 Nov 1979, *Mori 13016* (CEPEC!, K!, NY!); Mun. Lençóis. Arredores de Lençóis, caminho para Barro Branco, 400 m, 2 Mar 1980, *Mori & Funch 13351* (CEPEC!, K!, NY!); Mun. Ilhéus. Road from Olivença to Una, 2 km S. of Olivença, 0 m, 19 Apr 1981, *Mori 13662* (CEPEC!, K!, MO!, NY!); Mun. of Morro do Chapéu, 4 km S of Morro do Chapéu, on road to Utinga, 18 Jun 1981, *Mori 14558* (CEPEC!); Mun. Porto Seguro. ca 6–7 km na estr. que liga Trancoso ao Arraial D'Ajuda, 12 Dec 1991, *Sant'Ana 96* (CEPEC!, K!); Ilhéus, BA, 15 Dec 1984, *Sobral 3610* (F!, NY!); Mun. Ilhéus. Road from Ilhéus to Serra Grande, 11.3 km N of the Itaipe bridge leaving Ilhéus, 5 May 1992, *Thomas 9121* (CEPEC!, K!); Mun. Ilhéus. Road from Olivença to Serra das Trempes, 6 km from Olivença, 3 Feb 1993, *Thomas 9722* (CEPEC!). **ESPÍRITO SANTO:** Reserva Florestal da CVRD, Linhares. Final da estrada Parajú, 21 Jan 1993, *Nic Lughadha 151* (K!); **PARANÁ:** Jacarehy, 23 Mar 1911, *Dusen 11381* (S!); Jacarehy, 22 Mar 1914, *Dusen 14633* (NY!, S!); Jacarehy, 17 Mar 1909, *Dusen 8308* (NY!, S!); Mun. Paranaguá, Taboleiro do Guarani, 13 Jan 1966, *Hatschbach 13635* (MO!, NY!, US!); Mun. Paranaguá: Baia Paranaguá, Picaguera, 23 Apr 1969, *Hatschbach 21379* (MO!); Mun. Paranaguá, Rio da Vila, 26 Jan 1977, *Hatschbach 39738* (UEC!); Mun. Guaratuba, Rio da Divisa, 15 m, 13 Feb 1962, *Hatschbach 8952* (B!, F!); Guaratuba, 5 m, 3 Jan 1954, *Reitz 1516* (NY!, PACA!, US!); Guaratuba, 21 Feb 1952, *Reitz 4378* (PACA!, S!. US!); Mun. Guaratuba, Low coastal forest Guaratuba, 2 m, 21 Feb 1952, *Smith & Reitz 5742* (US!); **RIO DE JANEIRO:** Ilha Grande, Praia do Leste, 3 Dec 1980, *Araújo & Maciel 4149* (US!); Mun. Angra dos Reis. Ilha Grande, Reserva Biológica Estadual da Praia do Sul. Praia do

FIG. 33. *Gomidesia fenzliana* near Linhares, Espírito Santo. **a** habitat and habit; **b** infructescences and branches; **c** developing fruits, note closely connivent calyx lobes; **d** open flowers, note fully reflexed petals and style overtopping stamens, flower visitor is unidentified Syrphid fly, not observed to contact stigma; **e** bark, **f** inflorescence just before anthesis, note elongation of buds about to open; **g** same inflorescence with flowers at various stages of anthesis.


a
e
b
f
c
d
g

Sul, 28 Feb 1985, *Araújo & Pereira 6743* (NY!); In arenoso turfosis pr. Rio de Janeiro, *Beyrich s.n.* (BM!, K!, P!, W!); To the island of Boa Viagem (Niterói), 27 Mar 1826, *Burchell 2902* (K!, P!, US!); In insulae gubernatoris, 18 Mar 1875, Collector Unknown (R!); Mun. Cabo Frio, Massambaba, a 39 km da praia de Iguaba e a 14 km do trevo de Cabo Frio, 5 Feb 1986, *Fontella & Marquete 2282* (RB!); *Frolich s.n.* (S!); Estrada BR-5, pr. Arraial do Cabo, 30 Dec 1962, *Fromm & Santos 1338* (B!, R!); Restinga de Macaé, 10 m, 11 Jan 1985, *Gentry 49411* (MO!); Restinga de Macaé, 10 m, 11 Jan 1985, *Gentry 49411* (MO!); Estado de Guanabara; Barra da Tijuca, 30 Dec 1964, *Hoehne 5954* (K!, NY!, SP!, SPF!); Guanabara, Barra da Tijuca, 14 Feb 1933, *Kuhlmann s.n. RB 139829* (F!, NY!, RB!); Recreio dos Bandeirantes, Jan 1935, *Lulz & Cochran s.n. R 29268* (R!, US!); Estado de Guanabara. Restinga da Tijuca, *Machado s.n. RB75167* (RB!, US!); San Clemente, *Miers 3774* (K!); Mun. Cabo Frio, 28 Jan 1976, *Montouchet 2195* (R!, UEC!); Rio de Janeiro, 1832, *Riedel 196* (F!, K!, LE!, P!, S!, U!, W!); Cabo Frio, 6 May 1887, *Schenck 3848* (C!); Mun. Cabo Frio, Cabo Frio. Praia do Pontal, 0 m, 17 Apr 1952, *Smith 6632* (US!); Restinga de Cabo Frio, 18 Jan 1967, *Sucre 1382* (BR!, RB!, UB!); Estrada Barra Jacarepaguá, 16 Dec 1971, *Sucre 8107* (RB!); Mun. Cabo Frio, entre São Pedro d'Aldeia e a cidade de Cabo Frio, 16 Apr 1973, *Sucre 9955* (K!, NY!, RB!); SANTA CATARINA: Vargem do Macário, Governador Celso Ramos, 5 m, 20 Mar 1972, *Bresolin 516* (PACA!, R!); Barra do Sul, Araquari, 2 m, 2 Jan 1954, *Reitz & Klein 1500* (NY!); Praia Braba, Itajaí, 3 m, 10 Feb 1950, *Reitz 3253* (R!, S!, US!); Barra do Sul, Araquari, 5 m, 9 Jan 1953, *Reitz 5152* (PACA!); Barra do Sul, Araquari, 3 m, 8 Apr 1953, *Reitz & Klein 522* (F!, NY!, PACA!, U!, US!); SÃO PAULO: westward of Santos toward Cubatão, 24 Sep 1826, *Burchell 3128* (K!); Iguape, Estação Ecológica Juréia-Itatins, proximidades do maciço da Juréia, 300 m, 17 May 1990, *Cordeiro 633* (SP!); Cananéia, Ilha do Cardoso, Feb 1981, *Custódio 571* (MO!); Rodov. Bertioga–São Sebastião, 20 Mar 1975, *Leitão Filho 1487* (UEC!); Ubatuba, 21 Mar 1975, *Leitão Filho 1494* (R!, UEC!); Mun. Cananéia, Ilha do Cardoso, 20 May 1988, *Leitão Filho 20348* (UEC!); Ubatuba, Praia do Pequereassu, 1 May 1961, *Mattos 8933a* (K!); Ilha do Cardoso, perto de Cananéia, 0 m, 2 Feb 1978, *Prance 6937* (UEC!); Ilha do Cardoso, perto de Cananéia, 0 m, 2 Feb 1978, *Prance 6977* (UEC!); Saint-Hilaire C2 1678 (P!).

**Local Names.** Batinga Orelhinha (Espírito Santo), Murta (Espírito Santo). Murta is a name commonly applied to many different species of Myrtaceae in Brazil. The name batinga is applied to a number of different species of *Gomidesia*, while the qualifier orelhinha means little ear, a reference to the shape of the leaves.

Lacerda et al. (1993) list *G. fenzliana* as one of the principal species in the '*Clusia* open scrub' vegetation type which is frequent on secondary dunes in Brazilian coastal ecosystems. Legrand and Klein (1967) also considered *G. fenzliana* to be a characteristic species of stable dunes and described it as occurring in abundance along the northern coast of Santa Catarina. The southern distributional limit may be in Rio Grande do Sul. Mattos (1989) cites three collections from Torres but I have not seen this material and since the key conflicts with the description the identity of this material is uncertain. The most southerly collection I have seen in the course of this study is *Bresolin 516,* an inland collection from the south of Santa Catarina. Although apparently disjunct from the coastal populations this collection is morphologically very similar to them.

At the northern distributional limit the situation is more complicated. Specimens from the inland, high altitude populations often have more conspicuous, persistent indument and more coriaceous, oblong leaves with petioles short or absent. Since many intermediates exist and the coastal populations are in themselves extremely variable I do not consider that the inland populations merit recognition at species level. However, the pattern of variation in this area would appear to merit further detailed study as the character variation in the relatively few inland collections examined is suggestive of a cline: inland collections made at the same latitude as the northernmost coastal collections tend to have leaves of similar shape (but smaller size) to those seen in the coastal populations of Bahia while the northernmost inland collections, only 2 degrees further north, are so different that, were it not for the morphologically intermediate collections mentioned above, I would not hesitate to treat them as a distinct species. Recent intensive collecting in this area should result in the availability of a large number of new collections of this complex for study in the near future and it is hoped that these will permit the clarification of these patterns of variation.

In describing *Gomidesia fenzliana,* Berg cited an unusually large number of collections from B, M, W and the Sonder herbarium much of which is now at Melbourne. The syntypes are *Sellow s.n., Mart. hb. Fl. Bras. 683*, *Schott 1078*, *Luschnath s.n.* (all from Rio de Janeiro) and *Claussen 2100* from Minas Gerais. Contrary to his normal practice, when citing material of this species Berg did not specify which collections were referrable to each of the two varieties described. I suspect that var. *spathulata* was based on the *Luschnath* collection of which I have seen duplicates at BR and W and I have lectotypified this name accordingly. Of the remaining syntypes which are candidates for lectotype of the typical variety I exclude *Claussen 2100* since I have seen no material of *G. fenzliana* from Minas Gerais and I believe that the locality cited is based on the assumption that all Claussen collections are from Minas Gerais. The label for the W sheet of this collection gives no further detail than 'in brasilia'. The lack of a number citation for the Sellow syntype makes it unsuitable as a lectotype though I believe it was distributed from Berlin as *Sello 145*. Left with a choice between *Mart. hb. Fl. Bras. 683* and *Schott 1078* I preferred the former as lectotype because duplicates of this collection are very widely distributed.

**14. Gomidesia flagellaris** D.Legrand, Sellowia **13:** 279. 1961. Type. Brazil. Santa Catarina: Três Barras, Garuva, S. Francisco do Sul, *Reitz & Klein 5745* (holotype, MVM, n.v.; isotype, US!).

(Fig. 2C&D and 13a-d).

*Shrub* or *treelet* 2–4(–5 m) tall. Branchlets 10 cm below the terminal bud c. 1.5 mm in diameter, more or less rounded with a dense indumentum of appressed, straight, white hairs to 0.6 mm long, terminal bud 8 mm long x 2 mm wide with a dense indumentum of appressed, straight, straw-coloured hairs to 0.8 mm. Stipule lobes conspicuous, to 3 mm long. Petioles 3–4 mm long, 1–1.5(–2.5?) mm wide, slightly channeled, with a dense indumentum of appressed, straight, white hairs to 0.6 mm long. *Leaves* oblong to elliptic, usually narrowly so (67–)77–114(–140) mm long, 22–39 mm wide, (2.7–)3.0–3.5(–3.9) times longer than wide, apex acuminate or caudate, base acutely cuneate, margin flat or bent down or recurved, midrib impressed above, prominent below, lateral veins straight, more or less flat or very slightly raised above, slightly raised below, only slightly more conspicuous than the secondary laterals and sometimes difficult to distinguish from these latter, diverging at c. 70° from the midrib, secondary laterals simple, often more or less straight and equalling the laterals in prominence, marginal vein equalling the laterals in prominence and looping between them or almost parallel to the margin at a distance of 1–1.5(–2) mm from it, higher order venation inconspicuous, slightly raised especially in the vicinity of the marginal vein. Venation between marginal vein and margin inconspicuous. Indumentum absent above or scattered and consisting of appressed, curved, white hairs to 0.4 mm, moderately dense below, consisting of appressed, straight, pale hairs of mixed lengths to 0.6 mm. Gland dots indistinct above, distinct below, dark and slightly raised. Mature leaves chartaceous, markedly bicolorous, dark green above, pale golden green below. *Conflorescence* comprising 1(–2) pairs of uniflorescences in the axils of distal leaves. Uniflorescence a triad or occasionally a dichasium of 7 flowers, 17–67 mm long, reaching 1/3–1/2 the length of the subtending leaf, pendulous; peduncle 15–61 mm long i.e. c. 9/10 the length of the inflorescence, 0.7–0.8 mm wide, flattened, lateral branches none below the terminal cyme or cluster of cymes. *Mature flower buds* c. 4–5 mm long x 4–5 mm wide. Calyx lobes 1.6–2.1 mm long x 2.5–3.8 mm wide, depressed ovate, apex rounded, with a moderately dense indumentum of appressed, curved, white hairs to 0.4 mm externally, dense (near base) to moderately dense (near apex) internally, consisting of appressed, straight, white hairs to 0.2 mm long, hypanthium obconic, 2.2–2.5 mm long, prolonged c. 1.5 mm above the ovary, with a dense indumentum of appressed, straight, white hairs to 0.4 mm externally, indumentum dense internally, disk c. 2.9–3.5 mm diameter, indumentum dense, stamens 98–140, filament abruptly narrowed to thread-like portion near point of insertion on connective, anthers 0.6–0.7 mm long, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves retain curvature on dehiscence, connivent or held parallel, with margins flat, effective dorsal opening 1/3–1/2 the length of the anther, residual septum not visible, style 6–8 mm, with moderately dense indumentum in lower 2/3. Ovary 1–1.2 mm long, bilocular, ovules 2 per locule. *Fruit* globose, 7.5–13 mm diameter, crowned with the erect (or slightly spreading) imbricate calyx lobes. Mature seed one per fruit, c. 10 mm, testa mid-brown, hypocotyl glabrous.

**Distribution (Map 12) and ecology.** Occurs from the south of the state of São Paulo, through Paraná and into the north of Santa Catarina, alway on the coastal plain. Most collections seen are described as being from rain forest (mata pluvial) at altitudes of 10–150 m. Klein (1990) reported this species as confined to Floresta Ombrófila Densa (rain forest on Atlantic slopes) in lowland and submontane areas, up to an altitude of about 200 m. He considered it particularly characteristic of the associations occurring on the lower slopes of the Serra do Mar where it may reach densities of 10 to 12 plants per 100 m$^2$. In contrast, near the southern limit of its distribution, in the lower part of the Itajaí valley it is rather rare.

**Phenology.** *Gomidesia flagellaris* flowers from December through to February. Mature fruit have been observed from August to October.

**Specimens examined. BRAZIL. PARANÁ:** Mun. Antonina, localidad de Serrinha, 100 m, 11 1983, *Callejas & Hatschbach 1809* (K!, MO!, NY!, U!); Mun. Guaratuba, Serra de Araraquara, Morro do Cauví, 30 Dec 1963, *Hatschbach 11062* (B!); Mun. Antonina. Estr. Cacatu - Serra Negra, above Antonina, NW of the town, 19 Jan 1966, *Hatschbach & Haas 13552* (K!, NY!, P!, RB!, U!, US!); Morro do Tabaraquara, (Paranaguá), 100 m, *Hatschbach 14539* (US!); Mun. Guaratuba. Praia do Mendanha, 50 m, 20 Nov 1967, *Hatschbach 17889* (MO!); Mun. Guaraqueçaba. Rio do Cedro, 50 m, 14 Dec 1967, *Hatschbach 18116* (US!); Mun. Guaratuba, Serra de Araraquara, 75 m, 27 Feb 1968, *Hatschbach 18643* (C!); Mun. Morretes, Rio Mãe Catira, 150 m, 7 Aug 1968, *Hatschbach 19565* (C!); Mun. Guaraqueçaba. Rio de Costa, 10 m, 4 Feb 1971, *Hatschbach 26266* (C!, K!, S!, US!); Mun. Morretes. Rio Mãe Catira, 11 Jul 1977, *Hatschbach 40022* (UEC!); Mun. Morretes, Rio Bromado, 12 Jan 1979, *Hatschbach 41871* (C!, NY!, SPF!, UEC!); Mun. Antonina, Serrinha, 100 m, 29 Dec 1982, *Hatschbach 45974* (BR!, IBGE!, MU!); Mun. Antonina, Serrinha, 30 Nov 1983, *Hatschbach 47167* (BR!, MO!, UB!, US!); Mun: Paranaguá. Sítio do Meio, 30 m, 29 Dec 1962, *Hatschbach 9540* (U!); Mun. Paranaguá, Sertão do Indaial, 10 m, 26 Jan 1963, *Hatschbach 9825* (B!, US!); Mun. Antonina, along road to Guaraqueçaba, 100 m, 10 Dec 1981, *Landrum 3999* (MO!, NY!, RB!, US!); Forest on slope of Morro do Tabaquara, W. of Matinhos, 3 Jan 1967, *Lindeman & J.H. de Haas 3848* (U!). **SANTA CATARINA**: Cunhas, Itajaí, 30 m, 23 Jun 1955, *Klein 1420* (BR!, K!, NY!, S!, US!); Três Barras, Garuva, S. Francisco do Sul, 150 m, 25 May 1957, *Reitz & Klein 3990* (B!, F!, PACA!); Três Barras, Garuva, S. Francisco do Sul, 150 m, 19 Dec 1957, Reitz & Klein 5745 (US!); Locality not indicated, *Schrainer(?) s.n.* (R!). **SÃO PAULO:** Mun. Sete Barras - Reservas de Sete Barras, 50 m, 22 Dec 1979, *Benson 10891* (UEC!);

**Conservation.** Klein (1990) lists this species as rare, with an irregular and discontinuous distribution, though it is sometimes locally frequent. He reported it to be confined to the area between the Vale do Itajaí (Santa Catarina) and the Baia de Paranaguá (Paraná) in a rather narrow band along the coast and considered it likely to attain 'endangered' or 'vulnerable' status within a rather short period of time because of the destruction of its habitat due to land use for 'culturas ciclicas' (rotation cropping) and banana plantations. He advocated planting *G. flagellaris* in the Timbo Municipal Reserve, in the Itajaí valley as a step towards its conservation. However, since *G. flagellaris* was collected in São Paulo for the first time only in 1979 it seems likely that it is easily overlooked and may eventually prove to have a wider distribution than that known at present.

The fine flexuous peduncles suggest that the inflorescences are pendulous and this is also implied in Legrand and Klein's (1967) comment that the peduncles often hide themselves beneath the leaves. *Gomidesia cambessedeana* also exhibits flexuous peduncles and Klein has suggested that the two species may be related. They are easily distinguished however, since *G. flagellaris* lacks the erect indumentum of reddish brown hairs so conspicuous in *G. cambessedeana* and has rounded calyx-lobes quite unlike the acute calyx-lobes of *G. cambessedeana*.

Dichasia composed of seven flowers were observed in two collections of this species. This type of inflorescence has not previously been reported in *Gomidesia* but is well known in *Myrceugenia* (Landrum 1981).

Apparently *Gomidesia flagellaris* is likely to be confused with *Calyptranthes eugeniopsoides*, which Klein (1990) considered very similar both morphologically and in terms of habitat. He considered the paler green colour and dense adaxial indumentum of the young leaves of *G. flagellaris* to be one of the easiest characters to use to distinguish it from *C. eugeniopsoides.*

**15. Gomidesia freyreissiana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 19. 1857. Type. Brazil. Bahia: "ad Rio Mucuri," *Freyreiss s.n* (holotype, B, n.v., presumed destroyed; lectotype, P!, here designated).

*Tree* or *shrub* 1.5–7 m tall. Branchlets 10 cm below the terminal bud 3–4 mm in diameter, rounded or quadrangular, glabrous or with a sparse to moderately dense indumentum of appressed, straight, pale hairs to 0.8 mm long; terminal bud c. 4 mm long or proliferating. Stipule lobes to 0.6 mm long, yellowish. Inter-petiolar ridge absent. Petioles 4–9 mm long, 1–2 mm wide, channeled, with a sparse to moderately dense indumentum of appressed, straight, white hairs 0.6–0.8 mm or more long. *Lamina* oblong or elliptic, 59–116 mm long, 30–53 mm wide, 2–2.5 times as long as wide; apex acute or obtuse, truncate or rounded at very tip; base cuneate or decurrent; margin bent down or recurved; midrib sulcate near base to slightly raised near apex above, prominent below; lateral veins more or less straight, raised above, raised or prominent below, diverging at c. 60–70° from the midrib; secondary laterals composite, straight, sometimes almost equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping between them; higher order venation conspicuous, raised above and paler than the lamina, slightly raised below; venation between marginal vein and margin conspicuous, including secondary arches and submarginal vein. Indumentum absent above, sparse below, consisting of appressed, straight or curved, pale, straw-coloured, brown-based hairs up to 0.4–0.5 mm long. Gland dots above conspicuous, pale, distinct below, raised. Mature leaves chartaceous. *Conflorescence* comprising two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect complex thyrsoid of c. 15–35 flowers, 65–100 mm long, reaching c. 8/10–5/4 the length of the subtending leaf; peduncle 43–57 mm long i.e., c. 1/2–2/3 the length of the inflorescence, 1.2–2 mm wide, flattened; lateral branches 2–3 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 3.9–4.2 mm long x 3.8–4.2 mm wide. Calyx lobes shallowly depressed ovate, 1 mm long x 2.6 mm wide, apex rounded, with a sparse indumentum of appressed, straight, white hairs externally, sparse to moderately dense or dense internally, margin ciliate; hypanthium 2.2 mm long, prolonged c. 0.8 mm above the ovary, densely pubescent in lower half, moderately dense to sparse towards apex externally, dense internally; disk c. 2.4 mm diameter, densely pubescent. Stamens c. 127 per flower; filaments narrowing abruptly to point of insertion on connective, anthers c. 0.5 mm long, apex more or less truncate, vertical displacement of thecae marked, thecal halves losing curvature at dehiscence, divergent, thecal margins recurved after dehiscence, residual septum visible, oblique. Style c. 8 mm, with moderately dense indumentum in lower 1/3 consisting of white hairs to 0.3 mm; stigma distinctly capitate. Ovary 1.7 mm long, 4–5-locular, ovules 2 per locule.

**Distribution (Map 13) and ecology.** *Gomidesia freyreissiana* has been collected in the states of Rio de Janeiro and Espírito Santo and just over the border in the extreme south of Bahia. The scant ecological data available suggest a tendency to occur in flooded vegetation.

**Phenology.** *Gomidesia freyreissiana* has been collected in flower in late November and mid-December, rather earlier than most species of the genus.

**Specimens examined. BRAZIL.** BAHIA: 'ad Rio Mucuri in prov. Bahiensi, *Freyreiss s.n.* (P!). ESPÍRITO SANTO: Linhares, Reserva Florestal da CVRD, 29 Nov 1982, *Silva 365* (CEPEC!, CVRD!); Linhares, Reserva Florestal da CVRD, 14 Dec 1982, *Silva 373* (CEPEC!, CVRD, HRB!). RIO DE JANEIRO: Mun. Magé, Rio Guapimirim, 23 Nov 1977, *Araújo 1957* (GUA!); Mun. Silva Jardim, Reserva Biológica de Poço das Antas, 20 m, 5 Nov 1982, *Martinelli 8834* (K!); Atafona, 1939, *Sampaio s.n.* (R!); Atafona, Mar 1939, *Sampaio 8104* (R!); *Sellow s.n.* (BR!). STATE NOT INDICATED: *Beyrich 658* (LE!); Maracaibo, *Merkel s.n.* (C!); Macaraiba, *Merkel s.n.* (C!); *Sellow s.n.* (P!); *Sellow 658* (W!).

**Local names:** Batinga de Baixada (Espírito Santo). The name batinga is applied to a number of different species of *Gomidesia* in this area. The qualifier 'baixada' is suggestive of low-lying or marshy areas.

*Gomidesia freyreissiana* is one of the less distinctive species known from only a handful of collections. It resembles *G. schaueriana* in its unusually high locule number (4–5 in *G. freyreissiana*, 4 in *G. schaueriana*) and in its densely pubescent hypanthium which contrasts markedly with the calyx lobes. It differs from *G. schaueriana* in its chartaceous leaves (coriaceous in *G. schaueriana*) and in its generally more sparse indumentum. In the past *G. freyreissiana* has been confused with *Myrcia lacerdana* O.Berg ('*lacerdoana*', '*lacerdaeana*'). The two species are rather similar vegetatively but *M. lacerdana* differs in having distinctive calyx lobes which are much longer than broad and, of course, in its myrcioid anthers. I have also seen the name *Myrcia nigropunctata* (O.Berg) N.J.E. Silveira applied to material of *G. freyreissiana*. *M. nigropunctata* is easily distinguished by its smaller, more coriaceous leaves and by its hypanthium which is glabrous externally. Furthermore, both these species of *Myrcia* have trilocular ovaries.

Berg's description of *G. freyreissiana* was based on two collections seen at Berlin which he cited in the following form 'habitat ad Rio Mucuri in prov. Bahiensi: Freyreiss; nec non in prov. Rio de Janeiro: Sellow'. Since the Berlin collections are almost certainly no longer extant, a lectotype must be chosen from among the other material seen by Berg. I have examined a number of sheets annotated by Berg as *G. freyreissiana*. Most are unnumbered Sellow collections which bear Herb. Reg. Berol. labels and are almost certainly isosyntypes, i.e. duplicates of the Sellow collection mentioned by Berg. However, the W sheet is numbered *Sello II n. 658* and the LE sheet is numbered *Beyrich 658*, suggesting some confusion of collector or number. For this reason I prefer to choose as lectotype the *Freyreiss s.n.* collection at P which bears the type locality and determination in Berg's hand. I have seen no duplicates of this collection.

Also annotated by Berg as *G. freyreissiana* is a fragment mounted on the same sheet as *Beyrich 658* with an original label which reads 'Myrtus c Maracaibo Brasilia'. This appears to be a duplicate of a collection represented at C by two sheets labelled 'Maracaibo Brasil Merkel' and 'Macaraiba Brasil D. Hornemann' respectively. I have been unable to trace any such locality within Brazil and am tempted to conclude that the word is a vernacular name rather than a findspot. The *Sampaio* material cited above is placed here with hesitation. The sheets examined almost certainly represent duplicates of a single collection but at the time of writing I have only the unnumbered sheet to hand. The leaves bear a strong resemblance to those of the type but the fruit are immature and so have not been included in the description.

**16. Gomidesia gestasiana** (Cambess.) D.Legrand, Notul. Syst. (Paris) **15:** 261. 1958.
*Myrcia gestasiana* Cambess. *in* Saint-Hilaire, Fl. Bras. merid. **2:** 303. 1832. Type. Brazil. Rio de Janeiro: "In monte Tijuca prope Rio de Janeiro," *Saint-Hilaire s.n.* (lectotype, P!, here designated; isotypes, P! (2 sheets)).

Fragile *shrub* to 2 m tall. Branchlets 10 cm below the terminal bud 4 mm in diameter, rounded or slightly flattened, glabrous; terminal bud 8 mm long. Stipule lobes not seen. Interpetiolar ridge more or less marked. Petioles 4 mm long, 2.5 mm wide, channeled, minutely puberulent. *Lamina* oblong, narrowly elliptic or narrowly oblong, 93–171 mm long, 29–50 mm wide, 2.8–3.6(–4.4) times as long as wide; apex acute or acuminate, rounded at very tip; base rounded or acutely or obtusely cuneate; margin flat or bent down, recurved near base; midrib raised and channeled above, prominent below; lateral veins more or less straight, slightly raised above and below, diverging at c. 70–80° from the midrib; secondary laterals simple, straight, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and scarcely curving between them, almost parallel to the margin; higher order venation inconspicuous, slightly raised above and below; venation between marginal vein and margin inconspicuous. Indumentum sparse to moderately dense above, consisting of fine, white, straggling hairs to 0.6 mm, glabrous below, except for midrib which bears a dense indumentum consisting of reddish brown tangled hairs of varying lengths and orientations. Gland dots indistinct above or distinct and slightly impressed, distinct below, dark. Mature leaves membranaceous to chartaceous. *Conflorescence* comprising 1–2 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 9–15 flowers or fewer, 25–31 mm long, reaching c. 1/3 the length of the subtending leaf; peduncle 12–19 mm long i.e., c. 1/2–2/3 the length of the inflorescence, 2–3 mm wide, flattened; lateral branches 1 or 2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 5 mm long x 4 mm wide. Calyx lobes triangular, 1.5 mm long x 2 mm wide, apex acute, with a moderately dense indumentum externally, glabrous internally or with moderately dense indumentum towards apex, margin ciliate; hypanthium vertically ribbed, c. 3 mm long, prolonged c. 1.2 mm above the ovary, indumentum dense externally and internally; disk c. 2.6 mm diameter, indumentum dense. Stamens c. 89 per flower; anthers 0.5 mm long, filaments not tapered to point of insertion, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves retain curvature on dehiscence, connivent or held parallel, thecal margins flat or slightly reflexed, effective dorsal opening c. 1/4 the length of the anther, residual septum occasionally visible, vertical. Style c. 7 mm, with moderately dense indumentum in lower 1/2; stigma punctiform. Ovary c. 1.8 mm long, bilocular, ovules 2 per locule. *Fruit* not known.

**Distribution (Map 14) and ecology.** Apparently endemic to the Tijuca forest area of Rio de Janeiro.

**Conservation:** The only collection apart from the type was made in the early 1970s in an area that has been the subject of ongoing study by staff of GUA. The fact that *G. gestasiana* has not been recollected in recent years suggests that population sizes may be rather small.

**Phenology.** Material with unopened buds and finished flowers was collected in December.

**Specimens examined. BRAZIL.** **RIO DE JANEIRO:** In monte Tijuca prope Rio de Janeiro, *Saint-Hilaire s.n.* (P!); Morro Queimado, 600 m, 1 Dec 1971, *Sucre 8022* (RB!).

*Gomidesia gestasiana* appears to be closely related to *G. crocea* and the similarity is reflected in the fact that both the collections I examined had previously been determined as *G. crocea*. Judging by his determination slips, Legrand appears to have considered relegating *Myrcia gestasiana* to the synonymy of *G. crocea*, along with *G. jacquiniana* and *G. langsdorffii*, but he subsequently made the new combination *G. gestasiana* with the comment that the species was very close to *G. crocea* but differed in its smaller leaves. Other more significant differences between *G. gestasiana* and *G. crocea* are discussed under the latter species.

The name *G. gestasiana* has been applied incorrectly to recent collections of *G. sonderiana* (e.g. *Andreata 307A, 617*), with the effect that the binomial has been misapplied more often than it has been correctly applied. However, given that the total number of collections in question is fewer than a dozen, I prefer to restore correct usage than to attempt to conserve names for what are, by any standards, rather rare and little known taxa. *Gomidesia gestasiana* resembles *G. sonderiana* in having smooth, whitish bark and few-flowered inflorescences but differs in leaf venation and in anther morphology. In leaves of *G. gestasiana* the marginal vein scarcely curves between the laterals, following a course almost parallel to the leaf margin, while in leaves of *G. sonderiana* the marginal vein loops markedly between the laterals. In the stamens of *G. sonderiana* the filament tapers to a pale, thread-like apex which is inserted on a well-developed connective stub whereas in the stamens of *G. gestasiana* the filament scarcely tapers towards its apex and is inserted on the connective at more or less the same level as the thecae.

Not having had the opportunity to examine Saint-Hilaire's material, Berg treated *G. gestasiana* under *Myrcia* with an expression of doubt. His description is rather shorter than that provided for other species and is clearly based on Cambessedes' original description. Legrand (1958) studied some of the Saint-Hilaire collections held at P and transferred half a dozen of Cambessedes' *Myrcia* species to *Gomidesia*, making new combinations where required. One of the three Saint-Hilaire sheets of *G. gestasiana* at P bears Legrand's annotation (as described above) and an isotype label, while the other two sheets lack any annotation by Legrand and are labelled isotype and type respectively. Unfortunately the latter sheet is the least informative of the three, bearing very young inflorescences with no open flowers. I therefore choose the sheet annotated by Legrand as lectotype of *G. gestasiana*.

**17. Gomidesia glazioviana** (Kiaersk.) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 22. 1959.

*Myrcia glazioviana* Kiaersk., Enum. Myrt. bras. 111. 1893. Type. Brazil. Rio de Janeiro: Serra de Alto Macahé de Nova Friburgo, *Glaziou 17005* (holotype, C!; isotypes, BR!, K!, P! (2 sheets), R!).

*Tree* to 4 m tall. Branchlets 10 cm below the terminal bud c. 3.5 mm in diameter, rounded, more or less glabrous; terminal bud 10 mm long with a dense indumentum of erect or ascending, straight, pale or brownish hairs to 1 mm underlain by a mat of tangled trichomes. Stipule lobes to 0.6 mm long. Inter-petiolar ridge not seen. Petioles 3–4 mm long, 1 mm wide, flat. *Lamina* narrowly ovate or elliptic, 24–27 mm long, 11–13 mm wide, 2.1–2.2 times as long as wide; apex acute (or obtuse), rounded at very tip; base acute; margin bent down or recurved; midrib sulcate or impressed near base, impressed or flat near apex above, prominent below; lateral veins straight, indistinct or very slightly raised above, raised below, diverging at c. 70° from the midrib; secondary laterals simple, nearly equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation inconspicuous above, raised below; venation between marginal vein and margin inconspicuous. Indumentum absent above, dense below, consisting of erect, straight, whitish hairs underlain by a tangled mat of pale, brownish, felted hairs. Gland dots indistinct above and below. Mature leaves chartaceous. *Conflorescence* comprising 1–2 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 5–9 flowers, c. 32–34 mm long, reaching or just exceeding the length of the subtending leaf; peduncle 22–26 mm long i.e., c. 3/4 the length of the inflorescence, c. 1 mm wide, slightly flattened; lateral branches 1 or 2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 3.5 mm long x 3.2 mm wide. Calyx lobes shallowly deltate, 1.2 mm long x 1.4 mm wide, apex acute, with a moderately dense indumentum of appressed, crisped, white hairs to 0.3 mm externally, indumentum dense internally; hypanthium c. 2.3 mm long, prolonged c. 1.4 mm above the ovary with a dense indumentum of erect, curved, felted, brown hairs to 0.6 mm, dense internally; disk c. 2.8 mm diameter, indumentum dense. Stamens c. 90 per flower; anthers 0.5 mm long, vertical displacement of thecae apparently slight, thecal margins recurved after dehiscence, residual septum visible, oblique. Ovary 0.9 mm long, bilocular (or trilocular?), ovules 2 per locule. *Fruit* globose, c. 5 mm diameter, crowned with the erect, imbricate calyx lobes or with a collar formed by the free part of the hypanthium which persists after the calyx lobes have fallen. Developing seed two per fruit, mature seed not seen.

**Distribution (Map 15) and ecology.** Known only from Macaé de Cima in the Atlantic rain forest of Rio de Janeiro.

**Phenology.** The type material collected in February had largely finished flowering, while fruit were collected in October.

**Specimens examined. BRAZIL. RIO DE JANEIRO:** Serra do Alto Macahé di Nova Friburgo, 19 Feb 1888, *Glaziou 17005* (BR!, C!, K!, P!, R!); Mun. Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, Caminho para os Pirineus. Sítio Sophronites, 1100 m, 14 Aug 1989, *Peron 876* (NY!).

Legrand transferred *Myrcia glazioviana* to *Gomidesia*, making the new combination *G. glazioviana* and citing the type material of the typical variety and of var. *villosa* as well as two other collections ( *Glaziou 3762, 3763*) which are quite different from the type material and are probably referrable to *Myrceugenia*. The type of var. *villosa* ( *Glaziou 16999*) is referrable to *Gomidesia montana* as circumscribed here. *Gomidesia glazioviana* is clearly close to *G. montana* but the latter species differs in having longer calyx lobes, less tangled indumentum and leaves which are generally dark brown above when dry (those of *G. glazioviana* remain green). The felted indumentum of curling hairs and the caducous calyx lobes are reminiscent of *G. spruceana* which differs from *G. glazioviana* in having much larger leaves with raised venation on the upper surface.

**18. Gomidesia grandifolia** (Cambess.) Mattos & D.Legrand, Loefgrenia **67:** 17. 1975.

*Myrcia grandifolia* Cambess., *in* Saint-Hilaire, Fl. Bras. mer. **2:** 298. Type. Brasil. São Paulo: *Saint-Hilaire D 786* (lectotype, P!; isolectotypes, F! (fragment), P!).

Fig. 34.

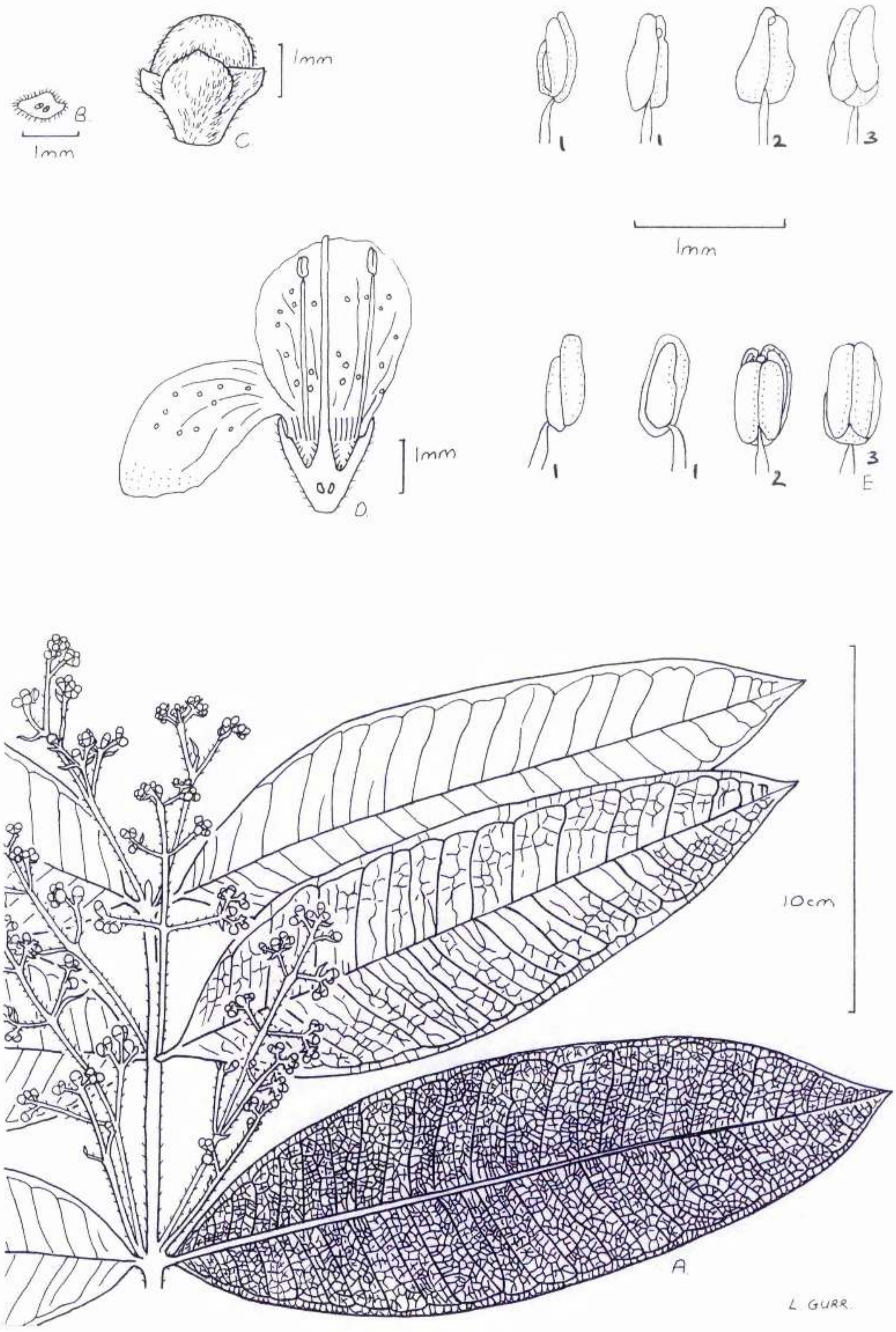
*Gomidesia jacquiniana* O.Berg, Linnaea **27:** 8. 1855. Type. Brazil. Rio de Janeiro: "ad radicem M. Serra de Taguahy," Mar 1818, *Pohl 5754* (lectotype, W!, here designated; isolectotypes, F! (fragment), W!).

*Myrcia ticuensis* Kiaersk., Enum. Myrt. bras. 107-109. 1893. Type. Brazil. Rio de Janeiro: "Serra da Bocaina, pres de S. José do Barreiro," 12 Feb 1876, *Glaziou 8381* (lectotype, C!; isolectotypes, K!, LE!, P!, R!).

*Gomidesia ticuensis* (Kiaersk.) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 15. 1959.

*Treelet* or *shrub,* height not recorded. Branchlets 10 cm below the terminal bud 3–3.5 mm in diameter, rounded or slightly flattened sometimes slightly ridged, with a moderately dense indumentum of erect or ascending, straight or curved, yellow or yellowish-brown, hairs to 0.7 mm long; terminal bud 6–8 mm long or proliferating. Stipule lobes to 2 mm. Inter-petiolar ridge absent. Leaves subopposite. Petioles 6–12 mm long, 1.5–2.5 mm wide, flat or slightly channeled. *Lamina* elliptic, narrowly ovate or narrowly oblong, 125–190(–260) mm long, 44–74(–112) mm wide, 1.8–4.3 times as long as wide; apex abruptly acuminate, occasionally acuminate; base acutely or obtusely cuneate; margin flat or bent down, occasionally recurved towards base; midrib sulcate above, filled with dense indumentum, prominent below; lateral veins straight or curved, sulcate to impressed above, prominent below, diverging at c. 70–80 ° from the midrib; secondary laterals composite, branching irregularly in the outer portion of the leaf, rarely equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation conspicuous, impressed above, raised below; usually paler than the lamina, venation between marginal vein and margin conspicuous, submarginal vein occasionally visible. Indumentum moderately dense to sparse above, consisting of white, irregularly disposed hairs, moderately dense on all orders of venation below, consisting of erect, straight, yellowish-brown hairs, c. 0.9 mm long. Gland dots indistinct above and below. Mature leaves chartaceous. *Conflorescence* often ill-defined comprising inflorescences irregular in size and disposition borne on leafless stems or in the axils of distal leaves or, when well-defined, comprising 2–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect complex thyrsoid of c. 59 flowers, up to 85 mm long, reaching c. 1/2 the length of the subtending leaf; peduncle c. 40 mm long i.e., c.1/2 the length of the inflorescence, 2 mm wide, flattened; lateral branches 2–3(–5) sub-opposite pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 4–4.2 mm long x 4–4.3 mm wide. Calyx lobes triangular, c. 1.8–2 mm long x 2.5–3.3 mm wide, apex acute or short-acuminate or rounded but appearing acute because of indumentum, with a dense indumentum of straight hairs up to 1 mm long externally, indumentum shorter and less dense internally; hypanthium 1:7–3 mm long, prolonged c. 0.8–1.7 mm above the ovary, with a dense indumentum of appressed, straight, brown hairs c. 0.5 mm long externally, indumentum dense internally; disk c. 1.8 mm diameter, densely pubescent. Stamens c. 115 per flower; filament tapering to pale apex; anthers c. 0.8–1 mm long, apex shallowly to deeply emarginate, gland inconspicuous, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent or gaping slightly, thecal margins in plane of curvature or slightly inrolled, effective dorsal opening 1/4–1/3 the length of the anther, residual septum often

FIG. 34. *Gomidesia grandifolia*. **A** Conflorescence and foliage; **B** Transverse section of ovary; **C** Flower bud; **D** Longitudinal section of flower; **E** Anthers in lateral (1), dorsal (2) and ventral (3) view. **A** & **C** from *Glaziou 8381*, **B**, **D** & **E** from *Glaziou 10782*. Drawn by L. Gurr.


1mm
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visible. Style 8.5–10.5 mm, with dense, appressed indumentum in lower 2/3, glabrous towards apex; stigma minutely capitate. Ovary c. 1.2–1.7 mm long, bilocular, ovules 2 per locule. *Fruit* globose, 10–13 mm diameter, crowned with the connivent to erect calyx lobes. Mature seed 2–3 per fruit, c. 10 mm long, testa pale with dark patches, hypocotyl glabrous.

**Distribution (Map 16) and ecology**. Infrequent in the understorey of forest in the Serra da Mantiqueira (and Serra do Mar). The fact that *G. grandifolia* has been collected from three Brazilian states belies its rather narrow distribution, which cannot be delimited with precision because of the ambiguous nature of some localities given for old collections (see discussion).

**Phenology**. Flowering collections have been made in January, March and April and fruiting collections in July and August.

**Specimens examined. BRAZIL. MINAS GERAIS:** Santa Rita de Jacutinga, 28 Jul 1970, *Urbano 8957* (RB!). **RIO DE JANEIRO:** Serra da Bocaina, pres de S. José do Barreiro, 12 Feb 1876, *Glaziou 8381* (K!, C!, R!, LE!, P!); Rezende, 13 Jun 1930, *Ignacio 1743* (RB!); "In via ad Basso do Serra, in montosis attioribus," Mar 1818, *Pohl 5754* (F! (fragment), W!). **SÃO PAULO:** Joanópolis, 30 Apr 1946, *Gonçalves & M. Kuhlmann 1345* (NY!, RB!, SP!); Eugênio Lefevre, rodovia para Campos do Jordão, 1250 m, 14 Jan 1965, *Handro 1110* (SP!); Serra da Mantiqueira, 1450 m, 16 Mar 1939, *Kuhlmann & A. Gehrt s.n. SP 40059* (NY!, SP!). **STATE UNCERTAIN:** Rio de Janeiro?: "ad Serra do Ticu, Palmital, route du Picu," 11 Apr 1879, *Glaziou & Netto 10782* (C!, F!, K!, LE!, P!); Minas Gerais: Serra do Picu, Aug 1878, *Netto & Glaziou R25190* (R!, US!);

*Gomidesia grandifolia* is reminiscent of a rather large-leaved form of *G. affinis*. It differs from *G. affinis* in its larger leaves and flowers, distinctive venation and more closed anthers. Duplicates of recent collections of this infrequently collected species have been variously determined as *G. affinis*, *G. anacardiifolia* or *G. spectabilis*. The collection *Gonçalves and Kuhlmann 1345* is included here with doubt. The vegetative parts are very similar to the type material of *G. ticuensis* (treated here as conspecific with *G. grandifolia*) but the more delicate inflorescence, smaller flowers and deeply emarginate anthers set it apart from the other material cited above.

In describing *G. jacquiniana*, Berg cited *Plinia crocea* Vell. as a synonym with an expression of doubt (?). He commented that his new species greatly resembled *P. crocea* Vell. but that the latter did not agree with respect to leaf base (clearly shown as auriculate in Vellozo's plate). The only other element cited by Berg in the protologue is *Pohl 5754* which Berg saw in Vienna. One of the two sheets of this collection from W is here designated lectotype of *G. jacquiniana*. Both sheets bear flowering specimens. An unnumbered *Pohl &*

*Schott* collection at W is also annotated as *G. jacquiniana* in Berg's hand. This specimen, which bears a deeply ridged fruit, was not cited by Berg but seems likely to have been the basis for his description of the fruit of *G. jacquiniana* which includes more details than were provided by Vellozo. The *Pohl & Schott* collection is in fact referrable to *G. crocea*, a species which was treated by Berg only in the supplement to Flora Brasiliensis, where it was likened to *P. crocea* but not based on it.

Niedenzu subsequently made the combination *G. crocea* (Vell.) Nied. citing *G. jacquiniana* as a synonym. Presumably Niedenzu interpreted *G. jacquiniana* as being based on *Plinia crocea* and intended to correct Berg's failure to take up the epithet *crocea*. It would seem that Niedenzu had overlooked the supplement to Flora Brasiliensis, and so was unaware that he was publishing a later homonym.

In the same year Kiaerskou published *Myrcia ticuensis* based on flowering material which I consider to be conspecific with *Pohl 5754*. The unusual epithet appears to derive from a misreading of the label of one of the Glaziou syntypes which is annotated 'Palmital, route du Picu' in Glaziou's hand. Kiaerskou cited the locality as 'Serra do Ticu'. As the name is here placed in synonymy the error is unlikely to cause any further confusion. The locality in question is open to discussion however. There are two uplands called 'Serra do Palmital' in the general area of distribution, one in São Paulo and one in Minas Gerais. Of these, the Minas locality seems the more likely candidate as this area is rather close to the border with Rio de Janeiro. A third possibility seems more likely still: that the reference to the Serra do Picu refers to the area now known as the Serra de Queluz. Brade (1952) treated these two localities as synonymous and showed the Serra do Picu as an area some 10 to 15 km north of the town of Queluz in the state of São Paulo and bounded to the north and north east by the border with the state of Rio de Janeiro and to the north west by the border with Minas Gerais.

Legrand recognised *M. ticuensis* as a *Gomidesia* and made the necessary new combination. However, he listed *G. jacquiniana* as a synonym of *G. crocea* (Vell.) O.Berg, clearly on the assumption that Berg's *G. crocea* was based on the Vellozo species.

Legrand and Mattos (1975) transferred *Myrcia grandifolia* to *Gomidesia*, citing *Krukoff 10439* from las Yungas, Bolivia. Although I agree that the type of *Myrcia grandifolia* is indeed referrable to *Gomidesia* I do not consider the material Legrand and Mattos to be correctly placed in this species. Only one specimen is cited: *Krukoff 10439* from Las Yungas, Bolivia, deposited at MVM. I have not had the opportunity to examine this specimen. However, I have studied a number of duplicates of this collection (deposited at K, MO, NY, US, and S) and I consider them close to *G. lindeniana*.

Despite the superficial resemblance to *G. affinis*, I suspect that the closest relative of *G. grandifolia* may be *G. reticulata* which has a similar inflorescence type and anther morphology. The geographic ranges of these two species are also strikingly similar.

**19. Gomidesia grazielae** Nic Lughadha sp. nov. ined. Type. Brazil. Bahia: Itacaré, 6 Jan 1967, *Belém 2999* (holotype, CEPEC!; isotype, UB!).

*Treelet* or *shrub* to 25 m tall. Branchlets 10 cm below the terminal bud c. 8 mm in diameter, flattened, with a dense indumentum of erect, straight or curved, reddish-brown hairs, c. 0.8 mm long; terminal bud c. 13 mm long. Stipule lobes not seen. Inter-petiolar ridge prominent. Petioles absent but lamina sometimes tearing away from the the proximal part of the midrib to produce a false petiole up to 5 mm long, x 3 mm wide. *Lamina* elliptic, 175–200 mm long, 85–102 mm wide, c. 1.9–2.1 times as long as wide; apex abruptly short-acuminate; base obtusely cuneate or rounded; margin bent down or recurved or revolute; midrib sulcate above, prominent below; lateral veins more or less straight or slightly curved, sulcate or impressed above, prominent below, diverging at c. 80 ° from the midrib; secondary laterals composite, irregular, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation impressed above, raised below; venation between marginal vein and margin conspicuous. Indumentum moderately dense to sparse above, consisting of erect or appressed pale hairs to 0.7 mm, moderately dense below, consisting of erect, straight or crisped, whitish brown-centred hairs to c. 0.6 mm long. Gland dots indistinct above and below. Mature leaves coriaceous, convex in fresh state and splitting along midrib when dried under pressure, markedly bicolorous, mid- or dark brown above, olive green below. *Conflorescence* comprising one or two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 145 flowers, 136 mm long, reaching c. 2/3 the length of the subtending leaf; peduncle 65 mm long i.e., c. 1/2 the length of the inflorescence, 5–6 mm wide, flattened and channeled; lateral branches 4–5 below the terminal cyme or cluster of cymes. *Mature flower buds* 8–9 mm long x 5.5–6 mm wide. Calyx lobes triangular or hemiorbicular, 1.8–2.3 mm long x 3.7–4.7 mm wide, apex obtuse or rounded, with a dense indumentum of appressed, straight, brown hairs to c. 0.3 mm long externally, dense internally consisting of appressed, straight, pale hairs to 0.2 mm; hypanthium c. 3.8–5 mm long, scarcely prolonged (0.3 mm or less) above the ovary, with three or four irregular longitudinal ridges, indumentum dense externally consisting of ascending, curved, brown hairs to 0.4 mm externally, indumentum dense internally; disk c. 2.5 mm diameter, indumentum dense. Stamens c. 119–175 per flower; filament narrowing abruptly to point of insertion on connective which is prolonged below thecae in a short, sterile stub; anthers 1–1.1 mm long, apex truncate to shallowly emarginate, vertical displacement of thecae marked to slight, thecal halves retain curvature after dehiscence, thecal halves connnivent with margins flat in plane of curvature, effective dorsal opening c. 1/5 the length of the anther, residual septum not usually visible. Style c. 10 mm, with dense indumentum in lower 1/5–2/3; stigma minutely capitate. Ovary 3.3–4.2 mm long, bilocular, ovules 2 per locule. *Fruit* globose, 19–21 mm diameter, crowned with the erect to slightly connivent calyx lobes. Mature seed one per fruit, c. 11–13 mm long, testa pale, hypocotyl with dense indumentum of hairs to 1 mm long.

**Distribution (Map 17) and ecology.** *Gomidesia grazielae* is endemic to the coastal forests of Bahia and has been collected at about 150 m above sea level.

**Phenology.** Flowering collections have been made as early as November and December but the main flowering peak is in January. Fruiting collections have been made from March through to August.

**Specimens examined. BRAZIL. BAHIA:** Ramal a esquerda na estrada Ubaitaba/Itacaré a 4 km do loteamento da Marambaia, 20 Nov 1991, *Amorim 464* (CEPEC!); Itacaré, 6 Jan 1967, *Belém 2999* (CEPEC!, UB!); Maraú, mata litorânea, margem de igarapé, *Belém 3483* (CEPEC!, NY!); Reserva Florestal de Porto Seguro-CVRD/BA. Aceiro próx. ao córrego Águas Claras, lado direito, 10 Jan 1989, *Folli 851* (K!); Mun de Belmonte. Estação Exp. Gregório Bondar, km 58 da Rod. Belmonte/Itapebi, 17 May 1979, *Mattos Silva 381* (CEPEC!, NY!); Mun. Santa Cruz Cabrália. Estação Ecológica do Pau-Brasil e arredores, cerca de 16 km a W de Porto Seguro, 2 Jul 1978, *Mori 10208* (CEPEC!, NY!); Mun. Santa Cruz Cabrália. Ramal para a Torre de Embratel com a entrada no km 25.6 da Rodovia BR 367 (Eunápolis/Porto Seguro), 150 m, 4 Jul 1979, *Mori 12068* (CEPEC!); Mun. Uruçuca. Estrada que liga Uruçuca com Serra Grande, a 28 km ao NE de Uruçuca, 2 Dec 1979, *Mori 13061* (CEPEC!, K!, NY!); Mun. Sta Cruz Cabrália. Estação Ecológica do Pau-Brasil e arredores, cerca de 16 km a W de Porto Seguro, 22 Mar 1978, *Mori 9838* (CEPEC!, K!, NY!); Maraú. Faz. Raquel, 6 Aug 1967, *Pinheiro 203* (CEPEC!); Maraú, 25 Nov 1971, *Santos 2215* (CEPEC!); Parque Nacional de Monte Pascoal/Porto Seguro, 15 Jan 1973, *Santos 2698* (CEPEC!); Mun. Belmonte. Estação Experimental Gregório Bondar, 27 Nov 1987, *Santos 4319* (CEPEC!); Mun. Itacaré. Marambaia, 1 km N and 2.5 km W of junction Marambaia rd and rd from BR 101 to Itacaré (BA 654), 6 km W of Itacaré, 16 May 1992, *Thomas 9397* (CEPEC!); Maraú. Faz. Raquel, 6 Aug 1967, *Vinha 55* (CEPEC!).

**Local names:** cumbuca, murta cumbuca, murta cambuca (Bahia).

This distinctive new species resembles *Gomidesia crocea* but differs in its larger bullate leaves and its smooth fruits. A large tree, *G. grazielae* has been collected repeatedly over the past thirty years by staff of the Cocoa Research Institute in Itabuna, Bahia. It is one of dozens of new species of Myrtaceae collected from the Atlantic rain forest of this area, many of which have yet to be described. Material of *G. grazielae* has generally remained undetermined or been annotated as *Myrcia* sp. However one or two sheets have been identified as *G. crocea* or *G. langsdorffii* (here treated as synonymous with *G. crocea*).

This species is dedicated to Dra Graziela Maciel Barroso, specialist in Brazilian Myrtaceae, whose energy, enthusiasm and expertise have inspired and guided me in this study.

**20. Gomidesia innovans** (Kiaersk.) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 23.

*Myrcia innovans* Kiaersk., Enum. Myrt. bras. 100. 1893. Type. Brazil. Rio de Janeiro: Petrópolis. Alto do Imperador. *Glaziou 12000* (holotype, C!; isotypes, BR!, K!, LE!, P!, R!).

*Treelet* or *shrub* to 2.5 m tall. Branchlets 10 cm below the terminal bud 2.5–3 mm in diameter, slightly flattened or more or less rounded, glabrous or with a scattered to moderately dense indumentum of straight, more or less appressed, pale hairs to 0.1–0.2 mm long, giving a pruinose appearance to the twig; terminal bud proliferating. Stipule lobes to 0.8 to 1.6 mm long. Inter-petiolar ridge absent, at least at some nodes. Petioles 3–7 mm long, 1–1.5 mm wide, channeled. *Lamina* narrowly ovate to lanceolate or narrowly elliptic, 59–113 mm long, 21–38 mm wide, 2.6–3.9 times as long as wide; apex acuminate or long acuminate, rounded at very tip; base cuneate or decurrent; margin flat or bent down, recurved or revolute near base; midrib sulcate above, prominent below; lateral veins more or less straight, flat or very slightly raised above and below, diverging at c. 60–70 ° from the midrib, secondary laterals simple, equalling or almost equalling the laterals in prominence and often difficult to distinguish from them; marginal vein equalling the laterals in prominence and curving between them; higher order venation inconspicuous above and below; venation between marginal vein and margin inconspicuous. Indumentum sparse to moderately dense above and below, consisting of straight appressed, pale hairs to c. 0.1–0.2 mm long. Gland dots indistinct above, distinct below, dark and slightly raised. Mature leaves chartaceous to coriaceous, markedly bicolorous when dry, dark brown above, pale olive green below. *Conflorescence* comprising 1–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect metabotryoid or thyrsoid of c. 9–27 flowers, 31–50 mm long, reaching c. 1/2–3/5 the length of the subtending leaf; peduncle 18–28 mm long i.e., c. 1/2–3/5 the length of the inflorescence, 1–1.5 mm wide, flattened; lateral branches 2–3 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 5–6.5 mm long x 4.5–6.5 mm wide. Calyx lobes shallowly depressed ovate or narrowly tranversely elliptic, c. 1.2 mm long x 3.3 mm wide, apex rounded or obtuse, with a sparse to moderately dense indumentum externally and internally consisting of appressed, straight, white hairs c. 0.1–0.2 mm long; hypanthium (terete) 3.2 mm long, prolonged c. 1.2 mm above the ovary, with a dense indumentum of appressed, straight, white hairs c. 0.1–0.2 mm long externally in proximal half, becoming moderately dense distally; disk c. 3.7 mm diameter, indumentum dense. Stamens c. 85 per flower; anthers 0.8 mm long, apex truncate or shallowly emarginate, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent, thecal margins flat, effective dorsal opening 1/4 the length of the anther, residual septum not usually visible. Style c. 8 mm, with sparse to moderately dense indumentum in lower 2/3, glabrous above; stigma minutely capitate. Ovary 1.2–1.6 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 13 mm diameter, crowned with the connivent to erect, imbricate calyx lobes. Mature seed 2 per fruit, c. 10.5 mm long, hypocotyl glabrous.

**Distribution (Map 18) and ecology.** *Gomidesia innovans* appears to be endemic to the state of Rio de Janeiro where it occurs in Atlantic rain forest.

**Phenology.** Flowering material has been collected in February and fruiting material in July.

**Specimens examined. BRAZIL. RIO DE JANEIRO:** Petrópolis, au Alto do Imperador, *Glaziou 12000* (BR!, C!, K!, LE!, P!, R!); Mun. Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, Sítio Sophronites, 1400 m, 17 July 1987, *Pessoa 222* (NY!); Baía de Sepetiba, Ilha Furtada, 4 Dec 1967, *Sucre 2435* (RB!).

With its strikingly bicolorous leaves and flower buds *G. innovans* is strongly reminiscent of collections of *G. tijucensis* from Rio de Janeiro. It differs in its coriaceous leaves and stout inflorescences and in its anther morphology which resembles that of *G. reticulata*. When describing *Myrcia innovans* Kiaersk. (1893) commented that he considered it related to *G. schaueriana* and *G. poeppigiana*. Like *G. innovans, G. schaueriana* has bicolorous flower buds and coriaceous leaves but the species differ in leaf shape (long acuminate in *G. innovans*, acute or obtuse in *G. schaueriana*) and, perhaps more importantly, in anther morphology (closed in *G. innovans*, open in *G. schaueriana*). For discussion on the affinities of *G. poeppigiana* see under Doubtful Names.

In my experience, *G. innovans* has most often been confused with *G. warmingiana*. When describing the latter species (as *Myrcia warmingiana*) Kiaerskou mentioned that he considered it related to the former (as *M. innovans*). The confusion may have begun with Legrand (1959) who transferred *M. innovans* and *M. warmingiana* to *Gomidesia*, making the required new combinations *G. warmingiana* and *G. innovans* and citing *Glaziou 12000*, the holotype of *G. innovans*, as the only material studied under each of the two new combinations! The fact that the two species occur sympatrically (e.g. at Macaé de Cima) may also have contributed to their being mistaken for each other. *Gomidesia warmingiana* differs from *G. innovans* in its smaller flowers with ridged hypanthium, acute calyx lobes and more open anthers. All but the latter character are visible in fruiting collections too. In the vegetative state *G. warmingiana* can be recognised by its chartaceous leaves (usually coriaceous in *G. innovans*) with a more abrupt acumen and more conspicuous higher order venation. The name *G. innovans* has been applied repeatedly and incorrectly to collections of *Myrcia anceps* (Spreng.) O.Berg. *Myrcia anceps* is a very distinctive species with strikingly winged internodes. It resembles *G. warmingiana* (and not *G. innovans*) in having carinate, ellipsoid fruit.

**21. Gomidesia lindeniana** O.Berg, Linnaea **29:** 208. 1858. Type. Cuba. Guinea: Sommet de la Guinea, Prov. de Santiago, 213 m, Sep 1844, *Linden 2123* (holotype, LE!).

Fig. 35-37 (also 2A&B and 14a-d&e-h).

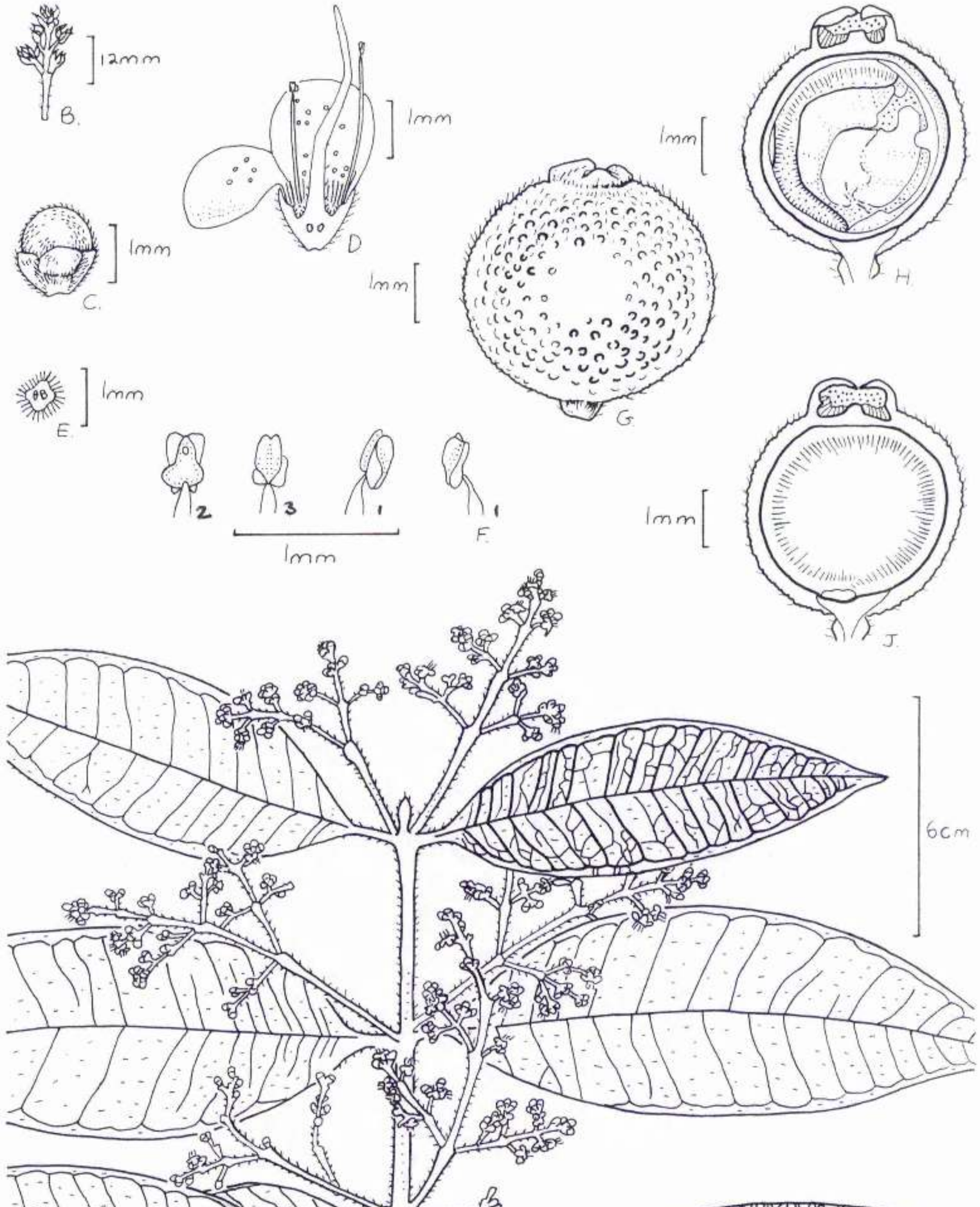
*Myrcia fenzliana* O.Berg, *in* Martius, Fl. Bras. **14(1):** 196. 1857. non *Gomidesia fenzliana* O.Berg, 1857. Type. Brazil. Minas Gerais: *Sellow 986* (holotype, BR!).

*Myrcia lindeniana* (O.Berg) C.Wr., in Sauvalle, Anal. Acad. Ci. Habana **5:** 420. 1868.

*Myrcia sintenisii* Kiaersk., Bot. Tidsskr. **17:** 257. 1890. *illegit nom. nov.* for *Gomidesia lindeniana* O.Berg in the genus *Myrcia* as *Myrcia fenzliana* is cited in synonymy.

*Tree, treelet* or *shrub* (0.8–)2–12(–30) m tall. Branchlets 10 cm below the terminal bud 4.5 mm in diameter, slightly compressed or more or less rounded, with a dense indumentum of erect, straight or curved or crisped, brown or blackish hairs c. 0.5–1 mm long; terminal bud 7–15 mm long. Stipule lobes not seen. Inter-petiolar ridge absent. Petioles c. 6 mm long, 2 mm wide, channeled. *Lamina* elliptic, lanceolate or ovate, 57–190 mm long, 28–74 mm wide, 1.5–2(–4) times as long as wide; apex short or long acuminate; base acutely cuneate or acuminate or rounded or obtuse; margin recurved or revolute; midrib sulcate or impressed above, prominent below; lateral veins more or less straight, impressed above, prominent below,

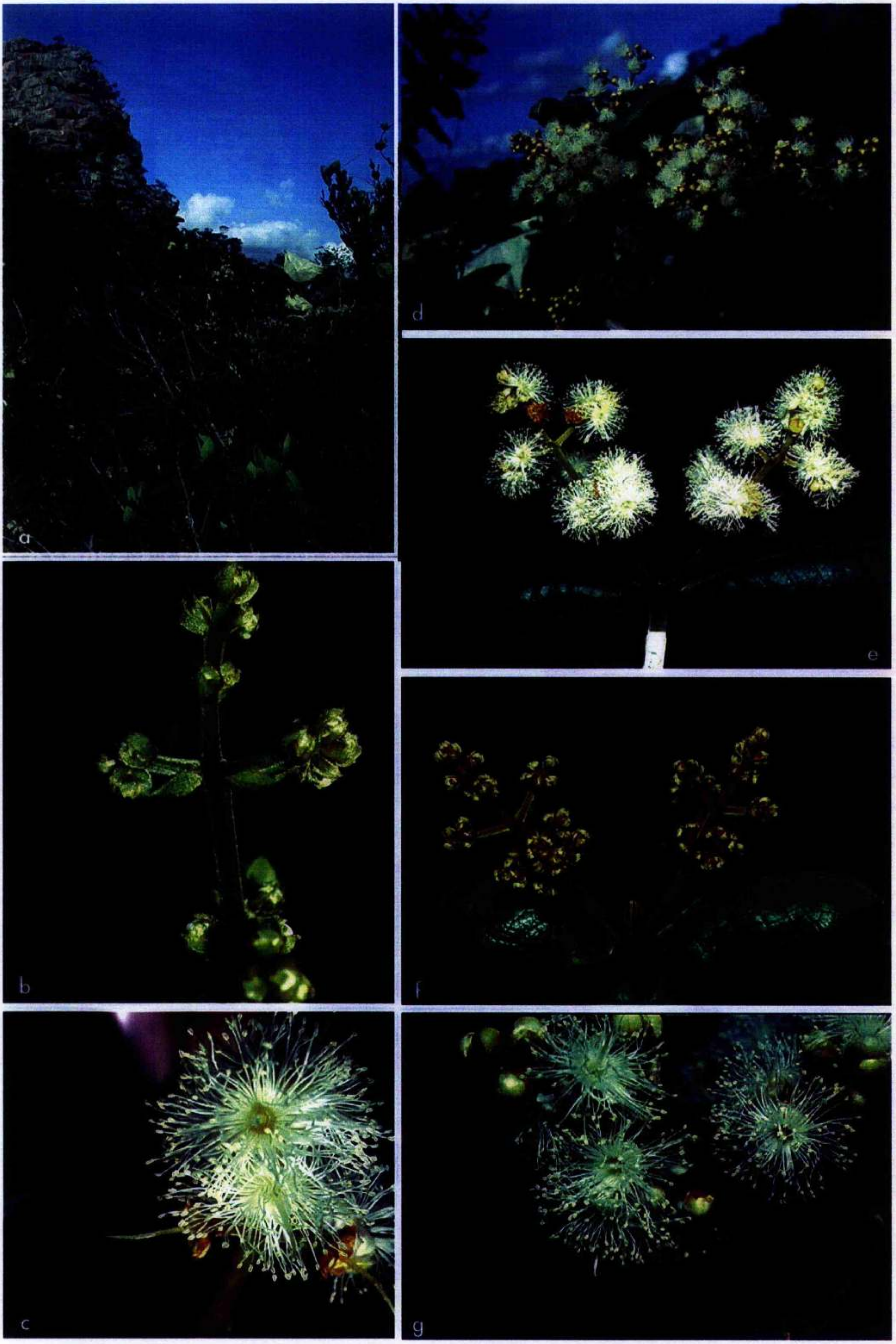
FIG. 35. *Gomidesia lindeniana*. **A** Conflorescence and foliage; **B** Portion of young inflorescence showing bracts; **C** Flower bud; **D** Longitudinal section of flower; **E** Transverse section of ovary; **F** Anthers in lateral (1), dorsal (2) and ventral (3) view; **G** Fruit; **H** Longitudinal section of fruit showing seed with testa removed; **J** Longitudinal section of fruit showing seed with testa intact. **A** & **C** - **F** from Irwin 12288, **B** from *Azevedo 398*, **G** - **J** from *Heringer 173*. Drawn by L. Gurr.


12mm
B.
1mm
D
1mm
C.
1mm
1mm
G
H.
1mm
E.
2
3
1
1
F.
1mm
1mm
J.
6cm
A.
L. GURR.

diverging at c. 60–70° from the midrib; secondary laterals composite, rarely equalling the laterals in prominence; marginal vein equalling the laterals in prominence and curving between them; higher order venation inconspicuous or slightly raised above, raised below; venation between marginal vein and margin conspicuous or concealed by rolled margin. Indumentum sparse to moderately dense above, consisting of appressed, straight, white hairs of varying orientation c. 0.4–1 mm, moderately dense below, consisting of erect, straight or curved, straw-coloured or reddish-brown hairs, c. 1 mm long. Gland dots indistinct above and below. Mature leaves coriaceous, usually markedly convex in fresh state and folded or split along midrib when dried under pressure; more or less bicolorous when dry, dark brown above, pale to mid-brown below. *Conflorescence* comprising 1–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. (20–)30–180(–250) flowers, (37–)45–100(–200) mm long, reaching c. 3/4 the length of the subtending leaf; peduncle (15–)23–33 mm long i.e., c. 1/4–2/5 the length of the inflorescence, (1.5–)2–3 mm wide, more or less flattened; lateral branches 4–5(–6) pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 3.2–4.5 mm long x 2.3–2.5 mm wide. Calyx lobes shallowly triangular, 0.8–1.1 mm long x 1.5–2.3 mm wide, apex acute or right-angled with a dense indumentum externally consisting of appressed, curved yellowish-brown hairs c. 0.5–0.8 mm, indumentum moderately dense internally; hypanthium 1.1–1.9 mm long, prolonged c. 0.5–0.8 mm above the ovary, with a dense indumentum externally consisting of erect or ascending, curved, whitish or brownish hairs to 0.5–0.6 mm, indumentum dense internally; disk c. 2–2.8 mm diameter, indumentum dense. Stamens 86–151 per flower; filament not or abruptly tapered to point of insertion on connective, anthers c. 0.5–0.7 mm long, apex truncate or very shallowly emarginate, vertical displacement of thecae marked, thecal halves losing curvature on dehiscence, held parallel or diverging, thecal margins recurved, effective dorsal 1/3–1/2 or most of the length of the anther, residual septum visible, oblique or almost tranverse. Style 6–7 mm, glabrous except at very base; stigma punctiform. Ovary c. 0.9–1.4 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 7–9(–11) mm diameter, crowned with the connivent imbricate calyx lobes. Mature seed 1–2(–4?) per fruit, to 7 mm long, testa mid-brown, hypocotyl glabrous.

**Distribution (Map 19) and ecology.** *Gomidesia lindeniana* is the most widely distributed member of the genus with two major centres of distribution in the Antilles (Cuba, Hispaniola, Jamaica, Puerto Rico and the Lesser Antilles) and in central and southeastern Brazil (Goiás, Distrito Federal, Minas Gerais and São Paulo). There are isolated populations in central Bahia and eastern Bolivia. In addition there are scattered collections from Venezuela and Colombia (and unconfirmed, fruiting material from Guyana and Peru) which may link the two

FIG. 36. *Gomidesia lindeniana* near Catolés, Bahia. **a** habitat and habit; **b**, **f** very young inflorescences, several weeks before flowering; **c** flowers, **d** flowering branches, note markedly convex leaves; **e**, **g** flowers photographed an hour before dawn, note style overtopping stamens.


a
b
c
d
e
f
g

main centres of distribution. *Gomidesia lindeniana* has been collected at altitudes of 400–1950 m, rarely as low as 200 m and then in a very humid region. The Caribbean collections were made in dwarf forest at middle and higher elevations (Liogier, 1994) or in montane forest (Proctor in Adams 1972). In Brazil *G. lindeniana* is generally collected from gallery forest within the *cerrado* (savanna) region of central Brazil but it also occurs in more open *cerrado* vegetation and between rocks in open vegetation at higher altitudes e.g., in the *campo rupestre* of Central Bahia.

**Phenology.** In Brazil, *Gomidesia lindeniana* flowers in January and February while in the Caribbean populations the flowering period is July to October with peak flowering in August.

**Representative specimens examined. BOLIVIA**. Department of Santa Cruz. Province of Chiquitos. South slope of the Serrania de Santiago; 5 - 10 km east of town of Santiago de Chiquitos, 875 m, 20 Jul 1983, *Daly 2157* (MO!, NY!); Dpto. Santa Cruz, Prov. Chiquitos. Serrania de Santiago, near Santiago de Chiquitos. 5 km ENE of Santiago, 800 m, 21 Nov 1989, *Daly 6298* (NY!).

**BRAZIL. BAHIA:** Mun. Rio de Contas, Pico das Almas. Vertente leste. Trilha Faz. Silvina - Queiroz. 1500 m, 28 Nov 1988, *Harley 26666* (CEPEC!, K!); Mun. Abaira, Campo da Pedra Grande, 1500 m, 25 Mar 1992, *Harley 53344* (CEPEC!, HUEFS!, K!, SPF!). **DISTRITO FEDERAL:** Fazenda Água Limpa/UNB. Mata ciliar do córrego Olho d'água da Onça, 17 Dec 1989, *Alvarenga 338* (K!); Parque Nacional de Brasília, 1100 m, 12 Aug 1979, *Guimarães 674* (RB!); Reserva Biológica da Águas Emendadas, 1025 m, 5 Aug 1970, *Heringer 11968-B* (NY!, UEC!); Brasília. (Reserva Biológica de Águas Emendadas), 2 Aug 1975, *Heringer 14816* (K!, NY!, UB!, UEC!); Escola Fazendaria, 31 Jan 1976, *Heringer 14897* (IBGE!, K!, UB!); Brasília. Várzea Bonita, 27 Feb 78, *Heringer 16835* (NY!, UB!); Reserva Ecológica do IBGE, 10 Oct 1977, *Heringer & de Paula 173* (IBGE!, K!, NY!, UEC!); Cachoeira do Rio Saia Velha, 1080 m, 2 Jun 1985, *Heringer 18679* (RB!, SP!, SPF!, UB!, UEC!); Bacia do Rio São Bartolomeu, 10 Dec 1979, *Heringer & Filgueiras 2897* (IBGE!, K!, MO!, NY!, US!); Bacia do Rio São Bartolemeu, 9 Jan 1980, *Heringer & Filgueiras 3104* (IBGE!, K!, MO!, NY!, US!); Reserva Ecológica do IBGE, 15 May 1978, *Heringer 492* (K!, MO!, NY!, SPF!); Recor, 26 Jun 1978, *Heringer & Paula 553* (IBGE!, K!, NY!); Bacia do Rio São Bartolomeu, 21 Jul 1981, *Heringer 7179* (K!, MO!); Chapada da Contagem, ca. 15 km E. of Brasília, 1050 m, 30 Jan 1966, *Irwin & Souza 12142* (B!, F!, NY!, S!, UB!, US!); Fazenda Vargem Bonita, ca. 10 km. S. of Brasília, 975 m, 5 Feb 1966, *Irwin & Grear 12288* (F!, MO!, NY!, RB!, UB!, US!); Fazenda Vargem Bonita, ca. 10 km S. of Brasília, 1000 m, 18 Jul 1966, *Irwin & Grear Jr. 18261* (F!, K!, MG!, MO!, NY!, US!); slopes of Chapada de Contagem, ca. 20 km E. of Brasília, 850 m, 16 Aug 1964, *Irwin 5213* (F!, NY!, RB!, UB!, US!); Parque Municipal do Gama, ca. 20 km. S. of Brasília, 850 m, 3 Sep 1964, *Irwin & Soderstrom 5894* (MO!, NY!, UB!, US!); ca.

FIG. 37. *Gomidesia lindeniana* near Brasília, Distrito Federal. **a** habitat; **b** habit, **c** *Melipona* bee visiting inflorescence tagged to assess natural fruit set; **d** flower; **e** bark; **f** inflorescence; **g** *Melipona* bee leaving flower.


a
b
c
d
e
f
g

23 km S.W. of Brasília on road to Anápolis, 4 Sep 1964, *Irwin & Souza 5968* (MO!, NY!, US!); Ao Sul da Cabeça do Córrego Palmeiras, 1000 m, 24 Aug 1981, *Kirkbride 4399* (K!); Brasília, Gama, 20 Mar 1964, *Pereira 9039* (F!, NY!, RB!); Gallery forest at Fazenda Vargem Bonita, 1025 m, 18 Jul 1966, *Ramos & Hunt 6675* (K!, MO!, NY!, SP!); Fazenda Água Limpa (University of Brasília field station), near Vargem Bonita, c. 18 km. SSW of Brasília TV tower, 2 Sep 1976, *Ratter & Fonseca 3526* (K!, NY!, UB!); Fazenda Água Limpa (University of Brasília field station), near Vargem Bonita, c. 18 km SSW of Brasília TV tower, 15 Oct 1976, *Ratter & Fonseca 3776* (E!, K!, UB!). **GOIÁS:** Margem da rodovia Brasília - Anápolis, 16 Dec 1965, *Belém 1998* (CEPEC!, NY!, UB!); Alto de Chapada dos Veadeiros, 15 Feb 1979, *Filgueiras 390* (NY!); Luizânia, 24 Nov 1975, *Heringer 14894* (UB!); Pico dos Pirineus, ca. 20 km N.W. of Corumbá de Goiás, near road to Niquelândia, Goiás, 1400 m, 28 Jan 1968, *Irwin & Maxwell 19389* (F!, MO!, NY!, RB!, US!); Cerrado and Gallery margin ca. 22 km NE of Catalão, 875 m, 22 Jan 1970, *Irwin & Onishi 25130* (MO!, NY!, US!); Serra do Pirineus, ca. 20 km E. of Pirenópolis, 1000 m, 14 Jan 1972, *Irwin 34040* (MO!, NY!, UB!); Chapada dos Veadeiros, Estrada Alto Paraiso/Colinas a 13 km de Alto Paraíso, 6 Dec 1988, *Mendonça 1114* (IBGE!, RB!); **MINAS GERAIS:** 1838, *Claussen 727* (C!, P!); Sabará, Jan 1916, *Hoehne 6827* (R!); Serra do Espinhaço. 32 km W of Montes Claros, road to Água Boa, 1000 m, 23 Feb 1969, *Irwin & Reis dos Santos 23749* (F!, NY!, UB!); Serra da Anta. Cerrado summit of chapada, ca. 10 km. NW of Paracatu, 900 m, 3 Feb 1970, *Irwin & Onishi 25877* (F!, K!, MG!, MO!, NY!, UB!, US!); Ca. 5 km SE of Paracatu, 675 m, 6 Feb 1970, *Irwin & Onishi 26211* (NY!, UB!); ca. 12 km W of Corinto, 600 m, 4 Mar 1970, *Irwin & da Fonseca 26913* (K!, MO!, NY!, UB!, US!); Belo Horizonte, Carapuça, 17 Jan 1933, *Mello Barreto 5193* (F!); Mun. Belo Horizonte. Navio, 5 Sep 1932, *Mello Barreto 7365* (F!); Jardim Botânico, Belo Horizonte, 3 Feb 1939, *Mello Barreto 8670* (R!); Navio, Belo Horizonte, 5 Sep 1932, *Mello Barreto 961* (RB!); Joaquim Felício, Serra do Cabral. Campos próximos da pequena Capelinha no alto da Serra, 1160 m, 12 Feb 1988, *Pirani 2184* (SPF!); Perdizes, 11 Aug 1987, *Stehmann NP975* (RB!); Mun. Ibiá, 2 Mar 1989, *Walter 23* (K!, IBGE!, RB!, UB!). **SÃO PAULO:** Pinhal, 12 Nov 1947, *Kuehn 1491* (NY!); Mun. Assis, Estação Experimental do Instituto Florestal, Feb 1988, *Leitão Filho 20098* (UEC!); Mun. Assis, estação experimental do Instituto Florestal, Feb 1988, *Leitão Filho 20125* (UEC!).

**COLOMBIA:** Santander, Eastern Cordillera. Mesa de los Santos, 1500 m, 926, *Killip 15060* (NY!); Huila, E. side of Cuchillo del Gigante, 2 km W. of Santa Ana, 1830 m, 12 Feb 1944, *Little 7212* (US!); Huila, 10 km ESE of Baraya, 1950 m, 2 Nov 1944, *Little 8924* (US!).

**CUBA:** Oriente, Loma del Gato, Cobre Range, Maestra, 1 Aug 1945, *Chrysogone 4812* (NY!); Oriente, in Sierra Maestra in Loma del Gato, 800 m, 9/ 922, *Ekman 15678* (S!); Oriente, prope Guantánamo in Monte Libanon prope Monterus, 500 m, 27 Nov 1922, *Ekman 15801* (S!); Oriente, in Sierra Maestra in monte alto El Gigante, 1100 m, 4 Jan 1923, *Ekman 16083* (S!); Oriente, Sierra Maestra, Loma del Gato, 1100 m, 29 Mar 1916, *Ekman 7012* (S!); Oriente, Sierra Maestra, La Gran Piedra, 1175 m, 29 Oct 1916, *Ekman 8162* (NY!, S!); Oriente, Loma del Gato, Sierra Maestra, 1000 m, Jul 1921, *Leon & Clement 10047* (NY!, US!); Oriente, Cordillera de la Gran Piedra, Sierra

Maestra, 1200 m, 18 Mar 1956, *Lopez F. 2609* (US!); Oriente, La Perla to Santa Ana, 660 m, 11 Feb 1911, *Shafer 8613* (NY!); Oriente, Gran Piedra, 1500 m, Mar 1911, *Shafer 9000* (NY!); In Cuba Orientali, *Wright 162* (K!, NY!).

**DOMINICA:** Ridge below summit of Morne Anglais, Elfin woodland, 1100 m, 16 Apr 1990, *Pendry 342* (BM!); Morne Anglais, 1200 m, 30 May 1888, *Ramage s.n.* (BM!); Morne Anglais (Couliaboune), near summit, 1105 m, 25 Jul 1964, *Wilbur 7937,* (US!).

**DOMINICAN REPUBLIC**. Pico Higua, 29 Sep 1938, *Canela* (P!); La Estrellata, Cordillera Central: Sureste de Colônia Rio Limpio, en la Loma Nalga de Maco, 1750 m, Apr 1983, *Dod s.n.* (MO!, NY!); Barahona, Bei Paradis, 600 m, Jul 1911, *Fuertes 925B* (BM!, K!, S!, US!); La Vega, Cordillera Central, Prov. La Vega, Constanza; Loma Canelilla, en el nacimiento del arroyo Canelilla, 1520 m, 22 Jan 1986, *Garcia 911* (MO!, NY!); Barahona, Near crest, on trail to Pedernales from Puerto Escondido and El Águacate, 1950 m, 24 Apr 1950, *Howard 12590* (BM!, U!, US!); Montiada Nueva, forested hillslopes S.E. of Polo, 1050 m, Aug 1946, *Howard & Howard 8518* (BM!, NY!, US!); Rio Grande, Constanza, 1250 m, Jul 1973, *Liogier 19484* (NY!); La Palma, Constanza, 1000 m, 30 Mar 1974, *Liogier & Liogier 21506* (NY!); Azua, Sierra Martín Garcia, en el Naranjo 2.5 km al sureste de El Águacate, 1290 m, 12 Sep 1984, *Mejia & Pimentel 1248* (NY!); Santiago Rodriguez, Cordillera Central: Cabirmar, en la orilla del arroyo Los Guanos, 8.4 km al sureste de Los Ramones en el camino hacia Manaclas, 630 m, 16 Jul 1985, *Mejia & Pimentel 1460* (NY!); Constanza, 1190 m, May 1910, *Turckheim 3340* (BR!); Santiago, Arr. Loma Bajita, Distr. of San José de las Matas, 750 m, 25 May 1933, *Valeur 878* (K!, LE!, NY!, US!); Barahona, Sierra de Baoruco. 4 km arriba el pueblecito rural de "Entrada de Cortico" en el camino a El Gajo, 1245 m, 19 Jan 1982, *Zanoni & Mejia 18896* (NY!); La Vega, Cordillera Central. 8.6 km desde el poblado rural de La Sal en el camino a La Palma: este del poblado arriba Loma la Golondrina, 1100 m, 13 Apr 1982, *Zanoni & Mejia 19998* (NY!); Barahona, Sierra de Baoruco: 7.2 km desde la carretera de Cabral-Polo, en el camino a la Entrada de Cortico Y El Gajo, 1290 m, 4 May 1982, *Zanoni & Mejia 20349* (NY!); Peravia, Cordillera Central: Oeste del poblado de Quita Pena: en la Loma Junumuçu (22 km. de Rancho Arriba en el camino a Quita Sueño y Quita Pena, 1375 m, 23 Sep 1983, *Zanoni & Pimentel 27327* (NY!); Barahona, Sierra de Baoruco. 10 km de La Cienaga en camino a Aguita Blanca y El Platón ( = Cruce de Charco Blanco-Majagualita-Aguita Blanca), 1000 m, 22 May 1984, *Zanoni 30181* (NY!, US!); Barahona, Sierra de Baoruco: Loma "Pie Pol" (Pie de palo en el mapa) de La Guasara de Barahona, 1250 m, 25 Mar 1987, *Zanoni & Pimentel 38688* (MO!, NY!); La Vega, Cordillera Central: Parque Nacional J.A.Bermudez: Prov. La Vega: en el sendero entre la caseta de Parques Nacionales en Los Tablones (de La Ciénaga de Manabo) y Loma Alto de La Cotorra, 1510 m, 12 May 1987, *Zanoni 39172* (MO!, NY!).

**GUADELOUPE.** Abord des Mamelles de Bouillante, 1025 m, 19 Dec 1944, *Bena 5484* (US!); Mammelles (Sommet), 19 Dec 1944, *Bena 841* (P!); 1944, *Bena 842* (P!); *Bena s.n.* (P!); Basse-Terre, Upper slopes and summit of Vent Souffle, Monts Caraibes, 590 m, 19 Nov 1959, *Proctor 20053* (BM!, US!); Bords Riv. Range, 1946, *Stehle 11* (P!).

**HAITI.** Massif de la Hoffe, western group, Corail, road to Dufreuil, 200 m, 28 Sep 1928, *Ekman H10734* (S!); Massif de la Selle, ridge between Morne Franchant and Morne Brouet, in thickets on the slope of Riviere Thebaud, 1700 m, 31 Jul 1924, *Ekman H1223* (S!); Dept. Artibonite. Montagnes Noires, in forest on the limestone cap of Morne Basil, 1375 m, 14 Nov 1924, *Ekman H2496* (S!); Massif de la Selle, Fourcy, 1540 m, 13 Feb 1925, *Ekman H3232* (NY!, S!); Sud, Morne de la Hotte in decliv, austral. mont. occid, Ma Blanche, 800 m, 8 Aug 1917, *Ekman H622* (S!); Gros Cheval, Morne des Commissaires, 28 Oct 1943, *Holdridge 1811* (BM!, NY!, US!); Vicinity of Marmelade, Departement du Nord, 800 m, 19 Dec 1925, *Leonard 8237* (US!); Summit Mt. Piment, 24 Jul 1905, *Nash & Taylor 1190* (NY!); La Brande to Mt. Balance, 1050 m, 15 Aug 1905, *Nash & Taylor 1714* (NY!, US!); Marmelade, 1020 m, 24 Aug 1903, *Nash 723* (NY!); Massif de la Hotte (extremo del oeste): Dept. Sud: Morne mansinte, la loma alta al norte de Tiburón, 1088 m, 26 Jan 1985, *Zanoni & Mejia 33232* (NY!).

**JAMAICA.** Below Vinegar Hill, 1050 m, 12 Jun 1896, *Harris 6282* (BM!, NY!); Below Vinegar Hill, 1000 m, 5 Jun 1896, *Harris 6348* (BM!, NY!); Below Vinegar Hill, 900 m, 7 Oct 1896, *Harris 6589* (BM!, US!); Below Vinegar Hill, St. Georges, 12 Sep 1896, *Harris 9348* (BM!); without locality, *Hart s.n.* (NY!).

**MONTSERRAT.** Hermitage, 400 m, 15 Nov 1944, *Beard 444* (K!, NY!, U!); Slopes of Chance's Mountain, 23 Feb 1980, *Howard 19723* (BM!, LE!, MO!, NY!, US!); Montserrat, *Ryan s.n.* (C!).

**PUERTO RICO.** Mount Morales, near Utuado, 19 Mar 1906, *Britton & Marble 1061* (NY!, US!); Monte Torrecilla, 1000 m, Mar 1915, *Britton & Cowell 5619* (NY!, US!); Cerro de Las Pinas, near Las Cruces, 660 m, 29 Mar 1922, *Britton & Matz 6885* (NY!); Maricao state forest: Along Hwy. 120, 800 m, 3 Apr 1985, *Croat 60909* (NY!); Near Camp Guavate, Cayey, 13 Aug 1940, *Gregory 73* (NY!); In forest, Cercadillo to Carite, 700 m, 10 Feb 1983, *Liogier & Liogier 33913* (NY!); Caribbean Natl. Forest. Toro Negro Division, 15 Aug 1950, *Little 13657* (NY!); Adjuntas, Bosque Ins. Guilarte. Summit of Monte Guilarte, 1190 m, 6 Aug 1952, *Little 14858* (BM!, NY!); Toro Negro Forest, Road to Cerra da punta, 900 m, 19 Jun 1954, *Little 16311* (BM!, NY!, US!); Near tower, Monte del Estado, Maricao forest, 840 m, 4 Aug 1966, *Little 21700* (BM!, NY!, US!); Patillas, Bo. Real, 19 Apr 1940, *Otero 725* (NY!); Prope Barranquitas, 30 Oct 1885, *Sintenis 2399b* (C!); Ayindas, in monte Capaes, 29 Mar 1886, *Sintenis 4041* (K!, LE!); Adjuntas, in monte Cedro, 1 Jun 1886, *Sintenis 4436* (BM!, NY!); Prope L(?)ares in sylva primaeva ad Buenos Aires, 24 Jan 1887, *Sintenis 6080* (K! (2 sheets), US!, W!); Col. inter Bayamón et Águas Buenas, 450 m, Sep 1887, *Stahl 720* (C!, S!); Mpio de Cayey, rte 7714 (Ruta panorámica) ca. 2 miles from rte 738 at electric towers, 4 Aug 1988, *Taylor & J. Ackerman 8147* (NY!); Santana, Sábana Grande, 12 Sep 1936, *Velez 988* (NY!).

**ST KITTS.** Forest slopes of Mt. Misery, 1901, *Britton & Cowell 568* (NY!, US!).

**VENEZUELA.** Barinas, Alto del Aguada, 1300 m, 20 Feb 1955, *Bernardi 1998* (NY!); Mérida, Pueblos del Sur, Jun 1955, *Bernardi 2268* (NY!); Monagas, Between Montaña de Aguacate and Colorado, along Rio Caripe, east of Caripe, 750 m, 19 Apr 1945, *Steyermark 62240* (F!).

**Local names.** Goyavier batard (Guadeloupe); cieneg(u)illo (Puerto Rico), Araçá da mata, (Brazil); Aoquey Blanco (Dominican Republic); Grand Merisier (Lesser Antilles); Cordoban (Cuba).

The convex, coriaceous leaves with acuminate apices and the much-branched inflorescences are usually sufficient to distinguish *G. lindeniana* from other species of *Gomidesia.* It is more often confused with some of the large-leaved species of *Myrcia.* The varied determinations which I have recorded for *Claussen 727*, a flowering collection of *G. lindeniana* from Minas Gerais, provide a good illustration of this confusion. Assorted duplicates of this collection have been annotated as *Myrcia* sp., *Myrcia grandiflora*, *Myrcia sellowiana* and *Myrcia anacardiaefolia* (here treated as *G. anacardiifolia*). Flowering specimens of *G. lindeniana* can easily be distinguished from *Myrcia* on the basis of anther morphology but fruiting material can be more problematic. Typically, *G. lindeniana* has a more or less globose fruit with closely connivent calyx lobes while the species of *Myrcia* with which it is confused are usually those with markedly ovoid or obovoid fruit and divergent calyx lobes. In spite of its wide distribution *G. lindeniana* is one of the more uniform species of the genus. There appears to be a tendency for the Caribbean material to have slightly larger flowers and fruits but these differences are insufficient to justify their recognition as a separate species.

Berg (1858) described *G. lindeniana* as a new species to be inserted after *G. hilariana* in his treatment of *Gomidesia* for Brazil, thus indicating that he considered these species to be closely related. However, he did not discuss its affinities or its distinctive characters. Given Berg's rather narrow species concepts it is scarcely surprising that he did not compare *G. lindeniana* to his own *Myrcia fenzliana*. This latter species was described in Flora Brasilenisis on the basis of a *Sellow* collection from Minas Gerais for which Berg cited neither collection number nor herbarium. He compared *Myrcia fenzliana* to *M. brunnea* Cambess. (here treated as *G. brunnea*) from which he considered *Myrcia fenzliana* distinct by virtue of its leaf shape and inflorescence. It was Kiaerskou (1890) who first pointed out the similarities between *G. lindeniana* and *Myrcia fenzliana* O.Berg, citing both in synonymy under the superfluous new name *M. sintenisii* Kiaersk. with the remark that he was obliged to coin a new name because of the existence of the binomials *Myrcia lindeniana* and *Gomidesia fenzliana!* Kiaerskou's taxonomy was more reliable than his nomenclature; I concur with him in considering the Cuban type of *G. lindeniana* and the Brazilian type of *Myrcia fenzliana* as conspecific. However, if the species is treated within *Myrcia* the name *Myrcia fenzliana* should be taken up. When the species is treated in *Gomidesia* the name *G. lindeniana* is correct, as the name *G. fenzliana* had already been used by Berg for another species by the time *G. lindeniana* was published. The names *Myrcia brunnea* and *Gomidesia brunnea* have been treated as synonymous with *G. lindeniana* by a number of specialists, myself included, but now that I have had the opportunity to examine the type material of *G. brunnea* I consider it to represent a distinct species. The differences between the taxa are discussed under *G. brunnea*.

**22. Gomidesia lutescens** (Cambess.) D.Legrand, Notul. Syst. (Paris) **15:** 262. 1958.
*Myrcia lutescens* Cambess., *in* Saint-Hilaire Fl. Bras. merid. **2:** 301. 1832. Type. Brazil. Minas Gerais: "In sylvis primevis montium prope vicum Itabira," *Saint-Hilaire B1 768* (lectotype, P!; isolectotypes, F!, P!).

*Myrcia nobilis* O.Berg, *in* Martius, Fl. bras. **14 (1):** 195. Type. Brazil. 'in Brasilia meridionali', *Sellow 1045* (holotype, B, n.v., presumed destroyed; lectotype BR!, here designated; isolectotypes K!, P!).

*Treelet* or *shrub* 3–4 m tall. Branchlets 10 cm below the terminal bud 5–8 mm in diameter, compressed, minutely puberulent or with a dense indumentum of erect, crisped or brown hairs to 0.3 mm long; terminal bud c. 15 mm long with a dense induemntum of erect or appressed, straight or curving, pale or dark brown hairs to 0.6 mm. Stipule lobes to 6 mm long. Inter-petiolar ridge indistinct or distinct and horizontal or inverted V-shaped. Petioles c. 18–20 mm long, 4–5 mm wide, channeled, with a dense indumentum of erect, crisped, brown hairs to 0.8 mm. *Lamina* ovate to narrowly ovate, 67–166 mm long, 33–95 mm wide, 1.7–2.7 times as long as wide; apex acute or short acuminate; base truncate, obtuse or rounded; margin bent down or recurved; midrib shallowly sulcate or impressed above, prominent below; lateral veins more or less straight or slightly curved, raised or slightly raised above, prominent below, diverging at c. 60–70° from the midrib; secondary laterals simple or composite, occasionally equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation distinct, slightly raised above, raised below especially near marginal vein; venation between marginal vein and margin distinct, including submarginal vein. Indumentum absent above except on midrib, dense below, consisting of erect, straight or crisped, brown hairs, c. 0.8 mm long, underlain by mat of felted pale hairs of varying length and orientation. Gland dots barely distinct above, dark and slightly impressed, indistinct below. Mature leaves coriaceous, markedly bicolorous, drying dark brown above, ochraceous below, often splitting along midrib when dry. *Conflorescence* comprising one or two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 100–200 flowers, 107–123 mm long, reaching c. 2/3–3/2 the length of the subtending leaf; peduncle c. 35 mm long i.e., c. 1/3 the length of the inflorescence, 2–3 mm wide, quadrangular or deeply striated; lateral branches 5–7 subopposite pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 4.2 mm long x 3.8 mm wide. Calyx lobes depressed ovate or shallowly triangular, 1.4–1.7 mm long x 2.2–2.3 mm wide, apex obtuse, with a dense indumentum of ascending, crisped, brown hairs to 0.7 mm externally, and a dense indumentum of appressed, crisped, pale hairs to 0.2 mm internally, hypanthium c. 1.4 mm long, prolonged c. 0.7 mm above the ovary, indumentum dense externally and internally; disk c. 1.8–3.3 mm diameter, indumentum dense. Stamens > 70 per flower (counted from open flower); filament not or scarcely narrowed to the point of insertion on connective, anthers c. 0.55–0.65 mm long, apex obtuse or very shallowly emarginate, vertical displacement of thecae slight, thecal halves lose curvature on dehiscence, divergent, with margins recurved, residual septum usually visible (but sometimes very faint), vertical. Style c. 6–7 mm, with moderately dense to dense indumentum in lower 1/2; stigma minutely capitate, distinctly papillate. Ovary c. 0.8 mm long, bilocular, ovules 2 per locule. *Fruit* globose to ovoid, c. 5 mm diameter, with a dense indumentum of felted ochraceous hairs, crowned with the connivent calyx lobes. Mature seed one or two per fruit, c. 4 mm long, testa dark, hypocotyl glabrous.

**Distribution (Map 20) and ecology.** *Gomidesia lutescens* is endemic to the Serra do Cipó area of Minas Gerais where it occurs in *campo rupestre* vegetation at altitudes of c. 1300 m.

**Phenology.** *Gomidesia lutescens* flowers in January and February. Fruiting material has been collected in September.

**Specimens examined. BRAZIL.** **MINAS GERAIS:** Serra do Cipó, Km 142 - estrada de Conceição. Mun. Conceição. Campo, 16 Apr 1935, *Brade 14782* (F!); Serra do Cipó, Km 134, 14 Feb 1963, *Duarte 7825* (RB!); Diamantina, Rio dos Cristais, 15 Jan 1963, *Duarte 7885* (RB!); Serra do Espinhaço. Serra do Cipó, ca. km 120 (ca. 145 km N. of Belo Horizonte), 1300 m, 15 Feb 1968, *Irwin & Maxwell 20114* (F!, K!, MO!, NY!, RB!); Serra do Cipó, Km 142 - estrada de Conceição. Mun. Conceição, 16 Apr 1935, *Mello Barreto & Brade 1205* (F!); 'Habitat in Brasilia meridionali' *Sellow 1045* (BR!, K!, P!); Mun. Jaboticatubas: Km 114 ao longo da rodovia Lagoa Santa - Conceição do Mato Dentro - Diamantina. Serra do Cipó, 5 Sep 1972, *Semir 3372* (SP!); Mun. Jaboticatubas: Km 142 ao longo da rodovia Lagoa Santa - Conceição do Mato Dentro - Diamantina, Dec 1973, *Semir 4884* (UEC!).

In view of its anther morphology, raised leaf venation and crisped indumentum *G. lutescens* appears to be closely related to *G. spruceana*, another species with a narrow distribution in the mountains of Minas Gerais. However, the two species are easily distinguished since *G. spruceana* has much smaller leaves (< 50 mm long), few-flowered inflorescences and very pale indumentum. Vegetatively *G. lutescens* bears a strong resemblance to *Myrcia mischophylla,* an extremely variable species with a distribution extending from the Serra do Cipó north to the *campos rupestres* of central Bahia. In the Serra do Cipó *G. lutescens* is easily distinguished from *Myrcia mischophylla* by virtue the narrower, long-acuminate leaves and paler indumentum of the latter species. However, a study of the variation in this species over the whole of its range is needed.

**23. Gomidesia magnifolia** O.Berg, *in* Martius, Fl. bras. **14 (1):** 531. 1859. Type. Brazil. Rio de Janeiro: "prope Macahé," *Riedel 1320* (lectotype, LE!, here designated; isotypes, F! (fragment), K!, LE! (4 sheets)).

*Myrcia magnifolia* (O.Berg) Kiaersk., Enum. Myrt. bras. 107. 1893.

*Shrub 3.6–6* m tall. Branchlets immediately below the terminal bud 13–17 mm in diameter, somewhat flattened and deeply channeled, with a dense indumentum of erect or appressed, straight, pale brown hairs, to 1 mm long; terminal bud 65–75 mm long or proliferating. Stipule lobes not seen. Inter-petiolar ridge prominent. Petioles absent. *Lamina* oblong or elliptic, 560–640 mm long, 225–245 mm wide, 2.4–2.8 times as long as wide; apex abruptly acuminate but often damaged and then appearing truncate; base truncate or slightly amplexicaul; margin bent down or recurved or revolute; midrib sulcate above, prominent below; lateral veins more or less straight, impressed or rarely sulcate above, prominent below, diverging at c. 80° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation conspicuous, flat or slightly raised above, raised below; venation between marginal vein and margin conspicuous. Indumentum very sparse or absent above, except on midrib and laterals which bear a dense indumentum of mostly appressed, straight, pale hairs to 1.5 mm long, moderately dense below consisting of erect, straight, brownish hairs to 1 mm or more, denser on midrib. Gland dots not visible above, distinct below. Mature leaves chartaceous. *Conflorescence* comprising 1(–2?) pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect complex thyrsoid or panicle of > 30? flowers, 200–270 mm long, reaching c. 2/5–1/2 the length of the subtending leaf; peduncle 80–120 mm long i.e., c. 1/3–>2/5 the length of the inflorescence, 9–10 mm wide, markedly arched and flattened; lateral branches 4–7 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* not seen. Calyx lobes (in fruit) depressed ovate, c. 4.5 mm long x 5.5 mm wide, apex obtuse or rarely acute (perhaps acute in bud?), with a dense indumentum internally and externally consisting of short (< 0.5 mm), appressed hairs; disk c. 6.7 mm diameter, staminal ring glabrous, top of ovary densely pubescent. Stamen number unknown, anthers to 1.3 mm long, apex obtuse, vertical displacement of the thecae slight, thecal halves retaining curvature after dehiscence, connivent, thecal margins inrolled, effective dorsal opening c. 1/10 the length of the anther, residual septum not visible. Style (only lower portion seen adhering to fruit) > 10 mm long, with a moderately dense indumentum of straight pale hairs to 1.5 mm in lower 1/3; stigma not seen. Ovary bilocular, ovules 2 per locule. *Fruit* depressed globose, 14 mm in diameter including c. 10 vertical ridges obscured by the dense indumentum of straight, brownish, erect hairs to 1 mm long, crowned with the erect or connivent, imbricate calyx lobes. Mature seed probably one per fruit, not seen, cotyledons leaf-like, hypocotyl densely pubescent.

**Distribution (Map 21) and ecology.** Known only from Atlantic forest to the north of the city of Rio de Janeiro.

**Phenology.** The little evidence available is contradictory. Only fruiting collections are known and collection dates are available only for the type material. The sheet at LE, here selected as lectotype, is clearly dated June 1833 The date on the Kew isotype, II 1833, must be considered a transcription error. Similarly, Berg's comment in the protologue 'florebat Junio: Riedel' must be interpreted as a slip of the pen since his description is clearly based on immature fruiting material and no flowers are described.

**Specimens examined. BRAZIL. RIO DE JANEIRO:** In silvis ad Alcantara, *Lund s.n.* (C! (2 sheets)); Poço d'Antas, *Pessoa 725* (RB!); prope Macahé, June 1833, *Riedel 1320* (F! (fragment), K!, LE! (5 sheets)).

Until recently I considered *Gomidesia magnifolia* as probably extinct since it was known only from two collections made more than 150 years ago. Apart from the type the only fertile material I had seen was an unnumbered, undated Lund collection from Alcantara which seems likely to have been made on the same collecting trip as the type collection; Riedel and Lund are known to have travelled together in Rio de Janeiro in 1833. However, in the early 1990s, phytosociological research carried out at Poço d'Antas by the Projeto Mata Atlântica team of the Jardim Botânico do Rio de Janeiro led to the rediscovery of this species. I am grateful to Dra Graziela Maciel Barroso for drawing my attention to the existence of this material which I have since had the opportunity to examine at RB. The material is as yet unmounted, unlabelled and undistributed but I understand that it was collected by S.V.A. Pessoa et al. in secondary vegetation at the study site. The sterile collection *Guimarães 1416* from the same locality is almost certainly referrable to this species too.

Berg compared *Gomidesia magnifolia* to *G. amplexicaulis* (from which he considered *G. magnifolia* distinct because of its tomentose indumentum, its leaves which he described as not at all amplexicaul and its truncate sepals) and also to *G. linkiana* and *G. pohliana* (from which it differs in its sessile, non-bullate leaves). The Vellozo plate of *Eugenia amplexicaulis*, on which *G. amplexicaulis* is based, cannot be referred with certainty to any known species. For a more detailed discussion of this problem see under *G. crocea*.

Legrand commented that he had not seen stamens of *G. magnifolia* but from its general features he deduced that it belonged in Sect. *Elytroteca*, subsect. *subaequales* and there grouped it with *G. martiana* and *G. spectabilis* on the basis of its fruit which he considered non-costate. Having examined a few anthers, found adhering to fruits of the type and of *Pessoa 725*, I can confirm that their morphology is such that they are indeed referrable to that subsection. The pubescent hypocotyl (visible in the recent collections) also supports this placement. However dissection also revealed that the fruit is in fact costate, though this character is obscured by the dense, persistent tomentum. This suggests that, within the subsection *subaequales*, *G. magnifolia* may be more closely related to *G. crocea* than to *G. martiana* or *G. spectabilis*.

Berg cited no number for the Riedel collection on which this species is based. His statement on the location of the type is 'v. in hb. hort. bot. Petrop.' I have examined five sheets of *G. magnifolia* from LE. All are numbered *Riedel 1320* and annotated by Berg. Among these I have selected as the lectotype the sheet with the most comprehensive label data, much of which is repeated in the protologue.

**24. Gomidesia martiana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 12. 1857. Type. Brazil. Rio de Janeiro: *Sellow s.n.* (isotypes, BR!, K!, P! (2 sheets)).

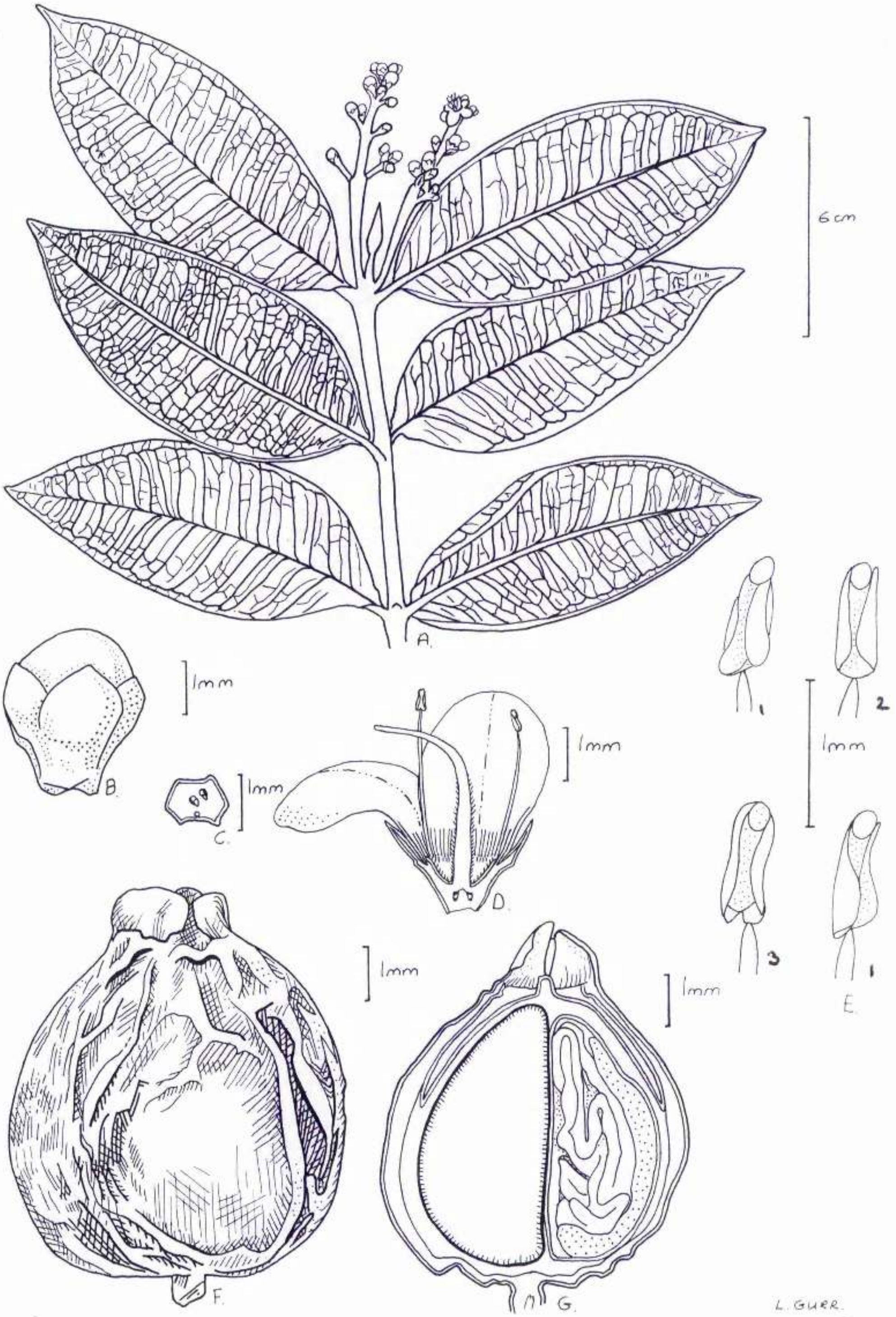
Fig. 38 & 39 (also 11d&e).

*Myrcia vittoriana* Kiaersk., Enum. Myrt. bras. 102. 1893. nom. nov. for *G. martiana* O.Berg non *M. martiana* O.Berg

*Myrcia vittoriana* var. *piratiningensis* Kiaersk., Enum. Myrt. bras. 102. 1893. Type. Brazil. Rio de Janeiro: Piratininga, Oct 1872, *Glaziou 5872* (holotype, C!; isotype, K!).

*Tree, treelet* or *shrub* (2–)3–8(–12) m tall. Branchlets 10 cm below the terminal bud 3–4 mm in diameter, more or less rounded, with a dense indumentum of farinaceous hairs (described in detail under Anatomy); terminal bud proliferating. Stipule lobes not seen. Interpetiolar ridge faint. Petioles 4–7(–10) mm long, 2–3 mm wide, channeled. *Lamina* narrowly ovate to lanceolate, 105–195 mm long, 40–64 mm wide, 2.1–2.8(–3.8) times as long as wide; apex acuminate to abruptly acuminate; base cuneate, obtuse, rounded or auriculate; margin flat, bent down, recurved or revolute; midrib slightly raised to flat or slightly impressed and channeled above, prominent and striated below; lateral veins straight or very slightly curved, raised above and below, diverging at c. 70–80° from the midrib; secondary laterals composite, more or less straight, sometimes almost equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation very slightly raised above and below; venation between marginal vein and margin inconspicuous. Submarginal vein visible when margin is flat. Indumentum sparse to moderately dense above, consisting of straight, white hairs to 0.8 mm above, moderately dense to dense below, consisting of bulbous-based, brown hairs. Gland dots indistinct above, occasionally distinct below, dark and slightly raised. Mature leaves coriaceous or occasionally chartaceous. *Conflorescence* comprising 1–2 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect complex thyrsoid of c. 26–70 or more flowers, 54–87 mm long, reaching c. 1/2–1/3 the length of the subtending leaf; peduncle 25–50 mm long i.e., c. 1/2–2/3 the length of the inflorescence, 2.5–3.5 mm wide, flattened and striated; lateral branches 3–5 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 4–5.7 mm long x 3–4.3 mm wide. Calyx lobes depressed ovate or obovate, deltate or shallowly triangular, 1.4–2.2 mm long x 2.1–3.5 mm wide, apex obtuse or rounded, with a moderately dense to dense indumentum outside and a moderately dense indumentum inside; hypanthium 1.7–2.6 mm long, prolonged c. 1–1.3 mm above the ovary with a dense indumentum inside and outside; disk c. 2.3 mm diameter, indumentum dense. Stamens 48–103 per flower; anthers c. 1 mm long, apex with prominent gland, vertical displacement of thecae marked, thecal margins recurved after dehiscence, thecal halves more or less parallel, effective dorsal opening c. 1/4 the length of the anther, residual septum usually visible, more or less vertical. Style c. 9 mm, with dense indumentum in lower 1/3, moderately dense near point of inflexion and glabrous towards apex, prominently glandular; stigma indistinct or occasionally minutely capitate. Ovary 0.5–0.8(–

FIG. 38. *Gomidesia martiana.* **A** Conflorescence and foliage; **B** Flower bud; **C** Transverse section of ovary; **D** Longitudinal section of flower; **E** Anthers in lateral (1), dorsal (2) and ventral (3) view; **F** Fruit; **G** Longitudinal section of fruit showing seed with testa removed (right) and seed with testa intact (left). **A** from *Landrum 4165*, **B** & **C** from *Machado s.n.*, **D** from *Landrum 4165, Machado s.n.* and *Sucre s.n.*, **E** from *Sucre s.n.*, **F** & **G** from *Araujo 181*. Drawn by L. Gurr.


6 cm
A.
1mm
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1
2
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L. GURR.

1.3) mm long, bilocular or occasionally trilocular, ovules 2 per locule. *Fruit* globose to subconical, wrinkled, c. 11 mm diameter, crowned with the strongly connivent calyx lobes closed over the free, domed apex of the ovary and the persistent style base. Mature seed two per fruit, c. 8–9 mm long, testa pale, hypocotyl c. 11–13 mm long, slightly pubescent near point of insertion on cotyledons.

**Distribution (Map 22) and ecology.** *Gomidesia martiana* is frequent in *restinga* vegetation in the states of Bahia, Espírito Santo and Rio de Janeiro at altitudes of 0–50 m. The most northern records are from one of the few remaining remnants of *mata atlântica* in the state of Pernambuco. A single collection from São Paulo (Bairo do Gomes) appears to represent the southern limit of this species but cannot be pinpointed precisely; it may refer to a suburb of São Paulo. Lacerda et al. (1993) listed *G. martiana* as one of the principal species (along with species of *Eugenia* and *Myrcia*) in the 'Myrtaceae closed thicket' a vegetation type which is characteristic of the secondary dune but may also occur on the landward slope of the primary dune. Further south (e.g., in Paraná) the closely related *G. spectabilis* sometimes occurs in *restinga*, perhaps occupying the niche filled by *G. martiana* in tropical coastal areas. *Gomidesia martiana* occurs inland in degraded forest (*nativo)* on white sand near Linhares, Espírito Santo and, most intriguingly, at 500 m above sea level in the Vale Encantado in Rio de Janeiro.

**Conservation**. Threatened only insofar as all *restinga* species are threatened by habitat destruction through burning, selective cutting of commercial species, cattle grazing, removal of sand for commercial purposes and the construction of housing developments and seaside vacation resorts (Lacerda et al. 1993).

**Phenology**. Over most of its range *Gomidesia martiana* usually flowers in January, with flowering occasionally continuing into February. However in Espírito Santo flowering seems to begin earlier, in November or December and mature fruit have been collected as early as February. Fruits of *G. martiana* have been collected in every month from January through to July but many of these are likely to have been immature. Mature fruit have been collected in Rio de Janeiro in April and June and in Bahia in July. Thus the fruit maturation period may be from two to five months.

**Specimens examined. BRAZL.** BAHIA: Mun. Una, Reserva Biológica do Mico-leão (IBAMA). Entrada no km 46 da Rod. BA-001 Ilhéus-Una., Apr 1993, *Amorim 1239* (CEPEC!); Santa Cruz Cabrália, 31 Oct 1966, *Belém 2791* (CEPEC!, UB!); Maraú, 12 Jan 1967, *Belém 3056* (CEPEC!); Belmonte, 30 Jan 1967, *Belém 3206* (CEPEC!, UB!); Mun. Maraú, Rodovia BR 030, trecho Ubaitaba-Maraú, a 45 km de Ubaitaba, 25 Feb 1980, *Carvalho 170* (CEPEC!); Mun. Una, Reserva

FIG. 39. *Gomidesia martiana* near Linhares, Espírito Santo. **a** habitat viewed from look-out tower; **e** habitat; **b** habit; **c** inflorescence in bud; **d** infructescence; **f** immature fruits; **g** inflorescence in flower, note fully reflexed petals.


a
b
c
d
e
f
g

Biológica do Mico-leão (IBAMA). Entrada no km 46 da Rod. BA-001 Ilhéus-Una, 28 Jun 1993, *Carvalho 4248* (CEPEC!); S(anta). C(ruz). Cabrália. Res. Bio. Pau-brasil, 5 Jan 1972, *Euponino 137* (CEPEC!); Km 10 da rod. P(orto). Seguro a Eunápolis, 29 Mar 1972, *Euponino 253* (CEPEC!); Mun. Alcobaça. Km 5 - 8 da Rod. BA 001, trecho Alcobaça/Caravelas, 15 m, 4 Jul 1979, *Hage 257* (CEPEC!); Mun. Canavieiras, Banal a 21 km na Rod. Canavieiras/Una. BA-001. Ramal da Faz. Campo Lucio, 4 Jun 1981, *Hage & E.B. dos Santos 892* (CEPEC!, NY!); Coast road between Alcobaça and Prado, 10 km NW of Alcobaça and 4 km N along road from the Rio Itanhentinga, 0 m, 15 Jan 1977, *Harley & Mayo 17947* (CEPEC!, K!, MO!, NY!, SPF!, U!); ca. 5 km. SE of Maraú near junction with road to Campinho, 25 m, 14 May 1980, *Harley 22043* (CEPEC!); About 5 km North from turning to Maraú, along the Campinho road, 25 m, 17 May 1980, *Harley & Bromley 22178* (CEPEC!, K!, U!, MO!, NY!, SPF!); Mun. Una, Reserva Biológica do Mico-Leão (IBAMA). Entrada no km 46 da Rod. BA -001 Ilhéus/Una, 7 Jan 1993, *Jardim 05* (CEPEC!); Mun. Ilhéus, estrada Olivença-Maruim, entre os Kms 7 - 10, 50 m, 19 May 1985, *Martinelli & Zuloaga 11096* (F!, RB!); Mun. Ilhéus. Rodovia Ilhéus / Ponto do Ramo / Itacaré. Entre km 6 e 12 ao Norte de Ilhéus, próximo ao litoral, 17 Apr 1986, *Mattos Silva 2051* (CEPEC!); Mun. Alcobaça. Rodovia Alcobaça/Prado (BA 001), km 3, 5 m, 29 Mar 1989, *Mattos Silva 2649* (CEPEC!); Mun. Maraú. Rodovia BR 030, trecho Maraú/Porto de Campinhos, a 19 km de Maraú. ca de 14 km a L do entroncamento, 13 Jun 1979, *Mattos Silva 445* (CEPEC!, SPF!); Mun. Itacaré. Cerca de 1 km ao S de Itacaré, beira-mar, 7 Jun 1978, *Mori & Santos 10144* (CEPEC!, K!, NY!); Mun. Maraú. Rod. BR 030, trecho Ubaitaba/Maraú, 45-50 km a leste de Ubaitaba, 50 m, 12 Jun 1979, *Mori & Carvalho 11960* (CEPEC!, K!, NY!); Mun. Una. Estrada Olivença/Una, a 26 km ao S de Olivença, 0 m, 31 Dec 1979, *Mori & F.P. Benton 13267* (CEPEC!, K!, NY!); Mun. Alcobaça. Rod. BA 001, a 5 km ao Sul de Alcobaça, 15 m, 17 Mar 1978, *Mori & Mattos Silva 9613* (CEPEC!, K!, NY!, US!); Mun. Una. 8 km ao norte de Comandatuba, 3 Jan 1989, *Santos 236* (CEPEC!); Mun. Una, 4 km N of Comandatuba, ca. 10 km S. of Una, 18 Feb 1988, *Thomas & Pirani 6025* (K!, NY!, SPF!); Ilhéus. Road from Olivença to Maruim. 5 km W of Olivença, 1 Feb 1992, *Thomas 8993* (CEPEC!, K!); Mun. Ilhéus, road from Olivença to Maruim, 6.1 km W of Olivença, 1 May 1992, *Thomas 9044* (CEPEC!, K!); Mun. Ilhéus. Road from Ilhéus to Serra Grande, 11.3 km N of the Itaipe bridge leaving Ilhéus, 5 May 1992, *Thomas 9137* (CEPEC!, K!); Parque Nacional de Monte Pascoal, 22 Mar 1968, *Vinha 109* (CEPEC!); Ubaitaba-Maraú, 13 Dec 1967, *Vinha & A. Castellanos 47* (US!). **ESPÍRITO SANTO:** Linhares, Reserva Florestal da CVRD, 27 Nov 1989, *Farias 344* (CVRD!); Reserva Biológica de Comboios, IBAMA - Regência, 4 Jan 1991, *Folli 1254* (CVRD!); Reserva florestal CVRD, Linhares, 22 Jan 1991, *Folli 1268* (CVRD!); Reserva florestal da CVRD, Linhares, 1 Mar 1991, *Folli 1302* (CVRD!); Rod. BR-101; Res. Flor da Sooretama (mun. Linhares), 8 Apr 1984, *Hatschbach 47734* (CEPEC!, MO!, MU!, US!); Rancho Alto (mun. Linhares), 7 Dec 1984, *Hatschbach 48700* (BR!, MG!); Mun. Linhares. Reserva florestal da Cia. Vale do Rio Doce, 14 Dec 1981, *Lima 1663* (RB!); Conceição da Serra, 15 Dec 1962, *Mattos & H. Bilcalho 10803* (US!); Linhares. Reserva florestal de CVRD, 31 Jan 1985, *Peixoto 3019* (MO!); Reserva Biológica de

Guriri, projeto TAMAR, S. Mateus, 8 May 1991, *Souza 79* (CVRD!); Reserva de Linhares, 1 Feb 1972, *Sucre 8387* (K!, NY!, RB!). **PERNAMBUCO:** Recife, Dois Irmãos. Mata de Dois Irmãos, 13 Oct 1967, *Andrade-Lima 67-5080* (IPA!, K!). **RIO DE JANEIRO:** Restinga de Jacarepaguá, Pedra de Itaúna, 25 Apr 1973, *Araújo 181* (RB!); Recreio d. Bandeirantes. Restinga Itapeva, Mar 1932, *Brade & Sampaio s.n.* (R!); Mata de Restinga, N. of restinga de Macaé, 10 m, 11 Jan 1985, *Gentry 49468* (MO!); Guanabara, Barra da Tijuca, 10 Dec 1931, *Kuhlmann s.n. RB139517* (NY!, RB!); Maricá, Restinga de Maricá, between ocean and Lagoa de maricá, ca. 40 km E of Rio de Janeiro, 21 Jan 1982, *Landrum 4165* (NY!); Mun. Macaé, estrada para Carapebus, Faz. Jurubatiba, 9 May 1987, *Lima 2893* (K!); Restinga de Sernambetiba, Recreio dos Bandeirantes, 6 Dec 1938, *Markgraf 3776* (RB!); Ilha da Marambaia, Praia Grande, 16 Jan 1986, *Rizzini 309* (RB!); Ilha da Marambaia, Praia Grande, 20 Jan 1987, *Rizzini 351* (RB!); Barra de Maricá, 5 Jan 1984, *Silva et al. 566* (R!); Alto da Boa Vista, Vale Encantado, 500 m, 4 Jan 1972, *Sucre s.n.* RB 153401 (CEPEC!, F!, K!, MG!, MO!, NY!); Restinga da Jacarepaguá, mata de restinga ao lado sul da Pedra de Itaúna, 4 Jun 1969, *Sucre 5415* (CEPEC!, K!, MO!, NY!, RB!); Serra da Mendanha, 450 m, 27 Nov 1969, *Sucre & Braga 6437* (K!, RB!); Estrada Alto da Boa Vista - Vale Encantado, 500 m, 4 Jan 1972, *Sucre 8199* (RB!); Estado de Guanabara, Lado Leste da Pedra de Itaúna, Jacarepaguá, 23 Mar 1972, *Sucre 8733* (RB!); Restinga da Marambaia, Rio Vermelho, 1 m, 3 Jun 1972, *Sucre 9178* (RB!); Estado Guanabara. Restinga de Jacarepaguá, Pedra de Itaúna, lado Sul da Pedra, 24 Apr 1973, *Vidal 280* (RB!). **SÃO PAULO:** Bairo de Gomes, São Paulo, 12 May 1930, *Serviço Florestal do Brasil* (RB!).

**Local names.** Batinga de Mussununga (Espírito Santo), Murta (Bahia). Murta is the common name for many species of Myrtaceae. Batinga appears to be more restricted in application and is often used for species of *Gomidesia* e.g, *G. fenzliana*, *G. freyreissiana.* Mussununga is the local name for an open type of *cerrado*/savanna vegetation in Espírito Santo.

*Gomidesia martiana* has often been confused with *G. spectabilis*. Indeed judging by determination slips, the two names are considered synonymous by some specialists. I consider the species closely related but distinct, and usually easily separable even in the vegetative state. *Gomidesia martiana* tends to have coriaceous leaves, which, when dry, are biscuit brown and similar in colour above and below, and the interpetiolar scar is faint, while leaves of *G. spectabilis* are chartaceous and usually stongly bicolorous when dry (dark green or brownish above and strikingly paler below), and the interpetiolar scar is prominent. In fertile material the differences are more numerous: *G. martiana* is distinct by virtue of the domed top of the ovary which is free in fruit and the hypocotyl which is pubescent only near its point of attachment to the cotyledodons, whereas in *G. spectabilis* the ovary is entirely fused to the hypanthium and the whole hypocotyl is densely sericeous.

Berg's description of *G. martiana* was based on Sellow material from B and herb. Schlechtendal. The B material is presumed to have been destroyed but the Schlechtendal herbarium is at CAS and HAL. Any Sellow material of *G. martiana* surviving there is likely to be the most appropriate choice for lectotype for this name. I have therefore refrained from lectotypifying *G. martiana* pending the outcome of a recent loan request to CAS and HAL.

**25. Gomidesia montana** (Cambess.) Nic Lughadha comb. nov.

*Myrcia montana* Cambess., *in* Saint-Hilaire, Fl. Bras. merid. **2:** 325. 1832. Type. Brazil. Minas Gerais: "In montibus Serra da Ibitipoca et Serra do Papagaio," *Saint-Hilaire D 501* (lectotype, P!, here designated; isotypes, P! (2 sheets)).

(Fig. 15e&f).

*Myrcia buxifolia* Gardner, Hooker's London Journal of Botany **4:** 101. 1845 Type. Brazil. Rio de Janeiro: Organ mountains, 1800 m, Mar 1841, *Gardner 5716* (lectotype, K!, here designated; isolectotype, K!).

*Aulomyrcia montana* (Cambess.) O.Berg, *in* Martius, Fl. bras. **14(1):** 61. 1857.

*Gomidesia clausseniana* O.Berg, *in* Martius, Fl. bras. **14(1):** 23. 1857. Type. Brazil. Minas Gerais: "Habitat in montibus Serra do Ouro Preto," *Mart, Herb. Fl. Br. n. 1235* (lectotype, M!, here designated; isolectotypes, K!, LE!, M!, NY!).

*Gomidesia kunthiana* O.Berg, *in* Martius, Fl. bras. **14(1):** 23. 1857. Type. Brazil: "Habitat in Brasilia meridionali," *Sellow s.n.* (holotype, B, *n.v.*, presumed destroyed; lectotype, BR!, here designated; isolectotypes, K!, P! (2 sheets)).

*Gomidesia kunthiana* var. *latifolia* O.Berg, *in* Martius, Fl. bras. **14(1):** 23. 1857. Inadmissible name to be replaced by *G. kunthiana* var. *kunthiana*.

*Gomidesia kunthiana* var. *angustifolia* O.Berg, *in* Martius, Fl. bras. **14(1):** 23. 1857. Type. Brazil: *Sello s.n.* (holotype, B, *n.v.*, presumed destroyed; lectotype, W!, here designated; isotype, F! (fragment)).

*? Gomidesia klotzschiana* O.Berg, *in* Martius, Fl. bras. **14(1):** 534. 1859. Type. Brazil. "Habitat in montibus Serra da Piedade prov. Minarum, nec non ad Petropolin prov. Rio de Janeiro," *Riedel s.n* (holotype, LE, n.v.).

*Myrcia glazioviana* var. *villosa* Kiaersk., Enum. Myrt. bras. 112. 1893. Type. Brazil. Rio de Janeiro: "Serra dos Órgãos, au sommet," *Glaziou 16999* (holotype, C!; isotype, K!).

*Myrcia kunthiana* (O.Berg) Kiaersk., Enum. Myrt. bras. 112. 1893.

*Myrcia kunthiana* var. *latissima* Kiaersk., Enum. Myrt. bras. 113. 1893. Type. Brazil. Rio de Janeiro: "Hautes Orgues," 27 May 1869, *Glaziou 3760* (lectotype, C!, here designated; isolectotypes, BR!, K!).

*Myrcia kunthiana* var. *microphylla* Kiaersk., Enum. Myrt. bras. 113. 1893. Type. Brazil. Rio de Janeiro: "Serra dos Órgãos, cote de Petrópolis," *Glaziou 16998* (holotype, C!; lectotype, BR!).

*Myrcia ouropretoensis* Kiaersk., Enum. Myrt. bras. 113. 1893. *Nom. superfl.* based on *Gomidesia clausseniana*, to be replaced by *M. clausseniana*.

*Shrub* or *subshrub* 0.8–1.5 m tall. Branchlets 10 cm below the terminal bud 1.5–2.5 mm in diameter, more or less rounded, glabrous with pale bark peeling in rectangular pieces or with a dense indumentum of erect, straight or curved, greyish hairs, to 0.8 mm long; terminal bud 4–4.5 mm long or proliferating, with a dense indumentum of ascending, straight, reddish hairs to c. 1 mm. Stipule lobes to 0.8 mm long. Inter-petiolar ridge not seen. Petioles 0.5–2 mm long, 0.7–1.5 mm wide, channeled, more or less glabrous or with a moderately dense to dense indumentum of appressed or ascending, straight or crisped, reddish brown or white hairs 0.5–2.0 mm. *Lamina* oblong to narrowly oblong or narrowly ovate, coriaceous, 11–29 mm long, 5.5–14 mm wide, 1.8–3 times as long as wide; apex acute or rounded or obtuse, rounded or obtuse at very tip; base truncate or rounded or acutely cuneate; margin bent down or recurved or revolute; midrib impressed above, raised or prominent below; lateral veins straight or curved, slightly impressed or slightly raised above, when raised sometimes slightly channeled, flat or very slightly raised below, sometimes not visible, diverging at c. 60–80° from the midrib; secondary laterals simple, sometimes equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping between them, or obscured by revolute leaf margin; higher order venation slightly raised above and below; venation between marginal vein and margin inconspicuous. Indumentum absent, scattered or moderately dense above, consisting of straight white hairs of varying orientation, 0.2–0.4 mm long; scattered or moderately dense below, consisting of erect, straight, white or reddish brown hairs, c. 0.3–1 mm long. Gland dots indistinct or impressed above, conspicous or distinct below, dark and slightly raised. *Conflorescence* comprising one or two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect triad or metabotryoid of 3–9 flowers, c. 11–47 mm long, reaching c. 2/3–3.5 times the length of the subtending leaf; peduncle 7–31 mm long i.e., c. 2/3–3/4 the length of the inflorescence, c. 0.5 mm wide, flattened; lateral branches none, or one or two pairs below the terminal cyme or cluster of cymes. *Mature flower* *buds* 3–4 mm long x 2.7–3.5 mm wide. Calyx lobes triangular, 1.8–2.5 mm long x 1.3–2 mm wide, apex acute, with a dense to moderately dense indumentum of appressed, straight, white hairs to 0.5 mm externally, glabrous internally, at least near base, glabrous or with moderately dense to dense indumentum towards apex, hypanthium 2–2.4 mm long, prolonged c. 1.6 mm above the ovary, indumentum dense near base externally, moderately dense to dense near apex, consisting of appressed or ascending, straight or curving, reddish-brown or whitish hairs to 0.4–2 mm; disk c. 3.5–4.2 mm diameter, indumentum dense. Stamens 94–118 per flower; anthers c. 0.55–0.6 mm long, filament not or scarcely tapering to the point of insertion on the connective, apex obtuse or truncate, vertical displacement of thecae marked, thecal halves lose curvature on dehiscence, thecal halves divergent with margins inrolled, residual septum visible, oblique to almost transverse. Style c. 5–7 mm long, with moderately dense indumentum in lower 1/2–2/3, glabrous towards apex; stigma punctiform. Ovary 1–1.2 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 6 mm diameter, crowned with the erect, imbricate calyx lobes or with a ring of hypanthial tissue left by the caducous calyx lobes. Mature seed 2 per fruit, c. 4.5 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 23) and ecology.** *Gomidesia montana* occurs in the mountains of Minas Gerais, Rio de Janeiro and São Paulo. It is reported from rocky outcrops in *campo rupestre* and forest margins at altitudes of 1500–2300 m.

**Phenology.** Peak flowering in *G. montana* is in January and February, with the main flowering season extending into March. Flowering collections have also been made in September while fruiting collections range from August to November.

**Specimens examined. BRAZIL.** MINAS GERAIS: Serra do Caparão, 2200 m, 9 Sep 1941, *Brade 16897* (F!, K!, NY!, RB! S!, US!); Serra do Caparão, Pico da Bandeira, 25 Sep 1941, *Brade 17015* (K!, NY!, RB!); Habitat in montibus Serra do Ouro Preto, prov. Minas Geraes, Feb 1839, *Claussen 12* (BR!); 'Environs de Rio Janeiro et d'Ouro Preto'. Cited in Glaziou's liste with the locality Itacolumy, pres Ouro Preto, Minas, *Glaziou 14828* (C!, P!); Cited in Glaziou's liste with the locality Serra de São José d'El Rei, Minas, *Glaziou 16072* (K!, LE!, P!); Near summit of Serra da Piedade, ca. 35 km E. of Belo Horizonte, near BR-31, 1900 m, 13 Jan 1971, *Irwin 30233* (NY!); Curvellas, Oct 1834, *Lund s.n.* (Habitat in montibus Serra do Ouro Preto, prov. Minas Geraes, *MartFlBrasHb 1235* (BR! (2 sheets), K!, LE!, M!, NY!, P!, US! (photo), W!); Mun. Ouro Preto. Parque Estadual do Itacolomi, 1650 m, 26 Dec 1987, *Peron 569* (RB!); Mun. Ouro Preto. Parque Estadual de Itacolomi, 1650 m, 18 Nov 1987, *Peron 572* (RB!); Serra da Piedade, Jan 1824, *Riedel s.n.* (NY!); Pico da Bandeira perto do Caparão. Beira de mata e campo aberto com pedras, 1900 m, 6 Sep 1977, *Shepherd 5788* (UEC!); Descida do Pico da Bandeira, 1500 m, 6 Aug 1969, *Souza 29* (RB!); Serra do Caparão, Macieiras, 15 Nov 1960, *Strang 226* (F!); Serra da Piedade, 2 Feb 1864, *Warming s.n.*

(C!). **Rio de Janeiro:** Serra dos Órgãos, Therezópolis, Pedra Assu, 2100 m, 8 Oct 1929, *Brade 9618* (R!, US!); Mont des Órgãos. T(?)etrópolis, *Glaziou 16049* (BR!, C!, K!, LE!, P!, R!, RB!, US!); Serra dos Órgãos. Campo das Antas, Mar 1883, *Palma 7402* (R!); Pedra do Sino, Serra dos Órgãos, Theresópolis, 2170 m, Feb 1952, *Vidal II-661* (R!); Pedra do Sino, 2150 m, *Vidal II-703* (R!). **São Paulo:** Parque est. de Campos de Jordão. São José dos Alpes, 22 Feb 1984, *Robim s.n.* SPSF 8393 (RB! 273736, UB!); Parque Estadual de Campos de Jordão, 1900 m, 16 Aug 80, *Ururahy 19* (RB!, HRB!).

As here circumscribed *Gomidesia montana* is an inclusive taxon characterised by its convex coriaceous leaves drying dark brown above and biscuit brown below and its open anthers. The number of binomials and trinomials listed in synonymy reflect the variability of this species. The *Lund s.n.* collection cited above probably that referred to by Legrand (1959) under *G. gaudichaudiana* (here treated as *G. eriocalyx*). Kiaerskou determined this specimen as *G. gaudichaudiana* but the anthers are clearly more open than those characteristic of the *eriocalyx* complex. Legrand noted this discrepancy, drew attention to the height of the plant (reported as being 25' ~ 8 m) and expressed the opinion that the specimen represented a new species in his Section Platyteca. I consider that the specimen is referrable to *G. montana* and that the label attached to the sheet may belong to a different collection. The fact that the label reads 'Laurus, arbor 25'....' lends support to this hypothesis, since in my experience Myrtaceae are rarely mistaken for Lauraceae.

Legrand suggested that *G. klotzschiana* should be placed in the synonymy of *G. clausseniana*. Berg's description is certainly consistent with this possibility. However, a search in LE failed to reveal the type material (R. Harley, pers. comm.) so *G. klotzschiana* is here treated as a doubtful synonym.

*Gomidesia montana* has often been confused with *G. eriocalyx* which differs in its larger flatter leaves (?) with venation always raised below and its distinctive, deeply emarginate anthers with thecal halves retaining curvature after dehiscence. I consider *G. montana* to be closely related to *G. spruceana* which also exhibits a markedly reduced inflorescence and calyx lobes which are glabrous towards the base internally and, probably, caducous in fruit.

**26. Gomidesia nitida** (Vell.) Nied., *in* Engl. & Prantl, Nat. Pflanzenfam. **3 (7):** 77. 1893.
*Eugenia nitida* Vell., Fl. flum. 281 (typ. cons. prop. *Mikan 1047*).

Fig. 40 & 41a-e (also 1C and 13e&f).

*Myrcia subsericea* A.Gray, U.S. Expl. Exped., Phan. 533. 1854. Type. Brazil. Rio de Janeiro:

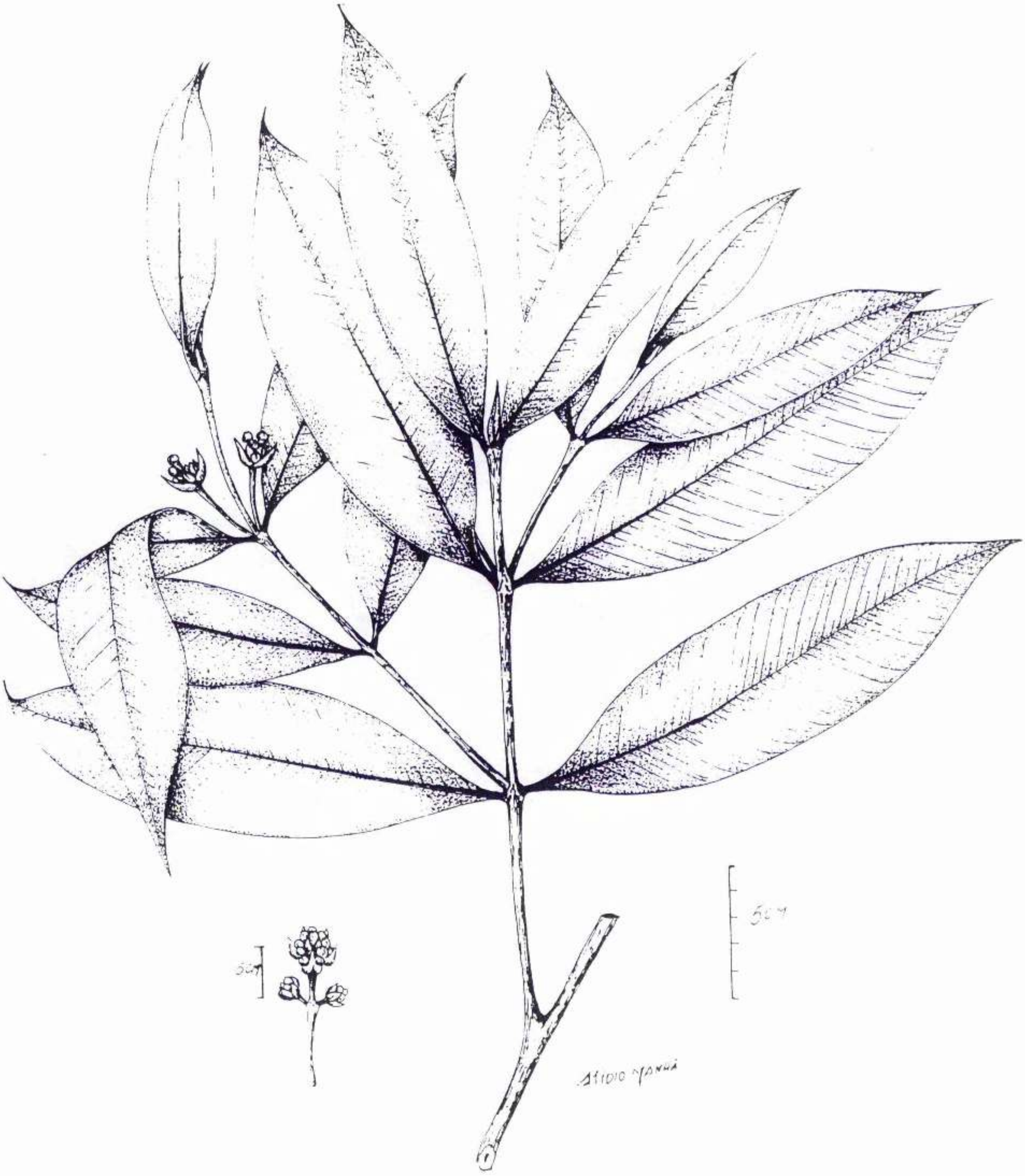
*Mikan/Pohl 1047* (lectotype W!, here designated; isolectotypes, F!, K!, W! (2 sheets)).

*Gomidesia chamissoeana* O.Berg, Linnaea **27:** 7. 1855. based on *Eugenia nitida* Vell.. Nom. illeg. superfl.

*Myrcia nitida* (Vell.) Kiaersk., Enum. Myrt. bras. 102. 1893. nom. illeg. non *Myrcia nitida* Cambess. 1832.

*Shrub* or rarely a *treelet* or *tree* (1.3–)2–4.5(–8) m tall. Branchlets 10 cm below the terminal bud 3–4 mm in diameter, slightly flattened in alternating planes so that in the pressed condition the branchlet often appears to widen just below the node, with a dense indumentum of straight, straw-coloured appressed hairs, to 0.8 mm long; terminal bud to 1.8 mm long or proliferating. Stipule lobes to 1.6 mm long. Inter-petiolar ridge distinct to conspicuous. Petioles 9–11 mm long, 1.5–2 mm wide, channeled. *Lamina* narrowly obong or lanceolate, 160–240 mm long, 33–51 mm wide, 3.8–5 times as long as wide; apex long-acuminate, often narrowly so (and the acumen frequently lost in herbarium material); base acutely cuneate and decurrent on petiole; margin flat or bent down and sometimes slightly undulating; midrib flat or raised and deeply channeled above, prominent below; lateral veins more or less straight, flat or very slightly raised above, very slightly raised below, diverging at c. 70° from the midrib; secondary laterals composite or apparently simple, sometimes equalling the laterals in prominence and difficult to distinguish from them; marginal vein more or less equalling the laterals in prominence and curving between them very close to the margin; higher order venation inconspicuous, very slightly raised above and below; venation between marginal vein and margin inconspicuous, submarginal vein sometimes visible. Indumentum absent above with the exception of crisped hairs in the channel of the midrib, extremely dense below, consisting of appressed, straight, pale, dark-based hairs, c. 0.3–0.4 mm long, giving a metallic sheen (silvery gold) to the surface. Gland dots distinct above, slightly raised and paler than the lamina, not visible below. Mature leaves membranaceous. *Conflorescence* comprising a single pair of uniflorescences in the axils of distal leaves. Uniflorescence an erect metabotryoid or crowded thyrsoid of c. (5–)11–30 flowers, 36–60 mm long, reaching c. 1/4–1/2 the length of the subtending leaf; peduncle 22–29 mm long i.e., c. 1/2–3/5 the length of the

FIG. 40. *Gomidesia nitida*. Fig. 3 from Gomes, 1992. Drawn by Atídio Manhã.


5cm
5cm
ATIDIO MANHÃ

inflorescence, 2.5–3 mm wide, flattened; lateral branches 2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 5–6 mm long x c. 4.3 mm wide. Calyx lobes broadly triangular to depressed ovate or hemi-orbicular, 1.3–2.3 mm long x 2.8–3.8 mm wide, apex rounded or obtuse, with a dense indumentum externally and internally; hypanthium 3.5–4.2 mm long, prolonged c. 2.5–2.8 mm above the ovary, densely pubescent internally and externally; disk c. 4–4.2 mm diameter, indumentum dense. Stamens 117–135 per flower; anthers 0.5 mm long, apex truncate or slightly emarginate, apical gland inconspicuous, vertical displacement of thecae marked, thecal halves held more or less parallel after dehiscence, the dorsal portions more or less flat, the ventral retaining curvature, thecal margins reflexed, thecal tissue extending below that of the connective, residual septum usually visible, vertical. Style 10–11 mm, with dense indumentum in lower 1/2–2/3; stigma capitate. Ovary 1.1–1.5 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 12–13 mm diameter, crowned with the hypanthial ring, the calyx lobes usually falling as the fruit matures. Mature seed 1 per fruit, c. 10–12 mm long, testa pale or dark, hypocotyl glabrous.

**Distribution (Map 24) and ecology.** Locally frequent in the Atlantic forest of Rio de Janeiro and adjacent Espírito Santo at 40–1180 m above sea-level. Usually an element of the understorey in dense shade. Occasional in secondary forest.

**Phenology.** *Gomidesia nitida* flowers from January to March with February collections being most frequent among the flowering specimens. Fruiting collections have been made from April through to December. Berg reported a *Sello* collection as flowering in June (as *G. chamissoeana*) but this seems likely to be an error for January.

**Specimens examined. BRAZIL. ESPÍRITO SANTO:** Mun. Cachoeiro de Itapemirim. Vargem Alta, 700 m, 5 May 1949, *Brade 19763* (RB!); Mun. Domingos Martins, estrada para a pedra azul, 1180 m, 19 Jan 1975, *Peixoto 483* (RB!); **RIO DE JANEIRO:** Campo Grande, 1841, *Allemão 302* (R!); P(arque). N(acional). Tijuca, Mata do Pai Ricardo, 11 Mar 1976, *Araújo 1032* (NY!); *Bowie & Cunningham 76* (MO!); Corcovado, 29 Jul 1946, *Duarte 178* (RB!); Corcovado, 5 Oct 1946, *Duarte 343* (RB!); Guanabara, Gávea, Parque da Cidade, 11 Feb 1947, *Duarte & P. Occhioni 927* (F!, NY!, RB!, U!, US!); Corcovado, 15 Feb 1903, *Dusen 1894* (NY!, S!); Mun. Rio de Janeiro, Parque Nacional da Tijuca, Mata do Pai Ricardo, 6 Mar 1978, *Ferreira 263* (RB!); Corcovado and Floresta da Tijuca, *Glaziou 2585* (BR!, C!, K!, P!); Corcovado, 23 Jan 1870, *Glaziou 3980* (C!, P!); Fazenda de Itatiaia, 20 Jan 1873, *Glaziou 6546* (C!, K!, P!, R!); Entre Sumaré e Corcovado, 19 May 1987, *Gomes 176* (RB!); Serra da Carioca, vertente Sul do Sumaré, pela rua Sara Vilela, 11 Jan 1988, *Gomes 290* (RB!); Serra da Carioca, vertente sul do Sumaré, entrada pela R. Sara Vilela, 11 Feb 1988, *Gomes 292* (RB!); Guanabara; Matas do Teixeira Borges, pr. ao Horto Florestal da Gávea, 26 Apr 1928, *Kuhlmann 755* (F!, K!, RB!, U!, US!); Corcovado, *Langsdorff s.n.* (LE!); *Mikan*

FIG. 41. *Gomidesia nitida* (**a** - **e**) and *Gomidesia schaueriana* (**f** - **h**).

*Gomidesia nitida* from Morro Queimado, Tijuca, Rio de Janeiro. **a** infructescence and branch; **b** bark; **c** finished flowers/developing fruits, note loss of some or all calyx lobes; **d** branch arranged to show strikingly bicolorous leaves and silver-gold indumentum on abaxial surface of young foliage; **e** finished flower/developing fruit, note densely pubescent disk and deciduous calyx lobes.

*Gomidesia schaueriana* from Estrada Vista Chinesa, Tijuca, Rio de Janeiro. **f** flowering branch; **g** finished flowers at various stages after anthesis; **h** bark.


a
b
c
d
e
f
g
h

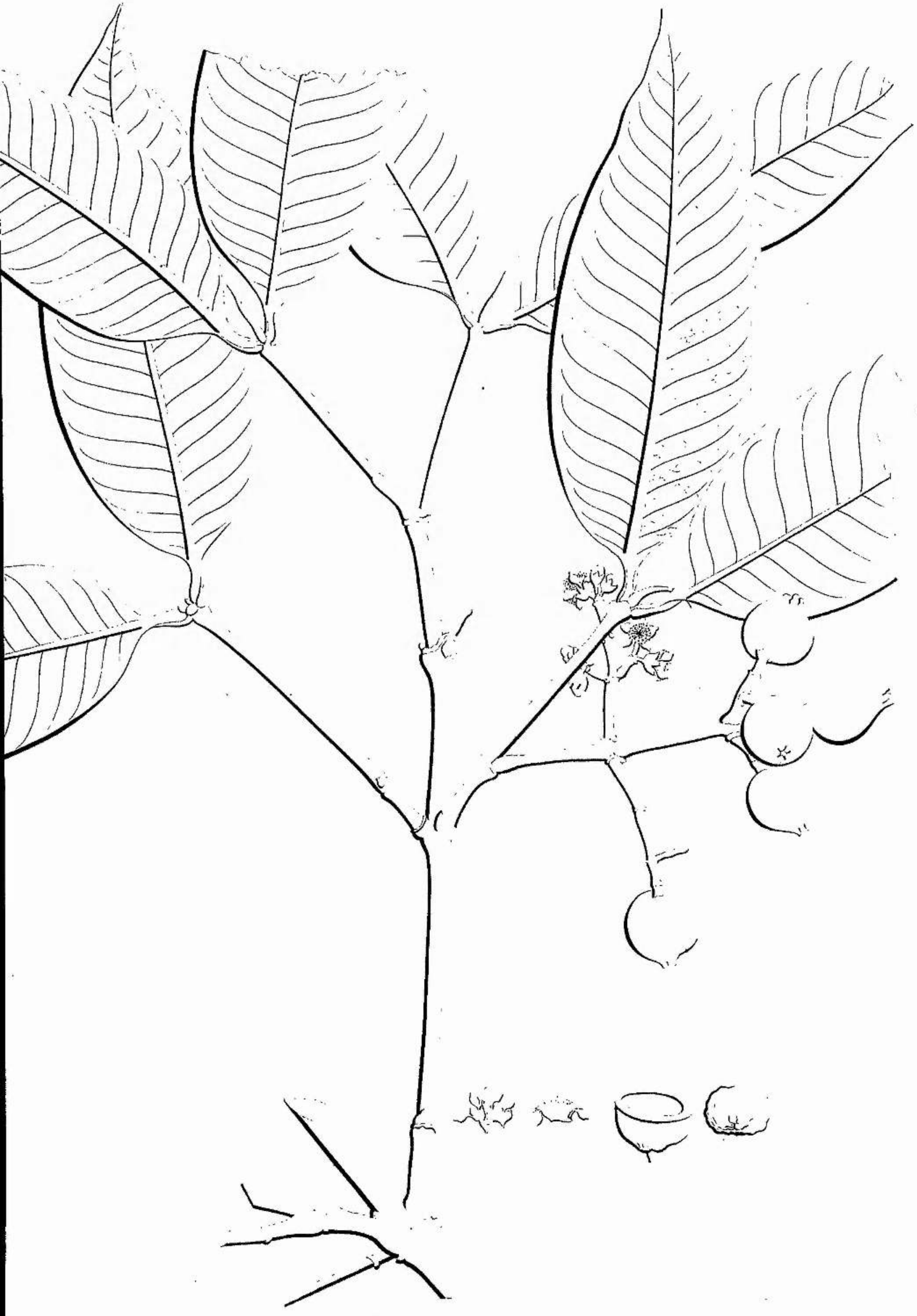
*1047* (F!, K!, W!); Mata de Vista Chineza, 21 Jan 1945, *Occhioni 259* (RB!); Estado de Guanabara, Sumaré, 23 Feb 1959, *Pereira & Duarte 4487* (BR!, RB!); Parque Nacional da Tijuca. Estrada do Sumaré, 24 Feb 1978, *Pinage 1* (RB!); Corcovado, 5 Apr 1917, *Porto 608* (RB!); Parque Nacional da Tijuca, Pedra do Beijo, próximo a Rua Lopes Quintas, 200 m, 10 Jan 1978, *Regina & Turma da UFRRJ 4* (K!, NY!, RB!); Corcovado, Feb 1833, *Riedel 1245* (K!, LE!, NY!, P!, S!, U!, W!); Estado de Guanabara, Pedreira da estrada da Vista Chineza, 400 m, 23 Jan 1968, *Sucre 2145* (RB!, S!); Mata da Lagoinha, 21 Aug 1968, *Sucre 3548* (RB!); Mata da Lagoinha, 12 Jan 1969, *Sucre 4399* (RB!); Mara (Mata) do Rumo, 10 Jan 1972, *Sucre 7362* (RB!); Mata do Rumo, 120 m, 12 Dec 1971, *Sucre 8096* (RB!); Est. da Guanabara, Grota do Pai Ricardo, 525 m, 22 Dec 1971, *Sucre 8157* (NY!, RB!); Mata do Rumo, 40 m, 28 May 1972, *Sucre & Silva 9161* (CEPEC!, K!, NY!, RB!); Vertente Sul do Morro do Sumaré, Jardim Botânico, subida pela Rua Sara Vilela, em direção a Cachoeira, 11 Nov 1988, *Vaz 502* (RB!).

*Gomidesia nitida* is the name in current use for this distinctive species of the mata atlântica of southern Brazil. The combination was made by Niedenzu in 1893 with *Eugenia nitida* Vell. as basionym. Included in synonymy of *G. nitida* was *G. chamissoeana*, a superfluous name published by Berg in 1855 with *E. nitida* Vell. as a synonym. All three names should therefore be (lecto)typified by a single plate in *Florae Fluminensis*.

The plate (reproduced here as Fig. 42) shows a leafy branch with prominent interpetiolar scars with a single panicle bearing buds, flowers and fruit. The leaves are somewhat less than three times as long as broad and fairly prominently veined. The fruit, which to judge by their size must be nearing maturity, are more or less globose but slightly tapered to the apex and crowned by five closely connivent calyx lobes. The analysis adds little further information but the accompanying text states that the leaves are ovate, oblong and extremely shiny.

This information along with the habitat cited (silvis maritimis = forest formations of the coastal plain) strongly suggests that the plant represented may be referrable to the species widely known today as *G. spectabilis*, one of the commonest species of Myrtaceae in Rio de Janeiro with a distribution extending over 800 km of the southern Brazilian coastal rain forest. Although this species has not been collected recently from the precise locality mentioned by Vellozo (Taguahy = Itaguaí) it is known to occur in nearby areas of the Serra do Mar. However it is also possible that the plant illustrated by Vellozo is referrable to the species now known as *G. martiana*, sister species to *G. spectabilis* and often confused with it in Rio de Janeiro where their distributions overlap. *Gomidesia martiana* is also frequent in Rio de Janeiro though it is near the southern limit of its wide distribution which extends over more than 1500 km to Pernambuco in the north. The most useful characters for distinguishing these two species cannot be seen clearly in the Vellozo plate but since *G. martiana* is most often

FIG. 42. *Gomidesia spectabilis?* Plate 35, from Vellozo's Florae Fluminensis **5** which appeared as "*Eugenia nitida.*"



Icos. Monog.
EUGENIA NITIDA
(Tab. 55.)

collected in restinga vegetation and tends to have less globular fruit and fainter leaf venation and interpetiolar scars, the specimen depicted is probably best accommodated in the species currently known as *G. spectabilis*.

Although the characters in the plate are insufficient to distinguish between *G. spectabilis* and *G. martiana* with certainty they are quite adequate to indicate that the plant illustrated is not referrable to the distinctive species currently known as *G. nitida*. This latter species differs from the illustration in its lanceolate leaves with inconspicuous venation and a long acuminate apex and in its rounded calyx lobes which generally fall as the fruit matures. In the field and herbarium it is immediately recognisable by virtue of the dense sericeous indumentum which imparts a metallic appearance (intermediate between silver and gold) to the abaxial surface of the leaves. Berg's description of *G. chamissoeana* undoubtedly refers to this distinctive species and this is confirmed by the additional material cited, *Mikan 1047*. Similarly the descriptive phrase which follows Niedenzu's new combination "*mit unterseits metallglanzenden, sehr lang lanzettlichen,*" clearly refers to the species currently known as *G. nitida*. Thus the name *G. nitida* has been consistently but incorrectly applied to the same species for the past century and a half. This same species was independently described by A. Gray in 1854 as *Myrcia subsericea*. Three specimens are cited in the protologue: *Wilkes s.n.*, *Macrae s.n.* and *Pohl 1047*. The latter specimen is almost certainly the same collection as that cited by Berg as *Mikan 1047*. Mikan and Pohl formed part of the same collecting expedition and their collections often bear no collector's name though they are immediately recognisable as they are numbered in a distinctive style. The name *M. subsericea* appears never to have been taken up, appearing only in the protologue and on the specimens cited therein.

To take up the name *Eugenia nitida* in the sense that seems to have been originally intended would have the following consequences: (a) the name *G. nitida* should be applied to the species hitherto known as *G. spectabilis*, the type species of the genus and (b) a new combination in *Gomidesia*, based on *Myrcia subsericea*, would be required for the species hitherto known as *G. nitida*. Considerable confusion would result from such changes, not least because these two species occur sympatrically in the mata atlântica of Rio de Janeiro. This confusion could be avoided by conserving the name *Eugenia nitida* Vell. with *Mikan 1047* as the conserved type. This measure would preserve the application of Vellozo's name as (mis)understood by Berg and Niedenzu and permit the use of the combination *G. nitida* (Vell.) Niedenzu in the sense in which it has always been applied.

A further complication arises from the consistent and persistent use of the later (by one year) homonym *Eugenia nitida* Cambess. for a completely different species common in the restinga vegetation of Rio de Janeiro and widely cited in vegetation descriptions and anatomical studies. *Eugenia nitida* Cambess. is correctly placed in the genus *Eugenia*. In contrast the species illustrated by Vellozo as *Eugenia nitida* would not nowadays be treated in that genus even if all the neotropical Myrtaceae were lumped in just three genera; given the paniculate inflorescence and pentamerous flower shown, no modern student of the group is likely to dispute that the plant depicted belongs in the Myrciinae rather than the Eugeniinae. Thus the illegitimate later homonym *E. nitida* Cambess. is generally applied to a common species of *Eugenia* while the earlier homonym *E. nitida* Vell. will almost certainly never be taken up again except as a basionym for combinations in the Myrciinae. I therefore intend to propose that *Eugenia nitida* Cambess. should be conserved against *Eugenia nitida* Vell. thus rendering the latter name unavailable for use but still permissible as a basionym for another name or combination based on the same (conserved) type (Art. 14.10).

The combined effect of these two proposals is to protect the current usage of names for two distinctive myrtaceous species with distributions centred on Rio de Janeiro and to remove a threat to the names of two more widespread species whose distributions extend over much of the eastern Brazilian seaboard and which are represented by hundreds of herbarium specimens in Brazil and elsewhere.

**27. Gomidesia palustris** (DC.) Kausel, Lilloa **32:** 348. 1966.

*Myrcia palustris* DC., Prodr. **3:** 246. 1828. Type. Brazil. São Paulo and Rio de Janeiro: "in paludosis ad S. Cruz et Mogy das Cruces," *Martius s.n.* (holotype, M!).

Fig. 43 (also 1H, 3C and 15g&h).

*Myrcia banisteriifolia* DC., Prodr. **3:** 246. 1828. '*banisteriaefolia*' Type. Brazil. São Paulo: "prope Ytú," *Martius s.n.* (holotype, M!).

*Myrcia garopabensis Cambess., in* Saint-Hilaire, Fl. Bras. merid. **2:** 324. 1832. Type. Brazil. Santa Catarina: "prope Armação de Garopaba," Saint-Hilaire *C2 1768 bis* (holotype, P!)

*Gomidesia banisteriifolia* (DC.) O.Berg, Linnaea **27:** 9. 1855. '*banisteriaefolia*'

*Myrcia palustris* DC. var. *bracteata* O.Berg, *in* Martius, Fl. bras. **14(1):** 191. 1857. Inadmissible name to be replaced by *Myrcia palustris* var. *palustris*.

*Myrcia palustris* DC. var. *stictophylla* O.Berg, *in* Martius, Fl. bras. **14(1):** 191. 1857. Type. Uruguay. Montevideo, *Sellow 1644* (holotype, B, n.v., presumed destroyed; lectotype, BR!, here designated; isolectotypes, C!, NY!, P!, S!).

*Myrcia palustris* DC. var. *acutata* O.Berg, *in* Martius, Fl. bras. **14(1):** 191. 1857. Type. Uruguay. Montevideo, *Sellow s.n.* (holotype, B, n.v., presumed destroyed)

*Myrcia palustris* DC. var. *angustifolia* O.Berg, *in* Martius, Fl. bras. **14(1):** 192. 1857. Type. Uruguay. Montevideo, *Sellow 2094* (holotype, B, n.v., presumed destroyed; lectotype, BR!, here designated, isolectotypes, K!, P! (2 sheets)).

*Gomidesia bergiana* D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 25. 1959. Based on *Myrcia palustris* var. *stictophylla* O.Berg and *Myrcia palustris* var. *angustifolia* O.Berg.

*Gomidesia garopabensis* (Cambess.) D.Legrand, Sellowia **13:** 281. 1961.

*Gomidesia palustris* (DC.) D.Legrand, *in* D.Legrand & Klein, Flora Ilustr. Catar. [MIRT]: 37. 1967.

*Gomidesia palustris* (DC.) D.Legrand var. *angustifolia* (O.Berg) Mattos, Loefgrenia **61:** 3. 1969.

*Shrub, treelet* or *tree* 0.5–6 m tall. Branchlets 10 cm below the terminal bud c. 1.5 mm in diameter, terete, glabrous; terminal bud 5–10 mm long with a dense indumentum of appressed or ascending, straight or curved, straw-coloured hairs to 0.6–0.8 mm. Stipule lobes to 1.4 mm long. Inter-petiolar ridge absent. Petioles c. 2 mm long, 0.5–1 mm wide, flat or slightly channeled. *Lamina* elliptic to narrowly elliptic or narrowly obovate, 25–51 mm long, 10–21 mm wide, 2.3–3.2 times as long as wide; apex acute or obtuse, rounded or obtuse at very tip; base acutely cuneate; margin bent down or recurved, often revolute near base; midrib impressed near base, flat near apex above, prominent below; lateral veins more or less straight, flat or slightly raised above, raised or slightly raised below, diverging at c. 50–60° from the midrib; secondary laterals simple, rarely almost equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping between them; higher order venation distinct, slightly raised above, raised below; venation between marginal vein and margin distinct. Indumentum sparse to moderately dense above, consisting of appressed straight white hairs to 0.7 mm, sparse to moderately dense below, consisting of erect, straight or curving, straw-coloured hairs, c. 0.3–0.8 mm long. Gland dots indistinct or distinct and dark above, distinct below, slightly raised. *Conflorescence* comprising one or two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 15–70 flowers, c. 29–52 mm long, reaching c. 4/5–5/3 the length of the subtending leaf; peduncle c. 20–22 mm long i.e., c. 2/5–3/4 the length of the inflorescence, 0.5–1 mm wide, slightly flattened; lateral branches 2–4 opposite or subopposite pairs below the terminal cyme or

FIG. 43. *Gomidesia palustris*. Fig. 35 from Bernardi's Contribucion a la dendrologia Paraguayana. II. Myrtaceae.

Fig. 35. — *Gomidesia palustris* (DC.) Legr.

cluster of cymes. *Mature flower buds* c. 3–4.5 mm long x 2.5–3.5 mm wide. Calyx lobes shallowly triangular or depressed ovate, 0.8–1 mm long x 1.5–1.6 mm wide, apex obtuse or rounded or minutely apiculate, with a moderately dense indumentum of appressed, pale hairs c. 0.3–0.8 mm externally, indumentum shorter and moderately dense internally; hypanthium 1.6–2.4 mm long, prolonged c. 1–1.3 mm above the ovary, indumentum dense externally, at least in proximal portion, consisting of appressed, straight or curved, white hairs to 1.0 mm long, indumentum moderately dense or dense in distal (free) portion; disk c. 2 mm diameter, indumentum dense. Stamens 68–76 per flower; anthers c. 0.45–0.6 mm long, filament abruptly narrowed to point of insertion on connective, apex truncate, obtuse, or shallowly emarginate, vertical displacement of thecae slight, thecal halves losing curvature on dehiscence, thecal margins recurved, residual septum visible, more or less vertical. Style c. 6–7 mm, with dense indumentum in lower 1/3–1//2; stigma punctiform. Ovary c. 0.6–1 m long, bilocular, ovules 2 per locule. *Fruit* globose, minutely puberulent, c. 5 mm diameter, crowned with the connivent or erect or spreading calyx lobes. Mature seed 2–4 per fruit, c. 4 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 25) and ecology.** *Gomidesia palustris* has a broad subtropical distribution extending from southern Brazil into Uruguay, Paraguay and Argentina from sea level to altitudes of 1000 m or more.

**Phenology.** Flowering collections of *Gomidesia palustris* have been made from December to February and, rarely, in November, April and May. Peak flowering is in December and January. Mature fruit have been reported from February through to September.

**Representative specimens examined. ARGENTINA.** Corrientes, Ituzaingo, ruta 38 at Rio Aguapey, 18 Feb 1982, *Landrum 4305* (NY!); Missiones, San Ignacio, Paraguari. a 1 km del rio Paraná, 290 m, 27 Mar 1958, *Montes 27612* (NY!); Corrientes, Estancia Garruchos, Dep. Santo Tome, Prov. Corrientes, 12 Feb 1960, *Pedersen 5417* (C!, US!); Misiones, Santa Ana, *Rodriguez 660* (NY!); Corrientes, Rio Aguapey y Ruta 38. Dep. Ituzaingo, Prov. Corrientes, 6 Dec 1981, *Tressens 1725* (C!); Misiones, Parque Nacional Iguazu. Sendero Yacaratia inferior, 16 Dec 1991, *Vanni 2870* (K!).

**BRAZIL. PARANÁ:** Palmeira, 22 Jan 1941, *Ceccato 2247* (S!); S. Mateus do Sul, 26 Dec 1929, *Gurgel 107* (NY!, RB!); Fluviópolis, 7 Mar 1929, *Gurgel RB37766* (RB!); S. Matheus, 27 Feb 1929, *Gurgel RB37768* (RB!); Mun. Porto Amazonas: Fazenda S. Luís, mata no rio Iguaçu, 800 m, 22 Dec 1963, *Hatschbach 10801* (B!); Mun. Pien, Pien, 9 Jan 1966, *Hatschbach 13469* (F!, NY!, US!); Mun. Paranaguá: Sertãozinho, 31 Jan 1966, *Hatschbach 13626* (MO!, NY!, US!); Mun. Lapa, Rio Passa Dois, 31 Dec 1967, *Hatschbach 18214* (F!, MO!, US!); Mun. Guaratuba, Rio Sai, 10 m, 5 Sep 1968, *Hatschbach 19672* (C!); Mun. Laranjeiras do Sul. Km. 127, 10 Dec 1968, *Hatschbach 20607* (S!); Almirante Tamandare: Timoneira, *Hatschbach 3582* (PACA!); Mun. Campo Largo, Retiro Grande, 3 Jan 1978, *Hatschbach 40718* (C!, MO!, MG!, NY!); Mun. Paranaguá. Rio Almeida, 3 Jan 1980, *Hatschbach 42668* (MO!, NY!); Mun. Teixeira Soares, Rod. BR-272, próx. Rio das Almas, 15 Jan 1981, *Hatschbach 43527* (HUCS!, MO!, MU!, US!); Mun. Piraquara, Florestalp. Piraquara, 830 m, 8 Dec 1946, *Hatschbach 552* (P!, PACA!); Jacarehy, in silva prim. reg. lit, 18 Mar 1914, *Jonsson 90a* (F!, K!, NY!, S!); União da Vitória, 29 Dec 1967, *Koczicki 44* (MU!); União da Vitória, perto da Ponte do Rio Iguaçu, 6 Nov 1964, *Mattos s.n.* (SP!, SPF!); Próximo de São Jerônimo da Serra, 7 May 1982, *Pires Furtado 187* (HRB!, RB!); Woods, Piraí do Sul, 20 Jan 1965, *Smith & Reitz 14871* (NY!, P!, R!, US!); **RIO DE JANEIRO:** Restinga de Jacarepaguá, 28 Feb 1932, *Brade 11394* (R!); Petrópolis, Quitandinha, Dec 1938, *Lutz s.n.* (R!); Morro das Abertas, acesso pela propriedade do Sr. José Krugue - Serraria, 26 Mar 1980, *Martau 251* (RB!); Restinga de Jacarepaguá, 6 Jan 1972, *Sucre 8211* (CEPEC!, F!, K!, MO!, NY!, RB! US!). **RIO GRANDE DO SUL:** Itapoan, S. of Porto Alegre, 22 Jul 1952, *Beetle 1700* (NY!); At Itapoan, S. of Porto Alegre, 22 Jul 1952, *Beetle 1701* (US!); Silvicultura, Sta. Maria, 23 Nov 1955, *Camargo 43* (PACA!); Mun. Taquari: Est. Exp. Pomicultura, 8 Dec 1957, *Camargo 2701* (B!, PACA!, S!); Porto Alegre. Passo de Dorneles, 26 Dec 1957, *Camargo 3090* (PACA!); Est. Ypiranga, Mar 1899, *Edwall s.n.* (SP!); Caracol p. Canela, Jan 1953, *Emrich s.n.* (PACA! (PACA 52848)); 1833, *Gaudichaud 1329* (P!); 1833, *Gaudichaud 1342* (P!); Fazenda Faxinal, Arroio dos Ratos, 3 Apr 1982, *Hagelund 13810* (C!, MO!, NY!); Fazenda Faxinal, Arroio dos Ratos, 23 May 1982, *Hagelund 13958* (C!, MO!, NY!); Pareci p. Montenegro, 1944, *Henz 27583* (PACA!); Pareci p. Montenegro, 1944, *Henz 27678* (PACA!); Pareci, p. Montenegro, 25 Nov 1945, *Henz 32781* (PACA!); Montenegro: Pareci Novo, 28 Dec 1945, *Henz 33014* (K!, PACA!); São Leopoldo, 22 Feb 1947, *Henz 35683* (MO!, NY!, PACA!); 1833, *Isabelle s.n.* (P!); Canguçu, ca. de 3 km a oeste da cidade, 21 Jan 1987, *Jarenkow 643* (PACA!); BR 101, KM. 6, Campo Bonito (ca. 8 km SW de Torres), 10 Feb 1983, *Krapovickas & C.L. Cristobal 38477* (C!, IBGE!); Pelotas na Estação Experimental Florestal do IBDF, 15 Jan 1981, *Mattos 22217* (RB!); Encruzilhada do Sul, na estação experimental, 22 Jan 1981, *Mattos 22384* (RB!); Canela, no caracol, 30 Nov 1982, *Mattos 24088* (RB!); Cerca de 5 km de Canela, 31 Mar 1982, *Mattos 24101* (RB!); Baração, 20 Feb 1986, *Neubert 154* (B!); Porto Alegre, Morro da Polícia, 18 Jan 1964, *Pereira 8481* (RB!); Tannenwald p. Saõ Leopoldo, Dec 1943, *Rambo 11187* (PACA!); Vila Manresa, p. Porto Alegre, Oct 1944, *Rambo 27442* (PACA!); Manresa p. Porto Alegre, Oct 1944, *Rambo 27472* (PACA!); S. Francisco de Paula, Vila Oliva, 30 Jan 1946, *Rambo 30808* (PACA!, U!); S. Leopoldo, 17 Dec 1948, *Rambo 38875* (BR!, P!, PACA!, W!); Steinkopf p. São Leopoldo, 20 Dec 1948, *Rambo 39021* (PACA!); Itapoan, p. Porto Alegre, 22 Dec 1948, *Rambo 39080* (BR!, P! PACA!); Espírito Santo p. Porto Alegre, 24 Dec 1948, *Rambo 39137* (PACA!, W!); Morro da Polícia p. Porto Alegre, *Rambo 39179* (PACA!); Campo do Varejão p. Itapoan, 29 Dec 1948, *Rambo 39315* (B!); Lami, p. Itapoan, 3 Jan 1949, *Rambo 39404* (PACA!); Morro das Abertas, p. Porto Alegre, 9 Jan 1949, *Rambo 39679* (PACA!); Pareci p. Montenegro, 14 Jan 1949, *Rambo 39716* (PACA!); Pareci p. Montenegro, 14

Jan 1949, *Rambo 39730* (PACA!); ad montem Ferrabraz p. Novo Hamburgo, 12 Jan 1949, *Rambo 39857* (PACA!); Sapucaia p. São Leopoldo, 9 Mar 1949, *Rambo 40446* (PACA!); Vila Manresa, p. Porto Alegre, 14 Mar 1949, *Rambo 40506* (PACA!); Sapucaia, p. São Leopoldo, 1 Apr 1949, *Rambo 40794* (PACA!); Est. Azevedo p. Montenegro, 6 May 1949, *Rambo 41433* (PACA!); Itapoan, 23 Dec 1949, *Rambo 44932* (PACA!); Itapoan, 23 Dec 1949, *Rambo 45180* (PACA!); in summo monte Itacolumi p. Gravataí, 11 Jan 1950, *Rambo 45286* (PACA!); Morro da Polícia, p. Porto Alegre, 16 Feb 1950, *Rambo 45834* (PACA!); Viamão p. Porto Alegre, 10 Apr 1950, *Rambo 46738* (B!, PACA!); Faz. do Arroio p. Osório, 14 Apr 1950, *Rambo 46773* (PACA!); Osório, *Rambo 46957* (PACA!); Vila Manresa p. Porto Alegre, 15 May 1950, *Rambo 47100* (PACA!); Lagoa dos Quadros p. Torres, 18 Jan 1951, *Rambo 49707* (PACA!); Palmares ad Lagoa dos Patos, 8 Jan 1952, *Rambo 51741* (PACA!, US!); Osório: Morro Grande, 10 Jan 1952, *Rambo 51801* (PACA!, S!); Vila Oliva p. Caxias, 24 Feb 1954, *Rambo 55052* (PACA!); Vila Oliva, p. Caxias, 8 Feb 1955, *Rambo 56596* (PACA!); Canela, 900 m, 5 Jan 1960, *Richter 14185* (B!); Morro Teresópolis, 28 Apr 1975, *Rosa & Martau s.n. HAS 1725* (F!); Pedreira Santa Luzia, Pelotas, 20 May 1959, *Sacco 1219* (F!); Pareci Velho, p. Montenegro, 21 Nov 1945, *Sehnem 1485* (HUCS!, PACA!); Glória, Porto Alegre, 200 m, 3 Feb 1950, *Sehnem 4415* (HUCS!, PACA!); Linha Campestre p. Montenegro, 450 m, 15 Dec 1949, *Sehnem 4449* (HUCS!, PACA!); Faz-Crisanto Soares. São Lourenço do Sul, 20 m, 11 Dec 1965, *Sehnem 8575* (C!, F!, HUCS!, PACA!); Pesqueiro. Montenegro, 28 Dec 1966, *Sehnem 8980* (PACA!); Guaíba, na Estação Experimental Agronômica, da UFRGS, 24 Jan 1985, *Silveira 2545* (R!, RB!); Proc. Morro Santana, Porto Alegre, 30 Jan 1983, *Sobral 1409* (F!); Porto Alegre, Morro Santana, 20 Feb 1983, *Sobral 1480* (F!, SPF!); Itapuã, Viamão, 13 Jan 1985, *Sobral 3713* (F!, MO!); Mun. Guaíba: Parque Estadual do Turvo, Tenente Portela, 15 Apr 1983, *Sobral & Jarenkow 1920* (NY!); Centro Agronomico, 19 Jan 1964, Strang 550 (F!); Est. Ecol. Taim, Rio Grande, Mar 1987, *Waechter 1827* (F!). SANTA CATARINA: Garopaba, 6 m, 18 Jan 1971, *Bresolin 96* (PACA!); Caputera, (mun. Laguna), 12 Feb 1978, *Hatschbach 40979* (BR!, C!, MU!); Rio Vermelho, Ilha de S. Catarina, 2 m, 17 Jan 1966, *Klein & Bresolin 6520* (HUCS!); Florianópolis: Canavieiras, Ilha de S. Catarina, 2 m, 17 Jan 1966, *Klein & Bresolin 6532* (HUCS!); Florianópolis: Morro das Pedras, sul da Ilha de S. Catarina, 2 m, 16 Feb 1966, *Klein & Souza Sob. 6670* (HUCS!); Lages, 18 Feb 1958, *Mattos s.n.* (PACA!); Sombrio p. Ararangua, 2 Feb 1946, *Rambo 31496* (PACA!); Sombrio p. Ararangua, 5 Dec 1945, *Rambo 31954* (PACA!); Sombrio, 10 m, 5 Dec 1945, *Reitz 1783* (S!); Sombrio, 15 m, 6 Feb 1946, *Reitz 1869* (S!, US!); Urubici - S. Joaquim, 800 m, 30 Dec 1948, *Reitz 2913* (C!, R!, S!, US!); Porto Belo: Canto Grande, 2 m, 15 Jul 1950, *Reitz 3605* (US!); Anita Garibaldi, 700 m, 13 Apr 1963, Figueirdo, p. Bom Retiro, 1000 m, 28 Dec 1948, *Reitz 3688* (P!, PACA!, R!, W!); Campo Alegre, *Reitz 3707* (PACA!, US!); Campo do Massiambu, Palhoça, 5 m, 18 Dec 1952, *Reitz 4851* (NY! U!); Campo Massiambu, Palhoça, 5 m, 5 Feb 1953, *Reitz 5583* (NY!); Campo de Massiambu, Palhoça, 5 m, 5 Feb 1953, *Reitz 5618* (F!, NY!, PACA!, U!, US!); *Reitz 14788* (US!); Laguna: restinga litorânea, 5 m, 29 Feb 1952, *Reitz & Klein 210* (PACA!, S!, US!); Laguna, 5 m, 5 Jun 1952, *Reitz & Klein 267*

(K!, PACA!, US!, W!); Palhoça: Campo do Maciambu, 2 m, 12 Mar 1953, *Reitz & Klein 362* (PACA!); Campo Massiambu, Palhoça, 2 m, 14 May 1953, *Reitz & Klein 621* (B!, US!); Sombrio: Pirão Frio, 10 m, 28 Jan 1960, *Reitz & Klein 9457* (US!); Rancho Queimado: Serra da Boa Vista, 700 m, 27 Dec 1960, *Reitz & Klein 10612* (B!); Rancho Queimado: Serra da Boa Vista, São José, 700 m, 3 Mar 1961, *Reitz & Klein 10842* (NY!); Canoinhas: próximo da cidade, 750 m, 5 Jan 1962, *Reitz & Klein 11542* (BR!, K!); Campo Alegre: Pinheiral, between Postema and Morro Iquererim, 950 m, 31 Jan 1957, *Smith & Klein 10504* (K!, NY!, R!, RB!, S!, US!); Mun. Mafra: 16 km northwest of Mafra on the road to Barras (20 km), 825 m, 13 Mar 1957, *Smith & Klein 12124* (R!, US!); Mun. Porto União: 7 km south of Porto União on the road to Matos Costa (42 km), 775 m, 20 Dec 1956, *Smith & Reitz 8862* (R!, US!); **São Paulo:** Mun. Cananéia: Cananéia Island, several km north of city of Cananéia, 2 m, 17 Feb 1965, *Eiten & W.D. Clayton 6189* (K!, SP!, UB!, US!); Paranapiacaba (via-férrea São Paulo - Santos). Estação Biológica, 800 m, 10 May 1970, *Handro 2135* (K!,US!); Mun. Itapecirica da Serra, perto de Juquitiba, 920 m, 4 Apr 1961, *Mattos 8879* (NY!, SP!); Gaibota, Mun. Itanhaém, 0 m, 7 Feb 1978, *Mizoguchi 391* (MO!, NY!); Santos-Sorocaba, Feb 1875, *Mosen 3382* (P!); Wet ground by a little stream. Munic. Santo André: Rio Grande da Serra, 7 Jan 1969, *Pedersen 8966* (C!); Est. de São Paulo, Mun. Cananéia, Ilha Comprida, 25 Feb 1983, *Pirani 540* (K!); *Riedel 703* (US!).

**PARAGUAY:** Cordilleras, Tobati, Cerro Tobati, 28 Dec 1973, *Arenas 278* (K!, NY!); Cordillera de Peribebua, *Balansa 3045* (K!, P!); Cerro- Hu, pres de Paraguari, 15 Dec 1882, *Balansa 4493* (P!); In silvula ad Estero Yukeri, Itapuã, 14 Nov 1978, *Bernardi 18608* (F!, MO!, U!); Tucuru Pucu: Alto Paraná, *Fiebrig 6129* (K!, US!); Paraguari Department, Ybycui National Park, Mar 1980, *Hartshorn 2498* (NY!); Villarrica, Nov 1934, *Jorgensen 3654* (K!); Dep. La Cordillera, By the Pirareta waterfall, near Piribebuy, 18 Dec 1965, *Pedersen 7580* (K!, P!, US!); Colônia Independência, 13 Nov 1945, *Rojas 13036a* (U!, W!); Guaíra, Colônia Independência, 250 m, 21 Dec 1986, *Schinini & Bordas 25074* (K!); Depto. Cordillera Tobati, Cerro Tobati, 297 m, 6 Apr 1988, *Soria 2169* (NY!).

**URUGUAY.** Montes de Tacuarembo, Dec 1900, *Arechavaleta 6* (W!); Riviera: Ataques, *Herter 94125* (MO!); Rivera, Franqueras, *Legrand 4141* (NY!); Montevideo, *Sellow 1644d* (P!, U!, W!); Montevideo, *Sellow d2094* (P!).

**Local Names.** Cambuí (Santa Catarina). Guamirim (Santa Catarina), Guamiru (Paraná). The name Cambuí is also applied to *G. rosangelae* in NE Brazil. For other species of *Gomidesia* known as Guamirim see under *G. affinis*.

Although the map suggests a more or less continuous distribution through the eastern part of subtropical South America, in ecological terms *Gomidesia palustris* has two distinct strongholds: the *restinga* vegetation along the coast of southern Brazil and the inland steppe vegetation (*campos*) of subtropical South America. Absent from the rain forest which separates these two biomes, it is frequent in copses in the Araucaria formations (*pinheiral*) where it often occurs sympatrically with *G. sellowiana*. Danilevicz et al. (1990) noted that *G. palustris* occurs as a shrub in restinga vegetation while elsewhere it may grow to be a tree.

The long-standing confusion regarding the application of the names *G. palustris* and *G. sellowiana* may be attributable to their general similarity of habit, leaf size etc. and to their largely overlapping distributions. Legrand (1936) appears to have fallen prey to this confusion in his account of the Myrtaceae of Uruguay, correctly treating *G. sellowiana* and *G. hartwegiana* as synonymous but then citing only material of *G. palustris*. However by 1967 he was clearly familiar with material of both species in the field and in the herbarium and gave a very detailed account of their distinguishing features. He emphasized (a) the nature of the indumentum - finer, slightly longer and more flexuose in *G. palustris*; (b) the density of the higher order venation - alveoles at least 0.5 mm long in *G. palustris*, smaller in *G. sellowiana*; (c) calyx lobes 'less deltoid' in *G. palustris*, obtuse or sub-obtuse; (d) the differences in anther morphology. I have not found the shape of the calyx lobes helpful in distinguishing these species but my studies confirm the utility of the other characters discussed by Legrand. In addition I have found differences in the angle of the lateral veins particularly useful in sorting large amounts of material whose identity can subsequently be confirmed by examination of the anthers. In dehisced anthers of *G. sellowiana* most of the surface visible is the external surface of the thecae which are held parallel to each other or slightly divergent so that the oblique or transverse residual septum is just visible. In *G. palustris* much of the exposed surface of the dehisced anther is the inner surface of the thecae and the residual septum can clearly be seen to be more or less vertical.

Legrand (1959) was the first to realise that elements of *Myrcia palustris* were referrable to *Gomidesia*. He published the nomen nudum *G. bergiana* for two of Berg's four varieties of *M. palustris*. It is not clear whether he intended to exclude the other two varieties or simply had not had access to their types. Subsequently he realised that these varieties are conspecific with *Myrcia garopabensis* and made a new combination in *Gomidesia* for all this material. However, he appears to have intended to include the type of *M. palustris* within this taxon, thus rendering his new name illegitimate. Eventually, in 1967, Legrand treated all of these names under the new combination *G. palustris*, still with an expression of doubt regarding the basionym. However, just one year before, Kausel had made the same new combination and the name *G. palustris* is therefore credited to him.

**28. Gomidesia pubescens** (DC.) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 20. 1959.

*Myrcia pubescens* DC., Prodr. **3:** 247. 1828. Type. Brazil. Minas Gerais: *Martius s.n.* (lectotype, M!, here designated).

Fig. 44 (also 15j&k).

*Gomidesia aubletiana* O.Berg, *in* Martius Fl. bras. **14 (1):** 27. 1857. Type. Brazil. *Pohl 1050* (lectotype, W!, here designated; isolectotypes, F!, K!, W!).

*Gomidesia casaretteana* O.Berg, *in* Martius Fl. bras. **14 (1):** 20. 1857. Type. Brazil. Minas Gerais: "ad Formigas et Serra de Grão-Mogor," *Martius s.n.* (lectotype, M!, here designated).

*Gomidesia mikaniana* O.Berg, *in* Martius Fl. bras. **14 (1):** 21. 1857. Type. Brazil. Minas Gerais: "ad Formigas et Serra de Grão-Mogor," *Martius s.n.* (holotype, M!).

*Gomidesia raddiana* O.Berg *in* Martius Fl. bras. **14 (1):** 26. 1857. Nom. superfl. based on *Myrcia pubescens DC.*

*Gomidesia widgreniana* O.Berg *in* Martius Fl. bras. **14 (1):** 26. 1857. Type. Brazil. Minas Gerais: *Widgren 546* (holotype, MEL, n.v., isotypes S!, US!).

*Gomidesia haenkeana* O.Berg *in* Martius Fl. bras. **14 (1):** 515. 1858. Type. Bolivia. Chiquitos, *Haenke s.n.* (holotype, M!).

*Myrcia minensis* Kiaersk., Enum. Myrt. bras. 110. 1893. Nom. superfl. based on *G. widgreniana* O.Berg non *Myrcia widgreniana* (O.Berg) Mattos 1968 (= *Aulomyrcia widgreniana* O.Berg).

*Myrcia minensis* var. *subcordata* Kiaersk., Enum. Myrt. bras. 110. Type. Brazil. Rio de Janeiro: "Morro Queimado par le cote du Chemin du Macaco," 18 Dec 1879, *Glaziou 10792* (lectotype C!; isolectotypes, K!, LE!, P!).

*Myrcia schenckiana* Kiaersk., Enum. Myrt. bras. 114. 1893. Type. Brazil. Rio de Janeiro: Tijuca, 21 Jan 1887, *Schenck 2182* (holotype, C!).

*Gomidesia pubescens* var. *casaretteana* (O.Berg) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 20. 1959.

*Gomidesia pubescens* var. *widgreniana* (O.Berg) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 21. 1959.

*Shrub, treelet* or *tree* 1.8–16 m tall. Branchlets 10 cm below the terminal bud c. 2–2.5 mm in diameter, rounded to subquadrangular, minutely puberulent; terminal bud c. 6–12 mm long, with a dense indumentum of appressed, straight or curving, pale brown hairs to 0.5–0.7 mm long. Stipule lobes c. 0.8–1.2 mm long. Inter-petiolar ridge apparently absent or distinct and

FIG. 44. *Gomidesia pubescens* near Brasília, Distrito Federal. **a** habitat; **b** young vegetative growth; **c** inflorescence in bud; **d** inflorescence in flower with unidentified beetle, not observed to contact stigma; **e** bark; **f**, **g** immature and mature fruit, note closely connivent calyx lobes; **h** flowering branch, note buds and fruits present on same branch; **j** flower, pink style noted on only a single tree of this population; **k** inflorescence.


e
f
g
b
h
c
i
d
k

transverse. Petioles 4–7 mm long, 1.5–2 mm wide, channeled, with a moderately dense indumentum of ascending, straight or curved, pale brown hairs c. 0.5–0.7 mm long. *Lamina* ovate or wide ovate or suborbiculate, 52–78 mm long, 30–46 mm wide, 1.4–1.7 times as long as wide; apex obtuse or rounded, occasionally shallowly emarginate; base truncate or rounded, rarely obtusely cuneate; margin bent down or recurved; midrib sulcate above, prominent below; lateral veins more or less straight, flat or slightly impressed or slightly raised above, raised or prominent below, diverging at c. 70–80 ° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein almost equalling the laterals in prominence and curving between them; higher order venation conspicuous, raised and pale above and below; venation between marginal vein and margin conspicuous, slightly raised. Indumentum absent or scattered to sparse above, consisting of white hairs of varying length and orientation, scattered or sparse below, consisting of erect, straight or curved or crisped, pale brown hairs, c. 0.3–0.6 mm long. Gland dots indistinct above, indistinct or conspicuous below, dark and slightly raised. *Conflorescence* comprising one or two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 20– > 100 flowers, c. (25–)65–77 mm long, reaching c. 3/2 the length of the subtending leaf; peduncle 30–50 mm long i.e., c. 2/5–2/3 the length of the inflorescence, 1–1.5 mm wide, flattened; lateral branches 2–4 below the terminal cyme or cluster of cymes. *Mature flower buds* c. 4 mm long x 2.5 mm wide. Calyx lobes widely deltate or shallowly triangular, 0.9–1 mm long x 1.1–1.6 mm wide, apex acute or obtuse and apiculate, with a moderately dense indumentum of appressed, straight or curved, white hairs to 0.3 mm externally and internally; hypanthium 2–2.2 mm long, prolonged c. 0.9–1.4 mm above the ovary, with a dense indumentum of ascending, straight or curved, brown hairs to 1 mm externally, dense internally; disk c. 1.6–2.6 mm diameter, indumentum dense. Stamens 47–65 per flower; filament tapered or scarcely tapered to point of insertion on connective, anthers c. 0.6 mm long, apex truncate or shallowly emarginate, vertical displacement of thecae marked, thecal halves lose curvature on dehiscence, held parallel or slightly divergent with margins recurved, effective dorsal opening 1/3–1/2 the length of the anther, residual septum visible, oblique, almost transverse. Style c. 7–8 mm, with moderately dense indumentum in lower 1/3–1/2; stigma punctiform. Ovary c. 0.8 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 7 mm diameter, with a moderately dense indumentum of straight, pale hairs to 0.3 mm, crowned with the erect, calyx lobes. Mature seed one per fruit, c. 6 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 26) and ecology.** *Gomidesia pubescens* occurs in gallery forest and between rocks in upland areas (600–1700 m) in southeastern and central Brazil. There are disjunct populations in central and western Bolivia and in Ceará.

**Phenology.** The main flowering period for *G. pubescens* is in January and February but flowering collections have also been made in April, May and June.

**Representative specimens examined. BOLIVIA.** Apolo, 4 Mar 1902, *Williams 17* (NY!, K!); Apolo, 1460 m, 25 Feb 1902, *Williams 323* (K!, NY! (2 sheets)).

**BRAZIL. DISTRITO FEDERAL:** Brasília, mata inundada entre o Guará e o Setor de Indústria, 21 Feb 1980, *Chagas e Silva 370* (IBGE!, K!, NY!); Convênio Florestal de Brasília, 30 May 1960, *Gomes 1020* (RB!). **ESPÍRITO SANTO:** Mun. Cachoeira de Itapemirim, Vargem Alta, Morro do Sal, 20 May 1984, *Ferreira 3383* (GUA!). **GOIÁS:** Granja Samambaia. Rio Corumbá. 120 km de Brasília, 1 Jan 1967, *Heringer 11245* (UB!); Gallery margin. 20 km N.W. of Corumbá de Goiás, near Pico des Pirineus, 1250 m, 26 Jan 1968, *Irwin & Maxwell 19251* (F!, NY!, UB!). **MINAS GERAIS:** Serra do Espinhaço, Eastern slopes of Pico do Itambé, 1700 m, 11 Feb 1972, *Anderson & Stieber 35818* (F!, MO!, NY!, R!, UB!, US!); 10 km by road SW of Rio Jequiti and Mendanha on road to Diamantina, 15 Apr 1973, *Anderson & Fryxell 8944* (MO!, NY!, UB!, US!); Grão Mogol. Vale do riacho Ribeirão, 900 m, 3 Sep 1986, *CFCR 10054* (NY!, SPF!); Grão Mogol. Vale do Rib. das Mortes acima da cidade, 970 m, 4 Sep 1986, *CFCR 10100* (NY!, SPF!); Grão Mogol. Bacia do Ribeirão da Morte, 950 m, 4 Nov 1987, *CFCR 11477* (NY!); Grão Mogol, Vale do Rio Itacambiruçu, ao longo da Estrada para Cristália, 750 m, 10 Dec 1989, *CFCR & P.T.Sano 12402* (NY!); Grão Mogol: Vale do Rio Itacambiruçu, longo da Estrada para Cristália, 750 m, 10 Dec 1989, *CFCR & P.T. Sano 12415* (NY!); Grão Mogol: Estreito do Riacho Ribeirão, 925 m, 16 Jun 1990, *CFCR & J.R. Pirani 13144* (NY!, SPF!); Grão-Mogol: estreito do Riacho Ribeirão, 950 m, 6 Sep 1990, *CFCR 13421* (NY!, SPF!); Grão Mogol. Rib. dos Bois, 850 m, 2 Sep 1986, *CFCR 9997* (NY!, SPF!); Locality not stated, 1840, *Claussen 199A* (BR! (3 sheets)); 10 km N O de Grão Mogol, 22 Oct 1978, *Hatschbach 41639* (SPF!); Serra do Espinhaço: ca. 27 km SW of Diamantina on road to Gouveia, 1300 m, 15 Jan 1969, *Irwin & Reis dos Santos 22036* (MO!, NY!, RB!, UB!, US!); Rocky river bank, Rio Itacambiruçu, and adjacent rocky cerrado, ca. 10 km west of Grão Mogol, road to Cristalina, 900 m, 19 Feb 1969, *Irwin & Reis dos Santos 23571* (F!, MO!, NY!); Diamantina, 17 Jan 1947, *Romariz 105* (RB!); In virgultis ad Brumado (inter Barbacena et Lagoa Santa), 3 May 1866, *Warming s.n.* (C!). **RIO DE JANEIRO**: Pico da Tijuca, 30 Nov 1972, *Almeida de Jesus 2157* (RB!); Pico da Tijuca, 1000 m, 2 Jun 1929, *Brade 10471* (R!, US!); Morro Queimado, 17 Jan 1932, *Brade 11286* (R!, US!); Morro Queimado, 22 Jan 1948, *Brade RB62177* (RB!); Morro Queimado, 27 Dec 1867, *Glaziou 2582* (BR!, C!, P!, (4 sheets) R!); Locality not stated, 1821, *Langsdorff s.n.* (P!); Alto do Morro Queimado, 14 Dec 1944, *Occhioni 260* (RB!); Alto da Tijuca, *Schwacke s.n. R121491* (R!); Morro Queimado, 600 m, 1 Dec 1971, *Sucre 8027* (RB!). **SÃO PAULO:** No alto da Serra, *Andrade 107* (R!, US!); locality not stated, *Riedel 728* (US!).

**Local names.** Marmelo bravo (São Paulo)

Although *Gomidesia pubescens* is one of the most broadly distributed species in the genus (second only to *G. lindeniana*) it is known from relatively few collections. The distribution pattern is suggestive of a species which was formerly more widely distributed and which, with climatic warming has suffered a contraction in its distribution and is now confined to cool upland areas or islands of relatively cool temperatures such as is found in Brasília.

Berg distinguished no less than six species among the material treated here as *Gomidesia pubescens*. Three of these ( *G. casaretteana*, *G. mikaniana* and *G. raddiana*) were based on material which de Candolle (1828) had named *Myrcia pubescens* but he failed to take up the epithet *pubescens* for any of them. Examination of the Martius material at M has permitted the lectotypification of *M. pubescens*, the sheet chosen being that on which Berg based *G. raddiana*. The other three names were based on previously undescribed material collected by Pohl, Haenke and Widgren ( *G. aubletiana, G. haenkeana* and *G. widgreniana* respectively). Kiaerskou (1893) treated *G. widgreniana* in *Myrcia* and described two further new taxa in this complex. Legrand (1959) made the necessary new combination *G. pubescens* and took a broad view of this species, including all of the names mentioned above except *G. aubletiana*. He commented that *G. pubescens* was insufficiently known with respect to variation and distribution. This observation is equally true today and my circumscription of *G. pubescens* differs from that of Legrand only in the inclusion of G. *aubletiana*. Having studied only a photo of the type of *G. aubletiana*, Legrand treated it as a distinct species which he considered closely related to *G. elliptica* and *G. hilariana* (here treated as synonyms of *G. eriocalyx*. This echoes Berg's original placement of *G. aubletiana* with *G. gaudichaudiana* (here treated as a synonym of *G. eriocalyx)* and, later, *G. spruceana* in a group united by leaves with cordate bases. I consider this group entirely artificial and, having studied the type material and similar collections from Minas Gerais and Goiás, I have no hesitation in treating *G. aubletiana* as a synonym of *G. pubescens*.

Cambessedes' (1832) circumscription of this species is broader still and appears to have included *G. fenzliana*. The two species are superficially rather similar and are occasionally to be found mounted on the same herbarium sheet, though I have not found any instance in which this appears to have been the result of a mixed collection in the field. *Gomidesia fenzliana* usually has leaves with acutely cuneate or acuminate bases and higher order venation less conspicuous than in *G. pubescens*. *Gomidesia fenzliana* tends to have broader buds with calyx lobes obtuse or rounded and broader than those seen in *G. pubescens*. Stamen numbers in *G. fenzliana* are approximately double those in *G. pubescens* and the vertical displacment of the thecae is less marked.

**29. Gomidesia reticulata** (Cambess.) O.Berg, *in* Martius, Fl. bras. **14 (1):** 15. 1857.
*Myrcia reticulata* Cambess., *in* Saint-Hilaire Fl. Bras. merid. **2:** 304. 1833. Type. Brazil. Minas Gerais: "prope praedium Rancho de Medeiro ad iter quod ducit a Sebastianopoli," *Saint-Hilaire s.n.* (holotype, P!; isotypes, F! (fragment), P! (2 sheets)).

Fig. 45 & 46 (also 1D and 12g-j).

*Gomidesia reticulata* var. *angustifolia* O.Berg, *in* Martius, Fl. bras. **14 (1):** 16. 1857. Type. Brazil. Rio de Janeiro: "ad Fazenda de Mathias Ramos & Pirahi," *Pohl 1022* (lectotype, W!, here designated; isolectotypes, K!, W!).

*Gomidesia reticulata* var. *latifolia* O.Berg, *in* Martius, Fl. bras. **14 (1):** 15. 1857. Inadmissible name to be replaced by *G. reticulata* var. *reticulata*. Berg treated the type of *G. reticulata* as var. *latifolia*.

*Treelet* or *shrub* 2–4 m tall. Branchlets 10 cm below the terminal bud 2–4 mm in diameter, flattened or more or less rounded, with a moderately dense indumentum of erect or ascending, straight or curved brown hairs, 0.8–1 mm long; terminal bud 5–9 mm long or proliferating. Stipule lobes to 2 mm long. Inter-petiolar ridge absent. Petioles 5–10 mm long, 1.5–2 mm wide, channeled. *Lamina* lanceolate, 115–180(–230) mm long, (26–)33–40(–61) mm wide, (3–)3.2–5.5 times as long as wide; apex long- or short-acuminate or attentuate; base obtusely or acutely cuneate; margin flat or bent down or recurved, especially near base; midrib sulcate above, prominent below; lateral veins more or less straight, sulcate above, raised or prominent below, diverging at c. 60–70° from the midrib; secondary laterals composite, rarely equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation deeply impressed above, raised below; venation between marginal vein and margin conspicuous. Indumentum sparse to scattered above, moderately dense to sparse below, consisting of erect, straight or curved, whitish hairs, c. 0.8 mm long. Gland dots distinct above and below. Mature leaves chartaceous. *Conflorescence* comprising 2–3(–4) pairs of uniflorescences in the axils of distal leaves. Phylloscopic accessory uniflorescences occasional. Uniflorescence an erect thyrsoid of c. 29 flowers, 42–80 mm long, reaching c. 1/2 the length of the subtending leaf; peduncle 12–45 mm long i.e., c. 1/4–1/2 the length of the inflorescence, c. 1 mm wide; lateral branches 3

FIG. 45. *Gomidesia reticulata*. Plate 142 from Saint-Hilaire's Flora Brasiliae meridionalis, which appeared as "*Myrcia reticulata*."

pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 3.7–4.5 mm long x 3.4–4 mm wide. Calyx lobes depressed ovate, 1.0–2.0 mm long x 2.4–3.6 mm wide, apex rounded, with a dense indumentum of straight hairs up to 1 mm long externally, indumentum shorter and less dense internally; hypanthium 2.4 mm long, prolonged c. 1.6 mm above the ovary, indumentum dense externally consisting of appressed, curved, pale brown hairs to c. 0.8 mm long, dense internally; disk c. 2.9–3.6 mm diameter, indumentum dense. Stamens 79–105; filament not tapered to point of insertion on connective, anthers 0.6–0.8 mm long, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent, with margins flat or inrolled, effective dorsal opening 1/4–1/3 the length of the anther, residual septum not usually visible. Style 9.2–10 mm, with moderately dense indumentum in lower 1/3; stigma capitate. Ovary 0.8–1.2 mm long, bilocular, ovules 2 per locule. *Fruit* globose, 9–14 mm diameter, crowned with the connivent to erect, imbricate calyx lobes. Mature seed 1 per fruit, c. 8.5–9 mm long, testa pale, hypocotyl glabrous.

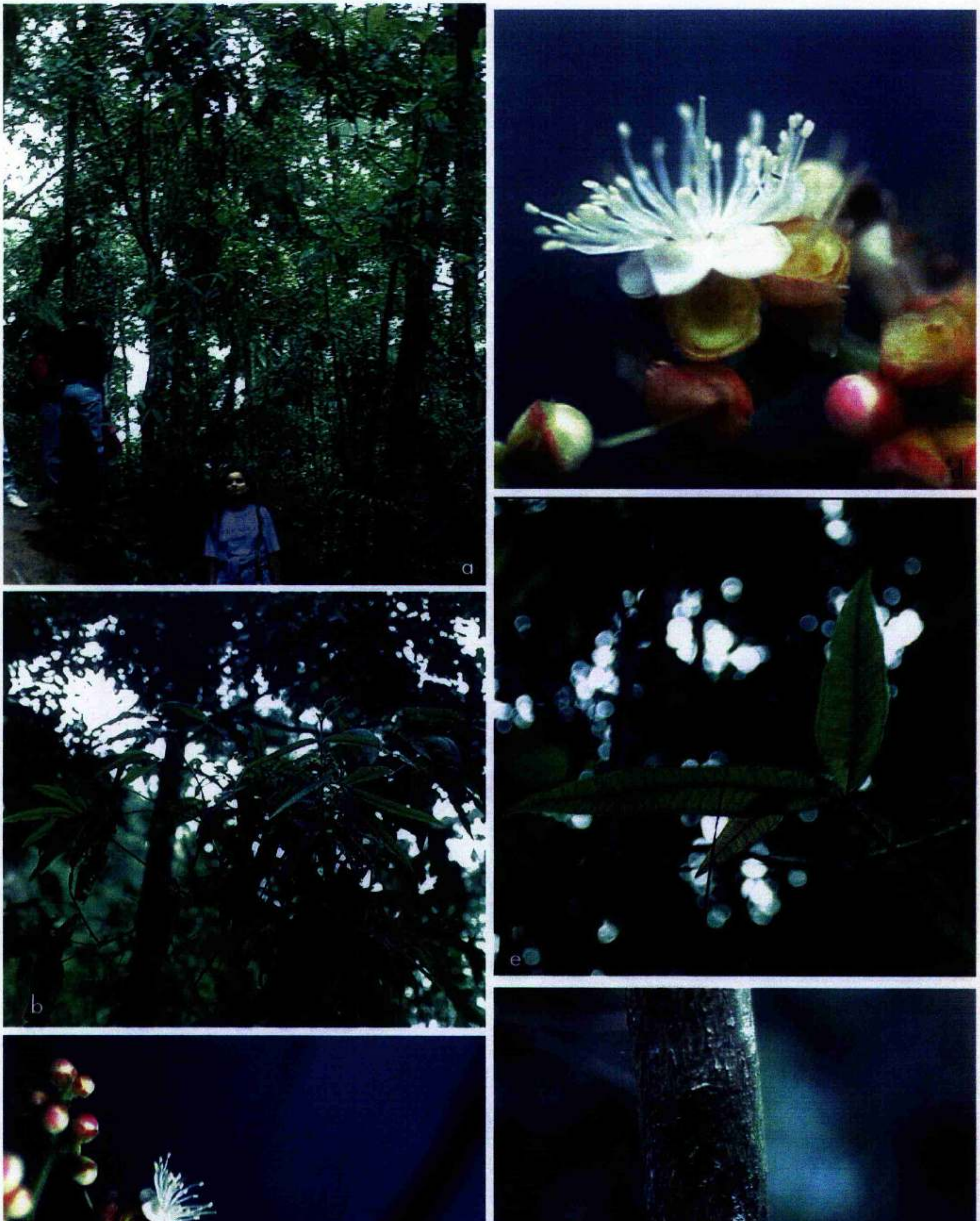
**Distribution (Map 27) and ecology.** Most of the specimens seen were collected in Itatiaia, in or about the National Park at altitudes of 400–1235m, often in secondary forest. There are additional collections from Juiz de Fora, Vassouras and (Nova) Friburgo.

**Conservation:** This rather narrow endemic is fairly common within the confines of the Itatiaia National Park, appears to thrive in secondary forest and is therefore under no immediate threat.

**Phenology.** Flowering material has been collected in January and February (though many collections still in very young bud at this time). Immature fruit have been collected in April, May and July while specimens collected in May, July and September bear mature fruit.

**Specimens examined. BRAZIL.** **MINAS GERAIS:** 'ad juiz de fora cp. leg.' *Collector unknown s.n.* (R!). **RIO DE JANEIRO:** Parque Nacional Itatiaia, 7 Jan 1960, *Barth J56* (US!); Itatiaja, 800 m, 20 Feb 1936, *Brade 15072* (B!, RB!); Itatiaia, 900 m, Jan 1938, *Burret 16034* (NY!, RB!); Friburgo, Faz. Santa Bárbara, 8 Feb 1953, *Capell s.n.* RB 83110 (F!, RB!); Mun. Resende; Itatiaia National Park, 1235 m, 24 Jul 1966, *Eiten & Liene T. Eiten 7338* (US!); Fazenda de Itatiaia, 20 Jan 1873, *Glaziou 6546* (C!, K!, P!, R!); Parque Nacional de Itatiaia, 830 m, 3 Feb 1967, *Lindeman & J.H. de Haas* 4181 (U!); Itatiaia, Jan 1939, *Luiz 32* (RB!); Rezende, perto de Marombas, no Parque Nacional de Itatiaia, 14 Jul 1967, *Mattos 14802* (SP!); Rezende, Parque Nacional de Itatiaia, 29 Sep 1969, *Mattos 15479* (SP!); Itatiaia, Parque, Lagoa Azul, 800 m, 26 May 1961, *Pereira 5702* (RB!); Itatiaia, Maromba, 1100 m, 4 Mar 1962, *Pereira 6987* (M!); Road between Monte Serrat and Ponte Maromba, Mt. Itatiaya, 1000 m, Jan 1929, *Smith 1617* (F!, S!); Itatiaia, 21 Apr 1962, *Strang 361* (K!); Vassouras, 400 m, Apr 1976, *Sucre 11193* (K!, NY!, RB!).

FIG. 46. *Gomidesia reticulata* at Itatiaia, Rio de Janeiro. **a** habitat and habit (slender, pole-like stem of *G. reticulata* is heavily disguised as a ruck-sack strap); **b** flowering branch, note bullate surface of leaves; **c** buds and flower; **d** flower, note style just overtopping stamens and distinct, capitate stigma; **e** leaves; **f** bark.


a
b
c
e
f

**Local names and uses.** Hoehne (1979) mentions *Gomidesia reticulada* (sic) in his treatment of the indigenous fruits of Brazil. He comments that although it is known by the vernacular name Jaboticaba Branca the paniculate inflorescence is sufficient to demonstrate that it should not be grouped with the other Jaboticabeiras which bear fasciculate flowers in the axils of leaves or even at leafless nodes. Among the 'other Jaboticabeiras' Hoehne included various species traditionally placed in the genus *Myrciaria*, most of which Sobral (1993) considers more correctly assigned to the genus *Plinia*. The name Jaboticaba Branca has also been applied to *Myrciaria aureana* Mattos (Silva, 1991) and to *Myrciaria phitrantha* (Kiaersk.) Mattos (Mattos, 1989).

Berg distinguished two varieties. His *G. reticulata* var. *latifolia* was based on *Myrcia reticulata* Cambess and therefore, as the typical variety, should be named *G. reticulata* var. *reticulata*. *Gomidesia reticulata* var. *angustifolia* was considered distinct from the typical variety because of its lanceolate leaves (oblong-lanceolate in var. *reticulata*), its trilocular ovary (bilocular in var. *reticulata*) and its style which exceeded the stamens in length (style shorter than the stamens in var. *reticulata*). The variation in leaf shape evident among the three Saint-Hilaire sheets on which *Myrcia reticulata* was based encompasses almost the entire range of leaf shape encountered in the species as whole. I dissected flowers and fruits respectively of two of the three syntypes of *G. reticulata* var. *angustifolia* and found no evidence of a trilocular ovary. All material dissected of this species was found to have bilocular ovaries. *Gomidesia reticulata* var. *angustifolia* is therefore relegated to synonymy since, even if the reported difference in relative style and stamen length were found to be consistent, it would be insufficient to justify recognition of a variety.

Records of *G. reticulata* from Santa Catarina are attributable to misidentifications by Legrand of material to which he later gave the name *G. affinis* var. *catharinensis* (*Klein 2008, Plaumann 360, Reitz & Klein 1593, 1987, 2714, 3671*). At the time of first publication of this name (as a *nomen nudum*) Legrand indicated that he considered the variety as occupying an intermediate position between *G. affinis* and *G. reticulata*. However when he eventually validated the name, eight years later, he discussed the new variety's affinities with *G. affinis* var. *affinis* and with *G. hebepetala* (here considered conspecific) and did not mention *G. reticulata*. This variety is here treated as a distinct species, *G. catharinensis*.

Three sheets of Saint-Hilaire material of *Gomidesia reticulata* were seen at P. These appear to represent a single collection. Two of the specimens bear threaded tags with the no. *2456* and small printed 'ISOTYPE' labels. The third specimen bears an unnumbered threaded tag and a small printed 'TYPE' label. This latter sheet is therefore considered to be the holotype of *Gomidesia reticulata*.

From the three collections on which Berg based *G. reticulata* var. *angustifolia*, the obvious choice for a lectotype is *Pohl 1022* because: (i) the only precise locality cited by Berg for this variety is that of *Pohl 1022*, (ii) the Pohl collection is preferred over the Sellow collection because no number was cited for the latter, (iii) the Pohl collection is of flowering material and is therefore preferred over *Schott 1071* which is of fruiting material. Both sheets of *Pohl 1022* seen from W bear determinations in Berg's hand; however only one bears the full locality as cited by Berg in his original description and for this reason that sheet is here designated lectotype.

The type locality for *Myrcia reticulata* "Rancho de Medeiro, ad iter quod ducit a Sebastianopoli ad provinciam Minas Geraes", probably refers to a site which Saint-Hilaire (1974a) mentioned as Morro da Boa Vista ou dos Arrependidos. In a footnote he added that a traveller gave this peak the name Morro de Mideiros and that there was a place nearby called Medeiro, in which case the peak should more correctly be called Morro de Medeiro (or Medeiros). From his description of his journey it may be deduced that this peak must be somewhere between Matias Barbosa (21° 53' S 43° 20' W) and Juiz de Fora (21° 45' S 43° 20' W). Pohl (1976) also mentioned passing through Medeiros before arriving at Alto do Marmelo on his way to Juiz de Fora and it is tempting to speculate that his unlocalized, unnumbered collection of *G. reticulata* from Minas Gerais may have been made in the same area where the type was collected.

The only precise locality cited by Berg for *G. reticulata* var. *angustifolia* is 'Fazenda Mathias Ramos et Pirahi'. The same phrase appears on one of the two sheets of *Pohl 1022* at W. From Pohl's account of his travels it is clear that, while based in Fazenda Mathias Ramos in or near the Serra de Itaguaí, he made an excursion to the Rio Piraí near its confluence with the Rio Paraiba. Thus the collection *Pohl 1022* is likely to have been made upriver from Vassouras in the state of Rio de Janeiro.

**30. Gomidesia rosangelae** Nic Lughadha sp. nov. ined. Type. Brazil. Alagoas: Santo Antônio, 21 Sep 1954, *Falcão et al. 1195* (holotype RB!; isotypes, F!, K!, NY!, RB!).
*Gomidesia blanchetiana* var. *alagoensis* D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 12. 1959. Type. Brazil. Bahia: *Blanchet s.n.* Nom. nud.

*Shrub* or *slender tree* 1.5–8 m tall. Branchlets 10 cm below the terminal bud 3.5–4 mm in diameter, rounded to slightly compressed, with a moderately dense to dense indumentum of appressed, ascending or erect, straight, golden brown hairs of varied lengths c. 0.1–0.4 mm;

terminal bud c. 8 mm long with a dense indumentum of erect, straight, golden brown or straw-coloured hairs to 0.5 mm. Stipule lobes c. 1–2.5 mm long. Inter-petiolar ridge, distinct, transverse. Petioles c. 1–2 mm long, 2–2.5 mm wide, channeled, with a moderately dense indumentum of appressed, erect, straight golden brown or straw-coloured hairs c. 0.4–0.5 mm long. *Lamina* ovate to wide ovate, 49–96 mm long, 34–54 mm wide, 1.4–1.8 times as long as wide; apex obtuse or acute or minutely apiculate; base rounded or truncate or very shallowly cordate; margin bent down or recurved or revolute; midrib sulcate or shallowly sulcate or impressed near base above, flat near apex, prominent below; lateral veins straight or curved, impressed or flat or very slightly raised above, raised below, diverging at c. 70–80° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein equalling the laterals in prominence and curving between them; higher order venation indistinct or very slightly raised above, slightly raised or raised below, especially near marginal vein; venation between marginal vein and margin inconspicuous or obscured by revolute margin. Indumentum sparse to moderately dense above, consisting of appressed, straight, pale or golden brown hairs c. 0.2–0.5 mm, sparse to moderately dense below, consisting of erect or appressed, straight or curved, golden brown or pale hairs, c. 0.3–0.6 mm long. Gland dots indistinct or distinct above, dark and impressed, distinct below, dark and slightly raised. Mature leaves coriaceous, drying mid to dark brown above, biscuit brown below. *Conflorescence* comprising two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 19–65 flowers, 75–89 mm long, reaching c. 9/10 to the whole length of the subtending leaf; peduncle 35–42 mm long i.e., c. 2/5–1/2 the length of the inflorescence, 2–3 mm wide, terete or flattened; lateral branches 2–4 below the terminal cyme or cluster of cymes. *Mature flower buds* 4.5–6.5 mm long x 4–6 mm wide. Calyx lobes hemi-orbicular or depressed ovate, 1.3–2 mm long x 2.1–3 mm wide, apex obtuse or rounded, with a moderately dense indumentum of appressed, straight or curved, pale hairs to 0.2 mm long, moderately dense internally; hypanthium 1.8–3 mm long, prolonged c. 0.7–1 mm above the ovary, with a dense indumentum of appressed, straight, pale hairs to 0.4 mm externally, dense internally; disk c. 2.8 mm diameter, indumentum dense. Stamens c. 69–85 per flower; anthers c. 0.7–0.95 mm long, filament tapering or narrowing abruptly to point of insertion on connective stub, apex shallowly emarginate, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, held parallel or slightly divergent, with margins flat (in plane of curvature), connivent or overlapping, effective dorsal opening 1/5 the length of the anther, residual septum occasionally visible, vertical. Style c. 6 mm, with dense indumentum in lower 1/3, moderately dense in middle 1/3, glabrous towards apex; stigma indistinct. Ovary

1.2 mm long, bilocular, ovules 2 per locule. *Fruit* depressed globose, c.10 mm diameter, crowned with the connivent calyx lobes. Mature seed 2 per fruit, c. 7.5 mm long, testa pale, hypocotyl with a tuft of appressed straw-coloured hairs at point of insertion on cotyledons, otherwise glabrous.

**Distribution (Map 28) and ecology.** *Gomidesia rosangelae* has a distribution confined to northeast Brazil, occurring in the states of Alagoas and Sergipe and in the north of Bahia. It has been collected in diverse habitats from *restinga* to savanna vegetation, rain forest, secondary forest and on the boundary between savanna and dry forest.

**Phenology.** *Gomidesia rosangelae* has been collected in flower in late November and December. Mature fruit have been collected in April.

**Specimens examined. BRAZIL.** ALAGOAS: Santo Antônio, 21 Sep 1954, *Falcão et al. 1195* (F!, K!, NY!, RB!); near Maceió, Feb 1838, *Gardner 1303* (K!); Mun. Coruripe, Parque da Usina Guaxuma, 17 Mar 1980, *Lyra 43* (SPF!); Mun. Maceió, Reserva Biológica do IBDF, 10 Apr 1984, *Lyra-Lemos 878* (SPF!). BAHIA: Ao norte de Alagoinhas, 14 Feb 1980, *Araújo 216* (RB!, CEPEC!, HRB!); locality not indicated, Collector not indicated *SP48269* (SP!); Camacari, 6 Apr 1991, *Ferreira 361* (HRB!); Área controle da Caraíba Metais. Junto fábrica, 30 Nov 1982, *Noblick 2198* (NY!); Área Controle da Caraíba Metais. Lamarão do Passe, 30 Nov 1982, *Noblick 2199* (HRB!, HUEFS!); Área controle da Caraíba Metais, 1 Dec 1982, *Noblick 2320* (CEPEC!, HUEFS!); Área controle da Caraíba Metais, 9 Dec 1982, *Noblick 2400* (CEPEC!, HUEFS!); Alagoinhas, Inhamupe, 14 Dec 1980, *Pinto 21/80* (HRB!). SERGIPE: Serra de Itabaiana, 8 Dec 1975, Collector not indicated *RB174022* (RB!); Mata do Crasto, Mun. Sta Luzia do Itanhy, 15 Mar 1995, *Landim 237* (K!); Mata do Crasto, Mun. Sta. Luzia do Itanhy, 15 Sep 1995, *Landim 634* (K!).

**Local names.** Cambuí (Bahia). This name is also applied to *Gomidesia palustris* in Santa Catarina.

*Gomidesia rosangelae* is strongly reminiscent of *G. martiana* with which it shares characters such as the coriaceous leaves which turn mid-brown on drying and the hypocotyl with a patch of pubescence near the point of insertion on the cotyledons. However, it lacks the Type II hairs characteristic of *G. martiana*, being rather closer to *G. springiana* in terms of the nature and distribution of the indumentum.

Legrand intended to treat this taxon as a variety of *G. blanchetiana*. He published the nomen nudum *G. blanchetiana* var. *alagoensis* under which was cited an unnumbered Blanchet collection from C 'Blanchet s/n (C) typ' and *Falcão 1195* which he saw at IPA. The only Blanchet material from C of which I am aware is *Blanchet 3415*, the type of *G. blanchetiana* and, since no material is cited under that name, I consider it most probable that the citation *Blanchet s.n.* actually referred to the typical variety and that it was accidentally transposed from the previous page. There are several such transpositions in this paper, and together with more minor typographic errors, they render Legrand's rather telegraphic text deceptively difficult to interpret. On the basis of the material available to date I consider *G. rosangelae* to be distinct from *G. blanchetiana,* differing in its broader, more coriaceous leaves (chartaceous in *G. blanchetiana*) with very short petioles (1–2 mm in *G. rosangelae*, c. 8 mm in *G. blanchetiana*) and short hairs.

The epithet honours Rosangela P. Lyra-Lemos, curator of the Maceió herbarium.

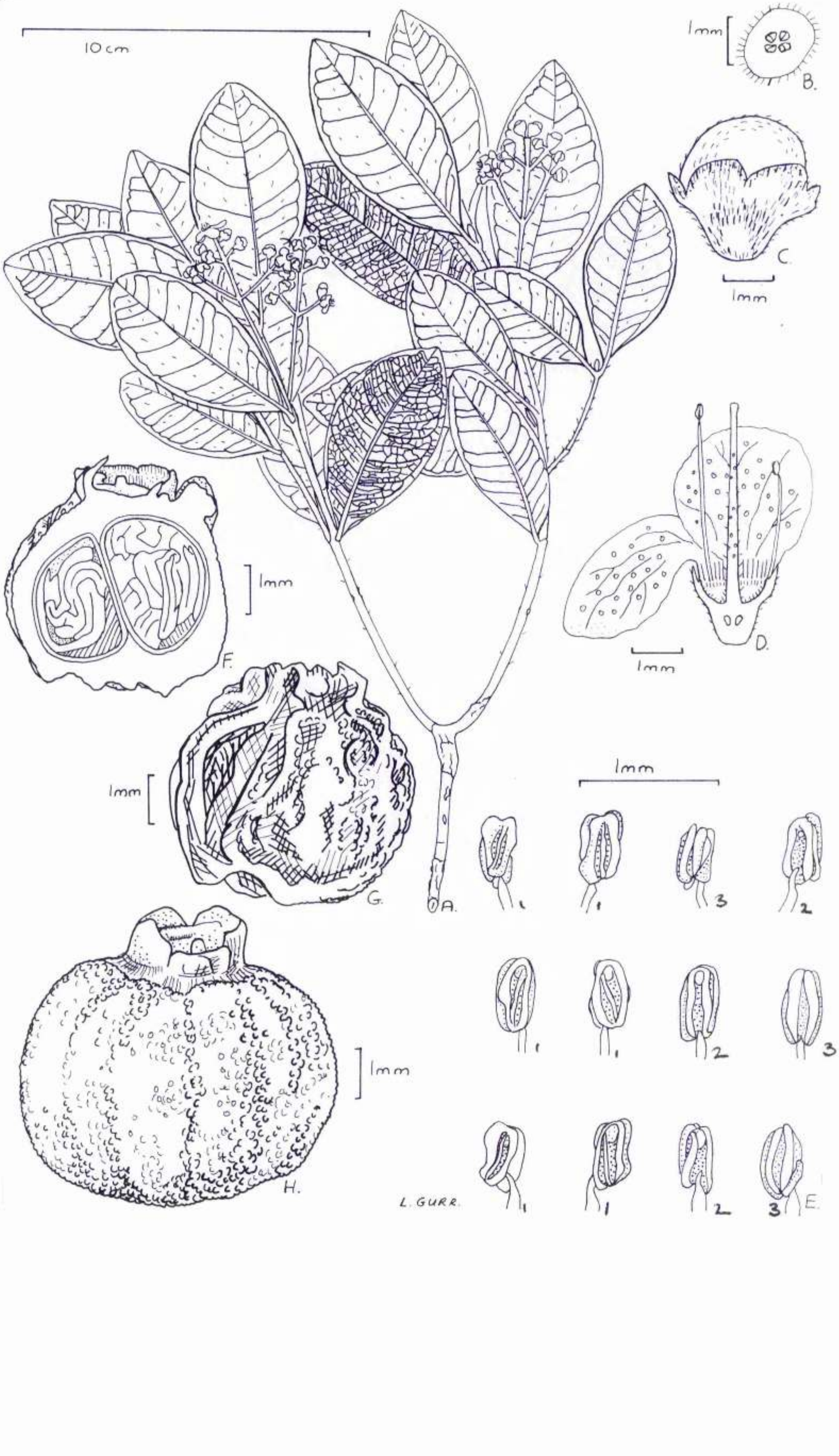
**31. Gomidesia schaueriana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 18. 1857. Type. Brazil. *Sellow 552* (holotype, B, n.v., presumed destroyed; lectotype, BR!, here designated).

Fig. 41f-h & 47 (also 2F and 15m&n).

*Myrcia brasiliensis* Kiaersk., Enum. Myrt. bras. 102. 1893, based on *Gomidesia schaueriana* non *Myrcia schaueriana* O.Berg, *in* Martius, Fl. bras. **14(1):** 163.

*Tree* or *treelet* 3–20 m tall. Branchlets 10 cm below the terminal bud 2.5–3.5 mm in diameter, terete, glabrous or with a scattered to moderately dense indumentum of straight, appressed white hairs to 0.2 mm long; terminal bud 4–9 mm long with a dense indumentum of appressed or ascending, straight, white or straw-coloured hairs 0.7–1 mm long. Stipule lobes c. 0.8–1 mm long. Inter-petiolar ridge absent. Petioles 3–7 mm long, 1–1.5 mm wide, channeled, glabrous or with a moderately dense indumentum of appressed, straight or curved hairs c. 0.4–1 mm long. *Lamina* elliptic or rarely wide elliptic or narrowly obovate, 44–70 mm long, 22–32 mm wide, (1.9–)2.1–2.8 times as long as wide; apex acuminate, acute, obtuse or rounded; base acutely or obtusely cuneate or decurrent; margin flat, bent down or recurved, recurved or revolute near base; midrib sulcate or impressed near leaf base, flat or slightly raised towards apex above, prominent below; lateral veins more or less straight, slightly raised or raised above, raised below, diverging at c. 50–60° from the midrib; secondary laterals composite, not equalling the laterals in prominence; marginal vein equalling the laterals in prominence and curving between them; higher order venation raised or slightly raised above and below; venation between marginal vein and margin inconspicuous. Indumentum absent or scattered above, consisting of appressed, straight, white hairs to 0.2 mm, moderately dense, sparse or scattered below, consisting of appressed or erect, straight or curved, whitish, brown-

FIG. 47. *Gomidesia schaueriana*. **A** Conflorescence and foliage; **B** Transverse section of ovary; **C** Flower bud; **D** Longitudinal section of flower; **E** Anthers in lateral (1), dorsal (2) and ventral (3) view; **F** Longitudinal section of fruit and two seeds; **G** & **H** Fruit. A - E from *Gehrt s.n.*, F - H from *Reitz and Klein 2083*. Drawn by L. Gurr.


10 cm
1mm
B.
C.
1mm
D.
1mm
1mm
F.
1mm
G.
A.
1mm
1
1
3
2
1
1
2
3
1mm
H.
L. GURR.
1
1
2
3
E.

based hairs, c. 0.3–0.6 mm long. Gland dots indistinct above, raised below. Mature leaves chartaceous to thinly coriaceous. *Conflorescence* comprising a single pair of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 5–19 flowers, 61–64 mm long, reaching c. 4/5–4/3 the length of the subtending leaf; peduncle 33–55 mm long i.e., c. 1/2–7/8 the length of the inflorescence, 1–2 mm wide, flattened; lateral branches 1or 2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 4.5 mm long x 5 mm wide. Calyx lobes hemi-orbicular, 0.8–1.3 mm long x 2.1–2.8 mm wide, apex rounded, indumentum sparse externally, dense near base internally, moderately dense to sparse near apex, hypanthium 1.5–1.8 mm long, prolonged c. 0.8–1.6 mm above the ovary, indumentum dense externally near base, moderately dense distally, dense internally; disk c. 2.8–3.4 mm diameter, indumentum dense. Stamens 98–189 per flower; filament abruptly narrowed to point of insertion, anthers 0.5–0.6 mm long, apex truncate, rounded or obtuse, vertical displacement of thecae slight, thecal margins recurved after dehiscence, effective dorsal opening the whole length of the anther, residual septum visible, oblique. Style c. 9 mm, with moderately dense indumentum in lower 1/2; stigma distinct, capitate. Ovary c. 1–1.7 mm long, 4-locular, ovules 2 per locule. *Fruit* depressed globose, 12–13 mm diameter, crowned with the connivent to erect calyx lobes. Mature seed 2–4 per fruit, c. 7–8 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 29) and ecology.** *Gomidesia schaueriana* occurs in southeastern Brazil from Rio de Janeiro south to the northern part of Rio Grande do Sul at altitudes of 5 to 1000 m. The southern limit appears to be near the town of Osório. *Gomidesia schaueriana* has been collected in a variety of habitats including river margins, várzea forest, mata atlântica, bamboo copse (taquaral), cloud forest,wet woodland and copses and, occasionally, restinga.

**Phenology.** Flowering may begin as early as November but the main flowering period for this species is from December to February. Mature fruit have been collected from April to August.

**Specimens examined. BRAZIL.** **PARANÁ:** Mun. Guaratuba, Rio da Divisa, 10 m, 14 Dec 1963, *Hatschbach 10823* (B!); Mun. Paranaguá: Picadão Cambará - Col. Limeira, 10 m, 21 Nov 1967, *Hatschbach 17897* (MG!, MO!, NY!, UEC!); Mun. Cerro Azul: Morro Grande, 27 Jan 1970, *Hatschbach 23438* (C!, K!, MO!, NY!, RB!, S!, US!); Mun. Guaraqueçaba, Rio Murato, 7 Dec 1972, *Hatschbach 30946* (C!, K!, MO!, S!); Colônia Pereira, (mun. Paranaguá), 15 m, 29 Dec 1988, *Hatschbach 52559* (HRB!); Mun. Campina Gde. do Sul. Jaguatirica, Rio Capivary, 16 Dec 1962, *Hatschbach 9685* (B!, U!); Serra Capivari Grande (mun. Campina Grande do Sul), 4 Feb 1985, *Oliveira 841* (HRB!); Mun. S. José dos Pinhais, Col. Santos Andrade, 17 Sep 1985, *Oliveira 927*

(MO!, UEC!); Candeias (Mun. Guaratuba), 23 Dec 1991, *Silva 1066* (HRB!). **RIO GRANDE DO SUL:** Torres, Passo de Torres, Feb 1987, *Hagelund s.n.* (F!); Faz. do Arroio p. Osório, 4 Jan 1950, *Rambo 45124* (PACA!); Lagoa da Pinguela p. Osório, 8 May 1950, *Rambo 47054* (PACA!); Lagoa dos Quadros p. Torres, 18 Jan 1951, *Rambo 49747* (B!); Morro Grande p. Osório, 10 Jan 1952, *Rambo 51767* (PACA!); Torres, 11 Feb 1954, *Rambo 54837* (B!, PACA!); Lagoa da Pinguela, Osório, 17 Jan 1961, *Sehnem 3591* (HUCS!, PACA!); Osório, Lagoa de Malvas, 17 Jan 1951, *Sehnem 5591* (HUCS!, PACA!); Faxinal, Torres, 22 Dec 1979, *Waechter 1508* (F!). **RIO DE JANEIRO:** Tijuca, Estr. da Vista Chineza, 25 Aug 1985, *Angeli 694* (NY!); Mata do Pae Ricardo, 7 Jun 1943, *Clarindo s.n.* RB48183 (RB!); Guanabara, Vista Chineza, 12 Jan 1962, *Duarte 6217* (U!, RB! 132189, F!, NY!, US!, S!, UB!); Restinga de Jacarepaguá, Pedra de Itaúna, lado norte, 18 May 1973, *Fontenelle 13* (NY!, RB!); Province of Rio de Janeiro Cited in Glaziou's liste along with 65, 2584, 3005, 20320 with the localities Haut du Corcovado et Petrópolis, *Glaziou 657* (BR!, C!, K!, P!, US!); locality as 657, *Glaziou 2584* (BR! C!, K!, P!, R!); locality as 657, *Glaziou 3005* (BR! C!, K!, P!); Vista Chineza, 31 May 1943, *Guerra s.n.* RB57603 (RB!); Guanabara, Tijuca, Estrada da Vista Chinesa, 18 Jan 1960, *Martins 145* (F!, K!, NY!, SP!); Alto da Boa Vista, Estrada da Chinesa, 16 Jun 1981, *Martins & Fernandes 160* (NY!, RB!); Vista Chineza, 20 May 1958, *Pereira 3764* (RB!); Guanabara, Mesa do Imperador, 10 Aug 1937, *Rosa s.n.* RB80697 (NY!, RB!); Guanabara, Vista Chineza, 20 Feb 1936, *Rosa s.n.* RB 80770 (NY!, RB!). **SANTA CATARINA:** Vargem do Macário, Governador Celso Ramos, 5 m, 14 Dec 1971, *Bresolin 419* (HRB!); Mun. Camboriú, estrada que liga SC 486-Camboriú (entroncamento para salto) a 6 km do asfalto (SC 486), 1 Apr 1981, *Campos & P.F. Leite 36* (MG!); São João do Sul, 6 Sep 1977, *Hagelund 11519* (C!); São João do Sul, 23 Jan 1976, *Hagelund 9970* (C!); Capoeira no Hoffmann, Brusque, 30 Jun 1950, *Klein 118b* (US!); Morro da Ressacada, Itajaí, 150 m, 20 Feb 1956, *Klein 1875* (B!, NY!, PACA!, US!); Estação Florestal I. N. P., Ibirama, 300 m, 6 Mar 1956, *Klein 1889* (B!, NY!, PACA!, US!); Horto Florestal I.N.P., Ibirama, 250 m, 19 May 1956, *Klein 1993* (B!, BR!, F!, K!, PACA!); Horto Florestal I.N.P., Ibirama, 300 m, 14 Jun 1956, *Klein 2078* (PACA!, U!); Morro Costa da Lagoa. Ilha de Santa Catarina, Florianópolis, 250 m, 15 Feb 1967, *Klein 7230* (PACA!); Morro do Ribeirão, Ilha de S. Catarina. Florianópolis, 450 m, 14 Mar 1967, *Klein 7274* (PACA!); Morro do Ribeirão, Ilha de S. Catarina. Florianópolis, 400 m, 16 May 1967, *Klein 7407* (PACA!); Ratones, Ilha de S. Catarina, Florianópolis, 1000 m, 17 May 1967, *Klein 7418* (PACA!); Morro Costa da Lagoa, Ilha de S. Catarina. Florianópolis, 200 m, 22 Jun 1967, *Klein 7479* (HUCS!); Morro da Fazenda. Itajaí, 350 m, 12 Aug 1954, *Klein 816* (B!, NY!, PACA!, UB!, US!); Morro do Ribeirão, (mun.) Florianópolis, 500 m, 14 Feb 1969, *Klein 8214* (HUCS!, PACA!); Morro da Fazenda, Itajaí, 350 m, 28 Apr 1954, *Reitz & Klein 1814* (PACA!, U!); Pilões, Palhoça, 450 m, 20 Jan 1956, *Reitz 2554* (B!, BR!, K!, PACA!, US!); Pilões, Palhoça, 450 m, 24 Feb 1956, *Reitz 2745* (B!, F!, PACA!, SP!, US!); Brusque, 5 m, 4 Jan 1950, *Reitz 3231* (R!, S!); Campo do Massiambu, Palhoça, 5 m, 20 Dec 1952, *Reitz 5015* (NY!, PACA!, US!); Palhoça, 5 m, 22 Dec 1952, *Reitz 5041* (NY!, PACA!, US!); Campo Massiambu, Palhoça, 5 m, 14 May 1953, *Reitz & Klein* 598 (C!, K!, PACA!, US!);

Capoeira no Hoffmann. Brusque, 30 Jun 1950, *Veloso 118b* (RB!). **SÃO PAULO:** Iguape, Estação Ecológica Juréia-Itatins. Serra da Juréia, trilha do Imperador, em direção à Praia da Juréia, 24 Apr 1991, *Anunciação 50* (K!, SP!); Iguape, Estação Ecologica Juréia-Itatins. Margens do Rio Verde, 11 Mar 1992, *Aragaki 2* (K!, SP!); in the upper part of the ascent up the Serra de Cubatão - summit or Pico da Serra, 22 Dec 1826, *Burchell 3697* (K!); Iguape, proximidades da Serra da Juréia, Caminho do Imperador, 25 Apr 1990, *Catharino 1353* (SP!); Iguape, Estação Ecológica Juréia-Itatins. Serra da Juréia, trilha do Imperador, 16 Dec 1990, *Gomes da Silva 161* (K!, SP!); Iguape, Estação Ecológica Juréia - Itatins, caminho do Imperador, 15 May 1991, *Kawall 62* (K!, SP!); Iguape, Estação Ecológica Juréia-Itatins. Beira do Rio Verde, descendo em direção à foz, 19 Mar 1991, *Mamede 394* (K!, SP!); Salesópolis, na Estação Biológica de Boracéia, perto das margens do Rio Coruja, 27 Apr 1966, *Mattos 13493* (SP!); Ubatuba, 10 Oct 1967, Moreira de Souza s.n. (NY!); Santos, Sorococaba, Jan 1878, *Mosen s.n.* (P!); Santos, 25 Jan 1875, *Mosen 3380* (C!, P!); Iguape, Estação Ecológica Juréia-Itatins, caminho do Imperador, 14 Aug 1991, *Pereira 056* (SP!); Apiahy, *Puiggary 126* (P!, US!); Iguape, Estação Ecológica Juréia-Itatins, trilha para o alto do morro próximo ao alojamento, 25 Jun 1992, *Rossi 1051* (K!, SP!); Iguape, Estação Ecológica Juréia-Itatins, margem do Rio Verdes, 28 Nov 1991, *Rossi 965* (SP!).

**Local Names.** Guamirim, Guaramirim araçá, Guamirim facho (Santa Catarina). For other species known as Guamirim see under *G. fenzliana*. The name Guamirim facho appears to be used only for *G. schaueriana* while Guamirim araçá is also applied to *G. fenzliana*.

*Gomidesia schaueriana* is clearly closely related to *G fenzliana* and, judging by determination slips, some myrtologists treat the two names as synonymous, determining material from as far north as Bahia as *G. schaueriana*. Though there are intermediates, the majority of specimens can easily be referred to one or other species and the differing (but overlapping) distributions and ecological preferences support the recognition of two taxa. *Gomidesia fenzliana* differs from *G. schaueriana* in having broader, coricaceous leaves with rounded, obtuse or shallowly emarginate apices and (usually) many-flowered inflorescences. The flower buds of *G. fenzliana* tend to be slightly smaller than those of *G. schaueriana* and they lack the marked contrast seen in *G. schaueriana* between the density of the indumentum on the hypanthium and that on the calyx lobes. The diameter of the disk and of the mature fruit are also significantly smaller in *G. fenzliana* than in *G. schaueriana* (disk c. 2 mm in *G. fenzliana* and c. 3 mm in *G. schaueriana*; fruit c. 8 mm in *G. fenzliana* and c. 12 mm in *G. schaueriana*).

Legrand and Klein (1967) compared *G. schaueriana* to *G. fenzliana* and commented that obovate leaved forms of the former species, with apices rounded or only obtusely subacuminate look very like *G. fenzliana*. They considered that these forms can be distinguished mainly by the less coriaceous texture of the leaves in *G. schaueriana*, and by the inflorescences which are scarcely clothed in pilose hairs and a little narrower than those of *G. fenzliana*.

*Gomidesia fenzliana* is primarily a coastal species, most commonly collected in restinga vegetation, though inland populations occur in the north of its range. *Gomidesia schaueriana* is rarely reported from restinga, being more characteristic of the subtropcial Atlantic rain forest. Legrand and Klein (1967) commented that, on first sight, *G. schaueriana* might be taken for an ecological form of *G. fenzliana*, such are the similarities in bark, canopy shape and leaves. However they argue that if this were the case, one would expect the leaves of *G. schaueriana* to be larger than those of *G. fenzliana* since the former species is usually found in closed forest and is thus more shade-loving than *G. fenzliana* which is basically sun-loving.

**32. Gomidesia sellowiana** O.Berg *in* Martius, Fl. bras. **14 (1):** 21. 1857. Type. Brazil. São Paulo: *Houllet s.n.* (lectotype, BR!, here designated).

Fig. 48 (also 1B, 2E and 15p&q).

*Gomidesia hartwegiana* O.Berg *in* Martius, Fl. bras. **14 (1):** 22. 1857. Type. Brazil. Minas Gerais: *Widgren 544 1/2* (lectotype, S!, here designated; isolectotype, C!)
*Gomidesia sprengeliana* O.Berg, *in* Fl. bras. **14 (1):** 21. 1857. Type. Brazil. São Paulo: "in silvis Capões ad urbem Ypanema," *Martius s.n.* (holotype, M!).

*Shrub or treelet* 0.5–5 m tall. Branchlets 10 cm below the terminal bud 1.5–2 mm in diameter, rounded, more or less glabrous or with a scattered indumentum of erect, straight or curved, pale hairs to 0.5 mm or of variable length and orientation; terminal bud c. 5 mm long or proliferating, with a dense indumentum of appressed, straight, pale hairs to 0.8 mm long. Stipule lobes to 0.8–1.4 mm long. Inter-petiolar ridge absent. Petioles c. 4–5 mm long, 0.7–1 mm wide, flat or channeled with a sparse to moderately dense indumentum of appressed, straight or curved, pale or straw-coloured hairs to 0.5 mm. *Lamina* wide obovate or wide elliptic, 24–57 mm long, 9–28 mm wide, 1.4–2.1(–3) times as long as wide; apex rounded or obtuse or very shallowly emarginate, rarely acute then rounded at tip; base acutely or obtusely cuneate; margin flat or bent down or recurved; midrib sulcate or impressed near base above, flat near apex, prominent below; lateral veins straight, raised or slightly raised above, raised or (rarely) prominent below, diverging at c. 60–80 ° from the midrib; secondary laterals

FIG. 48. *Gomidesia sellowiana*. Plate 12 from Martius' Flora Brasiliensis **14 (1)**.

12.

GOMIDESIA Sellowiana.

composite, not or nearly equalling the laterals in prominence; marginal vein equalling or almost equalling the laterals in prominence and curving or looping between them; higher order venation conspicuous or distinct above, raised, conspicuous below, raised and paler than the lamina; venation between marginal vein and margin distinct. Indumentum sparse or absent above, consisting of appressed, straight or curved white hairs c. 0.2–0.4 mm, scattered or sparse below, consisting of appressed or ascending or erect, straight, straw-coloured hairs to c. 0.2–0.5 mm long. Gland dots indistinct above, or conspicuous and dark, conspicuous or distinct below, dark and slightly raised. Mature leaves coriaceous, not markedly bicolorous. *Conflorescence* comprising 1–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 11–> 100 flowers, 21–45 mm long, reaching c. 4/5–4/3 the length of the subtending leaf; peduncle 13–23 mm long i.e., c. 2/5–2/3 the length of the inflorescence, 0.5–1 mm wide, more or less terete or slightly compressed; lateral branches 2–5 below the terminal cyme or cluster of cymes. *Mature flower buds* 2.7–3.5 mm long x 2.2–3 mm wide. Calyx lobes depressed ovate or shallowly triangular, 0.6–0.7 mm long x 1–1.4 mm wide, apex obtuse but often appearing acute due to indument, with a dense to moderately dense indumentum of appressed, straight or curved, pale or brown hairs to 0.2–0.8 mm long externally, indumentum moderately dense internally, at least near apex, consisting of appressed, straight, pale hairs to 0.2 mm; hypanthium 1.4–1.8 mm long, prolonged c. 0.7–1 mm above the ovary with a moderately dense to dense indumentum of appressed, straight or curved, grey or brown hairs c. 0.2–1.2 mm; disk c. 1.2–1.6 mm diameter, indumentum dense. Stamens c. 60–94 per flower; anthers 0.5–0.55 mm long, filament slightly tapered or narrowing abruptly to point of insertion on connective or connective stub, apex truncate or shallowly emarginate, vertical displacement of thecae marked, thecal halves lose curvature on dehiscence, held parallel or slightly divergent, with margins slightly to strongly recurved, effective dorsal opening c. 1/3–1/2 the length of the anther, residual septum visible, oblique to transverse. Style c. 4 mm, with moderately dense indumentum in lower 1/3; stigma distinctly capitate, papillate. Ovary 0.4–0.75 mm long, bilocular, ovules 2 per locule. *Fruit* globose, 5.5 mm diameter, crowned with the erect calyx lobes. Mature seed 2 per fruit, c. 5 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 30) and ecology.** *Gomidesia sellowiana* is distributed from Minas Gerais to Rio Grande do Sul. I have seen no material of this species from Argentina, Paraguay or Uruguay. Records from these areas are erroneous and due largely to misidentifications of *G. palustris*. *Gomidesia sellowiana* is primarily an upland species with most records from 800 to 2100 m above sea level, and just a handful from 400–600 m above sea level. In Santa Catarina it is abundant in and considered characteristic of the *Araucaria* forest formations while it also occurs on hilltops in the Atlantic forest region. Further north *Gomidesia sellowiana* montane cloud forest and rain forest and in open rocky habitats at high altitude, including the *campos de altitude*.

**Phenology.** *Gomidesia sellowiana* flowers from November to April with peak flowering in January and February. There appears to be a second minor flowering epsiode in June. Fruiting collections have been made from June to December, with mature fruits being reported from October to December.

**Representative specimens examined. BRAZIL.** MINAS GERAIS: Parque Estadual de Ibitipoca / Lima Duarte, 23 Jun 1987, *Andrade 966* (RB!); Serra de Ibitipoca, 27 Sep 1970, *Krieger 9236/4* (RB!); Mun. Delfim Moreira. São Francisco dos Campos, 7 Jun 1950, *Kuhlmann 2449* (SP!); Caldas, 10 May 1874, *Mosen 1848* (S!); Mun. Pasa Quatro. Distrito de Pinheirinhos. Sertão dos Martins, 1600 m, Feb 1979, *Nunes 105* (RB!); Mun. Ouro Preto. Parque Estadual do Itacolomi, 1650 m, 7 Sep 1987, *Peron 270* (RB!); Mun. Ouro Preto. Riacho Tripui, entre ALCAN e Tripui, 8 Feb 1987, *Peron 48* (RB!); Mun. Ouro Preto, Estação Ecológica do Tripui, 1300 m, 15 Nov 1988, *Peron 741* (RB!); Caldas, Feb 1845, *Regnell 547 III* (P!, US!); Serra de Ibitipoca, Pico do Pião, 1590 m, 12 May 1970, *Sucre 6736* (NY!); Serra de Ibitipoca, 1615 m, 28 Sep 1970, *Sucre 7200* (RB!). PARANÁ: Mun. Morretes, Pico Olimpo, 1547 m, 15 Jan 1950, *Hatschbach 1735* (PACA!); Lageado, Mun. Campo do Tenente, 25 Jan 1968, *Hatschbach 18482* (US!); Mun. Campina Gde. do Sul. Pico Caratuva, 1950 m, 8 Feb 1968, *Hatschbach 18576* (MO!); Mun. Guarapuava: Cachoeira dos Turcos, 13 Feb 1969, *Hatschbach 21171* (MO!); Mun. Campina Gde. do Sul, Serra Capivari Grande, 1500 m, 8 Feb 1972, *Hatschbach 26307* (C!, NY!, S!, US!); Mun. Colombo, Capivary, 23 Jan 1963, *Hatschbach 9660* (B!); União da Vitória, 29 Dec 1967, *Koczicki 43* (MU!); Mun. Quatro Barras, Morro Mãe Catira, *Kummrow & F.J. Zelma 2684* (US!); Curitiba - Mandirituba, 14 Jan 1964, *Pereira 8319* (RB!); Guarapuava, Rio Coitinho, 1000 m, 15 Dec 1965, *Reitz & Klein 17683* (B!, NY!, P!, US!); Morro 7 (mun. Quatro Barras), 6 Jun 1989, *Ribas 124* (HUEFS!). RIO DE JANEIRO: Locality not stated, *Capell s.n.* (RB!); locality not stated, 1821, *Langsdorff s.n.* (P!); Mun. Santa Maria Madalena, Parque Estadual do Desengano, Pedra do Desengano, 1785 m, 5 Oct 1988, *Martinelli 13132* (K!); Mun. Santa Maria Madalena, Parque Estadual do Desengano, Pedra do Desengano, vertente NW, 1750 m, 20 Dec 1988, *Martinelli 13240* (RB!); Parque Estadual do Desengano, Pedra do Desengano, 1825 m, 28 Jun 1989, *Martinelli 13356* (RB!). RIO GRANDE DO SUL: Lageadinho p. Bom Jesus, Feb 1958, *Camargo 3131* (PACA!); Cambará do Sul. Itaimbezinho, 6 Feb 1983, *Jarenkow s.n.* (SPF!); Serra da Rocinha p. Bom Jesus, 14 Jan 1942, *Rambo 8731* (PACA!); Bom Jesus, arr. Cap. Grande, 16 Jan 1942, *Rambo 8970* (PACA!); Serra do Fachinal, p. São Francisco de Paula, 14 Feb 1946, *Rambo 32132* (PACA!); Tainhas p. São Francisco de Paula, 17 Feb 1946, *Rambo 32319* (PACA!); Serra da Rocinha p. Bom Jesus, 28 Feb 1946, *Rambo 32453* (PACA!); Serra da Rocinha, p. Bom Jesus, 14 Feb 1947, *Rambo 35294* (PACA!); Cambará p. São

Francisco de Paula, Feb 1948, *Rambo 36801* (PACA!); Faz. Englert, p. São Francisco de Paula, 8 Feb 1941, *Rambo 4470* (PACA!); Serra da Rocinha, p. Bom Jesus, 18 Jan 1950, *Rambo 45323* (PACA!); Taimbesinho, p. São Francisco de Paula, 30 Jan 1950, *Rambo 45561* (PACA!); Sta. Rita p. Farroupilha, 13 Mar 1950, *Rambo 46265* (PACA!); Taimbesinho p. S. Fr. de Paula, 18 Dec 1950, *Rambo 49395* (B!, S!); Taimbesinho, p. São Francisco de Paula, 21 Feb 1951, *Rambo 50060* (PACA!); Taimbesinho, p. São Francisco de Paula, 21 Feb 1951, *Rambo 50146* (PACA!); Taimbesinho, p. S. Fr. de Paula, 21 Feb 1951, *Rambo 50154* (B!); Passo do Socorro p. Vacaria, 26 Dec 1951, *Rambo 51440* (PACA!); Passo do Socorro p. Vacaria, 28 Dec 1951, *Rambo 51703* (PACA!); Jaquirana, p. S. Fr. de Paula, 20 Feb 1952, *Rambo 52023* (PACA!, S!); Morrinhos p. São Francisco de Paula, 7 Feb 1952, *Rambo 52127* (PACA!, S!); Serra da Rocinha p. Bom Jesus, 3 Feb 1953, *Rambo 53796* (PACA!); Taimbesinho, p. S. Fr. de Paula, 20 Feb 1953, *Rambo 53939* (S!); Faz. Englert p. S. Fr. de Paula, 1 Jan 1954, *Rambo 54739* (B!); Vila Oliva, p. Caxias, 8 Feb 1955, *Rambo 56637* (PACA!); Taimbesinho, p. São Francisco de Paula, 950 m, 24 Feb 1951, *Sehnem 5652* (PACA!, B!); Serra do Fachinal, p. São Francisco de Paula, 23 Feb 1951, *Sehnem 5653* (PACA!); Bom Jesus, a ca. de 15 km da cidade na rodovia para Vacaria, 5 Feb 1985, *Silveira 2073* (RB!, R!); Cambará do Sul, na estrada para a Fortaleza a cerca de 4 km da cidade, 18 Mar 1983, *Silveira 560* (RB!); Faxinal, Cambará do Sul, Mar 1986, *Sobral 5066* (SPF!); André da Rocha, Nova Prata, Aug 1984, *Stehmann s.n.* (F!); Esmeralda, Fazenda da Guabiroba, 850 m, 12 Sep 1987, *Wasum 3205* (HUCS!, MO!, NY!, US!). SANTA CATARINA: Mun. Lajes, Índios, 950 m, 16 Dec 1967, *Lourteig 2240* (P!, US!); Perto de Ponte Alta na estrada para Rio do Sul, 29 Jan 1964, *Pereira 8719* (RB!); Lages, 10 Jan 1951, *Rambo 49612* (PACA!); Lages, 10 Jan 1951, *Rambo 49613* (PACA!); Morro do Campo Alegre, São Francisco do Sul, 1300 m, 7 Oct 1960, *Reitz 10075* (B!, BR!); Serra da Boa Vista, São José, 1000 m, 24 Jan 1961, *Reitz & Klein 10708* (B!); Serra da Boa Vista, São José, 1000 m, 2 Mar 1961, *Reitz 10790* (US!); Pilões, Palhoça, 450 m, 3 May 1956, *Reitz 3214* (B!, NY!, US!); Morro Spitzkopf, Brusque, 360 m, 9 Mar 1950, *Reitz 3452* (PACA!, S!, US!); Morro do Iquererim, Campo Alegre, 1500 m, 5 Sep 1957, *Reitz 4771* (B!, NY!, US!); Capetinga, Campo Ere, Chapeco, Jan 1952, *Reitz 4790* (PACA!, S!, US!); Morro do Iquererim, Campo Alegre, 1500 m, 18 Oct 1957, *Reitz 5232* (US!); Serra da Boa Vista, S. José, 1200 m, 24 Oct 1957, *Reitz 5387* (US!); Mata, Serra da Boa Vista, S. José, 1200 m, 24 Oct 1957, *Reitz & Klein 5406* (K!, US!); Serra da Boa Vista. S. José, 1300 m, 2 Feb 1953, *Reitz 5455* (PACA!, US!); Serra da Boa Vista, S. José, 1100 m, 4 Feb 1953, *Reitz 5489* (K!, NY!, PACA!, US!, W!); Morro do Iquererim, Campo Alegre, 1300 m, 10 Jan 1958, *Reitz 6129* (U!, HBR 15133, US!, PACA!); Morro do Iquererim, Campo Alegre, 1300 m, 5 Feb 1958, *Reitz 6433* (US!, PACA!); Serra da Boa Vista, S. José, 1000 m, 7 Sep 1960, *Reitz 9841* (NY!); Taimbesinho - Ararangua, 900 m, 15 Feb 1956, *Reitz C1515* (S!); Morro do Baú, Itajaí, 850 m, 29 Jan 1948, *Reitz C2060* (S!); Mun. Campo Alegre, pinheiral. upper fazenda of Ernesto Scheide, Campo Alegre, 1000 m, 1 Feb 1957, *Smith 10569* (R!, US!); Mun. Porto União: Pinheiral between Matos Costa and Calmon (22 km). 47 km S. of P.U, 1000 m, 5 Feb 1957, *Smith 10861* (US!); Mun. Caçador. Pinheiral 17 km north of Caçador, 1025 m, 7 Feb 1957, *Smith 10984* (R!, US!); Mun. Lajes, pinheiral, 2 km east of Índios, 850 m, 11 Feb 1957, *Smith & R. Klein 11235* (R!, US!); Mun. Lajes, 13 km east of Capão Alto, 950 m, 12 Feb 1957, *Smith 11328* (R!, US!); Mun. Videira: Mixed forest, Parque da Uva, 750 m, 26 Oct 1964, *Smith 12970* (F!, NY!, R!, US!); Mun. Campo Alegre: Campo and pinheiral, 4 km south of Campo Alegre on the road to Jaraguá do Sul, 950 m, 6 Nov 1956, *Smith 7325* (B!, R!, RB!, US!); Mun. Lajes, forest 3 km along the Estrada de Rodagem Federal, south of Lajes, 900 m, 3 Dec 1956, *Smith 8124* (B!, F!, P!, R!, RB!, US!); Low gallery forest above general tree line. Mun. Campo Alegre, slopes of Morro Iquererim, 1400 m, 9 Dec 1956, *Smith 8516* (R!, US!); Mun. Caçador, Pinheiral, 8 km north of Caçador, 1025 m, 21 Dec 1956, *Smith 8972* (R!, S!, US!); Mun. Jocaba, pinheiral, campos of Palmas, 77 km west of Caçador, 24 Dec 1956, *Smith & Reitz 9193* (R!, US!); Mun. Xanere, Pinheiral and ruderal 17 km north of Abelardo Luz, 550 m, 25 Dec 1956, *Smith 9198* (US!); Mun. Chapeco: Campo. Fazenda Campo São Vicente, 24 km west of Campo Ere, 950 m, 27 Dec 1956, *Smith 9336* (US!); Mun. Chapeco, pinheiral. Fazenda Campo São Vicente, 24 km west of Campo Ere, 950 m, 27 Dec 1956, *Smith 9519* (R!, US!). **SÃO PAULO:** Mun. Atibaia. Pedra Grande, 1300 m, 21 Nov 1989, *Bernacci 21012* (UEC!); about the village of São Bernardo, 18 Jan 1827, *Burchell 3974* (K!); São Paulo, about 1m. NW by N from the Tanque de Zunica as far as the Caveira Santa, 3 Feb 1827, *Burchell 4136* (FHO!, K!, P!, US!); at Morumbe, 4 Mar 1827, *Burchell 4381* (K!); Morumbe, 9 Mar 1827, *Burchell 4469-2* (K!); locality not indicated, 1833, *Gaudichaud 698* (P!); Route Santos a St. Paul, Jan 1839, *Guillemin 296* (P!); São Paulo, Alto da Lapa, 13 Mar 1947, *Hoehne s.n.* (K!, SPF 13515, F!); Alto da Lapa. Cap. S. Paulo, 11 Feb 1947, *Hoehne 13609* (SPF!); Butantã, 16 Feb 1950, *Joly 872* (NY!); perto do km 71 da Rodovia Santa Izabel-Igaratá, 13 Dec 1964, *Mattos 12155* (SP!); Cunha, 1 km ao norte de Paraibuna, na cabeceira do Rio Paraibuna, 12 Jun 1968, *Mattos 15325* (SP!); Mun. Moji das Cruzes: 1.5 km NW de Moji das Cruzes, 28 Aug 1960, *Mattos & N.F. Mattos 8142* (US!, MO!); Campos do Jordão, 1570 m, 21 Nov 1980, *Rubens 197* (HRB!, R!); locality not indicated, 12 Feb 1906, *Usteri 153b* (K!).

**Local names.** Guamirim (Santa Catarina). For other species of *Gomidesia* known by this name see under *G. affinis*.

*Gomidesia sellowiana* has often been confused with and misidentified as *G. palustris*. The differences between the species are discussed under *G. palustris*. Although much has been made of the similarities between *G. palustris* and *G. sellowiana* (e.g. Legrand & Klein, 1967) in this study I found the distinction between *G. pubescens* and *G. sellowiana* much more problematic. Characters useful for distinguishing these species are outlined under *G. pubescens*. In the northern part of its range, material of *G. sellowiana* is frequently misidentified as *Myrcia itambensis*. Apart from the differences in anther morphology, these species are easily distinguished by examining the venation on the abaxial surface of the leaf -

the reticulum is conspicuous in *G. sellowiana* but indistinct or apparently absent in *M. itambensis*.

**33. Gomidesia sonderiana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 533. 1859. Type. Brazil. Rio de Janeiro: *Riedel 351* (neotype, LE!, here designated; isoneotypes, LE! (2 sheets), P!).

*Myrcia dolichopetala* Kiaersk., Enum. Myrt. bras. 106. 1893. *nom. illeg. superfl.*

*Shrub 2–3* m tall. Branchlets 10 cm below the terminal bud 2 mm in diameter, terete, glabrous with outer bark exfoliating in semicylindrical pieces exposing pale smooth inner bark or with a sparse to moderately dense indumentum of appressed, straight, greyish hairs to 0.4 mm long; terminal bud 6–14 mm long or proliferating with a dense indumentum of appressed, straw-coloured or brownish hairs. Stipule lobes to 0.8 mm long. Inter-petiolar ridge distinct or indistinct. Petioles 4–7 mm long, c. 1.2 mm wide, channeled with a moderately dense to dense indumentum of reddish-brown hairs of mixed lengths to 0.6 mm. *Lamina* narrowly oblong, elliptic or narrowly elliptic, 96–139 mm long, 30–41 mm wide, 2.6–3.4 times as long as wide; apex acuminate, sometimes abruptly so; base rounded cuneate or decurrent; margin flat or bent-down; midrib sulcate or impressed above, prominent below; lateral veins more or less straight or sharply down-curved near midrib, raised above and below, diverging at c. 70–80° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving or looping between them; higher order venation distinct, very slightly raised above and below; venation between marginal vein and margin distinct, submarginal vein usually visible. Indumentum absent or scattered above consisting of appressed, white hairs of varying length and orientation, absent or scattered below, consisting of appressed, straight or curved, brownish hairs to 0.8 mm long intermixed with some Type II hairs??. Gland dots distinct or indistinct above, indistinct below, dark and slightly raised. Mature leaves chartaceous. *Conflorescence* comprising 2–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 3–17 flowers, 27–30 mm long, reaching c. 1/4–1/3 the length of the subtending leaf; peduncle 14–16 mm long i.e., c. 1/2 the length of the inflorescence, 1–2 mm wide, flattened; lateral branches 1 or 2 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 5 mm long x 4 mm wide. Calyx lobes shallowly triangular, 1.4 mm long x 2.2–2.3 mm wide, apex acute or rounded though sometimes appearing apiculate due to indumentum, with a dense indumentum of straight hairs up to 1 mm long externally, indumentum shorter and less dense internally; hypanthium more or less pentagonal in cross-section, c. 2.4 mm long, prolonged c. 1.6 mm above the ovary with a dense indumentum internally and externally consisting of more or less appressed, straight or curved, pale hairs to c. 0.5 mm; disk c. 1.4 mm diameter, with a dense indumentum of very short (Type II?) hairs. Stamens c. 86–94 per flower; anthers c. 0.8 mm long, including connective stub, filament tapering to a very fine thread towards the well-defined connective stub, apex shallowly to deeply emarginate, thecal halves retain curvature after dehiscence, held parallel after dehiscence, vertical displacement of thecae marked, thecal margins flat or slightly recurved after dehiscence, effective dorsal opening 1/3–1/2(–2/3) the length of the anther, residual septum rarely visible, more or less vertical. Style c. 8 mm, with dense indumentum in lower 1/3, moderately dense to sparse indumentum in middle 1/3, glabrous and conspicuously glandular in upper 1/3; stigma minutely capitate, distinctly papillate. Ovary c. 1.5 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 13 mm diameter, crowned with some or all of the calyx lobes which abscise as the fruit matures. Mature seed 1 per fruit, testa pale, hypocotyl densely sericeous.

**Distribution (Map 31) and ecology.** Known only from the state of Rio de Janeiro.

**Phenology.** Flowering collections have been made in November and December.

**Specimens examined. BRAZIL. RIO DE JANEIRO:** Itaipuaçu, Pico Alto Moirão, 25 Nov 1981, *Andreata 307* (RB!); Itaipuaçu, Pico Alto Moirão, 16 Nov 1983, *Andreata 617* (RB!); locality not stated, *Gaudichaud 765* (P! (2 sheets)); Pão de Assucar, 5 Dec 1948, *Palacios-Balegno-Cuezzo 2892* (R!); locality not stated, *Riedel 351* (LE! (3 sheets). P!).

Like most of the new taxa of *Gomidesia* which Berg published in 1859, *G. sonderiana* was based on a Riedel collection seen in 'hb. hort. bot. Petrop.' for which no number was cited. Unusually, the material studied was in fruit. On reading Berg's detailed description of *G. sonderiana* I was reminded of *Riedel 351*, annotated by Berg with the unpublished name *G. anacardiaefolia* var. *acuminata*. This material had puzzled me from the outset of this study as I considered it to represent a distinct species, bearing little resemblance to *G. anacardiifolia*. I have since examined 4 sheets of *Riedel 351* (3 from LE and one from P) and found them to correspond closely to Berg's description of *G. sonderiana*. Further support for the idea that *G. sonderiana* was based on *Riedel 351* is provided by the manner in which Berg numbered his new taxa and indicated where they should be inserted in his published classification. *Gomidesia sonderiana* was numbered 8b with the direction 'ante *Gomidesiam ancardiaefoliam* inseratur', a placement entirely appropriate for a taxon which Berg considered to be so closely allied to *G. anacardiifolia* that he had earlier contemplated treating it as a variety of that polymorphic species. Thus there is a strong probability that *Riedel 351*, annotated by Berg as ' *G. anacardiaefolia* d *acuminata*' later formed the basis for *G. sonderiana*. It must be acknowledged, however, that the case has not been proved beyond doubt and that one further piece of evidence might be interpreted as pointing to another conclusion entirely. One of the sheets of *Pohl 1022* here designated lectotype of *G. reticulata* var. *angustifolia* bears the annotation ' *G. sonderiana*' in Berg's hand but this annotation has been crossed out and corrected to *G. reticulata*, also in Berg's hand. Initially I was tempted to interpret this as an indication that *G. sonderiana* might resemble *G. reticulata*. However, in the light of similar situations where Berg changed his mind on paper, I eventually concluded that no great significance should be attached to the slip. For instance, material initially annotated by Berg as *G. langsdorffii* was later corrected by him to *G. eriocalyx*, but it is extremely unlikely that Berg confused these two species which differ in almost every respect. On the balance of the evidence I consider it almost certain that *Riedel 351* is the type of *G. sonderiana*. I have seen no material determined as *G. sonderiana* apart from the single sheet mentioned above. As far as I can establish the name has never been taken up since it was published in 1859.

Kiaerskou (1893) transferred *G. sonderiana* to *Myrcia* (along with all the other species of *Gomidesia* studied by him). He published the new name *M. dolichopetala*, explaining that this was necessary because of the existence of *Aulomyrcia sonderiana* which he transferred to *Myrcia* in the same publication. However since he also published the new name *Myrcia rabeniana* for *Aulomyrcia sonderiana* he failed to take up the epithet *sonderiana* which was still available in *Myrcia* and thus both new names in *Myrcia* are superfluous and illegitimate. I have not seen the Riedel collection (herb. hort. Petropolit. 1298) cited by Kiaerskou but, since the description he provides is of flowering material, it cannot have been based on the material seen by Berg in fruit.

In summary, *Riedel 351* corresponds closely to the description of *G. sonderiana* but cannot be demonstrated with certainty to be the original material on which that species was based. In order to preserve what I believe to be the original and only sense in which the name has been applied I intend to designate *Riedel 351* as neotype of *G. sonderiana*.

The distinct connective stub and the sericeous hypocotyl indicate that *G. sonderiana* is referrable to the *G. spectabilis* group. However, its affinities within that group remain unclear.

**34. Gomidesia spectabilis** (DC.) O.Berg, Linnaea **27:** 7. 1855.

*Myrcia spectabilis* DC., Prodr. **3:** 248. 1828. Type. Brazil. Rio de Janeiro: "in sylvis locis editis secus Viam publicam Paulinam," *Martius s.n.* (holotype, M!).

Fig. 49 (also 11f-h).

*Myrcia browniana* Gardner, Hooker's London Journal of Botany **2:** 354. 1843. Type. Brazil. Rio de Janeiro: *Gardner 423* (lectotype K!, here designated; isolectotype, K!).

*Gomidesia browniana* (Gardner) O.Berg, Linnaea **27:** 7. 1855.

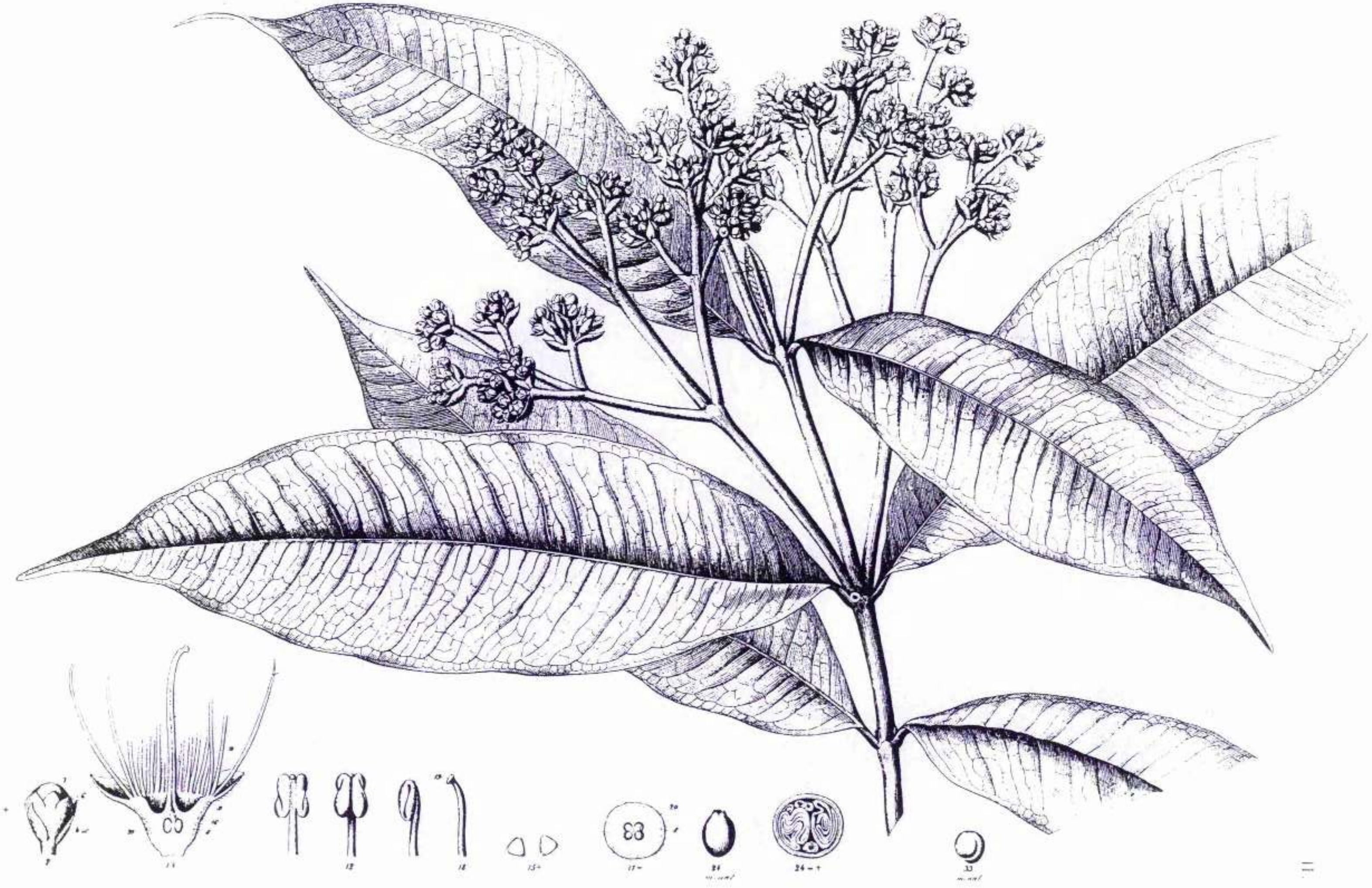
*Gomidesia spectabilis* var. *genuina* O.Berg, *in* Martius, Fl. bras. **14 (1):** 13. 1857. Inadmissible name to be replaced by *G. spectabilis* var. *spectabilis*. Berg treated the type of *G. spectabilis* as var. *genuina*.

*? Gomidesia spectabilis* var. *farinosa* O.Berg, *in* Martius, Fl. bras. **14 (1):** 12. 1857. Type. Brazil. Rio de Janeiro: "prope Venda de Batatas," *Beyrich s.n.* (holotype, B, n.v., presumed destroyed).

*? Gomidesia spectabilis* var. *ovata* O.Berg, *in* Martius, Fl. bras. **14 (1):** 12. 1857. Type. Brazil. Rio de Janeiro: *Gaudichaud s.n.* (holotype 'hb. Kunth', n.v.; possible isotype, P!)

*Tree, treelet* or *shrub* to (2.5–)4–8(–10) m tall. Branchlets 10 cm below the terminal bud c. 5 mm in diameter, rounded or slightly flattened and channeled,with a farinaceous surface overlaid with a moderately dense to dense indumentum of appressed or erect or ascending, straight or curved, whitish, dark-based hairs to 6 mm; terminal bud c. 30 mm long or proliferating. Stipule lobes to 1.2 mm long, soon caducous. Inter-petiolar ridge conspicuous. Petioles 6–7 mm long, 1.5–3 mm wide, channeled. *Lamina* narrowly elliptic to oblong, 150–320 mm long, 41–65 mm wide, 3.2–4 times as long as wide; apex acuminate to long-acuminate; base obtuse or rounded with margin decurrent onto petiole and minutely auriculate; margin flat or bent down; midrib flat or impressed and channeled above, prominent below; lateral veins more or less straight, flat or very slightly raised above and paler than the blade, slightly raised below, more conspicuous than the secondary laterals and easy to distinguish from them, diverging at c. 60–65° from the midrib; secondary laterals composite, not equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation just discernible above, distinct and very slightly raised below; venation between marginal vein and margin distinct, sub/paramarginal vein distinct. Indumentum moderately dense above consisting of appressed, fine, white hairs soon falling, moderately dense below, consisting of farinaceous hairs, especially on the veins admixed with scattered straight hairs of irregular posture up to 1 mm long. Gland dots not

FIG. 49. *Gomidesia spectabilis*. Plate 11 from Martius' Flora Brasiliensis **14 (1)**.



GOMIDESIA spectabilis, β genuina.

distinct above, occasionally distinct below. Mature leaves chartaceous. *Conflorescence* comprising two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid (or rarely a metabotryoid) c. 9–90 flowers, 40–130 mm long, reaching c. 1/3–1/2 the length of the subtending leaf; peduncle 25–40 mm long i.e., c. 2/5 to 2/3 the length of the inflorescence, 2–4 mm wide, flattened; lateral branches 1–4 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 4.5–6(–7) mm long x 3.5–5 mm wide. Calyx lobes broadly triangular to suborbicular, 1.8–2.3 mm long x 2.7–3 mm wide, apex obtuse, acute or apiculate, sometimes asymmetrically so, with a dense indumentum externally, more or less glabrous internally except for sparse hairs near apex and a band of puberulence near base; hypanthium to 3.8 mm long, prolonged c. 1.7 mm beyond the summit of the ovary, with a very dense appressed indumentum internally and externally; disk c. 2.4–3 mm diameter, indumentum dense. Stamens c. 100 per flower; anthers 1.2 mm long, apex truncate or very shallowly emarginate, vertical displacement of thecae marked to slight, thecal halves retaining curvature after dehiscence, sometimes gaping, thecal margins flat or very slightly recurved after dehiscence, connivent, effective dorsal opening up to 2/3 the length of the anther, residual septum occasionally visible, connective extends below the thecae, filament tapered to point of insertion. Style c. 8 mm, with a dense indumentum in lower 1/3, becoming sparsely pubescent distally and glabrous in the distal 1/4; stigma not distinct. Ovary 1.7–1.8 mm long, bilocular, ovules 2 per locule. *Fruit* ellipsoid, 11–14 mm diameter, up to 20 mm long, crowned with the connivent calyx lobes leaving only a small aperture through which the disk is visible. Mature seed one (to three) per fruit, c. 13 mm long, testa pale or dark, hypocotyl densely sericeous.

**Distribution (Map 32) and ecology.** *Gomidesia spectabilis* is frequent in SE Brazil from the states of Rio de Janeiro and São Paulo south through Paraná to Santa Catarina at altitudes of 10–1100 m above sea level. The most northerly collection seen for this study was from an apparently disjunct population in eastern Minas Gerais while the most southerly collections seen by this author are from Santa Catarina. Legrand and Klein (1967) report collections from the extreme south of the state of Santa Catarina but it appears that the species has not yet been recorded over the border in Rio Grande do Sul (Mattos, 1989). Over most of its range *G. spectabilis* occurs as a characteristic species of the middle layer of the Atlantic Coastal Forest and it is often one of the most important species in this stratum, especially in the most humid areas. However, in Paraná *G. spectabilis* is frequently collected in restinga vegetation where it may occupy the niche that *G. martiana* fills further north. Legrand and Klein were probably referring to the same habitat when they highlighted the abundance and frequency of *G. spectabilis* in the quaternary plains along the coast in the area between Tubarão and Torres

**Phenology.** Most flowering collections were made in January but flowering may begin in December and continue through February and into March. Fruiting collections have been made from March through to December with peak fruiting from April to August and mature fruit being reported from June onwards.

**Representative specimens examined. BRAZIL.** **MINAS GERAIS:** Estação Experimental Coronel Pacheco, 20 Dec 1940, *Heringer 532* (RB!, SP!). **PARANÁ:** Volta Grande, 7 Aug 1911, *Dusen s.n.* (S!); Morretes, Marumby, regio Casilaris, 14 Aug 1911, *Dusen s.n.* (S!); Serra do Mar, Itupava, 17 Sep 1908, *Dusen 6724* (S!); Mun. Morretes, Entre Pilão de Pedra e Cabrestante, 27 Feb 1965, *Hatschbach 12404* (NY!, US!); Mun. Antonina, Rio Cotia, 16 Sep 1965, *Hatschbach 12768* (NY!, US!); Mun. Antonina, Rain forest along road Cacatu-Serra Negra above Antonina, 19 Jan 1966, *Hatschbach & Lindeman 13550* (K!, NY!, U!, US!); Mun. Guaraqueçaba, Serrinha, 100 m, 6 Jul 1967, *Hatschbach 16682* (US!); Mun. Paranaguá, Rio das Pombas, 25 Jul 1967, *Hatschbach 16774* (US!); Mun. Guaraqueçaba, Fda. Abobreira, 35 m, 15 Dec 1967, *Hatschbach 18149* (MO!, US!); Mun. Guaratuba, Serra de Araraquara, 35 m, 21 Dec 1967, *Hatschbach 18165* (F!, MO!, NY!, P!, S!, US!); Mun. Paranaguá, Rio Cachoeira, 1 km abaixo do Pico Torto, 400 m, 18 Jan 1969, *Hatschbach 20834* (C!, NY!, US!); Mun. Guaraqueçaba, Serra Negra, 35 m, 8 Jan 1970, *Hatschbach 23310* (C!, NY!); Mun. Guaraqueçaba, Rio do Cerco, 13 m, 5 Feb 1971, *Hatschbach 26280* (C!, S!); Mun. Antonina. Sapitanduva, 20 May 1973, *Hatschbach 32175* (UEC!); Mun. Morretes, Rio Bromado, 24 Jan 1979, *Hatschbach 41951* (NY!, SPF!, UEC!); Mun. Guarequeçaba, Tagacaba, 8 May 1985, *Hatschbach 49347* (MG!); Mun. Antonina: Res. Biol. de Sapitanduva, 6 Jun 1985, *Hatschbach 49389* (MG!, MO!); Mun. Campina Gde. Sul, Serra do Espia, 1000 m, 20 Jan 1963, *Hatschbach 9852* (B!, U!); Mun. Paranaguá. Sítio do Meio, 10 m, 26 Jan 1963, *Hatschbach 9870* (B!, F!, U!); Serra do Mar, Volta Grande, 400 m, 3 Jul 1914, *Jonsson 621a* (S!). **RIO DE JANEIRO:** Tijuca, Estr. da Vista Chineza, 15 Jan 1960, *Angeli 74* (F!); Mun. Silva Jardim, Res. Biol. Poço das Antas, 24 Oct 1979, *Araújo 3356* (GUA!); Mun. Silva Jardim, Reserva Biológica de Poço das Antas, 8 Nov 1979, *Araújo 3415* (GUA!); Environs de Rio de Janeiro. Theresópolis, 22 Mar 1880, *Glaziou 12008* (BR!, C!, K!, LE!, P!); *Glaziou 2586* (BR!, C!, R!); Mun. Magé, ca. 3 km ESE de Santo Aleixo, 7 Apr 1984, *Guedes 728* (RB!); Serra do Tinguá, 7 Apr 1944, *Guerra s.n. RB55437* (RB!); Reserva Biológica Poço das Antas, *Guimarães 1410* (RB!); Floresta da Tijuca, near chapel, 13 Jan 1982, *Landrum 4123* (MO!, NY!, US!); Mun. Nova Friburgo, Distrito Macaé de Cima, estrada para o Sítio Sophronites, 1100 m, 6 Jun 1989, *Lima 3585* (NY!); Estrada de Vista Chinesa entre o no 510 e a curva do Surucuçu à beira do riacho, Jun 1985, *Oliveira 5* (GUA!); Inhumirin et Mandiocca, 1823, *Riedel s.n.* (NY!); Theresópolis, 13 Mar 1917, *Sampaio 1656* (R!, US!). **SANTA CATARINA:** Porto das Canoas. S. Francisco, 15 Jun 1951, *Klein 16e* (US!); Morro da Ressacada, Itajaí, 100 m, 24 Jan 1956, *Klein 1817* (PACA!); Horto Florestal I.N.P., Ibirama, 450 m, 15 Jun 1956, *Klein 2111* (PACA!, U!); Mata do Hoffmann, Brusque, 50 m, 13 Jan 1950, *Klein 37* (NY!); Porto das Canoas, S. Francisco do Sul, 30 m, 15 Jun 1951, *Klein 45* (PACA!); Morro da

Ressacada, Itajaí, 100 m, 24 Jan 1956, *Klein 1817* (PACA!); Cunhas, Itajaí, 15 m, 4 Jan 1955, *Klein 965* (PACA!, NY!, US!); Azambuja, Brusque, 35 m, *Reitz 2203* (K!, NY!, PACA!, S!, U!, US!, W!); Três Barras, Garuva, S. Francisco do Sul, 60 m, 22 Jun 1957, *Reitz 4481* (PACA!); Sabiá, Vidal Ramos, 750 m, 28 Jan 1958, *Reitz 6327* (NY!, PACA!, US!); Três Barras, Garuva, S. Francisco do Sul, 50 m, 17 Apr 1958, *Reitz 6675* (B!, NY!, PACA!, US!); Brusque, Mata do Hoffmann, 27 Apr 1950, *Veloso 6* (RB!). **SÃO PAULO:** Iguape, Estação Ecológica Juréia-Itatins, Serra da Juréia, 25 Apr 1991, *Carvalhaes 18* (K!, SP!); Ao lado da barragem de Represa do Ribeirão do Campo - SABESP, 900 m, 7 May 1980, *Collares 9* (HRB!, RB!); Biritiba Mirim, Estação Biológica de Boracéia, 830 m, 16 Sep 1983, *Custódio 1541* (K!); Biritiba Mirim, Estação Biológica de Boracéia, 830 m, 29 Mar 1984, *Custódio 2323* (K!); Biritiba Mirim; Estação Biológica de Boracéia, 820 m, 7 Jul 1983, *Custódio 36* (K!); Boracéia, between Moji das Cruzes and Biritiba-Mirim crest of Serra do Mar, 800 m, 3 Feb 1987, *Custódio 4522* (MO!); Boracéia, between Moji das Cruzes and Biritiba-Mirim, crest of Serra do Mar, 850 m, 4 Feb 1987, *Custódio 4629* (MO!); Iguape, Estação Ecológica Juréia-Itatins, 16 Aug 1990, *Ferreira 194* (K!, SP!); Mun. Iguape. Est. Ecol de Juréia, 20 Jul 1983, *Figueiredo 14766* (IBGE!, UEC!); Carlos Botelho State Park, Riberão Branco, Km 55, ca. 23 km S of Park Headquarters, 560 m, 2 Sep 1987, *Gentry 58809* (MO!); ca. 40 km N de Registro; Reserva Florestal de Sete Barras, 4 Aug 1977, *Gibbs & H. F. Leitão Filho 5625* (UEC!); Iguape, Estação Ecológica Juréia-Itatins, Serra da Juréia, 13 Dec 1990, *Gomes da Silva 131* (K!, SP!); Iguape, Estação Ecológica Juréia-Itatins, Serra da Juréia, 12 Dec 1990, *Gomes da Silva 94* (K!, SP!); Salesópolis, Boracea, 10 Feb 1960, Handro 916 (SP!); São Paulo, Cidade Jardim, 12 Nov 1951, *Hoehne s.n.* SPF 13965 (K!); Iguape, Estação Biológica Juréia-Itatins, margem do Rio Verde, 25 Jul 1991, *Kawall 73* (SP!); Ubatuba, Estação Experimental de Ubatuba, 24 Jun 1986, *Kirizawa 1669* (SP!); Nucleo Picinguaba, 23 May 1989, *Kirizawa 2170* (SP!); Salesópolis, Boracea, Estação Experimental de Boracea, 5 Aug 1948, *Kuhlmann 1673* (K!, NY!, SP!); Moji das Cruzes, 17 Feb 1950, *Kuhlmann 2364* (NY!, SP!); Salesópolis, Boracea, 28 Oct 1954, *Kuhlmann 3088* (K!, NY!, SP!); Iguape, Reserva Ecológica da Juréia, 25 Jun 1990, *Mamede 240* (K!, SP!); Iguape, Reserva Ecológica da Juréia, 21 Jun 1990, *Mamede 278* (K!, SP!); Iguape, Estação Biológica Juréia-Itatins, Serra da Juréia, 13 Jun 1991, *Mamede 446* (K!, SP!); Salesópolis. na Estação Biológica de Boracéia, 14 Apr 1967, *Mattos 14758* (SP!); Ubatuba, Horto Florestal, 1 May 1961, *Mattos 8928* (K!); Sete Barras. Fazenda Intervales. Saibadela, *Mello-Silva 566* (K!, SPF!); Santos, Sororocaba, Jan 1875, *Mosen 3385* (P!); Mun. São Sebastião, Boicucanga, Serra do Mar, 26 Jul 1983, *Pirani 747* (SPF!); Mun. Iguape. Estação Ecológica de Juréia, 13 May 1983, *Rodrigues 14694* (UEC!); São Paulo, Biritiba Mirim, Estação Biológica de Boracéia, 820 m, 3 Feb 1984, *Romaniuc Neto 108* (K!); Iguape, Reserva Ecológica Juréia-Itatins, 14 May 1991, *Rossi 867* (K!, SP!); Mun. Ubatuba, Estação Experimental do IAC, 29 Mar 1979, *Silva 10138A* (UEC!); Mun. Ubatuba, Est. Experimental do Inst. Agr. de Campinas, 23 Oct 1978, *Silva 10987* (UEC!); Mun. Iguape. Mata de Baixada, praia do Grajaú, 10 Dec 1981, *Stubblebine 13189* (UEC!). **STATE NOT INDICATED:** *Saint-.Hilaire s.n.* (P!).

**Local names.** Guapiroca, Pau de Arco, (São Paulo); Guamirim, Guarupunga mach, (Paraná); Cabiúna do Campo, Guaramirim Vermelho (Rio de Janeiro); Guarmirim branco, Guarmirim vermelho (Santa Catarina).

**Uses.** Legrand and Klein (1967) list note that this species is used for firewood and planks in Santa Catarina. Heringer (no. 532) comments that it has no known use.

Berg recognised three varieties of *G. spectabilis*, of which the second, var. *genuina*, was based on *Myrcia spectabilis* DC. and so should have been named *G. spectabilis* var. *spectabilis*. The three varieties were distinguished on the basis of a combination of indumentum and leaf-shape characters. I have seen type material only of the typical variety but the detailed descriptions and Berg's narrow species concepts suggest that the other two varieties are likely to be conspecific. The mixed collection *Gaudichaud 765* includes a single sheet of *G. spectabilis* (along with two sheets of *G. sonderiana*) but does not seem a good candidate for isotype.

*Gomidesia spectabilis* was doubtfully designated as type species of the genus by Britton and Wilson (1925) and this choice was confirmed by McVaugh (1956a). McVaugh justified the choice on the grounds that Berg saw the type specimen in flower in the herbarium of Martius, and because the species is illustrated in Flora Brasiliensis in such a way as to show well the generic character.

*Gomidesia spectabilis* differs from *G. martiana* in its less coriaceous, markedly bicolorous leaves with more conspicuous secondary laterals and higher order venation, in its densely sericeous hypocotyl, and in the complete fusion of the hypanthium to the ovary wall in fruit. See under *G. martiana* for a more detailed discussion of these sister species and under *G. nitida* for a possible threat to the application of the name *G. spectabilis*.

**35. Gomidesia ? springiana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 13. 1857. Type. Brazil. Minas Gerais: "ad Rio das Pedras," *Sellow s.n.* (holotype B, n.v., presumed destroyed).

*Gomidesia springiana* var. *coriacea* O.Berg, *in* Martius, Fl. bras. **14 (1):** 13. 1857. Inadmissible name to be replaced by *G. springiana* var. *springiana.*

*Gomidesia springiana* var. *membranacea* O.Berg, *in* Martius, Fl. bras. **14 (1):** 14. 1857. Type. Brazil. São Paulo: "ad viam de Cubatao in finibus São Paulo," *Sellow s.n.* (holotype, B, n.v., presumed destroyed).

*Myrcia springiana* (O.Berg) Kiaersk., Enum. Myrt. bras. 102. 1893.

*Tree, treelet* or *shrub* 3–10(–20) m tall. Branchlets 10 cm below the terminal bud 3.5–6 mm in diameter, somewhat compressed, with a moderately dense indumentum of appressed, straight, pale hairs to 0.3 mm long; terminal bud 7–16 mm long with a dense indumentum of appressed, straight, pale hairs c. 0.4–0.8 mm. Stipule lobes to 1 mm long. Inter-petiolar ridge faint or distinct and transverse. Petioles 5–6 mm long, 1.5–3.5 mm wide, flat or slightly channeled, with a sparse to moderately dense indumentum of appressed or ascending or erect, straight, pale hairs to 0.3 mm. *Lamina* elliptic or narrowly oblong, 118–305 mm long, 33–121 mm wide, 2.0–2.6(–5) times as long as wide; apex abruptly short acuminate; base acutely cuneate and minutely auriculate; margin flat or bent down or recurved; midrib sulcate or impressed or flat above, prominent below; lateral veins straight or slightly curved, slightly raised or flat or slightly impressed above, slightly raised below, diverging at c. 70–80 ° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein slightly less prominent than the laterals and curving or looping between them; higher order venation inconspicuous above, very slightly raised, distinct below, darker than the lamina; venation between marginal vein and margin inconspicuous or distinct, submarginal vein distinct above. Indumentum absent above, or scattered and consisting of appressed, straight, white hairs to 0.3 mm long, sparse below, consisting of appressed, straight, straw-coloured hairs, c. 0.1–0.3 mm long. Gland dots indistinct above, distinct below, dark and slightly raised. Mature leaves chartaceous to coriaceous, drying markedly bicolorous, dark brown or mid-brown above, pale olive green below. *Conflorescence* comprising two pairs of uniflorescences in the axils of distal leaves. Phylloscopic accessory uniflorescences occasional. Uniflorescence an erect thyrsoid of c. 27–57 flowers, 70–210 mm long, reaching c. 1/2–3/5 the length of the subtending leaf; peduncle 40–52 mm long i.e., c. 1/5–3/5 the length of the inflorescence, 2–6 mm wide, markedly flattened; lateral branches 4–6 pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 6 mm long x c. 4.5 mm wide. Calyx lobes depressed ovate, 1.6–1.7 mm long x 2.2–2.8 mm wide, apex obtuse to rounded, with a dense to moderately dense or sparse indumentum of appressed, straight, pale hairs to 0.1 mm long externally, indumentum sparse internally; hypanthium 3–3.2 mm long, irregularly furrowed, prolonged c. 0.7–1.2 mm above the ovary, with a dense indumentum externally consisting of appressed, straight, pale brown hairs to c. 0.1–0.2 mm long, indumentum dense internally; disk c. 2.4–3.2 mm diameter, indumentum dense. Stamens c. 53–92 per flower; anthers c. 1–1.3 mm long, filament tapered to very fine point or thread like portion at insertion on well-developed connective stub, apex truncate or shallowly or deeply emarginate (or rarely distinctly apiculate), vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent or held parallel with margins slightly recurved or flat or connivent or overlapping, effective dorsal opening 1/6–1/7 the length of the anther, residual septum not visible or visible and vertical. Style 10 mm, with moderately dense indumentum in lower 1/2; stigma minutely capitate. Ovary 1.8–2.5 mm long, bilocular, ovules 2 per locule. *Fruit* globose, 11–15 mm diameter, crowned with the connivent to erect, imbricate calyx lobes. Mature seed one or two per fruit, c. 9 mm long, testa pale, hypocotyl densely sericeous.

**Distribution (Map 33) and ecology.** *Gomidesia springiana* is now known only from collections from the Atlantic forest of southern Bahia (and Espírito Santo, see discussion).

**Phenology.** Flowering collections have been made from November to March. Peak flowering appears to be in November, rather earlier than many other species of *Gomidesia*. Fruiting collections have been made from February to July.

**Specimens examined. BRAZIL.** **BAHIA:** 8 km S. de Itacaré, 15 Oct 1968, *Almeida 158* (CEPEC!); Mun. Uruçuca, Distrito de Serra Grande. 7.3 km na estrada Serra Grande/Itacaré, Fazenda Lagoa do conjunto Fazenda Santa Cruz, Jul 1991, *Carvalho 3450* (K!); Entre Eunápolis e Tabela, Km 21, 28 Nov 1970, *Emmerich 3521* (CEPEC!, R!); Mun. Ilhéus, espírito do CEPEC (Centro de Pesquisas do Cacau), km 22 da Rodovia Ilhéus/Itabuna (BR 415), 50 m, 4 Mar 1981, *Hage 500* (CEPEC!, NY!, SPF!); 13 km North along road from Una to Ilhéus, 50 m, 23 Jan 1977, *Harley & Mayo 18176* (K!, MO!, NY!, U!); Mun. Ilhéus. Fazenda Barra do Manquinho. Ramal com entrada no km 10 da Rod. Pontal/Olivença, lado direito. 3 km a Oeste da Rod, 5 Feb 1982, *Mattos Silva 1404* (CEPEC!, NY!); Entre Eunápolis e Tabela, Km 21, 28 Nov 1970, *Mello Filho 2983* (CEPEC!); Mun. Uruçuca. Nova estrada que liga Uruçuca a Serra Grande, a 28 -30 km de Uruçuca, 1 May 1979, *Mori 11752* (K!, NY!, UB!); Mun. Cachoeira. Fazenda Cabonha, 8 Jun 1975, *Pereira de Souza s.n.* ALCB 10168 (CEPEC!, Herb. Leal Costa 10168); Rod. Una a Comandatuba. Faz. de Antônio de Pimenta, 26 Oct 1971, *Pinheiro 1652* (CEPEC!); Km 2 da rod Guaratinga p/Tabela, 29 Mar 1973, *Pinheiro 2060* (CEPEC!); Habitat quoque in siccis saxosisque prope Castel novo in districtu Ilheos prov. Bahiensis, Nov 1821, *Riedel 482* ( K!, LE! (5 sheets), P!, S!, US! (photo), W!); 8 km S de Itacaré, 15 Oct 1968, *Santos 158* (CEPEC!, HUEFS!); Rod. Itaimbé, Km 3 a 4 Itamari, 12 Nov 1971, *Santos 2125* (CEPEC!); Mun. Ilhéus, Área do Cepec, 5 Dec 1978, *Santos 3416* (CEPEC!, HRB!, HUEFS!, RB!); Mun. Ilhéus. Área do CEPEC (Centro de Pesquisas de Cacau), km 22 da Rodovia Ilhéus/Itabuna (BR 415), 50 m, 4 Nov 1982, *Santos 3809* (CEPEC!, SPF!); Mun. Uruçuca. 7.3 km N of Serra Grande on road to Itacaré, 6 May 1992, *Thomas 9173* (K!); Mun. Uruçuca. 7.3 km N of Serra Grande on road to Itacaré, 7 May 1992, *Thomas 9209* (K!). **ESPÍRITO SANTO:** Linhares, Reserva Florestal da CVRD, 5 Feb 1972, *Spada 4* (RB!); Linhares, Reserva Florestal da CVRD, 5 Feb 1972, *Sucre 8476* (K! (2 sheets), NY!).

**Local names.** Murta (Bahia). A name applied to many different species of Myrtaceae.

The Espírito Santo material cited above is included with some misgivings. The material appears to represent a single collection divided between two collectors. The specimens resemble *G. springiana* in having anthers with well-defined connective stub and thecal halves retaining curvature after dehiscence. They differ in having broader buds and leaves which dry are a similar brown in colour above and below and have lateral and marginal veins distinctly raised. I dissected a number of fruit which appeared to be mature but none contained a normally developing seed. In each case the fruit contained three non-developing ovules and one apparently malformed seed, with many concave surfaces and an embryo in which the hypocotyl was discernible but the cotyledons were disproportionately small and ill-developed. The possibility of a hybrid origin for this material might repay investigation as it was collected in a reserve where a number of *Gomidesia* species occur sympatrically.

The collection *Mattos Silva 1195* from Fazenda Guanabara, Ilhéus may also belong here. It differs from the material described above in having more coriaceous leaves which appear to have been markedly convex in the fresh state.

The application of the name *G. springiana* to this taxon is provisional. The Sellow collections at B on which *G. springiana* was based must be presumed to have been destroyed and I have seen no duplicates which could be interpreted as isotypes. However, when amplifying the description of *G. springiana* var. *membranacea*, Berg (1859) cited a Riedel collection, from Castel Novo, Bahia. Duplicates of this collection, *Riedel 482,* have been widely distributed. A number of these sheets bear the annotation *G. springiana* var. *membranacea* in Berg's hand. At present these would appear to be the only candidates for the neotypification of this name but I hesitate to designate a neotype before the other possibilities discussed below have been thoroughly explored.

Legrand (1959) mentioned a phototype of *G. springiana* on the basis of which he noted a resemblance to *G. gestasiana*. No indication is given of the source of the phototype but it may be possible to obtain it from MVM.

There may be an earlier name for this taxon. A Salzmann collection of the taxon here treated as *G. springiana* bears the name *Myrcia hayneana* DC. I have seen only a microfiche image of the type of *M. hayneana* from G-DC and the reproduction is not of sufficient quality to determined the application of the name.

For these reasons the material treated here is provisionally identified as *G. springiana* pending a visit to G-DC, a repeated loan request to MVM and further investigation of this problem. Finally, it should be noted that Berg himself appears to have been confused regarding *G. springiana* and *G. poeppigiana*. Of the five duplicates of *Riedel 482* at LE Berg annotated three sheets as *G. springiana* var. *membranacea* and the other two sheets as ' *Gomidesia poeppigiana* Bg.?' For further discussion of *G. poeppigiana* see under Doubtful names and excluded taxa.

**36. Gomidesia spruceana** O.Berg, *in* Martius, Fl. bras. **14 (1):** 534. 1859. Type. Brazil. Minas Gerais: "in locis saxosis prope Cachoeira," Dec 1824, *Riedel 1303* (lectotype, LE!, here designated; isolectotypes, K!, P!, U!)

*Gomidesia spruceana* var. *acutifolia* O.Berg, *in* Martius, Fl. bras. **14 (1):** 535. 1859. Inadmissible name to be replaced by *G. spruceana* var. *spruceana*.
*Gomidesia spruceana* var. *obtusifolia* O.Berg, *in* Martius, Fl. bras. **14 (1):** 535. 1859. Type: Brazil. Minas Gerais: 'in locis saxosis prope Cachoeira' prov. Minarum, Dec 1824, *Riedel 1303* (lectotype, LE!, here designated; isolectotype, P!)

*Shrub* 1 m tall. Branchlets 10 cm below the terminal bud c. 2 mm in diameter, terete, with a dense indumentum of curling, white, felted hairs of indeterminate length and varying orientation; terminal bud c. 8 mm long with dense indumentum. Stipule lobes to 2 mm long. Inter-petiolar ridge not seen. Petioles 3 mm long, 2 mm wide, channeled. *Lamina* wide ovate, ovate or wide oblong, 25–47 mm long, 15–36 mm wide, 1.3–1.7 times as long as wide; apex acute, obtuse or rounded; base subcordate; margin bent down or recurved; midrib impressed above, prominent below; lateral veins straight, raised above, prominent below, diverging at c. 60° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein slightly less prominent than the laterals and curving between them; higher order venation slightly raised above and below; venation between marginal vein and margin inconspicuous. Indumentum moderately dense above, dense below, consisting of curling, whitish hairs of indeterminate length and varying orientation. Gland dots distinct above, slightly impressed, indistinct below. Mature leaves coriaceous. *Conflorescence* comprising one or two pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect compact metabotryoid (?) of 5–9 flowers, 25–38 mm long, reaching c. 9/10 the length of the subtending leaf; peduncle 13–23 mm long i.e., c. 1/2–3/5 the length of the inflorescence, 2 mm wide, terete; lateral branches a single pair below the terminal cyme or cluster of cymes. *Mature flower buds* not seen. Calyx lobes deltate, 2.7 mm long x 2.5 mm wide, apex acute, with a dense indumentum of crisped white hairs up to 1.2 mm long externally, and a moderately dense indumentum of appressed, straight, white hairs to 0.2 mm internally, becoming glabrous towards base; hypanthium 3.2 mm long, prolonged c. 2.2 mm above the ovary with a dense indumentum of yellowish white erect hairs to 1.2 mm externally, dense internally; disk c. 4 mm diameter, indumentum dense. Stamens number unknown; anthers c. 0.5 mm long, apex obtuse, vertical displacement of thecae slight, thecal halves lose curvature on dehiscence, held parallel, thecal margins recurved, effective lateral opening the whole length of the anther, residual septum visible, more or less vertical. Style c. 7 mm, indumentum dense in lower 1/3, moderately dense in middle 1/3; stigma punctiform. Ovary 1 mm long, bilocular, ovules 2 per locule. *Fruit* unknown.

**Distribution (not mapped) and ecology.** Known only from the type whose precise locality is discussed below.

**Phenology.** Known only from flowering material which was collected in December.

**Specimens examined. BRAZIL.** **MINAS GERAIS:** Cachoeira, *Riedel 1303* (lectotype, LE!, here designated; isolectotypes, K!, LE!, P!).

I have been unable to establish the origin of the type material with any degree of certainty. The name Cachoeira was often used to refer to a gold-mining area close to Ouro Preto visited by many of the nineteenth century travellers. The town of Cachoeira do Campo is now situated there. The movements of Langsdorff and his party (which included Riedel) have been described by a number of recent historians. However, I have found no indication that Riedel (or any of the party) were in the vicinity of Ouro Preto in December 1824. On the contrary Bertels et al. (1981), quote from a letter in which Langsdorff reported leaving the Serra da Lapa on December 4th having spent fourteen days there due to rain and arriving, on December 11th, in Tejuco (Tijuco, now Diamantina). He had travelled to Serra da Lapa from Barra do Jequitiba, already far to the north of Ouro Preto. Bertels et al. (1981) noted that the expedition party started the return journey (from Diamantina) on December 29th and more or less as far as Santa Luzia and Gongo Soco it followed a different route to that by which it had travelled north, visiting areas until then unknown to them. Thus *G. spruceana* would appear to have been collected from central Minas Gerais but since the locality cannot be pinpointed with certainty is has not been mapped.

Berg described two varieties of *G. spruceana* on the basis of leaf shape: var. *acutifolia* and var. *obtusifolia*. I take var. *acutifolia* to be the typical variety and the name should therefore be replaced by var. *spruceana*. I have examined two sheets of *Riedel 1303* from LE annotated by Berg as *G. spruceana* var. *acutifolia* and *G. spruceana* var. *obtusifolia* respectively. Curiously the latter sheet bears several small specimens with acute leaves while the material on the other sheet is obtuse-leaved. Presumably the labels were switched at some point after Berg annotated the material. The same discrepancy may be observed in the two sheets of *G. spruceana* at P while the acute-leaved duplicates at K and U are also annotated as var. *obtusifolia*. Clearly the labels were switched before the material was distributed from LE. Since the material appears to be uniform in all respects but leaf shape I have chosen not to maintain Berg's varieties. As lectotype I have designated the LE sheet bearing the acute-leaved material since this is clearly the material he considered typical.

Berg indicated that *G. spruceana* should be inserted in his treatment immediately following *G. aubletiana,* in an artificial section comprised of species with cordate or subcordate leaves. Legrand treated *G. spruceana* in the synonmy of *G. gaudichaudiana* without explanation. He does not appear to have examined the type in which the anthers, though variable, bear no resemblance to those characteristic of *G. gaudichaudiana* (here treated as a synonym of *G. eriocalyx*). I consider *G. spruceana* to be closer to *G. montana* with which it shares the rather open anther morphology and the coriaceous subsessile leaves. Some of the anthers of the type are distinctly myrcioid in appearance and it seems more than likely that an earlier binomial exists for this species in *Myrcia*. A number of recent collections from Grão Mogol and environs in Minas Gerais resemble *G. spruceana* in leaf venation, and in the morphology of the calyx lobes and anthers. They differ from the type of *G. spruceana* in having much larger leaves with ochraceous indumentum and less reduced inflorescences. They may merit recognition as a separate species.

**37. Gomidesia squamata** Mattos & D.Legrand, Loefgrenia **67:** 14. 1975. Type. Brazil. Paraná: Quatro Barras, Rio Taperavi, *Hatschbach 10997* (holotype, MVM n.v.).

*Shrub* to 1.8 m tall. Branchlets 10 cm below the terminal bud c. 1 mm in diameter, more or less rounded, glabrous, terminal bud to 9 mm long, with a dense indumentum of appressed, white hairs to 0.3 mm long. Stipule lobes 1.2 mm long, pale. Inter-petiolar ridge absent. Petioles 2–3(–6) mm long, 0.5–1 mm wide, channeled. *Lamina* elliptic, markedly bicolorous, 61–86 mm long, 28–32 mm wide, 2–2.8 times as long as wide; apex acute; base cuneate; margin flat or bent down; midrib sulcate near base, flat or slightly raised near apex above, prominent below; lateral veins straight, slightly raised above, raised below, diverging at c. 60–

70° from the midrib; secondary laterals composite, never equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence, barely curving between them more or less parallel to the margin, higher order venation slightly raised above and below; venation between marginal vein and margin distinct. Indumentum absent above, scattered below, consisting of appressed, pale, brown-based hairs, to 1.2 mm long. Gland dots slightly raised above and below. Mature leaves membranaceous to chartaceous. *Conflorescence* comprising a single pair of uniflorescences in the axils of distal leaves. Uniflorescence an erect monad or triad of 1–3 flowers, 17 mm long, reaching c. 1/4 the length of the subtending leaf; peduncle 11 mm long i.e., c. 2/3 the length of the inflorescence, c. 1 mm wide, lateral branches none below the terminal cyme or cluster of cymes. *Mature flower buds* 5 mm long x 3.5 mm wide. Calyx lobes hemi-orbicular, 0.6 mm long x 1.6 mm wide, apex rounded or obtuse, with a dense indumentum of straight hairs up to 1 mm long externally, indumentum shorter and less dense internally; hypanthium 3.7 mm long, prolonged c. 2.5 mm above the ovary, indumentum dense, consisting of appressed, curved, white hairs to 1.2 mm long; disk c. 2.1 mm diameter, indumentum dense. Stamens not counted; filament tapered to pale, thread-like portion at point of insertion on connective, anthers 0.9–1.0 mm long, apex shallowly or deeply emarginate, vertical displacement of thecae marked, thecal halves retaining curvature after dehiscence, connivent or gaping, thecal margins slightly inrolled or flat, effective dorsal opening c. 1/4 the length of the anther, residual septum often visible, vertical. Style c. 9 mm, glabrous or with moderately dense indumentum in lower 1/3; stigma minutely capitate. Ovary 1.2–1.3 mm long, bilocular, ovules 2 per locule. *Fruit* not seen.

**Distribution (Map 34) and ecology.** Known only from the Serra do Mar in the east of Paraná where it has been collected in rain forest and in 'scrub' vegetation at altitudes of 1000m or more.

**Phenology.** Collected in flower in late March

**Specimens examined. BRAZIL.** **PARANÁ:** Morro Mãe Catira (Mun. Quatro Barras), 1000 m, 30 Mar 1967, *Hatschbach 16222* (MBM!, US!); Serra do Mar, scrub on small top near source of Rio do Corvo, ca. 35 km ENE of Curitiba, 1050 m, 30 Mar 1967, *Lindeman & Haas 5113* (NY!, U!).

Since I have not seen type material of *Gomidesia squamata* the description provided is based on two duplicates of *Hatschbach 16222*, one of the two paratypes mentioned by Legrand in the protologue. I have seen only one other specimen which I consider referrable to *G. squamata* and, coincidentally, this collection, *Lindeman & Haas 5113,* was made on the same day as the paratype examined. Mattos and Legrand (1975) did not discuss the affinities or diagnostic characters of their new species but *Gomidesia squamata* is clearly very close to *G. anacardiifolia*, indeed the collection *Lindeman & Haas 5113* was determined as *G. riedeliana* (here treated as a synonym of *G. anacardiifolia*) by Legrand in 1972. On the basis of the scant material available to me I have chosen to recognise *G. squamata* as a distinct species differing from *G. anacardiifolia* in its very slender branchlets and membranous leaves. The abundant indumentum which Legrand and Mattos emphasized in the original description also occurs in the collection *Hatschbach 16862* but this material differs from that described above by virtue of its stouter branchlets and less diaphanous leaves. I have examined only the C sheet which bears a single securely mounted fruit. Study of other duplicates of this collection and other collections from this area will be important in determining whether the admittedly slight differences between the species are consistently correlated.

**38. Gomidesia tijucensis** (Kiaersk.) D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 23. 1959.

*Myrcia tijucensis* Kiaersk. Enum. Myrt. Bras. 102. 1893. Type. Brazil. Rio de Janeiro: Tijuca. *Glaziou 6886* (lectotype, C!, see discussion; isolectotypes, BR!, F!, P!, S!).

Fig. 50 (also 2G, 3E and 15r&s).

*Gomidesia acuminatissima* D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 24. 1959. Nom. nud. Type. Brazil. Rio de Janeiro: Mesa do Imperador. *Occhioni 254* (RB!, 2 sheets).

*Tree, treelet* or rarely *shrub* 6–15(–25) m tall. Branchlets 10 cm below the terminal bud 1.5–2 mm in diameter, terete, glabrous or with a moderately dense indumentum of appressed, straight or curved, straw-coloured, brown-based hairs to c. 0.3 mm long; terminal bud c. 3 mm long or proliferating. Stipule lobes 0.6–1.0 mm long, dark-purple. Inter-petiolar ridge absent, at least at some nodes. Petioles 3–5.5 mm long, 0.5–0.9 mm wide, flat or channeled with a sparse to moderately dense indumentum of appressed, pale hairs to 0.4 mm long. *Lamina* elliptic, ovate or narrowly ovate, 44–71 mm long, 16–33 mm wide, (1.9–)2.4–3(–4.5) times as long as wide; apex acuminate, obtuse or rounded at very tip; base acutely or obtusely cuneate, rounded or decurrent; margin flat, bent down, or revolute; midrib sulcate near leaf base above, to slightly raised near apex, prominent near base below to raised near apex; lateral veins more or less straight or slightly curved, raised above and below, diverging at c. 60–70° from the

FIG. 50. *Gomidesia tijucensis*. Fig. 111 from Mattos' Myrtaceae do Rio Grande do Sul.

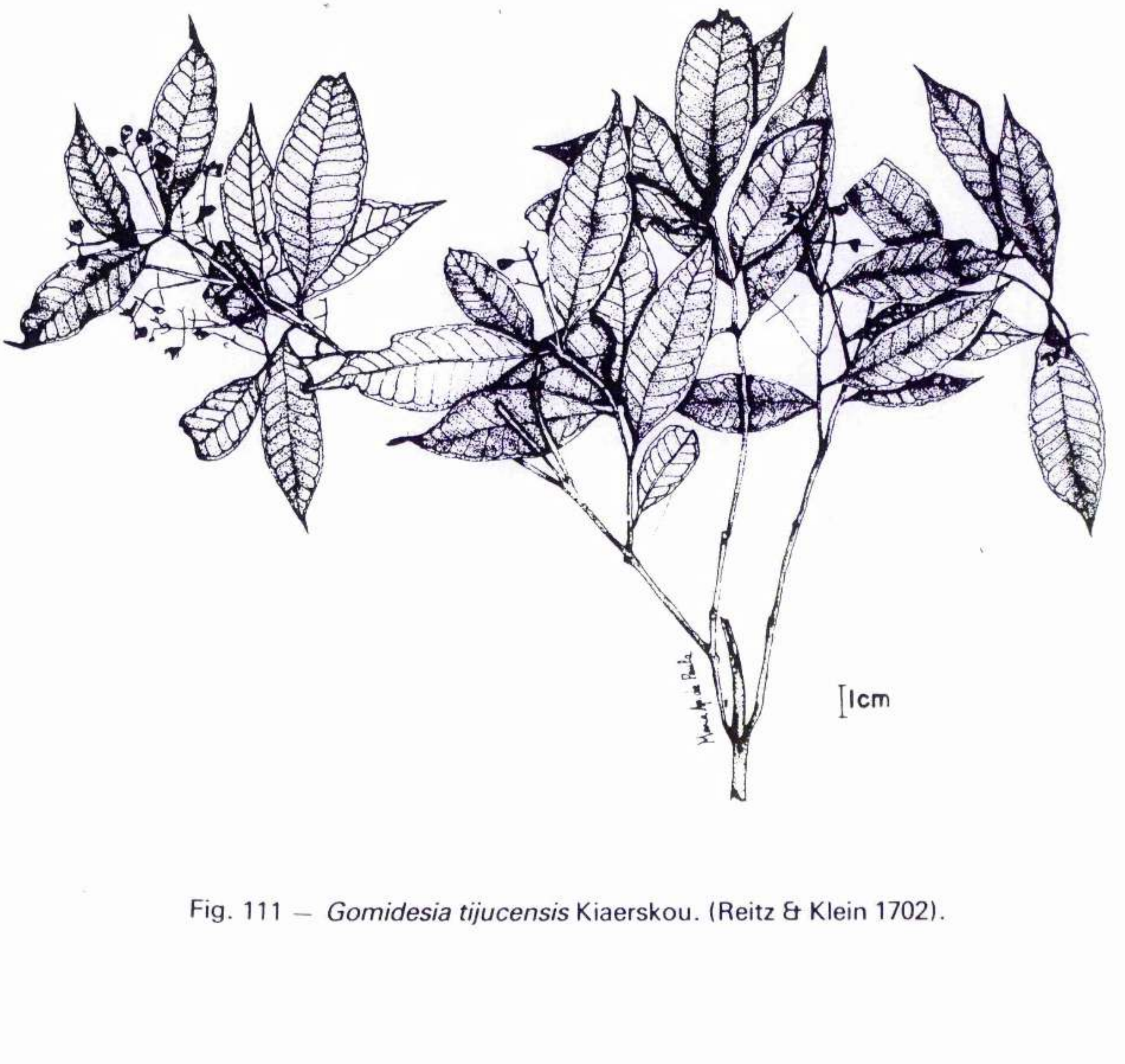


Fig. 111 — *Gomidesia tijucensis* Kiaerskou. (Reitz & Klein 1702).

midrib, only slightly more conspicuous than the secondary laterals and sometimes difficult to distinguish from these latter; secondary laterals composite, straight or slightly curved, almost equalling the laterals in prominence, occasionally branching near margin; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation distinct, raised above and below; venation between marginal vein and margin inconspicuous. Indumentum absent or sparse above, consisting of scattered, appressed, pale hairs of variable length to 0.5 mm, sparse or scattered below, consisting of appressed, straw-coloured, brown-based hairs to 0.9 mm long. Gland dots indistinct above, distinct or indistinct below. Mature leaves chartaceous. *Conflorescence* comprising 2–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid, panicle or metabotryoid of c. 7–17 flowers, 42–57 mm long, reaching c. 1/2–4/5 the length of the subtending leaf; peduncle 19–28 mm long i.e., c. 1/2 the length of the inflorescence, c. 1 mm wide, flattened, straight or curved, lateral branches 3(–4) pairs below the terminal cyme or cluster of cymes. *Mature flower buds* c. 2.5–3.8 mm long x 2.6–3.5 mm wide. Calyx lobes broadly triangular to hemi-orbicular 0.8–0.9 mm long x 1.3–1.7 mm wide, apex rounded, obtuse or rarely acute, with a sparse indumentum of straight hairs up to c. 0.5 mm long externally, indumentum shorter internally; moderately dense to dense near base, sparse towards apex, margin ciliate; hypanthium c. 1.4–1.6 mm long, prolonged c. 0.6–0.8 mm above the ovary, with dense indument in lower half externally; moderately dense in upper half; disk c. (1.2–)2–2.4 mm diameter, densely pubescent. Stamens c. 90–102 per flower; filament more or less tapered below point of insertion on anther; anthers c. 0.4–0.5 mm long, apex shallowly emarginate, vertical displacement of thecae marked but variable, thecal halves held more or less parallel after dehiscence, dorsal halves somewhat flattened, ventral halves retaining curvature, margins recurved, effective dorsal opening c. 1/3–1/2 the length of the anther, residual septum usually visible, oblique, almost transverse. Style c. 7 mm, glabrous or with moderately dense indumentum in lower 1/3, sparse indumentum in middle 1/3 and glabrous towards apex; stigma minutely capitate, distinctly papillate. Ovary c. 1 mm long, bilocular, ovules 2 per locule. *Fruit* globose, c. 10 mm diameter, crowned with the connivent to erect, imbricate calyx lobes. Mature seed 1 per fruit, c. 7 mm long, testa mid-brown, cotyledons leaf-like, slightly fleshy, folded into a bundle, hypocotyl glabrous.

**Distribution (Map 35) and ecology.** *Gomidesia tijucensis* occurs in Atlantic forest in the state of Rio de Janeiro and in southern São Paulo, Paraná, Santa Catarina and northern Rio Grande do Sul at altitudes of 20–800 m above sea level. Legrand and Klein (1967) considered this species to be exclusive to and characteristic of the Atlantic coastal rainforest. They reported it to lack pronounced affinities for particular zones, having a regular distribution throughout the forests both on the plains and on slopes where it maintains high frequency and abundance values. They noted that despite being rather indifferent in character it appeared to prefer fertile várzeas along rivers, and lower slopes as well as areas with slight gradients where its abundance makes it particularly notable. As a species characteristic of the more advanced associations of the Atlantic Forest formation it scarcely occurs in the forests on the coastal quaternary plains.

**Phenology.** In Paraná and Santa Catarina *G. tijucensis* can begin flowering in late December but peak flowering time is late January to February. In Rio de Janeiro flowering collections have been made in December and January and also in April, May and June, suggesting two flowering episodes per year.

**Specimens examined. BRAZIL.** **PARANÁ:** Mun. Antonina, Forest along Rio Cotia near Antonina, 450 m, 20 Jan 1966, *Hatschbach & Lindeman* 13573 (C!, K!, MO!, NY!, U!, US!); Mun. Guaraqueçaba, Rio do Cedro, 75 m, 14 Dec 1967, *Hatschbach 18129* (C!, F!, MO!, NY!, US!); Mun. Campina Grande do Sul, Serra Virgem Maria, 30 Jan 1969, *Hatschbach 20960* (C!, MU!, UEC!, US!). **RIO DE JANEIRO:** Parque Nacional da Serra dos Órgãos. Terezópolis, 22 Jun 1942, *Constantino 127* (RB!); Serra dos Órgãos, Terezópolis, Jun 1942, *Constantino & O.C. Goes 177* (RB!); Petrópolis, 1947, *Goes 25* (RB!); Vallee de Jacarepaguá, 29 Dec 1869, *Glaziou 3977* (C!, K!, P!) Petrópolis, 800 m, Jun 1986, *Sucre 11385* (RB!); **RIO GRANDE DO SUL:** Santa Cristina do Pinhal, Taquara, 13 Nov 1982, *Waechter s.n.* (F!, SPF!). **SANTA CATARINA:** Mata do Hoffmann, Brusque, 31 Sep 1950, *Klein 12* (US!); Mata do Maluche, Brusque, 50 m, 10 Jan 1952, *Klein 31* (PACA!); Mata do Hoffmann, Brusque, 50 m, 13 Jan 1950, *Klein 37* (NY!); Mata do Maluche, Brusque, 50 m, 26 Jul 1951, *Klein 47* (PACA!); Mata do Hoffmann, Brusque, 50 m, 17 Feb 1950, *Klein 50* (PACA!); Morro Costa da Lagoa, Ilha de S. Catarina, Florianópolis, 300 m, 15 Feb 1967, *Klein 7237* (PACA!); Morro Costa da Lagoa, Ilha de S.Catarina, Florianópolis, 300 m, 15 Feb 1967, *Klein 7243* (HUCS!, PACA!); Morro da Ressacada. Itajaí, 200 m, 9 Feb 1954, *Reitz 1526* (NY!); Morro da Fazenda, Itajaí, 300 m, 4 Mar 1954, *Reitz & Klein 1702* (NY!, PACA!, U!, US!); Morro da Fazenda, Itajaí, 30 m, 23 Sep 1954, *Reitz & Klein 2079* (B!, PACA!, NY!, S!, U!, US!); Cunhas, Itajaí, 20 m, 24 Sep 1954, *Reitz 2094* (PACA!, U!); Horto Florestal I.N.P., Ibirama, 300 m, 3 Feb 1956, *Reitz & Klein* 2594 (B!, NY!, PACA!, U!, US!); Brusque, 50 m, 23 Feb 1950, *Reitz 3361* (S!); Serra do Matador, Rio do Sul, 500 m, 29 Dec 1958, *Reitz 6093* (NY!, US!); Correa, Corupa, Jaraguá do Sul, 600 m, 13 Jan 1958, *Reitz 6200* (BR!, K!, US!); Vargem Grande, Lauro Muller, 450 m, 15 Jan 1959, *Reitz 8268* (B!, BR!); Serra do Matador, Rio de Sul, 550 m, 25 Jan 1959, *Reitz & Klein 8296* (B!, BR!, K!); Garapuvu, Vista Alegre, Sombrio, 20 m, 29 Jan 1960, *Reitz 9480* (B!, NY!, US!); Garapuvu, Vista Alegre, Sombrio, 30 m, 14 May 1960, *Reitz 9689* (B!, US!); Brusque, Mata Maluche, 26 Jul 1951, *Veloso 12*. **SÃO PAULO:** Iguape, Reserva Ecológica da Juréia, 20 Sep 1990, *Mamede 336* (SP!); Iguape, Reserva Ecológica da Juréia, 100 m, 18 Dec 1990, *Mamede 385* (SP!).

**Local names**. Brazil: Ingabau (Santa Catarina), Guamirim Ferro (Santa Catarina). For other species known by these names see discussion below.

**Uses.** Legrand and Klein (1967) mention the use of this species for firewood and planks.

*Gomidesia tijucensis* may be distinguished from other species in the genus by its acuminate leaves with very dark petioles, and its two-tone flower buds in which the pale, densely pubescent hypanthium contrasts markedly with the almost glabrous, brown or blackish calyx lobes.

As circumscribed here *G. tijucensis* appears to include two slightly different groups which may eventually be found to merit recognition as separate species. The Rio de Janeiro group includes the type material and a handful of other flowering specimens characterised by leaves which dry almost perfectly flat and markedly discolorous (typically dark brown above and pale or olive green below) and inflorescences in which the lateral flower buds of the terminal cyme often greatly overtop the central bud. The second group includes most (all?) of the more southerly collections (except, perhaps, those from São Paulo) and is characterised by less strikingly discolorous leaves which are slightly undulate when dry, with margins bent down or recurved and inflorescences in which the lateral buds of the terminal cyme overtop the central bud infrequently and then only by one or two millimetres. At present I am reluctant to segregate this latter group as a new species because the characters discussed are rather variable and by no means strictly correlated. Further study, including more fruiting material from Rio de Janeiro, is needed to resolve this problem. Interestingly, Legrand appears to have considered recognising the southern collections as a separate species, as some Santa Catarina duplicates were determined by him as *G. sericiflora* D.Legrand. However, this name does not appear to have been published and in their treatment of *G. tijucensis* for Santa Catarina Legrand and Klein (1967) give no indication that the bulk of the material studied by them differed from the type in any way.

Kiaerskou (1893) considered *G. tijucensis* to be closely related to *G. freyreissiana*. Legrand grouped *G. tijucensis* with *G. nitida*, *G. velutiflora*, *G. warmingiana* and *G. innovans*.

The vernacular names Ingabaú and Guamirim Ferro are by no means exclusive to *Gomidesia tijucensis* but are also used for diverse species of *Myrcia,* some of which have been confused with *G. tijucensis*. Ingabaú, the vernacular name most commonly applied to *G. tijucensis,* is also used for a taxon treated by Legrand and Klein (1969) as *Myrcia leptoclada* DC. Legrand's application of this latter name appears to have undergone considerable change over the years. Most of the material I have seen determined by Legrand as *Myrcia leptoclada* dates from the 1950's and was determined within a year or two of collection e.g. *Reitz 2199,* *3116, 3660, 8795, 8938, 8947*. These are, without exception, fruiting collections which I consider referrable to *G. tijucensis*. Legrand appears to have reached the same conclusion at some point before the publication of his treatment of *Gomidesia* for Santa Catarina and all these collections are cited there under *G. tijucensis*. By the time he prepared his treatment of *Myrcia* for the same Flora (Legrand & Klein, 1969) Legrand was applying the name *M. leptoclada* in quite a different sense, to a true *Myrcia* species. Curiously, Legrand made no reference to his previous application of the name, nor to the possibility of confusion with *G. tijucensis*. I have not seen any of the collections cited under *Myrcia leptoclada* in the Flora of Santa Catarina but I have examined a duplicate of *Hatschbach 19916* determined by Legrand in 1973 as *M. leptoclada* DC. var *glazioviana* Kiaersk. This material has smaller flowers than *G. tijucensis* and the anthers are clearly myrcioid. It remains to be established whether Legrand's later application of the name is in fact correct; McVaugh (1969) was of the opinion that 'true *M. leptoclada* does not occur in South America' but he did not discuss the variety distinguished by Kiaerskou (1893). From the point of view of our understanding of *Gomidesia*, the most important outcome of all this confusion is that many widely distributed collections of *G. tijucensis* have been mis-identified as *M. leptoclada* DC., not only by Legrand but by other myrtologists following his example. Both *M. leptoclada s.s.* and var. *glazioviana* have flower buds glabrous externally and so are easily distinguished from *G. tijucensis*. Fruits of *G. tijucensis* are more or less globose (and usually one-seeded?) while those of *M. leptoclada s.s.* usually bear marked sulcae indicating the development of two or three seeds.

The other vernacular name reported for *G. tijucensis* is Guamirim Ferro, a name also applied to a number of other species of *Myrcia* including *M. arborescens* O.Berg, *Myrcia bicarinata* (O.Berg) D.Legrand, *M. dichrophylla* D.Legrand, *M. hatschbachii* D.Legrand, *M. richardiana* O.Berg and, most notably, *Myrcia sosias* D.Legrand (Legrand & Klein, 1969). The latter species differs from *G. tijucensis* in its smaller flowers with myrcioid anthers, in its larger, ovoid fruits and in its leaves which terminate in a narrow, whip-like acumen which usually does not exceed 1 mm width at 5 mm from the leaf apex. It is not uncommon for specimens of *Myrcia sosias* to be determined in error as *G. tijucensis*. Even the author of *Myrcia sosias* confused the two species on occasion e.g. *Hatschbach 18489*, a flowering collection of *G. tijucensis,* was determined by Legrand as *M. sosias*.

When making the new combination *G. tijucensis* for *Myrcia tijucensis* Kiaersk., Legrand cited the two Glaziou syntypes as follows: *Glaziou* 6886 typ., 3977 (C). I take this to indicate a choice of *Glaziou 6886* as lectotype. This specimen is, in any case, the obvious choice for lectotype as the specific epithet is derived from the locality in which it was collected, Tijuca. The other syntype, *Glaziou 3977*, is reported as having been collected in Jacarepaguá.

Of the several nomina nuda published in Legrand's (1959) synopsis, *G. acuminatissima* is one of only two which were not subsequently validated. Legrand appears to have realised that the collection in question, *Occhioni 254*, fell within the range of variation seen in *G. tijucensis* in Rio de Janeiro and the specimen is cited under *G. tijucensis* in the Flora Ilustrada Catarinense treatment (Legrand & Klein, 1967).

**39. Gomidesia velutiflora** Mattos & D.Legrand, Loefgrenia **67:** 15. 1975. Type. Brazil. Rio de Janeiro: Estrada da Vista Chinesa perto da Cutia, 3 Feb 1941, *Gonçalves s.n.* (holotype, MVM, n.v. ; probable isotypes, RB! (2 sheets)).

(Fig. 15t&v).

*Tree* 12–15 m tall. Branchlets 10 cm below the terminal bud 2.5 mm in diameter, slightly flattened or more or less rounded, with a moderately dense to dense indumentum of appressed, straight, straw-coloured hairs, to 0.6 mm long; terminal bud 7–14 mm long. Stipule lobes not seen. Inter-petiolar ridge faint or apparently absent. Petioles 7–8 mm long, 1 mm wide, deeply channeled. *Lamina* lanceolate or rarely narowly ovate, (76–)115–165 mm long, (27–)34–49 mm wide, (2.8–)3–3.5 times as long as wide; apex long acuminate; base acutely cuneate, decurrent onto petiole for 2–3 mm; margin bent down; midrib near leaf base raised towards apex above, prominent below; lateral veins more or less straight, raised above, and below, diverging at c. 60–70° from the midrib; secondary laterals composite, occasionally equalling the laterals in prominence and then difficult to distinguish from them; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation distinct, slightly raised above and below; venation between marginal vein and margin inconspicuous. Indumentum moderately dense above, consisting of appressed, fine, straight, white hairs to 0.4 mm, moderately dense below, consisting of appressed, brown-based, pale hairs to 0.4 mm intermixed with shorter appressed hairs lacking a conspicuous dark base. Gland dots indistinct above and below. Mature leaves chartaceous. *Conflorescence* comprising 1–3 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect complex thyrsoid, panicle or metabotryoid of c. 13–50(–80) flowers, 33–60 mm long, reaching c. 1/4–1/3 the length of the subtending leaf; peduncle 10–19 mm long i.e., c. 1/4–1/2 the length of the inflorescence, 1–1.5 mm wide, more or less terete; lateral branches 3–4(–5) pairs below the terminal cyme or cluster of cymes. *Mature flower buds* 2.5–3 mm long x 2.5 mm wide. Calyx lobes shallowly triangular, c. 0.7 mm long x 1.3 mm wide, apex acute, with a moderately dense indumentum externally, indumentum shorter and less dense internally; hypanthium irregularly longitudinally ridged, c. 1.2 mm long, prolonged c. 0.5 mm above the ovary densely pubescent internally and externally; disk c. 1.7 mm diameter densely pubescent. Stamens c. 80 per flower; anthers 0.35–0.55 mm long, apex truncate or shallowly emarginate, vertical displacement of thecae slight to marked, thecal margins recurved after dehiscence, effective dorsal opening c. 1/3 the length of the anther, residual septum visible, oblique. Style to c. 5 mm, with moderately dense indumentum in lower 1/3; stigma minutely capitate. Ovary c. 1.0 mm long, bilocular, ovules 2 per locule. *Fruit* not seen.

**Distribution (Map 36) and ecology.** Apparently endemic to the Floresta da Tijuca in Rio de Janeiro. However the locality cited for *Sodre 150* has yet to be pinpointed with certainty and this may represent an extension to the known range. The collections are all from forest and one (*Duarte 6265*) is cited as being from primary forest but in fact the Tijuca forest is secondary in origin, having been replanted, in the latter half of the last century. Most of the plantings were of native species from the region.

**Phenology.** Peak flowering appears to be in February and March but flowering collections have also been made in December (with many buds unopened).

**Specimens examined. BRAZIL.** RIO DE JANEIRO: Entre Silvestre e Hotel das Paineiras, 16 Mar 1962, *Duarte 6265* (F!, K!, LE!, NY!, RB! U!); Estrada da Vista Chineza perto da Cutia, 3 Feb 1941, *Gonçalves 131* (RB! 80774); Mata do Horto Florestal, 24 Dec 1927, *Pessoal do Horto Florestal s.n.* RB 136305 (RB!); Vista Chinesa, 22 Jan 1934, *Rosa 140* (RB! 81401); Maciço da Pedra Branca, Pico da Serra Nogueira, 3 Mar 1989, *Sodre 150* (GUA!).

*Gomidesia velutiflora* is easily recognised by its lanceolate, acuminate leaves which turn dark brown on drying, its young branchlets with exfoliating bark and its densely velutinous flower buds. It is unlikely to be confused with any other species of *Gomidesia* but the small flowers and flat, rather nondescript leaves may lead to it being mis-identified as *Myrcia*. There is a distinct possibility that fruiting collections of *G. velutiflora* await discovery among the undetermined *Myrcia* collections in Rio de Janeiro herbaria. At the time of my study visits in RB and R, I had just become familiar with the species in flower and I may have failed to recognise it in the fruiting state. In habit and anther morphology *G. velutiflora* bears a marked resemblance *to G. tijucensis*. The latter differs in its markedly bicolorous leaves and its more delicate inflorescence.

The name *G. velutiflora* first appeared as a *nomen nudum* in Legrand's (1959) synopsis and was subsequently validated by Legrand and Mattos (1975). The holotype, *Gonçalves s.n.*, was cited as having been deposited in MVM and no isotypes were cited. I have not seen the holotype. However, two sheets deposited at RB appear to represent isotypes. Both were collected at 'Estrada da Vista Chinesa, perto da Cutia' on the same day as cited for the holotype. One is numbered *Fr. Gonçalves 131* and also bears the herbarium number RB 80774. The collector of the second is cited as *Francisco Gonçalves da Silva* and the sheet nears the numbers *(101)* and *781 N.E.* though neither of these appears to be the collector's own number. This information is written on a label printed by the Serviço Florestal do Brasil. Two further collections (paratypes) were cited in the protologue: *E. Pereira 4528* and *Paulino Rosa s.n. (RB 81401)*. A duplicate of this latter collection which I have examined at RB bears the collector's number *140*. It should be noted, however, that a further sheet, RB 80770, bears exactly the same label information as RB 81401, including the collector's number, although the specimen mounted thereon is of *Gomidesia schaueriana*. Since *G. schaueriana* also occurs in forest along the Estrada Vista Chinesa it is just possible that this discrepancy is the result of a mixed collection. However, given the striking differences in leaf shape and flower size between the two species, it seems more likely that some label confusion occurred after the material entered the herbarium.

**40. Gomidesia warmingiana** (Kiaersk.) D.Legrand in Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 23.

*Myrcia warmingiana* Kiaersk., Enum. Myrt. bras. 104. 1893. Type. Brazil. Rio de Janeiro. *Glaziou 17673* (lectotype, C!).

*Treelet* or *tree 3–7* m tall. Branchlets 10 cm below the terminal bud 2.5–3 mm in diameter, terete, glabrous or minutely puberulent; terminal bud 20 mm long with a dense indumentum of appressed, straight, straw-coloured hairs to c. 1 mm long. Stipule lobes to c. 2 mm long, subulate, dark, fleshy. Inter-petiolar ridge absent. Petioles 5 mm long, 2 mm wide, channeled, with a moderately dense to dense indumentum of appressed, straight, straw-coloured hairs to 0.7 mm *Lamina* oblanceolate, chartaceous, 110–116 mm long, 33–46 mm wide, 2.5–3.3 times as long as wide; apex abruptly acuminate, rounded at very tip; base cuneate; margin flat or bent down, recurved near leaf base; midrib sulcate near base, flat or slightly raised near apex above, prominent below; lateral veins straight, slightly raised above and below, diverging at c. 70° from the midrib; secondary laterals composite, equalling the laterals in prominence; marginal vein more or less equalling the laterals in prominence and curving between them; higher order venation distinct, very slightly raised and paler than the lamina above, darker below; venation between marginal vein and margin inconspicuous. Indumentum absent above, moderately dense below, consisting of appressed, straight, straw-coloured hairs to c. 1 mm long. Gland dots indistinct above, distinct below, dark and slightly raised. *Conflorescence* comprising 2 pairs of uniflorescences in the axils of distal leaves. Uniflorescence an erect thyrsoid of c. 5–9(?) flowers, 64 mm long, reaching c. 3/5 the length of the subtending leaf; peduncle 42 mm long i.e., c. 2/3 the length of the inflorescence, c. 1.5 mm wide, flattened; lateral branches one pair or none below the terminal cyme or cluster of cymes. *Mature flower buds* 4 mm long x 3.5 mm wide. Calyx lobes triangular to trullate, 1.8–2.1 mm long x 1.8–2 mm wide, apex acute or right-angled, with a moderately dense indumentum internally and externally; hypanthium five-ridged, 3.2 mm long, prolonged c. 1.7 mm above the ovary with a dense indumentum of appressed, straight hairs to 0.2 mm long in lower 2/3 externally, moderately dense in upper 1/3; disk c. 2.5 mm diameter, indumentum dense. Stamens c. 105 per flower; filament not tapering perceptibly to point of insertion, anthers c. 0.5 mm long, apex shallowly to deeply emarginate, vertical displacement of thecae marked, thecal halves losing curvature after dehiscence, held parallel or slightly more divergent, thecal margins recurved, effective lateral opening the whole length of the anther, residual septum visible, oblique or occasionally almost transverse. Style c. 9 mm, with moderately dense indumentum in lower 2/3; stigma punctiform, distinctly papillate. Ovary 1.5 mm long, bilocular, ovules 2 per locule. *Fruit* ovoid to obconic, longitudinally ridged, c. 9 mm diameter, 20 mm long, crowned with the connivent calyx lobes. Mature seed one per fruit, c. 11 mm long, testa pale, hypocotyl glabrous.

**Distribution (Map 37) and ecology.** *Gomidesia warmingiana* appears to be endemic to the area of Macaé de Cima, Rio de Janeiro where it occurs on slopes it Atlantic rain forest at approximately 1300 m above sea level.

**Conservation.** Most collections are from the conservation area so there is no immediate threat to the survival of this species

**Phenology.** The only flowering material I have seen is the type which is undated. I studied immature fruit in the field in March 1994 (*Nadruz 997)* and mature fruit were collected in July.

**Specimens examined. BRAZIL.** **RIO DE JANEIRO:** Macaé de Cima, *Glaziou 17673* (C!, P!); Mun. Nova Friburgo, Dist. de Macaé de Cima, Sítio Sophronitis, 1300 m, 22 Mar 1994, *Nadruz 997*

(K!); Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, Nascente do Rio das Flores, 26 Jul 1988, *Pessoa 338* (NY!).

Kiaerskou considered *G. warmingiana* to be related to *G. innovans* and the two names appear to have been used interchangeably by some botanists. The differences between these two species are discussed under *G. innovans*. When I visited herbaria in Rio de Janeiro I was as yet unclear as to the distinctions between these species. The following collections which I saw unmounted at RB are all from Macaé de Cima and are probably referrable to *G. warmingiana* but require re-examination before they can be determined with certainty: *I.A. de Araújo 22*; *M. Peron 842*; *S.V.A. Pessoa 244, 478*. Fruiting collections from Magé including *Lima 2288* and *Martinelli 9936*, previously determined by me as *G. warmingiana,* are not in fact referrable to that species as is evidenced by their smooth fruits and rather widely spaced lateral venation. Determination of these specimens must await flowering material. Vegetatively *G. warmingiana* resembles a number of species of *Marlierea* which also exhibit leaves with rather closely spaced lateral venation and conspicuous gland dots.

When making the new combination *G. warmingiana,* Legrand (1959) cited only the holotype of *G. innovans*, *Glaziou 12000.* Since there are a number of obviously misplaced lines in the text of this paper I consider this citation to represent a typographical error rather than a reflection of any intention on Legrand's part to merge the species. In the protologue of *Myrcia warmingiana* Kiaersk. (1893) cited two *Glaziou* collection numbers which differed only by a single digit: *17173* and *17673*. In his list Glaziou cited only the latter number under *M. warmingiana*. I have seen no Glaziou collection numbered 17173 and I consider it probable that the number was cited due to a copying error for 17673. If this is the case, the sheet of *Glaziou 17673* annotated by Kiaerskou and deposited at C is automatically the holotype. I hereby designate that sheet lectotype in order to ensure its status in the unlikely event of the collection *Glaziou 17173* being found to represent the same species.

## Doubtful names and excluded taxa

*Gomidesia bonnetiasylvestris* Steyerm. in Fieldiana, Bot. **28:** 1016. 1957. Type. Venezuela. Bolívar: Ptari-tepuí, 2000 - 2200 m, 2 Nov 1944, *Steyermark 59768* (holotype, F!; isotype, U!). = *Myrcia bonnetiasylvestris* (Steyerm.) Steyerm., Ann. Miss. Bot. Gard. **71:** 330. 1984.

The type material bears a strong vegetative resemblance to *G. fenzliana*. A single dehisced anther in a capsule mounted on the F sheet (the holotype) is clearly myrcioid with the curvature of the thecal halves completely reversed so that only the interior surface of the locules is exposed. No further anthers were seen on this specimen. I therefore concur with Steyermark in considering this species best accommodate in *Myrcia.*

*Gomidesia gardneriana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 22. 1857. Type. Brazil. Rio de Janeiro: 'ad Corrego das Pombas,' *Sellow s.n.* (holotype, B!, presumed destroyed).

I have seen no material identified as this species by Berg or by any subsequent worker. The name does not appear in Legrand's (1959) synopsis. In the protologue Berg compared *G. gardneriana* to *G. sellowiana* from which he considered it distinct by virtue of its more sparse indumentum, and leaves which were more rigid, with obtuse apex and base, revolute margin, the two surfaces differing in colour, opaquely punctate and with a stout petiole. The ovary was described as sulcate and the calyx lobes longer and more acute than in *G. sellowiana*, and almost glabrous. This description suggests that *G. gardneriana* may belong in *G. sellowiana* or in *G. pubescens* as delimited in the present treatment. However in the absence of any original material its placement cannot be determined.

*Gomidesia klotzschiana* O.Berg, *in* Martius, Fl. bras. **14(1):** 534. 1859. Type. Brazil. "Habitat in montibus Serra da Piedade prov. Minarum, nec non ad Petropolin prov. Rio de Janeiro," *Riedel s.n* (holotype, LE, n.v.).

Although I have not seen the type material I believe this name may be referrable to the synonymy of *G. montana*. See discussion under this name in Systematic Treatment.

*Gomidesia minutiflora* D.Legrand & Mattos [Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 26] Loefgrenia **67:** 15. 1975. Type. Brazil. Bahia: Ilheus, *Blanchet s.n.* (holotype, NY!).

Legrand first published the name *G. minutiflora* without description in his synopsis stating only that it was based on a *Blanchet* collection from Bahia which was deposited at NY and which had been determined as *Aulomyrcia detergens*. Mattos and Legrand subsequently validated the name citing a *Blanchet s.n.* collection at NY as the holotype. The locality given was Ilhéus, Bahia and it may be assumed that the specimen in question is the same one referred to previously by Legrand. I have examined a *Blanchet s.n.* NY sheet which fits the description, having been annotated as *Aulomyrcia detergens* and subsequently, by Legrand, as ' *Gomidesia* sp. probablemente especie no descrita aun'. Legrand's sketch of a flower dissection is mounted on the sheet along with a specimen which has suffered extensive insect damage. Examination of a few anthers retrieved from the detritus revealed a morphology closely resembling that of *Myrcia fallax*. The anthers are minute (c. 0.2 mm) and in the dehisced state they present a more or less flat dorsal surface while the ventral view shows the interior of the two thecae with the margins of the two inner thecal halves (one from each theca) meeting to form a vertical ridge in the centre and the outer thecal halves are divergent so that the base of the anther appears deeply emarginate or bilobed. There is no residual septum. The more or less flat or slightly concave pubescent disk and the distribution of indumentum elsewhere are also suggestive of *Myrcia fallax*.

*Gomidesia myrcioides* Mattos & D.Legrand [Comun. Bot. Mus. Hist. Nat. Montevideo **37:** 27] Loefgrenia **67:** 14. 1975. Type. Bolivia. Santa Cruz, 450 m, 4 May 1916, *Steinbach 2182* (holotype, MVM, n.v.).

The history of this name is similar to that of *G. minutiflora*, above. These two species constitute Legrand's invalidly published Sect. *Micranthera*. Although I have been unable to obtain access to the type material I believe that *G. myrcioides* is likely to be referrable to *Myrcia*. The flowers are described as minute (as small or smaller than those of *G. minutiflora*) and I believe that Legrand may have misinterpreted the anther morphology. The anthers are not described in any detail in the protologue, which merely refers to '*stamina generis*'.

*Gomidesia poeppigiana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 14. 1857. Type. Brazil. Rio de Janeiro. *Sellow s.n.* (holotype, B, n.v., presumed destroyed).

Like *G. gardneriana*, *G. poeppigiana* was described by Berg on the basis of Sellow material deposited in B and subsequently destroyed. I have been unable to locate any *Sellow* material likely to represent an isotype of this name. The only specimens I have seen determined as *G. poeppigiana* are two duplicates of *Riedel 482*, annotated by Berg with an expression of doubt. For further discussion of this material see under *G. springiana*. The description and Berg's placement of this species are indicative of an affinity with *G. blanchetiana and G. springiana.*

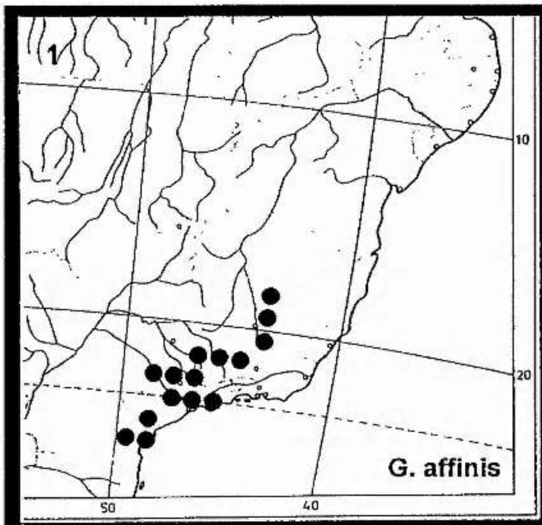
*Gomidesia willdenowiana* O.Berg, *in* Martius, Fl. bras. **14 (1):** 19. 1857. Type. Brazil. Rio de Janeiro: 'juxta S. Anna, prope Villa de S. João do Principe (S. João Marcos),' *Sellow s.n.* (holotype, B, n.v., presumed destroyed; possible isotype, LE!).

This is another Berg name based on Sellow material deposited at Berlin and subsequently destroyed. The LE specimen cited above seems a good candidate for isotype as it matches the description well and was annotated by Berg as *G. willdenowiana*. The inflorescence is long-peduncled and bears rather small buds but in the absence of further material it is difficult to establish whether these are mature. The ovary is 4–5-locular, suggesting an affinity with *G. schaueriana*, and I suspect that *G. willdenowiana* may be referrable to the synonymy of that species. The leaf morphology is consistent with such a placement.

Maps 1-37 (on facing and following pages).

Distribution patterns of individual species of *Gomidesia* plotted by degree square.

Each dot represents one or more collections known from that square.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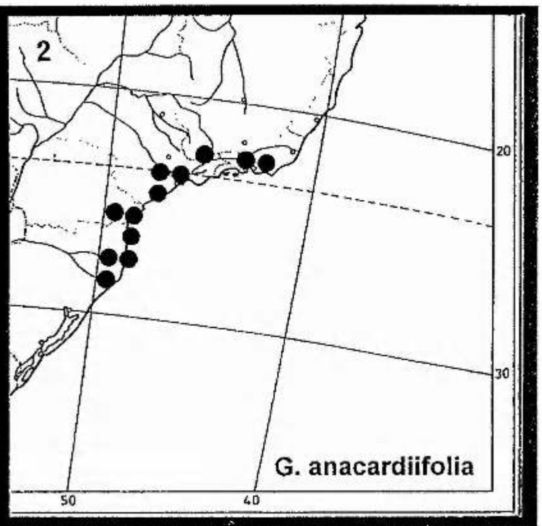
G. affinis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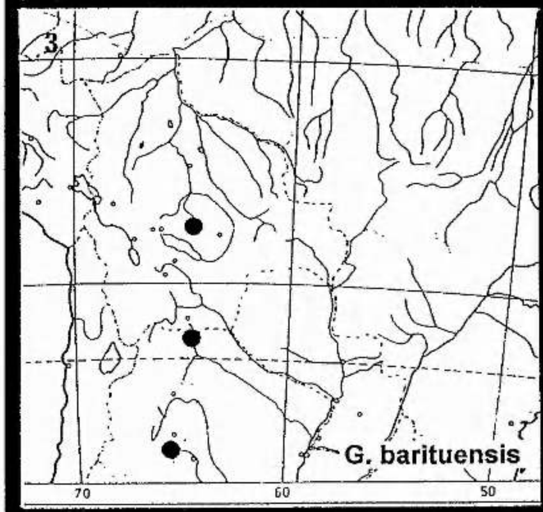
G. anacardiifolia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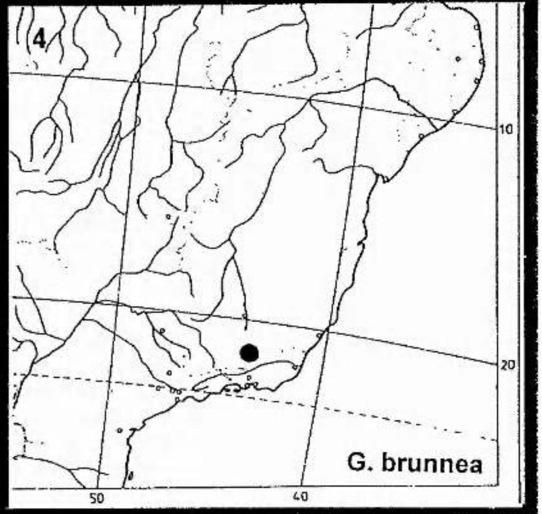
G. barituensis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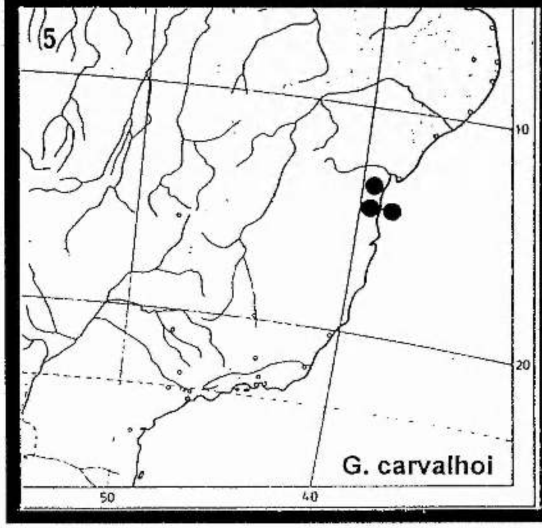
G. brunnea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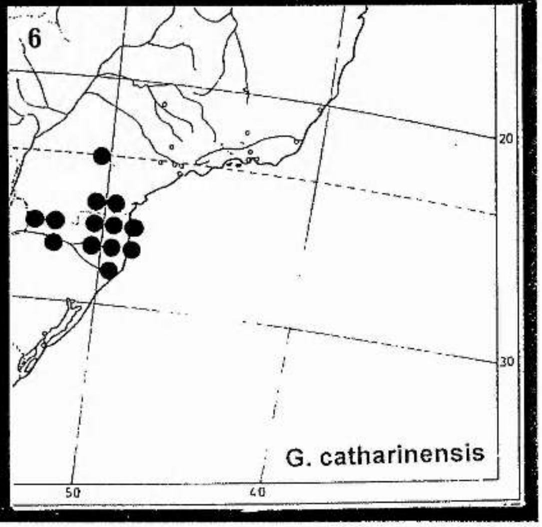
G. carvalhoi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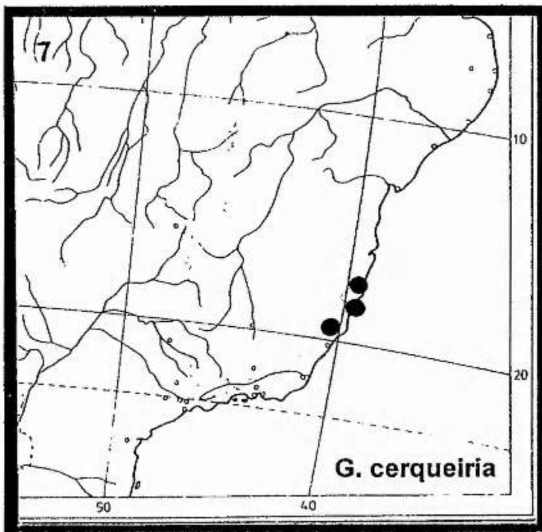
G. catharinensis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G. cerqueiria
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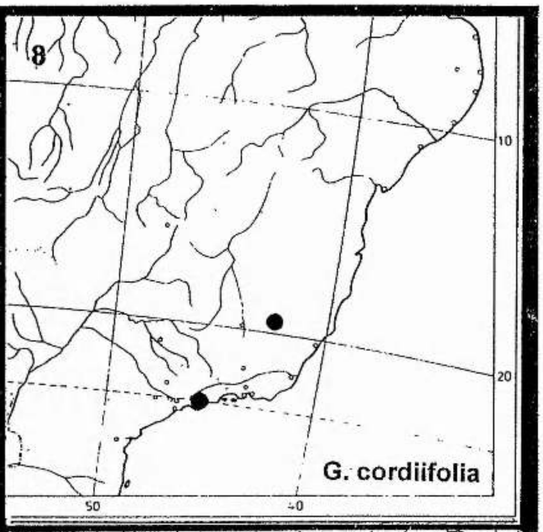
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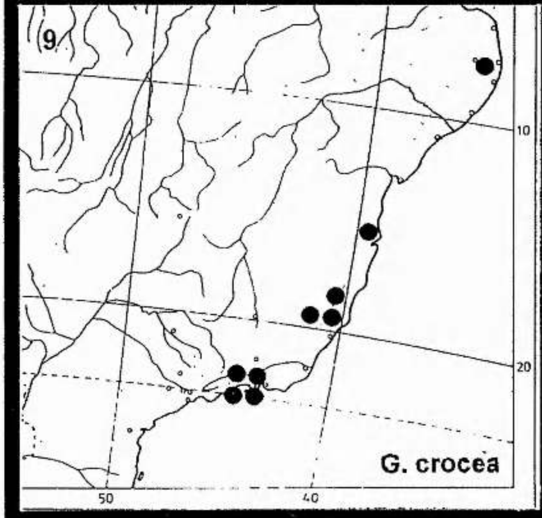
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G. crocea
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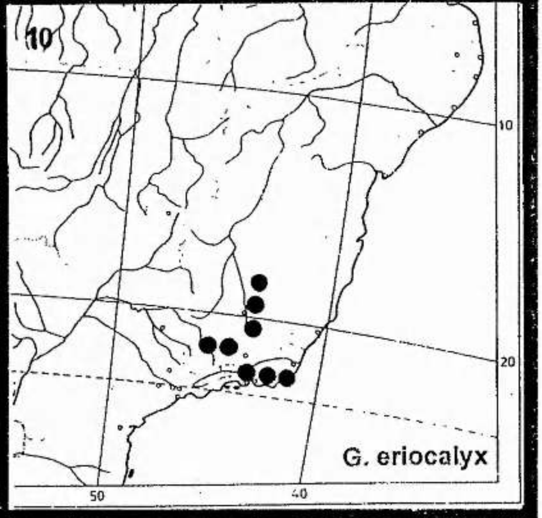
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G. eriocalyx
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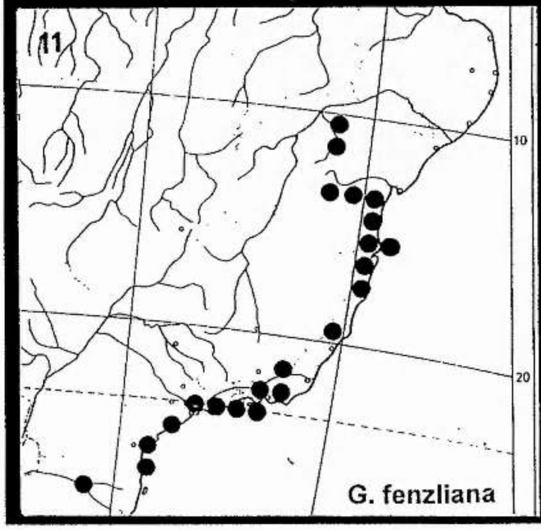
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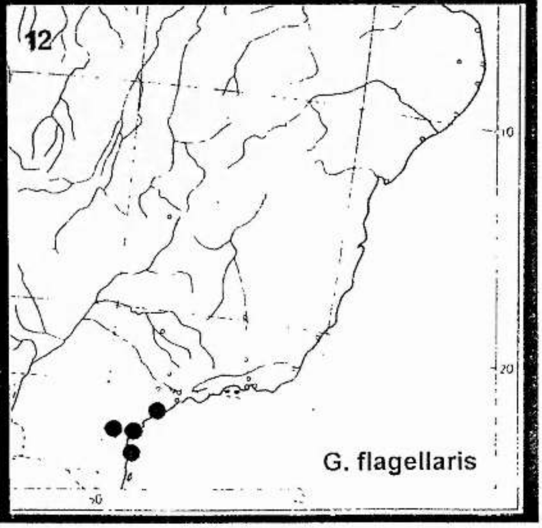
G. fenzliana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G. flagellaris
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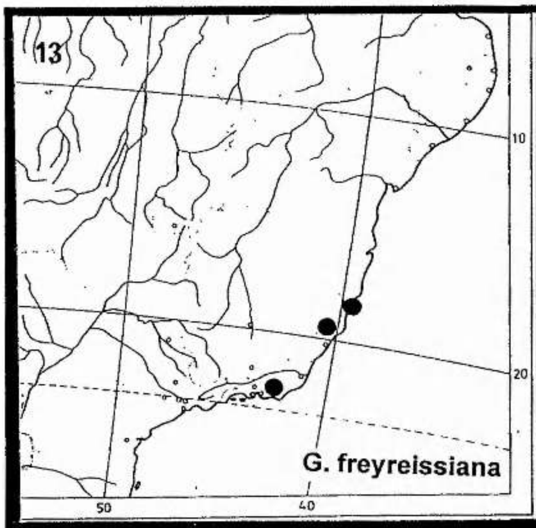
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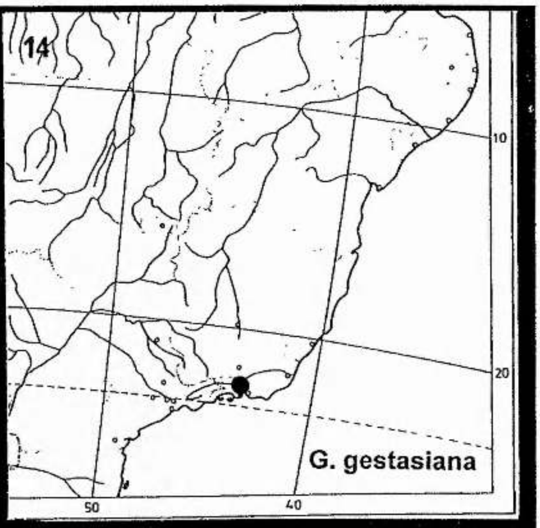
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G. gestasiana
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G. glazioviana
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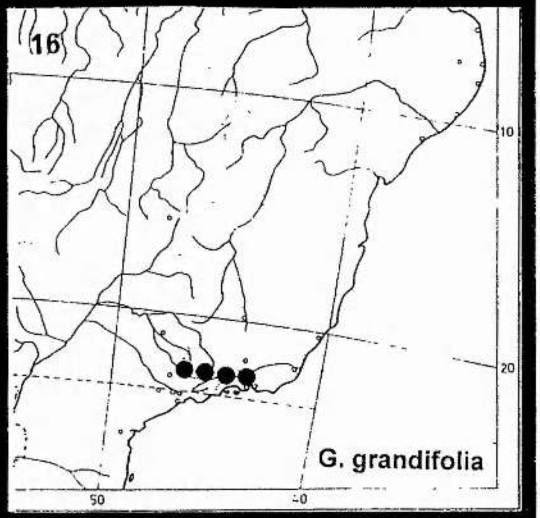
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G. grandifolia
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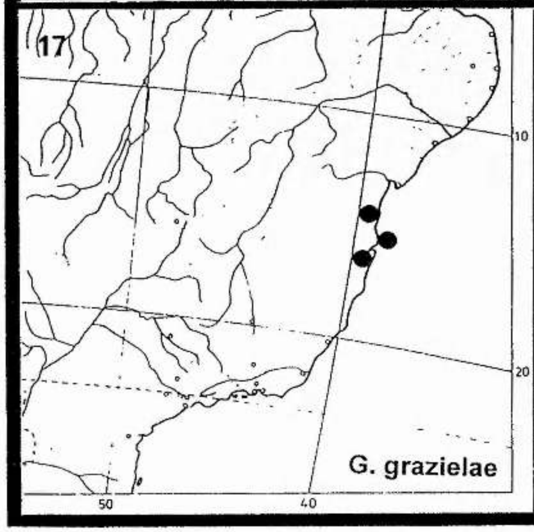
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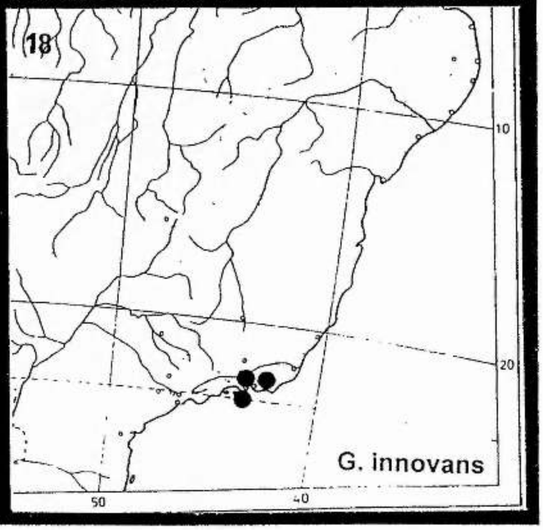
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G. innovans
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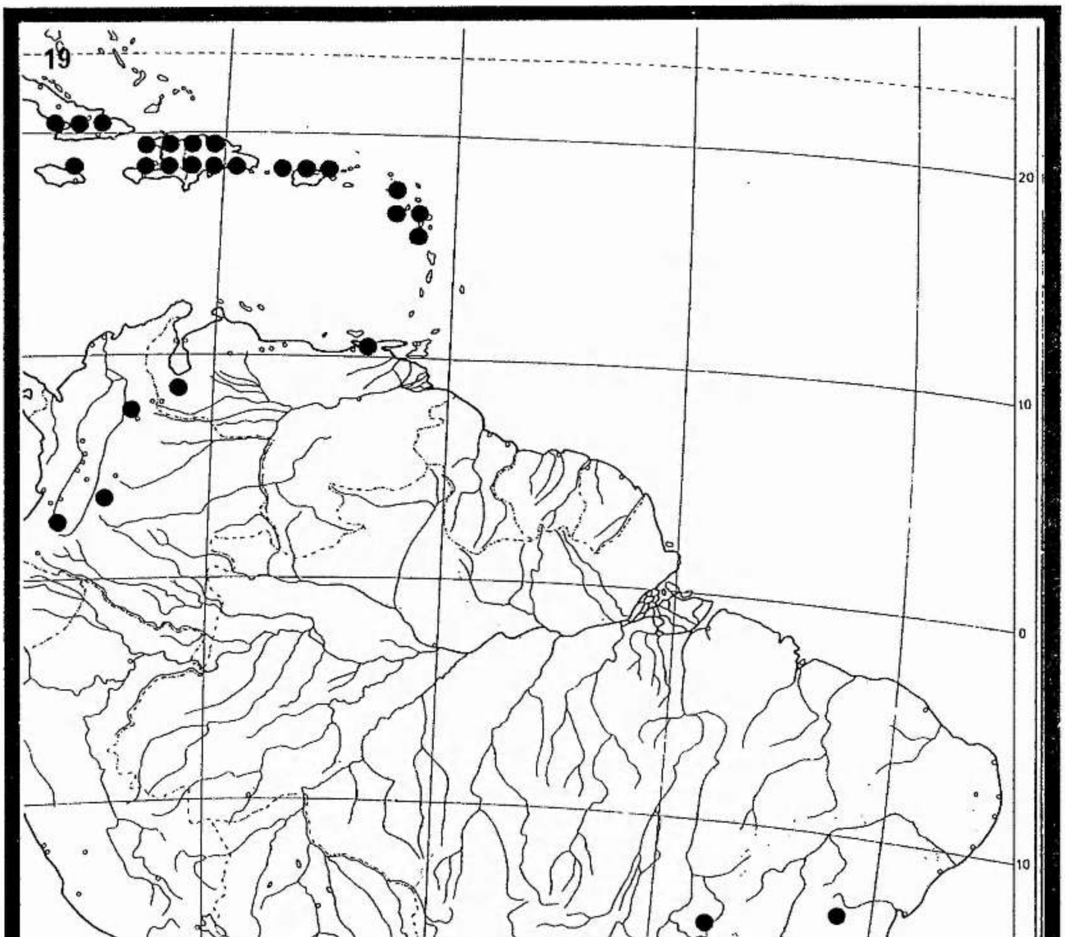
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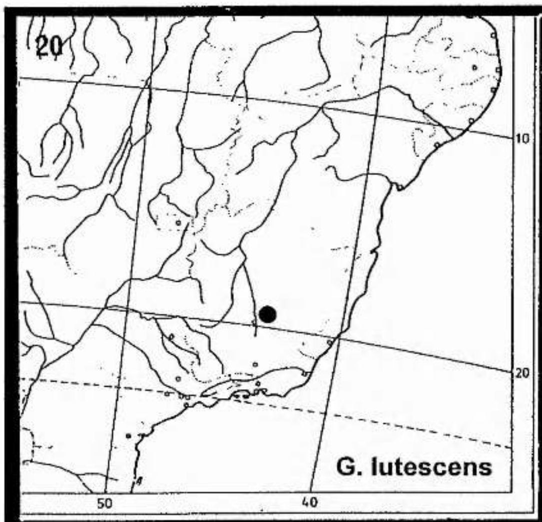
G. lindeniana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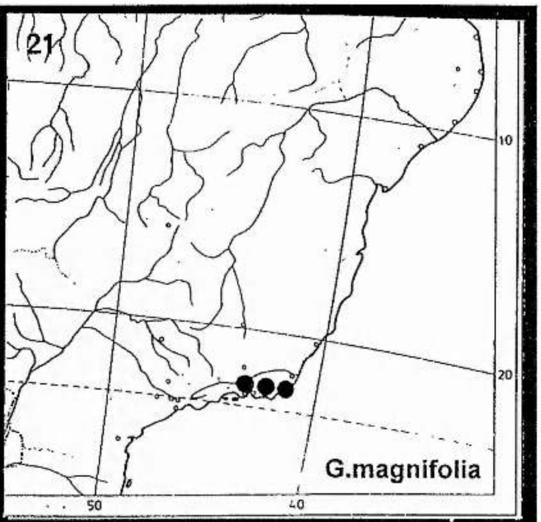
G. lutescens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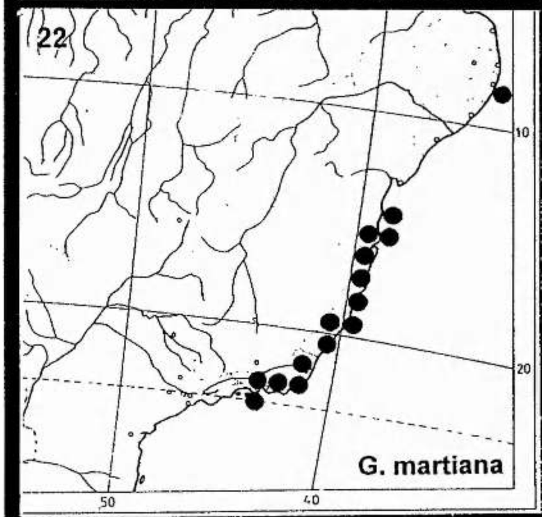
G.magnifolia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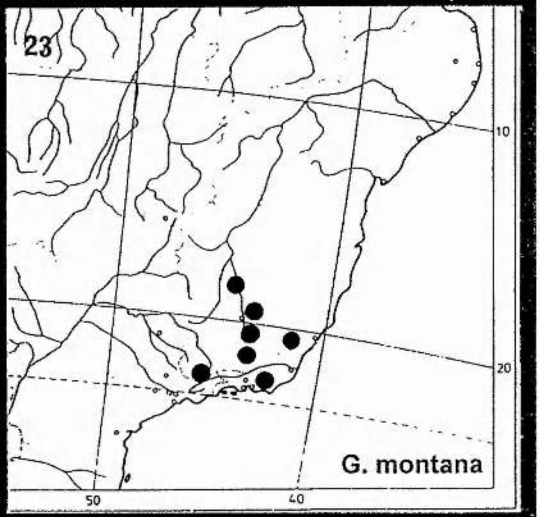
G. martiana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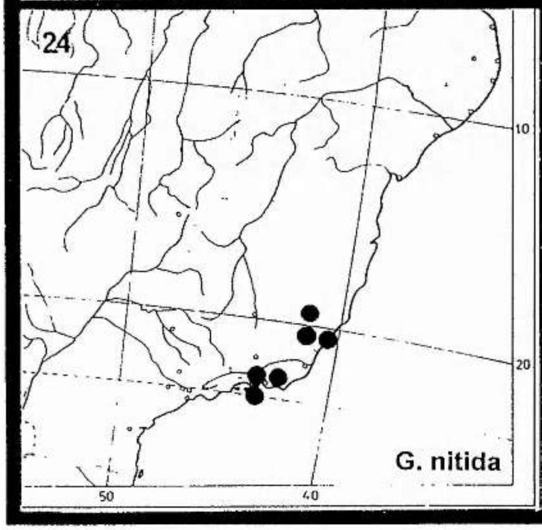
G. montana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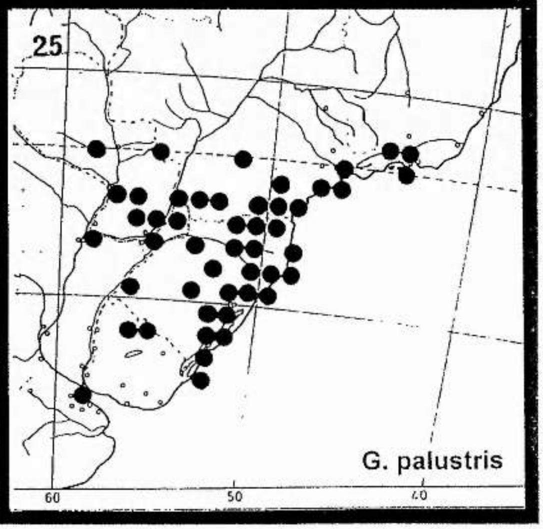
G. nitida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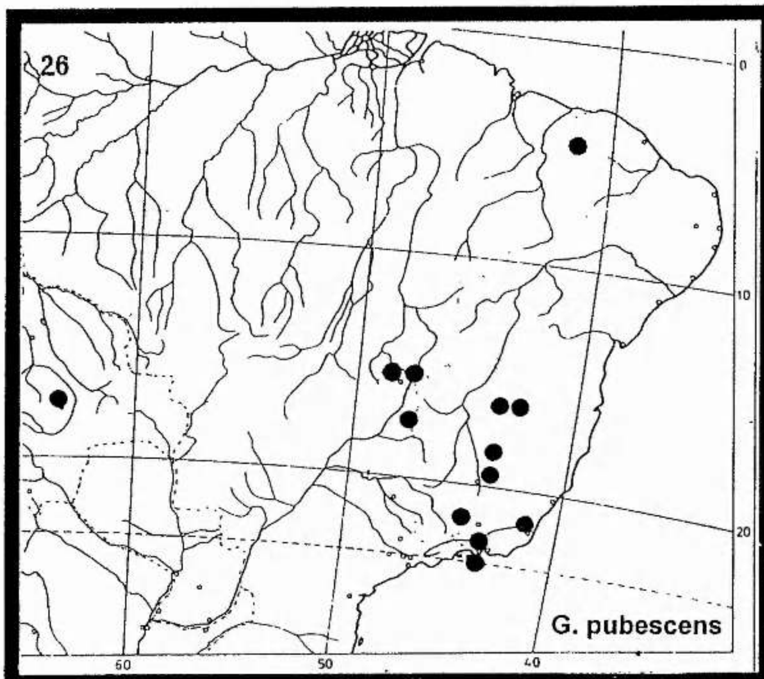
G. palustris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G. pubescens
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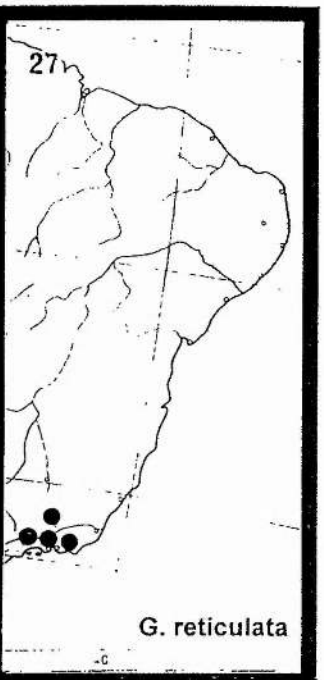
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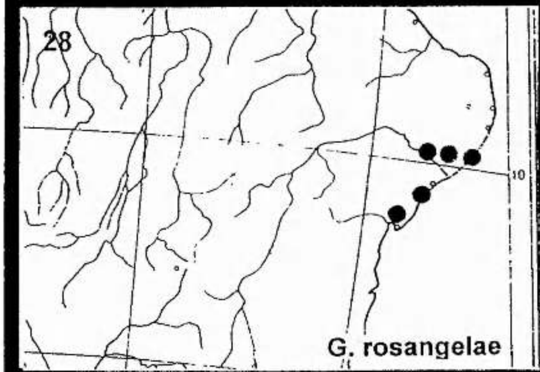
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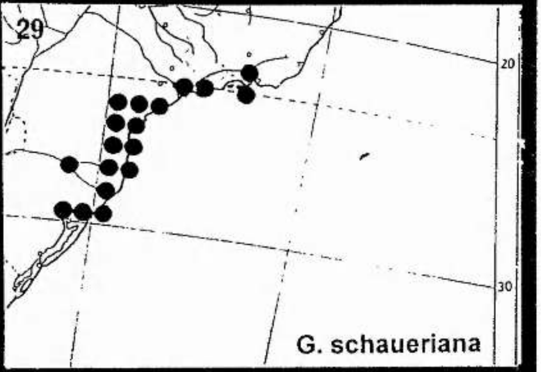
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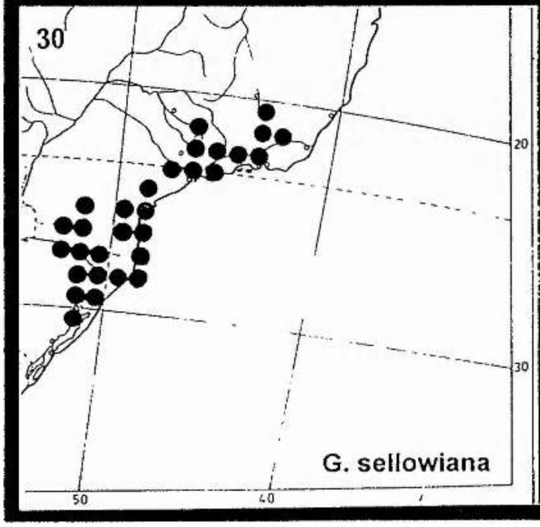
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G. sellowiana
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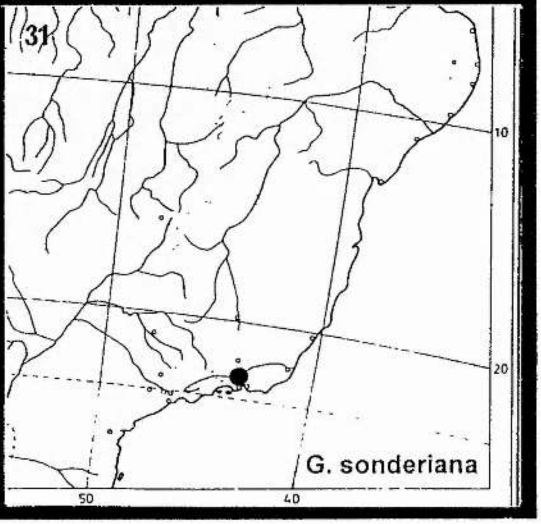
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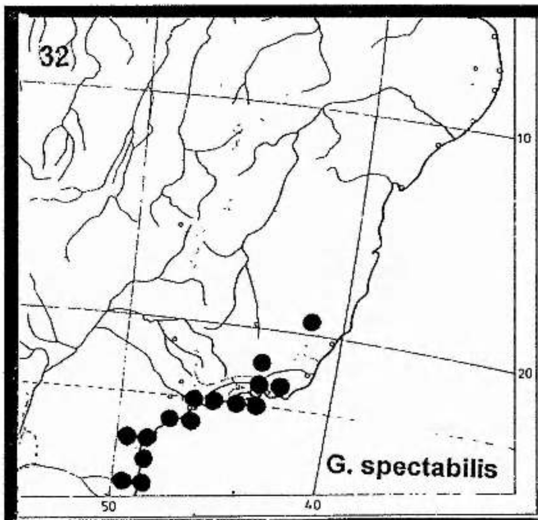
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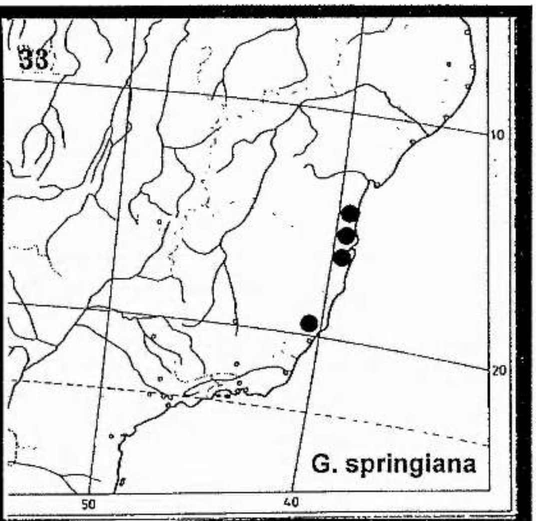
G. spectabilis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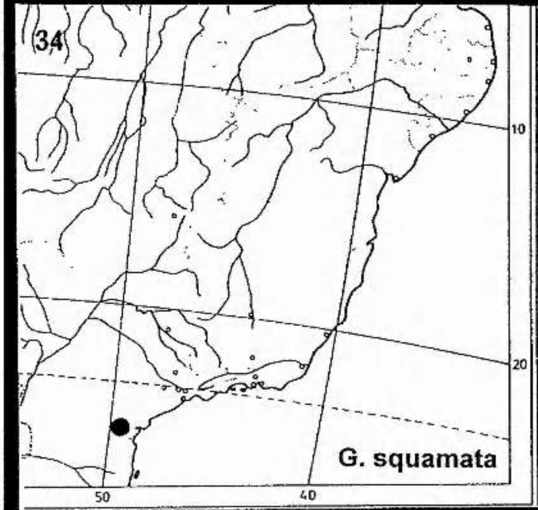
G. springiana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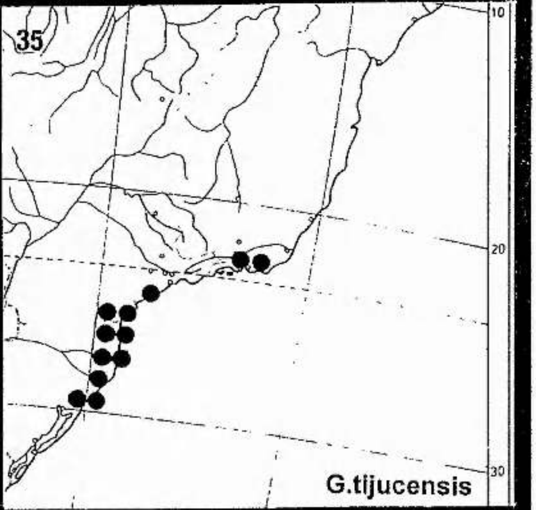
G. squamata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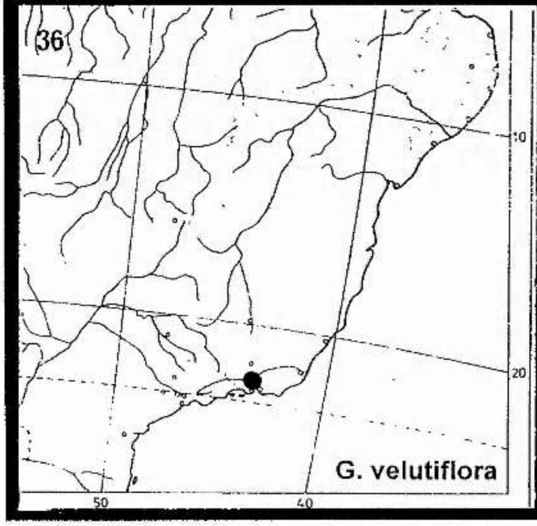
G.tijucensis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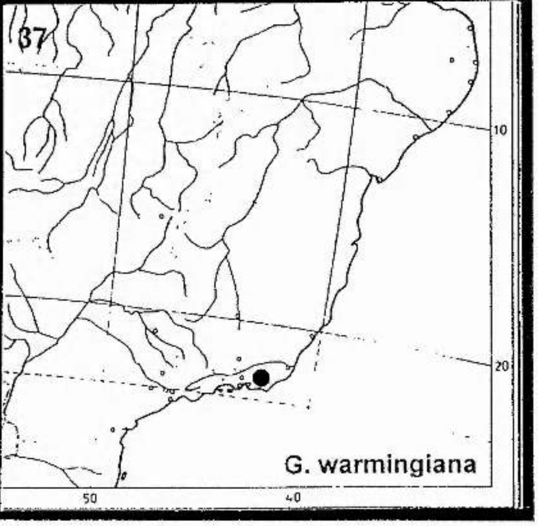
G. velutiflora


37

G. warmingiana

## Numerical list of accepted taxa

[with abbreviated epithets used in Table 4, Fig. 21 and synoptical key]

| | |
|---|---|
| 1. G. **affinis** (Cambess.) D.Legrand | [aff] |
| 2. G. **anacardiifolia** (Gardner) O.Berg | [ana] |
| 3. G. **barituensis** Legname | [bar] |
| 4. G. **blanchetiana** O.Berg | [blan] |
| 5. G. **brunnea** (Cambess.) D.Legrand | [bru] |
| 6. G. **cambessedeana** O.Berg | [camb] |
| 7. G. **carvalhoi** Nic Lughadha | [graz] |
| 8. G. **catharinensis** (D.Legrand) Nic Lughadha | [cath] |
| 9. G. **cerqueiria** Nied. | [cerq] |
| 10. G. **cordiifolia** (DC.) Nic Lughadha | [cord] |
| 11. G. **crocea** O.Berg | [croc] |
| 12. G. **eriocalyx** (DC.) O.Berg | [erio] |
| 13. G. **fenzliana** O.Berg | [fenz] |
| 14. G. **flagellaris** D.Legrand | [flag] |
| 15. G. **freyreissiana** O.Berg | [frey] |
| 16. G. **gestasiana** (Cambess.) D.Legrand | [gest |
| 17. G. **glazioviana** (Kiaersk.) D.Legrand | [glaz] |
| 18. G. **grandifolia** (Camb.) Mattos & D.Legrand | [gran] |
| 19. G. **grazielae** Nic Lughadha | [graz] |
| 20. G. **innovans** (Kiaersk.) D.Legrand | [inn] |
| 21. G. **lindeniana** O.Berg | [lind] |
| 22. G. **lutescens** (Cambess.) D.Legrand | [lut] |
| 23. G. **magnifolia** O.Berg | [mag] |

| | |
|---|---|
| 24. G. **martiana** O.Berg | [mart] |
| 25. G. **montana** (Cambess.) Nic Lughadha | [mont] |
| 26. G. **nitida** (Vell.) Nied. | [nit] |
| 27.G. **palustris** (DC.) Kausel | [pal] |
| 28. G. **pubescens** (DC.) D.Legrand | [pub] |
| 29. G. **reticulata** (Cambess.) O.Berg | [ret] |
| 30. G. **rosangelae** Nic Lughadha | [ros] |
| 31. G. **schaueriana** O.Berg | [scha] |
| 32. G. **sellowiana** O.Berg | [sell] |
| 33. G. **sonderiana** O.Berg | [sond] |
| 34. G. **spectabilis** (DC.) O.Berg | [spec] |
| 35. G. **springiana** O.Berg | [spri] |
| 36. G. **spruceana** O.Berg | [spru] |
| 37. G. **squamata** Mattos & D.Legrand | [squa] |
| 38. G. **tijucensis** (Kiaersk.) D.Legrand | [tij] |
| 39. G. **velutiflora** Mattos & D.Legrand | [vel] |
| 40. G. **warmingiana** (Kiaersk.) D.Legrand | [warm] |

## Index to scientific names

New names and new combinations are in **boldface,** synonyms are in *italics.*

Page numbers refer to the first page of the species account under which the name in question is treated (but not always as a synonym).

# Case Studies in the Reproductive biology of *Gomidesia*

## Introduction

The aim of the research described below was to obtain an understanding of the reproductive biology of some of the species of the genus *Gomidesia*, a subject on which no published data were available. Some level of knowledge of the breeding systems occurring in the genus was considered to be of great potential importance in interpreting the patterns of variation encountered within and between populations and species, a perennial problem in the Myrtaceae. In addition it was hoped to throw light on the functional significance of characters employed in constructing classifications and in particular to investigate the incidence of buzz-pollination in this, the only genus of the Myrtoideae to exhibit functionally poricidal anthers. Time and funding permitted detailed fieldwork on only a fraction of the species recognised in the genus so the populations to be studied were selected to represent both narrowly endemic and broadly distributed taxa, from habitats as diverse as *campo rupestre*, *cerrado*, gallery forest and *mata atlântica* and to include the extremes of anther morphology encountered in the genus. In total, populations of four different taxa of *Gomidesia* were studied in the Brazilian states of Bahia (1992) and Espírito Santo (1993) and in the Distrito Federal (1994) [Table 6]. A general account of the materials and methods common to these studies is provided below and variations are explained in the individual species treatments. Descriptions of the populations studied and their habitats are presented together with the results obtained for individual species and the discussion thereof.

## Materials and Methods

### Flowering phenology and natural fruiting success

A minimum of five (but more usually ten to twenty) fertile trees of the species to be studied were located and labelled using strong plastic tags with wire fixings. The most easily accessible tree was usually chosen for detailed observations of flowering phenology and natural fruiting success. Before the onset of flowering, sufficient conflorescences on this tree were selected to yield at least 135 buds (200 - 400 was normal). These conflorescences were individually labelled with masking tape and/or loops of waterproof paper at the internode below the first pair of leaves subtending the conflorescence and numbers of buds per inflorescence were recorded. The marked conflorescences were monitored daily. As flowers

Table 6. Location and habitat of *Gomidesia* species included in this study.

| Species | Study Site | near | State | Location | Habitat | Habit | Study Period |
|---|---|---|---|---|---|---|---|
| *G. fenzliana* O.Berg | Catolés | Abaira | BA | 13° 15' S 41° 55' W | High altitude gallery forest | Tree | Jan - Mar 1992 |
| *G. lindeniana* O.Berg | Catolés | Abaira | BA | 13° 14' S 41° 54' W | Campo Rupestre | Shrub | Feb - Apr 1992 |
| *G. cerqueiria* Nied. | Reserva CVRD | Linhares | ES | 19° 12' S 40° 02' W | Atlantic Forest | Treelet | Jan - Mar 1993 |
| *G. pubescens* (DC.) Kausel | Reserva IBGE | Brasília | DF | 15° 57' S 47° 52' W | Planalto gallery forest | Tree | Jan - Mar 1994 |
| *G. lindeniana* O.Berg | Reserva JBB | Brasília | DF | 15° 52' S 47° 50' W | Cerrado | Tree | Jan - Mar 1994 |

BA = Bahia, CVRD = Companhia Vale do Rio Doce, DF = Distrito Federal, ES = Espírito Santo, IBGE = Instituto Brasileiro de Geografia e Estatistica, JBB = Jardim Botânico de Brasília opened they were individually tagged with lengths of cotton and daily counts were made of buds, flowers opening on that day and flowers or floral remains persisting from previous flowering days. In addition to these detailed observations, more general records of flowering were maintained for other trees on which a number of conflorescences had been tagged for use in breeding system studies (see below). For each of these trees the presence or absence of open flowers in the marked conflorescences and on the tree as a whole was recorded on a daily basis. Daily observations on all trees continued for three to seven weeks after the onset of flowering in the population. Some five to eight weeks later the tagged inflorescences were collected and numbers of buds, persisting ovaries and developing fruits were recorded. Developing fruits were soaked in dilute detergent solution and dissected, and the relative sizes of the ovules (and/or young seeds) within were recorded.

### Anthesis and pollination

Timing and mode of anthesis were documented for flowers in different individuals. Visitors to flowers were observed and, when possible, collected for identification. Flower descriptions were prepared on the basis of field observations and fixed material stored in 70% alcohol.

### Breeding system

The breeding system was assessed by performing hand-pollinations on bagged flowers. Inflorescences in bud were tagged and bagged. Greaseproof paper bags were used when weather conditions permitted but in particularly wet and windy weather they were substituted by fine-mesh nylon bags which proved more resistant to tearing. Bags were fastened around the base of the conflorescence or one or two internodes below it using lengths of plastic-coated wire. Bagged conflorescences were monitored on a daily basis. When anthesis occurred open flowers were individually tagged with lengths of coloured thread. Unopened buds in the same inflorescence were removed only where this was necessary to permit unambiguous tagging of the open flowers. One of the following treatments was then applied to the open flowers before the bags were replaced.

1. Hand self-pollination
2. Hand cross-pollination
3. Automatic self-pollination (control, no further treatment applied)
4. Emasculation

Flowers in treatments 1 - 3 were not emasculated. Hand pollinations were carried out by brushing dehisced anthers against the stigma. In the case of *G. cerqueiria* the apically dehiscent anthers were removed from the donor flower and opened on a clean watch glass using a scalpel blade which was then used to apply pollen to the stigma of the recipient flower. The time of each pollination and the pollen source(s) were recorded. As all species presented dry stigmas, receptivity could not easily be assessed. Pollinations were carried out at least 30 minutes after anthesis and before midday i.e. several hours before the first flowers began to show signs of wilting. For self-pollinations the anthers were taken from the same flower. For cross-pollinations the anthers were taken from recently collected flowers from plants at least 50 m (and sometimes up to 1 km) away from the recipient plant. Emasculations were carried out using fine scissors immediately after anthesis and before anther dehiscence.

Treated flowers were monitored on a daily basis and subsamples of treatments 1 - 3 were fixed in cold 70% FAA at intervals of 2 - 28 days after pollination in the case of selfs, 2 - 25 days after pollination in the case of crosses and 1 - 15 days after flowering in the case of automatic pollinations. Due to the narrow window of time available for emasculation and the painstaking nature of the operation it was not possible to emasculate a sufficient number of flowers to permit subsampling on the scale described for the other treatments.

Flowers fixed up to one week after hand-pollination were used to study pollen tube growth in the style and ovary using leuco-aniline blue stain and fluorescence microscopy (Martin, 1959) with a Leitz labolux microscope fitted with ploemak incident lighting and uv filters. Some of the older material was sectioned by rotary microtome, either at 14 µm embedded in paraffin wax, or at 5 µm in historesin. Sections were stained with Delafield's haemotoxylin or alcian blue/safranin (Johansen, 1940). In addition whole ovules/seeds were observed using clear-squash techniques (Herr, 1971; Stelly et al., 1984) and differential interference contrast (DIC) optics (Herr, 1973). [See Appendix 2].

The remaining flowers in treatments 1 - 3 and all the emasculated flowers were left in situ to determine fruit set. Daily monitoring and subsequent collection and examination of persisting ovaries and developing fruits were carried out as described above for natural fruiting success assessment.

### Descriptive indices

To aid in the interpretation of data and, in particular, to facilitate between-species comparisons, indices of flowering synchrony, pre-emergent reproductive success, self-incompatibility and automatic selfing were calculated as follows:

**Flowering synchrony** (hereafter referred to as synchrony) was quantified at both individual and population level, following the method of Augspurger (1983). Individual synchrony is a composite measure of the overlap of a given individual's flowering days with those of all individuals in the study population. $X_i$, the index of synchrony for individual i is defined as:

$$X_i = \left(\frac{1}{n-1}\right)\left(\frac{1}{f_i}\right)\sum_{j=1}^{n} e_{j\neq i}$$

where $e_j$= number of days both individuals i and j are flowering synchronously, $j \neq i$;

$f_i$ = number of days individual i is flowering;

n = number of individuals in population.

When X = 1, perfect synchrony occurs, i.e. all flowering days of individual i overlap with all flowering days of each other individual, $j \neq i$, in the population.

When X = 0, no synchrony occurs, i.e. no overlap occurs among any of the flowering days of individual i and any other individual, $j \neq i$, in the population.

Population synchrony is simply the mean of the values of individual synchrony. These indices do not reflect the differences in the number of open flowers on an individual from day to day but rather measure overlap of days when an individual has at least one open flower.

**Pre-emergent reproductive success** (hereafter PERS) was estimated by measuring the fruit/flower (Fr/Fl) ratio and the seed/ovule (S/O) ratio in each species. PERS is the product of (Fr/Fl) and (S/O) and is the percentage of all ovules maturing into seeds. Wiens et al. (1987) demonstrated that among outcrossing species PERS averaged about 22%, whereas in inbreeding species the average PERS was approximately 90%. They interpreted PERS as a measure of selective forces acting on the embryo phenotype during development. In outcrossing, genetically heterozygous organisms a greater proportion of potential progeny are lost during the pre-emergent phase of the life-cycle than the post-emergent phase.

PERS = % natural fruit set x no. of seeds per fruit/no. of ovules per fruit

**The index of automatic self-pollination** (hereafter IAS) was obtained for self-compatible species by comparing percentage fruit set following automatic selfing and hand-selfing. The IAS reflects the relative success of automatic selfing and vector-mediated selfing, the vector being the experimenter in the case of the controlled pollinations undertaken here or the pollinating insect in the natural situation. Fully autogamous plants score 1, while partially autogamous plants have values between 1 and 0. Self-compatible species mechanically prevented from intra-flower selfing would score 0 (Ruiz & Arroyo, 1978).

IAS = % fruit set in automatic selfs / % fruit set in hand selfs.

**The index of self-incompatibility** (hereafter ISI) reflects the relative fruiting success of selfed and crossed flowers. Fruit set results rather than seed counts were used as the basis of estimates of ISI following Bawa (1974) and Bullock (1985). This latter author commented that seed counts had not been more important than fruits to the conclusions of other studies. As numerous subsequent authors have calculated ISI on the basis of fruit set alone this method was preferred in the present study for the purposes of comparability. Bawa (1974) and Ruiz and Arroyo (1978) considered species with an ISI of 0.2 or less to be self-incompatible while Bullock (1985) considered 0.25 the threshold value above which species were considered self-compatible.

ISI = % fruit set in selfed flowers / % fruit set in crossed flowers.

## Case Study 1: *Gomidesia fenzliana* near Catolés, Bahia

### Study site

Reproductive biology studies of *G. fenzliana* were carried out in the mountains above Catolés, between Abaira and Piatã, Bahia, Brazil during the period January to March 1993. The study ran concurrently with a floristic survey of the area undertaken by staff of the Royal Botanic Gardens, Kew and the University of São Paulo. This latter survey is the most recent of a series of inventories conducted at points along the Serra do Espinhaço, a 1000 km mountain range which runs through the states of Minas Gerais and Bahia. These mountains are best known for the spectacular and unique *campo rupestre* vegetation which occupies their upper reaches. This vegetation type is discussed further under Case Study 2.

*Gomidesia fenzliana* is not a characteristic species of *campo rupestre* as such. Rather it is generally found at the margins of gallery forests which occur along the streams in this area. Two of the three populations of *G. fenzliana* encountered near Catolés occurred in gallery forest vegetation. Of these, one (Tijuquinho) was too distant and difficult for daily access. The other population was found in sparse gallery forest on a steep slope, towards the top of which the forest petered out into a bamboo thicket which gave the site its name, Taquara (Fig. 32a). Just over the ridge, in the valley of the Cigano river, a third population was discovered with trunks growing up between huge rocks on a much dissected rocky plateau which appeared rich in bromeliads but bereft of other typical *campo rupestre* vegetation (Campo do Cigano, Fig. 32b). The situation of these latter trees permitted access to their canopies by clambering on adjacent rocks while the height of the Taquara trees necessitated the construction of a platform and the manipulation of various boughs so that sufficient flowering branches could be reached.

Flowers of *G. fenzliana* are described in detail in the Systematic Treatment. From the point of view of reproductive biology the characters of importance are that the ovary is trilocular with two ovules per locule and that the anthers exhibit only a slight vertical displacement of the pollen sacs, the thecal margins losing curvature on dehisence and held parallel to each other or slightly divergent (Fig. 14j-n). Thus pollen is exposed laterally along the whole length of the anther.

Results obtained for *G. fenzliana* are outlined below and summarised in Table 7.

## Table 7

Summary of results for *Gomidesia fenzliana*

| **Treatment:** | | **Natural** | **Cross-pollinated** | **Self-pollinated** |
|---|---|---|---|---|
| | | | | |
| % Fruit set | | 9 (12/202) | 46 (28/61) | 20 (42/206) |
| | | | | |
| Developing seeds per ovary: | mean | 2.3 | 1.96 | 1.78 |
| | mode (range) | 1 (1-6) | 1 (1-6) | 1 (1-4) |
| | | | | |
| PERS | | 3.5 | | |
| | | | | |
| Persisting at intervals after hand-pollination: | @ 10 days | | 60 (58/96) | 52 (133/253) |
| | @ 20 days | | 39 (22/56) | 35 (50/143) |
| | | | | |
| Resulting ISI | | | 0.43 | |
| | | | | |
| Breeding system | | | ' self-compatible' | |

## Flowering Phenology and Natural Fruiting Success

**Population and synchrony.** The onset of the flowering episode observed was gradual. A single individual in the Cigano population had a few open flowers in the first week in February (i.e. towards the end of the rainy season). The same individual flowered again on February 12th, and on February 13th open flowers were observed on this tree and two more of the five trees under observation. The remaining two trees began flowering nine and ten days later respectively. Trees which had begun flowering did not, in general open new flowers each day. With the exception of one individual in the Cigano population a flowering day for a particular tree tended to be followed by one or two days on which that individual did not open any flowers. This pulsed effect was particularly evident in the first weeks of flowering and during this period a loose synchrony was detected among the trees which had begun flowering. Later in the flowering episode this pulsed synchrony seemed to break down, and the tree in which the onset of flowering was latest proceeded to open flowers on 20 out of 26 consecutive days. This tree had a synchrony index of 0.38, the lowest among those monitored. One of the Taquara individuals scored the highest synchrony value of 0.72 and the population index was 0.59 for the period observed. Unopened buds remained on all trees on the last day of the observation period (March 28th) but some of these had already begun to dry out and fall, and the major flowering period can be said to have ended approximately six weeks after the first flowers opened.

**Conflorescence.** Conflorescence size is rather variable in this species. In the study populations a conflorescence may consist of anything from 4-40(-60) buds arranged in one to three pairs of inflorescences each of 2-20 buds. Once flowering begins, an individual conflorescence opens from 0 to 12 flowers each day. 0 was the modal number in conflorescences which had begun flowering but such a conflorescence tended to open at least one flower on most flowering days until all flowers had opened. The mean number of open flowers per flowering conflorescence on flowering days was 2.9 and the modal number was 1. The flowering life of an individual conflorescence ranged from 7 to 23 days and spanned two to eight flowering days. Apical buds on sub-apical branches tended to open first.

**Flowering and natural fruit set.** Less than half of the buds present at the start of the observation period produced flowers that opened normally. About 25% of buds fell without opening and < 1% remained unopened at the end of the observation period. A further 25% of buds opened partially, exposing the stigma, but did not exhibit the sequence of events described below as a normal anthesis. Most flowers which opened (normally or otherwise) fell four to five days after anthesis. Only 4.4 % of the buds originally present persisted to form fruit. This figure is equivalent to 5.9 % of the flowers whose stigmas were exposed and 9 % of the flowers which opened 'normally'. This latter figure is used in the discussion of fruiting success hereafter. Dissection of the fruits collected permitted the identification of two distinct size classes of ovules/seeds. Most measured 0.6 mm or less along their largest dimension and had a concave appearance. These were termed non-developing ovules. Larger structures, usually > 1 mm with mostly convex surfaces were termed developing. The modal number of developing seeds per fruit was 1 and the mean was 2.3 (range 1-6). Thus the PERS for the species is 3.5%. Developing seeds tended to be evenly distributed across the three locules, i.e. locules containing two developing seeds were rare in fruits containing only two or three developing seeds.

### Anthesis and Pollination

**Anthesis.** Observations of anthesis were made for this species on several days and the timing was found to be variable both between flowers on a given tree and from day to day. With experience, flowers which were about to open could be distinguished by an almost imperceptible elongation of the exposed dome of petals. Shortly after dawn the outer petal, which was often suffused pink, separated itself a little from the dome formed by the other petals. An interval of up to 20 minutes elapsed before the opposite petal started to rise exposing the upper portion of the still folded style. The filaments of the incurved stamens then became visible as the other petals started to pull away from them. About one hour after the onset of anthesis, the filaments of a group of stamens (perhaps 10% of the total) began to rise and to straighten and, over the next 30 - 40 minutes all of the stamens and the style rose to above the level of the petal apices. The style was still slightly bent and the filaments had a crumpled appearance. As the style straightened the stamens lost their crumpled appearance and splayed out from their incurved/erect position to a more or less patent position. The petals accompanied the stamen movement until they were patent to reflexed. Anther dehiscence occurred in some stamens c. 90 minutes after anthesis but was not synchronous, even within a flower. A strong sweet scent was detectable at this time.

Many exceptions to the general pattern described above were observed. The most common abnormality was for the upper portion of the style to be trapped by (stuck to?) a petal apex thus preventing the flower from opening normally. Another phenomenon commonly observed was flowers in which the petals and style rose normally but the stamens failed to unfurl. Such part-opened flowers represented a significant proportion of total flower production on some flowering days. They were excluded from experimental treatments but their effect is discussed under natural fruiting success.

**Visitors.** During numerous observation periods covering the interval from anthesis to 16.00 h (by which time the flowers had wilted) very few visitors were observed and no principal pollinator was identified. Most observation periods passed without a sighting of a single visitor and most of the visitors collected were observed in a single half-hour period from 11.30 a.m. till noon on a single day. These were mainly Diptera which exhibited gleaning behaviour and were not observed to make contact with the stigma of any flower.

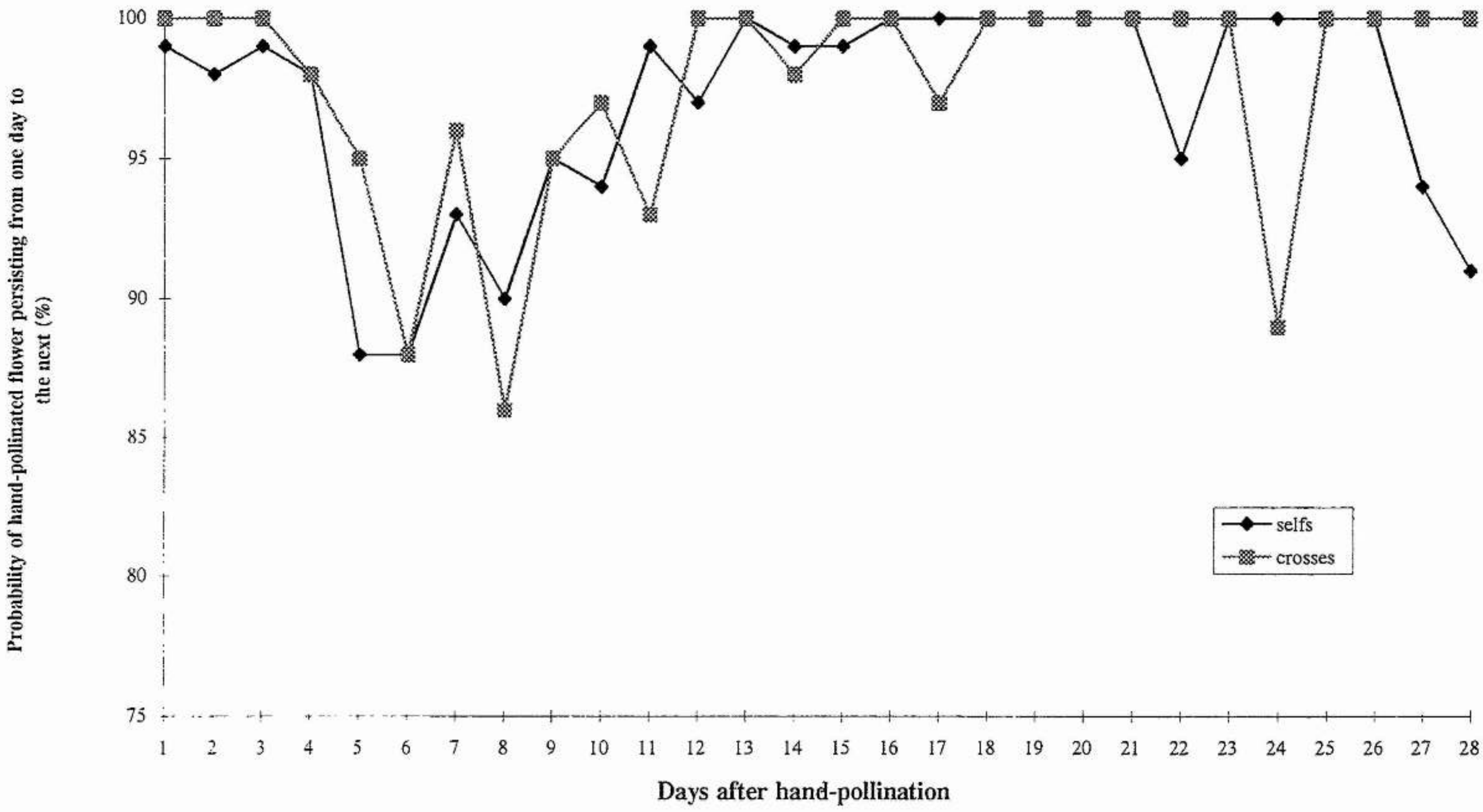
### Breeding system

**Hand-pollinations.** There was massive fall-off of hand-pollinated flowers in the first ten days after pollination. Fig. 51 presents fall-off level in terms of the probability of a retained ovary persisting on the tree from one day to the next. Fall-off peaked between days 4 and 6 for selfed flowers and on days 5-6 and 7 -8 for crossed flowers. Ten days after pollination the proportion of crossed flowers retained was significantly greater than that of selfed flowers (60% and 52% respectively; chi-square = 6.5, df = 1, p = 0.01). Fall-off continued at a greatly reduced level for the next ten days (days 11 - 20 after treatment) and on day 20 there was no significant difference between the numbers of selfed and crossed ovaries persisting (35% and 39% respectively; chi-square = 1.1, df = 1, p = 0.29). By the time the fruits were collected however, crossed ovaries were present in significantly higher numbers than selfed ovaries (46% and 20% respectively; chi-square = 54.0, df = 1, p < .0001). The resultant ISI value is 0.43. The discrepancy in the number of crosses retained between 20 days and the collection day is due to the inclusion in the fruit-set result of later cohorts of pollinated flowers for which 20 day data were not available i.e. flowers pollinated on or after March 9th.

**Automatic pollinations and emasculations.** Flowers left for automatic self-pollination and those emasculated also exhibited massive fall-off on days 1 - 10. All emasculated flowers had fallen by six days after anthesis. Fall-off in automatically self-pollinated flowers peaked at six to eight days after anthesis and on day 10 levels of ovary retention in automatically selfed flowers were statistically equivalent to those in hand-selfed flowers. 20-day data are not available for automatically selfed flowers but levels of fruit set in this treatment are statistically equivalent to those in hand-selfed flowers. This apparent uniformity masks a

FIG. 51. Loss of hand-pollinated flowers in *Gomidesia fenzliana.*

Loss of hand-pollinated flowers of *Gomidesia fenzliana*



substantial difference between two cohorts of automatically pollinated flowers. Those tagged in February had a fruiting success of 9% whereas the cohort tagged in mid-March had 20% fruiting success. An IAS value of 0.69 was calculated on the basis of the pooled data from these two cohorts.

**Fruit dissections.** Fruit dissections revealed that the modal number of developing seeds in developing fruits of all treatments was 1, with means of 1.96 in crosses (range 1-6), 1.78 in selfs (range 1-4) and 1.14 in automatic self-pollinations (range 1-2). Numbers of developing seeds in crossed and selfed fruit did not differ significantly from those for natural fruit set (Crosses: $t = -0.57$, $df = 52.7$, $p = 0.56$; Selfs: $t = -1.26$, $df = 42.7$, $p = 0.21$). Numbers of developing seeds in fruits arising from flowers left to self-pollinate automatically were significantly lower than those for natural fruit set ($t = -3.53$, $df = 33.0$, $p = 0.001$). Fruits resulting from natural pollination and controlled cross pollination occasionally were found to contain five or six developing seeds whereas fruits resulting from hand self-pollination contained a maximum of four developing seeds and no fruit resulting from automatic self-pollination was found to contain more than two developing seeds .

**Fluorescence microscopy.** Fluorescence microscopy revealed the presence of numerous pollen tubes in fixed material of most crossed, selfed and automatic pollinations at two days after pollination and beyond. At least some of these tubes had reached the base of the style by two to three days after pollination and fluorescence could often be detected in the micropylar region. However, the thickness of the integuments rendered the tracking of the pollen tubes within the ovule difficult and it was often impossible to say with certainty whether or not penetration had occurred. Thus, although possible penetration events were observed in 2- and 3-day old material and definite penetrations in 4- and 5-day old fixations, the results are not suitable for statistical analysis. In general, however, whenever pollen tubes were plentiful in the style most of the ovules appeared to have been penetrated, in both selfed and crossed pistils.

**Differential Interference Contrast Microscopy.** These observations were confirmed by the DIC optics images obtained of ovules dissected out from older developing fruits. The 10- and 13-day fixations of selfed and crossed ovaries revealed a globular proembryo in most ovules for which a clear image could be obtained (Fig. 52a, b, c). Due to the limitations of the technique, failure to discover an embryo in a particular ovule could not be interpreted as proof of its absence as it could equally be ascribed to the faint nature of the images being studied. It

FIG. 52. Differential Interference Contrast images of ovules of *Gomidesia fenzliana* from ovaries fixed after experimental hand-pollination. (Scale bar = 10 µm, except in **b** where scale bar = 100 µm)

**a** Pro-embryo (large arrow) in ovary of cross-pollinated flower at day 10. Note prominent nucleus within embryo (small arrow) and fusion nucleus (small arrow). Compare with optical section **c**, below.

**b** Pro-embryo (arrowed) in ovary of self-pollinated flower at day 10.

**c** Same ovule as in **a** but in different plane of focus, showing another prominent nucleus (small arrow) within the pro-embryo (large arrow).

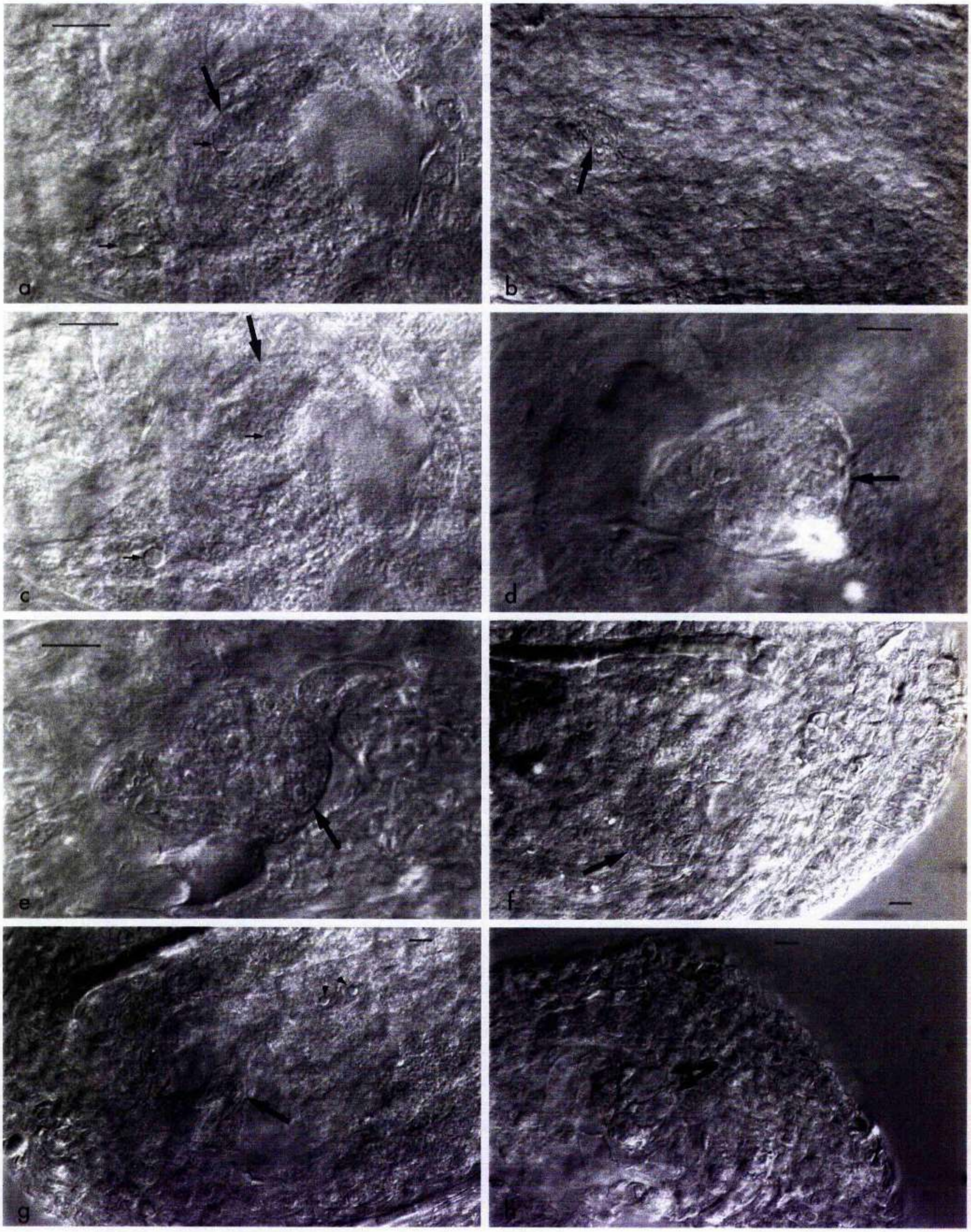
**d** Highly refractive embryo (arrowed) in ovary of self-pollinated flower at day 13.

**e** Embryo (arrowed) in ovary of self-pollinated flower at day 18.

**f** Embryo (arrowed) in ovary of cross-pollinated flower at day 18.

**g** Unfertilised egg sac in ovary of cross-pollinated flower at day 18. Note egg cell (large arrow) and polar nuclei (small arrows).

**h** Degenerating synergids (arrowed) in ovary of cross-pollinated flower at day 18.


a
b
c
d
e
f
g
h

can, however, be stated with certainty that in at least some selfed and crossed ovaries of this age class all six ovules contained developing embryos.

DIC images of older ovules were poorer still. In 15-day fixations proembryos were detected in two (or occasionally three) out of six ovules and in 18-day samples most ovaries had just two developing embryos. The embryos observed at this point were still globular, generally more than eight-celled and had a clearly defined suspensor (Fig. 52e, f). In some ovules in which proembryos were not discovered highly refractive areas were encountered within the embryo sac. Their shape, size and position relative to the synergids suggested that they might be interpreted as abortive embryos. In other cases refractive areas were seen in otherwise normal embryos (Fig. 52d). Not all the seeds scanned fell into this pattern of developing or abortive embryos however. One 15-day selfed ovary included an ovule in which the synergids, egg nucleus and fusion nucleus could be clearly discerned. One 18-day crossed ovary contained an ovule with an apparently unfertilised sac still intact with two polar nuclei clearly visible (Fig. 52g). In other ovules of the same treatment only degenerating synergids could be detected (Fig. 52h).

**Histological Sections.** Sections of 25 - 27 day old selfed ovaries revealed the deposition of tannins in the integuments and in the synergids. Developing embryos (Fig. 53 f, g, h) and endosperm (Fig. 53e) were clearly visible in two (or occasionally three) seeds per ovary. In the other ovules the embryo sac appeared to have collapsed (Fig. 53d).

## Discussion

The pulsed flowering pattern exhibited by this species, at least in the early part of the flowering episode, is referrable to the the pulsed annual pattern described by Newstrom et al. (1994). This pattern was reported by Proença and Gibbs (1994) for two myrtaceous species (*Myrcia rhodosepala* and *Blepharocalyx salicifolius*) in the *cerrado* of Central Brazil and by Oliveira et al. (1991) for *Vellozia squamata* (Velloziaceae) in the same habitat. This pattern is characterised by pauses embedded in the major flowering episode. Proença and Gibbs (1994) recorded pauses of four to seven days whilst some of the pauses documented by Oliveira et al.(1991) exceeded ten days in duration. The pauses reported here for *G. fenzliana* were shorter, typically about two days, and the assumption that the flowering episode in which they were interspersed was an annual one has not been tested. Nonetheless, as this is the pattern which appears to best fit the data available, the question arises as to what triggers the mini-cycles. Proença and Gibbs (1994) related the onset of flowering in *Blepharocalyx salicifolius* to a sharp increase in relative humidity and found that subsequent flowering pulses

FIG. 53. Post-pollination events in *Gomidesia lindeniana* (**a-c**) and post-fertilisation in *G. fenzliana* (**d-f**)

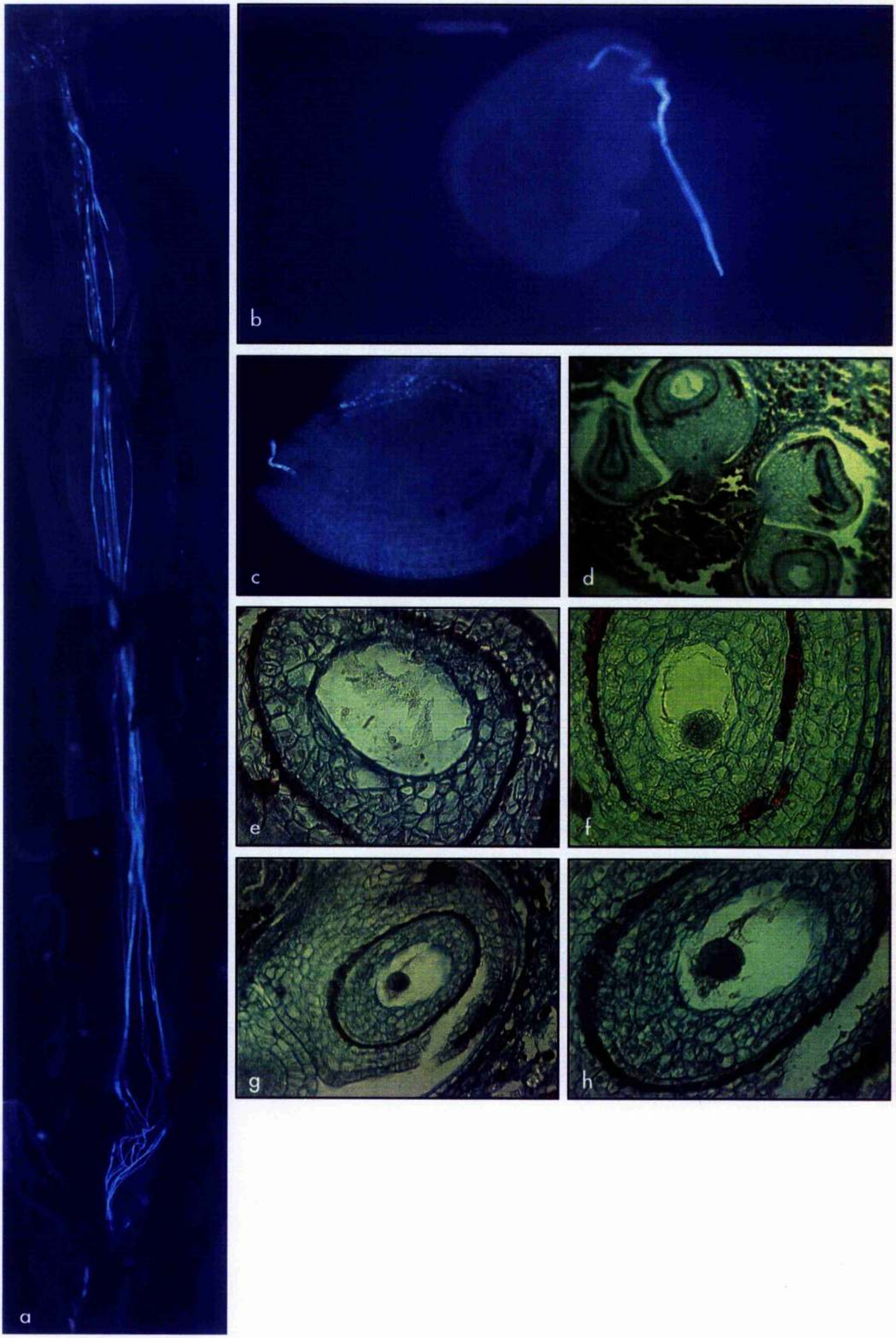
**a** Self pollen tubes growing to the base of the style in *G. lindeniana* (Brasília). Fixed c. 48 hours after anthesis. (x 42)

**b, c** self pollen tubes entering micropyle in *G. lindeniana* at 4 and 3 days after anthesis respectively. (b: x 110, c: x 180)

**d** T.S. of ovary in *G. fenzliana* at 26 days after self-pollination (x 84)

**e, g, h** TS of ovary of *G. fenzliana* at 27 days after self-pollination, note free nuclear endosperm (**e**) and developing embryo (**g, h**). (e: x 450, g: x 200, h: x 400)

**f** LS of ovary of *G. fenzliana* at 27 days after self-pollination (x 350)


a
b
c
d
e
f
g
h

within the flowering episode corresponded to days on which relative humidity exceeded 80%. This pattern did not hold true for *Myrcia rhodosepala* however. Meteorological data are not available for the Catolés area (nearest meteorological station is at Piatã more than 20 km away and at much lower altitude) so this theory cannot be tested for the present species. No obvious association between weather and flowering patterns was detected during fieldwork. However, it should be noted that the flowering episode studied coincided with an unusually heavy and extended rainy season. Continuous heavy rains throughout the Chapada Diamantina in early 1992 caused huge local floods, while the Rio São Francisco burst its banks, inundating extensive areas of lowland (Harley, 1995). Even when the rains eased in mid-February it was not unusual for the trees under observation to remain shrouded in mist for most of the day.

Adverse weather conditions could conceivably be responsible for the failure of many hundreds of flowers to open fully, for the dearth of insect visitors to the flowers, and consequently for the rather low levels of natural fruiting success recorded. The low PERS of 3.5 % would generally be considered indicative of a a primarily outbreeding species (Wiens et al., 1987) but the IAS of 0.69 indicates that mechanical selfing is fairly common in this species. The similiarity in levels of fruit set between flowers bagged and left to self-pollinate and natural (untreated) flowers was initially interpreted as an indication that automatic self-pollination might be the main mechanism responsible for fruit set in natural flowers during the study period. However, the fact that naturally pollinated fruits were found to contain significantly more developing seeds than those resulting from automatic self pollination strongly suggests that the former benefited from a pollen source not available to the latter. Fruits resulting from controlled self-pollination were also found to contain more developing seeds than automatically selfed fruits so it may be that pollen deposition via automatic pollination is too little and/or too late to fertilise most of the ovules in a flower.

With an ISI of 0.43 this species must be considered self-compatible but the experimental evidence leaves little doubt that some mechanism of discrimination against fruits resulting from self-pollination is in operation. That this discrimination is post-zygotic also seems to be beyond doubt, but the exact timing of the rejection of selfs cannot be discerned from the data presented here as they do not permit the separation of two levels of rejection: that of individual embryos *vs* that of whole fruit. Embryo failure could be detected in selfs and crosses from about two weeks post-pollination and we may postulate higher levels of embryo failure in selfs than in crosses, resulting in greater numbers of selfed fruits which have no developing embryos and which ultimately fall. However, as ovary retention is statistically equivalent in selfs and crosses at 20 days it is equally possible that the embryo failures observed merely represent a thinning process which occurs in all developing fruits irrespective of parentage and that the differential rejection of selfed fruits occurs at some later stage.

Numbers of developing seeds in maturing fruits resulting from cross and self pollinations did not differ statistically but it must be borne in mind that this comparison is between successful selfs and successful crosses. The failure to find selfed fruits in which more than four seeds were developing is consistent with a situation in which selfed ovules are more likely to abort than crossed ovules and therefore selfed fruit are likely to be outcompeted by crossed fruit which contain more developing seeds and represent a better sink for resources.

The levels of fruit set after different treatments reported here for *G. fenzliana* are strikingly similar to those described for *Eucalyptus regnans* by Griffin et al. (1987). These authors demonstrated the occurrence of preferential outcrossing in this large mass-flowering forest tree and provided strong evidence that differential embryo viability plays an important role in the breeding system control mechanism. They concluded that the post-fertilisation control mechanism was dependent upon both embryo genotype and maternal resource allocation. Their results are outlined in more detail in the General Discussion.

## Case Study 2: *Gomidesia lindeniana* near Catolés, Bahia

### Study site

Reproductive biology studies of *Gomidesia lindeniana* were carried out in the mountains above Catolés, Bahia, in the same area as and concurrently with the work on *G. fenzliana* described above. Unlike *G. fenzliana*, *G. lindeniana* occurs in open *campo rupestre* vegetation and in this habitat its distribution does not appear to be influenced by the location of water courses. Strictly speaking, *campo rupestre* is a mosaic of different vegetation types but many of the species considered characteristic of this habitat share xeromorphic features which are interpreted as adaptations to the extreme climatic conditions experienced in this exposed habitat. The physical and biological factors which influence *campo rupestre* vegetation were discussed in some detail by Harley (1995).

More than fifty individuals of *G. lindeniana* were found scattered over a steep, rocky hillside. However most of these trees bore either no inflorescences or very few and most showed no sign of having borne fruit in previous seasons, suggesting that these individuals were either rather young or growing near the limit of the altitudinal range of the species. Only in the valley at the bottom of this hillside (Pedra Grande) were freely flowering individuals found in sufficient quantity to permit experimental work. These trees formed a compact group growing among large boulders in a sheltered situation near the mouth of the valley (Fig. 36a). Their situation among boulders facilitated access to the canopy of most trees in this group. Initial suspicions that the individual trees might represent ramets rather than genetically different individuals were allayed when flowering behaviour was found to differ between trees.

Flowers of *G. lindeniana* are described in detail in the Systematic Treatment. The ovary is bilocular with two ovules per locule and the anthers exhibit marked vertical displacement of the pollen sacs, with the thecal halves losing curvature on dehiscence and held parallel to each other or slightly divergent with margins recurved. The pollen is exposed over the whole length of the anther in lateral view and over 1/3 - 1/2 the anther in dorsal view. (Fig 14e-h).

Results obtained for *G. lindeniana* are outlined below and summarised in Table 8.

### Flowering Phenology and Natural Fruiting Success

**Population and synchrony.** Of the nine trees in the study population one did not produce any inflorescences during the flowering period observed (though it had flowered previously). A further three trees had only one or two inflorescences and another with 33 inflorescences was accessible only with difficulty and not suitable for monitoring on a daily basis. Four trees

## Table 8

Summary of results for *Gomidesia lindeniana* at Catolés

| **Treatment:** | | **Natural** | **Cross-pollinated** | **Self-pollinated** |
|---|---|---|---|---|
| | | | | |
| % Fruit set | | 31 (131/425) | 39 (37/70) | 5 (12/254) |
| | | | | |
| Developing seeds per ovary: | mean | 2.2 | 2.0 | 1.4 |
| | mode (range) | 2 (1-4) | 1 (1-6) | 1 (1-3) |
| | | | | |
| PERS | | 17 | | |
| | | | | |
| Persisting at intervals after hand-pollination: | @ 8 days | | 48 (10/21) | 78 (156/199) |
| | | | | |
| Resulting ISI | | | 0.13 | |
| | | | | |
| Breeding system | | | ' self-incompatible' | |

were therefore monitored for their flowering phenology. Within five days of the first flower opening all four trees were in flower. Once an individual tree had commenced flowering it tended to open flowers on a daily basis. During the three week observation period only three days were recorded on which no flowers opened on any tree. Synchrony values for individual trees ranged from 0.65 to 0.95 with a population value of 0.78. The observation period did not extend to the end of the major flowering episode. However, it encompassed flowering in 89% of the buds present at the start of the flowering period.

**Conflorescence.** Conflorescence size is rather variable in this species. In the study population a conflorescence may consist of 5 - 82 buds arranged in one or two pairs of uniflorescences. Once flowering began, an individual conflorescence produced from 0 to 36 flowers each day. 0 was the modal number in conflorescences which had begun flowering but such a conflorescence tended to open at least one flower on most flowering days until all flowers had opened. The mean number of open flowers per flowering conflorescence was 8.45 and the modal number was 1. The flowering life of an individual conflorescence ranged from 2 - 14 days and spanned 2 - 10 flowering days.

**Flowering and natural fruit-set.** Some 6% of the buds originally tagged fell off before the onset of flowering in the tree chosen for detailed phenology and natural fruit-set observations. A further 8.4% were still present as buds at the end of the flowering period. Fall-off during the actual flowering period was negligible (< 2%). Ovary retention at the time of collection was 31% but the ovaries collected showed no signs of swelling. Dissections of retained ovaries revealed that the ovules could be sorted into two categories: apparently developing and non-developing. The mean number of developing seeds per ovary was 2.2 and fruits with one, two and three developing seeds were equally common. Fruits where all four seeds appeared to be developing were occasional. Where the number of developing seeds was two these were almost invariably arranged one in each of the two locules in the ovary. PERS as estimated at this point is 17 % but this may be an overestimate of the true value, as it is based on the assumption that all the ovaries persisting at this point will eventually form mature fruits.

### Anthesis and pollination

**Anthesis.** Observations of anthesis were made for this species on March 26th. Some temporal variation between trees was noted but the earliest flowers opened between 3 and 4 a.m. (Dawn at about 05.40 h). Flowers which were about to open could be distinguished by an almost imperceptible elongation of the exposed dome of petals. Petals peeled away from the dome one by one and when the petals were all more or less erect a few filaments forced their way through the opening between the petal apices. The style sometimes appeared at this stage too. As the filaments straightened and began to splay out, the petals became reflexed and a strong scent was discernible. At least some of the anthers dehisced at this stage, c. 50 - 60 minutes after the first petal movement. The stamens continued to straighten and the outer ones became reflexed giving a puff-ball appearance to the flower. By dawn most of the opening flowers had reached this stage.

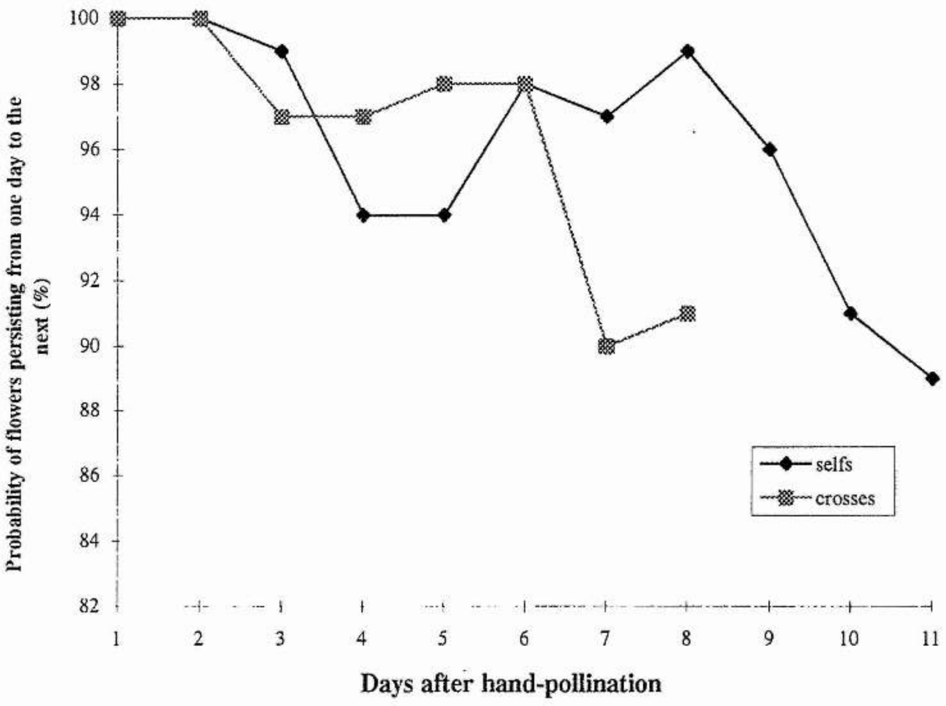
**Visitors.** Numerous observation periods covered the interval from anthesis to 16.30 h, by which time the stamens had begun to move upwards again towards an erect position. During wilting the filaments appeared to lose turgor and curl inwards rather than remaining parallel to the style. As a result the anthers were 1-2 mm below the level of the stigma in the wilted flower. The most common visitors were bees and buzzing behaviour was recorded on seven separate days. The earliest visitors were members of the genus *Andrena*. These were observed buzzing flowers on three occasions just before dawn. After dawn, the period between 06.00 h and 08.00 h was dominated by visits from *Bombus atratus*. Typically these bees exhibited buzzing behaviour, buzzing three or four times on a single flower in the early morning and just once or twice per flower later in the day. Gleaning behaviour was also observed in *Bombus atratus* on occasion. Gleaning behaviour was the norm in the other common visitor, *Apis mellifera* subsp. *scutellata*. These honeybees crawled over the stamens and were occasionally observed to contact the stigma. Other flower visitors observed to contact the stigma occasionally included Diptera.

### Breeding system

**Hand-pollinations.** There was substantial loss of hand-pollinated flowers in the first eight days after treatment (Fig. 54). Ovary retention at eight days was significantly lower in crosses than in selfs (48% and 78% respectively; chi-square = 75.6, df = 1, p < .0001). Data for later intervals before the fruit collection period are not available. Six to eight weeks after pollination 5% of selfed ovaries and 39% of crossed ovaries were retained on the tree (chi-square = 122.8, df = 1, p < .0001). None of these ovaries had swollen perceptibly but fruit dissections permitted the assessment of numbers of developing seeds per ovary. The modal number of developing seeds per ovary for both selfs and crosses was one. The mean number of developing seeds per crossed ovary was 2.0 (range 1-4) and did not differ significantly from that for natural pollination (t = -0.5, df = 43.9, p = 0.62). As in the case of naturally

FIG. 54. Loss of hand-pollinated flowers in *Gomidesia lindeniana* near Catolés, Bahia.

Loss of hand-pollinated flowers of *Gomidesia lindeniana*



pollinated ovaries, crossed ovaries with one, two and three developing seeds were equally common and ovaries where all four seeds appeared to be developing were occasional. The mean number of developing seeds in selfed ovaries was 1.36 (range 1-3), significantly less than in those naturally pollinated ($t = -2.77$, $df = 28.1$, $p < 0.01$). Most selfed ovaries examined contained only a single developing seed. Selfed ovaries with three developing seeds were occasional while no selfed ovaries were found to contain contain four developing seeds. If it is assumed that the ovaries fixed at 6 - 8 weeks after pollination would have gone on to swell and produce fruit, an ISI of 0.13 can be derived for this species. It can therefore be classed as self-incompatible.

**Automatic pollinations and emasculations.** No flowers left to self-pollinate automatically were persisting at the time of collection. The IAS therefore equals zero. No data are available for persistence of automatically pollinated flowers at eight days after anthesis. Due to lack of light and the necessity of balancing on boulders to reach the inflorescences, severe difficulties were encountered in carrying out emasculations in flowers of this species. Of fourteen flowers considered to have been satisfactorily emasculated two persisted until the collection period.

**Fluorescence microscopy.** Fluorescence microscopy revealed numerous pollen tubes in the styles of one day fixations of selfed, crossed and automatically selfed flowers. Ovule penetrations were observed in two day fixations of all treatments and appeared to be more frequent in selfed than in crossed flowers. By five to six days after pollination most ovules in selfed and crossed ovaries appeared to have been penetrated (c.15/24 in selfs, c. 18/24 in crosses), though the thickness of the integuments made it difficult to judge some cases with certainty. Numbers of penetrations were lower in automatically selfed flowers (c. 8/24) and examination of the styles of these flowers revealed that pollen tubes were few or absent in most cases.

**Histological Sections.** Sections of 9-day selfed and crossed flowers revealed the presence of pro-embryos and endosperm.

### Discussion

The flowering pattern observed seems similar to the cornucopia type described by Gentry (1974) which corresponds to the annual flowering of Newstrom et al (1994). The trees produced a large number of flowers over a period of a few weeks. The reason for the occasional non-flowering days embedded in this otherwise continuous flowering period is not apparent. No obvious relationship to weather conditions was detected during the observation period but the possibility that such correlations exist cannot be excluded.

The estimated PERS of 17 % is suggestive of a primarily outcrossing species (Wiens et al., 1987). The similarity of the results obtained for cross and natural pollination in terms of both ovary retention levels and numbers of developing seeds per ovary suggests that many of the naturally pollinated flowers may have received cross pollen.

The early anthesis and pre-dawn visitation of these flowers by buzzing bees is reminiscent of the process described by Renner (1989) for some Melastomataceae. In particular she commented that some species are pollinated 20 minutes before sunrise. Proença (1991) reported pre-dawn anthesis in *Siphoneugena densiflora* O. Berg (Myrtaceae) but noted that in this species the anthers do not dehisce until daybreak. In the other seven Central Brazilian species included in her study anthesis occurred shortly after daybreak (five species) or was not observed (two species).

On the basis of the fluorescence data it seems clear that the IAS of zero is due largely to lack of pollen deposition on stigmas of flowers left to self-pollinate automatically.

With an ISI of 0.13 this species clearly qualifies as self-incompatible. However, at eight days after pollination selfed ovaries were actually present in significantly greater numbers than crossed ovaries. The prevalence of selfs at this stage may be attributable to these flowers receiving larger or fresher pollen loads than those which were cross-pollinated as self pollen is, almost by definition, more readily available and fresher than cross-pollen. The fact that ovule penetrations appeared more frequent in two day fixations of selfed flowers than in crosses lends support to this idea. Whatever the explanation for the initial advantage held by selfs it is clear that some mechanism discriminating against selfed ovaries must have come into operation at least one week after pollination so that by the time of fruit collection most selfed ovaries had fallen. The histological results indicate that, by nine days after pollination, seeds of both selfed and crossed ovaries contained proembryos and endosperm. One can therefore conclude that the preferential outcrossing observed was maintained by some postzygotic effect rather than by a conventional SI mechanism. As no older material could be fixed from this population it cannot be ascertained from the data available whether the abortion of developing proembryos resulting from self-fertilisation occurred synchronously or by a gradual process of attrition. However the significantly lower numbers of developing seeds in retained ovaries of selfed flowers than in cross-pollinated flowers suggests that the latter could outcompete the former as a sink for resources. Thus competition could amplify the effect of the abortion of one or two inviable embryos in a selfed ovary.

The ovaries persisting in flowers which were emasculated are probably best interpreted as the result of contamination. Every effort was made to ensure that flowers were emasculated as soon as access to the stamens could be obtained without damaging the style. However lack of light rendered this procedure difficult and it was sometimes impossible to tell whether the anthers removed had actually dehisced already.

## Case Study 3: *G. cerqueiria* near Linhares, Espírito Santo

### Study site

Reproductive biology studies of *Gomidesia cerqueiria* were undertaken at the Forest Reserve of the Companhia Vale do Rio Docé, which is located between Linhares and São Mateus, in the north of the state of Espírito Santo, Brazil. This reserve comprises c. 22,000 hectares and includes about 25% of the extant primary forest cover of the state of Espírito Santo. Approximately 68% of the area of the reserve is covered by the dense uniform climax Atlantic rain forest, which is locally termed *tabuleiro* forest. It is in this tall forest with a relatively open understorey that populations of *G. cerqueiria* were discovered. This forest type is described in detail by Peixoto and Gentry (1990) who emphasized its unusually high species richness, its great density of trees greater than or equal to 10cm DBH, and its high density of lianas. They also highlighted the high diversity of Myrtaceae in their 1000 $m^2$ sample. Some 82 myrtaceous trees of more than 2.54 cm diameter were encountered, representing 31 species; Myrtaceae were considered second only to Leguminosae in terms of their diversity in this forest type. *Gomidesia cerqueiria* is unlikely to have been included in sampling for this study as trees of this species rarely exceed 2 cm in diameter.

For the present project two populations of *G. cerqueiria* were studied during the period January to March 1993. At Parajú a fairly dense population was encountered in undisturbed tabuleiro forest, apparently rather similar to that described by Peixoto and Gentry (1990) and situated only a few kilometres from the site of this latter study. A second, sparser but extensive population was subsequently discovered in rather more disturbed forest adjacent to the plant nursery (Viveiro) of the reserve. This Viveiro forest (Fig. 26a) has a much more dense understorey than the Parajú forest and boasts a network of trails (originally cut for zoological research work) which greatly facilitated the relocation of particular trees and the estimation of distances. The two study sites were situated at a distance of c. 10 km from one another as the crow flies (some 15 km by trail) and, in the absence of motorized vehicular transport, it was not possible to conduct experimental pollination work on both populations on a daily basis. In general, flowers pollinated in the Viveiro population were subsampled and fixed at differing intervals after anthesis, while flowers pollinated in the Parajú population were left to set fruit. These latter were monitored at first at daily intervals and, later in the season, at weekly intervals.

Flowers of *G. cerqueiria* are described in detail in the Systematic Treatment. The ovary is bilocular with 2 ovules per locule. The stamens are c. 50 in number (rather few compared to

**Table 9**

Summary of results for *Gomidesia cerqueiria*

| **Treatment:** | | **Natural** | **Cross-pollinated** | **Self-pollinated** |
|---|---|---|---|---|
| | | | | |
| % Fruit set | | 29 (39/135) | 13 (4/30) | 3 (1/34) |
| | | | | |
| Developing seeds<br>per ovary: | mean<br>mode (range) | 1<br>1 (1) | 1<br>1 (1) | 1<br>1 (1) |
| | | | | |
| PERS | | 7.2 | | |
| | | | | |
| Persisting at intervals<br>after hand-pollination: | @ 10 days<br>@ 20 days | | 24 (19/78)<br>22 (17/78) | 29 (16/56)<br>29 (16/56) |
| | | | | |
| Resulting ISI | | | 0.23 | |
| | | | | |
| Breeding system | | | 'borderline self-incompatible' | |

the other members of the genus) and the anthers are c. 1.3-1.5 mm long (the largest of the genus). The anther apex is deeply emarginate and the vertical displacement of the pollen sacs is marked. The thecal halves retain curvature on dehiscence and are connivent with margins inrolled. The effective dorsal opening is c. 1/8 the length of the anther so that the impression is of an apically poricidal structure (Fig. 13k&m, 14p&q).

Results obtained for *G. cerqueiria* are outlined below and summarised in Table 9.

### Flowering Phenology and Natural fruiting Successs

**Population and synchrony.** Differences in the timing of flowering between the study populations were apparent. When observations began in mid-January the Parajú population was already in the middle of its flowering episode. The Viveiro population, which was discovered a week later, appeared to be much nearer to the beginning of its flowering episode and included trees in which flowering had not yet commenced. Trees which had begun flowering usually opened new flowers each day. As neither the onset nor the end of flowering was observed for many trees synchrony values were not calculated. Similarly the exact duration of the flowering episode in either population as a whole cannot be stated but it is known to exceed five weeks and is estimated at six to seven weeks. The tree marked for phenology and natural fruit set had a flowering episode of 16 days duration, with 1 - 20 flowers open on each of these days.

**Conflorescence.** Conflorescence size is relatively small and uniform in this species. A conflorescence typically consists of a pair of uniflorescences each bearing 4 - 13 buds. Once flowering began an individual conflorescence produced from 0 to 5 flowers each day. 1 was the modal number of open flowers in conflorescences which had begun flowering. The mean number of open flowers per flowering conflorescence on flowering days was 1.88. The flowering life of an individual conflorescence ranged from 10 to 15 days and spanned 5 to 13 flowering days. The apical bud and the apical buds on lateral branches tended to be the first to open.

**Flowering and natural fruit set.** Some 97% of the buds present at the start of the observation period went on to produce normally opening flowers. The other 3% fell without opening and no buds remained unopened at the end of the observation period. Fall-off rates of flowers which had opened were negligible in the first week of flowering and increased sharply in the second week, coinciding with the flowering peaks at this time. They were still comparatively low however, and 81% of the flowers which had opened were still in situ at the end of the flowering period. Once flowering ceased fall-off rates again became negligible and remained so for at least ten days. Fall-off resumed between 27 and 40 days after the onset of flowering (exact dates unknown as daily observations were not made on this population at this time) and 47% of the total flowers were persisting by day 40. Fall-off continued at a lower rate until the collection period and 31% of ovaries were retained at day 86. These retained ovaries represented a spectrum of variation ranging from obviously non-developing floral remains weighing only 6 - 10 mg when dry to obviously developing fruits weighing 20 - 30 (-47) mg through a range of intermediates which were not easily assignable to developing or non-developing classes. All retained ovaries of > 10 mg dry weight were found upon dissection to have one ovule which was larger and paler than the other three and this was classed as developing. PERS calculations were therefore based on the assumption that all of these ovaries, 28.9% of the original buds, represent developing fruits, though it is acknowledged that this may result in an over-estimate. Maximal PERS in this species is therefore 7.2 %.

### Anthesis and Pollination

**Anthesis.** Observations of anthesis were made for this species on several days and the timing was found to be be variable both among flowers on a given tree and from day to day. With experience, flowers which were about to open could be distinguished by an almost imperceptible elongation of the exposed dome of petals (visible by torchlight, up to six hours before dawn). The earliest petal movements observed were at 04.30 h (dawn c. 05.00 h). The outer petal rose slowly, pulling away from the others in the dome. The remaining petals then rose, apparently pushed by the stamens which, when they first became visible, were adhering in clumps with filaments bent. As the petals separated, stray stamens sometimes escaped between them and the style became visible, already more or less erect. The petals moved from their erect position through a patent one until they were completely reflexed. The stamens separated from each other and gradually splayed out as their filaments straightened. In the fully open flower the stigma was held 1-2 mm above the level of the inner anthers. Some of the flowers reached this stage by half an hour after dawn while in others the outer petal was just beginning to move at this time and more than two hours after dawn stamens were still in a more or less erect position in some flowers. The time of anther dehiscence could not be determined with certainty and no scent was detected.

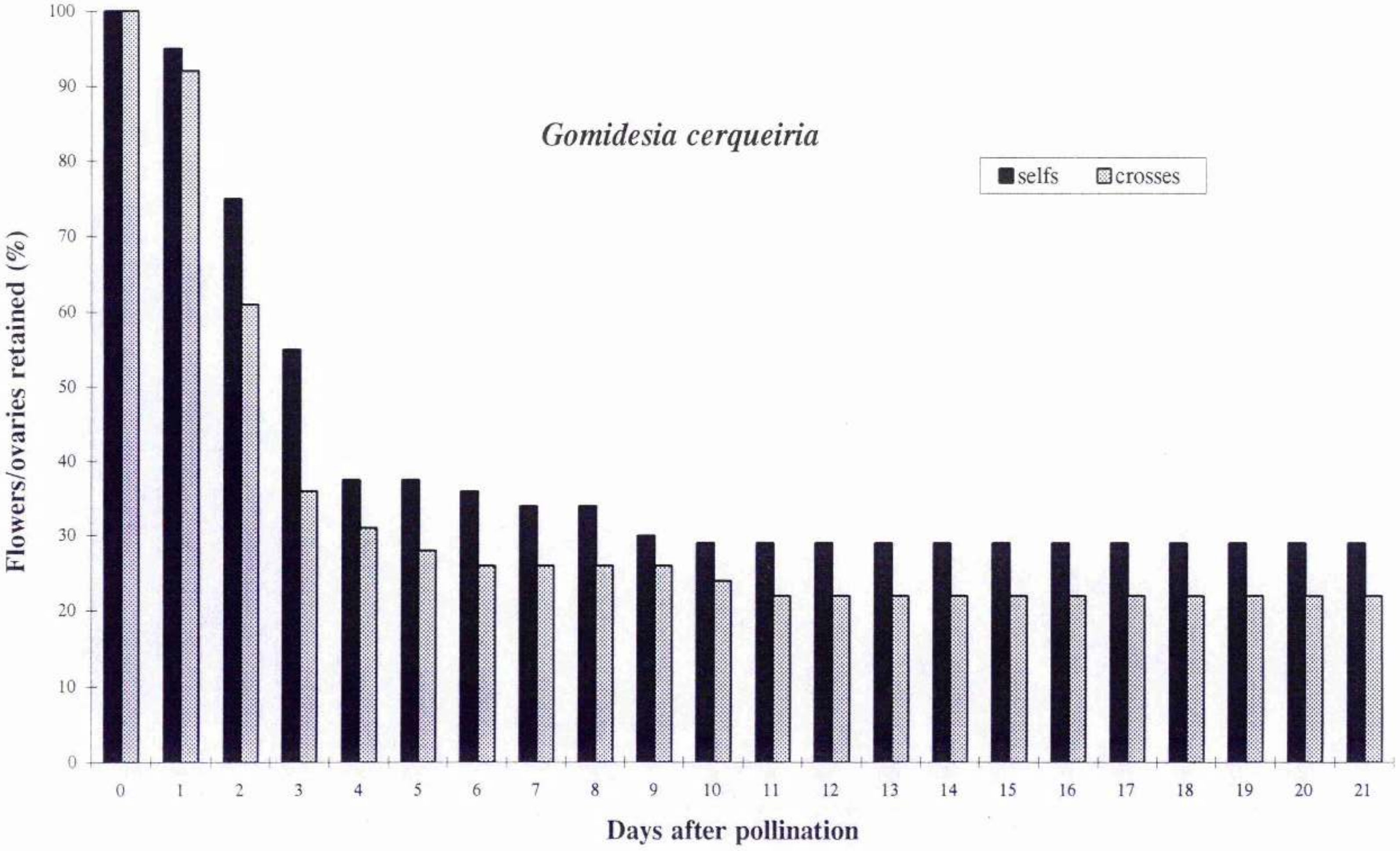
**Visitors.** Numerous observation periods covered the interval from anthesis (pre-dawn) to 16.00 h by which time the stamens had returned to a more or less upright position with filaments slightly curved and anthers held close to the style but 2 - 3 mm below the level of the stigma. Visitors were in general rare: on one of the peak flowering days for the phenology tree only one visitor was observed during five hours of morning observations. This lone visitor was a wasp which exhibited 'gleaning' behaviour at 07.35 h without apparent success. The presumptive pollinators are small bees. Bees tentatively identified as Fam. Anthophoridae Subfamily Nomadinae were captured at 06.45 h and 08.15 h. These exhibited buzzing behaviour as follows: positioning itself with its head towards the centre of the flower a bee would grasp a bundle of stamens (about one-sixth of the total ) and buzz for less than one second. Bees were observed to move and buzz again two to three times within the same flower before moving to another flower on the same inflorescence. Bees tentatively identified as *Augochlora* (Fam. Halicitidae, Augochlorini) were captured at 10.00 h and 11.45 h. They too exhibited buzzing behaviour and one bee was observed to return to the same flower several times when this was the only open flower on an inflorescence.

### Breeding System

**Hand-pollinations.** There was massive fall-off of hand-pollinated flowers in the first five days after pollination (Fig. 55). Beyond this point the curve flattened and at ten days after pollination there was no statistical difference between the numbers of selfed and crossed ovaries persisting (chi-square = 0.68, df = 1, p = 0.41). Fall-off between 10 and 20 days was negligible and there was no statistical difference between the numbers of selfed and crossed ovaries persisting in situ at 20 days (chi-square = 1.5, df = 1, p = 0.22). Fall-off resumed at some point after this, by which time daily monitoring had ceased. By eight weeks after pollination only a single selfed flower was persisting, representing 3% of the total flowers selfed and 10% of the selfed flowers that were present at 15 days after pollination (i.e. during the plateau period). The equivalent value for crossed flowers was four, representing 13% of the total flowers crossed and 57% of those that had persisted to 15 days. These differences are not statistically significant (chi-square = 3.18, df = 1, p = 0.075). All ovaries contained only one developing seed. The resulting ISI is 0.23, so the species rates as self-compatible.

**Automatic pollinations and emasculations.** Flowers left to automatically self-pollinate and those emasculated exhibited even higher rates of fall-off in the first few days after anthesis. At day 20 ovary retention levels in automatic selfs (7 %) and emasculations (5 %) did not differ significantly (chi-square = 0.32, df = 1, p = 0.57). No emasculated flowers persisted until the collection period ( the two flowers represented by the 5% above fell synchronously at 25 days after anthesis). Some 5 % of the automatically selfed flowers were still retained at 35

FIG. 55. Loss of hand-pollinated flowers in *Gomidesia cerqueiria.*


Gomidesia cerqueiria
■ selfs
▨ crosses
Flowers/ovaries retained (%)
100
90
80
70
60
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
Days after pollination

days after anthesis, at which point monitoring ceased. It cannot be assumed that these flowers would have gone on to set fruit as hand-selfed flowers are known to have fallen at ages > 35 days. Therefore the IAS cannot be calculated with any degree of confidence.

**Fluorescence microscopy.** Fluorescence microscopy of 4- and 5-day fixations of selfed and crossed flowers revealed pollen tubes extending to the base of most styles. Most ovaries had at least one penetrated ovule and one was the modal number of ovule penetrations in such ovaries. The mean number of penetrated ovules in ovaries which contained at least one penetrated ovule was 1.42 in crosses and 1.33 in selfs. Numbers of ovule penetrations were statistically equivalent in selfs and crosses ($t = 0.57$, $df = 38$, $p = 0.57$). The frequency distribution of penetrated ovules within ovaries was also equivalent for selfs and crosses (chi-square = 0.27, $df = 2$, $p = 0.87$).

**Differential Interference Contrast Microscopy.** DIC microscopy revealed the presence of a proembryo in a single ovule of most crossed ovaries at 15 days (6?/8), (Fig. 56a, b) Proembryos were detected in only 2/10 selfed ovaries . Possible degenerating embryos were detected in the seeds of a further two selfed ovaries. Similar results were obtained for 20 day fixations; only a single embryo was encountered in the six selfed ovaries screened while four of the six crossed ovaries screened contained at least one embryo and one had two seeds containing developing embryos (Fig. 56 d, e). Fixations made at 25 days produced very poor images but in at least one instance an embryo was clearly visible in the ovary of a self-pollinated flower (Fig. 56 e, f).

### Discussion

The flowering pattern exhibited corresponds to the cornucopia type described by Gentry (1974) and is equivalent to the annual flowering pattern of Newstrom et al. (1994). The flowering pattern observed was the most regular of all the species included in the present study. The infloresences are less showy than in the other species studied and the relatively small number of flowers opening per day, per inflorescence and per tree, suggested that this species may depend on traplining bees for pollen dispersal rather than producing a big display to attract opportunists.

The PERS of 7.2 % is suggestive of a primarily outcrossing species (Wiens et al., 1987).

Although anthesis began before dawn it occurred rather more slowly than in the other species studied. As this species is an understorey shrub in tall forest the light and warmth of day take longer to reach it than to reach the other species studied which were all in more or

FIG. 56. Differential Interference Contrast images of ovules of *Gomidesia cerqueiria* sampled after experimental pollinations. (Scale bar = 10 μm)

**a** Embryo (arrowed) in ovary of cross-pollinated flower at day 15.

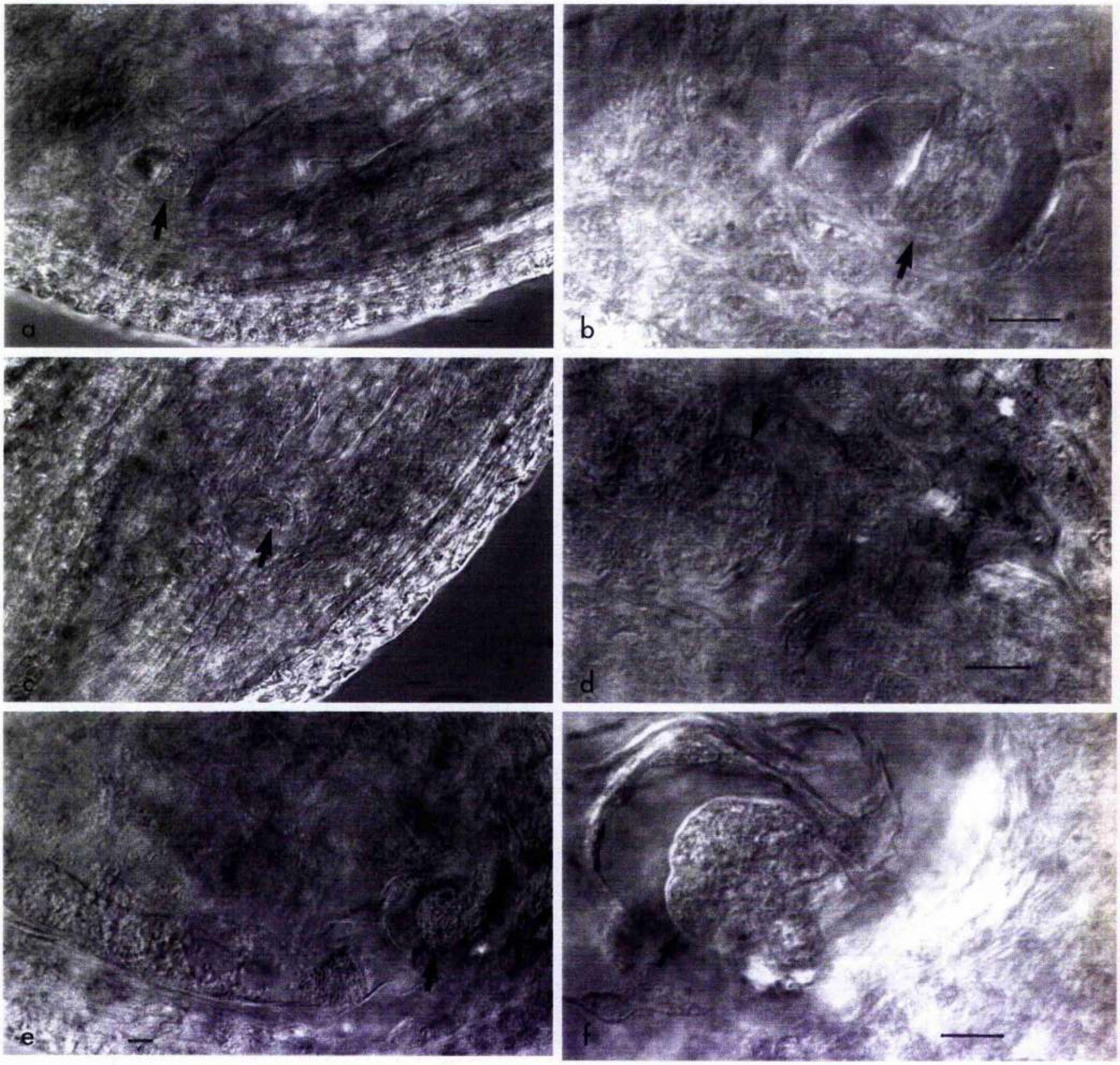
**b** Same embryo (arrowed) as in **a** but at higher magnification.

**c** Embryo (arrowed) in ovary of cross-pollinated flower at day 20.

**d** Embryo (arrowed) in ovary of another cross-pollinated flower at day 20.

**e** Embryo (arrowed) in ovary of self-pollinated flower at day 25.

**f** Same embryo (arrowed) as in **e** but at higher magnification.


a
b
c
d
e
f

less exposed habitats. Anther dehiscence, a drying-dependent phenomenon, can be expected to be delayed in such a situation.

With an ISI of 0.23 this species just qualifies as self-compatible. However, the differences between ovary retention levels in selfed and crossed flowers are nearly statistically significant suggesting that (a) there is some mechanism of discrimination against selfed ovaries and (b) that with larger sample sizes a statistically significant result may be obtained. Histological studies strongly support this possibility. Most 15- and 20-day fixations of crossed ovaries contained at least one developing pro-embryo whereas most selfed ovaries of equivalent age did not, and in two instances structures interpreted as degenerating embryos were detected in these selfed ovaries.

This is the only species studied in which the number of seeds in the mature fruit is fixed at one. As more than one ovule is often penetrated and fertilised one can infer the occurrence of ovule abortion in many developing fruits. The exact timing of this abortion is of relevance to the issue of whether any preferential outcrossing which may be found to exist in this species is maintained by an active self-incompatibility system or simply by inbreeding depression. The results indicate that in most cases the developing seeds have been reduced to one per ovary by 15 days after pollination. However, in one instance a 20-day crossed ovary was found to contain two developing embryos. No histological observations are available for older seeds but the continued fall-off of ovaries more than 20 days after pollination suggests that abortion continues during this period. The implications of this conclusion are further examined in the general discussion.

## Case Study 4: *Gomidesia pubescens* near Brasília, Distrito Federal

### Study site

Reproductive biology studies of *Gomidesia pubescens* were carried out at the Ecological Reserve of the Instituto Brasileiro de Geografia e Estatística (IBGE), Distrito Federal, Brazil during the period January to March 1994. This 1300 ha *cerrado* reserve is situated 33 km south of Brasília and shares boundaries with two other reserves, owned by the Univerisity of Brasília and the Brasília Botanic Garden respectively. In total these three reserves represent more than 7000 ha of protected *cerrado* and associated vegetation types. *Cerrado* vegetation is a mosaic varying from 10 -15 m tall savanna woodland with a more or less closed canopy excluding grasses, to low open grassland with no woody plants. The *cerrado* is dissected by rivers which are lined with 10 - 30 m tall gallery forest. Trees of *G. pubescens* were found along the margin of gallery forest, where the forest edge meets the marsh which separates it from the *cerrado* proper (Fig. 44a). The marsh is of the *vereda* type (Eiten, 1984) comprising low, tussocked, grassy vegetation dotted with palms (*Mauritia flexuosa*). Access to the canopy of trees under study was aided by plastic crates introduced for the purpose and by bending down lower branches and fixing them in accessible positions.

Flowers of *G. pubescens* are described in detail in the Systematic Treatment. The ovary is bilocular. The stamen number is c. 47 - 65 (in the lower part of the range for the genus as a whole) and the anthers are c. 0.6 mm long. The vertical displacement of the pollen sacs is marked and the thecal halves lose curvature on dehiscence, being held parallel or slightly divergent with margins recurved (Fig. 15j&k). Thus the pollen is exposed along the whole length of the anther in lateral view.

Results obtained for *G. pubescens* are outlined below and summarised in Table 10.

### Flowering phenology and natural fruit success

**Population and synchrony.** When observations began in mid-January the flowering episode appeared to have just begun in this population. All fourteen trees under study flowered on January 19th, many for the first time. Trees which had begun flowering did not in general open new flowers each day. In most cases a flowering day was followed by one or two (or rarely several) non-flowering days. There was a high degree of synchrony between the trees in the population with respect to flowering days. Synchrony values are not presented here because of the discontinuity of observations during the flowering period. For most trees flowering was over by the end of the first week in February though some individuals growing

### Table 10

Summary of results for *Gomidesia pubescens*

| **Treatment:** | | **Natural** | **Cross-pollinated** | **Self-pollinated** |
|---|---|---|---|---|
| | | | | |
| % Fruit set | | 10 (11/107) | 39 (45/114) | 5.5 (6/109) |
| | | | | |
| Developing seeds per ovary: | mean | 1.5 | 2.6 | 1.3 |
| | mode (range) | 1 (1-3) | 3 (2-4) | 1 (1-2) |
| | | | | |
| PERS | | 3.9 | | |
| | | | | |
| Persisting at intervals after hand-pollination: | @ 10 days | | 82 (93/114) | 72 (78/109) |
| | @ 20 days | | 72 (82/114) | 56 (61/109) |
| | | | | |
| Resulting ISI | | | 0.14 | |
| | | | | |
| Breeding system | | | ‘ self-incompatible’ | |

in shaded situations continued to flower sporadically beyond this date and still retained buds at the end of the observation period. The major flowering episode can therefore be estimated to be of approximately four weeks duration.

**Conflorescence.** A conflorescence may consist of anything from 18 to 45 or more buds arranged on one or two pairs of inflorescences. Once flowering begins an individual conflorescence produces from 0 to 15 flowers each day and tended to open at least one flower on most flowering days until all flowers had opened. Apical buds on subapical branches tended to open first.

**Flowering and natural fruit-set.** No estimate was made of bud fall-off before flowering in this population. Ovary retention at the time of collection of natural pollinated flowers was 10.3 % but most of the ovaries collected showed no signs of swelling. Fruit dissections revealed that ovules within these ovaries varied considerably in size and shape and that the ovules from a single ovary could usually be divided into two classes. Ovules which had mostly convex surfaces and a pale colour were termed developing seeds while darker structures with some concave surfaces were termed non-developing. Non-developing ovules often equalled developing ones in length but were considerably smaller in total volume. In a few ovaries the ovules were not so easily categorized as developing and non-developing but included intermediates between these two classes. The modal number of clearly developing seeds per retained ovary was 1 and the mean number was 1.5 (range 1-3). Fruits in which all four seeds appeared to be developing were not observed. The resulting PERS is 3.9 %.

### Anthesis and pollination

**Anthesis.** Anthesis in this species was not studied in detail but casual observations indicated that the process was comparable to the general patterns described for *Gomidesia fenzliana* in Catolés. Temporal variation in the process between trees was notable with shaded trees lagging behind those in the open. In these more exposed trees anther dehiscence occurred before 08.00 h (dawn at c. 06.00 h) in stamens which were not yet fully splayed. At this time stamens were not even visible in opening flowers of shaded trees.

**Visitors.** During several observation periods covering the interval from anthesis (pre-dawn) to mid-afternoon very few visitors were observed and only one was captured, a species of the genus *Melipona* which was gleaning at 9.20 h. Buzzing behaviour was observed on one occasion: a brown bee (possibly a *Melipona*?) visited three or four inflorescences and at least 20 flowers on a non-shade tree at 07.50 h. On another morning green iridescent bees (euglossines?) were observed visiting the flowers several times between 9.30 and 11.00 h. These latter bees did not exhibit buzzing behaviour but moved very rapidly and unpredictably and proved impossible to trap.

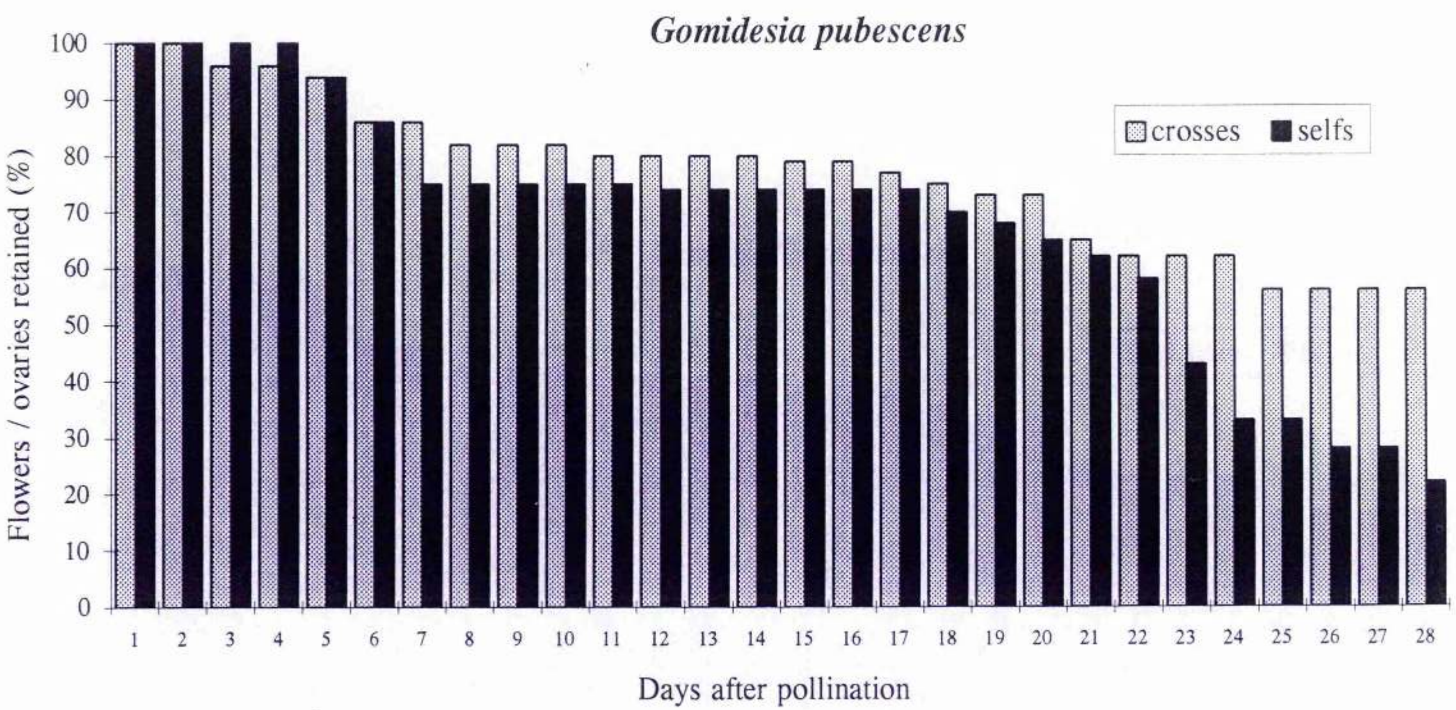
### Breeding system

**Hand-pollinations.** There was gradual fall-off of hand-pollinated flowers in the first ten days after pollination (Fig. 57). Fall-off peaked at five days after pollination for both selfed and crossed flowers. The percentage of crossed ovaries persisting (82%) was significantly greater than that of selfed ovaries (72%) by ten days after pollination (chi-square = 8.63, df = 1, p = 0.0033). Fall-off continued at a comparable level for the next ten days (days 11 - 20 after treatment) and by day 20 the numbers of selfed and crossed ovaries persisting (56 and 72 % respectively) had diverged even more (chi-square = 13.27, df = 1, p = 0.0003). During the fourth week after treatment the rate of fall-off of selfed flowers rose steeply while fall-off in crossed flowers stabilised so that on day 27 the percentage of selfed flowers persisting was less than half that of crossed flowers (22 and 56% respectively, chi-square = 59.85, df = 1, p < 0.0001). By the time of collection, some16-20 weeks after pollination 5.5% of selfed ovaries and 39% of crossed ovaries were still retained (chi-square = 59.05, df = 1, p < 0.0001). If it is assumed that all these retained ovaries would eventually mature into fruits the ISI can be estimated as 0.14 and the species rates as self-incompatible.

**Automatic pollinations and emasculations.** Of eighty-five flowers tagged, bagged and left to self-pollinate automatically only one persisted until the collection period. This result does not differ significantly from the retention rate for flowers which were self-pollinated by hand (chi-square = 3.06, df = 1, p = 0.08) but it is significantly lower than the retention rate for flowers left exposed to natural pollinating agents (chi-square = 4.69, df = 1, p = 0.03). The resulting IAS is 0.21. No emasculations were carried out in this population.

**Fruit dissections.** Fruit dissections of ovaries retained in experimental treatments yielded results similar to those obtained for natural pollinations: in most ovaries ovules could be classed without difficulty as developing or non-developing but in some case intermediates were observed. Three was the modal number of apparently developing seeds in ovaries retained after cross pollination and the mean was 2.6 (range 2-4). Numbers of developing seeds in crossed ovaries were significantly greater than in naturally pollinated ovaries (t = -

FIG. 57. Loss of hand-pollinated flowers in *Gomidesia pubescens.*


Gomidesia pubescens
crosses
selfs
Flowers / ovaries retained (%)
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Days after pollination

1.08, df = 16.7, p = 0.02). Sample sizes for retained ovaries of self-pollination and automatic selfing treatments were insufficient for statistical analysis but numbers of apparently developing seeds were lower in these ovaries than in crosses (range 1-2 in selfs).

**Fluorescence microscopy.** Due to low numbers of flowers available for pollination it was not possible to fix subsamples of flowers at regular intervals after pollination. However, some flowers which had been left to self-pollinate automatically were fixed one day after anthesis. Examination of this material using fluorescence microscopy revealed that some pollen tubes had reached the base of the style by this time and that at least one ovule had been penetrated.

### Discussion

This species displayed the pulsed bang flowering pattern discussed in relation to *G. fenzliana* but with a shorter major flowering episode and, apparently, a higher degree of synchrony than in this latter species. Means by which this high degree of synchrony may be maintained are considered in the general discussion.

The PERS of 3.9 % is suggestive of a primarily outcrossing species (Wiens et al., 1987).

The late anthesis and low visitation rates are reminiscent of *G. fenzliana* but unlike this latter population buzz-pollination was observed on one occasion in *G. pubescens* in Brasília.

The ISI of 0.14 indicates that the species should be considered self-incompatible. Although visitation rates appear to be rather low the fact that retention rates for naturally pollinated flowers are significantly higher than those of automatically self-pollinated flowers strongly suggests that the former benefit from some pollen source not available to the latter. The IAS of 0.21 is a little misleading as the ovary retention rates are statistically equivalent for automatic selfs and hand selfs. Automatic transfer of self pollen to the stigma may actually be fairly efficient in this species but may be of real importance to fruit set only when visitation rates are even lower than in the present population during period of observation.

On the basis of the (admittedly scanty) fluorescence data and on the timing of preferential abortion of selfed ovaries it may be tentatively concluded that some post-zygotic mechanism of discrimination against selfed ovaries is in operation in this population. Although histological results are not available for *G. pubescens*, on the basis of the data obtained for other species it seems highly probable that the many ovaries which are shed ten days or more after anthesis contain ovules which have been fertilised and embryos at various stages of development.

The superior retention rates of cross-pollinated flowers as compared to those which were left exposed for natural pollination are mirrored by the greater numbers of developing seeds in ovaries of the former. These results are consistent with an explanation of preferential outcrossing in which an ovary in which all seeds are the result of cross-pollination is likely to have a greater number of developing seeds (few or none being homozygous for recessive lethals) and therefore act as a more effective sink for resources, increasing its long term probability of survival and outcompeting other ovaries in which some or all the ovules received self pollen.

## Case Study 5: *G. lindeniana* near Brasília, Distrito Federal

### Study site

Reproductive biology studies on *G. lindeniana* were carried out at the Biological Reserve of the Brasília Botanic Garden concurrently with those on *G. pubescens* described above. This reserve is contiguous with the IBGE reserve which was the study site for *G. pubescens*, and encompasses a similar range of vegetation types. The population studied was situated on a steep, rocky, ridge above a river, with open, woody vegetation and little ground cover (Fig. 37a). *Gomidesia lindeniana* was one of the dominant species in this vegetation along with a species of *Vochysia*. Access to the canopy was facilitated by the steep slope on which the trees occurred and, occasionally, by standing on a vehicle parked below the trees at the bottom of the ridge.

Flowers of *G. lindeniana* are described in detail in the Systematic Treatment and floral traits of relevance to the present study of reproductive biology are summarised in Case Study 2. Late flowering of this species in Bahia in 1992 had resulted in a shorter study period than was desirable so the presence of a population of *G. lindeniana* in Brasília represented an opportunity to obtain a more complete data set for this species (see Table 11) and to examine between-population variation in pollination biology and breeding system. The two populations are compared in the discussion.

### Flowering Phenology and Natural Fruiting Success

**Population and synchrony.** The onset of the flowering episode in the population observed was rapid. The first open flowers were observed on January 18th and within five days most trees in the population were in flower. 16 trees were included in the phenology analysis. Trees which had begun flowering did not, in general, open new flowers each day. In most individuals a flowering day tended to be followed by one or more days on which that tree did not open any flowers. Two trees showed a tendency to flower on two or three successive days, one or more of which would coincide with a major flowering day for the population as a whole. During the three week continuous observation period ten days were recorded on which no flowers opened on any tree. Synchrony values for individual trees ranged from 0.53 to 0.93 with a population value of 0.76. The major flowering episode lasted approximately four weeks and some unopened buds were still present on a few trees at the end of this period. A high degree of synchrony was observed between flowering in this population and that in the population of *G. pubescens* studied on the nearby IBGE reserve (see general discussion).

## Table 11

Summary of results for *Gomidesia lindeniana* near Brasília

| **Treatment:** | | **Natural** | **Cross-pollinated** | **Self-pollinated** |
|---|---|---|---|---|
| | | | | |
| % Fruit set | | 35 (76/219) | 30 (30/99) | 0 (0/134) |
| | | | | |
| Developing seeds per ovary: | mean<br>mode (range) | 2.2<br>2 (1-4) | 2.3<br>2 (1-4) | N/A<br>N/A |
| | | | | |
| PERS | | 19 | | |
| | | | | |
| Persisting at intervals after hand-pollination: | @ 10 days<br>@ 20 days | | 53 (53/99)<br>46 (46/99) | 28 (28/134)<br>3 (4/134) |
| | | | | |
| Resulting ISI | | | ~ 0 | |
| | | | | |
| Breeding system | | | 'strictly self-incompatible' | |

**Conflorescence.** A conflorescence may consist of up to 477 buds arranged in one or two pairs of inflorescences each of 90 to 140 buds. Once flowering began an individual conflorescence opened from 0 to 70 flowers per day. 0 was the modal number in conflorescences which had begun flowering and there seemed to be a pattern whereby a conflorescence which had opened numerous flowers on a major flowering day would open none on the next major flowering day. Thus, although there was a high degree of synchrony between trees this was produced by the alternation of flowering between conflorescences on individual trees. However, the data were insufficient to test this pattern statistically. Apical buds on subapical branches tended to open first.

**Flowering and natural fruit- set.** Fall-off of unopened buds before flowering was negligible. In the inflorescences monitored no buds remained unopened at the end of the observation period (but this was not the case for the population as a whole, as noted above). Ovary retention at the time of collection was 34.7% but the ovaries collected showed no signs of swelling. Fruit dissections revealed that the ovules could be separated into two categories: apparently developing and non-developing. All ovules observed were a similar length (ca. 0.5 mm) in their longest dimensions but those termed developing seeds were pale. with mostly convex surfaces (plump) and therefore had a greater volume than those termed non-developing which were generally darker, had only one convex surface and appeared shrivelled. Two was the modal number of developing seeds in retained ovaries of natural pollinations and the mean number was 2.2 (range 1-4). Maximal PERS (based on the assumption that all the ovaries retained until the collection date would eventually have matured into fruit) is 19.35 %.

**Anthesis and pollination**

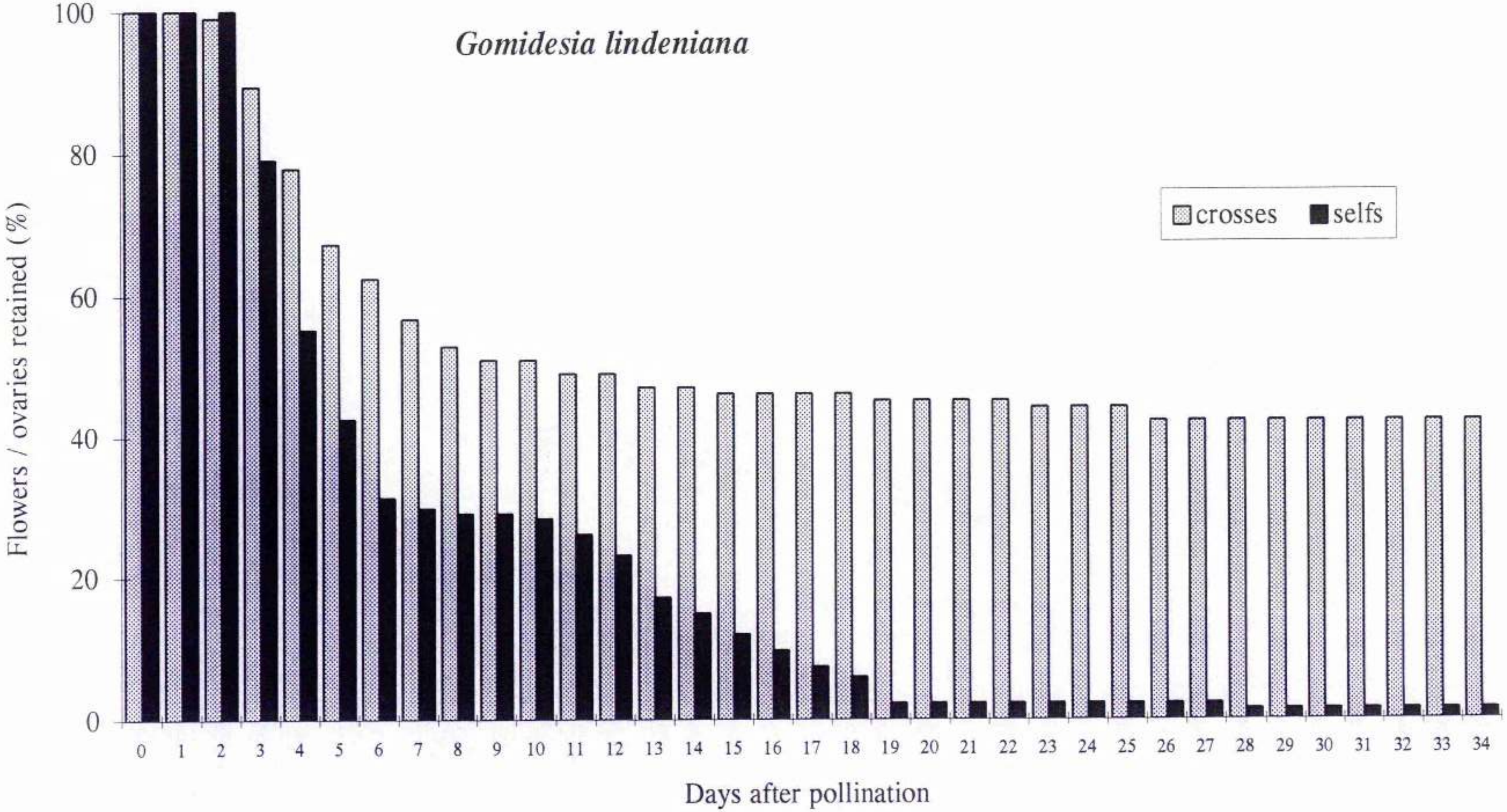
**Anthesis.** Observations of anthesis were made for this population on several occasions. Some temporal variation was noted but the earliest flowers opened at 06.00 h. (Dawn at about 06.30 h.). At least an hour before this, flowers which were about to open could be distinguished by an almost imperceptible elongation of the exposed dome of petals. As the first petal peeled away from the dome the style generally began to rise and straighten. In some (few) flowers the stigma was trapped under the edge of the second petal and the style did not rise until this petal too has peeled back from the dome. As the other petals separate the stamens begin to unfurl and as the filaments straighten the stamens gradually become splayed until the outer ones are patent or reflexed. By dawn some flowers still had not reached this stage but, in those that have, a strong fragrance could be detected and the anthers appeared to have dehisced.

**Visitors.** Numerous observation periods covered the interval from anthesis (pre-dawn) to mid-afternoon, by which time the stamens had begun to move upwards and inwards and the filaments appeared to lose turgor and curl inwards rather than becoming parallel to the style. As a result the anthers were held 1 - 2 mm below the level of the stigma. The most common visitors were bees but no buzzing behaviour was observed in this population. The earliest visitor observed (but unfortunately not captured) was a large brown bee which alighted on a newly opened flower a few minutes after dawn and flew off again immediately. The most abundant visitors were *Melipona* which visited the conflorescences in swarms (Fig. 36). These bees appeared to favour sunny branches and, perhaps for this reason, sometimes confined their gleaning behaviour to a single tree while adjacent flowering trees remained unvisited. Visits by *Melipona* were observed between 08.30 h and 10.30 h. Other visitors gleaning at this time of day included introduced *Apis mellifera*, some fast-moving iridescent blue-green bees which proved impossible to catch (Euglossines?), a very occasional *Lasioglossum* and some unidentified Diptera which did not appear to contact the stigma. The latest visitor observed to contact the stigma was a bee of the genus *Andrena* which was captured in the early afternoon.

### Breeding system

**Hand-pollinations.** There was massive fall-off of hand-pollinated flowers in the first ten days after pollination (Fig. 58). Fall-off was steepest on days 3 - 6 in selfs and on days 3 - 8 in crosses. Fall off was greater in selfs than in crosses. Differences in persistence of crossed and selfed ovaries were already discernible only five days after pollination; chi-square = 3.88, df = 1, p = 0.049. Ten days after pollination the percentage of crossed ovaries persisting was significantly greater than that of selfs (53% and 28% respectively; chi-square = 30.89, df = 1, $p < 0.0001$). For selfed ovaries fall-off was negligible on days 6 - 10 but it then resumed and by day 20 only 3% of hand-selfed ovaries were persisting. Crossed flowers, in contrast, had a longer initial fall-off period, of 3 - 8 days but, once the curve flattened, fall-off rates remained very low for at least 25 days. At day 20 the percentage of crossed ovaries persisting was significantly higher than that of selfs (46% and 3 % respectively; chi-square = 646.27, df = 1, $p < 0.0001$). By the final collection period no selfed ovaries from this cohort were persisting and 30% of crossed flowers were persisting. Retention levels for cross-pollinations did not differ significantly from those for natural pollinations (chi-square = 0.505187, df = 1, p =

FIG. 58. Loss of hand-pollinated flowers in *Gomidesia lindeniana* near Brasília, Distrito Federal.


Gomidesia lindeniana
crosses
selfs
Flowers / ovaries retained (%)
100
80
60
40
20
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
Days after pollination

0.48). These results indicate a completely self-incompatible species. However it must be noted that in another cohort of flowers self-pollinated by hand (and intended for subsampling at intervals after pollination) at least one selfed flower was retained on the tree until the collection period.

**Automatic pollinations and emasculations.** Flowers left for automatic self-pollination and those emasculated also exhibited massive fall-off in days 3 - 6 after flowering. 97% of flowers left to self-pollinate automatically fell within six days of anthesis and the remaining few fell within a week after this. The fall-off pattern was very similar in emasculated flowers but the ovary of one emasculated flower persisted to the end of the observation period and may have been capable of setting fruit.

**Fruit dissections.** Dissection of ovaries persisting after cross-pollination showed that the modal number of developing seeds was two, with a mean of 2.3 developing seeds per retained ovary (range 1-4). The frequencies of cross-pollinated ovaries containing different numbers of developing seeds did not differ significantly from those observed for naturally pollinated ovaries (chi-square = 0.50, df = 3, p = 0.92). Ovary retention levels in the other treatments were too low to allow statistical comparison of numbers of developing seeds per ovary (range 1-4).

**Fluorescence microscopy.** Fluorescence microscopy revealed the presence of numerous pollen tubes in fixed material of most crossed, selfed and automatically self-pollinated styles at two days after pollination (Fig. 53a). At least some of these tubes had reached the base of the style by this time and in some cases fluorescence was detected in the micropylar region. However, the thickness of the integument rendered the tracking of the pollen within the ovule difficult and it was often impossible to say with certainty whether or not penetration had occurred. Thus, although possible penetration events were observed in two day old material and definite penetrations in three, four and five day old fixations (Fig. 53b, c) the results are not suitable for statistical analysis. Penetrated ovules seemed to be at least as common in automatically pollinated material as in hand-selfed or crossed styles and in some ovaries all four ovules were definitely penetrated.

**Differential InterferenceContrast Microscopy.** Attempts to examine older material of this species using DIC optics were unsuccessful. Ovaries fixed 13 and 18 days after pollination proved completely opaque to these techniques.

**Histological Sections.** Serial sections of wax-embedded ovaries were no more informative. The embedding medium did not appear to have penetrated to the locules of the ovary or to the ovules and tannin deposits hindered the sectioning process.

### Discussion

The pulsed flowering pattern exhibited by this species is comparable to that recorded in *G. pubescens* in the adjacent IBGE reserve (with which it shows a high degree of synchrony as discussed below) and to that of *Gomidesia fenzliana* in Catolés. However, the range and mean of synchrony values calculated for the population are closer to those obtained for *G. lindeniana* in Catolés.

The apparent absence of buzz-pollinating bees visiting this population is curious. It cannot be attributed to the absence of such bees from the study area, as Proença and Gibbs (1994) and Oliveira and Sazima (1990) have reported buzzing activity in this area by bees including *Augochloropsis* sp., *Bombus atratus*, *Exomalopsis fulvofasciata, Melipona quinquefasciata, Ptiloglossa* sp, *Xylocopa frontalis* and *X. hirsutissima*. Nor is the lack of buzzing activity attributable to the form of the flower or of the anthers as buzzing behaviour was frequent in a population of same species in Catolés which exhibited similar flower and anther morphology. Perhaps an alternative pollen source in the area proved more attractive for the bees during the study period.

The PERS of 19.35 % is close to the mean PERS value reported by Wiens et al. (1987) for outcrossing species.

The statistical equivalence of ovary retention levels and numbers of developing seeds between the hand-cross-pollinated treatment and those left exposed to natural pollination indicate that natural pollen transfer is quite efficient. Fruit set would therefore appear to be resource-limited rather than pollen-limited in this population.

Results from early cohorts of flowers cross- or self-pollinated and left to fall or set fruit indicate a completely self-incompatible species. However, in a later cohort it was noted that the ovary of one self-pollinated flower persisted until the end of the study period. Thus, while it may be concluded that this species is self-incompatible it may not be completely so under all circumstances. One possibility that may merit further investigation is that the tree may be less likely to reject selfed flowers later in the season if the numbers of flowers being pollinated and fruits being set is lower than average. Thus, late in the flowering season a tree which has set less fruit than the resources available to it allow might become less discriminating as to the parentage of the developing embryos in the ovaries which it retains than it might have been earlier in the flowering season. Alternatively this low level of ovary retention in selfed flowers may be simply be attributable to contamination.

Contamination may also account for the single ovary persisting after emasculation. No ovaries were retained in flowers left to self-pollinate automatically though the fluorescence data indicate that the stigmas of these flowers received substantial pollen loads and that pollen tube growth in this treatment was comparable to that in the hand-pollinated treatments.

Ovule penetration appeared independent of pollen source and the timing of discrimination against selfed ovaries suggests that preferential outcrossing is maintained by a post-zygotic phenomenon. Abortion of selfed ovaries did not appear to be synchronous. Rather, fall-off of selfed ovaries was concentrated at certain intervals after pollination while at other times it was negligible. Although data on embryo development are not available for this species, if the timing of development is assumed to be roughly comparable to that of the other species studied, we may surmise that the peak in ovary fall-off after day 10, which is seen in selfs but not in crosses, occurs when the proembryo is at the globular stage.

# General Discussion

## Flowering Phenology and Natural Fruiting Success

Two different flowering strategies were encountered in the species studied. Flowering was of the more or less continuous 'cornucopia' type in *G. cerqueiria* and in the population of *G. lindeniana* near Catolés (hereafter Catolés *G. lindeniana*) while pulsed bang flowering was observed in *G. fenzliana*, *G. pubescens* and in the population of *G. lindeniana* near Brasília (hereafter Brasília *G. lindeniana*). Pulsed bang flowering has been reported for two other species of Brazilian Myrtaceae, *Myrcia rhodosepala* and *Blepharocalyx salicifolius* (Proença & Gibbs, 1994). These authors detected an association between abrupt increases in relative humidity and the onset of flowering in species of Myrtaceae with 'big-bang' flowering strategies. They suggested that the synchronization of pulsed bang species may be more complex. One pulsed bang species studied by them, *B. salicifolius*, commenced flowering the day after the largest daily increase (42%) in relative humidity of the year had been registered and thereafter opened flowers on all days in which humidity was high (c. 80% or higher) until all buds had opened. However, in the other pulsed bang species studied, *Myrcia rhodosepala*, several flowering days showed no discernible correlation with humidity changes. For the present study meteorological data from a station adjacent to the populations of *G. lindeniana* and *G. pubescens* studied in Brasília were compared to flowering patterns in these species but no clear associations could be discerned. Nonetheless, the high level of flowering synchrony exhibited between the two populations of these different species does seem to indicate that some common external factor is controlling flowering episodes in these two species and that this phenomenon might repay further investigation.

As Proença and Gibbs (1994) emphasized, the dry/rainy season transition offers great scope for humidity linkage of flowering events as this is the period of the year when the most marked fluctuations in humidity occur over the shortest time intervals. As discussed earlier (under Ecology: Phenology and Pollination) initiation of flowering at the dry/rainy season transition appears to be typical of the bulk of the neotropical Myrtaceae. This strategy may have the advantage of affording good (dry) conditions for pollination, allowing mature seeds to be dispersed as the rains arrive and facilitating germination and establishment before the onset of the next dry period (Proença & Gibbs, 1994). The *Gomidesia* species treated here, and the majority of the other members of the genus, differ markedly from the general myrtaceous pattern in their flowering seasonality, tending to begin flowering at the wet/dry season transition, several months later than many sympatric Myrtaceae species. The ecological implications of flowering which coincides with the period when the rains are beginning to taper off, rather than with the onset of the rains, have not been investigated in the present study. However, the lack of any perceptible swelling or maturation process in retained ovaries for many weeks after flowering suggests that the fruits of some species of *Gomidesia* (not *G. fenzliana*) may not mature until several months after flowering. In this respect they may resemble fruits of many species of *Myrceugenia* which Landrum (1981) reports as maturing 9 to 12 months after flowering. In *Myrceugenia* it is common to find fruits and flowers on the same plant. In this study fruits and flowers were observed on the same plant in *G. lindeniana* and *G. pubescens* while herbarium studies indicate that this phenomenon is occasional in other species of *Gomidesia*.

The seed/ovule ratios (PERS values) presented here for *Gomidesia* (3.5 -19 %) are all below the average for outcrossing species (22%, Wiens et al., 1987) and for woody plants in general (33 %, Wiens et al., 1989). The highest values were reported for *G. lindeniana* and and the two populations of this species studied had similar values (17%, 19%). The lowest values reported were for *G. fenzliana* and *G. pubescens* and the study populations of these two closely related species differed little in PERS (3.5%, 3.9 % respectively). The range of values for *Gomidesia* is comparable to the range of estimates for eight Central Brazilian species of Myrtaceae (0.3 -12.7 %) by Proença and Gibbs (1994). Low seed/ovule fecundity levels appear to be characteristic of the Myrtaceae in general, independent of breeding system. The highly self-incompatible *Thryptomene calycina* produces 4-7 % viable seed per ovule, while similar fecundity levels are typical of the partially self-compatible *Callistemon citrinus* (Beardsell et al., 1993b). In self-incompatible *Melaleuca* species only 1 - 2% of ovules form seeds (Barlow & Forrester, 1984). Still lower fecundity levels are characteristic of *Syzygium aromaticum* where one-seeded fruits are produced from ovaries containing c. 100 ovules in about 25% of the flowers borne by the plant (Pool, 1988) giving a PERS of 0.25 %. Beardsell et al. (1993b) considered that the similarity in fecundity of various members of the Myrtaceae with differing breeding systems suggests that similar limitations to seed set occur in diverse members of this family, despite differences in reproductive behaviour. The apparent superfluity of ovules was discussed by in the context of the Myrtoideae by Nic Lughadha and Proença (1996). Possible explanations include historical factors, insurance against the wastage of ovules inherent in a post-zygotic SI system or the provision of scope for female choice. Clearly an improved understanding of the basis of this phenomenon will require more detailed studies of the non-developing ovules/seeds in a range of species to establish whether they contain aborted embryos (at similar or different stages of development) or are unfertilised. In the meantime extreme caution should be exercised in inferring predominant outbreeding on the basis of low PERS values alone.

### Anthesis and Pollination

Anthesis occurred before dawn in three of the populations studied (*G. cerqueiria* and both populations of *G. lindeniana*) and was later (and more variable?) in the closely related *G. fenzliana* and *G. pubescens*. Only in Catolés *G. lindeniana* were flower visitors (bees of the genus *Andrena*) observed before dawn. Anthesis before daybreak has also been reported in Brazilian *Siphoneugena densiflora* and in Costa Rican *Eugenia salamensis*. In this latter species Frankie et al. (1983) observed pre-dawn visits by bees (see Nic Lughadha & Proença, 1996) but in *S. densiflora*, curiously, although flowers opened two to three hours before dawn the anthers did not dehisce until daybreak (Proença, 1991). Thus, the *Andrena* observations in *G. lindeniana* represent only the second record for the Myrtoideae of pre-dawn pollination, a phenomenon which is well-known in the neotropical Melastomataceae, most of which are buzz-pollinated. Renner (1989) commented that the rapid vibrations used by bees when harvesting melastome pollen presumably produce a high temperature of the flight muscles which may mean that this method of pollen collecting is particularly appropriate during the relatively cool early morning hours. She considered that ecological constraints must govern the activity of dark-coloured bees during the hottest hours. In the present study buzz-pollination was reported in two of the three populations with pre-dawn anthesis (*G. cerqueiria* and *G. lindeniana* at Catolés) but only in the latter species were buzzing visitors observed before dawn. Buzzing behaviour was also observed on one occasion in *G. pubescens*, at 07.50 h, shortly after anthesis.

When the observed incidence of buzzing behaviour is considered in relation to anther morphology, it can be seen that the species with the most closed anthers (*G. cerqueiria*) is buzz-pollinated while there are no reports of buzz-pollination (or indeed of visits by any putative pollinator) for the species with the least specialised anthers (*G. fenzliana*). However, the fact that buzz-pollination was prevalent in one population of *G. lindeniana* and apparently absent in another clearly indicates that the occurrence of buzzing behaviour cannot be predicted from anther morphology alone. Finally, buzz pollination is rare (observed on only one occasion) in *G. pubescens*, which has anthers which resemble those of *G. fenzliana* in degree of opening but differ in having a more pronounced vertical displacement of the pollen sacs. Thus, it seems likely that buzz-pollination may be increasingly important in anthers with increasing degrees of closure of the thecae, but observations on more species are needed in order to investigate this apparent trend. Interestingly, it could be argued that the pollen of *Gomidesia* is pre-adapted for buzz-pollination since, in the species for which data are available the pollen is relatively small (< 30 μm), fairly smooth and closer to being spherical than that of some other genera of the Myrtoideae (See Pollen Morphology).

The buzz-pollination syndrome was originally associated with poricidal anthers (Buchmann, 1983) but it is has become increasingly clear that bees also use vibration to aid pollen collection from non-poricidal anthers (Buchmann, 1985). Recent reports of buzz-pollination in flowers with longitudinally dehiscing anthers include two species of *Kielmeyera*, Guttiferae (Oliveira & Sazima, 1990) and, in the Myrtales, five species of *Diplusodon*, Lythraceae (Barros, 1989). A further report highly relevant to the present discussion is that of Proença (1992) who discussed the broad implications of her discovery of buzz-pollination by *Bombus* spp. in *Myrcia rhodosepala* and *Blepharocalyx salicifolius* and by *Ptiloglossa* bees in *Siphoneugena densiflora*, three myrtaceous species which lack poricidal anthers. She observed that bees vibrated only in flowers of species in which the hypanthial cups were prolonged beyond the ovary and ended in strongly reflexed sepals and petals. She therefore proposed that the hypanthial cup of bee-pollinated Myrtaceae represented an adaptation to buzz-pollination, its exact function in this regard remaining unclear. Two non-exclusive hypotheses were presented to explain the perceived correlation between the hypanthial cup and buzzing behaviour. The circular disk at the apex of the hypanthial cup may act as a 'hold' for the bees to grasp. Alternatively (or additionally) the cup may serve to reflex the sepals and the petals thereby replacing the usual 'petaloid' floral cue with a 'staminal' floral cue. Staminal cues could also be offered by flowers displaying bigger, stouter stamens or by calyptrate flowers in which petals are reduced or absent. The flowers of all the species of *Gomidesia* in this study exhibit prolonged hypanthia and strongly reflexed sepals and petals but not all were buzz-pollinated. Thus while these traits may be prerequisites for buzz-pollination their presence is not necessarily indicative of a buzz-pollinated species.

Combining Proença's (1992) reports of buzz-pollination in species of *Blepharocalyx*, *Myrcia* and *Siphoneugena* with the results of the present study it is clear that buzz-pollination must have arisen on several occasions within the Myrtoideae. Buchmann (1985) hypothesized that poricidal anthers evolved from regular anthers of pollen flowers in which bees were vibrating. Our Myrtoideae data are not inconsistent with this scenario. Dukas and Dafni (1990) considered that selection for reduced investment in pollen production could drive the evolution of poricidal anthers. Their proposed evolutionary pathway was derived from studies on Boraginaceae and began with polyandrous nectariferous flowers of a type not dissimilar to those assumed to be basal in the Myrtaceae (See Nic Lughadha & Proença, 1996). The model envisages flowers of an intermediate type in which access to pollen is restricted and which are visited chiefly for their nectar. Dukas and Dafni (1990) suggested that in times of pollen shortage bees could collect pollen from these stamens by occasional vibration in addition to typical nectar sipping. However they did not make explicit the means by which such occasional exploitation could lead to new floral adaptations resulting in an obligately buzz-pollinated flower.

**Breeding system**

The range of ISI values obtained for the study populations is presented in Table 12. Applying the criteria of Bawa (1974) and Bullock (1985), only *Gomidesia fenzliana* rates as self-compatible while *G. cerqueiria* is a borderline case and *G. lindeniana* and *G. pubescens* rate as self-incompatible. There is evidence for between-population variation in breeding system in *G. lindeniana* with the Brasília population rating as strictly self-incompatible while there is some fruit set from selfed flowers in the Catolés population. Thus the data obtained represent a continuum of results from apparent self-incompatibility to self-compatibility but in no case were selfed flowers as successful as crossed flowers. Most of the trees studied showed some degree of self-compatibility but the superior fruiting success of crossed flowers in every case indicates the operation of some mechanism to maintain preferential outcrossing in these populations. That this mechanism is post-zygotic has been established without doubt. However, the nature of the mechanism in operation remains open to discussion. Phenomena of this kind, loosely referred to as late-acting self-incompatibility (hereafter LSI), have been reviewed in detail by Seavey and Bawa (1986) and Sage et al. (1994). Seavey and Bawa (1986) classified LSI systems according to the site of rejection. The *Gomidesia* species studied here would be assigned to their third category 'post-zygotic rejection' of which only eleven instances (in seven families) were known to the authors at the time of their review. In the intervening decade numerous additional examples have been published of species which exhibit phenomena of this type, e.g. *Vellozia squamata*, (Oliveira et al., 1991); *Chorisia chodatii*, *C. speciosa*, *Tabebuia caraiba* and *T. ochracea* (Gibbs & Bianchi, 1993) as well as the examples discussed below.

**Distinguishing between true LSI and inbreeding depression.** Seavey and Bawa (1986) discussed the importance and the difficulties of distinguishing between active self-rejection (i.e. the operation of an LSI system) and the effects of inbreeding depression. Four criteria

Table 12. Summary of results of breeding system studies in selected species of *Gomidesia.*

|  |  | *G. cerqueiria* |  | *G. fenzliana* |  | *G. lindeniana* |  |  |  | *G. pubescens* |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Catolés |  | Brasília |  |  |  |
| % Natural fruit set |  | 29 |  | 9 |  | 31 |  | 35 |  | 10 |  |
| Mean developing ovules per fruit |  | 1 |  | 2.3 |  | 2.2 |  | 2.2 |  | 1.5 |  |
| PERS[1] |  | 7.2 |  | 3.5 |  | 17 |  | 19 |  | 3.9 |  |
| Crosses : Selfs |  | Cross | Self | Cross | Self | Cross | Self | Cross | Self | Cross | Self |
| persisting at | @ 10 days | 24 | 29 | **60** | **52** | **48**[2] | **78**[2] | **53** | **28** | **82** | 72 |
| intervals after | @ 20 days | 22 | 29 | 39 | 35 | * | * | **46** | **3** | 72 | 56 |
| hand-pollination[3] | @ collection | 13 | 3 | **46** | **20** | **39** | **5** | **30** | **0** | **39** | **5.5** |
| ISI[4] |  | 0.23 |  | 0.43 |  | 0.13 |  | ~0 |  | 0.14 |  |
| Breeding system[5] |  | SC/SI |  | SC |  | SI |  | strict SI |  | SI |  |

1. Pre-emergent reproductive success - see Methods.
2. Data collected @ 8 days after hand-pollination at which point daily monitoring of this population ceased.
3. Retention rates of ovaries after hand-pollination expressed as a percentage of the number pollinated.
   Differences between pairs of results presented in bold are statistically significant.
   Chi-square tests were performed on the raw data before conversion to percentages.
   Values for *G. fenzliana* @ collection include a second cohort not monitored daily but left to set fruit.
4. Index of self-incompatibility - see Methods
5. SC = Self-compatible, SI = Self-incompatible- for criteria applied see Methods

* = missing data

were listed which might help to determine whether zygote or embryo abortion is the result of delayed action SI or of inbreeding depression determined by the genotype of the zygote.

1. The timing of abortion: uniform embryo failures at a particular developmental stage would suggest LSI whereas embryos blocked at a variety of stages could more easily be interpreted as the result of inbreeding depression, with different recessive lethals taking effect at different points.

2. Between-plant variation in selfing success: where genetic load is responsible for low seed set after selfing one would expect plants with fewer detrimental recessives to approach normal seed-production. Uniformly low seed-set after selfing may be evidence of active self-rejection.

3. Dependence of abortion on the paternal rather than the progeny genotype: where SI is controlled by one or a few specific loci, cross-compatible and cross-incompatible groups should be detectable within the population.

4. Embryo rescue: embryos homozygous for lethal genes would not survive in tissue culture while those aborting because of their interaction with their female parent might be rescued by such means.

Klekowski (1988) challenged the first and third of these criteria, arguing that the mechanisms of self-sterility are insufficiently understood to permit predictions as to the timing of self-rejection and that inbreeding depression is consistent with the presence or absence of clear segregation ratios in progeny after selfing (because the lethal equivalent concept is based on the homozygosities of many genes with small detrimental effects). Klekowski added a fifth criterion to the list:

5. Induced mutations in ovarian self-incompatibility systems (or indeed in any SI system) should favour a shift from self-sterility to self-fertility whereas the opposite should be the case where inbreeding depression is involved.

Sage et al. (1994) reviewed recent progress in the study and interpretation of post-zygotic rejection. Several researchers have attempted to apply some of the criteria listed above to distinguish between post-zygotic SI and inbreeding depression in species with ovarian self-infertility. The occurrence of self-rejection at a continuum of embryonic stages was cited as evidence to support inbreeding depression as an explanation for decreased fertility after self-pollination in *Epilobium angustifolium* (Wiens et al., 1987), *Campsis radicans* (Bertin et al. 1989), *Crinum erubescens* (Manasse & Pinney, 1991). In contrast, post-zygotic failure in *Liquidambar styraciflua* occurred in a fairly restricted developmental phase when embryos were 4 - 6 celled (Schmitt & Perry, 1964). Although this could be construed as evidence in support of the operation of LSI in this species, Sage et al. (1994) comment that the synchronized embryo failure could equally be due to an inbreeding depression system that mimics ovarian LSI by virtue of the involvement of a large enough number of early-acting embryonic lethals. Gribel (1995) favoured genetic load as an explanation for self-sterility in *Ceiba pentandra* and *Pseudobombax munguba* because of the observed diversity of developmental stages shown by the ovules in self-pollinated flowers just before pistil abscission and variation in levels of self-sterility between trees in the study populations. Weller and Ornduff (1991) exploited the distylous breeding system of *Amsinckia grandiflora* to demonstrate unambiguously that self-sterility in this species is attributable to inbreeding depression.

**Can inbreeding depression mimic LSI?** With so many case studies tending to support inbreeding depression rather than SI as the explanation for post-zygotic self-rejection one might wonder why the problem is not generally considered to have been resolved. The objection most often offered against such an explanation for species showing high levels of self-sterility is the 'unrealistically high' number of genetic lethals required to produce near-uniform abortion of young embryos (Seavey & Bawa, 1986; Waser & Price, 1991; Sage et al., 1994). The level of self-fertility (S) corresponding to a given number of embyronic lethals (N) is given by $S = (0.75)^N$. Thus, at least ten embryonic lethals (equivalent to 94% self-infertility) would be necessary to produce a situation where inbreeding depression caused embryo death with sufficient frequency to mimic SI. It has been argued that these levels of embryonic lethals are unrealistic, both from an empirical point of view and also on theoretical grounds.

The empirical argument is based simply on comparison with published estimates of mean numbers of lethal equivalents in angiosperms. These are rather few and range in value from less than 1 to 12 (Levin, 1984; Klekowski, 1988). This would seem to suggest that only in species bearing genetic loads at the higher limits of the known range could preferential outcrossing be maintained by inbreeding depression. However, Sage et al. (1994) outlined several additional factors that should be taken into account when assessing genetic loads and their potential role in the maintenance of preferential outcrossing. Firstly, numbers of genetic lethals have been reported for a rather small and unrepresentative sample of the angiosperms but results for the few woody species studied show some of the highest estimates of genetic load to date (e.g. 9.6 in *Vaccinium corymbosum* (Krebs & Hancock, 1991), 13.8 in *Pseudobombax munguba* (Gribel, 1995), 11 -12 in *Liquidambar styraciflua* (Schmitt & Perry, 1964)). Large perennial species can be expected *a priori* to have much higher mutation rates per generation than small annual species because somatic mutations can accumulate during many mitotic cell divisions between meiotic events. On the basis of preliminary data on chlorophyll deficiencies Klekowski and Godfrey (1989) suggested that genomic lethal mutation rates may be more than an order of magnitude higher in trees than in annual plants. Secondly, it seems likely that numbers of lethal equivalents are underestimated in species that never mature more than a certain (small) fraction of their ovules. In such species the seed to ovule ratio may act as a soft-selection sieve resulting in artificially low estimates of numbers of genetic lethals especially where the load levels are genuinely rather low (Klekowski, 1988). Finally, as Sage et al. (1994) emphasized, an embryo which has the capability to survive to maturity may fail to do so simply because the ovary which contains it is aborted, perhaps because of the low number of other viable embryos present. Thus, the ratio of seeds resulting from selfing to the total number of ovules in all selfed flowers underestimates the number of selfed-embryos free from developmental lethals. In summary, the numbers of lethal recessives carried by individuals of woody species may be higher than previously estimated AND the genetic load necessary for a population to simulate SI may be lower than has been generally supposed. Together these conclusions may be interpreted as support for inbreeding depression as a plausible explanation for high levels of outcrossing in woody species with low PERS values. However, it should be noted that, since estimates of genetic load are based on relative survivorship of selfs and crosses, the argument becomes somewhat circular as in many cases the possibility that low self-survivorship is due to active self-rejection rather than to homozygosity for recessive lethals cannot be discounted.

The theoretical grounds on which the numbers of required lethals are deemed 'unrealistically high' have been mentioned often but are rarely discussed thoroughly. Seavey and Bawa (1986) comment that theoretical models of genetic load do not appear to anticipate genetic loads of a magnitude great enough to mimic SI, citing Dobzhansky (1970), Wallace (1970) and Wright (1977). Waser and Price (1991) calculated that about 8000 loci producing lethals would be required to explain a situation in which only 1% of selfed offspring survive and considered this number unrealistic, citing Lewontin (1974). Lande and Schemske (1985) concluded that even a moderate degree of selfing in a population would greatly reduce the level of inbreeding depression by purging recessive or nearly recessive lethal mutations. However, recent studies on *Arabidopsis thaliana,* which has the smallest known plant genome, have generated estimates of about 5000 loci producing recessive lethal mutations (Jurgens et al., 1991). In this context, the Waser and Price estimate of 8000 does not seem extraordinarily high. Furthermore, these latter authors' calculations were based on an assumed mutation rate of $10^{-6}$ per locus per generation to lethal alleles whereas recent studies on loci producing recessive chlorophyll deficiencies suggest that mutation rates are several orders of magnitude greater (Klekowski & Godfrey, 1989; Willis, 1992). Extrapolating from the chlorophyll deficiency data to lethals in general, Lande et al. (1994) suggested that the long-lived red mangrove may have a genomic mutation rate to recessive lethals as high as 0.2 per generation. They then proceeded to model the evolutionary dynamics of recessive or slightly dominant lethal mutations in partially self-fertilizing plants. They concluded that with genomic mutation rates to (nearly) recessive lethals of the order of 0.1 to 1.0 per generation, completely outcrossing populations can maintain large average numbers of lethals and very high early inbreeding depression. In such situations, where the mean number of lethals per mature plant exceeds 10, selective interference among loci creates a sharp discontinuity in the mean number of lethals maintained as a function of selfing rate. Purging of lethals is negligible unless the selfing rate approaches or exceeds a threshold level at which there is a sharp drop in the number of lethals maintained. Thus, Lande et al. (1994) have established that with high mutation rates to recessive lethals plant species may display very high inbreeding depression (sufficient to mimic LSI) despite intermediate selfing rates.

Since neither the empirical nor the theoretical objections to inbreeding depression as an explanation for post-zygotic rejection of selfs can be sustained in general terms, inbreeding depression must be considered along with active LSI as a potential explanation for observed post-zygotic preferential outcrossing phenomena. The relative explanatory power of these alternatives should be assessed in relation to the data obtained for individual species

**Inbreeding depression or LSI in *Gomidesia*?** Returning to the particular case of *Gomidesia* we can attempt to apply some of the general considerations discussed by Seavey and Bawa (1986), Klekowski (1988) and Sage et el. (1994). Obviously, of the criteria outlined by them some (4. and 5.) are irrelevant to the data available for *Gomidesia* and the others are of strictly limited application, nonetheless the exercise is not completely uninformative.

1. Is abortion of selfed embryos synchronous? The data on ovary retention suggest that abortion is not synchronous but that it is particularly common at certain intervals after pollination and absent or negligible at others. Typically, a period when fall-off is high immediately after pollination, is followed by a plateau period where fall-off is negligible, before the onset of another phase of gradual loss of selfed ovaries. Such a pattern could be considered consistent with genetic load hypotheses, with embryo abortion occurring at various developmental stages. However, the histological data show the error involved in interpreting fall-off patterns as a direct reflection of embryo abortion patterns. In *G. cerqueiria*, for instance, fluorescence microscopy of flowers sampled at the middle (day 15) and towards the

end (day 20) of the plateau period (during which ovary loss was negligible), revealed preferential abortion of embryos in selfed flowers during this period. Considerable embryo abortion also took place in *G. fenzliana* in seeds of a similar age, during a period when ovary fall-off was very gradual. Surviving embryos at 18 days after pollination were at the globular stage of development, generally more than eight-celled with a clearly defined suspensor. Preferential shedding of selfed ovaries occurred at some time after this date and whether it was due to the abortion observed cannot now be established.

2. Does self-sterility vary from tree to tree within a population? Unfortunately the experimental pollinations were not designed to test this possibility. There is, however, some circumstantial evidence to suggest that self-sterility varies between trees within a population (particularly in *G. pubescens*).

The data discussed so far indicate that self-sterility is incomplete and variable within and between populations of *Gomidesia* species and also that the timing of embryo abortion and rejection of selfed ovaries is variable. These observations provide some support for the genetic load model of post-zygotic discrimination rather than for active self-rejection. The situation is further complicated by the fact that embryo abortion must also occur in ovaries which ultimately mature into fruit, since in all cases studied the average number of ovules fertilised per ovary was considerably greater than the average number of seeds per mature fruit. The basis for embryo abortion in successful fruit has not been investigated in the present study but it is of interest to explore whether such abortion can be accounted for by invoking the same factors used to explain the post-zygotic maintenance of preferential outcrossing.

Competition among seeds seems, *a priori*, to represent the most parsimonious explanation for embryo abortion in outcrossed ovaries. Where developing embryos in the same ovary are competing for resources (as is presumed to be the case in *Gomidesia*) a positive feedback situation may develop with more vigorous embryos representing a more effective sink for resources and thus widening the gap between them and the less vigorous embryos which would ultimately abort. Broadening this resource allocation model to consider competition between ovaries it is not difficult to envisage a situation whereby the abortion of just one or two embryos due to homozygosity for recessive lethals could render a selfed ovary a less effective sink for resources and result in the ultimate abortion of that ovary even though it may have contained potentially viable embryos. The even distribution of developing embryos among the locules of an ovary is consistent with competition between seeds , assuming that competition is particularly intense between developing seeds occupying the same locule. However, this even distribution is also consistent with explanations which depend on maternal choice, e.g. the plant may 'allow' a maximum of one embryo per locule and cause the abortion of all but the most vigorous of the developing seeds in each locule. The fact that the non-developing ovules/seeds in an individual ovary are usually similar in size suggests that they abort more or less simultaneously rather than being gradually outcompeted one by one

Thus, 'female choice' or maternal control represents an non-exclusive alternative to competition as a determinant of the fates of ovules.. Just as LSI is difficult to distinguish from inbreeding depression so the operation of female choice within outcrossed ovaries may be difficult to distinguish from the unmodified effects of competition. However, one of the species studied here, *G. cerqueiria*, seems to represent a strong candidate for the operation of some degree of maternal control. In this species all mature fruits examined contained only a single seed, although in many ovaries two or three ovules were penetrated by pollen tubes and, in at least some cases, embryo development was initiated in more than one seed. The regularity with which the number of maturing seeds is reduced by abortion to one per fruit is suggestive of maternal control. Although simple competition between seeds for limited resources could also account for reductions in the number of seeds maturing per ovary, if this were the case one would expect occasional two-seeded fruits where two embryos of comparable vigour had acted as equally effective sinks for resources, each failing to gain a competitive edge over the other.

It seems that the results presented here for *Gomidesia* are best explained in terms of inbreeding depression operating in tandem with or followed by inter- and intra-ovarian competition and, perhaps, maternal selection. The data are consistent with a situation in which some embryos fail due to genetically based lethality and others lose out in the competition between the remaining potentially viable embryos. Once some embryos have gained the competitive edge the maternal plant may induce early abortion in the other seeds , thus producing cohorts of similarly sized abortive seeds . As the number and vigour of developing seeds is likely to influence fruit survivorship, a fairly low level of homozygosity for recessive lethals in selfed ovaries may be amplified into a marked preferential outcrossing effect. There is nothing in the data to indicate the operation of a late-acting self-incompatibility system such as was suggested by Proença and Gibbs (1994) for three of the eight Central Brazilian Myrtoideae species studied by them rather than the recessive lethal model favoured here.

**Preferential outcrossing elsewhere in the Myrtaceae.** Given the limited nature of the data available on SI in the Myrtoideae it seems appropriate to broaden the discussion to consider and compare reports of SI elsewhere in the Myrtaceae. This can be justified on the grounds that repeated sampling within a family has usually revealed identical mechanisms controlling SI (Charlesworth, 1985). Beardsell et al. (1993a) considered it likely that the same mechanism of SI should operate throughout the Myrtaceae. However, among the several myrtaceous breeding system studies cited by these authors the variation in the timing of operation of reproductive barriers after self-pollination is striking. Self pollen tubes were arrested at the base of the style in *Melaleuca hypericifolia* and *M. thymifolia* and in the ovarian cavity in *M. capitata* (Barlow & Forrester, 1984). In *Thryptomene calycina* self-pollen tubes were arrested on the placenta or at the micropyle (Beardsell et al., 1993b). Even within a genus the timing of discrimination against self pollen may vary considerably. In *Eucalyptus woodwardii* reduced seed crops following self-pollination were attributed to reduced ovule penetration by self pollen tubes (Sedgley & Smith, 1989). In contrast post-zygotic SI has been reported in *E. regnans* (Griffin et al., 1984, 1987), *E. spathulata, E. cladocalyx* and *E. leptophylla* (Ellis & Sedgley, 1992). Potts and Savva (1988) also concluded that some late-acting mechanism of SI was in operation in *E. morrisbyi*.

The ovarian SI reported in *Melaleuca* and *Thryptomene* has been tentatively interpreted as a gametophytic SI system (Barlow & Forrester, 1984; Beardsell, 1991) although no genetic analyses were undertaken. Another apparent candidate species for SI is *Melaleuca alternifolia* for which an extremely high outcrossing rate of 93% has been reported (Butcher et al., 1992). The genetic bases for post-zygotic discrimination are not so easily fathomed however. The species most thoroughly studied to date is *Eucalyptus regnans* F. Muell., a large mass-flowering forest tree with hermaphrodite flowers (Griffin & Cotterill, 1988; Griffin & Hand, 1979; Griffin et al.,1987; Sedgley et al., 1989). Isozyme analysis of mixed-pollinated material showed this species to be a preferential outcrosser (Griffin et al., 1987) yet studies employing bright field, fluorescence, phase contrast, Nomarski and scanning electron microscopy found no differences in rates of ovule penetration or in development of embryos between self- and cross-pollinated material up to 16 weeks after pollination (Sedgley et al., 1989). At this time embryos with two to sixteen cells were present in some seeds but some undivided zygotes were also observed. The timing of abortion of selfed seeds could not be established in this study but the authors considered it unlikely to occur before the eight-celled stage. There was no evidence for a self-incompatibility reaction, rather the evidence suggests that the control mechanisms for the preferential outcrossing observed in this species are dependent upon both embryo genotype and maternal resource allocation (Griffin et al., 1987). Individual trees showed a range of self-fertility after self-pollination and there was a reduction in mean seed yield relative to cross pollination consistent with the expression of recessive deleterious alleles in the developing inbred embryos. However, even in outcrossed capsules, the seed:ovule ratio was only about 20% (Griffin et al., 1987), and as this was much lower than the numbers of penetrated and fertilised ovules at 16 weeks it was inferred that considerable seed selection occurs during the later stages of seed development (Sedgely et al., 1989). Thus, a combination of inbreeding depression and maternal choice could be sufficient to explain the results obtained for *E. regnans*. Inbreeding depression had previously been demonstrated for growth and survival of seedlings of this species (Eldridge & Griffin, 1983).

Three species of *Eucalyptus* Section *Bisectaria, E. cladocalyx*, *E. leptophylla* and *E. spathulata* have also been studied in some detail and found to be highly self-incompatible. The preferential outcrossing observed in these species was found to be maintained by a post-zygotic mechanism operating in *E. cladocalyx* and *E. leptophylla* while the existence of mixed pre-zygotic and post-zygotic mechanisms was inferred in *E. spathulata*. Microscopic studies of embryo development were not undertaken for these species so the timing of operation of the post-zygotic mechanism cannot be ascertained from the data provided. Although the authors refer to the post-zygotic mechanism in operation as SI the data available are also consistent with explanations based on inbreeding depression

Other mating system studies of *Eucalyptus* have concentrated on estimating outcrossing levels in populations without investigating the mechanisms by which these levels are maintained. In general, such studies have indicated outcrossing with a significant amount of selfing. Outcrossing estimates for mass-flowering species of *Eucalyptus* tend to fall within the range 0.70 - 0.86 (Moran & Bell, 1983; James & Kennington, 1993) and thus are generally lower than might be expected in species with an active SI system but consistent with levels of inbreeding depression which could be produced by several lethal alleles. Barrett and Eckert (1990) commented on the uniformity of outcrossing rates within and between species in *Eucalyptus* and suggested that this might reflect a lack of genetic variation within *Eucalyptus* for floral mechanisms that would increase outcrossing rates. They considered that this phylogenetic constraint could have arisen during the evolution of this group's specialized floral morphology. James and Kennington (1993) interpreted their data for *Eucalyptus camaldulensis* in terms of selection against recessive homozygotes and maternal control of resource allocation. In their model, post-zygotic seed selection depends on each plant carrying a large number of seed-aborting recessive lethal factors in heterozygous condition. The intensity of selection operating against any particular genotype will be determined by the genotype of its neighbours and by the maternally controlled availability of resources. They demonstrated the use of this model in the successful interpretation of much of the published mating system data for *Eucalyptus*, including data for some species and situations previously considered anomalous.

Curiously James and Kennington (1993) do not discuss the results obtained by Potts and Savva (1988). These authors reported that 80% of trees of *Eucalyptus morrisbyi* were completely self-incompatible. Though such high levels of self-sterility might be interpreted as evidence to support the existence of an active self-rejection mechanism in this species, Ellis and Sedgely (1992) provide an equally convincing alternative explanation: *E. morrisbyi* is a rare Tasmanian endemic, very restricted in range and population size, and the high degree of self-incompatibility may be due to an accumulation of deleterious alleles in the population.

In summary, although ovarian SI has been demonstrated in some Myrtaceae, there is no evidence to indicate the existence of a post-zygotic self-incompatibility system in any species of Myrtaceae studied to date. A number of species, including the members of the genus *Gomidesia* treated here and many (most?) species of *Eucalyptus* exhibit preferential outcrossing which is maintained by some post-zygotic mechanism. On the basis of the data available to date, inbreeding depression seems to offer the most satisfactory explanation for this phenomenon. Estimates of genetic load for some of these species could represent a first step towards testing this hypothesis.

# Appendix 1

## Scanning electron microscope techniques for the study of anther morphology.

Dehisced anthers were taken from herbarium specimens or from flowers preserved in 70 % alcohol or Copenhagen mixture. Anthers from liquid preserved collections were dried before mounting using a Balzer Critical Point Drier 030. Herbarium material required no treatment before mounting. All anthers were mounted using Araldite, a proprietary adhesive which allowed some manipulation of the anther for a few seconds after it had been placed the stub. Thus a degree of consistency in the orientation of the anthers could be achieved. The stubs were then coated using a Bal-Tec SCD 050 sputter coater and examined with a Hitachi 2-2400 microscope fitted with a Polaroid camera using black-and-white Polaroid 665 film.

# Appendix 2

## Clear-squash techniques for the study of ovules and developing seeds.

Dissected ovules or developing seeds were placed on a microscope slide in a drop of modified Herr's clearing fluid (lactic acid-chloral hydrate-phenol-clove oil-histoclear, 2:2:2:2:1 by weight). For safety reasons, histoclear has been substituted for xylene, with apparently identical results. A cover slip was placed over the preparation prior to a preliminary examination of the preparation using a Leitz microscope with DIC (differential interference contrast) optics. Subsequently the cover slip was lightly and repeatedly pressed with a dissecting needle so that the cells of the preparation gradually became spread apart, facilitating more detailed observations of structures detected during the preliminary examination.

In cases where developing seeds were difficult to clear, because of the presence of large amounts of tannin, usually in the integument, a stain clearing technique was employed, involving haemalum and methyl salicylate as outlined by Stelly et al. (1984).

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# A SURVEY OF THE REPRODUCTIVE BIOLOGY OF THE MYRTOIDEAE (MYRTACEAE)[1]

*E. Nic Lughadha*[2] *and C. Proença*[3]

## ABSTRACT

The Myrtoideae usually present small, epigynous, 4–5-merous, polystemonous flowers that last one day. Bee-pollination in which pollen is the sole reward is the dominant pollination system. Nectar has been best documented in *Syzygium* but probably also occurs in other bee-pollinated genera. The most common bee visitors are Apidae: Meliponinae and Bombinae. Bird- and mammal-pollination occur in Old World *Syzygium* with nectar as the primary reward. Bird-pollination with petals as the reward occurs in New World *Acca* and *Myrrhinium*. General floral morphology is very uniform, while inflorescence types and flowering strategies are very diverse. Stigmas are dry and ovules are anatropous, hemicampylotropous or anacampylotropous and have an outer 2–6-layered integument and an inner 2-layered integument or a single integument. The ovary usually contains more ovules than will form seeds. Flowering strategies vary from mass-flowering types, in which the flowering episode typically takes only a few days, to steady-state types of up to 90 days duration. Flowering at dry/wet season transition is common in seasonal climates, and fire-induced flowering is found occasionally. Outbreeding is probably widespread, although both self-compatible and self-incompatible species exist. The self-incompatible species have self pollen tubes penetrating the micropyles, so preferential outcrossing may be maintained by a late-acting mechanism. Cryptic dioecy, in which female flowers have "mimic" sterile anthers occurs in several genera. Apomixis occurs in *Syzygium* and this has been reported to be linked to the polyembryony found in this genus. Myrtoid fruits are fleshy berries or drupes, dispersed by birds, bats, and other small mammals. Fruit size, color, texture, and number of seeds are all very variable. Seed coats may be absent to bony, but have a smooth surface. The endosperm is mainly digested by the developing embryo. Early embryology is relatively uniform but final embryo morphology varies widely across the genera. Germination times vary from 10 days to over 2 years and seed viability periods from 15 days to 1 year.

The reproductive biology of the Australian Myrtaceae has recently been the subject of a thorough review by Beardsell et al. (1993). The alliances traditionally assigned to the subfamily Leptospermoideae are the major focus of their account, reflecting not only the predominance of these groups in the Australian flora but also the widely acknowledged dearth of information on the reproductive biology of the Myrtoideae in general (e.g., van Wyk & Lowrey, 1988; Proença & Gibbs, 1994).

The present survey was compiled to complement that of Beardsell et al. (1993) by bringing together the scattered and often fragmentary data on the Myrtoideae. We use the term Myrtoideae in the traditional sense to embrace virtually all the fleshy fruited Myrtaceae. Thus we include Johnson and Briggs's (1984) monophyletic Myrtoideae sensu stricto, and their *Acmena* alliance (including *Syzygium*), although phylogenetic analysis has suggested that this latter group is more closely related to the leptospermoid *Eucalyptus* alliance than to the Myrtoideae s. str. (Johnson & Briggs, 1984). Conversely, we use the term Leptospermoideae in its broadest sense to include all Myrtaceae with capsular fruit. Where names have been changed to fit modern taxonomic concepts, the name that appeared in the original publication is cited in parentheses, e.g., *Syzygium paniculatum* (as *Eugenia paniculata*).

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The pantropical Myrtoideae as a whole has not received any synthetic taxonomic treatment since Niedenzu's (1893) synoptic account. There is no Old World equivalent to McVaugh's (1968) invaluable review of the American Myrtoideae. As a subfamily the Myrtoideae are rather less morphologically diverse than the Leptospermoideae. Approximately 60 genera are recognized for the estimated 2375 species of Myrtoideae, while the Leptospermoideae with less than half the number of species (1300) includes some 72 genera (species numbers from Schmid, 1980; generic estimates reflect the present authors' view of current taxonomic opinions). While this discrepancy may be interpreted as an artifact of our ignorance of the former group, most myrtologists would agree that the perceived homogeneity is real and has contributed to, rather than resulted from, the comparative taxonomic neglect which this subfamily has indisputably suffered. McVaugh (1968) described the species of American Myrtaceae as "distressingly alike in aspect and in most individual characters, making identification and classification of both genera and species a correspondingly difficult and tedious matter."

This homogeneity is portrayed in more concrete terms in Schmid's (1980) table of the "distinguishing organographic characters of the subfamilies of the Myrtaceae," the majority of which are based on reproductive organs. For each character a statement of the prevailing state within each subfamily is followed by a summary of the exceptions. Schmid expressed the estimated percentage of exceptions using precise and clearly defined qualifying terms: "very rarely" (signified $< 2\%$ of species), "rarely" (2–4%), "very occasionally" (5–10%), "occasionally" (5–30%) and "often" (31–60%). Hence a reasonably accurate impression of the variability of particular characters within the subfamilies can be gained. The qualifier "very rarely" is applied to the majority of the exceptions listed for the Myrtoideae. In the Leptospermoideae, however, exceptions are more or less evenly distributed across the range from "rarely" to "often" with "very rarely" being applied in only two instances. Thus the Myrtoideae emerges as a much more homogeneous group than the Leptospermoideae.

## INFLORESCENCE STRUCTURE

Inflorescences may be apical, subapical, axillary, supra-axillary, ramiflorous or cauliflorous in position. The authoritative analysis of inflorescence structure in the Myrtaceae by Briggs and Johnson (1979) documented an equally impressive range of structural form within the Myrtoideae. They range from many-flowered panicles and thyrsoids through dichasia, botryoids, metabotryoids, triads, and metaxytriads to monads and metaxymonads. In their brief description of adaptive syndromes, these authors drew attention to correlations between habitat, niche, and inflorescence arrangement. In particular, large panicles or aggregations of smaller inflorescences are reported by them as typical of forest and woodland species of Myrtaceae (myrtoid examples include species of *Myrcia* and its allies, *Blepharocalyx* (as *Temu*), *Pimenta*, *Xanthomyrtus*, species of *Syzygium* and its allies). However, in the undergrowth or understory of non-sclerophyllous communities, they noted that flowers are often in monads and/or triads that are not massed (myrtoid examples include *Myrceugenia*, *Psidium* spp., *Ugni*, *Myrteola*, *Myrtus* sensu stricto, *Rhodamnia*, *Lophomyrtus*, *Neomyrtus*, *Campomanesia*, *Luma*, and *Eugenia* spp.) (Briggs & Johnson, 1979). Ramiflorous or cauliflorous inflorescences have been linked to bat pollination (Crome & Irvine, 1986), and to bat or marsupial dispersal (see Fruit Characteristics and Dispersal Agents).

## FLOWER STRUCTURE

Flowers of the Myrtoideae are hermaphrodite (or very rarely unisexual), epigynous (or very rarely semi-epigynous), with (3–)4–5(–8) sepals and (0–)4–5(–6, 12) petals per flower. The perianth parts are free in bud or occasionally form a calyptra or operculum or rupture irregularly at anthesis. In several genera the individual calyx lobes or the hypanthial remnants are deciduous after anthesis. Petals are white, cream, pale pink, or (rarely) deep pink or red. Stamens are usually numerous but, when few, the androecium may be diplostemonous, haplostemonous, or obhaplostemonous (i.e., a univerticillate androecium with only antipetalous stamens; Schmid, 1980). Stamens are generally free and attached directly to the hypanthium, but fascicled stamens occur in a few species of *Syzygium* sometimes segregated as *Pareugenia* (Schmid, 1972a). Most Myrtoideae have a secretory cavity at the apex of the anther connective but this feature is lacking in a handful of species in various genera (Schmid, 1972a). Carpels, when present, are 2 or occasionally 3–18 per flower, and the number of ovules per ovary is usually many, occasionally few, and very rarely one. General flower structure varies little among species as compared to other larger families, but flower size may vary by an order of magnitude.

## ANTHER DEVELOPMENT AND MICROSPOROGENESIS

The anther is tetrasporangiate and dehiscence is by longitudinal slits. In *Gomidesia* the thecal margins are often strongly inrolled, so that the interior of the sacs and the pollen are only exposed over a small area at the apex (and often another small area at the base) of the anther. *Gomidesia* anthers have often been termed poricidal; however, they are more accurately described as longitudinally dehiscent and functionally poricidal. Terminally dehiscent anthers have also been reported in *Acmena*. The anther sacs, which are almost globose and somewhat divaricate, open by a terminal slit and are one of the diagnostic features of this genus (Merrill & Perry, 1938). Pollen grains of all Myrtoideae (and all Myrtaceae) studied to date are two-celled at anthesis (Schmid, 1984[1985]).

## POLLEN GRAINS

Patel et al. (1984) reviewed the palynological literature on the Myrtaceae. Pike's (1956) survey of 300 species in 71 genera remains the most comprehensive work on the subject to date. Although her study focused on the Leptospermoideae of the southwest Pacific area she also investigated representatives of the Myrtoideae, including some South American genera, and was forced to conclude "There appears to be no particular feature that separates the pollen of the Myrtoideae from that of the Leptospermoideae" (Pike, 1956: 46).

Barth and Barbosa (1972) confirmed the stenopalynous nature of the Myrtoideae on the basis of their survey of 140 species in 19 genera. They described myrtoid pollen as follows (translated from the Portuguese original with modern preferred terms (Punt et al., 1994) inserted [in brackets] after outmoded terms): "grains small to medium, oblate to peroblate, tricolporate with lalongate ora [endoapertures], goniotreme [angulaperturate] with triangular amb [polar view], surface of apocolpia and mesocolpia granular, smoother near the apertures. On average sexine is twice as thick as nexine 2 [endexine], which is constant in thickness. The sexine is tectate, the bacula [columellae] being responsible for the granular surface of the grains; undulations on the surface originate from the tectum. Nexine 1 [foot layer] is limited in occurrence; in general it is absent or reduced to fragments in grains with a thicker exine" (Barth & Barbosa, 1972: 468–469).

All these features common to the Myrtoideae are also characteristic of the Myrtaceae as a whole. Both Pike (1956) and Patel et al. (1984) recognized three pollen types in the Myrtaceae: (1) longicolpate, (2) syn- or parasyncolpate, and (3) brevi- or brevissimicolpate grains. All members of the Myrtoideae studied were reported to have grains of one or the other of the first two types, grains of type (3) being confined to certain members of the *Chamelaucium* group. However, Barth and Barbosa (1972) reported grains of all three types in the Myrtoideae and listed some 25 instances where both longicolpate and syncolpate grains were found in the same species, usually in the same collection, as most species in this study were represented by a single specimen. Similar variation was reported in about one third of the 18 species studied by Lieu and Melhem (1973), while most of the remaining species sampled had consistently longicolpate grains.

Pollen is released as free monads except in *Myrtus communis* L. and *Psidium cattleianum* Sabine (as *Psidium littorale* Raddi) where there is a mixture of free monads and tetrahedral tetrads (Patel et al., 1984). Dimorphic pollen occurs in association with cryptic dioecy in *Decaspermum parviflorum* (Lam.) A. J. Scott (Kevan & Lack, 1985) and in the South African species of *Eugenia* (van Wyk & Lowrey, 1988; van Wyk & Dedekind, 1985). Male flowers produce normal pollen grains and female (apparently hermaphrodite) flowers produce morphologically abnormal unviable pollen grains.

## STIGMA AND STYLE STRUCTURE

Beardsell et al. (1993) described stigmas in the Myrtaceae as unspecialized and generally of the "wet" type, citing the Heslop-Harrison and Shivanna (1977) review of the receptive surfaces of the angiosperm stigma. In fact, Heslop-Harrison and Shivanna (1977) recorded dry stigmas with unicellular papillae in five of the seven genera of Myrtaceae studied, including all three of the myrtoid genera in the survey (*Acca* (as *Feijoa*), *Eugenia*, and *Syzygium*). Dry stigmas were also reported for the six genera studied by Proença and Gibbs (1994) (*Blepharocalyx*, *Campomanesia*, *Eugenia*, *Myrcia*, *Psidium*, and *Siphoneugena*) and in *Gomidesia* (Nic Lughadha, pers. obs.) and thus appear to represent the norm in the Myrtoideae.

Stigmas are undivided or very rarely divided. Bifid or occasionally trifid stigmas are reported in the African species *Eugenia ancorifera* Amshoff (Amshoff, 1974), *E. aschersoniana* F. Hoffm., and *E. mossambicensis* Engl. (Amshoff, 1958). Schmid (1980) drew attention to the style and stigma of *Campomanesia guazumifolia* (Cambess.) O. Berg, which has been variously described as "shortly bifid," "broadly capitate," and "peltate." Most Myrtoideae have punctiform or capitate stigmas. Proen-

Table 1. Correlations between stigma diameter, ovule number, and pollen tubes.*

| Species (number of flowers per obs.) | Stigma diameter (mm) | Max. number of ovules | Max. number of pollen tubes |
|---|---|---|---|
| *Blepharocalyx salicifolius* (8 fls) | 0.1 | 12 | ±35 |
| *Campomanesia pubescens* (6 fls) | 0.74 | 78 | ±20 |
| *Campomanesia velutina* (4 fls) | 0.57 | 29 | ±50 |
| *Eugenia dysenterica* (3 fls) | 0.1 | 8 | ±15 |
| *Myrcia linearifolia* (3 fls) | 0.1 | 4 | 17 |
| *Myrcia rhodosepala* (3 fls) | 0.1 | 6 | 10 |
| *Psidium firmum* (3 fls) | 0.65 | 298 | ±120 |
| *Siphoneugena densiflora* (3 fls) | 0.1 | 13 | ±15 |

* Adapted from Proença (1991).

ça (1991) reported both types in a study of eight species and went on to demonstrate a positive correlation between stigma diameter and ovule number (Table 1). This was explained in terms of the need for the stigma of a multi-ovulate flower to support more germinating pollen grains. The dioecious *Pimenta dioica* (L.) Merr. and the putatively dioecious *P. guatemalensis* (Lundell) Lundell are exceptions, having very low ovule numbers (1–4 per ovary) and large peltate stigmas. Proença (1991) argued that the females of these dioecious species no longer need to minimize stigma size in order to avoid deposition of self-pollen and consequent inbreeding depression (in the case of a self-compatible species) or occupation of all the ovules by self-pollen tubes and subsequent abortion of the pistil (in the case of a self-incompatible species) and suggested that expanded stigmas optimize pollen collection from the pollinator's body, the only pollen source for a totally female plant. *Carpolepis elegans* (Montrouzier) J. Wyndham Dawson, the only known dioecious Leptospermoideae, also has a large peltate stigma in contrast to the punctiform stigmas of its hermaphrodite congeners (Dawson, 1992).

### OVARY STRUCTURE

The ovary comprises 2(3–18) fused carpels. The locules are generally multi-ovular, but the number of ovules is often reduced and very rarely each locule may contain only a single ovule. Axile placentation is the norm but parietal, basal, and apical placentation have also been reported (Schmid, 1980). Where placentation is axile a compitum (a passageway connecting the loculi) is often present. Carr and Carr (1961) commented that, because of their relationship to the stylar canal(s), such compita may increase the chance of fertilization where pollination is limited. Pollen tubes were observed growing through compita in *Siphoneugena densiflora* O. Berg and *Myrcia linearifolia* Cambess. (Proença, 1991).

### OVULE STRUCTURE AND MEGAGAMETOPHYTE DEVELOPMENT

The extremely uniform embryology of the Myrtoideae was noted by Mauritzon (1939). Recent reviews by Tobe and Raven (1983) and Beardsell et al. (1993) have shown that subsequent studies have added few genera to the list studied by Mauritzon and have done little to dispel the original impression of uniformity within the Myrtoideae.

Ovules of the Myrtoideae (as of the Myrtaceae as a whole) are generally described as anatropous, crassinucellate, and bitegmic. Mauritzon (1939) commented "I hardly exaggerate when I say that there is no other great family in the plant kingdom in which the ovules of the species so regularly have two invariably two-layered integuments." He then proceeded to describe the fusion of these two-layered integuments to form a single integument of four cell layers in material which he referred to as *Eugenia paniculata* Banks ex Gaertn. (almost certainly *Syzygium paniculatum* Gaertn.). Unitegmic ovules have also been reported in *Syzygium cumini* (L.) Skeels (Narayanaswami & Roy, 1960a; Roy & Sahai, 1962 (as *S. caryophyllifolium* (Lam.) DC.)), *Syzygium fruticosum* DC. (Roy, 1961 (as *Eugenia fruticosa* L.)), *Syzygium jambos* (L.) Alston (van der Pijl, 1934 (as *Eugenia jambos* L.)), *Syzygium malaccense* (L.) Merr. & L. M. Perry (van der Pijl, 1934; Roy, 1960 (as *Eugenia malaccensis* L.)), and *S. myrtifolium* (Roxb.) DC. (Roy, 1962 (as *Eugenia myrtifolia* Roxb.)). Van Wyk and Botha (1984) commented that those *Eugenia* species for which only a single integument has been described in the literature can probably all be referred to *Syzygium*. Tobe and Raven (1983) discussed the possible origin and significance of unitegmy in *Syzygium*. Few would dispute their conclusion that it represents a derived feature within the basically bitegmic Myrtales. However, their proposition that unitegmy "probably will be found in other genera when the family is better known embryologically" (Tobe & Raven, 1983: 86) has yet to be substantiated.

Mauritzon's generalization about myrtaceous integuments seems to hold true insofar as it concerns the inner integument: where this is distinct from the outer integument it is nearly always two cell layers thick (locally three cell layers thick in some South African *Eugenia* species (van Wyk & Botha, 1984)). However, the outer integument in the Myrtoideae has proved more variable than Mauritzon's survey led him to suspect. Petit (1908, quoted in Mattos, 1989) reported 4 cell layers in the outer integument of *Luma apiculata* (DC.) Burret (as *Myrceugenia apiculata* (DC.) Nied.) and commented that the outer integument may comprise even more layers in some species of *Eugenia* judging by the considerable thickness of the integument of *Myrcianthes pungens* (O. Berg) D. Legrand and *Eugenia uniflora* L. (cited as *Eugenia pungens* O. Berg, and *Stenocalyx michelii* O. Berg, respectively). Van Wyk and Botha (1984) described an outer integument four to six layers thick over the greater part of its free length in their detailed study of South African *Eugenia*.

This latter group of *Eugenia* also seems to represent an exception to the generalization that ovules of the Myrtoideae (and the Myrtaceae) are anatropous. Van Wyk and Botha (1984) reported hemi-campylotropous ovules (occasionally tending to be ana-campylotropous) and suggested that campylotropous ovules have frequently been taken as anatropous during cursory investigations.

In all Myrtoideae studied to date the micropyle is formed from both integuments. As in other Myrtaceae, embryo-sac formation in the Myrtoideae follows the *Polygonum*-type pattern and the antipodal cells are ephemeral (Tobe & Raven, 1983).

## FLOWERING

### FLOWERING SEASONALITY

Data on the time of initiation of flowering in the Myrtoideae have been compiled and discussed by Proença (1991) and Proença and Gibbs (1994). A tendency to flower at the dry/rainy season transition was distinguished, a pattern exhibited by 6 of the 8 species (in 6 different genera) studied by them in the Distrito Federal, central Brazil, and 7 out of 10 species of Myrtoideae investigated in other South American forest communities by other researchers (Frankie et al., 1983; Ferreira & Merona, 1987; Morellato et al., 1989). This pattern was clearly demonstrated in a floristic study of the Myrtaceae of the Serra do Cipó, Minas Gerais, Brazil, in which Kawasaki (1984, 1989) reported that the majority of the 50 species (in 11 genera) recorded for the area were found flowering in September and October (spring), after the first rains in the region. Two of these species had a second flowering period in February and March (late summer/early autumn), and a further five species flowered only during this latter period. In Costa Rican dry forest *Eugenia salamensis* Donn. Sm. was the only mass-flowering species (out of 21 mass flowerers studied) to bloom at the beginning of the wet season (Frankie et al., 1983). The other species (not Myrtaceae) bloomed during the long dry season. Ruiz and Arroyo (1978) reported flowering by *Eugenia* sp. at the beginning of the wet season in a Venezuelan deciduous forest. Proença and Gibbs (1994) proposed that flowering may be cued by abrupt increases in humidity, which are much more frequent at the dry/rainy season transition than during the remainder of the year. Landrum (1986) commented that most species of *Campomanesia* flower in the spring, usually in October in southeastern Brazil and adjacent regions. In contrast, most species of the temperate and subtropical South American genus *Myrceugenia* flower during the summer and autumn with a relatively small number of species flowering during late winter and spring (Landrum, 1981). Chilean Myrtaceae flower during the dry spring and summer (Landrum, 1988).

Southern African Myrtoideae exhibit a strong conformity to spring dry/wet season flowering, with 12 of the 15 species of *Eugenia* studied by van Wyk and Lowrey (1988) conforming to this pattern. The remainder flower in early summer (two species) or in winter (one species). Spring flowering is also reported as the norm in southern Australian Myrtaceae (Beardsell et al., 1993; O'Brien & Calder, 1993), though this generalization may be more applicable to the capsular dry-fruited Myrtaceae than to the Myrtoideae, as no specific examples from this latter group are cited. In fact, two detailed studies of Australian species of the genus *Syzygium* illustrate the variation in the time of flowering within this large genus. In Kuranda, northern Queensland, the rainforest tree *Syzygium tierneyanum* (F. Muell.) T. G. Hartley & L. M. Perry flowered in January (Hopper, 1980 ) while *S. cormiflorum* (F. Muell.) B. Hyland, another northern Queensland rainforest tree, had an extended flowering period ranging from at least late July to mid-November (Crome & Irvine, 1986). In Indonesia, however, at least one species of *Syzygium* does appear to demonstrate the dry/wet season transition spring flowering pattern discussed by Proença and Gibbs (1994): in Sulawesi trees of *Syzygium lineatum* (DC.) Merr. & L. M. Perry (as *Syzygium syzygioides* (Miq.) Merr. & L. M. Perry and subsequently corrected) flowered in February and March (spring) toward the end of what appeared to be "a fairly dry season"—precise information on climate was not available (Lack & Kevan, 1984). In the same area *Decaspermum parviflorum* (Lam.) A. J. Scott flowered in January and February, apparently toward the end of a short dry period (Kevan & Lack, 1985).

### FLOWERING DURATION, PATTERN, AND SYNCHRONY

Meager though the data on flowering seasonality may appear, information on flowering strategies is scarcer still. Proença and Gibbs (1994) described four flowering strategies observed in the Myrtaceae of the Distrito Federal, central Brazil. Of these, three corresponded to types described by Gentry (1974) viz., "big bang," "cornucopia," and "steady state" flowering, and the fourth, for which they coined the term "pulsed bang," is a modification of the big bang strategy from which it differs in its discontinuity: flowering days may be followed by intervals of several days when no flowers are open. Such pulsed bang flowering was reported in *Myrcia rhodosepala* Kiaersk. and in *Blepharocalyx salicifolius* (Kunth) O. Berg in central Brazil. Kevan and Lack (1985) described a similar pattern in *Decaspermum parviflorum* in Sulawesi. In this species flowering occurred regularly once in every two or three days with all plants in synchrony over the peak blooming time from late January to mid-February. The total flowering period of ca. 4 weeks was, however, considerably shorter than the ca. 8-week periods estimated for the central Brazilian pulsed-bang species.

Also in Sulawesi, *Syzygium lineatum* had a total flowering period of approximately the same duration as the nearby *Decaspermum parviflorum* (ca. 4–5 weeks) but, as far as we could tell, appeared to exhibit a typical cornucopia pattern (Lack & Kevan, 1984). *Siphoneugena densiflora* in central Brazil also exhibited the cornucopia strategy with many flowers being produced per plant over a period of a month or so and a population flowering period estimated at 8 weeks.

The distinction between the cornucopia strategy and the steady state strategy in which relatively few flowers are produced each day over a long period of time may be somewhat arbitrary in some instances. The central Brazilian shrubs *Psidium firmum* Berg and *Campomanesia pubescens* (DC.) Berg, with flowering periods of ca. 12 weeks, were considered steady state (Proença & Gibbs, 1994). The Amazonian tree *Psidium acutangulum* DC. had an even longer flowering period. Flowering was reported all year round with relatively few flowers being produced from January to March (Falcão et al., 1992). Similar patterns were reported for other Amazonian fruit crops studied by these authors, including *Eugenia stipitata* McVaugh and *Myrciaria dubia* (Kunth) McVaugh (Falcão et al., 1988, 1989). The term steady state seems inappropriate for these latter species, as monthly totals for flower production exhibit spectacular peaks and dips. A better example of steady state flowering is provided by the northern Queensland species *Syzygium cormiflorum*, which has a rather long flowering period (> 14 weeks) and apparently relatively few flowers open per day. Crome and Irvine (1986) commented that "flowers are not numerous" and that their experimental program was limited by "insufficient flowers."

*Syzygium tierneyanum*, also from northern Queensland, appears to represent the opposite extreme of flowering strategy, viz., the classic big bang. The species is described as bursting into flower and reaching its peak over a 12-day period. Hopper (1980) counted 334 flowers per cubic meter of lower canopy and estimated that a 20-m plant could carry ca. 300,000 flowers at its seasonal peak. The central Brazilian species *Eugenia dysenterica* DC. and *Campomanesia velutina* (Cambess.) O. Berg also exemplify the big bang strategy, albeit on a smaller scale (Proença & Gibbs, 1994), as does *Eugenia salamensis*, a dry forest species in Costa Rica (Frankie et al., 1983).

Two Costa Rican dry forest shrubs, *Eugenia oerstediana* O. Berg and *Psidium guineense* Sw., exhibit a multiple bang strategy, flowering several times a year in synchronized flowering episodes lasting less than two weeks (Suarez & Esquivel, 1987).

### LONGEVITY OF INDIVIDUAL FLOWERS

One-day flowers are the norm in the Myrtoideae. Species in which individual flowers last one day or less were reported from *Blepharocalyx*, *Campomanesia*, *Decaspermum*, *Eugenia*, *Myrcia*, *Myrciaria*, *Psidium*, *Siphoneugena*, and *Syzygium* (Hopper, 1980; Kevan & Lack, 1985; Peters & Vasquez, 1986/87; Proença & Gibbs, 1994). Stratton (1989) reported a mean floral longevity of 1.27 days, and a range of 1.1–1.5 days for three myrtaceous species in Costa Rican cloud forest. In this study of 110 species, in 35 families, taxonomic constraints at family level were the most important determinant of floral longevity, explaining 73% of the variance. Singh and Sehgal (1968) reported that the stigma of *Psidium guajava* L. is receptive for 2 or 3 days. Primack (1985), however, included the Myrtaceae in a list of families with long-lived flowers, which typically last 4–19 days. This generalization was very likely based on examples from the Leptospermoideae in which long-lived flowers appear to be common, e.g., flowers of *Leptospermum scoparium* J. R. Forst. & G. Forst. may last up to 3 weeks (Primack, 1980). Such longevity is rare in the Myrtoideae and where it occurs appears to be positively associated with large flower size, e.g., *Syzygium cormiflorum* has flowers of ca. 4 cm in diameter, which do not brown until one week after anthesis (Crome & Irvine, 1986).

### EFFECTS OF FIRE AND DROUGHT ON FLOWERING

In the Australian Myrtaceae flowering is not enhanced by fires. In fact, the flush of vegetative growth in recovering, fire-resistant species generally inhibits flowering for several seasons (Beardsell et al., 1993). In contrast, van Wyk and Lowrey (1988) reported that in southern Africa, grassland fires promoted new growth and flowering in the rhizomatous geoxylic suffrutex *Eugenia albanensis* Sond., and these authors considered that similar effects were likely in *E.* cf. *mossambicensis* and *E. pusilla* N. E. Br. Cesar (1980) reported three Myrtaceae (one *Campomanesia* sp. and two undetermined Myrtaceae) among 50 species that presented some form of fire-induced flowering in central Brazilian savanna grassland. *Eugenia myrcianthes* Nied. flowers very soon after burning in the same habitat (C. Proença, pers. obs.).

Sanaiotti and Magnusson (1995) studied the effects of annual fires on the production of fleshy fruits in a Brazilian Amazonian savanna. In *Eugenia biflora* DC. and *Myrcia sylvatica* (G. Mey.) DC. fruiting was dramatically reduced after fire, but recovery was rapid with fruiting reaching 50–90% of normal levels in the first year after burning and 50–100% in the second year.

Van Wyk and Lowrey (1988) considered drought conditions a major factor in delayed flowering in southern African *Eugenia,* while Falcão et al. (1988, 1989, 1992) reported flowering periods coinciding with precipitation minima in three Amazonian species, i.e., *Eugenia stipitata, Myrciaria dubia,* and *Psidium acutangulum.*

## BREEDING SYSTEMS

### DICHOGAMY

Beardsell et al. (1993) commented that all hermaphroditic species of the Myrtaceae studied so far, except for one protogynous species of *Verticordia,* have protandrous flowers, although there may be some overlap of male and female phases providing potential for self-pollination. Intervals of days or even weeks separating male and female phases are not uncommon in the Leptospermoideae, but the potential for such conspicuous protandry is significantly reduced in the Myrtoideae where flowers are generally short-lived. Furthermore, the detection of dichogamy in the Myrtoideae is rendered more difficult by the dry nature of the stigma, which does not permit visual assessment of receptivity.

From a theoretical viewpoint it seems unlikely that temporal separation of male and female functions should be widespread but undetected among the Myrtoideae with short-lived flowers which offer only pollen as a reward. Female-phase flowers would offer nothing to reward visitors and, as Renner (1989) commented, only mimicry or deception might account for visits to such flowers. That dichogamy should co-occur with nectar production seems more likely and this does in fact appear to be the case in at least three of the four genera where the existence of dichogamy has been postulated.

Dichogamy seems most likely to occur in *Syzygium,* where many species offer nectar as a reward; interestingly, this genus includes species with relatively long-lived flowers possibly affording more scope for temporal separation of male and female functions. In the context of the Myrtoideae the flowers of *Syzygium cormiflorum,* as already mentioned, are remarkably long-lived: styles do not brown until, on average, a week after anthesis, and they are not shed until about three weeks later (Crome & Irvine, 1986). According to these authors a flower could be successfully pollinated at anthesis, but they were unable to tell whether the stigma was actually receptive on the first day or whether the pollen retained viability until the stigma matured later. Thus protandry is possible but not confirmed in this species.

The only reliable report of protandry in the Myrtoideae that we have encountered to date is that of Grifo (1992) for *Myrcianthes.* In some species of this genus the stigma remains introrsely curved until after the anthers have released much of the pollen through longitudinal slits and are leaning outwards, away from the now erect and apparently receptive stigma. Grifo (1992) also reported nectar production in *Myrcianthes*—see Attractants and Rewards below.

Peters and Vasquez (1986/87) have documented protogyny in *Myrciaria dubia,* where the stigma is exserted first and the filaments of the numerous anthers expand later. These authors stated that anthesis occurs early in the morning, that the flowers are receptive to pollination for a period of 4–5 hours, and that by the time the anthers emerge to release the pollen the stigma is no longer receptive to pollination. The method of assessment of stigma receptivity was not discussed but in the accompanying diagram the stigma appears shrivelled in the flower with erect stamens. After pollination the stamens start to wilt and the whole hypanthial cup, with sepals, petals and stamens, abscisses on the following day, leaving only the ovary. Grifo (1992) commented that the monotypic *Amomyrtella* is also decidedly protogynous. The large peltate stigma of this species is exserted before the petals unfold (herbarium label for *Solomon 11018*).

Stylar extension post-anthesis is common in the Leptospermoideae. It appears to coincide with the onset of stigma receptivity and has been variously interpreted as a mechanism to favor outcrossing (Moncur & Boland, 1989) or as a mechanism to reduce interference from self-pollen (Lloyd & Webb, 1986; Webb & Lloyd, 1986). The phenomenon appears to be rarer in the Myrtoideae but has been reported from two species of *Syzygium*. In the flowers of *S. cormiflorum* the style expands to maximum length 4–5 days after opening and after the stamens are shed (Crome & Irvine, 1986). In contrast, in the one-day flowers of *S. lineatum*, the style reaches its full length 4 to 6 hours after anthesis, often while the anthers still have much pollen on them (Lack & Kevan, 1984).

### ANDROMONOECY AND DIOECY

Andromonoecy, which is common in the Leptospermoideae (Beardsell et al., 1993), has not been detected in the Myrtoideae. Interestingly, Beardsell et al. (1993) suggested that andromonoecy in the Australian Myrtaceae (Leptospermoideae) may represent a response to soils of low fertility and to drought, allowing optimal resource allocation for reproduction. The Myrtoideae, in contrast, though tolerant of poor soils appear to be drought avoiders, reaching their maximum ecological importance (as estimated by density and/or basal area) in areas of South America where there is a combination of coolish temperatures, a steady supply of water, and a poor, weakly acidic soil (Proença, 1991).

The term cryptic dioecy has been applied to dioecious breeding systems in which one or both of the functionally unisexual morphs appear to have perfect hermaphroditic flowers, making the dioecious condition difficult to detect (Mayer & Charlesworth, 1991). In populations of most cryptically dioecious species, plants with staminate flowers (male) co-exist with apparently perfect-flowered but functionally pistillate (female) plants whose anthers produce sterile or abnormal pollen, or are indehiscent. This situation is sometimes mistaken for androdioecy, in which functionally male and functionally hermaphrodite individuals co-exist.

Nic Lughadha (1994) summarized current knowledge on dioecy in the Myrtaceae, which has until recently been considered a relatively rare phenomenon (van Wyk & Lowrey, 1988). In the Myrtoideae, cryptic dioecy has been reported in *Pimenta dioica* (Chapman, 1964), in *Decaspermum parviflorum* (Kevan & Lack, 1985), and in all 15 species of *Eugenia* native to South Africa (van Wyk & Lowrey, 1988). With the exception of *Pimenta dioica*, which has structurally hermaphroditic flowers in both sexes, all of these species have male flowers with greatly reduced pistils, while female flowers appear perfect but generally have fewer stamens whose anthers do not produce viable pollen. In the typically small myrtaceous flower with its many stamens, both types of cryptic dioecy (apparently hermaphrodite and apparently androdioecious) may easily be overlooked by the casual observer and are probably more common than the few literature reports suggest.

Reduced styles and abortive ovaries have been reported for *Pimenta guatemalensis* (Lundell, 1968) and for three species of *Calyptranthes*, *C. fasciculata* O. Berg (Berg, 1857), *C. longifolia* O. Berg. and *C. speciosa* Sagot (McVaugh, 1958). In the *Flora of Peru*, McVaugh (1958) also noted short styles and apparent imperfect development of the hypanthium in *Myrcia aliena* McVaugh and suggested that this species may be partially or completely dioecious. A further two imperfect flowered species are among the thirty species of *Myrcia* described as new by McVaugh (1969). *Myrcia imperfecta* McVaugh and *M. myriantha* McVaugh (both from Mount Ayanganna, Guyana) were each based on a single collection with male flowers only and no vestige of a style. McVaugh commented that this was a condition rarely noted in *Myrcia* and that its significance was unknown, though the imperfect flowers of *M. imperfecta* could be abnormal. *Myrcia almasensis* Nic Lughadha from the Pico das Almas, Brazil, was based on apparently male material with a vestigial style and brought to four the total number of putatively dioecious species of *Myrcia*. Of course the possibility that some of these collections may represent andromonoecious species cannot as yet be discounted. Interestingly, many of these putatively dioecious neotropical Myrtoideae are from high-altitude areas. Sobrevila and Arroyo (1982) have discussed the abnormally high incidence of dioecy in a Venezuelan montane cloud forest as compared to other tropical forest communities.

Classical dioecy, where female flowers lack stamens completely, is unlikely to occur in the Myrtoideae. In flowers offering pollen as a sole reward to pollinators, which is the case for most Myrtoideae, selection tends to favor female flowers which mimic male flowers by retaining stamens, even though the pollen therein may be sterile (Lloyd, 1982). A possible mechanism for the evolution of dioecy in pollen-only taxa is outlined under Attractants and Rewards below.

Dioecy is unknown in the Australian Myrtaceae (Beardsell et al., 1993), and we consider it highly improbable that it has been extensively overlooked there. The only published example we have encountered of dioecy in the Leptospermoideae occurs in the small genus *Carpolepis*, which is endemic to New Caledonia (Dawson, 1992). *Carpolepis elegans* is dioecious and, apparently, more or less cryptically so. Male flowers include fertile stamens, a morphologically normal, but non-functional ovary, a full-length style, and a peltate stigma: female flowers are similar but the stamens are replaced by recurved staminodes whose anthers bear no pollen. The other two species of *Carpolepis* bear hermaphrodite flowers with punctiform stigmas. Dioecism has also been discovered in some species of the Myrtoideae of New Caledonia, and these are shortly to form the basis of a new genus (J. W. Dawson, pers. comm.).

The fact that dioecy is extremely rare in the Leptospermoideae yet appears to have arisen independently on at least half a dozen different occasions in the Myrtoideae can be interpreted as further evidence in support of the non-random association between dioecy and dispersal mode, which was described and discussed by Bawa (1980) and Givnish (1980, 1982). These authors argued that unisexuality is more likely to establish itself in taxa with large few-seeded animal-dispersed fruits than in taxa with other modes of dispersal. In species that produce nutrient-rich fruit an increase in female reproductive effort produces a disproportionate increase in female fitness due to selection for spatial and temporal peaks in fruit production. They consider that such an advantage to increasing female effort could, under certain circumstances, favor individuals that invest only as females or only as males.

### OUTCROSSING RATES

In most Myrtoideae, especially the small-flowered species, many flowers are produced per tree per flowering day. The potential for geitonogamy would therefore seem great. However the low PERS values [Pre-emergent reproductive success, the percentage of all ovules maturing into seeds expressed as: % natural fruit set × no. of seeds per fruit/no. of ovules per fruit, Wiens et al., 1987] typically found in the Myrtoideae (Proença & Gibbs, 1994; Nic Lughadha, unpublished data) are suggestive of predominantly outbreeding species. Electrophoretic studies have demonstrated the existence of high outcrossing rates in various species of *Eucalyptus* and *Melaleuca* with similar flowering patterns (Phillips & Brown, 1977; Moran & Bell, 1983; Griffin et al., 1987; Butcher et al., 1992). Beardsell et al. (1993) interpreted these high levels of outcrossing in spite of ample opportunities for geitonogamy as reflecting the operation of a barrier to self-pollination such as self-incompatibility. Proença (1991) suggested that high levels of outbreeding could be maintained even in self-compatible species through flowering strategies that favor trap-lining or opportunistic behavior by pollinators. In cultivated *Psidium guajava*, a relatively low level of outcrossing of 25–41% (mean = 36%) was reported by Soubihe Sobrinho and Gurgel (1962).

### SELF-INCOMPATIBILITY

Beardsell et al. (1993) considered that self-incompatibility is probably widespread in the Myrtaceae. They cited cases ranging from partial self-incompatibility to complete self-sterility with no seed production after selfing. No myrtoid examples of self-sterility were reported, but they considered it likely that the same mechanism of self-incompatibility operates throughout the Myrtaceae and acknowledged the need to examine more species in order to determine whether reduced seed-set after selfing is due to the expression of lethal recessive genes in the zygote or to a late-acting self-incompatibility system. The latter explanation was favored by Proença and Gibbs (1994) in their study of the reproductive biology of central Brazilian Myrtoideae. Of the eight species studied by these authors, three (*Blepharocalyx salicifolius, Campomanesia velutina,* and *Siphoneugena densiflora*) were apparently strictly self-incompatible and set no fruit when selfed. A further two species (*Myrcia linearifolia* and *Campomanesia pubescens*) exhibited partial self-incompatibility with ISI values [Index of Self-Incompatibility, expressed as the ratio of fruit set from selfed vs. crossed flowers] of 0.12 and 0.09, respectively. Self-pollen tubes were observed to penetrate ovules in all of these species and no differences were detected between self- and cross-pollinations with respect to the mean number of penetrated ovules per flower at 24, 48, or 72 hours after pollination. The time of abscission of selfed pistils varied between species from one week to one month after pollination, but rejection was synchronous within species, and no ovary enlargement was detected in crossed or selfed pistils up to the time of abscission of the latter. This represents the most detailed study of "self-incompatibility" in the Myrtoideae published to date but, as no material was fixed beyond 72 hours after pollination, we can only speculate as to the nature of the rejection mechanism in operation. More recent studies on *Gomidesia* have included fixations up to 28 days after pollination, and results obtained to date suggest that preferential outcrossing is sustained by a post-zygotic mechanism or effect (Nic Lughadha, unpublished data).

Complete self-sterility has also been reported in *Eugenia* sp. in secondary deciduous forest in Venezuela (Ruiz & Arroyo, 1978), in *Eugenia* sp. (presumably different) in montane cloud forest in Venezuela (Sobrevila & Arroyo, 1982), and in *Syzygium lineatum* in Sulawesi, Indonesia (Lack & Kevan, 1984). Bullock (1985) reported almost complete self-incompatibility in Mexican *Psidium sartorianum* Nied. (ISI 0.02). However, in none of these cases is any indication given of the timing or nature of the reproductive barriers operating after self-pollination.

Reports of self-compatibility in Myrtoideae are almost as numerous as those of self-incompatibility. Proença and Gibbs (1994) recorded three completely self-compatible species (*Eugenia dysenterica, Myrcia rhodosepala,* and *Psidium firmum*) that set statistically equal numbers of fruits after self- and cross-pollination. For the cultivated guava, *Psidium guajava,* self-pollination in isolated trees has been registered between 64% and 90% (Soubihe Sobrinho & Gurgel, 1962). In Peru, *Myrciaria dubia* showed 91% fruit set after geitonogamous pollination (Peters & Vasquez, 1986/87). In Venezuela, *Myrcia fallax* (Rich.) DC. showed significantly diminished fruit set after self-pollination as compared to cross-pollination; however, its ISI of 0.24 exceeded the threshold value of 0.2 arbitrarily set for self-incompatible species (Bawa, 1974; Sobrevila & Arroyo, 1982), and so this species was classed as self-compatible. *Syzygium cormiflorum* from northern Queensland also exhibited partial self-compatibility with 18–36% fertilization (estimates based on ovule enlargement) in self-pollinated flowers and 72.7–86.7% fertilization in cross-pollinated flowers (Crome & Irvine, 1986). In another northern Queensland tree species, *Syzygium tierneyanum,* bagged inflorescences set fruit in the absence of cross-pollination (Hopper, 1980). Beardsell et al. (1993) interpreted this result as demonstrating autogamy (in the sense of automatic self-pollination of a self-compatible species) but did not discuss the possibility of apomixis. Chantaranothai and Parnell (1994) obtained similar results in a study of breeding systems of Thai species of *Syzygium.* They found that all four species studied in detail were apparently self-compatible with self-pollination appearing to enhance seed-set. However, they further demonstrated that two of these species were actually apomictic (see below). Purseglove (1968) documented self-fertility in *Psidium guajava.* Schroeder (1947) reported results ranging from complete self-compatibility to almost complete self-incompatibility in different varieties of *Acca sellowiana* (O. Berg) Burret (as *Feijoa sellowiana* O. Berg).

### APOMIXIS

Davis (1966) reported apomixis as occurring widely within the Myrtoideae. Where apomixis occurs it is generally by adventitious embryony, although there is some evidence indicating the possibility of apospory. The resulting polyembryony is discussed in more detail under Embryo and Seed Development (see below).

Rye (1979) postulated a positive correlation between the widespread occurrence of apomixis in the Myrtoideae and the high frequency of polyploidy in this group, but commented that the only specific example was *Syzygium jambos* (cited as *Eugenia jambos*). A further example is *Syzygium cumini,* which exhibits adventitious polyembryony (though apparently not consistently: Narayanaswami & Roy, 1960a; Roy & Sahai, 1962 (as *S. caryophyllifolium*); Tiwary, 1926 (as *Eugenia jambolana* Lam.); van der Pijl, 1934 (as *Eugenia cumini* (L.) Druce); Chantaranothai & Parnell, 1994) and in which several authors reported varying levels of polyploidy (Mehra, 1976; Bir et al., 1980; Singhal & Gill, 1984; Singhal et al., 1984, 1985; Gill et al., 1989: as *E. jambolana* in each case, gametophytic counts 11, 22, and 33, sporophytic counts 22, 44, and 66). Whether this association extends to other polyembryonic members of the genus *Syzygium* and, more importantly, whether it is continued outside the genus remains to be investigated. *Luma apiculata,* the only other polyembryonic species of the Myrtoideae for which chromosome counts are available, lends no support to Rye's hypothesis as it is reported to have $n = 10$ (Titow de Tschischow, 1956), or about $2n = 22$ (Landrum, 1981). However, as there is circumstantial evidence that polyploidy may not be ubiquitous in this species, it is possible that these diploid counts may derive from non-polyembryonic material. The correlation cannot be tested further in the absence of chromosome counts for any other myrtoid genera in which polyembryony has been documented.

## POLLINATION BIOLOGY

### ATTRACTANTS AND REWARDS

Petals and/or stamens may act as the visual attractants in flowers of the Myrtoideae, but the stamens are generally the most conspicuous structures in the open flower. Scent also appears to play a role in attraction. The odors produced are generally described as sweet but flowers of *Syzygium cormiflorum* have a faint unpleasant smell (Crome & Irvine, 1986). Grifo (1992) described the flowers of *Myrcianthes* as smelling either sweet and similar to an apple-blossom or rather sour and similar to "well-seasoned sneakers." Chantaranothai and Parnell (1994) found that floral buds of *Syzygium jambos* and *S. megacarpum* (Craib) Rathakr. & N.C. Nair were sweetly fragrant during the period of swelling before anthesis. In southern African *Eugenia* species van Wyk and Lowrey (1988) did not discover any osmophores but found that the strong sweet odor was emitted either by the anther tisue and/or by the pollen grains.

Pollen is the principal reward available to visitors of most Myrtoideae flowers. Van Wyk and Lowrey (1988) found that the pollen of southern African *Eugenia* tested positive for lipids (in the form of oil droplets) and negative for starch. Moncur (1988) commented that sugars in pollen are pollinator rewards in *Acca sellowiana* (as *Feijoa sellowiana*). In several dioecious species, such as the southern African *Eugenia* and *Decaspermum parviflorum*, female flowers produce non-viable pollen-like material which may represent an important resource to insect pollinators (Kevan & Lack, 1985; van Wyk & Lowrey, 1988). Kevan and Lack commented that *D. parviflorum* is unusual among dioecious species in presenting pollen (and sterile pollen) as the main food reward and cited *Vitis* and *Solanum* as other examples of this phenomenon. However, pollen-only flowers also occur in other dioecious species such as *Actinidia chinensis* Planch. (Schmid, 1978), *Rosa setigera* Michx. (Kevan et al., 1990), and *Saurauia veraguasensis* Seem. (Haber & Bawa, 1984). It is noteworthy that female flowers of these species accrue neither of the major advantages proposed by Bawa (1980) for female flowers of dioecious species: they must still allocate resources to the production of stamens and sterile pollen and still run the risk of their stigmas becoming clogged with their own sterile pollen. This could be interpreted as an indication that the avoidance of inbreeding may represent a more important selective force in the maintenance of dioecy in these species than does the reallocation of reproductive resources (Mayer & Charlesworth, 1991). However, it should be borne in mind that reallocation of resources may take place on a whole-plant level, with male plants producing a more prominent floral display, more flowers, and/or more pollen per flower than female plants. This is certainly true of *D. parviflorum* (Kevan & Lack, 1985), and there is circumstantial evidence that it may be the case in other putatively dioecious Myrtoideae (Nic Lughadha, 1994). Givnish (1980) discussed the potential role of sexual selection in the evolution of dioecy in pollen-only taxa. Where pollen is the only reward then disproportionately many pollinators may be attracted to plants with heavy pollen loads. This advantage could drive the evolution of dioecy if male and female flowers mimic each other, as is the case in all dioecious Myrtoideae known to date (see discussion of dioecy above).

Besides the pollen and sterile pollen offered as the principal reward, *Decaspermum parviflorum* is also reported to produce minute quantities of nectar (Kevan & Lack, 1985). Most other reliable reports of nectar production that we have encountered refer to species of the genus *Syzygium*. Schmid (1972b) described an ovarian annular nectary in *S. aromaticum* (L. ) Merr. & L. M. Perry, *S. jambos*, *S. malaccense*, and *S. paniculatum* and cited Werth's (1901) account of the secretion of nectar in copious amounts into the concavity formed by the depressed top of the ovary in flowers of *S. jambos* (as *Jambosa vulgaris* DC.). Crome and Irvine (1986) measured copious but variable flow of weak nectar in *S. cormiflorum*. Small quantities of nectar of rather high sugar content are produced in flowers of *S. lineatum* (as *S. syzygioides*; Lack & Kevan, 1984). Nectar production is also reported from *S. tierneyanum* (Hopper, 1980) and *S. samarangense* (Blume) Merr. & L. M. Perry (Chantaranothai & Parnell, 1994).

Studies of genera of Myrtoideae other than *Syzygium* have generally failed to find any evidence of nectar production. Nectar is absent in flowers of southern African *Eugenia* species (van Wyk & Lowrey, 1988) and, apparently, in most South American Myrtoideae (Landrum, 1986; Proença & Gibbs, 1994; Nic Lughadha, unpublished data). Exceptions include the report by Pirani and Cortopassi-Laurino (1993) of bees collecting pollen and nectar from flowers of *Plinia glomerata* (O. Berg) Amshoff and that of Peters and Vasquez (1986/87) on nectar production in *Myrciaria dubia*. The other notable exception is the genus *Myrcianthes*, in which sweet-tasting nectar is secreted at the base of the staminal disk (Grifo, 1992). Grifo's descriptions of visitor behavior indicate that nectar is the principal reward offered by these species. Small insects may approach the flowers and feed on the nectar while entirely avoiding the numerous stamens, but larger insects become covered with pollen as they brush the anthers in search of nectar.

Nectar is widespread in the Leptospermoideae, and the nectar-producing *Chamelaucium* group emerged as sister to the Myrtoideae in cladistic analyses by both Johnson and Briggs (1984) and Grifo (1992) (along with the *Leptospermum* group in the former analysis). Grifo's (1992) cladistic analysis also indicated that *Myrcianthes* is "much more closely related to *Syzygium* than previously supposed" and that these genera are basal to the Eugeniinae in the Neotropics. We can therefore hypothesize that nectar production is basal in the Myrtaceae with the numerous pollen-only genera of the Myrtoideae arising as a result of secondary loss(es) of this facility. Renner (1989) has proposed a similar scenario to explain the distribution of nectar production among the neotropical melastomes. Her observation that the Melastomataceae that offer nectar are pollinated by a broader range of pollinator classes than the pollen-only species seems also to hold true for the Myrtaceae on the basis of the evidence available to date.

The role of the secretory cavity at the apex of the anther connective does not appear to have been investigated in any member of the Myrtoideae. In *Thryptomene calycina* (Lindl.) Stapf, a member of the *Chamelaucium* alliance (Leptospermoideae s.l.), Beardsell et al. (1989) demonstrated that the anther connective glands secrete a lipid-rich fluid which solidifies and serves as a food reward for pollinating insects. Although a similar role is possible for the anther connective glands of the Myrtoideae it seems unlikely that any visitor small enough to be attracted to the minute quantities of secretion that these glands might afford would contact the stigma regularly while collecting. Renner (1989) discussed a comparable paradox offered by the staminal glands of *Mouriri* (Memecylaceae) and noted Morley's (1976) suggestion that these glands may be involved in odor production. Van Wyk and Lowrey's (1988) observations on fragrant anthers and pollen in southern African *Eugenia* represent the only evidence we have encountered to support the hypothesis of an odor production role for the anther connective glands in the Myrtoideae. Of course, another possibility is that these structures serve no function in the flowers of the Myrtoideae and are simply vestigial remnants of an organ which is more or less ubiquitous in the Myrtaceae. The scattered examples of species whose anthers lack secretory cavities undoubtedly represent secondary losses of this feature.

The role of petals as an attractant and reward to visitors to *Acca* and *Myrrhinium* is discussed under Bird Pollination below.

### BEE POLLINATION

Bees (Apoidea) appear to be the most common pollinators of Myrtoideae, as they are of Myrtaceae as a whole. There is a strong association between the Myrtaceae and the short-tongued Colletidae, which are considered to be the most primitive flower-visiting bees (Michener, 1979). This relationship is most notable and best documented in Australia where nearly half of the bee species belong to the Colletidae and most of these are restricted to or collect pollen primarily from flowers of Myrtaceae (Armstrong, 1979). These include *Eugenia* and *Syzygium* as well as numerous non-myrtoid genera. Bees reported to collect pollen from *Eugenia* and/or *Syzygium* include *Euryglossina* and *Hylaeus* (Colletidae) as well as *Homalictus* and *Lasioglossum* (Halictidae) (Michener, 1965). When current taxonomic concepts are applied, most of these records are referrable to the genus *Syzygium*; only one species of *Eugenia* s. str. occurs in Australia (Hyland, 1983).

Proença and Gibbs (1994) suggested that the Myrtaceae–Colletidae association, so striking in Australia, probably exists to some extent in the Neotropics. They cited two neotropical examples of this association, viz., rapid pre-dawn pollen removal from *Eugenia salamensis* by *Ptiloglossa* spp. (Colletidae: Diphaglossinae) in Costa Rica (Frankie et al., 1983) and pollination of *Siphoneugena densiflora* by *Ptiloglossa* sp. in central Brazil (Proença, 1992). Colletidae are not particularly common in the Neotropics: e.g., in central Brazil, where the Proença and Gibbs study was carried out, only 5% of bee species are Colletidae (A. Raw, unpublished list based on 12,000 collections). Therefore one could argue that such reports are unlikely in the absence of some degree of association. However, a careful compilation of 33 reports of bee visitation in neotropical Myrtoideae (Table 2) showed that most registered visits are by Apidae: Meliponinae (14), followed by Apidae: Bombinae (9), Halictidae (4), Anthophoridae (4), Colletidae (2). In defense of the neotropical Myrtaceae–Colletidae association, it should be noted that both reports were of pre-dawn visitation, so that this phenomenon could be widespread but largely overlooked in studies based purely on diurnal observations.

The first report of buzz-pollination in the Myrtaceae was published by Proença (1992). She described buzz-pollination in *Siphoneugena densiflora* by *Ptiloglossa* sp., in *Myrcia torta* DC. (as *M. dictiophylla* (O. Berg) J. R. Mattos & D. Legrand) by *Augochloropsis*? sp. (Halictidae), and in *Myrcia rhodosepala* and *Blepharocalyx salicifolius* by *Bombus* spp. (Apidae: Bombinae). *Bombus* spp. (including *B. atratus* and *B. morio*) were considered the principal pollinators of a further five species of central Brazilian Myrtaceae (*Campomanesia pubescens*, *C.*

Table 2. Species of neotropical Myrtoideae with presumed pollinators or insect visitors to flowers.

| Species | Visitors | Behavior | Reference |
|---|---|---|---|
| *Blepharocalyx salicifolius* | Apidae: Bombinae<br>Apidae: Meliponinae<br>Halictidae | "visitors" | Proença & Gibbs (1994) |
| *Campomanesia pubescens* | Apidae: Bombinae | "visitors" | Proença & Gibbs (1994) |
| *Campomanesia velutina* | Apidae: Bombinae | "visitors" | Proença & Gibbs (1994) |
| *Eugenia dysenterica* | Apidae: Bombinae<br>Apidae: Meliponinae | "visitors" | Proença & Gibbs (1994) |
| *Eugenia salamensis* | Colletidae | "foraging" | Frankie et al. (1983) |
| *Eugenia stipitata* | Apidae: Meliponinae | "visiting" | Falcão et al. (1988) |
| *Eugenia* sp. 1 | Apidae: Meliponinae | "aggressive behavior" | Roubik (1989) |
| *Eugenia* sp. 2 | Halictidae | "visits" | Ruiz & Arroyo (1978) |
| *Eugenia* spp. | Apidae: Meliponinae | "collect pollen" | Absy & Kerr (1977) |
| *Myrcia linearifolia* | Apidae: Bombinae | "visitors" | Proença & Gibbs (1994) |
| *Myrcia rhodosepala* | Apidae: Bombinae<br>Anthophoridae: Xylocopinae | "pollinators" | Proença & Gibbs (1994) |
| *Myrcia torta* | Halictidae ? | "pollinators" | Proença & Gibbs (1994) |
| *Myrcia* sp. | Apidae: Meliponinae | "pollen in honey" | Vit & D'Albore (1994) |
| *Myrciaria dubia* 1 | Apidae: Meliponinae | "visiting" | Falcão et al. (1989) |
| *Myrciaria dubia* 2 | Apidae: Meliponinae | "pollinators" | Peters & Vasquez (1986/87) |
| *Pimenta dioica* | Anthophoridae: Xylocopinae<br>Anthophoridae: Anthophorinae<br>Halictidae | "visiting" | Chapman (1965) |
| *Plinia cauliflora* | Apidae: Meliponinae | "intensive exploitation" | Guibu et al. (1988) |
| *Plinia glomerata* | Apidae: Bombinae<br>Apidae: Meliponinae | "foraging" | Pirani & Cortopassi-Laurini (1993) |
| *Psidium acutangulum* | Apidae: Meliponinae | "visiting" | Falcão et al. (1992) |
| *Psidium firmum* | Anthophoridae: Xylocopinae<br>Apidae: Bombinae | "presumptive pollinator" | Proença & Gibbs (1994) |
| *Psidium guajava* 1 | Apidae: Meliponinae<br>Apidae: Bombinae | "foraging" | Camillo & Garófalo (1989) |
| *Psidium guajava* 2 | Apidae: Meliponinae | "intensive exploitation" | Guibu et al. (1988) |
| *Siphoneugena densiflora* | Colletidae | "presumptive pollinator" | Proença (1992) |
| Myrtaceae indet. spp. | Apidae: Meliponinae | "pollen in honey" | Vit & D'Albore (1994) |

Note. Visits by honeybees, introduced to the Neotropics, are excluded from this table.

*velutina, Eugenia dysenterica, Myrcia linearifolia,* and *Psidium firmum*), but no buzzing behavior was noted during observation of these species. The same species of *Bombus* exhibited a preference for *Psidium guajava* in secondary vegetation in southeastern Brazil (Camillo & Garófalo, 1989). *Bombus* spp. were reported to collect pollen and nectar from *Plinia glomerata* in São Paulo (Pirani & Cortopassi-Laurino, 1993). Visits by *Melipona quadrifasciata, Tetragonisca angustulata* (both Apidae: Meliponinae), and *Apis mellifera* were also recorded. Guibu et al. (1988) documented intensive exploitation of Myrtaceae by *Melipona quadrifasciata.* They listed *Psidium guajava* s.l. and *Plinia cauliflora* (Mart.) Kausel s.l. (as *Myrciaria cauliflora* (Mart.) O. Berg s.l.) among the species visited by these bees in São Paulo, Brazil.

Other species of the bee genus *Melipona* may be important pollinators of Myrtaceae in Amazonian Brazil. *Melipona rufiventris* and *M. seminigra* collected pollen of *Eugenia* spp. and other unidentified Myrtaceae near Manaus (Absy & Kerr, 1977; Absy et al., 1980). In the same area Falcão et al. (1988, 1989, 1992) recorded *Melipona lateralis* and

*M. pseudicentris* visiting cultivated *Eugenia stipitata*, *Myrciaria dubia*, and *Psidium acutangulum*. In the nearby Reserva Ducke, Roubik (1989) observed aggressive behavior of several species of *Trigona* (Meliponinae) on *Eugenia* sp. In Peru *Myrciaria dubia* is commonly pollinated by *Melipona fuscopilara* and *Trigona postica* (Peters & Vasquez, 1986/87). A recent study of pollen spectra in the honey of 48 species of *Melipona* in Venezuela (Vit & D'Albore, 1994) provides additional evidence of the importance of Myrtaceae to these bees: Myrtaceae spp. and *Myrcia* sp. were respectively the fifth and eighth most common pollen types in a list of 13. Ruiz and Arroyo (1978) reported visits to a Venezuelan *Eugenia* sp. by *Augochloropsis fulvofimbriata* (Halictidae) and by *Apis mellifera* and *Trigona testiceicornis* (Apidae).

Chapman (1965) saw solitary bees belonging to the genera *Ceratina* (Anthophoridae, Xylocopinae), *Exomalopsis* (Anthophoridae, Anthophorinae), and *Halictus* (Halictidae), as well as honeybees, visiting flowers of *Pimenta dioica* for pollen in Jamaica.

In a population of *Decaspermum parviflorum* in a forest clearing in Indonesia, Kevan and Lack (1985) recorded vigorous pollen collection during a 45-minute peak period by a variety of bees, mostly *Apis dorsata* (Apidae: Apiinae) and *Nomia* spp. (Halictidae: Nomiinae). *Nomia* and *Trigona* continued to glean during the rest of the day and perfunctory visits by *Xylocopa* spp. were also reported. In a nearby forest *Syzygium lineatum* (as *Syzygium syzygioides* and subsequently corrected) was visited sparingly and mainly for nectar (Lack & Kevan, 1984). Another study notable for the paucity of potential pollen vectors was that of van Wyk and Lowrey (1988). These authors provisionally considered that the 15 southern African species of *Eugenia* studied might be bee-pollinated, as honeybees were observed visiting *Eugenia* spp. in Pretoria and were also active in natural populations of *Eugenia capensis* Harv.

### BIRD POLLINATION

Bird pollination appears to be much less frequent in the Myrtoideae than in the Leptospermoideae. Ford et al. (1979) reported six species of birds visiting three species of *Syzygium* in Australia, but in no case was a bird actually seen to be carrying pollen. Honeyeaters were reported as the most commonly observed vertebrate visitors to flowers of *Syzygium cormiflorum* and *S. tierneyanum* in Australia (Hopper, 1980; Crome & Irvine, 1986). Hopper (1980) suggested that honeyeaters may be the most important pollinators of *S. tierneyanum* but acknowledged that the role of bats was neglected in his study. Crome and Irvine (1986) demonstrated experimentally that in *S. cormiflorum* birds were far less effective pollinators than bats, accounting for less than 25% of all successful pollinations. Both of these species have white or cream flowers, but Ford et al. (1979) noted a tendency for red stamens among large-flowered, bird-pollinated Australian Myrtaceae in general (mostly Leptospermoideae).

Two small neotropical myrtoid genera, *Acca* and *Myrrhinium*, have stiff red stamens reminiscent of those of many Australasian bird-pollinated Myrtaceae. Landrum (1986) noted that there is no nectar in the fresh flowers of *Acca sellowiana* and that in both genera the petals change color and become sweet and juicy just as the anthers dehisce. There are various reports of visiting birds eating the petals of *Acca sellowiana* (Kiaerskov, 1893; Knuth, 1906; McGregor, 1976; Vogel et al., 1984). In view of their isolated position within the Myrtoideae, Landrum (1986) hypothesized that the use of petals as an attractant in these two closely related genera (which he called the *Myrrhinium* complex) is very ancient. Schroeder (1947), however, observed extensive bee visitation in *Acca sellowiana* cultivated in California and found that flowers so visited set fruit ca. 16 times as well as flowers protected from visitation. Free (1993) also reported that bees are frequent visitors to the flowers of this species and assumed that they were responsible for most of the pollinations. In *Myrrhinium atropurpureum* Schott recently opened flowers have deep wine-red petals with a normal petal texture, crinkled filaments, and closed anthers; putatively receptive flowers have inflated, very pale lavender petals, stiff filaments, and dehisced anthers; the pale petals provide a dramatic contrast to the rest of the inflorescence, which is a uniform deep wine red, even to the axes, and the petal texture is unlike that of any other flower known to us, aerenchyma-rich, resembling the hollow structure of certain rubiaceous fruits such as *Coccocypselum* (C. Proença, pers. obs.). It seems likely that *Acca* and *Myrrhinium* evolved under selection for bird pollination (perhaps in areas with an impoverished bee fauna) without totally losing their adaptations to bee pollination, so that in cultivation *Acca sellowiana* at least still responds to bee pollination.

### MAMMAL POLLINATION

Long-tailed pygmy possums (*Cercartetus caudatus*) feed on *Syzygium cormiflorum* in northern Queensland (Hopper, 1980). Beardsell et al. (1993) suggested that the cauliflorous flowering of several

*Syzygium* species might facilitate access to the flowers by larger marsupials, which move up and down the trunks and larger branches. These authors also stressed that bats, being nocturnal and not easily studied, might be more significant pollinators of some Myrtaceae than had been thought previously. *Syconycteris australis* (Queensland blossom bat) appeared to be one of the minor pollinators of the night-flowering rainforest tree *Syzygium tierneyanum* (Hopper, 1980) and also made nocturnal visits to the flowers of the cauliflorous *S. cormiflorum* (Crome & Irvine, 1986) as did *Macroglossus lagochilus*, another small blossom bat. In *S. cormiflorum* flowers open at any time of the day or night, but bats were the single most important pollinators, although visits by birds to the flowers were more frequent and more numerous. Start and Marshall (1976) reported the bats *Eonycteris spelaea* and *Macroglossus minimus* feeding on *S. malaccense* in West Malaysia.

### WIND POLLINATION

Grifo (1992) considered wind-pollination possible but unlikely in *Myrcianthes.* Peters and Vasquez (1986/87) mentioned the possibility of wind-pollination in *Myrciaria dubia* and Moncur (1988) the same for *Acca sellowiana* (as *Feijoa sellowiana*), but in both of these studies bees were considered to be the most important pollinating agents.

## FRUITS

### FRUIT CHARACTERISTICS AND DISPERSAL AGENTS

The typical fruit of the Myrtoideae is a fleshy single-seeded, usually orange, red, or black berry, and the Myrtoideae have long been characterized as a fleshy-fruited subfamily or tribe. However, semi-dry to dry berries (i.e., leathery or pithy) have also been recorded, especially in *Eugenia* and related genera. Drupaceous fruits are reported for *Myrtella* and *Stereocaryum.* Subdrupaceous fruits, with variable levels of woodiness of the endocarp, are found in some species of *Eugenia* s.l., *Rhodomyrtus* (Schmid, 1980), and in *Acmena* (Hartley & Craven, 1977). Drupoid fruits with 1–3 pyrenes occur in *Eugenia* and *Hexachlamys* (Berg, 1857; Rotman, 1982). A very specialized "drupoid" fruit occurs in *Campomanesia.* It may be considered drupoid in that the single seeds developing in each of the locules adhere to the endocarp, as in a true drupoid fruit, but it differs in the texture of the endocarp, which can be woody or merely glandular-verrucose, simulating a false seed-coat (Landrum, 1982). The more primitive subtribe Myrtinae includes many species that have green or yellow, several- to many-seeded fruits.

Our knowledge of dispersal agents is mainly based on deductions from fruit morphology; few actual dispersal events have been reported. Fleshy perigynia have clearly evolved in association with zoochory. Briggs and Johnson (1979) highlighted two common secondary developments that may occur independently or in conjunction, viz., increase in fruit size and reduction in seed number. Proença (1991) suggested that single-seeded fruits, i.e., "packaging each seed separately," would enable the plant to abort inferior zygotes on an individual basis and to mature fruits at different rates, thus permitting more dispersal events for the same number of seeds.

Various dispersal mechanisms have been suggested for many-seeded fruits. Landrum (1986) considered that most species of *Campomanesia* best fit the mammal dispersed syndrome as defined by Janson (1983) based on an Amazon rainforest community, but Snow (1981) registered *Campomanesia* as forming part of the diet of specialized frugivorous birds. Motta Júnior et al. (1994) reported that *Dusicyon thous*, a small nocturnal Canidae, feeds on fruits of *Psidium* sp., *Campomanesia* sp., and *Plinia cauliflora* (as *Myrciaria cauliflora*). Seeds of *Campomanesia* sp. recovered from scats germinated successfully both *in situ* and in the laboratory, indicating that this small mammal is a potentially effective dispersal agent. The genus *Psidium* is cited by Snow (1981) as having fruits that form part of the diet of specialized frugivorous birds, but *Psidium firmum* is apparently consumed by small rodents (Proença, 1991). Evidence to this effect included a gnawed-through peduncle of an unripe fruit, marks of superficial bites on unripe fruit, ripe fruit torn open and the flesh partly eaten, and nearby scats which were identified as pertaining to *Rhipidomys* or *Oryzomys.* Cultivated *Psidium guajava* is eaten by parrots (M. A. S. Alves, pers. comm.), other birds (Advani, 1981), and bats (Funmilayo, 1980; Advani, 1982). Other multi-seeded fruits mentioned by Snow (1981) include those of *Decaspermum* and *Rhodamnia*, which are exploited by specialized frugivorous birds, and *Calycolpus*, exploited by specialized and unspecialized frugivorous birds. Kevan and Lack (1985) observed mistletoe-birds (Dicaeidae) feeding on the fruits of *Decaspermum parviflorum* and discussed bird dispersal in this dioecious species in relation to the selective pressure for the production of energy-rich fruits. Ant-dispersal by *Messor minor* (André) has recently been reported for *Myrtus communis*, the seeds of which bear elaiosomes (Aronne & Wilcock, 1994)

Johnson and Briggs (1984) suggested that in diverse lines of Myrtaceae, fruits with large, single seeds seem to be adapted to vertebrate dispersal in tropical forest. In the large genus *Syzygium*, one-seeded fruits are the norm, but mature fruits from different species may differ in diameter by an order of magnitude (Hyland, 1983). K. Fischer (pers. comm.) compared the morphology and nutritional and secondary chemistry of fruits of New Guinean species of *Syzygium* eaten by birds and by bats. In the species of *Syzygium* studied by her, fruits eaten by bats were both longer and wider than those consumed by birds but did not differ in nutrient composition or secondary chemistry. Among 16 wild fruits edible to man that were studied in Malawi, *Syzygium guineense* Guill. & Perry had the highest levels of iron and magnesium (Saka & Msonthi, 1994). Beardsell et al. (1993) noted that in many species of *Syzygium* the infructescences are borne at some distance from the tips of the branches thus allowing larger animals access to the fruits. They cited the extreme case of *Syzygium cormiflorum*, the berries of which develop on the main trunk and larger branches, and suggested that this arrangement enables larger marsupials to eat the fruits during tree to tree movements. Fruits of a cauliflorous species of *Myrciaria* are eaten by bats (Semir, 1984). *Eugenia* s.l. is cited as consumed by unspecialized frugivorous birds (Snow, 1981). Two unidentified species of *Eugenia* s. str. from Costa Rica are eaten by *Pharomachrus mocinno* (Trogonidae) and by *Aulacorhynchus prasinus* (Rhamphastidae), respectively (Wheelwright et al., 1984). Fruits of *Eugenia punicifolia* (Kunth) DC. are probably consumed by pheasant-like Tinamidae in central Brazil, and *Siphoneugena densiflora* fruits are eaten by *Miyarchus swansonii* (Tyrannidae), an opportunistic fly-catcher, and by other birds (Proença, 1990). Fruits of *Myrcia torta* DC. (as *Myrcia dictiophylla*) are eaten by *Neothraups fasciata* (Emberizidae), a generalist low-foraging tanager (Alves, 1992). Observations of *Blepharocalyx salicifolius* revealed that the fruits are swallowed whole by migratory *Elaenia chiriquensis* and *Tyrannus melancholicus* (both Tyraniidae) and by resident *Neothraups fasciata* (Emberizidae), all opportunistic frugivores that also feed on insects (Paes, 1993). Snow (1981) listed *Acmena, Eugenia, Myrcia*, and *Syzygium* as forming part of the diet of specialized frugivorous birds, while fruits of *Eugenia* and *Myrcia* are also exploited by non-specialized birds. He commented that while at least 13 genera of Myrtoideae provide fruits that are eaten by frugivorous birds, specialized and unspecialized, none seems to provide the staple diet of any frugivorous bird. In this respect the Myrtoideae resemble the Euphorbiaceae but differ from the Lauraceae, Burseraceae, and Palmae. Grifo (1992) saw monkeys of the genus *Alouatta* consuming the fruits of *Myrcianthes pungens* in Corrientes, Argentina. However, her observations suggested that the fruits, including the seeds, were chewed, thus considerably reducing the possibility that the monkeys were agents of dispersal.

## OVULE-SEED RATIOS AND REPRODUCTIVE CAPACITY

In the fruits of most Myrtoideae, including the many-seeded ones, the number of mature seeds is much smaller than the original number of ovules in the ovary from which the fruit is derived. Even in genera in which the ovule number is reduced to two in each of two (or three) locules, most ovules do not develop into mature seeds. This superfluity of ovules may simply represent a relictual situation, with these species being derived from taxa in which most or all ovules within the ovary would have matured into seeds (Caspar & Wiens, 1981). For example, Landrum (1981) envisaged an ancestor of *Myrceugenia* that developed all or nearly all its ovules into seeds while in present-day species few ovules develop into seeds. Alternatively, the superfluous ovules may provide scope for the exercise of female choice (Stephenson & Bertin, 1983) and/or allow for the wastage of ovules inherent in a post-zygotic "self-incompatibility" system. In the dioecious *Pimenta dioica* (and the putatively dioecious *P. guatemalensis*) the number of ovules scarcely exceeds the number of seeds per fruit (Landrum, 1986). We suggest that in these species there is no need for superfluous ovules, since all pollen tubes must originate from non-self pollen.

In the Australian Myrtaceae (largely Leptospermoideae), Rye and James (1992) identified reduction in ovule numbers and competitive selection among fertilized ovules as mechanisms leading to reduction in seed number. These trends were interpreted as the result, in part at least, of selection for larger seed size. In addition, they found that plant size is positively correlated with ovule number and seed set, and that the effects of all these factors tended to reinforce each other in determining the net reproductive capacity of the species.

Another factor that has been linked to reproductive capacity is chromosome number. Rye and James (1992) found that high reproductive capacity is associated with high dysploid chromosome numbers in four genera including *Eugenia*.

## EMBRYO AND SEED DEVELOPMENT

### EMBRYO DEVELOPMENT

The Myrtoideae apparently follow the onagrad pattern of embryo development but, as in the Myrtaceae as a whole, the process has scarcely been studied. The dearth of information in this area is acute, even in the context of our rudimentary knowledge of Myrtoideae biology in general, and may be attributable to the extreme difficulties experienced in fixation for histological studies in the family (Mauritzon, 1939; Davis, 1968; Beardsell et al., 1989, 1993).

### SEED-COAT

Beardsell et al. (1993) considered a seed-coat formed from both integuments as "a feature of all Myrtaceae so far examined." While this may summarize the situation in the Leptospermoideae it is far from true with respect to the Myrtoideae. Van Wyk and Botha (1984) reported testa formation from the outer integument only in some southern African *Eugenia* species and a pachychalazal seed-coat in others. Narayanaswami and Roy (1960b) described the testa in *Psidium guajava* (and in *P. cujavillus* Burm. f., now considered synonymous) as being formed from the outer integument only. The seed-coat appears to be entirely absent in *Acmena, Acmenosperma,* and *Waterhousea* (Hartley & Craven, 1977; Hyland, 1983).

McVaugh (1968) indicated that the testa varied in thickness from group to group in the neotropical Myrtoideae and may be membranous, leathery, cartilaginous, or bony. Where the seed-coat is hard (i.e., in most Myrtinae apart from Landrum's *Campomanesia* complex), an operculum in the seed-coat, located directly over the basal end of the hypocotyl, allows the embryo to emerge. Landrum and Stevenson (1986) detected a strong correlation between seed-coat texture and embryo structure but admitted the possibility that changes in embryo morphology naturally follow changes in seed-coat texture. Whatever the thickness, the testa is usually quite smooth and unsculptured.

In *Campomanesia* the thick glandular locule wall adheres to the delicate membranous testa of the single seed maturing inside the locule, as described above. The locule wall thus serves as a false seed-coat, to which Landrum (1982) attributed a protective function, hypothesizing that frugivorous birds or mammals would tear apart the fruits without biting into the glandular turpentine-smelling walls. Some field observations support this theory, as partially eaten fruits were found to have the locules intact (Landrum, 1986) but, as discussed above, some seeds are clearly ingested by small mammals (Motta Júnior et al., 1994). Proença (1991) suggested a possible co-adaptive role for the pseudotesta, interpreting it as a defense to prevent developing larvae of Tephritidae flies from migrating from infected to healthy locules. The situation in *Campomanesia,* where each locule harbors a single developing embryo, was compared to that in a species of *Berberis* in which high mortality of Tephritidae larvae was found to occur in single-seeded fruits when compared to several-seeded fruits (Herrera, 1984). Tephritidae are notorious predators of myrtaceous fruit crops (Malavasi & Morgante, 1980; Morgante & Malavasi, 1981; Tan & Lee, 1982; Burk, 1983).

### EMBRYO STRUCTURE

Embryo structure has been considered fundamental in the classification of the Myrtoideae since the time of De Candolle (1828). He distinguished three basic embryo types commonly referred to as eugenioid (with thick, fleshy cotyledons and a relatively insignificant hypocotyl), myrcioid (with leafy cotyledons that are much broader than the hypocotyl), and myrtoid/pimentoid (with a well-developed hypocotyl and relatively small, narrow cotyledons). Although most subsequent authors have used these differences as the basis for their classifications, little attention has been paid to the biological significance of these structures. One notable exception is the discussion by Landrum and Stevenson (1986) in which the various embryo types are interpreted as different responses to the same selective pressure for increased food storage in the embryo. Essential oil-secreting schizogenous glands occur in the embryos of *Pimenta racemosa* (P. Miller) J. W. Moore (as *Myrcia acris* DC.), *Luma apiculata* (as *Myrceugenia apiculata*), *Myrceugenia glaucescens* (Cambess.) D. Legrand & Kausel (as *Eugenia glaucescens* Cambess.), *Myrcianthes pungens* (as *Eugenia pungens*), and *Eugenia discolor* DC. and are absent from *Myrtus* sp., *Psidium, Acca* (as *Feijoa*), and *Eugenia uniflora* (as *Stenocalyx michelii*) (Petit, 1908). In a study of southern African *Eugenia,* four species had conspicuous glands and five species were described as "apparently eglandular but usually with a few obscure glands mainly associated with the radicular protuberance" (van Wyk, 1980). Hyland (1983) recorded oil glands in the embryos of 4 out of ca. 50 species of Australian *Syzygium* studied, i.e., *S. macilwraithianum* B. Hyland, *S. sayeri* (F. Muell.) B. Hyland, *S. velae* B. Hyland, and *S. wilsonii* B. Hyland. In the Leptospermoideae the embryo lacks oil glands (Petit, 1908).

ENDOSPERM

The endosperm is nuclear and is generally described as being digested by the developing embryo and therefore absent from the mature seeds (Tobe & Raven, 1983). However, studies by Petit (1908, cited in van Wyk & Botha, 1984) have shown that traces of endosperm are present in many myrtaceous seeds including those of the genera *Acca* (as *Feijoa*), *Myrtus*, and *Psidium* (all Myrtoideae). Van Wyk and Botha (1984) reported the presence of endosperm in mature seeds of some species of southern African *Eugenia*. They suggested that variation in the amount of endosperm formed in the young seed may be of taxonomic importance, whereas the quantity of endosperm that remains in mature seeds is variable within species and therefore less likely to prove taxonomically significant.

POLYEMBRYONY

Tobe and Raven (1983) described polyembryony as usual in *Syzygium* but our literature survey suggests that, though frequent, it is by no means the norm in this genus. The earliest reports are by Tiwary (1926), who concluded that all (six) of the species of *Syzygium* (reported as *Eugenia*) examined by him showed "the existence of some kind of polyembryony." However, as he interpreted early bifurcation of the plumule as evidence of polyembryony, he may have overestimated the frequency of this latter phenomenon within the genus. In only two of the species he examined (*S. cumini* and *S. jambos*, as *Eugenia jambolana* and *E. jambos*, respectively) was the presence of more than one embryo in the seed actually demonstrated.

Subsequent studies have confirmed the existence of polyembryony in *Syzygium jambos*, disputed its occurrence in *S. cumini* (van der Pijl, 1934; Henderson, 1949; Roy, 1953; Chantaranothai & Parnell, 1994) and in general indicated that the condition was far from ubiquitous in the genus. Van der Pijl (1934) reported polyembryony in *S. aqueum* (Burm. f.) Alston (as *Eugenia aquea* Burm.f.), *S. jambos* (as *E. jambos*), *S. javanicum* Miq. (as *E. javanica* Lam.), and *S. malaccense* (as *E. malaccensis*), but found no evidence for polyembryony in *S. cumini* (as *E. cumini*) on the basis of the examination of specimens of this species from four different localities and fruits obtained from the local market. Henderson (1949) found polyembryony in "some species" of the 138 in the genus *Eugenia* s.l. in Malaya, and Merrill and Perry (1938) reported that of the 45 species of *Syzygium* known from China, 5 are regularly polyembryonic (*S. jambos*, *S. buxifolium* Hook. & Arn., *S. megacarpum* (as *S. latilimbum* (Merr.) Merr. & L. M. Perry), *S. forrestii* Merr. & L. M. Perry, and *S. hancei* Merr. & L. M. Perry). Hyland (1983) described ca. 50 species of *Syzygium* occurring in Australia and recorded consistent polyembryony in *Syzygium paniculatum* and the presence of "two-seeded fruits" in *S. aqueum* (polyembryony? see *S. aqueum* above). Chantaranothai and Parnell (1994) found no evidence of polyembryony in *S. cumini*, nor in *S. megacarpum* or *S. formosum*, but confirmed the existence of polyembryony in *S. jambos* and *S. malaccense* and reported production of 2–6 seedlings from 1–3-seeded fruit in *S. siamense* (Craib) P. Chantaranothai & J. Parn. We concur with van Wyk and Botha's (1984) conclusion that most reports of polyembryony in *Eugenia* are probably referrable to the genus *Syzygium*.

Johnson (1936) counted 2–22 embryos in seeds of *Luma apiculata* (as *Eugenia hookeri* Steud.). However, Landrum (1986) revised *Luma apiculata* and, although he had obviously dissected seeds and examined embryos, did not mention the occurrence of polyembryony. Thus we may infer that polyembryony is not constant in this species.

Gurgel and Soubihe Sobrinho's (1951) study of myrtaceous fruit-bearing trees in Brazil is one of the most complete studies of polyembryony in the Myrtoideae to date. Sixteen species were investigated, representing five genera native to Brazil plus *Syzygium*, which is introduced and widely cultivated. The following species were found to be consistently monoembryonic: *Campomanesia* sp. (as *Myrtus mucronata* Cambess.), *Psidium guajava*, *Psidium guineense* (as *Psidium araça* Raddi), *Eugenia uniflora*, *Eugenia tomentosa* Cambess., *Eugenia uvalha* Cambess., *Eugenia myrcianthes* (as *Myrcianthes edulis* O. Berg), *Eugenia brasiliensis* Lam., *Eugenia lucescens* Nied. (as *Phyllocalyx luschnathianus* O. Berg), and *Gomidesia reticulata* O. Berg.

Gurgel and Soubihe Sobrinho (1951) found a high percentage of polyembryony in *Syzygium malaccensis* (66–97%) and *Syzygium cumini* (76–95%). One to eleven embryos were reported per seed. Repeated sampling of these species in successive years suggested the existence of a phenetic as well as a genetic component to the level of polyembryony. A low to medium percentage of polyembryony (33–70%), with one to five embryos reported per seed, was found in the following native Brazilian species: *Plinia cauliflora* (as *Myrciaria cauliflora*), *Plinia trunciflora* (O. Berg) Kausel (as

*Myrciaria trunciflora* O. Berg), and *Plinia edulis* (Vell.) Sobral (as *Eugenia edulis* Vell.), as well as a species cited as *Myrciaria trunciflora*, which Mattos (1989), based on the common name, claimed to be *Myrciaria coronata* Mattos. Sobral (1993) excluded this species from *Myrciaria* in his recent revision of that genus and stated that it is a *Plinia*. Rotman (1982) registered consistent polyembryony in *Guapurium peruvianum* (possibly = *Plinia*) but registered no polyembryony in *Plinia trunciflora*. Thus all low to medium polyembryonic species may be members of genus *Plinia*. Traub (1939) had already noted that polyembryony was usual in *Plinia cauliflora* (as *Myrciaria cauliflora* ) cultivated in Florida.

Observations on the origin of the embryos in polyembryonic seeds are few and disparate. Tiwary (1926) reported embryos originating from the egg cell (presumbly sexual), from the synergids and from the nucellus in *S. cumini* (as *Eugenia jambolana*). Narayanaswami and Roy (1960a) and Roy and Sahai (1962) also studied *S. cumini*, and the latter authors found that the fertilized egg degenerates along with the synergids. The upper half of the nucellus becomes proliferative and produces several embryos, one or more of which may survive, producing mono- or polyembryonic seeds in this species. Roy and Sahai (1962) also noted the occasional production of supernumerary embryo-sacs (by apospory or by the activity of more than one archesporial cell) but reported that ovules in which this occurs eventually degenerate. The multiple embryos in seeds of *S. jambos* are also of nucellar origin (van der Pijl, 1934), and Johnson (1936) tentatively suggested a nucellar origin for the embryos of *Luma apiculata* (as *Eugenia hookeri*). Gurgel and Souhihe Sobrinho (1951) confirmed that in *S. jambos* the sexual embryo often dies immediately after fertilization. However, they considered the adventitious embryos to be derived from the inner integument. Van der Pijl (1934) reported an integumentary origin for the multiple embryos of *Syzygium malaccense* (as *E. malaccensis*).

## REGENERATION FROM SEED

Beardsell et al. (1993) highlighted the lack of published data on the regeneration of the Myrtoideae of the tropical forests. They suggested that germination requires breakdown of the pericarp by weathering or ingestion by animals including birds, and reported that some species of *Syzygium* germinate after fermentation of the fruits. Tidbury (1949) also advocated fermentation of fruits. When fruits of *Syzygium aromaticum* (Clove Tree) were left to ferment for about three days the seeds were easily hulled, and such hulled seed produced "somewhat better seedlings" than unhulled. Germination was rapid, occurring within 12–14 days of sowing, and germination percentages were high, almost always above 90%. Hyland (1983) included seedling germination periods in his descriptions of some 50 Australian species of *Syzygium*. Germination periods ranged from 10 days to almost 10 months (300 days) and there was considerable within-species variation in germination time. In the same paper, species of *Acmena* were cited as having even longer germination times, ranging from 24 days to well over 2 years (860 days), while values for *Waterhousea* tended to be lower at 10–60 days. *Eugenia reinwardtiana* (Bl.) DC. and *Acmenosperma claviflorum* (Roxb.) E. Kausel were reported as having germination periods of 30–50 and 40–90 days respectively.

Ferreira (1982) studied germination of seeds of *Psidium acutangulum*, which had been treated with a 1% solution of a proprietary systemic fungicide after being removed from the fruit pulp. He found that germination occurred 30–100 days after sowing and that ca. 90% of seeds planted in loam (the most successful medium) germinated eventually. Lorenzi (1992) reported a similar range of germination times among 16 native Brazilian species (in eight genera) of Myrtaceae studied by him. The most rapid germination (10 days after sowing) was observed in *Eugenia pyriformis* Cambess., while some seeds of *Plinia edulis* (as *Marlierea edulis*) took up to 100 days to germinate. Gurgel and Soubihe Sobrinho (1951) reported germination times between 18 days (for *Psidium guajava*) and 73 days (for *Campomanesia* sp. as *Myrtus mucronata*). Levels of germination varied considerably (40–80%).

Lorenzi (1992) also reported seed viability periods. These were generally short (as little as 2 weeks in *Eugenia involucrata* DC.), but species of *Psidium* and *Acca* had longer seed viabilities of several months. Viability of seeds of *Psidium guajava* may exceed one year. *Blepharocalyx salicifolius* seeds lost viability within two months (Matos, 1994).

## CONCLUSIONS

As might be predicted from their morphology, the Myrtoideae emerge from this review as a rather uniform group with respect to their overall pollination and dispersal syndromes. Most species diverge little from the apparently highly successful combination of small, short-lived flowers offering pollen to attract bees as pollinators and fleshy fruits adapted to endozoochory. However, it is possible to observe that more morphological diversification has arisen in characters linked to seed dispersal and seedling establishment than in those linked to pollination biology. For such a large group, the species exhibit an impressive uniformity with respect to general flower structure and pollen morphology.

The rather narrow pollination spectrum is reminiscent of other large groups with faithful bee pollination, e.g., Malpighiaceae (Anderson, 1979), Melastomataceae (Renner, 1989), and Solanaceae (Symon, 1979). Renner (1989) has suggested that such a lack of diversification may be the result of being "stuck on an adaptive peak." However, the data available suggest that the Myrtoideae run the gamut of flower-visiting bee taxa and fully exploit differences in bee behavior, such as buzzing abilities and trap-lining, the more highly evolved Apidae bee family being dominant. This is reflected in the considerable diversity in flower size, flowering phenology, and especially flowering strategies encountered. The breeding systems of the Myrtoideae vary from dioecy and complete self-sterility (with late-acting variants) through to self-compatibility and apomixis, suggesting that the Myrtoideae have successfully capitalized upon their bee pollinators, and diversified their reproductive strategies accordingly, to establish themselves as important elements in many different life-zones and habitats. In this respect, the Myrtoideae are similar to the Leptospermoideae, although this latter group has coevolved primarily with the most primitive flower-visiting bee family, the Colletidae, while simultaneously developing a secondary evolutionary line of bird pollination, which is very rare in the Myrtoideae. Certain specialized features of the floral biology of the Leptospermoideae are absent in the Myrtoideae, e.g., secondary pollen presentation, wet stigmas, and the presence of ovulodes in the ovary. Conversely, buzz pollination is, as far as we know, limited to the Myrtoideae. Within the Myrtoideae s.l. nectar-rewarding bird pollination systems, post-anthesis stylar extension, unitegmic ovules, and apomixis have only been registered in *Syzygium* (of the *Acmena* alliance) and may be restricted to this group (although the possibility of polyembryonic *Plinia* of the Myrtoideae s. str. also being apomictic cannot be discarded as yet).

The endozoochorous fruits of the Myrtoideae seem to be adapted to many different classes of dispersers, and this characteristic is probably the most important ecological difference as compared to the largely wind-dispersed Leptospermoideae. The Myrtoideae show a great variety in size, color, texture, and seediness of fruits, with the seeds also varying significantly in size, seed coat structure, and embryo morphology. Pseudo-testa formation from the endocarp, testa formation from the outer integument only, oil glands in the embryo, and polyembryony are apparently restricted to the Myrtoideae.

Our knowledge of the reproductive biology of the Myrtoideae is still far from complete, and the following questions merit further investigation: Are inflorescence structure and flowering strategy correlated with habitat? Is flowering cued by abrupt fluctuations in humidity? How common is buzz pollination, and what are the adaptations and bees involved? Which birds are involved with bird pollination systems where petals are offered as a reward, why has this mechanism evolved, and how does it differ from nectar-rewarding bird pollination systems? How common is cryptic dioecy and what are the selective pressures maintaining this apparently expensive breeding system? What are the main agents of fruit dispersal and, in particular, how important is the role played by bats and other small mammals? Has co-evolution with parasites affected fruit and seed morphology? What is the nature of the mechanism which maintains preferential outcrossing and does more than one type of self-incompatibility exist in the family? Is there any relationship between apomixis, polyembryony, and chromosome number? The answers to such questions as these may have important and diverse implications. First, they may help to resolve some of the complex taxonomic problems in the Myrtoideae by helping to elucidate the functional significance of characters of taxonomic importance. Second, studies of breeding systems in particular should aid systematists, population geneticists, and ecologists in the interpretation of patterns of variation within and between populations and species. Third, this information may facilitate the genetic improvement of the several economically important species. Finally, a deeper understanding of the reproductive biology of a group that is of great ecological importance in several endangered tropical ecosystems may represent an invaluable contribution toward their conservation.

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