

INFORMATION TO USERS

This reproduction was made from a copy of a manuscript sent to us for publication and microfilming. While the most advanced technology has been used to photograph and reproduce this manuscript, the quality of the reproduction is heavily dependent upon the quality of the material submitted. Pages in any manuscript may have indistinct print. In all cases the best available copy has been filmed.

The following explanation of techniques is provided to help clarify notations which may appear on this reproduction.

1. Manuscripts may not always be complete. When it is not possible to obtain missing pages, a note appears to indicate this.
2. When copyrighted materials are removed from the manuscript, a note appears to indicate this.
3. Oversize materials (maps, drawings, and charts) are photographed by sectioning the original, beginning at the upper left hand corner and continuing from left to right in equal sections with small overlaps. Each oversize page is also filmed as one exposure and is available, for an additional charge, as a standard 35mm slide or in black and white paper format.*
4. Most photographs reproduce acceptably on positive microfilm or microfiche but lack clarity on xerographic copies made from the microfilm. For an additional charge, all photographs are available in black and white standard 35mm slide format.*

*For more information about black and white slides or enlarged paper reproductions, please contact the Dissertations Customer Services Department.

U·M·I Dissertation
Information Service

University Microfilms International
A Bell & Howell Information Company
300 N. Zeeb Road, Ann Arbor, Michigan 48106

8629677

Callejas, Ricardo

TAXONOMIC REVISION OF PIPER SUBGENUS OTTONIA (PIPERACEAE)

City University of New York

PH.D. 1986

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark ✓.

1. Glossy photographs or pages ✓
2. Colored illustrations, paper or print _____
3. Photographs with dark background ✓
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy ✓
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages _____
8. Print exceeds margin requirements _____
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) _____ lacking when material received, and not available from school or author.
12. Page(s) _____ seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Dissertation contains pages with print at a slant, filmed as received _____
16. Other _____

University
Microfilms
International

TAXONOMIC REVISION OF PIPER SUBGENUS OTTONIA (PIPERACEAE)

by

RICARDO CALLEJAS

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York.

1986

This manuscript has been read and accepted for the Doctoral
Faculty in Biology in satisfaction of the dissertation require-
ment for the degree of Doctor of Philosophy.

27 Aug 1982
date

James L. Luteyn
Chairman of Examining Committee
James L. Luteyn, New York Bot. Gdn.

Sept 18, 1982
date

Peter C. Chabora
Executive Officer
Peter C. Chabora

Arthur Cronquist
Arthur Cronquist, New York Botanical Garden

Durland Fish
Durland Fish, Fordham University

Joseph W. Rachlin
Joseph W. Rachlin, Lehman College

Dennis Stevenson
Dennis Stevenson, Barnard College

READER ONLY
William Burger, Field Museum of Natural History

Supervisory Committee

The City University of New York

ABSTRACT

TAXONOMIC REVISION OF SUBGENUS OTTONIA (PIPERACEAE)

by

Ricardo Callejas

Adviser: Professor James L. Luteyn

Ottonia is a distinct natural group in the large family Piperaceae. It was previously recognized as a genus, but is here placed as a subgenus of Piper. It consists of 21 species, 16 of which are restricted to the SE Atlantic Coastal forest of Brazil, the rest occurring in the Amazon basin and NE South America (P. darienense). The subgenus includes species with sessile and/or racemose inflorescences. None of these two groups, however, conform monophyletic units. Thus, this treatment does not recognize Ottonia as consisting only of species with pinnately nerved leaves and racemose inflorescences, as has been previously interpreted. Data from seed coat structure, seed morphology, primary stem anatomy, wood anatomy, leaf anatomy and leaf histology, and flower development were used to elaborate a cladistic analysis of the subgenus. That analysis was performed using as a sister group the subgen. Callianira. The sister group was selected base on a cladistic analysis generated for the entire genus Piper. Seed coat structure as well as seed morphology, and to certain extent leaf histology, proved to be of diagnostic value at species level. Of the 25

species previously recognized, 15 are placed on synonymy, and 36 names previously synonymized are relocated. Two species, Piper brevinodis (pedicellate flowers) and Piper ubatubensis (sessile flowers) are described as new. One species, Ottonia corei, from the Andes of Colombia is excluded and transferred to Piper.

ACKNOWLEDGEMENTS

The present is the manuscript of a dissertation submitted to the Graduate School in Biology (CUNY) in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Many people and institutions provided me with support and advice during many phases of my work.

I want to express my gratitude to the New York Botanical Garden for providing me with a graduate fellowship; at the institution staff members and students became a second family, in many cases a very important one. My special thanks in the Garden to my adviser and friend Dr. James Luteyn for his encouragement, advice and more important for all his patience with me... and my english, his incisive comments and painstaking reading of early drafts resulted in improving many parts of the dissertation. Also to Dr. Arthur Cronquist who kindly shared with me all his knowledge and on the not always clear subject of classification. To Dr. Rupert Barnabey for his careful and constructive comments on nomenclature and latin diagnosis. To my friends, students like me, Mr. John Pipoly and Mr. Douglas Daly for their interest and constructive criticisms on my dissertation as well as their help both in the field and the lab. My thanks and appreciation to Mr. Steve Churchill for all his advice and many hours of discussion on cladistics. Finally, at the Botanical Garden, many thanks to the staff and administration at the library, specially to

Lothian Lynas, and the Lieberman Lab, where Mr. Don Black was most helpful in instructing me on working in the dark room.

Anatomical and gross morphological data are an important part of the present treatment, many gaps in my knowledge as well as much of what I know now are the result of my friendship with Dr. Dennis Stevenson, who during the past three years was a critical reader and supportive friend in the lab. My deep gratitude to him.

Field work in Brazil and Paraguay was possible thanks to a Dissertation Improvement Grant from the National Science Foundation (BSR-8313150). Work in Brazil was possible with the help of local herbaria; in Bahia at Instituto de Pesquisas do Cacao, Mr. André Mauricio de Carvalho provided me with logistic support and help in the herbarium, in Paraná Dr. Gert Hatschbach and staff at the Herbario Municipal de Curitiba, in Rio de Janeiro, Dr. Elsie Guimarães and in São Paulo Mr. J. Pirani. To all them my thanks for their help and support in the field.

Finally to the staff members of the many herbaria in Europe, the United States and South America who kindly loaned thousands of specimens on which most of this work is based.

This dissertation is dedicated with love, gratitude and admiration to my wife Lucía.

TABLE OF CONTENTS

Introduction.....	1
Taxonomic History.....	2
Morphology	
Habit and Architecture.....	8
Seedlings.....	16
Leaf.....	17
Prophylls.....	20
Vesture.....	24
Inflorescence.....	26
Floral Bracts.....	28
Flowers.....	32
Fruit.....	35
Seeds.....	38
Pollen.....	43
Anatomy	
Materials and Methods.....	46
Wood Anatomy.....	49
Leaf anatomy.....	67
Primary Stem.....	73
Flower Development.....	85
Seed Coat.....	98
Ecology	
Habitat.....	108

Pollination.....	109
Phytochemistry and Physiological Action.....	111
Cladistics	
Introduction.....	115
Infrageneric Relationships of Subgenus <u>Ottonia</u>	123
Cladistic Analysis of Subgenus <u>Ottonia</u>	126
Discussion.....	139
Biogeography of Subgenus <u>Ottonia</u>	152
Systematic Treatment	
Generic Description.....	163
Notes on Keys and Species Descriptions.....	167
Key to Flower and/or Fruiting Specimens.....	168
Key to Sterile Specimens.....	174
Species Descriptions.....	180
Doubtful Names and Excluded Taxa.....	334
Numerical List of Taxa.....	338
List of Exsiccatae.....	340
Index of Local Names.....	356
Appendix I. A Cladistic Analysis of the Genus <u>Piper</u>	359
Literature Cited.....	408

List of Tables

Table I. Voucher specimens for anatomy, seed coat and pollen studies.....	40
Table II. Seed characters studied.....	51
Table III. Wood characters.....	61
Table IV. Leaf (anatomy & histology) characters.....	69
Table V. Character data matrix for subgen. <u>Ottonia</u>	141
Table VI. Character data matrix for <u>Piper</u>	402

List of Figures

Fig. 1. <u>Piper miquelianum</u> var. <u>miquelianum</u> , habit.....	15
Fig. 2. <u>Piper corcovadensis</u> var. <u>blanchetii</u> , habit.....	15
Fig. 3. <u>Piper miquelianum</u> var. <u>miquelianum</u> , nodal roots....	15
Fig. 4. SEM of papillate hairs.....	15
Fig. 5. Infructescence of <u>Piper corcovadensis</u> var. <u>blanchetii</u>	34
Fig. 6. Infructescence of <u>Piper miquelianum</u> var. <u>miquelianum</u>	34
Fig. 7. Infructescence of <u>Piper hayneanum</u>	34
Fig. 8. SEM of floral bract of <u>Piper darienense</u>	34
Fig. 9. SEM of floral bract of <u>Piper ottonoides</u>	34
Fig. 10. <u>Piper miquelianum</u> var. <u>miquelianum</u> , cross section of inflorescence.....	34
Fig. 11. SEM of floral bract of <u>Piper miquelianum</u> var. <u>miquelianum</u>	34
Fig. 12. Cross section of fruit of <u>Piper alatabaccum</u>	45
Fig. 13. <u>Piper anisum</u> , SEM of seed.....	45
Fig. 14. <u>Piper hoffmannseggianum</u> var. <u>hoffmannseggianum</u> , SEM of seed.....	45
Fig. 15. <u>Piper francovilleianum</u> , SEM of seed.....	45
Fig. 16. <u>Piper piscatorum</u> , SEM of seed.....	45
Fig. 17. <u>Piper bartlingianum</u> , SEM of seed.....	45

Fig. 18. <u>Piper piliovarium</u> , SEM of seed.....	45
Fig. 19. <u>Piper corcovadensis</u> var. <u>blanchetii</u> , SEM of pollen grains from anthers in the frontal plane.....	48
Fig. 20. <u>Piper corcovadensis</u> var. <u>blanchetii</u> , SEM of pollen grains from anthers in the sagital plane.....	48
Fig. 21. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 22. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 23. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 24. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 25. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 26. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 27. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 28. Wood anatomy of subgen. <u>Ottonia</u>	60
Fig. 29. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 30. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 31. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 32. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 33. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 34. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 35. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 36. Wood anatomy of subgen. <u>Ottonia</u>	64
Fig. 37. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u>	75
Fig. 38. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u>	75

Fig. 39. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	75
Fig. 40. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	75
Fig. 41. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	75
Fig. 42. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	75
Fig. 43. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 44. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 45. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 46. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 47. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 48. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 49. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 50. Leaf anatomy and leaf histology of subgen. <u>Ottonia</u> ...	77
Fig. 51. Primary stem anatomy of subgen. <u>Ottonia</u>	84

Fig. 52. Primary stem anatomy of subgen. <u>Ottonia</u>	84
Fig. 53. Primary stem anatomy of subgen. <u>Ottonia</u>	84
Fig. 54. Primary stem anatomy of subgen. <u>Ottonia</u>	84
Fig. 55. Primary stem anatomy of subgen. <u>Ottonia</u>	84
Fig. 56. Primary stem anatomy of subgen. <u>Ottonia</u>	84
Fig. 57. Flower development in subgen. <u>Ottonia</u>	93
Fig. 58. Flower development in subgen. <u>Ottonia</u>	93
Fig. 59. Flower development in subgen. <u>Ottonia</u>	93
Fig. 60. Flower development in subgen. <u>Ottonia</u>	93
Fig. 61. Flower development in subgen. <u>Ottonia</u>	93
Fig. 62. Flower development in subgen. <u>Ottonia</u>	93
Fig. 63. Flower development in subgen. <u>Ottonia</u>	95
Fig. 64. Flower development in subgen. <u>Ottonia</u>	95
Fig. 65. Flower development in subgen. <u>Ottonia</u>	95
Fig. 66. Flower development in subgen. <u>Ottonia</u>	95
Fig. 67. Seed anatomy and seed coat structure in subgen. <u>Ottonia</u>	103
Fig. 68. Seed anatomy and seed coat structure in subgen. <u>Ottonia</u>	103
Fig. 69. Seed anatomy and seed coat structure in subgen. <u>Ottonia</u>	103
Fig. 70. Seed anatomy and seed coat structure in subgen. <u>Ottonia</u>	103
Fig. 71. Seed anatomy and seed coat structure in subgen. <u>Ottonia</u>	103

Fig. 72. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>bartlingianum</u>	105
Fig. 73. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>darienense</u>	105
Fig. 74. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>hoffmannseggianum</u> var. <u>latifolium</u>	105
Fig. 75. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>francovilleanum</u>	105
Fig. 76. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>alatabaccum</u>	105
Fig. 77. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>piscatorum</u>	105
Fig. 78. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>anisum</u>	107
Fig. 79. Seed coat structure of subgen. <u>Ottonia</u> in <u>Piper</u>	
<u>hayneanum</u>	107
Fig. 80. One of four more parsimonious cladograms for subgen.	
<u>Ottonia</u>	145
Fig. 81. One of four more parsimonious cladograms for subgen..	
<u>Ottonia</u>	145
Fig. 82. One of four more parsimonious cladograms for subgen..	
<u>Ottonia</u>	145
Fig. 83. One of four more parsimonious cladograms for subgen..	
<u>Ottonia</u>	145
Fig. 84. Cladogram for subgen. <u>Ottonia</u>	147

Fig. 85A. Geographic distribution of <u>Piper francovilleum</u> , <u>P. scutifolium</u> , and <u>P. batubensis</u>	156
Fig. 85B. Geographic distribution of <u>Piper bartlingianum</u>	156
Fig. 86A. Geographic distribution of <u>Piper alatabaccum</u> , <u>P. hoffmannseggianum</u> var. <u>hoffmannseggianum</u> , <u>P. hoffmannseggianum</u> var. <u>latifolium</u> , and <u>P. piscatorum</u>	158
Fig. 86B. Geographic distribution of <u>Piper darienense</u>	158
Fig. 87A. Geographic distribution of <u>Piper brevinodis</u> , <u>P. guimaraesianum</u> , <u>P. klotszchianum</u> , <u>P. ottonoides</u> and, <u>P. villosobracteatum</u>	160
Fig. 87B. Geographic distribution of <u>Piper eucalyptophyllum</u> , <u>P. hayneanum</u> , and <u>P. rizzinii</u>	160
Fig. 88A. Geographic distribution of <u>Piper ovatum</u> var. <u>ovatum</u> , <u>P. ovatum</u> var. <u>boucheanum</u> , and <u>P. piliovarium</u>	162
Fig. 88B. Geographic distribution of <u>Piper miquelianum</u> var. <u>miquelianum</u> and <u>P. miquelianum</u> var. <u>hirtellum</u>	162
Fig. 88C. Geographic distribution of <u>Piper corcovadensis</u> var. <u>corcovadensis</u> and <u>P. corcovadensis</u> var. <u>blanchetii</u>	162
Fig. 88D. Geographic distribution of <u>Piper anisum</u>	162
Fig. 89. Illustration of <u>Piper ubatubensis</u>	190
Fig. 90. Illustration of <u>Piper bartlingianum</u> (=Ottonia	

<u>warakabocoura</u>).....	195
Fig. 91. Illustrations of <u>Piper corcovadensis</u> var. <u>corcovadensis</u> (=Ottonia <u>corcovadensis</u>) and <u>Piper</u> <u>hoffmannseggianum</u> var. <u>latifolium</u> (=Ottonia <u>pohlana</u>)	223
Fig. 92. Illustration of <u>Piper brevinodis</u>	253
Fig. 93. Illustration of <u>Piper hayneanum</u> (=Ottonia <u>macrostachya</u> and <u>O. macrophylla</u>).....	259
Fig. 94. Habitat of <u>Piper ovatum</u> var. <u>boucheanum</u>	332
Fig. 95. <u>Piper ovatum</u> var. <u>boucheanum</u> , close up of inflorescence.....	332
Fig. 96. <u>Piper miquelianum</u> var. <u>hirtellum</u> , close up of flowering branches.....	332
Fig. 97. <u>Piper corcovadensis</u> var. <u>blanchetii</u> , habit.....	332
Fig. 98. Cladogram for the Piperales.....	370
Fig. 99. Cladogram for <u>Piper</u>	378

INTRODUCTION

The aim of the present work is to provide a systematic treatment for a natural group of 21 species in the genus Piper (Piperaceae), traditionally segregated from it under the generic name Ottonia, but here treated as a subgenus.

While the systematic treatment of Ottonia was the prime objective of this work, the elucidation of relationships within Ottonia by a cladistic analysis implied finding the sister group. Since previous hypotheses on the relationships of Ottonia to Piper were found to be wrong, the construction of a rough cladogram for the entire genus Piper (using as outgroups, Peperomia and Saururaceae) was then performed.

According to the present treatment, and following the hypothesis in the cladogram for Piper, all natural groups so far resolved (including all previously described genera, but excluding Peperomia) are for the time being considered as subgenera of Piper.

The cladistic analyses here presented both for Piper and subgenus Ottonia are hypothetical, and as such should be tested. It is expected that the search for new characters (e.g. seed coat, tree architecture, etc.) as well as a better knowledge of the distribution of those previously known in Piper will allow better resolution of yet unresolved clades in the genus.

TAXONOMIC HISTORY

Some species of Piper, including those belonging to subgen. Ottonia, are known locally in Brazil as "jaborandi," a name often applied to taxa used for the treatment of toothache. Not surprisingly, early references to Ottonia include doubtful taxa of Piper known as "jaborandi." In 1648, Piso and Marcgrave described and illustrated several species of Piper which were of particular economic importance, among them, Jaborandi frutiscescens (the combination first used by Guillemin in 1836). The roots and leaves of this plant were used by the natives of Brazil. Whether or not it belonged to those species included in Ottonia is difficult to ascertain. Several authors including Vellozo (1822) and Guillemin (1836) used this name as a pre-Linnean synonym of Serronia jaborandi (= Piper anisum), or as specific epithet for Piper jaborandi (= Piper anisum). The first validly described Ottonia was Piper ovatum, a pedicellate-flowered taxon from Trinidad, described in 1796 by Vahl in his Eclogae Plantarum. Ignoring or not knowing of Vahl's publication, Sprengel (1820) described Ottonia anisum from Brazil as the type of a new genus with pedicellate flowers. Sprengel's generic description is very superficial and difficult to interpret as applying to a member of the Piperaceae. However the species description and a later illustration (A. de Candolle & Sprengel, 1820) leave no doubt

that the species belongs to the Piperaceae. Three decades after Sprengel's publication the Flora Fluminensis of Vellozo was published. In that work Vellozo described and illustrated the pedicellate-flowered P. jaborandi, a name he hoped would elucidate once and for all the true identity of the "jaborandi."

It was a species with pedicellate flowers and pinnately nerved leaves, not with palmately nerved leaves and sessile flowers as P. reticulatum (known under the same common name). Vellozo's description and illustration leave no doubt that the species had pedicellate flowers; however, both were superficial and the identity of the taxon, unless Vellozo's herbarium is found, will remain uncertain. In 1836 Guillemain and Gaudichaud described and illustrated a new genus Serronia, with S. jaborandi the type species. They probably ignored Sprengel's description or were unaware of the species' flower illustration, although they must have known the superficial and doubtful identity of J. frutiscescens and P. jaborandi. Serronia jaborandi was superbly described and illustrated compared to the descriptions and illustrations of J. frutiscescens and P. jaborandi, and it is not surprising that Endlicher (1836) accepted Serronia and placed Ottonia as a doubtful genus of the Piperaceae in his Genera Plantarum.

In 1839, both Miquel and Kunth, in separate works, published the first generic treatments for the Piperaceae.

Miquel included only generic descriptions and followed Endlicher's view accepting Serronia over Ottonia for the pedicellate-flowered species of neotropical pipers. He also included Ottonia in the tribe Zippeliae together with Zippelia, a monotypic genus from SE Asia with pedicellate flowers and echinate fruits. Kunth, on the other hand, described not only genera but many species. As contrasted with Miquel's position, Kunth realized that Ottonia and Serronia represented the same plant and since the former had priority it was the earliest valid name.

In his treatment Kunth (1839) included P. ovatum under O. vahllei, placed O. anisum in synonymy with his O. jaborandy (based on S. jaborandy), and described six new species. Furthermore, he included as species anomala, O. laeta (sessile flowers), O. leptostachya (short-pedicellate to subsessile flowers), and O. klotzchiana (sessile flowers). These were somewhat distinct from the typical Ottonia because of their sessile or nearly sessile flowers but were otherwise in agreement with the other generic characters (viz. pinnately nerved leaves, saccate-galeate floral bracts, 4 stamens, 4 carpels, sulcate drupes). In the same publication Kunth described Enckea, similar to Ottonia but distinguished by palmately nerved leaves and sessile flowers. According to Kunth the two genera were more closely related to each other than to any other groups.

In 1840 Moricand described S. acuminata, a species he soon realized was invalid and therefore transferred to Ottonia as O. blanchetii, both names appearing in the same publication. In 1844 Miquel, in Systema Piperacearum, included Ottonia with 12 species and placed Serronia in synonymy. His treatment did not differ substantially from that of Kunth's (1839). However two species, O. lessertiana and O. carpunya, included by Kunth (1839) because of their 4-staminate flowers and 3-5 stigmas, were doubtfully maintained by Miquel because they did not fit into any other genus in the Piperaceae.

From 1844 to 1847 Miquel described several new species in Ottonia, both with sessile and pedicellate flowers. It seems, however, that Miquel relied too heavily on mature fruits as diagnostic characters for Ottonia. As a result he often described the same species in different genera. In 1849 Presl, in his Epimeliae Botanicae, described two new species of Ottonia and transferred P. stipulaceum to Ottonia. Piper stipulaceum was a species from Mexico characterized by palmately nerved leaves and pedicellate flowers and was previously placed in Enckea by Kunth. Presl's transfer probably reflected Kunth's view on the close relationships between Ottonia and Enckea. In the same publication, Presl described Carpunya to accomodate those species placed by Miquel (1844) as doubtful under Ottonia (i.e. O. lessertiana and O. carpunya).

In the treatment of the Piperaceae for Martius' Flora Brasiliensis, Miquel (1852) included 19 species in Ottonia and divided it into two sections. Section Ottonia included species with pedicellate flowers, while sect. Carpunya included taxa with sessile flowers (several of which were previously placed by Kunth under his species anomalae).

The treatment of the Piperaceae for Flora Brasiliensis ended Miquel's involvement with neotropical Piperaceae and opened the road for a new specialist, C. de Candolle. De Candolle was more conservative than Miquel and lumped all the Piperaceae under two genera Piper and Peperomia. In his first major work on the family de Candolle (1869), in the Prodromus, divided Piper into nine sections and included Ottonia as a subsection of sect. Steffensia.

Subsection Ottonia contained 58 taxa divided into three groups: leaves pinnately nerved and with pedicellate flowers, leaves palmately nerved and with pedicellate flowers (including Zippelia), and species having pinnately nerved leaves with sessile flowers. From 1869 to 1920 de Candolle described large numbers of species in Piperaceae including many ottonias. By 1923 in his posthumous work, Clavis Piperacearum, de Candolle divided Piper into 11 subgenera, one of which, subgen. Ottonia, included 31 species and comprised only those taxa in Piper with pedicellate flowers (groups one and two of the Prodromus).

De Candolle's view of the Piperaceae and subgen. Ottonia in particular remained unchanged until 1930 when William Trelease, in a revision of the geography of Piperaceae, returned Ottonia to generic rank and segregated those species with palmated nerved leaves under the new genus Arctottonia. In a revision of Ottonia Trelease (1935) included 70 taxa, many of which were newly described. Trelease also segregated from Ottonia those species with sessile flowers and placed them under Piper.

Trelease's concept of Ottonia as a distinct genus remains unchallenged to date. Since 1935, several new species with pedicellate flowers have been described. In 1952 Rizzini described O. angustifolia. In 1956 Yuncker described a plinerved species with pedicellate flowers from Chocó (Colombia) as O. corei, which he erroneously interpreted as being intermediate between Ottonia and Arctottonia. In 1972 in his posthumous work, The Piperaceae of Brazil, Yuncker reduced the number of species in Ottonia to 31 and described one species, P. piliovarium, with both sessile and pedicellate flowers. Yuncker was the last specialist in the Piperaceae and since then only sporadic descriptions of new species of Ottonia have appeared. A recent study of the genus (Guimarães, 1984), while lumping several species, still followed Trelease's view.

MORPHOLOGY

Habit and Architecture

Members of subgen. Ottonia are small to medium-sized shrubs 0.4-5 m tall. Often species are described as dwarf plants, repent or lianescent shrubs. These variations in the habit are in apparent response to environmental conditions and strongly correlated with plant architecture. It seems advisable to discuss habit of the plant in the terms of its architecture, so variation seen in the field can be more easily understood.

Hallé et al. (1978) defined an architectural model as the growth program of a tree (here an inclusive term for herbs as well as trees) which determines its successive architectural phases. In contrast the architecture of a tree is the morphology at any given time (Hallé et al, 1978). Size or dimension of a plant, or its growth habit, do not define nor are they comparable to an architectural model; thus a vine, tree, or herb may all display the same model. Functional characters to define a model are axis orientation, axis differentiation, growth periodicity, flower or inflorescence position, and changes in branching as a result of flowering outcome. Based on such characters Hallé et al. (1978) defined 23 models, many of which cut across taxonomic groups and may serve for

descriptive purposes. Models are significant in that any alteration in growth form for a particular plant will tend to occur within the structural and developmental constraints of a given model. However, this is not always true and variations are probably due to plasticity in architectural parameters as well as response to different environmental conditions. Furthermore, a single plant may go through several architectural phases during the course of its ontogeny, and it may become difficult to recognize a specific model for a species. Thus to some extent the ecological and evolutionary significance of a model remains to be seen. Fortunately work has already been started in that direction (Ashton, 1978; Fisher & Hibbs, 1982; Remphrey, 1983).

Architectural models in the Piperaceae have been described for few species (see Hallé et al., 1978), but more recently and in greater detail for a large number of taxa in both Piper and Peperomia (Blanc & Andraos, 1981, 1983). Ottonioid species have not yet been described architecturally, but observations presented here are similar to those of Blanc and Andraos (1981) for Piper unguiculatum.

In subgen. Ottonia the main stem (originating from the seedling axis) is orthotropic, it never reaches more than a few centimeters in height, and it rarely branches distally. Germination is epicotylar and the seedling axis is correlated with the lack of leaf transition (scales). Once the seedling

axis has produced leaves (all long-petiolate), buds in the axils start development giving rise to a series of orthotropic shoots, each more vigorous and taller than the previous (Fig. 1). There are generally 2-4 shoots, but in some species one may find up to 17, especially in those species which often grow in light gaps (Piper bartlingianum). The first shoots are no more than the branches of first order and in contrast with higher orders, orthotropic instead of plagiotropic.

In contrast with the seedling axis, orthotropic shoots display at first a series of long internodes previous to the first branching node (Fig. 1). Those series of internodes are associated with small scale leaves which have well developed sheathing bases but which are otherwise indistinguishable from the prophylls. Also these scale leaves, unlike the prophylls, are not associated with axillary branches.

The first branching node is marked by the appearance of a foliage leaf displaying a well developed sheathing base which is symmetric and basally acute. The lamina of the leaf is typically elliptic-lanceolate (Fig. 2). Correlated with the number of orthotropic shoots, a well formed root system is developed. Furthermore, in old individual plants, secondary growth becomes prominent at the base, particularly in the seedling axis, which becomes irregularly shaped. Branches from the aforementioned first branching node will follow immediately with both the main stem and the axillary branch

displaying similar vigorous growth, and simulating a dichotomy. Branching thereafter is diffuse with inflorescences appearing on second or third order branches.

Compared with orthotropic shoots, flowering branches are all sympodia and modularly constructed. Each module consists of three units: a basal prophyll, a foliage leaf, and a terminal inflorescence (see illustration of P. brevinodis, Fig. 92) (the number of modules being 4-7). Flowering branches are plagiotropic (in two species orthotropic), and distichous. A well marked distinction between an erect monopodial shoot and modular sympodial branches defines Petit's architectural model. The series of orthotropic shoots emerging from a basal corn, each shoot more vigorous than the preceding, are elements of Tomlinson's architectural model which is rather common in the monocots and which is related to the elaboration of a basal anchoring system, which provides support for plants where secondary growth is either absent (monocots) or reduced.

Reiteration in Petit's model is prominent in the aerial branches and to some extent (subgen. Ottonia) in the basal portions of the plant. Generally the prophyll on each module subtends another bud, itself protected by a single prophyll. This bud will develop if the branch breaks and repeats the model of the parental stem. The same applies for the buds in vegetative nodes, especially at the first branching node when often 4-5 stems seem to arise from a single node. As was pre-

viously mentioned variation in habit is strongly correlated and restricted by the architectural model; furthermore, leaf shape, leaf size, and the extent of basal branching are all directly linked to the aforementioned model.

In subgen. Ottonia normal individuals consist of 2-3 orthotropic shoots, and are generally restricted to shady places in the forest understory. More numerous shoots are present when species grow in light gaps or along sandy riverbanks (e.g. P. miquelianum var. hirtellum, and P. bartlingianum). In this case the taller shoots reach to 5 m and bend by their own weight (most probably because of reduced secondary growth), thus resembling a lianescent habit. The large number of shoots in open conditions is probably the result of additional sunlight, a factor often claimed to promote reiteration (Hallé et al., 1978). While most species have monopodic orthotropic shoots with long basal internodes, P. francovilleanum has shoots which branch 1-2 cm above the seedling axis, and there are no scales or long internodes before the first branching node. Furthermore, all the flowering branches are orthotropic not plagiotropic, each individual consisting of one flowering branch which produces one inflorescence per season. Piper francovilleanum is apparently endemic to the forests occurring at the base of the Guiana Shield in NW Amazonia of Venezuela and Brazil, a sector with considerable variation in soil composition and high numbers of endemics (Huber et al.,

1984; Steyermark, pers. comm.). It is not known, however, to what extent soil composition may explain the oddities of P. francovilleanum. A similar condition to that found in the aforementioned species occurs in P. hoffmannseggianum var. hoffmannseggianum, apparently endemic to the forest edge of restinga in coastal Bahia (Brazil). That variety grows on sandy soils and often in open sandy dunes. It also has orthotropic flowering shoots, consisting of numerous inflorescences as is normal in all other species of subgen. Ottonia. Compared with the taxa mentioned before, the other extreme is found in P. miquelianum var. miquelianum, populations of which may cover extensive areas of the forest understory. The individual plants are connected to each other by horizontal shoots (Fig. 3) which arise from the basal corn. These shoots root first at the nodes and then become erect some distance from the parent plant, eventually detaching and establishing new individuals. This phenomenon, which eventually results in large clones, is found in all ottonias, but large populations are apparently restricted to P. miquelianum var. miquelianum. The change in orientation of the orthotropic shoot may be correlated with the need to exploit a habitat with a patchy distribution of resources, but often is also the result of an orthotropic shoot bending by its weight because of lack of support, and then eventually rooting at the nodes. Leaf variation, as in branching and habit, is often linked to

- Fig.1-4. 1. Piper miquelianum var. miquelianum (Callejas et al. 1836). Mature individual showing multiple orthotropic shoots with long internodes at the base, and below the first branching nodes. X 0.40.
2. Piper corcovadensis var. blanchetii (Callejas et al. 1896), habit, observe that leaves at branching nodes are smaller than those at flowering nodes. X. 0.50.
3. Piper miquelianum var. miquelianum (Callejas et al. 1836), horizontally oriented orthotropic shoots with nodal roots. X 0.50.
4. Piper miquelianum var. miquelianum (Callejas et al. 2034), SEM photomicrograph of papillate-like hairs (adaxial surface of the leaf), X 3000.
- Scale= 102 ~~µm~~



the architecture of the plant and more specifically to the nature of a node. Such variation is discussed below under Leaf.

Seedlings

The following description is based on collections of five species (see below). Seedlings were found to occur with the parent plants. They were restricted to the wet forest floor or along streams with relatively broad banks (e.g. in P. anisum). Several features of the seedling axis, especially the absence of leaf dimorphism, confirm for subgen. Ottonia previous descriptions for species of Fiper (Duke, 1965).

The first leaf above the cotyledonary node is a long-petiolate entire eophyll (Tomlinson's terminology, 1960), that is wide ovate and basally truncate. No transition of leaf size or shape is observed between the eophyll and the next adult foliage leaf. All metaphylls along the seedling axis are long-petiolate with a conspicuous stipule-like margin along the entire length of the petiole, a character otherwise associated with branching nodes in aerial stems (see Habit and Architecture). The seedling axis never reaches more than a few centimeters (15-20) in height and rarely branches distally. Foliage leaves of seedlings have thin translucent laminae. In P. corcovadensis, P. miquelianum, and P. anisum the lamina is variegated, with a distinct white-silver stripe along the

adaxial surface of the midvein. Seedlings in P. piscatorum and P. hoffmannseggianum are glabrous but in the three species aforementioned they are densely villous. The latter are glabrous as adult plants or display a different vesture. Those species with long-villous seedlings are closely related to several species which display variegated and long-villous leaves in adult stages (e.g. P. villosobracteatum). While germination was not observed in the field, the aforementioned seedling description suggests that germination in subgen. Ottonia is phanerocotylar (Duke, 1965), agreeing with the rest of the genus Piper (Johnson, 1902; Duke, 1965, 1969).

Leaf

Historically authors have argued that in Piperaceae floral characters are too difficult to detect, are too variable, or simply that discontinuities in the flower are absent (Trelease, 1936; Trelease & Yuncker, 1950; Yuncker, 1972). It does not come as a surprise then that the taxonomy of Piper has been based almost entirely on leaf morphology. One cannot dismiss the importance of leaf characters in the Piperaceae, but unfortunately some botanists have misinterpreted it. In Trelease's (1935) revision of Ottonia, he described 45 new species, most based entirely on leaf size. Variation in leaf size and shape is correlated to a certain

extent with the nature of a particular node, and extremes are normally present along a single branch.

Leaves in subgen. Ottonia are simple, alternate, and exstipulate. They are pinnately nerved with the intervenular spaces equally spaced (e.g. P. eucalyptophyllum, P. rizzinii), or more often unequally spaced. Leaves range from wide ovate to elliptic, rarely lanceolate. They are basally acute and generally symmetric, often acute decurrent with the petiole (P. alatabaccum), or oblique and asymmetric and then lobulate, or the leaves are obtuse, cordate and symmetric (P. brevinodis). The lobes in one species (P. francovilleanum) house ant colonies. Leaves may be short- or long-peltate. Short-peltate leaves are common at branching nodes, rarely at flowering nodes and may be restricted to a single leaf on an entire individual (P. bartlingianum), a single branch order (P. bouchenaum), or at random (P. klotzschianum). Long-peltate leaves are found in P. scutifolium and P. guimaraesianum and, in these cases all leaves are long-peltate. In the living condition leaves are thin-membranous and translucent (P. brevinodis, P. anisum, P. villosobracteatum) or more often chartaceous. Normally leaves are plain, or rarely bullate and pouched beneath as in P. brevinodis. They are glossy green above and light green beneath, sometimes variegated adaxially (P. villosobracteatum and P. francovilleanum, but not all leaves or all specimens). Normally leaves are light green or

brownish when dry. In a few taxa (P. bartlingianum, P. alata-baccum) the midvein and secondary veins dry white and the intervenular regions green, giving a characteristic edged appearance to the leaf, but only if specimens were previously fixed in FAA. In P. corcovadensis var. corcovadensis leaves dry blackish, less often brownish. Young leaves are covered by short 1-2-celled papillate hairs (see Vesture), while adult leaves are glabrous throughout or sparsely pubescent along veins. Less often leaves are long-villous, and rarely both long-villous and short-hirtellous (P. francovilleum). In P. guimaraesianum the long-villous leaf hairs extend adaxially to the midvein, unlike other species in subgen. Ottonia. Oil containing idioblasts (oil cells) are present in all leaves but are evident only in the dry condition in few species as revealed by their orange, reddish, or black coloration. In P. hayneum and P. eucalyptophyllum leaves display reddish oil cells if they are fixed in FAA. Some populations from NE Bahia (Callejas et al. 1925) do not show any sign of oil cells regardless of the fixing method. Glandular dotted leaves are often found in single individuals in species otherwise not displaying oil cells (P. hoffmannseggianum var. latifolium, Robert s.n. (K); P. anisum, Pickel 2789 (R)).

Although leaf characters help to distinguish many species, they are of only limited use in P. corcovadensis, P. miquelianum, and P. anisum, which species account for nearly

half of the names in subgen. Ottonia. Most of those names refer to taxa in which leaf size or shape, and presence or absence of oil cells were the diagnostic features. Interpretation of leaf variation in those species is better understood by analyses of the particular nodes. At the vegetative branching nodes leaves are elliptic-lanceolate, symmetrical, acute based, and smaller than those at flowering nodes where leaves are of different shape, larger, asymmetric, and acute or more often obtuse based. In the three species mentioned above, individuals are profusely branched and reiteration is common in many aerial branches.

All Mexia collections of P. anisum from Minas Gerais, show specimens with branches where reiteration has occurred in all vegetative nodes. Thus most leaves are elliptic-lanceolate, while a few are basally obtuse as is the case for flowering nodes. Both Trelease (1935) and Yuncker (1973) misinterpreted this variability which led to much of the taxonomic confusion surrounding those three taxa (for other examples see discussion under P. miquelianum var. hirtellum).

Prophylls

Turpin (1819) first used the term prophyll to indicate the first reduced leaf occurring at the base of both vegetative and flowering branches. There is typically one prophyll

in monocots and two in dicots. In monocots the prophyll usually has a constant position being adaxial, and bekeeled. These characters were often used to interpret the monocot prophyll as the equivalent of two prophylls (as in dicots) which had fused adaxially to form a single organ (Goebel, 1932). Thus based on putative homologies authors relied on the prophyll as evidence to derive monocots from dicots. Balser (1944), after an extensive survey on the subject, noticed inconsistency in the use of the term prophyll as well as variation in number and interpretation to which the term had been subjected. He concluded that "in a narrow sense, as originally used, the prophyll describes a structure preceding the leaves since there is no purpose other than to indicate the basal leaf or leaves on a branch."

Compared with most dicots, Piperaceae have a single prophyll instead of two. In Piper, prophylls are often called stipules (Kunth, 1839; Miquel, 1843; Smith, 1975). Miquel (1844) believed their position to be of systematic value at the generic level (but then he compared stipular margins of sheathing leaf bases with prophylls). Burger (1972) discussed prophyll morphology and indicated that variation in size, as well as presence or absence along branches, could be a useful diagnostic character. That author observed that in many species the prophyll at flowering nodes was hidden by a well developed sheathing leaf base. Furthermore in those taxa

the leaf base probably acted as a protective structure for the emerging shoot and thus replaced the function of the prophyll. Species with hidden prophylls were then described by Burger as having the flowering shoots emerging from within the leaf base and free from the prophyll. Burger added that in many species of Piper prophylls were present at flowering nodes, but absent at vegetative nodes. The use of the prophyll as proposed by Burger has been criticized as difficult to use (Howard, 1973; Steyermark, 1984), especially since in many species the prophylls are early caducous, and thus position of the emerging flowering shoot in relation to the prophyll is difficult to ascertain.

As far as I can see the description of a shoot emerging from within a leaf base and free from the prophyll is somewhat misleading. Since all prophylls are associated with an axillary branch, an emerging shoot whether flowering or vegetative will always be enclosed by the prophyll and therefore emerge from within it. The observation of a prophyll at a flowering node and its absence in a vegetative one, relates to the lack of reiteration in the vegetative node which when damaged produces a new bud enclosed in a prophyll. This new bud repeats the pattern of the parental plant and the prophyll generally leaves a prominent scar. My own survey of the prophyll structure in Piperaceae confirmed some discontinuities found by Burger (not including those discussed above), and additionally indicated that prophyll size (as large as or

smaller than the flowering node), texture, presence or absence after inflorescence development, shape, apex, and vestiture were useful taxonomic characters.

In subgen. Ottonia prophylls are hidden by sheathing leaf bases only at vegetative nodes. They are 2-7 mm long, chartaceous, and densely short-papillate. In most species prophylls are early caducous at flowering nodes, although in P. francovilleanum and P. villosobracteatum they are persistent at all nodes. In the former species prophylls are apically long-attenuate, unlike other species, in which are apically acuminate. In P. anisum and P. brevinodis prophylls are thin-membranous and translucent, while they are chartaceous in other taxa. In P. brevinodis there are up to seven reduced internodes between each flowering node, consisting of a single prophyll which leaves a prominent scar after falling (Fig. 92).

While prophyll variation within subgen. Ottonia was of limited use, it nevertheless proved significant for distinguishing its members from others which displayed vegetative features of subgen. Ottonia (e.g. pinnately nerved leaves, architecture of the plant, etc.) and were difficult to separate when sterile. Indeed, P. anonifolium, P. piresii, and their relatives (subgen. Isophyllon) are very similar to P. hoffmannseggianum and P. rizzinii (subgen. Ottonia), but are separated by the papyraceous, apically truncate, and glabrous prophylls of the former compared to the chartaceous, apically

acuminate, and densely papillate prophylls of subgen. Ottonia.

Vesture

Vesture in subgen. Ottonia consists of hairs and oil-containing idioblasts (oil cells or glands, as used currently in Piperaceae). Loss of hairs in adult organs and/or changes in coloration of oil cell content restrict somewhat the emphasis placed on vesture as a taxonomic character. The varied morphology of trichomes has often been interpreted differently by specialists and terminology for the most part has been inconsistent. I follow the criteria suggested by Theobald et al. (1979) for trichome description.

In subgen. Ottonia hairs are simple and uniseriate. Based on length one may recognize three types:

1) Papillae-like hairs which are thin, translucent clavelliform, 2-celled, and 50 μ m long (Fig. 4). Unless high magnification is used (70x) their trichome nature is very difficult to establish. At lower magnifications (10-20x) they look more like papillae, especially when they consist of a single cell. This type of trichome has been variously described for several species of Peperomia (Deferrari, 1977) and Piper (Mohandas et al., 1982) where it generally occurs covering the surface of young organs (leaves, prophylls, floral bracts). In subgen. Ottonia these hairs are especially prominent on the ovary walls at all stages, unlike other spe-

cies in selected outgroups (see CLADISTICS).

2) Villous hairs are thin, white to yellowish, translucent, spreading, 20-30-celled, and 1.5-3 mm long. They are found in the adult stages of P. francovilleanum, P. brevinnodis, P. guimaraesianum, and P. villosobracteatum, but more often in seedlings of several species (see Seedlings) which in adult stages are glabrous or display a different type of hair.

3) The third type of hair, and the most common in subgen. Ottonia, is variable in most features, thus a definite term is rather difficult. They are straight or curved, thin or thickened, 4-9-celled, 0.5-1.2 mm long, and generally white but turning brown, yellowish, or reddish when dry. In most cases an entire set of hairs displaying different features is present on the same plant specimen, and the terms hirtellous or strigose are ambiguous. Where they occur I describe the plant parts as densely pubescent if the hairs obscure the organ or organ parts, otherwise as sparsely pubescent. This type of hair is present in leaves along the veins beneath, stems, petioles, peduncles, and the proximal or/and distal portion of floral bracts. In P. francovilleanum this type of hair occurs with villous trichomes, and the species is described as having dimorphic pubescence.

Oil cells in subgen. Ottonia are present in all species in almost every organ. Color of the cell content as well as changes associated with drying techniques were previously explained (under Leaf) and apply as well to other organs. In

several taxa, herbarium specimens display oil cells by a raised surface where they occur (floral bracts, stamens, fruits, leaves) generally prominent and colored (reddish, orange). In that case I describe the particular organ as glandular dotted.

Inflorescences

Inflorescences in subgen. Ottonia are solitary spikes or racemes, terminal to a subtending leaf as revealed in the sympodial construction of flowering branches (see illustration of Piper ubatubensis, Fig. 89). A minimum of three to a maximum of seven inflorescences occur in a single branch. Maturation of inflorescences is acropetal along the branch and will begin only after several inflorescence buds are already formed. Generally a single flowering branch will provide inflorescences for two seasons. In the particular case of P. francovilleanum, the orthotropic sympodial flowering branch may display up to 13 flowering nodes, and inflorescence development and maturation will occur sequentially. Thus a sympodial branch in that species will usually display a single inflorescence at the uppermost flowering node. Inflorescences are erect and white to cream-colored in flower, remaining erect in fruit, or the flowering portion is curved in flower and fruit as in P. scutifolium and P. ubatubensis (Fig. 89).

They are pendulous at all stages in P. francovilleanum.

Infructescences are green or blackish-colored in all species.

The distinction between racemes and spikes (an important taxonomic character at the specific level) becomes apparent only after fertilization has occurred, in which case the pedicels if present will start elongating during fruit maturation. In those species with short-pedicellate flowers (e.g. P. ovatum and P. piliovarium), the pedicel does not elongate with fruit maturation and the fruits generally obscure the pedicel to the extent of appearing sessile. Thus inflorescences may appear spike-like rather than racemose (see P. piliovarium previously described as a sessile-flowered species by Yuncker, 1973).

A single inflorescence may have from 60 flowers as in P. ottonoides to nearly 600 as in P. bartlingianum. Maturation along the inflorescences is acropetal (Fig. 2), but fruits mature at random (Fig. 5). At anthesis inflorescences are 2.5-4 cm long becoming 6-10 cm long in fruit. Occasionally in P. miquelianum var. hirtellum inflorescences are 14-18 cm long, whereas in P. miquelianum var. miquelianum they barely elongate in fruit and rarely exceed 3 cm (Fig. 6).

Development of inflorescences in the seedlings of P. hoffmannseggianum var. hoffmannseggianum, normally a rare event in subgen. Ottonia, seems rather common although fruits rarely mature. In those seedlings the inflorescences generally become

fasciated, the rachis is apparent at all times in racemose inflorescences, and varies from sparsely pubescent to glabrous. In those species with spicate inflorescences, the rachis is obscured at anthesis and becomes apparent only in fruit. At that time it may be seen that the rachis is sparsely pubescent to glabrous if the flowers are widely spaced (Fig. 7) or densely short-fimbriate if tightly congested. At anthesis rachis pubescence is white for all species, but it becomes reddish in P. anisum and brownish in P. bartlingianum when dry. The flowering portion of the inflorescence is longer than the peduncle in all taxa. The peduncle is rugose, densely papillate, and sparsely pubescent in early stages, generally becoming glabrous at maturity. Inflorescence dimensions are not strongly altered in the dry condition at which all measurements were made.

Floral Bracts

In what seems to be the first classification of Piperaceae, Kunth (1839) indicated that floral bracts were of diagnostic value at both generic and species levels. In subgen. Ottonia the wide variation displayed by the bract confirms Kunth's view. In fact, based on such variation, 13 of the 21 species in the subgenus can be easily keyed on overall morphology of floral bracts. Bracts unfortunately have rarely

been used as taxonomic characters in Piperaceae (but see de Candolle, 1869, 1923). They are often included in the species description but only occasionally do the authors discuss floral bract variation or its diagnostic value (Burger, 1972; Steyermark, 1984). As with most floral structures in the family, bracts are very small and their morphology tends to be easily distorted after drying. Unless one dissects and boils each flower or inflorescence, variation for the most part will go unnoticed. Floral bracts display a different shape at anthesis compared with fruiting stages, a factor that may have contributed to inconsistencies in terminology. Thus in subgen. Ottonia bracts have been described as saccate-galeate (Kunth, 1839), cucullate (de Candolle, 1869), conchaeformis or angular subpeltate (Yuncker, 1950, 1973), cupulate (Trelease & Yuncker, 1950), etc.

To establish a definitive terminology for floral bracts in Piperaceae is beyond the present treatment. Nevertheless given the importance of floral bracts in the taxonomy of subgen. Ottonia (see CLADISTICS), a detailed description of the bract is given here. This description may apply in many cases to other species in Piper.

Bracts in the fresh condition are white or ochroleucous becoming orange in the distal portion and white proximally when dry. Bract measurements include the width of the lamina (the distal portion), and the height of the bract. The latter is

here defined for those species with a distinct pedicel as being from the tip of the proximal portion of the lamina to the base of the pedicel (Fig. 8). All measurements were made on material previously boiled in water.

Two portions are easily distinguished in the bract: an upper extended portion called the lamina, and a basal subtending narrow portion called the pedicel. In Piper major discontinuities in the floral bract occur in the laminar portion and to a lesser degree in the pedicel which itself may be present or absent (Fig. 9).

Bract shape is strongly correlated with floral development. The peltiform floral bract is initiated much earlier than the flower it subtends. Dorsiventral symmetry is established from the beginning before the bract's definite form is attained. The bract is epipeltate, not hypopeltate as currently described (de Candolle, 1866) (for detailed explanation see Endress, 1975). Secondary edges or margins are formed in those portions of the bract which are in contact with the flower, with these zones of protection originating from vacuolated not meristematic cells (Schmitz, 1872; Endress, 1975).

In subgen. Ottonia the bract at anthesis is inflexed (Figs. 10, 11), protecting and covering the flower, and is better described as cupulate. As the stigma becomes receptive, the inflorescence begins to elongate and the bract becomes

reflexed exposing the flower. At this point bracts display the typical shape of the fruiting stages. The lamina consists of a distal portion (at anthesis covering and in direct contact with the flower) and a proximal portion (which gives the cupulate appearance of the bract at anthesis). These two portions are discontinuous, the distal portion being expanded and thin translucent while the proximal portion is callosed and galeate. Therefore, I use the term saccate-galeate to describe the floral bract, other terms being ambiguous.

In subgen. Ottonia bracts may be pedicellate or sessile. In P. ottonoides and P. darienense they are sessile at all stages. In P. ottonoides the bract is sessile and the distal portion is decurrent with the rachis (Fig. 9), unlike any other species in subgen. Ottonia. In P. villosobracteatum the distal portion has a tuft of long-villous hairs. In Piper anisum, P. scutifolium, P. piliovarium, and P. ubatubensis the distal portion is densely short-pilose at anthesis, becoming glabrescent in fruit. Floral bracts are densely glandular dotted (see Vesture) on both the lamina and the pedicel in P. hayneanum, P. eucalyptophyllum, and P. rizzinii. In P. ovatum only the pedicel is glandular dotted. In P. hoffmannseggianum the floral bracts are sessile at anthesis but become pedicellate during fruit development. When present, the pedicel may be densely pubescent, or sparsely pubescent to glabrous.

In Piper bartlingianum, the bracts are sessile in all sta-

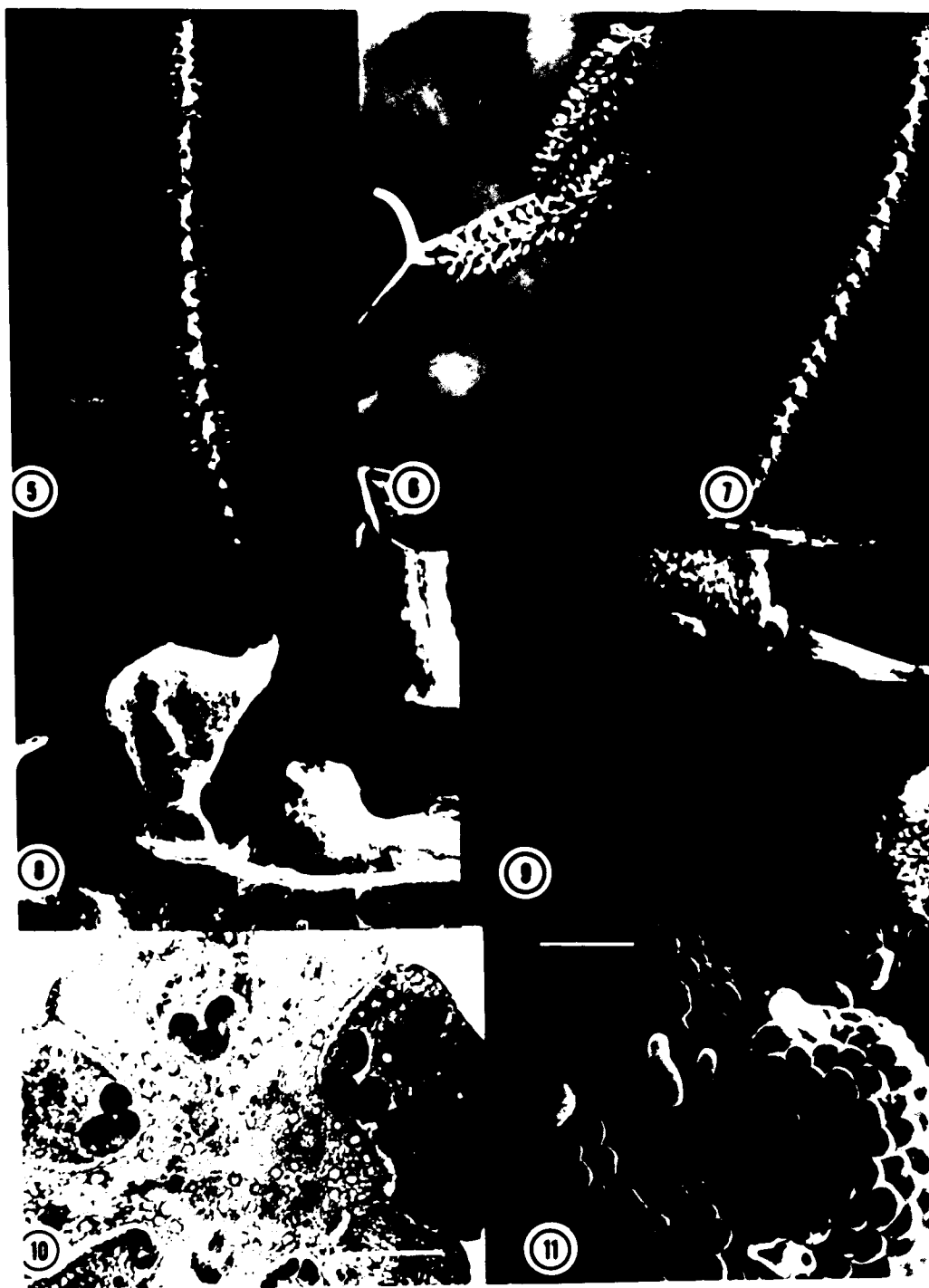
ges, becoming inflexed toward the rachis (as when covering the flower). Therefore, their distinctive morphology is only apparent at anthesis. In this species the bracts are less than 0.2 mm wide and less than 0.1 mm in height, the smallest in subgen. Ottonia.

Aside from its protective nature in early flower development, the bract may also serve as a pollination attractant reflected in the banding pattern displayed in many inflorescences in Piper. The pattern is often reinforced by the distinct ornamentation of the lamina, which may consist of hairs (distributed along the margins or upper surface of the lamina), glands, papillae, etc. Banded patterns are not present in any species in subgen. Ottonia; however, in their absence, one may assume that ornamentation of the bract at anthesis serves an attractant role for pollination. Their role is unknown in those species in which bracts lack any type of ornamentation as in P. klotzschianum, P. darienense and P. ottonoides.

Flowers

Flowers are naked, bisexual, subtended by a floral bract, and arranged in helical fashion in spicate or racemose inflorescences in which individuals are borne on short-terete pedicels. In subgen. Ottonia flowers are 4-merous, a number

- Fig. 5-11. 5. Close up of infructescence of Piper corcovadensis var. blanchetii (Callejas et al. 1846). X 10.
6. Close up of infructescence of Piper miquelianum var. miquelianum (Callejas et al. 1608). X 6.
7. Close up of infructescence of Piper hayneanum (Callejas et al. 1608). X 5.
8. SEM photomicrograph, floral bract (lateral view) of Piper darienense (Callejas 342). X 100.
9. SEM photomicrograph, floral bract (upper view) of Piper ottonoides (Prance et al. 1981). X 55.
10. Inflorescence, cross section, observe the inflexed floral bracts which cover the young floral buds, in Piper miquelianum var. miquelianum (Callejas et al. 1895). X 40.
Scale= 166 μ m.
11. SEM photomicrograph, floral bract (upper view).
Material examined as in Fig. 10. X 500. Scale= 350 μ m.



which is very consistent within a single inflorescence. The four stamens arise in two distinct planes unlike any other member in Piper. Stamens in the frontal plane are larger and better developed than those in the sagital plane, which are poorly developed or in which the pollen grains are collapsed. Anthers are tetralocular, bivalvate, and dehisce latrorsely. The connective protrudes beyond the anthers and is glandular dotted apically. Filaments are articulate and after anthesis leave the basal portion attached to the fruit walls. The syncarpous gynoecium is composed of four carpels which are slightly separated at the stigmatic portion. Four prominent stigmatic lobes are decurrent with the ovary wall and in immature stages are straight giving the impression of a true style. A true style is present in only one species, P. ubatubensis. At all stages, but most noticeable when immature, the ovary walls are densely papillate, but in P. anisum and P. piliovarium they are short-pubescent. Flowers are sessile or pedicellate, or pedicellate and sessile within the same inflorescence as in P. piliovarium. Pedicel length is quite variable before fruit maturation and attaining its final length once the first pair of anthers in the frontal plane dehisce.

Fruit

The single fleshy drupaceous fruit in subgen. Ottonia is

ovoid to ellipsoid or irregularly spherical, rounded in cross section (Fig. 12), 1-5 mm long and 0.7-3 mm in diam., glossy green when fresh, and turning white to cream, brownish or black when dry. At all stages it is densely short-papillate. Both the outer and more particularly the inner pericarp layers are rich in oil-containing idioblasts (Fig. 12). These are yellowish to translucent, often reddish or orange and then opaque in color, and appear raised in P. hayneanum and P. eucalyptohyllum. Based on field and herbarium data, fruit maturation takes at least four months. Fruit shape in many species is a very consistent character, but in those taxa with widely spaced flowers (sessile or pedicellate) it tends to be too variable to be of diagnostic value. Traditionally in subgen. Ottonia fruit shape has been used as a diagnostic character at the species level (Trelease, 1935; Yuncker, 1973; Guimarães, 1984). Recently Guimarães (1984) illustrated and partially described the fruits of all taxa with pedicellate flowers in subgen. Ottonia. She correctly interpreted the distinctive morphology of the fruits at mature and immature stages (many of which were previously misinterpreted by others), but still relied too heavily on shape of the fruit. Most of the variation in fruit shape is found in the apical portion where the stigmatic lobes may or may not be straight, therefore a fruit can be described as short-apiculate, umbonate, stylose, etc. The orientation of stigmatic lobes is

strongly modified by drying techniques and therefore is not a valid character for separation of species.

Compared with those species having pedicellate flowers, taxa with tightly congested flowers display less variability in fruit shape. Thus in P. bartlingianum fruits are distinctly obovoid and easily separated from those of P. alatabaccum, which are wide ovoid with four prominent pericarpic bulges. Fruits in P. alatabaccum are very similar to but larger than those found in P. francovilleanum. Fruits in the three aforementioned taxa are short-apiculate to truncate, and stigmatic lobes are not as prominent as those found in other species. In P. darienense immature fruits are distinctly umbonate becoming globose-ovoid when mature, very similar but larger than those in P. ottonoides.

When dry the single seed determines to a large extent fruit shape. Species in subgen. Ottonia are usually described as having 4-ribbed and sulcate fruits, a somewhat misleading description since in the fresh condition fruits are not ribbed or sulcate. In the present treatment both immature and mature stages of the fruit are described so confusion is avoided. In subgen. Ottonia correlation between fruit and pedicel length has previously been stressed as an important character for those species with pedicellate flowers (Kunth, 1839; Miquel, 1844; Trelease, 1935). For all species with pedicellate flowers, pedicel length is the same prior to fertilization

followed by pedicel elongation. In P. ovatum and P. piliovarium the pedicel does not elongate. The following descriptions include pedicel length only when the fruit is fully matured or after the anthers in the frontal plane have dehisced.

Fruit dispersal in the genus Piper has been discussed by Fleming (1977, 1981). In those species observed the major agent for dispersal was phyllostomatid bats, particularly those of the genus Carollia. To a lesser extent birds are also responsible for fruit dispersal (Snow & Snow, 1971). In P. amalago fruits may be dispersed as single units or the entire infructescence is dispersed. No observations on fruit dispersal were made on any species in subgen. Ottonia and the significance for seed dispersal in species with pedicellate flowers is not yet clear.

I have observed numerous insect larvae in the fruits of P. alatabaccum but without apparent damage to the seed or its development.

Seeds

In subgen. Ottonia seeds offer numerous characters not previously recognized in Piper (but see Quisumbing, 1930). In many instances these are proving to be of diagnostic value at the species level. The large number of fruits in a single

inflorescence, the almost invariant morphology of the seed in herbarium material, and their easy removal from the fruit (by boiling 5-10 minutes) makes the study of seed characters straightforward compared to other floral characters which are so easily distorted upon drying (e.g. fruits, bracts, number of stamens). Seed characters (including measurements) are provided in Table I.

Seed measurements for each species are based on 25 counts per inflorescence on five specimens chosen at random. Values in Table I refer to means. Seed length does not include the apex. Shape of the seeds is described according to the terminology of the Systematics Association Committee (Taxon, 1962). As in flower development, one may distinguish two planes in the seed, a sagittal and a frontal (following the terminology of Tucker, 1982b). However, the terms are not used since once the seed has been removed from the fruit, the planes are easily confused or without much practical value as in those seeds having radial symmetry.

Seeds in subgen. Ottonia are meloniform (Lindley, 1848), 4-ribbed, sulcate, ranging from ellipsoid to obovoid, 0.6-1.7(-2) mm long and 0.5-1.7 mm in diam., basally concave or convex, and apically cuspidate. The seed coat is reticulate (see Seed Coat). The seed color is imposed by the endotegmen which is filled with tannins (Fig. 12). Seeds are brown to grayish when living turning glossy orange, dark reddish or

TABLE I
SEED CHARACTERS STUDIED

Abbreviations: sha=seed shape, siz=seed size, sym=seed symmetry, ris=rib shoulder, riu=rib sulcus, awo=anticlinal wall outline, cfa=cell facet, cec=edge appearance, ceo=cell edge orientation, n-ellips.=narrow ellipsoid, w-ellips.=wide ellipsoid, + = present, - =absent.

	Seed Body					Seed Coat (Exotegmen)			
	sha	siz	sym	ris	riu	awo	cfa	cec	ceo
<u>P. alatabaccum</u>	w-ellips.	1.2x0.6	radial	+	-	V-shaped	concave	granulose	raised
<u>P. anisum</u>	ellipsoid	1.6x1.3	radial	-	-	∩-shaped	concave	verrucose	raised
<u>P. bartlingianum</u>	obovoid	1.2x0.8	radial	-	-	straight	convex	verrucose	plane
<u>P. bracteo-villosum</u>	ellipsoid		radial	-	-				
<u>P. brevinodis</u>	ellipsoid		radial	-	-				
<u>P. corcovadensis</u>	ellipsoid	1.2x1.8	radial	-	-	∩-shaped	concave	verrucose	raised
<u>P. darienense</u>	ovoi-ell.	3.0x3.7	radial	-	-	straight	concave	verrucose	raised
<u>P. eucalyptophyllum</u>	ellipsoid	1.3x1.0	radial	-	-	∩-shaped	concave	verrucose	raised

TABLE I
-continued-

	sha	siz	sym	ris	riu	awo	cfa	cec	ceo
<u>P. francovilleum</u>	w-ellips.	0.6x0.5	radial	+	-	V-shaped	concave verrucose	raised	
<u>P. guimaraesianum</u>	ellipsoid	1.3x1.2	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. hayneum</u>	ellipsoid	1.7x0.8	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. hoffmannseggianum</u>	w-ellips.	1.5x1.5	bilateral	-	+	straight	concave verrucose	raised	
<u>P. klotzchianum</u>	ellipsoid	1.0x1.7	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. miquelianum</u>	ellipsoid	2.0x1.6	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. ottonoides</u>	w-ellips.	0.6x0.4	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. ovatum</u>	ellipsoid	2.1x1.7	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. piliovarium</u>	glob-ell.	1.6x0.8	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. piscatorum</u>	w-obovoid	1.5x1.0	asymmetr.	-	-	straight	concave verrucose	raised	
<u>P. rizzinii</u>	ellipsoid	1.9x1.5	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. scutifolium</u>	n-ellips.	1.0x0.7	radial	-	-	Ω -shaped	concave verrucose	raised	
<u>P. ubatubensis</u>	ellipsoid	1.0x0.5	radial	-	-	Ω -shaped	concave verrucose	raised	

black when dry. Nearly 90% of seed volume is starchy perisperm. The minute embryo is situated at the seed apex and is surrounded by an endospermous-like membrane.

Seeds are 4-ribbed and sulcate (Fig. 13). From the longitudinal position of the ribs along the two planes of the seed, one may distinguish seeds with radial or bilateral symmetry. Bilateral seeds have a pair of ribs in one plane which are more prominent and wider as seen from above and are normally obtuse and with a sulcus (Fig. 14). This type of seed is unique to P. hoffmannseggianum. Radial seeds have ribs equally developed in all planes (Fig. 15). Only in P. piscatorum are the seeds asymmetric (Fig. 16). Aside from symmetry planes one may distinguish a more inclusive set of characters, viz. seed shape and size, rib width in frontal section, and presence or absence of a rib shoulder. In P. francovilleianum and P. alatabaccum seeds are black when dry, wide ovoid, and the ribs narrow in frontal section and forming distinct shoulders (Fig. 15). Those seed characters provided the strongest arguments for supporting the relationship of those species and added a character by which P. alatabaccum could be differentiated from P. bartlingianum. The latter species had seeds glossy orange when dry, obovoid, and with ribs narrower in the frontal plane (Fig. 17) which are very similar to those in P. darienense, a taxon with larger seeds. The species mentioned above are all sessile-flowered taxa and in each case possess a

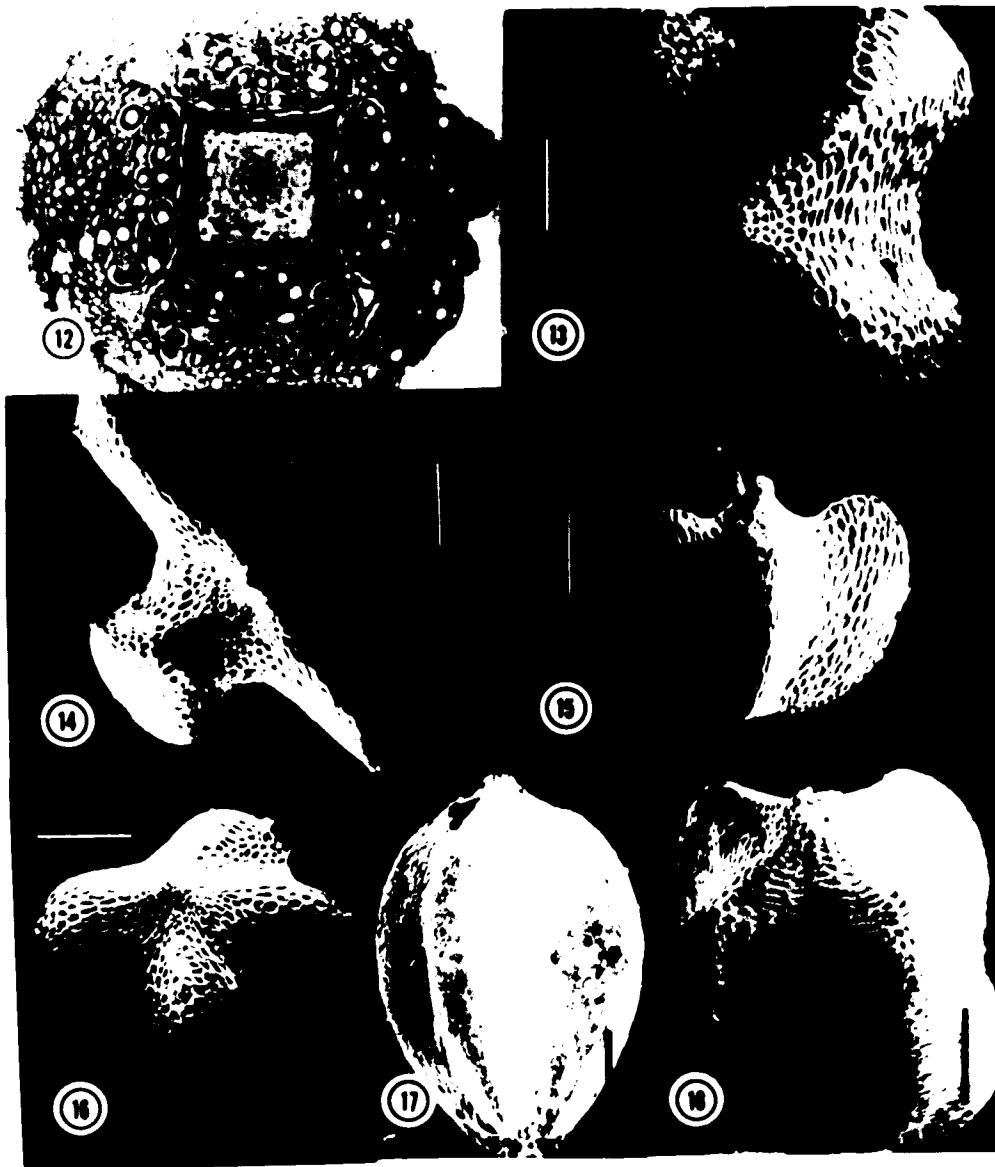
unique seed type. Seeds in the rest of the subgenus, which include both sessile and pedicellate-flowered taxa, present fewer variations. They are brownish to blackish when dry, globose, ovoid, or spherical, and long-apiculate. The ribs in frontal section are distinctly wider in the seeds of P. anisum (Fig. 13), and P. piliovarium (Fig. 18) when compared with other species, such as P. bartlingianum (Fig. 17).

Pollen

Pollen in Piper is monosulcate, anatrivotomonosulcate or inaperturate (Barth & Barbosa, 1972; Smith, 1975; Walker, 1978; Yi-zhen, 1982). In subgen. Ottonia, Barth and Barbosa (1972) described the pollen of P. hayneanum (= Ottonia macrostachya). Their description was very similar to the one here provided. Sampling of pollen grains for all species of subgen. Ottonia revealed the following features: pollen globose to spherical (Fig. 19), minute, 9-12 μ m, monosulcate, aperture of colpoid type, exine psilate. Most pollen grains collapsed along the aperture (Fig. 20). Barth and Barbosa (1972) described the tectum as smooth and rarely perforate, and the apertures as covered by granulations of sexine. No significant variation in pollen structure was found in the subgenus. However, pollen grains from anthers in the sagittal plane were often collapsed, either because they rarely mature, or because

Fig. 12-18. Fruit and seeds of subgen. Ottonia.

12. Piper alatabaccum (Plowman et al. 12641),
cross section of the fruit showing the single
containing seed. X 44.
13. SEM photomicrograph. Piper anisum (Callejas et
al. 1637), top view of seed. X 60. Scale= 430
14. SEM photomicrograph. Piper hoffmannseggianum
var. hoffmanseggianum (Matos Silva 1812), top
view of seed (displaying bilateral symmetry).
X 60. Scale= 430 μm .
15. SEM photomicrograph. Piper francovilleianum
(Huber & Colchester 8383), lateral view of
seed. Observe the prominent ribs shoulders.
X 60. Scale= 430 μm .
16. SEM photomicrograph. Piper piscatorum (Daly
& Callejas 1377), top lateral view of seed
(asymmetric). X 60. Scale= 430 μm .
17. SEM photomicrograph. Piper bartlingianum
(Mori et al. 9166), frontal view of seed. X
60. Scale= 430 μm .
18. SEM photomicrograph. Piper piliovarium
(Carauta 2394), lateral view of seed. X 60.
Scale= 430 μm .



the stamens fall before the anthers dehisce.

ANATOMY

Materials and Methods

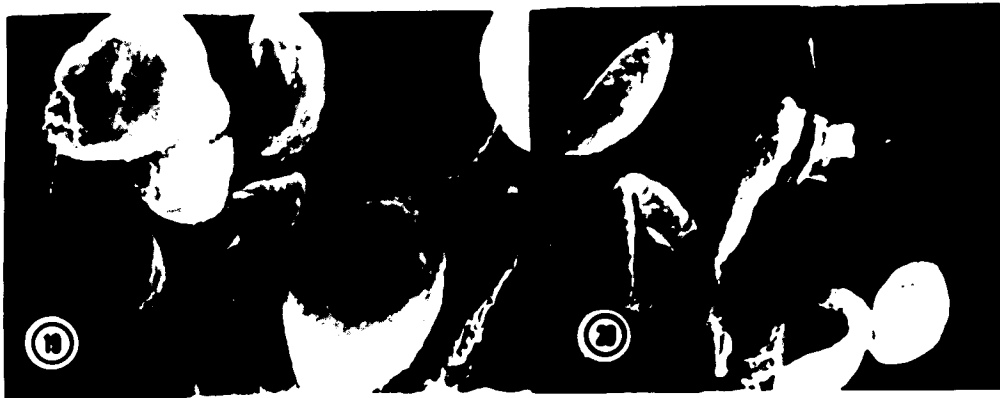
Field collections for studies of the primary stem, leaf, and flower anatomy were fixed in FAA and after 24 hours transferred to 70% ETOH. All material was embedded in paraplast plus (56-57°C) and cut with a rotary microtome into sections 5 um thick for flowers and inflorescence and 10-15 um for leaves and stem. They were stained in a safranin-fast green ETOH series (Johansen, 1940) or in safranin-chlorazol black E (Stevenson, 1980). Leaf clearings were stained with safranin using the technique of Payne (1969). Some leaf sections from dry herbarium material were softened in water, then cut with a razor blade using parafilm as described by Fhrolich (1984). Sections were then stained in a safranin-fast green ETOH series. Leaf architecture is described according to the terminology of Hickey (1973), while flower anatomy follows terminology used by Tucker (1982a, 1982b)

Wood specimens were cut into 3-4 cm long cylinders, immersed in a solution of glycerin and 60% ETOH, and left for softening for three weeks. They were then air-pumped and trimmed on a sledge microtome into sections 15-20 um thick, stained progressively in 5% aqueous iron-hematoxylin (Camp,

Fig. 19-20. Pollen grains of subgen. Ottonia.

19. SEM photomicrograph. Piper corcovadensis
var. blanchetii (Callejas et al. 1902),
pollen grains (from anthers on the stamens
along the frontal plane). X 3000.

20. SEM photomicrograph. Piper corcovadensis
var. blanchetii (Callejas et al. 1902),
pollen grains (from anthers on the stamens
along the sagital plane). X 3000.



1930), and counterstained with a 1% phenolic Bismarck brown Y series. Maceration was made by sonication and using a modification of Jeffrey's technique as given by Schmidt (1982). Terminology follows the AIWA committee for wood terminology (1957).

Seed material for SEM was gently boiled in water for 10 minutes and sonicated for 5 minutes, then air dried or fixed and dehydrated in an alcohol-freon series. They were critically-point dried in freon and then gold coated. The seed coat is described according to the terminology of Barthlott (1982). Wood specimens for SEM include sections cut with a razor blade and then air dried. Flowers, pollen, and leaf sections for SEM were dehydrated in an alcohol-freon series then critically-point dried in freon. All SEM material was gold coated with 10 um of gold for two minutes. All photographs were taken with a Jeol-SEM microscope at 25 Kv. Photographs of microtome sections were taken with an Olympus BH-2 with a PM-10AD photomicrographic system and with a Nikon Labophot microscope with an HFX-11 automatic camera attachment. Technical PanFilm at ASA 50 was used for all photographs. Voucher specimens examined are listed in Table II.

Wood Anatomy

The description of wood in subgen. Ottonia is based upon

examination of 12 specimens representing seven species (Table III). All measurements represent means. For each feature 25 measurements were made for five sections.

Few Piper species have been surveyed for wood anatomy (Araujo & Mattos Filho, 1974; Bailey & Tupper, 1918; Balfour, 1958; Carlquist, 1975; Cozzo & Cristiani, 1950; Datta & Dasgupta, 1977; Harrar, 1946; Metcalfe & Chalk, 1950; Patel & Bowles, 1980). Nevertheless wood structure in the genus seems to follow one general pattern, one that is also present in subgen. Ottonia. No species of this subgenus have been previously examined for wood anatomy. Metcalfe and Chalk (1950) cite P. jaborandi (= P. anisum) for which they give a short description on vessel perforation; however, other features in the primary stem of their specimens do not match with those found here in subgen. Ottonia, and it is possible that the species cited by them is not P. anisum.

General. Colored heartwood absent; growth rings indistinct; medullary bundles present; wood hard, brown to blackish; all species with a mild anise scent; economic value none.

Anatomical. Wood diffuse porous. Pores more or less evenly distributed and with an occasional tendency towards oblique arrangement (more conspicuous in large bundles) (Fig. 21); solitary (50-70% average for all samples) (Fig. 21), in radial multiples of 2-3 (Fig. 22), in tangential multiples of

TABLE II

VOUCHER SPECIMENS FOR ANATOMY, SEED COAT, AND POLLEN STUDIES

Abbreviations: flw=flower development, frs=fruit section, lfc=leaf clearing, poll=pollen, pst=stem section, pts=petiole section, sec=seed coat, wom=wood maceration, wos=wood section).

Species	Collection	flw	frs	lfc	lfs	poll	pst	pts	sec	wom	wos
<u>P. alatabaccum</u>	<u>Plowman et al. 12641</u>	x	x	x	x	x			x		
	<u>Prance et al. 5027</u>	x		x		x			x		
<u>P. anisum</u>	<u>Callejas et al. 1637</u>	x	x	x	x	x	x	x	x	x	x
	<u>Callejas et al. 1637b</u>	x	x	x	x	x			x	x	
<u>P. bartlingianum</u>	<u>Daly & Callejas 1200</u>	x		x	x	x			x	x	x
	<u>Plowman & Davis 12540</u>	x		x					x		
	<u>Mori et al. 9166</u>			x					x		
<u>P. brevinodis</u>	<u>Sucre 10133</u>	x		x		x					
<u>P. corcovadensis</u> var.											
<u>corcovadensis</u>	<u>Sucre 6356</u>	x		x		x			x		

TABLE II

-Continued-

Species	Collection	flw	frs	lfc	lfs	poll	pst	pts	sec	wom	wos
<u>P. corcovadensis</u> var.											
<u>corcovadensis</u>	<u>Sucre 7838</u>					x			x		
<u>P. corcovadensis</u> var.											
<u>blanchetii</u>	<u>Callejas et al. 1902</u>	x	x	x	x	x	x	x	x		
	<u>Hatschbach 45235</u>	x		x		x			x		
	<u>Prance & Silva 59567</u>			x					x		
<u>P. darienense</u>	<u>Callejas 342</u>	x		x		x			x		
	<u>Folsom 7829</u>			x					x		
	<u>Burger s.n.</u>	x		x					x		
<u>P. eucalyptophyllum</u>	<u>Callejas et al. 2142</u>	x	x	x		x		x	x		
<u>P. francovilleanum</u>	<u>Huber & Colchester 8383</u>	x	x	x		x			x		
	<u>Wurdack et al. 43537</u>	x		x					x		
<u>P. guimaraesianum</u>	<u>Peixoto et al. 438</u>	x		x		x			x		

TABLE II

-Continued-

Species	Collection	flw	frs	lfc	lfs	poll	pst	pts	sec	wom	wos
<u>P. miquelianum</u> var.											
<u>miquelianum</u>	<u>Callejas et al. 1868</u>	x		x	x	x	x	x	x	x	x
	<u>Callejas et al. 1870</u>	x		x	x				x	x	
	<u>Callejas et al. 2034</u>			x	x				x		
	<u>Callejas et al. 2038</u>			x					x		
<u>P. miquelianum</u> var.											
<u>hirtellum</u>	<u>Callejas et al. 1894</u>	x		x	x	x		x	x		
	<u>Callejas et al. 1895</u>			x	x				x		
	<u>Callejas et al. 1897</u>	x		x	x				x		
<u>P. ottonoides</u>	<u>Prance et al. 1981</u>			x							
	<u>Frame et al. 147</u>								x		
<u>P. ovatum</u> var. <u>ovatum</u>	<u>Tamayo 2154</u>			x		x			x		

TABLE II

-Continued-

Species	Collection	flw	frs	lfc	lfs	poll	pst	pts	sec	wom	wos
<u>P. ovatum</u> var.											
<u>boucheanum</u>	<u>Callejas et al. 1554</u>	x	x	x	x	x		x	x		
	<u>Callejas et al. 1569</u>			x	x	x		x	x		
	<u>Carvalho & Callejas 2048</u>			x	x			x	x		
<u>P. pilovarium</u>	<u>Carauta 2394</u>			x				x	x		
<u>P. piscatorum</u>	<u>Daly & Callejas 1377</u>	x	x	x	x				x		
	<u>Daly & Callejas 1540</u>			x					x		x
<u>P. rizzinii</u>	<u>Pirani & Yano 717</u>	x		x					x		
<u>P. scutifolium</u>	<u>Hoehne s.n.</u>	x		x				x	x		
<u>P. ubatubensis</u>	<u>Davis et al. 59786</u>			x					x		
<u>P. villosobracteatum</u>	<u>Duarte 4012</u>			x							

TABLE II

-Continued-

Species	Collection	flw	frs	lfc	lfs	poll	pst	pts	sec	wom	wos
<u>P. hayneanum</u>	<u>Callejas et al. 1608</u>	x	x	x	x	x	x	x	x	x	
	<u>Callejas et al. 1608b</u>	x	x	x					x	x	
<u>P. hoffmannseggianum</u>											
var.	<u>Mattos Silva 1812</u>	x		x	x	x		x	x	x	x
<u>hoffmannseggianum</u>	<u>Carvalho & Plowman 1448</u>								x	x	x
<u>P. hoffmannseggianum</u>											
var. <u>latifolium</u>	<u>Callejas et al. 1779</u>	x	x	x	x	x	x	x	x	x	x
	<u>Carvalho & Callejas 2021</u>	x		x	x	x	x	x	x	x	x
	<u>Carvalho & Callejas 2047</u>	x			x				x		x
<u>P. klotzchianum</u>	<u>Belém 713</u>	x		x		x			x		
	<u>Heringer 16041</u>	x		x					x		

2-3 (Fig. 23), in clusters of 2-4 (Fig. 24); angular in cross-section; tangential diam. (14-)50-112(-190) μm ; pore frequency ranging from 32-50 per sq. mm; vessel member length (190-)200-380(-150) μm ; vessel perforation plates simple, end wall transversely or obliquely oriented, often with a tail at one extreme (Fig. 25); intervacular pitting scalariform (Fig. 26), ray to vessel contact not seen in any specimen examined, vessel-parenchyma pitting as in vessel to vessel but narrower (Fig. 27), pits simple; vessel to fiber pitting transitional, pits circular and small (Fig. 27); spiral thickenings absent (present only in protoxylem elements). Tyloses absent. Fiber-tracheids (Fig. 28), and libriform fibers (Fig. 28) thin to very thick-walled, 1-4 mm thick, sometimes occluding the lumen; lumina in fiber tracheids 13-20 μm in diam., (400-)900-1300(-1800) μm in length; both types of inaperturate elements often septate (Fig. 29), in most specimens septate fiber-tracheids are more numerous than septate libriform fibers; 1-2(-3) septum/fiber; spiral thickenings absent; pits vestured to transitional (Fig. 30); tracheids present in all samples, with bordered scalariform pitting (Fig. 26). Wood rays only multiseriate (Fig. 31), (3-)6-13.1(-18) cells wide, above 10 mm in height or as long as the internodes; homocellular; cells typically square or upright, intermingled (Fig. 32); ray cells with simple pitting, often storied (Fig. 33), sheath cells irregularly distributed. Parenchyma paratracheal,

mostly vasicentric, forming complete sheaths around the vessels (Figs. 22, 27, 29), one cell thick, occasionally scanty, well developed, in strands of 2-3 cells; pits simple (Figs. 27, 34), smooth, scalariform to the vessels (Fig. 27), parenchyma-parenchyma pitting transitional (Fig. 27). Starch grains abundant in both septate and non-septate fibers (Figs. 28, 35), and ray cells (Fig. 33). Some crystals present in rays and fibers (Fig. 36). Oil cells absent. Mucilage canals not observed.

Note: Starch grains were only present in ray cells in one sample of P. hoffmannseggianum var. hoffmannseggianum (Carvalho & Callejas 1144). Axially united rays were present in one sample of P. hoffmannseggianum var. latifolium (Callejas et al. 2047). Dissected rays were found in one sample of P. bartlingianum (Daly & Callejas 1200).

An outstanding feature of the secondary xylem of subgen. Ottonia is the rather uniform similarity displayed by the wood specimens, despite the fact that specimens were selected from different localities and different habitats. Differences such as frequency of simple pores vs. clusters, or tangential or radial multiples are apparently correlated with specimen age. Young plants are almost exclusively solitary-porous. On the other hand older plants tend to display other pore arrangements, but always with a tendency to occur near the stem periphery. This observation has otherwise been previously

Fig. 21-28. Wood anatomy of subgen. Ottonia.

21. Piper bartlingianum (Daly & Callejas 1200).

Transverse section. Notice the lack of rings and the differences in the arrangement of the pores in the vascular bundles. X 40.

22. Piper piscatorum (Daly & Callejas 1540).

Transverse section showing the radial arrangement of pores. X 440.

23. Piper anisum (Callejas et al. 1637),

transverse section showing the tangential arrangement of pores, notice also the surrounding axial parenchyma. X 500.

24. Transverse section showing pores arranged in clusters. (Material examined and magnification as in Fig. 23).

25. Piper corcovadensis var. blanchetii (Callejas et al. 1902), wood maceration, simple perforate vessel with a long tail at one of the extremes. X 800.

26. Piper bartlingianum (Daly & Callejas 1200), SEM photomicrograph, tangential section showing the intervascular pitting (at the center), and a tracheid with simple bordered pitting (at the left). X 1500.

Fig. 21-28. Wood anatomy of subgen. Ottonia. Cont.

27. Piper corcovadensis var. blanchetii (Callejas et al. 1902). SEM photomicrograph, transverse section showing the parenchyma (arrow)-vessel pitting. X 1000.
28. Piper anisum (Callejas et al. 1637b). Wood maceration, showing a fiber tracheid with numerous strach grains (arrow). X 800.



TABLE III
WOOD CHARACTERS

Species	#Rays/mm ²	Vessel diam.			Vessel length	Vessel freq.	d.b.h.
		(um)			(um)	(mm ²)	(cm)
		av	min	max			
<u>P. anisum</u>	1.1	46	18	85	200-310	62	4.0
<u>P. bartlingianum</u>	1.4	75	50	130	210-370	32	5.0
<u>P. corcovadensis</u>	1.3	52	37	75	220-390	58	3.5
var. <u>blanchetii</u>							
<u>P. hoffmassenggianum</u>	0.6	30	126	190	330-370	67	3.0
var. <u>hoffmasseng.</u>							
<u>P. hoffmassenggianum</u>	1.3	76	45	148	200-380	48	4.2
var. <u>latifolium</u>							
<u>P. ovatum</u>	1.3	62	37.5	125	190-370	39	4.5
<u>P. piscatorum</u>	0.8	32	14	45	235-365	32	2.1

Fig. 29-36. Wood anatomy of subgen. Ottonia.

29. Piper ovatum var. boucaneanum (Callejas et al. 1540). Wood maceration, close up of a septate fiber tracheid containing starch grains. X 1000.
30. Piper bartlingianum (Daly & Callejas 1200). SEM photomicrograph, tangential section, close up of slit-like pitting in libriforme fibers. X 3000.
31. Piper piscatorum (Daly & Callejas 1540). Tangential section showing the wide multiseriate rays. X 150.
32. Radial section, close up showing the homocellular rays. Notice the absence of procumbent ray cells. (Material examined as in Fig. 31). X 400.
33. Piper anisum (Callejas et al. 1637). SEM photomicrograph, radial section showing storied ray cells. X 1100.
34. Piper hoffmannseggianum var. latifolium (Callejas et al. 1779). Wood maceration showing a parenchyma cell (center). X 750.
35. Piper anisum (Callejas et al. 1637). SEM photomicrograph. Radial section showing ray cells with numerous starch grains. X 1100.

Fig. 29-36. Wood anatomy of subgen. Ottonia. Cont.

36. Piper hoffmannseggianum var. hoffmannseggianum
(Mattos Silva 1812). SEM photomicrograph
showing calcium oxalate crystals in libriforme
fibers. X 3000.



cited for Macropiper excelsum (Patel & Bowles, 1980). It is important to mention that pore distribution in the stele displays distinct arrangements for small and large bundles (small bundles are branches of large bundles). In the former, the pores are more or less evenly distributed, while in the latter, they tend to occur only along the center of the bundle (Fig. 21).

No significant differences were found in vessel diameter between species or within taxa. Only in specimens of P. hoffmannseggianum var. hoffmannseggianum were vessels comparatively narrower than in other taxa. Probably such differences are correlated with the dry habitat of that species (sandy restinga areas) compared with the more mesic sites (forest understory) of all other taxa. Several characters found in the wood of subgen. Ottonia had not been reported in other members of the genus Piper; they include: presence of starch grains in both septe and non-septate fibers and in ray cells, and presence of crystals (probably calcium oxalate) in ray cells and tracheids. Presence of starch grains has been reported by Johnson (1902) in the primary stems of Macropiper excelsum; however, Patel and Bowles (1980), after examination of the same species, did not report starch grains in the wood. It is rather unlikely that such characters are restricted to subgen. Ottonia, especially since a character such as the presence of starch grains seems to be variable

within species (see above for M. excelsum). Likewise some wood characters common in Piper are not present in subgen. Ottonia, such as the presence of scalariform thickenings, and rays without procumbent cells. Patel and Bowles (1980) noticed that septa are more common in long than in short fibers in Macropiper excelsum. This condition is very similar in subgen. Ottonia in which septa in fiber-tracheids are more common than in libriform fibers. Storied arrangement of fibers and/or parenchyma cells has been reported for P. arboreum (Cozzo & Cristiani, 1950) and Macropiper excelsum (Patel & Boles, 1980). In subgen. Ottonia storied structure was observed only in ray cells.

As already noticed by Metcalfe and Chalk (1950), Carlquist (1962, 1985), and Patel and Bowles (1980), wood in Piperaceae is unusual because of the presence of simple perforation plates and scalariform pitting, large pits, vasicentric parenchyma, and storied structure. All of these features are not expected to occur together (simple perforation plates and scalariform pitting); however, Carlquist (1962, 1975) has advanced a theory of paedomorphosis for such wood structures. According to that author, wood in Piperaceae is in a permanent juvenile stage, very much like in Begoniaceae (Carlquist's 1985 description of the wood for that family is remarkably similar to that given here and other families with large number of herbaceous species).

Leaf Anatomy

Techniques and descriptive terminology are given under Materials and Methods. Description and distribution of oil containing idioblasts (here described as oil cells following common terminology in Piperaceae) are given under Habit and Architecture, and in Histology since they are closely associated with the venation in some species of subgen. Ottonia. Although oil cells in Piper differentiate relatively early in the ontogeny of the leaf, much before the veinlet is formed (Chibber, 1913), they should not be considered components of venation. To date descriptions of leaf anatomy in Piper are known for fewer than 15 species.

Datta and Dasgupta (1977), upon examination of leaf histology in six species of Piper, gave a list of characters consistent at the species and generic level. Descriptions for single taxa by other authors (Chibber, 1913, Piper methysticum; Sabatino & Silva, 1975, P. regnellii) seem to confirm Datta and Dasguptas' observations. Data here presented for subgen. Ottonia revealed important characters in leaf histology and to lesser extent in architecture. The distribution of the most important characters is given in Table IV.

Architecture. Leaves in subgen. Ottonia have involute ptyxis (Fig. 37) and the venation is pinnate brochidodromous

with 8-18 pairs of secondary veins, the lower 2-3 pairs departing at acute angles, the remaining upper ones departing at obtuse angles. The intercostal areas are commonly of different width throughout the lamina, rarely equally spaced, abruptly curved and loop connected, joining superadjacent secondaries at acute angles. A fimbriate marginal vein is formed by fusion of veins of higher orders (Fig. 38). The areoles are well developed and pentagonal (Fig. 38) or rectangular towards the margins (Fig. 38). The intersecondary veins are simple, linear to curved, running almost parallel to the secondaries. Veinlets are simple and unbranched in the pentagonal areoles (Fig. 38), terminated by a single tracheid (Fig. 39), rarely by three or more tracheids (Fig. 40), enclosed by parenchyma cells (Fig. 40), more commonly ending in a single oil cell. Midvein, secondary, and tertiary veins are surrounded by distinct parenchymatous sheaths. Venation of higher orders has complete or incomplete sheaths, less often sheaths are absent. Sheath cells are thin to very thick-walled, simple pitted (Fig. 41), running parallel to adjacent tracheids or at right angles (Fig. 41). Oil cells are commonly found in association with veins; they are 10-12 μ m in diam. (Fig. 39), thin-walled, fully or partially filled with oil. Oil cells are in direct contact with sheath cells and surrounded by spongy parenchyma cells (Fig. 41), less often in direct contact with tracheids (Fig. 42). They are absent in

TABLE IV

LEAF (ANATOMY & HISTOLOGY) CHARACTERS

Abbreviations: uh=upper hypodermis, ueao=upper epidermis anticlinal wall outline, leao=lower epidermis anticlinal walls outline, ocid=oil-containing idioblast distribution, ndlp=presence of distinct cell layers in palisade, ntev=number of tracheids at veinlet end, caox=calcium oxalate crystals in the mesophyll, + =present, - =absent.

	uh	ueao	leao	ocid	ndlp	ntev	caox
<u>P. alatabaccum</u>	-	sinusoid	sinusoid	mesophyll	+	3	+
<u>P. anisum</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. bartlingianum</u>	-	sinusoid	sinusoid	mesophyll	+	3	+
<u>P. brevinodis</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. corcovadensis</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. darienense</u>	+	curved	sinusoid	veins & mesoph.	-	1	+
<u>P. eucalyptophyllum</u>	+	curved	sinusoid	veins	-	1	-
<u>P. francovilleianum</u>	-	sinusoid	sinusoid	mesophyll	+	3	+
<u>P. guimaraesianum</u>	-	curved	sinusoid	veins & mesoph.	-	1	-

TABLE IV
-continued-

	uh	ueao	leao	ocid	ndlp	ntev	coxc
<u>P. hayneanum</u>	+	curved	sinusoid	veins	-	1	-
<u>P. hoffmannseggianum</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. klotzchianum</u>	-	straight	straight	veins & mesoph.	-	1	-
<u>P. miquelianum</u>	-	curved	sinusoid	veins & mesoph.	-	1	+
<u>P. ottonoides</u>	-	straight	straight	veins & mesoph.	-	1	-
<u>P. ovatum</u>	-	curved	sinusoid	veins & mesoph.	-	1	+
<u>P. piliovarium</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. piscatorum</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. rizzinii</u>	+	sinusoid	sinusoid	veins	-	1	-
<u>P. scutifolium</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. ubatubensis</u>	-	curved	sinusoid	veins & mesoph.	-	1	-
<u>P. villosobracteatum</u>	-	curved	sinusoid	veins & mesoph.	-	1	-

the ending of veinlets in marginal areoles.

In the subgenus veinlets of the marginal areoles are simple and unbranched in all species, and not restricted to P. pseudottonia (here under P. klotzchianum) as stated by Falcão-Ichaso and Guimarães (1974). In most species veinlets ended with a single tracheid, but in P. bartlingianum, P. alatabaccum, and P. francovilleum the endings consisted of three tracheids which were surrounded by parenchymatous sheath cells (Fig. 40). Those three species also have oil cells restricted to the mesophyll and not in contact with veins as other taxa. In P. hayneum, P. eucalyptophyllum, and P. rizzinii oil cells are restricted to the veins, and are in contact with bordering sheath cells (Fig. 44). In P. piscatorum oil cells, when occurring along the veinlets, are in direct contact with tracheids many of which are oriented at right angles (Fig. 43). The above mentioned characters have not been previously described in the genus Piper, restricted to subgen. Ottonia, they are not present in selected species of the outgroups used for a cladistic analysis (see CLADISTICS).

Histology. The cuticle is smooth on both epidermises and thin to very thick (2.5-8.5 μ m thick). The upper epidermis is essentially unilayered (Fig. 45), however it is interrupted by small crystalline pearl glands or 1-2-celled papillate hairs, the anticlinal walls in paradermal sections are curved, less

often straight or sinusoid. A unilayered adaxial hypodermis is present along the midvein region in all taxa, but occurs elsewhere only in the lamina of three species (Table IV, see also Fig. 45); its cells are distinctly larger than epidermal cells and are thin-walled with curved anticlinal walls. The mesophyll is dorsiventral and well differentiated; fusiform pallisade cells are in 1-2 layers around the veins (Fig. 46); oil cells are present, but crystals are absent. The spongy mesophyll consists of 2-4 layers with rounded cells that are tightly packed with small lacunae; all layers have cells of similar size and shape; in some species only two layers are present in which the upper is composed of cells leaving small intercellular lacunae and surrounding oil cells (Fig. 47), and the lower has larger cells leaving larger lacunae and is devoid of oil cells (Fig. 48); crystals are commonly absent (Table IV). An abaxial hypodermis is present in all taxa; its cells are distinctly larger than the others in any tissue, and are thin-walled and devoid of oil cells or crystals (Fig. 45); there are large lacunae which correspond to substomatal chambers. The lower epidermis is the same as the upper but lacks pearl glands; the anticlinal walls are commonly sinusoid (Fig. 49), rarely curved; oil cells are absent; stomata are restricted to the abaxial epidermis, where they are tetracytic and raised, and the guard cells are simple, rounded and unornamented (Fig. 50); calcium oxalate crystals are present in

all taxa in the midvein region.

In summary, with regards to histology, characters of significance at the species level include: 1) presence or absence of an upper hypodermis (in subgen. Ottonia restricted to P. darienense, P. rizzinii, P. hayneanum, and P. eucalyptophyllum), 2) presence of calcium oxalate crystals in the mesophyll (detected in P. miquelianum, P. ovatum, and P. francovilleanum), 3) spongy mesophyll which in most species consists of several layers, all with cells of similar sizes and shapes (however in P. bartlingianum, P. alatabaccum, and P. piscatorum consisting of two layers, as described above), and 4) the lower hypodermis which in subgen. Ottonia is quite distinct from those previously described for other species of Piper, especially in the presence of large lacunae formed by neighboring cells.

Primary Stem

Many authors (Kunth, 1839; Miquel, 1844; C. de Candolle, 1869; Burger, 1977; Cronquist, 1981; Dahlgren, 1985) have pointed out that Piperaceae are unusual among dicotyledons due to the presence of several characters otherwise found only in monocotyledons (e.g. one prophyll, often trimerous flowers, sheathing leaf bases, stelar structure, etc.). Among those characters, stelar structure has generated much attention,

Fig. 37-42. Leaf anatomy and leaf histology of subgen. Ottonia.

37. Piper hoffmannseggianum var. latifolium
(Callejas et al. 1779). Branching node showing
the leaf base with a well developed sheath and
the involute ptyxis. X 0.6.
38. Piper klotzchianum (Belén 713). Leaf clearing
close up of the marginal areoles and the
fimbriate vein (fv). X 24.
39. Piper piscatorum (Daly & Callejas 1377).
Leaf clearing, close up of ending of a veinlet
with surrounding tracheids (1-2) and partially
filled oil containing idioblasts. X 400.
Scale= 10 μ m.
40. Piper francovilleianum (Huber & Colchester
8383). Leaf clearing, close up of ending of a
veinlet surrounded by 3 tracheids. X 80.
Scale= 6 μ m.
41. Piper darienense (Callejas 342). Leaf clearing
close up of tertiary vein surrounded by promi-
nent parenchyma cells (notice the thick walls).
X 110. Scale= 6 μ m.
42. Cross section of the leaf showing the
distribution of oil containing idioblasts (oi)
along tertiary veins. In this case in contact
with a parenchyma cell. (Material examined as
in Fig. 41). X 350.

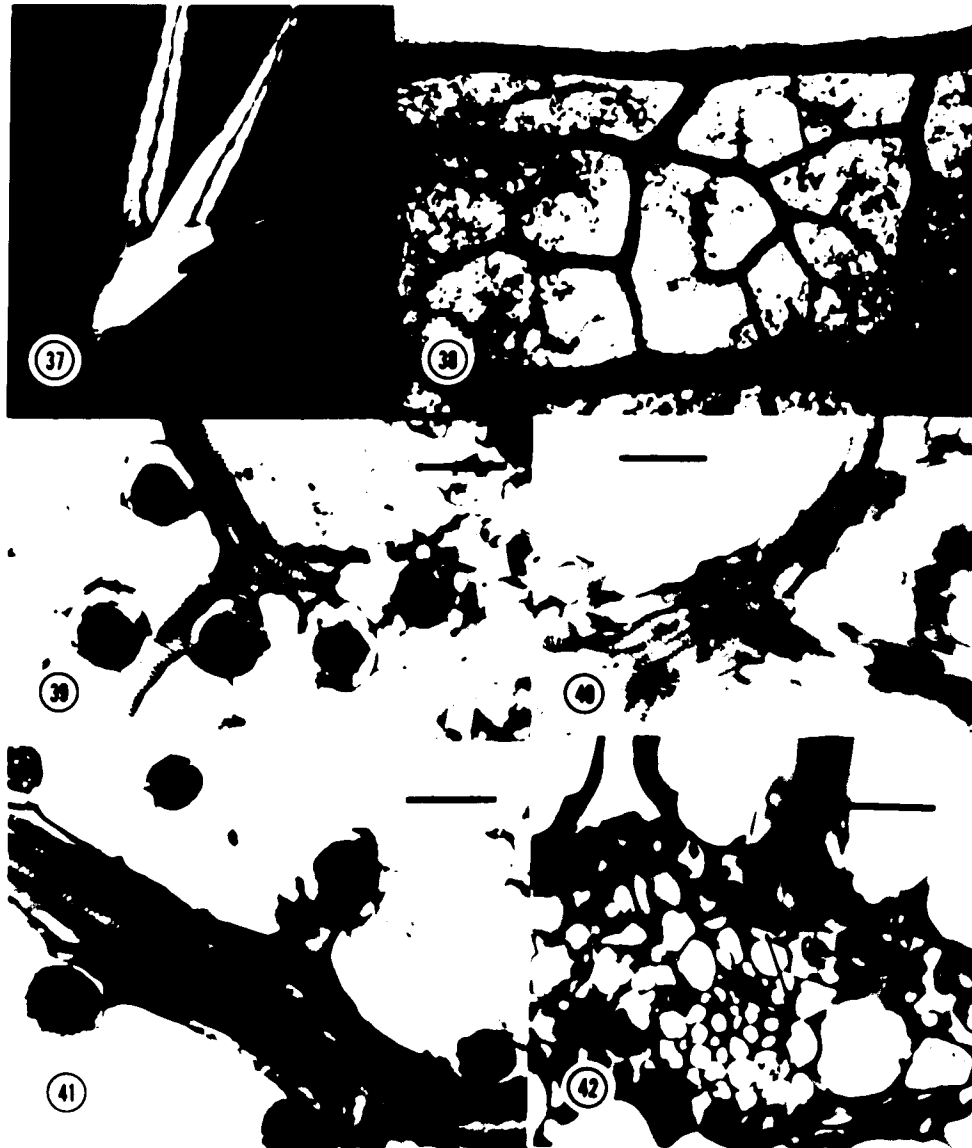
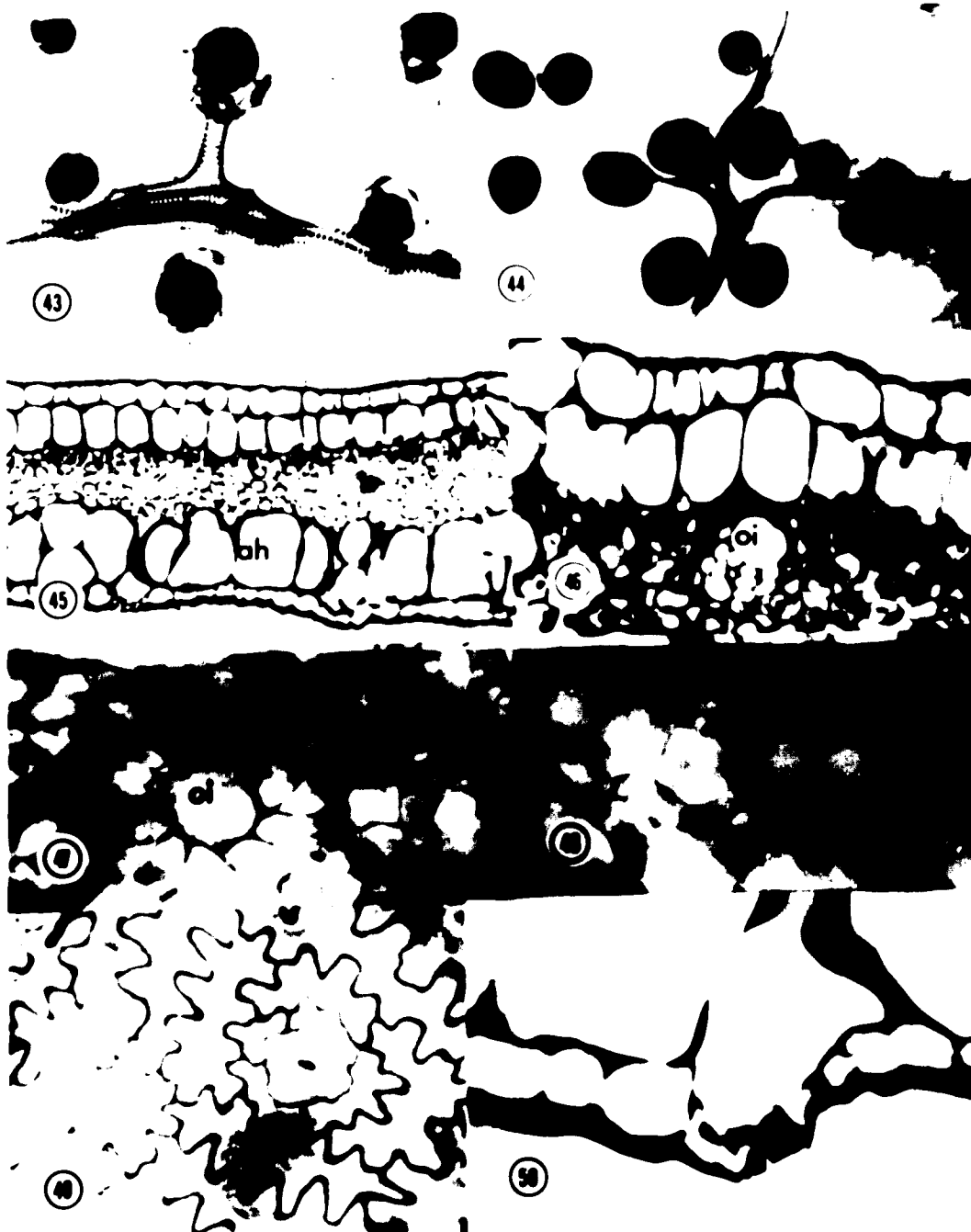


Fig. 43-50. Leaf anatomy and leaf histology of subgen. Ottonia.

43. Piper piscatorium (Daly & Callejas 1540).
Leaf clearing showing oil containg idioblast
in direct contact with tracheids. X 800.
44. Piper hayneanum (Callejas et al. 1608). Leaf
clearing. Oil containing idioblasts restricted
along the tertiary veins. X 450.
45. Piper darienense (Callejas 342). Leaf cross
section. An adaxial hypodermis is present.
Note the prominent size of cells in the
abaxial hypodermis (ah). X 220.
46. Piper anisum (Callejas et al. 1637). Leaf,
Cross section, close up of palisade tissue.
X 400.
- 47-48. Piper bartlingianum (Daly & Callejas 1200).
Leaf clearing, showing the two types of cells
in the mesophyll. (oi= oil containing
idioblast). (both X 800).
49. Piper rizzinii (Pirani & Yano 717). Leaf
clearing, abaxial epidermis showing a single
tetracytic stoma and the epidermal cells with
sinusoid anticlinal walls. X 400.
50. Piper piscatorium (Daly & Callejas 1540).
Cross section of a stoma. X 1000.



especially with regards to the presence of medullary bundles in Piper and the lack of a distinct vascular ring in the stele of Peperomia. Consequently studies of the primary stem in Piperaceae have been more concerned with nodal vasculature than with purely descriptive histology. De Candolle (1866) provided data on the distribution of stem tissues of several species of Piper. De Bray (1886), in his work on the nodal anatomy of Piperales, described superficially the stem structure of nearly 20 species in Piper and Peperomia. Bond (1931) noticed the presence of an endodermis in the stem of many species of Piper, and in a long dissertation described the ontogeny and distribution of that tissue. Isolated studies on single species, e.g. Chibber (1912) in Piper betle, and Hoffstadt (1916) in P. methysticum have revealed the presence of mucilage canals in the stem of many species of Piper. More recently Datta and Dasgupta (1979) and Konoshima and Miyagawua (1976) have described the structure of the primary stem in many species of Piper from the Old World tropics. In the latter study the structural variation in the stem was used to support the division of Piper into several subgenera.

No description of the primary stem structure in subgen. Ottonia has been published previously. Metcalfe and Chalk (1950) described superficially the stelar structure of P. jaborandi (= P. anisum). Their description however seemed to be based on a different species (see below).

Stem anatomy in subgen. Ottonia is quite uniform with insignificant variation found among the species and specimens examined. The epidermis is one cell thick and often interrupted by the presence of papillate hairs, less often by pearl glands. The stem cortex in the region bordering the epidermis consists almost exclusively of angular collenchyma, 3-7 cells thick (Fig. 51). This collenchymatous region is continuous, forming a complete ring, but usually undergoes rupture as the stem increases in diameter. In many specimens some collenchyma cells become sclerenchyma, fibers form caps abutting the vascular bundles becoming prominent. These caps are separated from the bundles themselves by an inner parenchymatous cortex in which oil containing idioblasts, and calcium oxalate crystals (Figs. 51, 52) are ubiquitous. A distinct endodermis delimits the cortex and vascular cylinder (Fig. 51) and forms a more or less continuous ring displaying considerable accommodation to the increasing bulk of the vascular tissues. Secretory cells are often present in the endodermis.

Embedded in a medullary fibrous ring, the vascular cylinder is formed by a more or less distinct ring of collateral vascular bundles separated by wide primary rays. Cells in these rays are rich in calcium oxalate crystals and starch grains, both of which are retained after the cells become lignified. A ring of medullary bundles is centripetal to the

vascular cylinder (Fig. 53). These bundles display similar structure to those in the outer vascular cylinder, but without being separated by medullary rays. Clusters of calcium oxalate crystals tend to form more or less distinct sheaths around these bundles (Fig. 54). The pith (except for the presence of medullary bundles) consists of thin-walled parenchyma cells with numerous oil containing idioblasts and calcium oxalate crystals.

The presence of a collenchymatous cortical ring, medullary fibrous ring, medullary bundles, and endodermis are common to all species here examined and not strikingly different in structure from other species reported in the literature. Additionally calcium oxalate crystals and oil containing idioblasts seem almost universal for the family. One exception to the above histological description is that of Metcalfe and Chalk (1950) for P. jaborandy. According to those authors, in P. jaborandy (= P. anisum) the xylem and phloem in the outer vascular cylinder have numerous mucilage canals. Furthermore the vascular cylinder is not separated from the pith by a medullary fibrous ring.

While mucilage canals have been previously reported for many species of Piper, I have not seen them in any species here examined and they seem to be rare in shrubby neotropical taxa. The presence of a medullary fibrous ring is prominent in all species where it becomes most obvious at the beginning of

secondary growth.

While no precise observations or ontogenetic studies were made on the endodermis, its presence in the stem is certainly striking. Bond (1931) studied its occurrence in the stem of Piper and observed that the casparian strip was of exceptional size with the walls of the endodermal cells often pitted both tangentially and radially. Furthermore in some species extra-casparian strips were developed in unusual positions on the walls of the endodermal cells. It was Bond's contention that in Piper the endodermis was a vestigial structure and of no primary significance for the plant. In this regard, Fahn (1982) noted that when present, the endodermis in the stem is usually more common in underground stems than in aerial, and was often also associated with flowering stages or with the presence of a starch sheath in herbaceous dicotyledons.

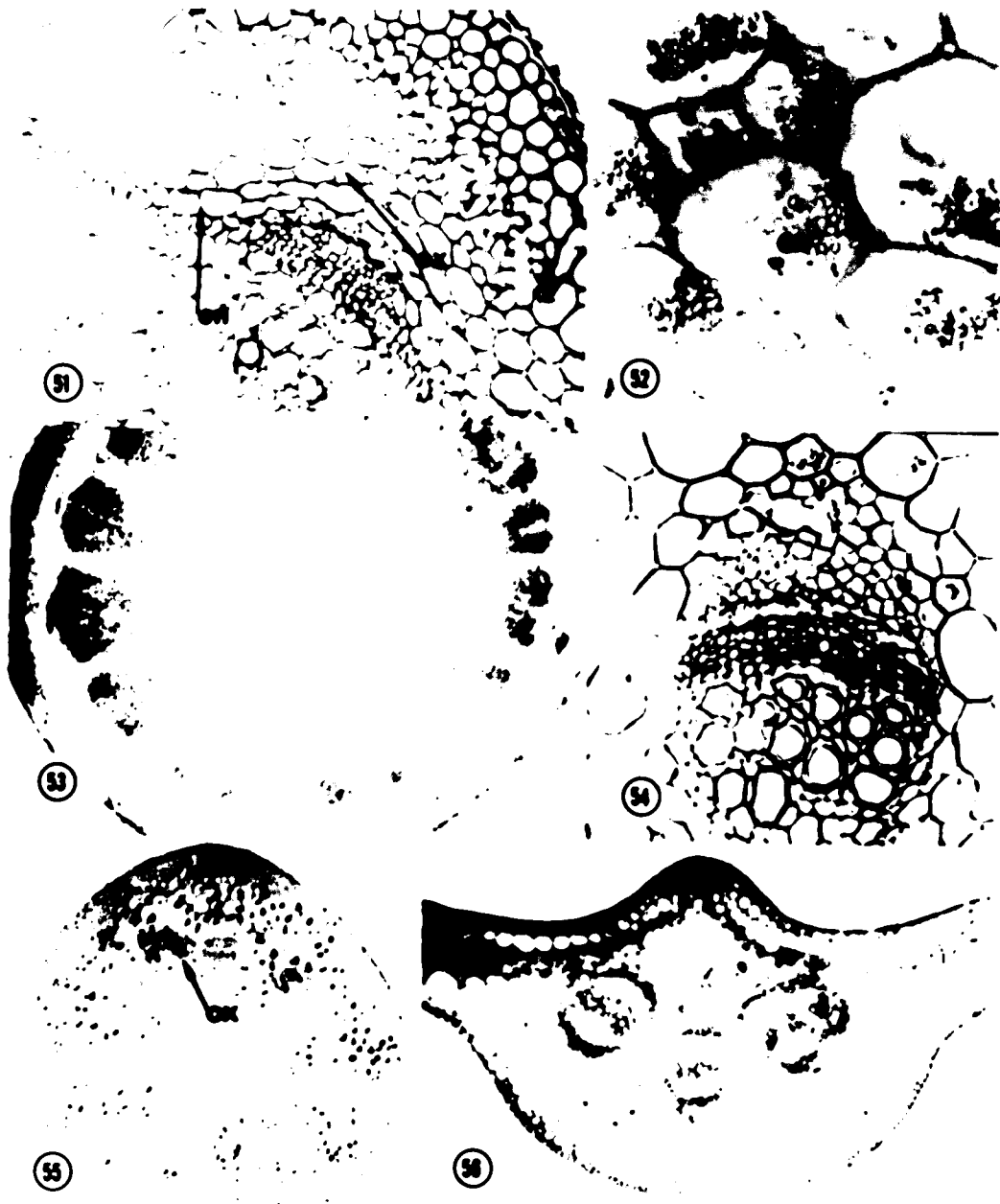
As was mentioned before the presence of medullary bundles in Piperaceae has been a subject of much research. In an elegant study De Bray (1886) surveyed nodal anatomy in the Piperales. His findings, while restricted to few taxa, seemed a reflection of a more or less general pattern in the family. According to De Bray, and supported by Datta and Dasgupta (1979), nodes are multilacunar in Piper, with 3-7 traces leaving equal numbers of lacunae, one exception is P. cubeba in which the nodes are three trace unilacunar (coincidentally in this species there are no medullary bundles). Medullary

bundles vary in number of rings as well as number of individual bundles. Thus, in some species there are two rings of bundles, while more generally there is only one. In the outer peripheral vascular cylinder two types of bundles are distinguished, large and small ones, less often there are no differences in size. The large bundles produce lateral branches at different levels below the node, and lateral branches from these bundles fuse. Similarly, the medullary bundles divide to produce lateral and middle traces. The middle traces move obliquely outwards and fuse with the peripheral laterals below or above the region of their fusion. These fusion bundles, described by De Bray, supply the leaves in the next upper node as do the main bundles of the lower node (Datta & Dasgupta, 1979).

The multilacunar node in Piper is often associated with a well developed sheathing leaf base, which is often described as a stipule or the base as having stipular margins. Majumdar and Pal (1961), in comparing species of Piper with Scindapsus (Araceae), came to the conclusion that leaves in Piper are exstipulate but with prominent sheathing leaf bases. Similarly Werbering (1970) described the leaves in Piper as having vaginal lobes or transitional forms approaching the character of true stipules.

Fig. 51-56. Primary stem anatomy of subgen. Ottonia

51. Piper hoffmannseggianum var. latifolium
(Callejas et al. 1779). Cross-section of stem.
A collenchymatous region is apparent towards
the periphery, calcium oxalate crystals (ox)
are abundant in the parenchymatous region of
the cortex, this one separated from the
vascular cylinder by the endodermis (en).
X 800.
52. Close up of the parenchymatous region of the
cortex showing the calcium oxalate crystals
(ox). (Material examined as in Fig. 51).
X 1000.
53. Cross-section of mature stem showing the
vascular bundles separated by the wide rays,
and the prescence of medullary bundles. (Ma-
terial examined as in Fig. 51). X 40.
54. Close up of medullary vascular bundle.
(Material examined as in Fig. 51). X 800.
55. Piper hoffmannseggianum var. hoffmannseggianum
(Mattos Silva 1812). Cross-section of petiole,
just above nodal region. Calcium oxalate
crystals (ox) are abundant towards the
periphery. X 40.
56. Piper hayneanum (Callejas 1608). Leaf cross-
section showing the midvein region. X 44.



No detailed investigation of the vascular anatomy of subgen. Ottonia was performed. However nodal structure of several species revealed a multilacunar node with a variable number of leaf traces (5-9) and an equal number of gaps. A cross-section of the petiole revealed that the traces remain free and form a distinct U-shaped ring (Fig. 55). There are no medullary bundles. The vascular bundles are surrounded by parenchyma containing large quantities of calcium oxalate crystals and almost forming distinct sheaths. Oil containing idioblasts are abundant in the pith. A well developed angular collenchyma layer is apparent on the periphery of the petiole. Little anastomosing occurs along the midvein and there is little change along the midvein of tissue distribution apparent in the petiole (Fig. 56). Calcium oxalate crystals are present along the midvein of all species and extend into the lamina itself in only a few. Structure of the petiole as well as the number of traces in it were previously described for P. jaborandy by Datta and Dasgupta (1979) who cited seven traces and seven lacunae. Their data was supposedly extracted from Metcalfe and Chalk (1950) who nevertheless did not make any reference to the number of traces or lacunae for P. jaborandi.

FLOWER DEVELOPMENT

Since the first treatment on flower development of

Piperaceae by Schmitz in 1872, it has been generally agreed by others that flowers in the family are radially symmetric with members arranged as trimerous whorls. This character has been used to support the position of the family in the Magnoliidae (Cronquist, 1982). Consequently it has been argued that in Piperales flowers are more likely to be derived as result of a reductionary series from a flower with many parts as in Magnoliaceae. That position has been recently challenged by Burger (1977) (who rests on the arguments of Raju (1961) that the flower of Saururus is an inflorescence) who put forward the hypothesis by which the flowers in Piperales are more likely to be the result of fusion of several flowers in the inflorescence of a chloranthaceous ancestor. His hypothesis has been framed in the context of a theory in which the trimerous arrangement of floral parts in monocotyledons and Piperales may indicate a more recent common ancestor for both groups than is generally recognized.

Tucker (1975, 1976, 1982a, 1982b, 1985), based on the floral diagrams presented by Schmitz (1872) and later by Eichler (1875-1878), questioned the initiation of trimerous whorls in the Piperales. It was her contention that the data provided by those authors suggested a different type of symmetry. Through a series of detailed studies, Tucker (see references above) found that flowers in the order display bilateral symmetry. Such symmetry results from paired or solitary initiation of

stamens rather than whorled, and thus differs from the radial helical arrangement found in the Magnoliidae. Furthermore, in Saururaceae (Tucker, 1975, 1976, 1985), adnation of floral parts in members of the family is strongly correlated with common uncommitted primordia which precedes bract and floral (Houttuynia and Saururus) or stamen (Anemopsis) initiation. It was her conclusion that at least on flower ontogeny there was no evidence to support a relationship between the Piperales and Magnoliidae. No data was found to suggest that flowers in Saururus resulted from condensation of an inflorescence or that flowers in the order were initiated in trimerous whorls. In short, flower structure in the family is rather specialized and of restricted distribution (bilateral symmetry, common primordia) with regard to other groups of plants.

Tucker's findings not only provided another derived feature supporting the monophyly of Piperales (and its isolated position in dicotyledons), but also disclosed a wide spectrum of variation in the number and arrangement of stamens and carpels in Piper. It was then worth examining flower ontogeny in subgen. Ottonia and, determining to what extent it deviated from that observed by Tucker (1982a, 1982b) in other species of Piper. Schmitz (1872) had already provided a floral diagram of Ottonia laeta (= Piper hoffmannseggianum). According to him, in that species, carpels are alternate to the stamens, with the pair of stamen in the frontal plane in

a 3-9 position rather than 5-7 position as in other species in Piper. Tucker (1982b) reproduced Schmitz's diagram but with a reverse order of stamen initiation. In it the first pair of stamens arise in the sagital rather than the frontal plane. This is most unusual since no species in Piper studied by her seemed to have this order of initiation. Additionally she referred the diagram to P. marginatum. The floral ontogeny of that species (Tucker, 1982) (palmate-nerved leaves, 3 carpels, stamens in frontal plane in a 5-7 position, anthers dehiscence upwards) does not correspond to the diagram nor does its taxonomic position. It was then necessary to verify Schmitz's data and compare it with that offered by Tucker.

The following description relates in large extent to stamen initiation as well as position, rather than vascularization which has already been provided by Schmitz (1872), and seems not to deviate from that described by Tucker in other species of Piper. While large numbers of species (Table II) were examined, the description is based on P. miquelianum (pedicellate flowers), other taxa being mentioned when they deviate in some aspect from that present in that taxon.

Inflorescences in P. miquelianum are terminal and first subtended by a leaf, both of which are enclosed in a single prophyll (Fig. 57). Bract primordia arise along the flanks of the inflorescence a significant distance from the apex. In P. miquelianum the apex at its peak of activity is nearly 430

um high (Fig. 57), but diminishes toward cessation, when floral bract primordia begin to arise near the summit. Most species do not deviate in length of the inflorescence apex; only in P. bartlingianum (sessile flowers) and P. corcovadensis meristems at their peak of activity may reach to 600 um in length.

Floral bracts are normally initiated by periclinal divisions in a T2 layer of the inflorescence meristem (Fig. 58). The small floral bract enlarges to become more or less clavate, becoming inflexed as to overtop and mask the floral apex. When the bracts have attained 40-56 um high, a floral primordium is initiated at its axil. At first it is a small mound which soon widens tangentially as a result of lateral initiation of two distinct growing sites corresponding to the first pair of stamen primordia (Fig. 59). By this time the floral bract possesses a large number of oil containing idioblasts as well as papillate hairs at its flanks (Fig. 60).

This first pair of stamens arises simultaneously. They are initially of equal size (Fig. 60), in a flower with the convex floral apex lying at the center. Flowers in neighboring orthostiches in the inflorescence are more or less at similar stages of development and widely spaced from each other (Fig. 61). Papillate hairs occur along the rachis in most species or 4-6-celled trichomes in taxa with sessile and congested flowers (e.g. P. hoffmannseggianum, Fig. 66). Just before the initiation of a single stamen primordium in the

anterior portion of the floral apex along the sagittal plane (Fig. 62), the first pair of stamens has already diverged in size (Fig. 63). The floral apex then appears somewhat tilted to the side. The third stamen, initiated on the anterior side, is soon followed by a fourth stamen opposite to the third (Fig. 64). This second pair of stamens along the sagittal plane is decussate to the first pair and equidistant from it. Thus the pair of stamens in the frontal plane appears in a 3-9 position. Stamens in the sagittal plane display distinct sizes from the beginning of initiation (Fig. 64). They arise sequentially rather than simultaneously as in the frontal plane. When sporocytes have undergone differentiation, the floral apex in longitudinal section (Fig. 65) appears apiculate, marking the beginning of carpel initiation. The four carpels arise in two distinct pairs in the frontal plane (at anterior and posterior positions). The stamens are inserted just below the gynoeceum (Fig. 66) and the flower is more or less distant from the rachis. In pedicellate flowers zonal growth below the level of attachment of the stamens marks initiation of the pedicel. Position of stamens and sites of initiation of carpels in the flower result in all parts being alternate with each other (Fig. 66).

No exception to the initiation of floral parts as described above was found among the species studied. There were no significant differences between species with pedi-

Fig. 57-62. Flower development in subgen. Ottonia.

All from Piper miquelianum var. miquelianum
(Callejas et al. 1870).

57. SEM photomicrograph. Young terminal inflorescence subtended by a leaf, the inflorescence meristem is somewhat tilted and about 430 μ m long, numerous floral bract primordia had already been initiated along the flanks of the inflorescence. X 100. Scale= 172 μ m.
58. Inflorescence, median longisection. Close up of initiated floral bract primordia towards the apex of the inflorescence. X 400.
59. SEM photomicrograph, young flowers with two stamen primordia initiated along the frontal plane. At this stage the stamens are of equal size. A floral bract (b) has been removed for easy view. X 600. Scale= 50.
60. Cross-section of flower in similar stage as that one in Fig. 59. Oil containing idioblasts are already present in the floral bract. X 800.

Fig. 57-62. Flower development in subgen. Ottonia. cont.

61. SEM photomicrograph, upper view of young flowers, with two lateral stamens (ls) along the frontal plane, and a third one being initiated in the anterior side of the sagittal plane. Some flowers with the floral apex tilted and the two stamens in the frontal plane already diverging in size. X 600.

Scale= 50 μ m.

62. SEM photomicrograph, close up of labeled flower in Fig. 61. X 1000. Scale= 10 μ m.



Fig. 63-66. Flower development in subgen. Ottonia. Fig. 63-65 from Piper miquelianum var. miquelianum (Callejas et al. 1870). Fig. 66 from P. hoffmannseggianum var. latifolium (Carvalho & Callejas 1880).

63. Cross-section of 2 staminate flower. The two stamens in frontal plane showing large difference in size, the concave floral apex lying at the center. X 800.
64. SEM photomicrograph. Four-staminate flower. Differences in size between the stamens in the two planes is evident and correlated with the time of initiation of lateral stamens in the frontal plane (ls) followed by that of stamens in the sagital plane, at the anterior (a) and posterior (p) positions. X 2000. Scale= 110 .
65. Cross-section of flower. Differentiation of sporocytes has already started. The floral apex at the center is apiculate and marks the beginning of carpel initiation. X 1100.
66. SEM photomicrograph, 4-carpelate flower. The two pairs of carpels (c) are alternate to the stamens. The stamens in frontal plane (ls) had been removed. X 3000. Scale= 110 ~~µm~~.



cellate and sessile flowers. Number of members in the single flower along the inflorescence remains constant. Solitary bracts, but no unisexual flowers, were found at the inflorescence apex.

Flower ontogeny in subgen. Ottonia agrees with that already described by Tucker (1982a, 1982b) for Piperaceae (bilateral symmetry, paired and/or single initiation of stamens). It does not fit however, the initiation of stamens in the group as illustrated by Tucker, but it concurs with that of Schmitz (1872).

As compared with other species in Piper, flower ontogeny in Ottonia differs in some aspects. The first pair of stamens in the frontal plane diverges in size before initiation of the third pair, and occurs at a 3-9 position. Number of floral parts is consistent in all flowers observed. Relevant to subgen. Ottonia and most likely to be derived in the group is the alternate position of floral parts. Such an hypothesis rests on the interpretation of possible evolutionary trends in Piperales. In it ottonioid flowers display one of several novelties (stamens and carpels alternate) resulting from the constraints in accomodating large numbers of primordia in a relatively small floral apex. A transformation series involving reduction of parts and shifting of stamen position can be framed in the following theory.

In Saururaceae an evolutionary trend involving reduction

of floral parts is already evident when comparing the 6-staminate and 4-carpellate flowers of Saururus with those of Houtunnya (3-merous) or Anemopsis (3 carpels). There is no a priori reason to consider that a reduction has occurred in the Saururaceae. But as seen in Piperaceae, reduction of parts occurs in almost every group in the family (see CLADISTICS). Such reductions are strongly correlated with the packing of large numbers of flowers in the inflorescence, formation of striate banded patterns, and changes in the plane of anther dehiscence (from vertical to horizontal, i.e upwards). Thus, Peperomia may very well represent an extreme point in such a trend with its 1-carpellate, 2-staminate flowers in which the anthers dehisce upwards. If reduction is an advanced feature, then the number of floral parts in Saururus may be interpreted as primitive. Occurrence of four carpels and six stamens is very rare in Piperales (subgen. Enckea and Arctottonia) and in all cases in basal groups (see CLADISTICS). It may be related to developmental constraints in accomodating large numbers of parts in a small floral apex. However in isolated cases, such constraints may have been overcome by strong selection favoring persistence of many parts. Not surprisingly in species with many floral parts both in Piperaceae and Saururaceae the ontogeny has somehow deviated from the general pattern. In Saururus, the first pair of stamen and carpel primordia is initiated along the sagital

plane (Tucker, 1975, 1976), unlike other species in Piperales (i.e. initiated along the frontal plane). In that genus the second pair of carpels is then initiated in the center of the floral apex. Crowding of parts is then reduced in the sagittal plane (as result of shifting of initiation sites in the floral apex from frontal to sagittal). In Piperaceae species with six stamens and four carpels are extremely unstable in the number of parts, especially related to the presence or absence of a fourth carpel (e.g. Piper amalago (subgen. Enckea), Tucker, 1982b). In subgen. Ottonia four carpels are very consistent in all flowers, but unlike in Enckea (the most basal outgroup of Ottonia) packing of four carpels has been overcome by reduction of stamens from six to four (present in a Enckea-like ancestor) and shifting of stamen position (analogous to that of Saururus) from a 5-7 to a 3-9 site.

Seed Coat

In Piper development of seed integuments has been described for P. nigrum by Kanta (1963) and Prakash and Kin (1982), P. medium and P. aduncum by Johnson (1902), P. betle by Yoshida (1960), as well as for Pothomorphe peltata by Swamy (1944). Integumentary primordia appear almost simultaneously just after the archaeosporial cell has become distinguishable (Johnson, 1902). The inner integument grows faster than the

outer and forms the micropyle (Prakash & Kin, 1982). The outer, slower growing integument rarely covers the ovule (Nikiticheva, 1981). When fully developed both integuments consist of two to four layers (Fig. 67). In subgen. Ottonia the two integuments are separated by a cuticular layer (Fig. 68) which remains distinguishable even after the nucellus has become differentiated into perisperm. By the time an embryo sac is well developed the outer layers of the outer integument are more or less degenerated (Yoshida, 1960). As embryo sac maturation progresses the outer layers of the inner integument become crushed against the inner layer of the outer integument (Yoshida, 1960). Generally two layers remain, the outer and inner of the inner integument, the exotegmen and the endotegmen, respectively. The endotegmen, which forms the main mechanical tissue of the mature seed coat, is generally filled with tannins (Johnson, 1902) (Fig. 69). From the initiation of the integumentary primordia to the formation of the seed coat, the integuments remain separated from the perisperm by the single-layered nucellar dermis (Fig. 69).

Examination of the mature seed coat in subgen. Ottonia revealed remarkable structural diversity particularly in relation with the exotegmen. In subgen. Ottonia the outer periclinal wall tears off and the inner periclinal wall becomes the main structural component of the seed coat very much like in Cordylanthus (Scrophulariaceae) (Chuang & Heckard, 1972). No

significant variation was found in the endotegmen; this layer consisting of tetragonal or pentagonal elongate cells with straight walls. The facet of the cells is at level with the anticlinal walls (Fig. 70). Towards the apex of the seed, the anticlinal walls become raised obscuring the cell facet (Fig. 71).

Based on variation found in the exotegmen, one may distinguish three types of seed coat structure (Table 1): 1) in P. bartlingianum, P. darienense, and P. hoffmannseggianum the cells are pentagonal-isodiametric with straight to more or less irregularly curved anticlinal walls (Figs. 72, 73), the edges at level with the anticlinal walls or the facet of the cell convex and thus the anticlinal walls appear immersed (Fig. 73, P. bartlingianum), or often the facet of the cell is concave and the anticlinal walls appear slightly raised (Fig. 74, P. hoffmannseggianum), 2) in P. francovilleanum and P. alatabaccum the cells are elongated and many sided, anticlinal wall curvature is V-shaped (most prominent in P. francovilleanum, Fig. 75), and edges are slightly raised and either verrucose in P. francovilleanum or granulose in P. alatabaccum (Fig. 76), and 3) the third type, found in the rest of the species, is characterized by anticlinal walls with a distinctive omega-shaped curvature (Fig. 77), the edges are prominent and may cover 1/4-1/2 of the cell facet (Fig. 78), and the cells are many-sided and oriented perpendicular to the

axis of the seed (Fig. 79). Examination of selected species in the outgroup (see CLADISTICS) revealed that the first type of seed coat is rather common while the second and third types were restricted to subgen. Ottonia. Additionally the structure of the endotegmen is invariant in the outgroup and subgen. Ottonia.

Although not all the types of seed coat are useful for phylogenetic analyses, they nevertheless provide good complementary characters for species delimitation. Thus, the seed coat of P. darienense provides the best argument to separate this taxon from P. piscatorum and P. ovatum, both of which overlap the former in many other characters. Similarly, P. piscatorum displays a seed coat structure (Fig. 77) which supports its separation from P. hoffmannseggianum (Fig. 74). The type of seed coat found in P. alatabaccum and P. francovilleum confirms their relationships both of which have also the same type of seed (see Seed). This is important because P. francovilleum is a highly derived taxon in subgen. Ottonia, and it is extremely difficult to establish with certainty its relationships. While providing a most interesting set of characters, seed coat structure, unfortunately, is very uniform in those taxa with pedicellate flowers, with most variation related to the extent of which the edges cover the cell facet (Figs. 78, 79).

Fig. 67-71. Seed anatomy and seed coat structure of subgen.

Ottonia.

67. Piper alatabaccum (Plowman et al. 12641).

Fruit, longitudinal-section. Both integuments already well differentiated, the outer integument partially collapsed against the inner fruit walls. The inner integument (ii) with 3-4 distinct layers. X 600.

68. Piper bartlingianum (Plowman & Davis 12540).

SEM photomicrograph. Seed coat. A cuticular layer covering the exotegmen (outer layer of the inner integument). This cuticular layer separates the two integuments. X 1000.

69. Piper alatabaccum (Plowman et al. 12641).

Fruit, cross-section with single containing seed. The perisperm fills nearly 90% of the seed (pe) and is separated from the endotegmen (et) by the nucellar dermis (nu). The exotegmen is lying against the fruit walls, these with numerous oil containing idioblasts (oi). X 1000.

70. Piper corcovadensis var. corcovadensis. SEM

photomicrograph of the endotegmen. X 1000.

71. As in Fig. 70, but toward the apex of the

seed. X 600.

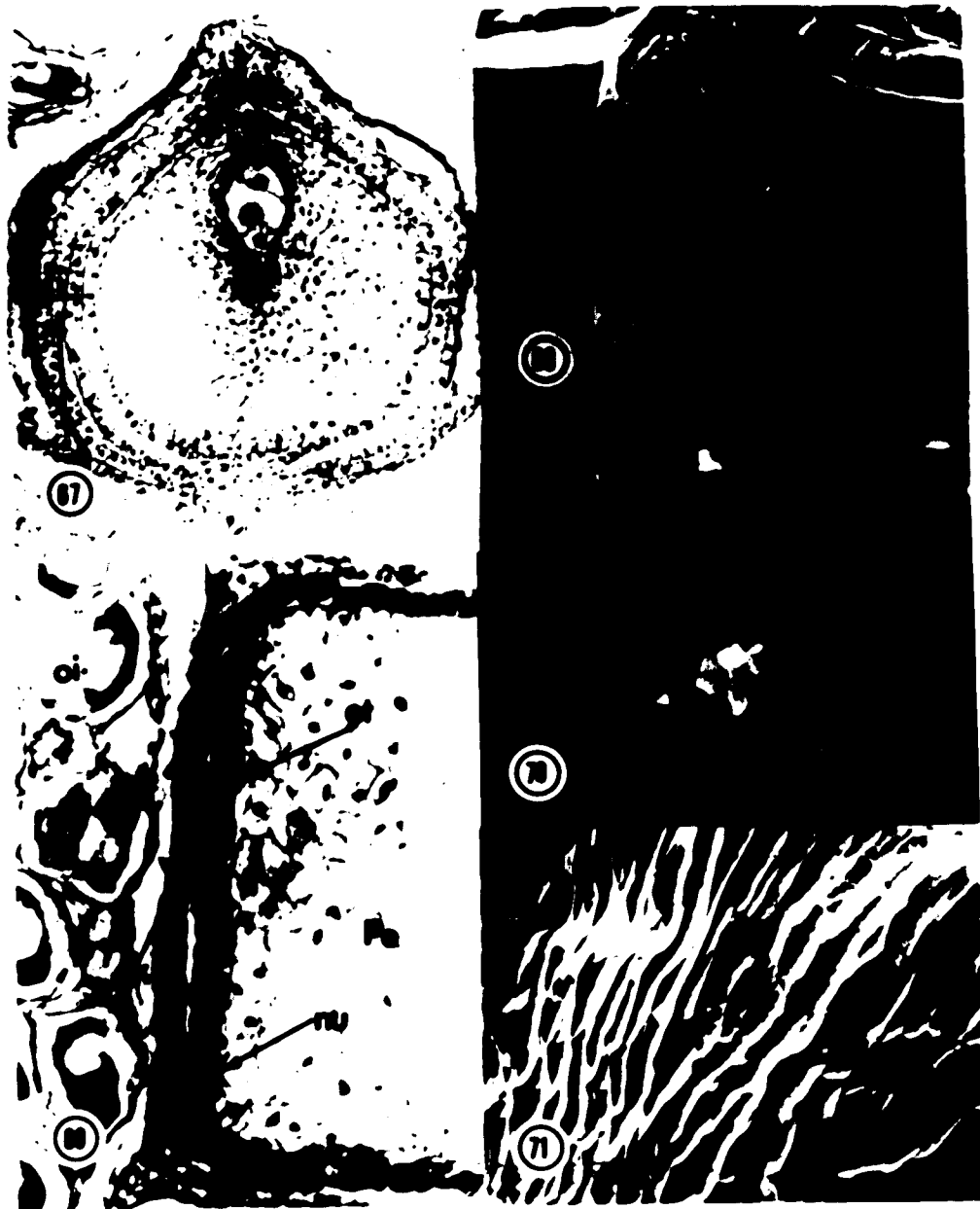


Fig. 72-77. SEM photomicrographs of the seed coat in subgen.

Ottonia. Showing:

72. Piper bartlingianum (Mori et al. 9166).

X 600.

73. Piper darienense (Folsom 7829). X 450.

74. Piper hoffmannseggianum var. latifolium
(Callejas et al. 1779). X 600.

75. Piper francovilleum (Wurdack et al. 43537).

X 650.

76. Piper alatabaccum (Plowman et al. 12641).

X 600,

77. Piper piscatorum (Daly & Callejas 1377).

X 600.

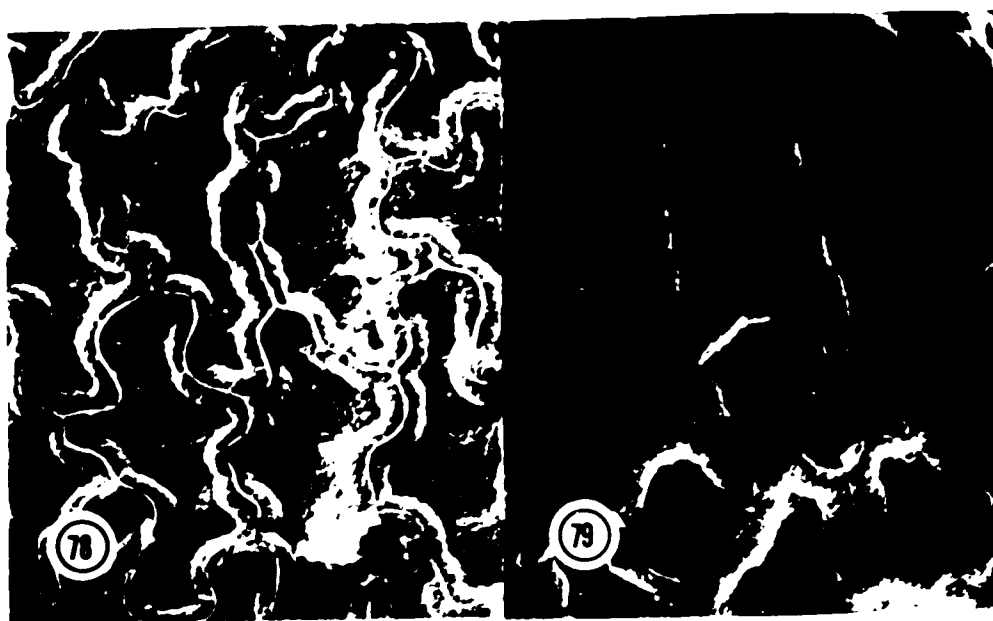


Fig. 78-79. SEM photomicrographs of the seed coat in subgen.

Ottonia. Showing:

78. Piper anisum (Callejas et al. 1637b). X 500.

79. Piper hayneanum (Callejas et al. 1608). X 400.



ECOLOGY

Habitat

Members of subgen. Ottonia are small to medium size shrubs occurring in the understory of lowland neotropical forests. Within this life zone and range of distribution species are found growing along sandy banks of rivers in fully exposed sites (e.g. P. bartlingianum), or rarely in non-forested areas. Piper hoffmannseggianum var. hoffmannseggianum often occurs in restingas (sea level) along the coastal forest of Bahia (Brazil), where plants are normally found as epiphytes in the root system of Attalea funifera. Little-disturbed habitats are preferred by most taxa, but a few widespread species (P. corcovadensis, P. miquelianum, P. anisum) grow in secondary forests where they are often a common element of the understory. Most species grow at elevations between 50-400 m. Piper francovilleianum however is normally found from 50 to 1500 m in NW Amazonia where it grows at the base of the Guiana Shield in the riverine forests to the wooded slopes of the sandstone bluffs.

Flowering and fruiting occur throughout the year in P. bartlingianum, while in other species flowering individuals are generally found from January to August, and fruiting

restricted from October to February. Insect damage is almost absent in living plants, although in P. alatabaccum insect larvae are normally found in the fruit, they apparently do no damage to the seed.

The species are rare for the most part, many of them still known from less than a dozen localities. In subgen. Ottonia 14 taxa are known to occur in the Atlantic coastal forest of Brazil, an ecosystem whose rapid destruction certainly qualifies several species as endangered since less than 1% of the original area remains undisturbed according to Mori et al. (1981).

Pollination

Flowers in subgen. Ottonia lack nectar as may be the case for all Piperaceae. Pollen, therefore, in the absence of any other attractant, becomes the main if not the only reward. Flowers are protogynous as evidenced by dehiscence of anthers long after immature fruit has already been formed. In species with pedicellate flowers stamen dehiscence occurs after the pedicel has attained its maximum length. Flowers are self-incompatible as seems to be the case for most species of Piper (Gomés Pompa & Vásquez Yanes, 1974; Prakash, 1982). Field observations in subgen. Ottonia revealed Trigona bees and small flies as the most active visitors to the inflorescences. Both

have been reported as the main pollination agents in Piper (Semple, 1974). As seen from floral development, stamens arise in pairs along two distinct planes. Those in the first, frontal plane, shed pollen before those in the sagittal plane. In this latter plane anthers often do not open or the stamens fall, or the pollen grains collapse. In pedicellate flowers pollen is released from the anthers only after the pedicels have attained their final length.

In those taxa with sessile flowers onset of the staminate stage is difficult to discern. Usually inflorescences elongate prior to shedding of pollen. Whether inflorescences are at pistillate or staminate stages they seem to be equally visited by insects. In the staminate stage pollen is probably the main attractant. As is the case for many protogynous nectarless flowers at the pistillate stage, attraction of pollen feeders to ottonia flowers is probably classified as temporary deceit. As suggested by Faegri and van der Pijl (1979), attraction in the type of flowers found in ottonias may be by the sight of still unripe anthers. But this has to be confirmed. In some species of Piper (e.g. P. brachypodon) inflorescences at pistillate stages are variously colored (a result of pigments in the floral bracts) and thus color may be another attractant.

In subgen. Ottonia inflorescences in all stages are white to cream-colored, becoming greenish in fruit. Some species

(e.g. P. anisum) have inflorescences with strong anise odors (present in infrutescences as well). Species with pedicellate flowers, as compared with those having sessile flowers, retain their individuality during the staminate stages. In such cases the stamens surround and obscure the fertilized ovary. Whether or not this represents a more effective attractant for pollen (compared with sessile flowers) is yet to be explained.

PHYTOCHEMISTRY AND PHYSIOLOGICAL ACTION

Species of subgen. Ottonia have been extensively used by natives in South America, and to lesser extent in Central America, as a source of remedies for a variety of illnesses. Reports on the medical properties of several species appeared as early as 1648 (Piso & Margrave, Historia Naturalis Brasiliae). In the last century much attention was devoted to the therapeutic effects of decoctions of subgen. Ottonia (Dunstan et al., 1895), and since then several active compounds have been isolated (see Makapugay et al., 1983). I did not attempt to perform chemical screenings or isolation of active compounds in subgen. Ottonia. Only a brief summary of the phytochemistry of the group and the physiological action of several compounds is given here.

The present treatment recognizes 21 species, 12 of which are known in Brazil under the common name jaborandi (or local

variations of it, e.g. joao-borandin, jaborandinho, jambú, etc.). The name has its origins in the Tupí-Guaraní language. The etymology of the word is rather obscure but it probably refers to the properties of a diverse group of plant species which prevent or treat poisoning in animals (Coursino de Moura, 1884).

Outside Piperaceae the name jaborandi is applied to many plant species but more specifically to Pilocarpus (Rutaceae). The effects of Pilocarpus and Piper substances are very similar. Not surprisingly, species in both genera are customarily placed in popular pharmacopias as taxonomic synonyms (Penna, 1946). Less often the chemical compounds of Pilocarpus are erroneously reported as being extracted or present in Piper species (Guimarães, 1984).

In Pilocarpus (for a complete review see Kaastra, 1982), several species are known to produce pilocarpine an ester alkaloid of wide use in ophtalmology for the treatment of glaucoma. At the end of the last century and beginning of the present, pilocarpine became very popular in Europe as a pharmaceutical to treat several afflictions. Its effects were praised as diaphoretic, silagoge, and local anaesthetic. Many people in Brazil who were aware of similar effects produced by species of subgen. Ottonia became interested in the group as a potential source of useful pharmaceuticals (Coursino de Moura, 1884). The wide use of ottonias as local anaesthetics and

effective remedies for toothache prompted several works on the species therapeutic effects (Calvet, 1887; Coursino de Moura, 1884)

Abundant literature exists on the physiological effects of ottonias known as jaborandi. However since plant material was rarely described or even mentioned, it is difficult to determine the true identity of the particular species being used. Thus by 1887 Julio Calvet, a Brazilian medical student, wrote an extensive dissertation on the Brazilian jaborandi. Calvet was probably the first to describe the physiological effects of ottonia decoctions. Calvet's experiments led him to the conclusion that ottonioid species were effective as diaphoretic but not as silagoges. Unfortunately, according to Coursino de Moura (1884), Calvet's experiments were too superficial, and since he gave no indication of the plant used his conclusions were dubious.

Coursino de Moura (1884), aware of Calvet's inaccuracies, prepared a similar dissertation. In his work, Coursino de Moura, described and illustrated the species used. The author described the taxon as Piper jaborandi (=P. anisum); however, his illustration corresponds to P. hoffmannseggianum var. latifolium. Using leaf and root decoctions he administered different doses to patients in the local hospital and carefully monitored their reactions. Physiological effects observed included: excessive sweating, salivation, somnolence,

increased body temperature, difficulties in swallowing and breathing, and increase in pulse rate. The effects tend to disappear after 24 hours. Coursino de Moura's observations agreed with those reported in the literature by plant collectors. More important the effects of Ottonia compounds simulate those of pilocarpine. Coursino de Moura concluded that the species were useful as diaphoretics and as treatment for toothache. His observations suggested however that the excessive salivation produced by the plant products precludes its uses in minor surgical procedures. It is important to mention that local users in Brazil note that continued root chewing causes tooth loss.

Coursino de Moura's work did not go unnoticed and in 1895 Dunstan and Garnett isolated the active principles from the roots of Ottonia ovata (= P. ovatum) obtained from Trinidad and therefore dispelled any doubt of the species identity. The main active principle, an amide derivative, piperovatine, has since been isolated by others from the same species (Price & Pinder, 1970; Hansël et al., 1980). More recently piperovatine has been recovered from leaf and root extracts of Ottonia anisum (Giesbrecht et al., 1981), P. corcovadensis (Soares Costa et al., 1981), and P. miquelianum var. hirtellum (Makapugay et al., 1983). I have not seen voucher material from the first two species; however, the voucher specimen from the Makapugay work is beyond any doubt the variety given above

(in that work the authors cited the species as P. frutescens, an erroneous determination).

Makapugay et al. (1983) confirmed that the numbing effects on mouth parts produced by roots of Ottonia species corresponded to those of piperovatine. Such confirmation suggested that piperovatine was very likely to be present in other species of the Ottonia-complex. The amide is not exclusive to ottonioid species however, and has been isolated from Piper callosum (Pring, 1982) and P. nigrum (Sokolov, 1952). The presence of piperovatine in P. callosum is not surprising since that species is known to be used as diaphoretic and anaesthetic (Murça Pires, pers. comm.). However the presence of such a compound in P. nigrum should be examined more critically. If present in that species, then piperovatine could be an active compound widespread in the genus Piper.

The use of species of subgen. Ottonia as local anaesthetics and silagoges is only one of several for the group. Local names and other uses aside from the aforementioned are given after the description of each species.

CLADISTICS

A survey of the published schemes of classification proposed for Piperaceae (Miquel, 1839; Kunth, 1839; De Candolle, 1869, 1923) reveals several views concerning the monophly of Ottonia as well as its closest relatives in the family. It is

the purpose of this section to evaluate such hypotheses in light of a cladistic analysis.

Cladistics or phylogentic systematics is a classification technique. It was originally proposed by Hennig (1966), and in its basic tenets, follows many of Darwins original ideas on evolutionary theory. According to Hennig (1966) classifications should reflect phylogenies if we are going to look at them as reflecting an evolutionary process (see Nelson 1984, for a different view). Within such classifications groups should be monophyletic and ranked according to the branching sequence of their ancestry in such a way that sister groups are given equal rank.

Criticisms of the cladistic school have been directed mainly at the validity of the three tenets mentioned above (Mayr, 1978, 1984). It has been argued that phylogenies as such can not be reconstructed from extant species alone, but only if a fossil record is present. The impossibilities of an adequate fossil record (Eldredge, 1978; Nelson, 1972), as well as ambiguities in polarizing ancestral characters in fossils (Cracraft, 1982) has been argued by some, thus making it extremely difficult to reconstruct phylogenies by relying on fossils. Consequently many have given up the reconstruction of phylogenies as an impossible task. Classifications are then being constructed as simple measurements of degree of similarity or to reflect gaps in evolution, most often

resulting in a conflict between ranking and monophyletic units.

Hennig did not deny the problems concerning the fossil record, but restated the problem of phylogeny reconstruction in a different way. An approach to the phylogeny of a three species group could be attempted not by asking if A was the ancestor of B or C, but rather if B and C have a more recent common ancestor with each other than any of them have with A. Thus a diagram depicting relationships in terms of recency of common ancestry (a cladogram) should provide a fair approach to phylogeny. This diagram while less specific than a phylogenetic tree yet provides as much information as the tree (by now it should be clear that a cladogram is not a tree but rather a general statement of many trees; see Nelson & Platnick, 1982; Eldredge & Cracraft, 1983; Ax, 1985).

A basic tenet of Hennigian principles is that similarity alone can not reveal a genealogy. Rather, if evolution is to be accepted as "descent with modification", then groups should be characterized by the acquisition of evolutionary novelties. Recency of common ancestry will then be inferred by shared derived features. This reasoning will lead to the notion that all characters in a phylogeny represent evolutionary novelties at some point. Since each has a different generality, their distribution will result in a hierarchy. (For example, zygomorphic flowers appear to be derived in Piperales; however,

that character state (one of two states in character "flower symmetry") will not be informative about the relationships within the order. On the other hand, a single ovule, which is derived in Piper and Peperomia will specify a more inclusive group (the two genera above) members of which share a more recent common ancestor with each other than with Saururaceae).

Discovery of synapomorphies implies, however, that we have to distinguish between primitive and derived character states, i.e. to establish polarity. Many approaches have been proposed to determine polarities (See Crisci & Stuessy, 1976, for arguments on common equals primitive; Stevens, 1980, for a review of many different techniques). Among them, ontogeny and outgroup comparison have become prominent (see Brooks & Wiley, 1985; Kluge, 1985; and Nelson, 1985, for a discussion on the ins and outs of both approaches). The outgroup approach was more or less implicit in the writing of some Hennig contemporaries (Maslin, 1950). It has been explicitly stated in an operational form by Watrous and Wheeler (1981). The method is based on a simple methodological technique: in a group of species (the ingroup) the state of a two character states system, occurring in the most closely related outgroup (the sister group being the most important one) and the ingroup is likely to be primitive, while that restricted to the ingroup is advanced. This technique has been criticized on the basis that statements of character polarity of this kind for phylo-

genetic reconstruction implies a previous knowledge of phylogeny (Guedes, 1983). Donoghue and Cantino (1984), and later Madison et al. (1984) have demonstrated that even in the absence of a well-corroborated sister group, the outgroup comparison technique is still possible to use. In their outgroup substitution approach, Donoghue and Cantino (1984) suggested to first construct cladograms with each of the outgroups before proposed as possible sister groups of the study group, then search for areas of congruence among the resulting cladograms. This approach has been used recently by Gilmartin et al. (1986) in determining the most likely sister group of a monophyletic group in the genus Tillandsia. When outgroups are well known however, the global parsimony approach of Madison et al. (1984) may be an adequate model. In it both ingroup and outgroup relationships are resolved simultaneously. The results are cladograms which are globally parsimonious (i.e. those which minimize the number of ad hoc hypothesis, homoplasies, to explain the phylogeny of the group (Farris, 1983). The model is powerful, but restricted by the lack of knowledge on the cladistic relationships of most study groups (plants and animals as well).

While the outgroup method provides a powerful tool for establishing character polarity, it does rest ultimately on choosing the right outgroup. Furthermore, in the case of having a solid hypothesis for the outgroup, the analysis may

still result in many equally parsimonious cladograms. That is, some character-state distributions suggest different phylogenies for the ingroup. Noncongruence of this kind results from the extensive homoplasy displayed by many characters in living organisms. Characters may be acquired independently, reverse, or be lost many times. Normally however, examining the cladograms may reveal that some of the polarity statements were wrong, or the characters were coded incorrectly, or the data at hand were not enough to provide a solid hypothesis on the genealogy. Also some of the species may not belong to the study group or, on the other hand, some taxa were left out from it. All these possible problems then require a cladistic analysis of characters, statements on the monophyly of the study group, polarity assessments, species delimitations, etc. By doing this the method provides hypotheses which are subject to testing. Eventually the cladogram may be refuted in part or in full or new data may be congruent with the old and suggest a solid hypothesis for the genealogy of the study group.

Due to the lack of a formal classification in Piper and the poor resolution in the current taxonomy of the genus, a hypothesis on the relationships of subgen. Ottonia is difficult to assert. In order to evaluate hypotheses on the relationships of Ottonia I decided to elaborate a cladistic analysis for the entire genus Piper. This analysis is here provided as an appendix to the present treatement. It is based on an

almost uninterrupted seven year study of neotropical representatives of Piper and to lesser extent on species in the Old World tropics. The data base for the analysis is then based largely on herbarium specimens, field collections, and local floras. Other types of information, such as anatomy, histology, embryology, chemistry, etc., have been gathered from the literature. Names for many of the terminal groups recognized in Piper had been previously published in the classification schemes put forward by Kunth (1839) and Miquel (1839), but also to a lesser degree by de Candolle (1869, 1923) and Trelease (1935). Certainly not all 1000 species in the genus were examined, rather only representatives within each potential monophyletic unit. The ins and outs of this analysis are provided in Appendix 1. A list of characters, data matrix and a tentative list of all groups (or species complex when no formal names have been proposed) with their descriptions, distribution, number of species is given as well.

It should be understood that the cladogram for Piper is a preliminary hypothesis which in many respects (lack of resolution in many groups) is still poorly supported. Nevertheless it provides a framework for discussing not only the possible relationships of Ottonia but also of many other groups whose position in the family is poorly understood.

Before going into a formal discussion of the position of Ottonia in Piper, several important points should be made.

All terminal groups in the cladogram of Piper are here interpreted as subgenera, including Ottonia. The reason for this derives from the fact that if Ottonia (as a natural group) is going to be recognized as a genus, then a decision should be made on the ranking of the other terminal groups. In many cases, this will imply the transfer of large number of species from Piper, with the resulting new combinations. In subgenus Chavica this would involve at least 250 species and in Steffensia (including most species in the neotropics) nearly 400. Many nomenclatural problems surround the taxonomy of the genus and creation of new names will be detrimental for the taxonomy of the group. On the other hand, accepting the present system is absurd. Piper as currently defined is a large heterogeneous genus surrounded by an indeterminate number of satellite genera which are connected with Piper in no specific way. The classification is not stable, nor does it provide information retrieval. Recognized genera have been based on gaps or discontinuities (e.g. pedicellate flowers in Ottonia, axillary inflorescences in Trianaepiper, etc.) found in many groups, but without consideration of the monophyly of those groups. This had serious consequences, the most evident being the recognition of paraphyletic groups. For example based on the hypothesis on the monophyly of Ottonia, there is no natural group in the subgenus which consists only of species

with pedicellate flowers. However, assuming that the present hypothesis is wrong, then we still have to make a decision on the rest of the species which share all the synapomorphies of Ottonia except the pedicellate flowers. Either we recognize that group as a genus, or else as is presently done, we leave it in Piper. Then Piper will be defined by the absence of characters (no pedicellate flowers), furthermore it will imply that the sister group of Ottonia (i.e. with sessile flowers) shares a more recent common ancestor with Piper than with Ottonia, or that all shared derived features between Ottonia and its sister group have evolved independently. In that case we have to search for another possible sister group, one which so far does not seem to exist in Piper.

That is my reasoning for the decision to place Ottonia within Piper. In this connection the cladogram for Piper (Fig. 99) provides an initial step towards a system of classification for the genus.

Infrageneric Relationships of subgenus Ottonia.

Based on the cladogram for Piper (Fig. 99), the following hypotheses can be put forward on the relationships of Ottonia.

Subgenus Ottonia is a natural group in Piper defined by

the following synapomorphies: saccate-galeate floral bracts, stamens in a 3-9 position and alternate with the carpels, 4-ribbed seeds, and leaves pinnate-brochidodromous throughout. It is one of four terminal groups in a most basal clade in the lineage of the neotropical species of Piper. It is most closely related to subgen. Schilleria (Piper callosum, P. aequale and relatives, see Appendix 1; including Carpunya sensu Presl, not sensu Miquel (1856)), a group with which it has in common 4-staminate flowers, brochidodromous venation, and floral bracts with entire (not lobulate) margins in the anterior extreme of the distal portion (the lamina). As in subgen. Ottonia most species in Schilleria are restricted to the southeastern forests of Brazil. Subgenus Schilleria differs from subgen. Ottonia in its 3-carpellate fruits, seeds triangular angulate, and stamens in a 5-7 position. Both subgenera have as a sister group a clade containing subgen. Enckea and subgen. Arctottonia. These two groups have in common leaves with basal acrodromous venation. Pedicellate flowers occur in both subgen. Arctottonia and Ottonia, and in both cases in groups which have a restricted distribution (subgen. Ottonia in SE Brazil, subgen. Arctottonia in N Mexico), thus indicating an independent evolution for the pedicellate flowers in both groups.

These four subgenera are characterized by the occurrence of isobutylamides of the piperovatine type, and leaves with two

distinct callosities at the base. Other synapomorphies may include the shoot apex emerging from within the prophyll with the inflorescence being free from the leaf base.

The relationships outlined above seem to agree with those proposed by Kunth (1839), who, based on the similarities of Ottonia and Enckea (number of carpels, similar floral bracts, widely spaced flowers), suggested that one might consider the latter as a subgenus of the former. Kunth indicated also his reluctance to lump both groups under Ottonia based on the apparent distinct arrangement of stamens in Ottonia as compared with those in Enckea. Both Miquel (1844) and later Presl (1852) were impressed by the similarities of P. carpunya and P. lessertianum with Ottonia. Miquel (1844) placed both taxa in Ottonia based mostly on the leaf venation; Presl went a step further and described both groups under his new genus Carpunya, which included also species of Ottonia with sessile flowers. Presl argued that the lack of banded patterns in the inflorescence, leaf venation, and persistence of four stamens at the base of the fruit (which he erroneously interpreted as a perygonium) seemed to confirm a close relationship between Ottonia and Carpunya. Piper lessertianum and P. carpunya are more closely related to P. callosum and distantly to P. aequale both of which were originally placed by Kunth in his genus Schilleria.

There is no indication as suggested by Miquel (1844) that Zippelia is the most closely related group to Ottonia. That monospecific taxon (from SE Asia), while of uncertain relationships, does not share any of the synapomorphies of Ottonia. It seems most closely related to subgen. Piper (partially adnate floral bracts). On the other hand it is the only species of Piper in the Old World tropics with bisexual pedicellate flowers, and is unique in the Piperales by its glochidiate fruits and the wide laminar (?) connective.

De Candolle's (1823) hypothesis on the relationship of Ottonia suggested that the group consisted of all species of Piper with bisexual pedicellate flowers (i.e. Acrtottonia, Zippelia, and species with pedicellate flowers in Ottonia). Such an hypothesis, however, is not supported by the cladogram and would require at least 10 more homoplasies to explain such a grouping.

Cladistic analysis of subgen. Ottonia

Given the hypothesis that subgen. Callianira is the sister group of subgen. Ottonia, a cladistic analysis for the latter was then performed. It was important to determine from the cladogram to what extent all species with pedicellate flowers form a distinct monophyletic unit in the subgenus.

The cladogram was elaborated by the outgroup technique, with statements on ancestral characters made at the ingroup rather than at the outgroup node (Wiley, 1981). As suggested by Madison et al. (1984) polarizing at the outgroup node results in cladograms which are globally parsimonious. This provided the cladistic structure of the sister groups. Since no analysis has yet been performed in subgen. Schilleria, distribution of many characters are not known; furthermore, the taxonomy of that group should be examined before we know the real number of taxa (especially with regards to the taxonomy of Piper aequale). For this reason I have restricted the analysis for character polarity to seven taxa in Schilleria which I believe conform to a potential monophyletic unit in that subgenus, and includes P. callosum, P. concinnum, P. xylosteoides, P. sprengelianum, P. carpunya, P. aequale, and P. mikanianum. Five specimens of each species were examined for gross morphological characters and seed coat structure. Due to the restrictions imposed on herbarium specimens, leaf histology was only examined in P. xylosteoides (Callejas et al. 2001) and P. callosum.

Fifty-five characters (with no intraspecific variation) were scored for the 21 species. Since not all characters could be weighted unambiguously, all are given equal weight. Some may represent transformation series (vesture of the floral bract), but were scored in binary form (indicating 0 for primitive and 1

for advanced). Seed coat structure was not possible to determine in all species and was scored in the data matrix as missing (indicated by ?). The same was applied to some characters in leaf histology (i.e. distribution of calcium oxalate crystals).

Cladograms were generated from the data matrix (Table. V) using Swofford's PAUP (phylogenetic analysis using parsimony) program version 2.3 (Swofford, 1984) in an IBM computer 3081 at Triangle Universities Computation Center (Duke University, Durham, NC). Among the correct options available, the following were used: MAXTREE=50 (maximum number of equally parsimonious trees to be printed), HOLD=5 (number of trees to be held at each step in the tree construction), SWAP=local (rearrangement of tree topologies in search of shorter trees) used in conjunction with MULPARS=yes (discovering equally parsimonious trees before they are input to the branch swapping procedure). Character state optimization (OPT) uses Farris' method (1970) (solving ambiguities in ascribing ancestral states). Trees are rooted using an hypothetical ancestor plesiomorphic for all characters.

The list of characters and their polarity follows and precedes the discussion of the cladograms. Some of the polarities are not discussed because the character distribution has already been discussed in MORPHOLOGY or/and ANATOMY.

Characters and character-state polarity:

1. Stamen position in the frontal plane.

3-9 position=1

5-7 position=0

Data from Tucker (1982a, 1982b) and the present treatment. See flower development for more extensive discussion on the possible derived nature of stamen position in subgen. Ottonia.

2. Stamen size in the frontal plane.

One distinctly larger than the other=1

Both stamens of equal size=0

Tucker (1982b). In all species of Piper so far examined, stamens in the frontal plane do not diverge in size at any stage. Stamen divergence in size in subgen. Ottonia occurs before the initiation of the third stamen in the anterior median position along the sagittal plane, and is maintained thereafter. Judging from the size of stamens in the frontal plane in species of the sister group, the character seems to be derived in subgen. Ottonia.

3. Stamen anther vestiture.

With prominent raised oil containing idioblasts=1

Oil containing idioblasts, absent or impressed, but never raised=0

While restricted to few species in subgen. Ottonia, it

is not unique in the subgenus and occurs elsewhere in subgen. Isophyllon. It is absent in subgen. Callianira (otherwise not to be confused with the prescence of oil glands at/or throughout the connective).

4. Flower insertion.

Pedicellate=1

Sessile=0

In using only the sister group, the pedicellate condition is advanced. If secondary outgroups are considered (subgen. Arctottonia and Enckea) the assesment is equivocal. This is because both conditions occur in those groups. Judging however, from the flower development, the condition may have arisen independently within each type of flower (those with four stamens as in subgen. Ottonia and six in subgen. Arctottonia). As will be seen in the cladograms, the assesment on the polarity of this character is supported by several other independent synapomorphies.

5. Stigmas.

On a style=1

Sessile=0

The style is not to be confused with the apicular portion in many fruits derived from the long-decurrent stigmatic lobes, as in Piper callosum (subgen. Callianira).

6. Seed outline.

Four-ribbed=1

Angular=0

7. Seed plane of bisection.

Asymmetric=1

Symmetric=0

Asymmetric seeds in P. piscatorium result from the unequal development of the four ribs (see Seed).

8. Type of symmetry.

Bilateral=1

Radial=0

9. Rib outline.

Sulcate=1

Not sulcate=0

10. Rib departure at the fruit apex.

Forming distinct shoulders, concave=1

Not forming shoulders, convex=0

11. Rib in frontal plane.

3 times longer than wide=1

10-15 times longer than wide=0

12. Floral bract distal portion.

Long-decurrent with the rachis=1

Free from the rachis=0

13. Vesture on the distal portion of the floral bract.

Long-villous=1

Papillate=0

The long-villous floral bracts are restricted to P. bracteo-villosum in subgen. Ottonia, and are otherwise absent in the sister group. Long-villous bracts are known elsewhere in Piper from P. monzonensis (subgen. Isophyllon), P. mirmecophyllum (subgen. Chavica) and a new species, yet not described from Espírito Santo in subgen. Isophyllon (Hatschbach et al. 48623)

14. Vesture on the distal portion of the floral bract.

Short-pubescent=1

Papillate=0

As in character 13, this refers to the vesture on the posterior extremity of the distal portion. No to the presence of marginal trichomes (i.e. marginally ciliate).

15. Floral bract vesture

With prominent raised oil containing idioblasts=1

Oil containing idioblasts impressed=0

16. Flower spatial arrangement.

Widely spaced=1

Tightly congested=0

All species with racemose inflorescences have widely spaced flowers, but there are also few species with sessile flowers. This character is not the same as character 4.

17. Inflorescence position at the flowering node.

Pendulous=1

Erect=0

Pendulous inflorescences are unknown in the sister groups. They are known elsewhere in Piper in many species of subgen. Macrostachys.

18. Flowering portion orientation (at fruit).

Curved=1

Straight=0

Curved flowering portions are common in Piper especially in species of subgen. Steffensia (Piper aduncum and relatives), becoming erect however at fruiting stages probably as result of the rachis lignification.

19. Vesture of rachis.

Fimbriate=1

Sparsely pubescent=0

The character is often correlated with tightly congested flowers; however, in subgen. Callianira it is absent. It is otherwise present in the basal sister group of subgen. Ottonia and in few species of subgen. Enckea (e.g. Piper sanctum)

20. Vesture of rachis.

Densely papillate=1

Glabrous=0

21. Fruit size.

5-7 mm long=1

1-2.3 mm long=0

22. Floral bract insertion at fruit.

Remaining sessile=1

Becoming pedicellate=0

23. Floral bract size.

5-10 times shorter than the fruits=1

2 times shorter or equal to the fruits=0

24. Floral bract orientation at fruit.

Remaining inflexed=1

Becoming refelexed=0

25. Fimbriate rachise vesture.

Brownish=1

White=0

26. Fruit vesture.

Pubescent=1

Glabrous=0

27. Pedicel vesture.

Pubescent=1

Glabrous=0

28. Pedicel length.

Shorter than the fruits=1

As long as or longer than the fruits=0

Pedicels are present only in subgen. Ottonia; therefore, polarities on many states in this character cannot be

assessed precisely by outgroup comparison. In the present case, as well as in character 27, the polarization was based on the distribution of the different states in subgen. Artoccttonia.

29. Anticlinal walls in the seed coat.

V-shaped=1

Straight=0

30. Edges of cells in the anticlinal walls of the seed coat.

Granulose=1

Verrucose=0

31. Distribution of oil containing idioblasts in the leaf.

Absent in the mesophyll (i.e. restricted to the veins)=1

Present in the mesophyll=0

32. Oil containing idioblasts along the veins.

In contact with tracheids=1

In contact with parenchyma cells=0

33. Number of cell types in the palisade.

Two=1

One=0

34. Veinlet endings.

With 3-4 tracheids=1

With 1 tracheid=0

35. Calcium oxalate crystals in the mesophyll (excluding the midvein region)

Present=1

Absent=0

36. Anticlinal walls of upper epidermis cells.

Sinusoid=1

Curved=0

37. Anticlinal walls of lower epidermis cells.

Straight=1

Sinusoid=0

38. Leaf insertion.

Long-peltate=1

Subpeltate=0

39. Adaxial hypodermis.

Present=1

Absent=0

40. Leaf base.

Decurrent with the petiole=1

Not decurrent with the petiole=0

41. Leaf vesture.

Long-villous=1

Short-pubescent=0

Three types of trichomes occur in subgen. Ottonia, 1-2-celled papillate hairs, 3-4-celled hairs (stiff, opaque erect), and 16-25-celled villous hairs (thin, translucent, flexuous). The first type is a synapomorphy for all Piperaceae. The second type is one class of many which includes, hirtellous, hispidulous, and is the com-

monest in the family. Long-villous hairs are more restricted and occur in isolated taxa in many subgenera. Villous hairs are not homologous with the second type of hairs (Mohandas & Shah, 1982). Long-villous trichomes do not occur in any species examined of subgen. Callianira.

42. Vesture along the leaf margin.

Present=1

Absent=0

Marginally ciliate leaves are absent in subgen.

Callianira. The character occurs in Piper regardless of whether leaf lamina is pubescent or glabrous.

43. Long-villous leaves adaxially.

Villous along the midvein=1

Glabrous along the midvein=0

The character was polarized using P. francovilleanum as an ingroup.

44. Short-pubescent leaves abaxially.

Short-pubescent along the midvein=1

Glabrous along the midvein=0

45. Leaf size (l/w ratio).

9-16 times longer than wide=1

Less than 4 times longer than wide=0

46. Myrmecophyllous domatia.

Present=1

Absent=0

47. Leaf lamina

Bullate=1

Plane=0

48. Fimbriate vein vestiture.

Short-hirtellous=1

Glabrous=0

Presence of hairs along a fimbriate vein is apparently restricted to subgen. Ottonia. It is not correlated with the presence of pubescence on other parts of the lamina. It occurs in species with glabrous or pubescent leaves. It does not seem to be present in taxa with long-villous hairs.

49. Prophyll's apex.

Long-attenuate=1

Acuminate=0

50. Prophylls distribution along the flowering branches.

Persistent at all nodes=1

Early caducous=0

51. Number of internodes between flowering nodes.

5-7=1

1-2=0

52. Floral bract size in distal portion.

Broad (=0.5-0.8 mm wide)=1

Narrow (=0.2-0.3 mm wide)=0

53. Fruit bulges.

Present=1

Absent=0

54. Number of inflorescences along flowering branches.

1=1

5-9=0

55. Anticlinal walls in the seed coat.

Omega-shaped=1

Straight=0

Discussion

The analysis resulted in 50 equally parsimonious and topologically very similar trees. Each tree had a length of 76 and a consistency index (CI) of 0.724 (CI indicates the relative number of homoplasies in the data, from a relation between the number of characters and state changes in the tree; PAUP considers both reversal and parallelisms equally).

While the initial number of trees was 50, these included many sets which differed only in the position of terminal taxa in an unresolved polytomie. This was due to the fact that PAUP considers every apparent resolution of a polyotomie as a different tree. Swofford (1984) indicated that apparent resolutions of a polyotomie in equally parsimonious trees are considered as being different, so the user can distinguish between some of the following: 1) cases in which all resolutions are equally acceptable but the polyotomie occurs regardless of character reconstruction (e.g. the polyotomie including P. bracteo-villosum, P. guimaraesianum and P. brevi-

nodis (Fig. 83) is unresolved in all trees, some of them differing only in the position of these taxa in the polytomie), and 2) cases in which in equally parsimonious trees some characters, reconstruction resolves some of the polytomies (e.g. in some trees P. darienense appears in a basal polytomie (Fig. 81) if character 48 is placed at the root of the tree, in other trees there is a perfect dichotomy, but only if character 48 appears above the root of the tree (Fig. 80)).

Thus all trees in the final output can be reduced to four cladograms representing two basic cladogram configurations (a basal polytomie, or a dichotomy, Figs. 80. 81). Each configuration with two variants (related to whether or not a polytomie is resolved, Figs. 82, 83). Since all cladograms are equally parsimonious, not much confidence can be placed in the alternate solution of a polytomie.

Albeit the uncertainties in choosing a cladogram, all of them nevertheless showed significant congruences. Thus four clades appeared consistently in all cladograms, these for the sake of the discussion will be abbreviated as A (clade of P. francovilleanum, P. alatabaccum, and P. bartlingianum), B (P. darienense), C (clade of P. piscatorum and P. hoffmannseggianum), and D (clade containing all species with pedicellate flowers plus taxa with sessile flowers, P. ubatubensis, P. scutifolium, P. klotzchianum, P. ottonoides). One of the four resulting cladograms is illustrated in Fig. 84.

TABLE VI

CHARACTER DATA MATRIX FOR SUBGENUS OTTONIA

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alatabac	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Anisum	1	1	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Bartling	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Brevinod	1	1	0	1	0	1	0	0	?	0	1	0	0	0	0	1	0	0	0	0
Corcovad	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Darienen	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucalypt	1	1	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Francovi	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Guimarae	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Hayneanu	1	1	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Hoffmann	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0
Klotzsch	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Miquelia	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Ottonoid	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0
Ovatum	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Piliovar	1	1	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Piscator	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Rizzinii	1	1	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Scutifol	1	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0
Ubatuben	1	1	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0
Vill-bra	1	1	1	1	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	0

TABLE V

-continued-

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Ancestor	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alatabac	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0
Anisum	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Bartling	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0
Brevinod	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0	0	0
Corcovad	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dsrienen	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Eucalypt	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Francovi	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0
Guimarae	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0
Hayneanu	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hoffmann	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Klotzsch	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Miquelia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ottonoid	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Ovatum	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Piliovar	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Piscator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rizzinii	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Scutifol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ubatuben	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vill-bra	0	0	0	0	0	0	0	0	?	?	?	0	0	?	0	0	0

TABLE V

-continued-

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alatabac	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Anisum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Bartling	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brevinod	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	?
Corcovad	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Darienen	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Eucalypt	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Francovi	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	1	0
Guimarae	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?
Hayneanu	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Hoffmann	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Klotzsch	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Miquelia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ottonoid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ovatum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Piliovar	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Piscator	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Rizzinii	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Scutifol	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Ubatuben	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Vill-bra	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	?

Fig. 80-83. Cladistic analysis of subgen. Ottonia.

80-81. Two main cladogram configurations resulting from the cladistic analysis.

82-83. Two variants for each of the cladogram configurations in Figs. 80, 81. E= Piper brevinodis, P. guimaraesianum and P. villosobracteatum, F= P. hayneanum, P. rizzinii and P. eucalyptophyllum, G= P. anisum, P. piliovarium, P. scutifolium and P. ubatubensis, H= P. klotzchianum and P. ottonoides. Refer to the text for details. Circles indicate parallelisms, stars indicate reversals.

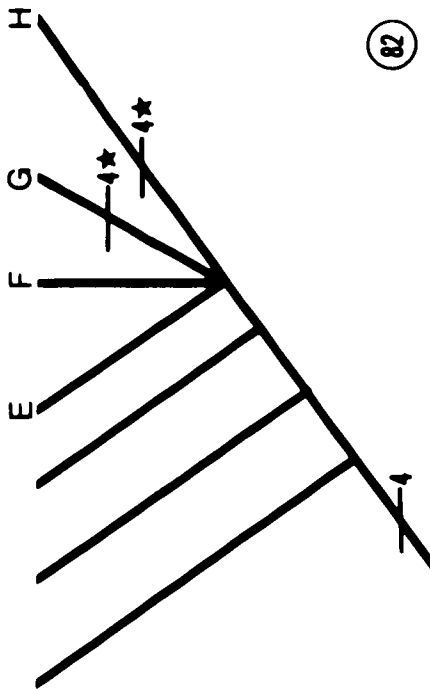
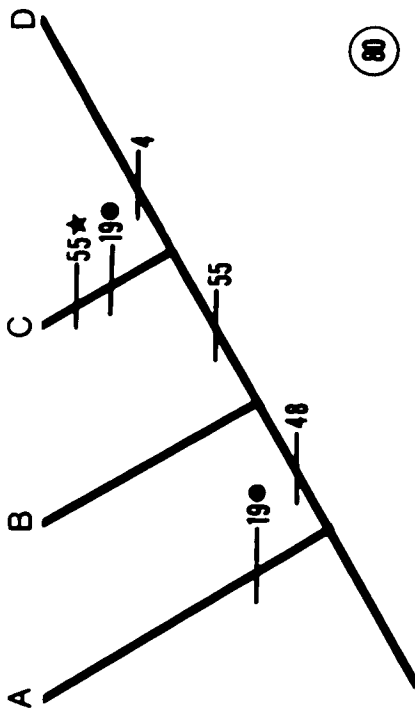
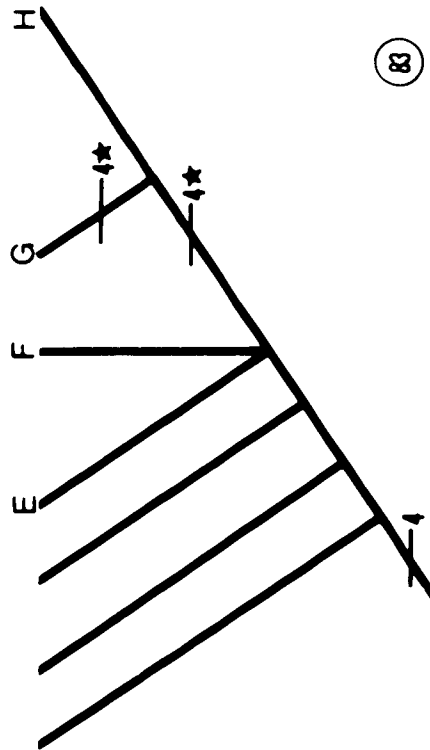
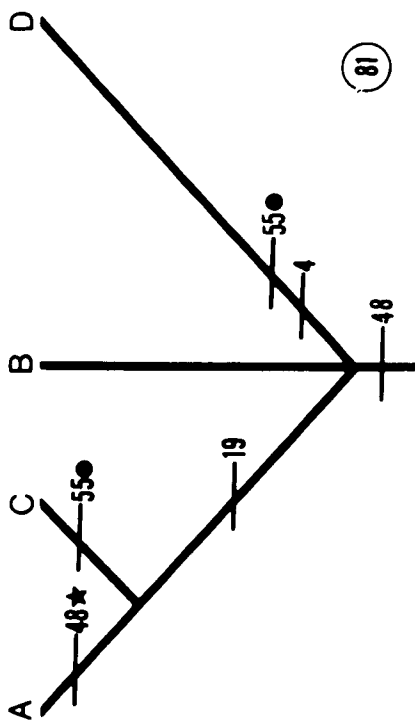
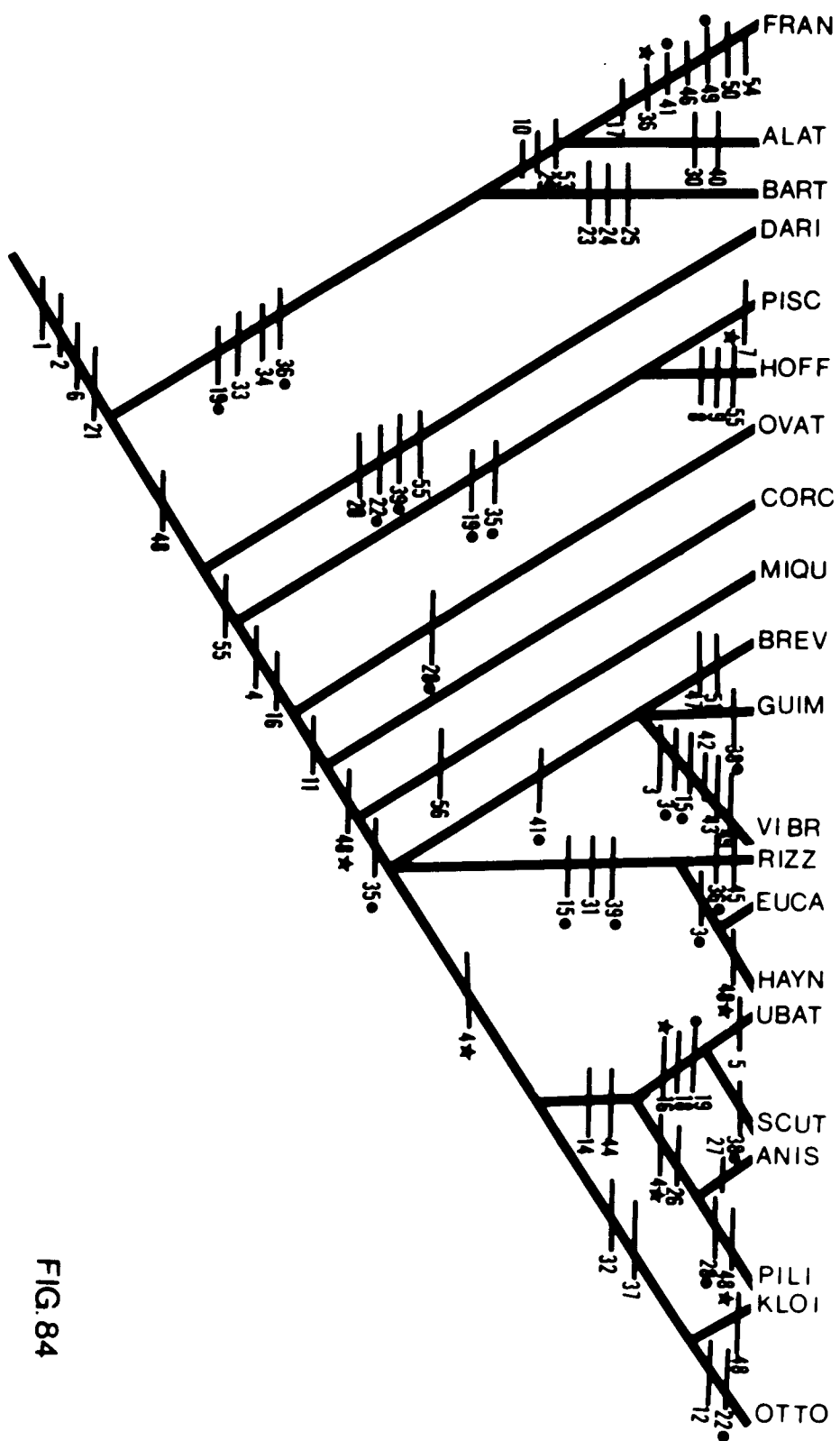


Fig. 84. Cladogram for subgen. Ottonia.

Circles indicate parallelisms, stars indicate
reversals. See text for details.



Lack of resolution in the cladograms resulted in the different positions for clade B, which appeared as a sister group of clade A, but only in a cladogram with a basal polytomie. The placement of the former clade assumes that character 19 arose only once in clade A and B, but that character 55 arose independently in P. piscatorum from all other species in subgen. Ottonia. I prefer the alternate solution, character 19 as an independent gain and 55 as a reversal (Fig. 80) because I have more confidence in the consistency of seed coat structure (55), than in the relatively simple character fimbriate rachises (19). Furthermore it appears that character 19 may have arisen independently many times in portions of the cladogram, otherwise supported by strong synapomorphies (fimbriate rachises arose independently also in P. scutifolium and P. ubatubensis). In taking the cladogram in Fig. 84 as an hypothesis on the cladistic structure of subgen. Ottonia, one has yet to consider that a major lineage (including clades B, C, and D) is supported by a rather weak synapomorphy. Character 48 (hirtellous fimbriate vein), while apparently restricted to subgen. Ottonia, nevertheless displays too much homoplasy as judged from the fact that it seems to reverse itself four times. Additionally, one may still consider that in some species the low number of specimens sampled (e.g. P. ubatubensis, P. piliovarium) does not allow one determination of the extent of variation in this character. Elimination of this

character resulted in the partial collapse of a dichotomous cladogram and a polytomie below the node of P. miquelianum. Also P. klotzchianum and P. hayneanum appeared as taxa without synapomorphies. Uncertainties due to character 48 can be solved only with additional data, the degree of congruence then indicating to what extent the taxa supported by character 48 are distinct clades.

Relevant to the systematics of subgen. Ottonia is clade D, which is supported by four synapomorphies (4, 16, 11, 35), one of which, character 4 (pedicellate flowers), shows multiple reversals (or alternatively (Figs. 82, 83) as being gained independently, but in either case resulting in equally parsimonious cladograms). As earlier stated (list of characters and state polarity), polarity for insertion of the flowers (pedicellate or sessile) is equivocal when one considers secondary outgroups. If the character is taken from the analysis, however, a clade including both sessile and pedicellate flowers is still supported by three synapomorphies. This would imply that in either case the pedicellate condition arose independently within subgen. Ottonia or was lost several times. Furthermore it supports the suspicion that a group with pedicellate flowers does not conform to a distinct clade in subgen. Ottonia. A cladogram elaborated by hand, and with the prior assumption that the species with pedicellate flowers are a distinct clade, is much less parsimonious than the ones

here presented (10 more homoplasies). In it character 48 occurs six times, while character 35 appears as an independent gain three times. In this cladogram character 48 does not support any major clade, character 4 does not show any reversal, but then characters 11, 16, 14, 44, and 55 appear independently many times. Again I agree much more with a cladogram allowing for few reversals in character 48 and no homoplasy in otherwise more complex characters.

Resolution of some terminal groups in clade D, however, is far from being achieved. Thus, P. brevinodis, P. guimaraesianum, and P. bracteo-villosum appear as a polytomie, the relationships of which are yet not clear in subgen. Ottonia (Fig. 84). Such unresolved clades could be caused by the poor number of specimens sampled for each species (otherwise known from the type collections, and in the case of P. brevinodis from immature specimens), and the fact that some characters which may be useful to separate the species (i.e. based on leaf shape P. guimaraesianum and P. bracteovillosum appear as very distinct from P. brevinodis) were not used in the cladistic analysis (i.e. leaf shape was found to be quite variable within some taxa). Despite the lack of resolution in portions of the cladogram, many clades agree well with previous groups proposed in subgen. Ottonia (Yuncker, 1973). Piper corcovadensis, P. miquelianum, and P. ovatum appear as basal to all other species in clade D. Those three taxa are

all widespread species, and based on the character analysis, are the less derived ones. They overlap each other in most characters and a more conservative taxonomy may result in lumping all of them. Piper corcovadensis appears without any synapomorphy. In the particular case of that species, the most variable one, the taxon as here circumscribed may include more than one entity, probably corresponding to var. blanchettii. Based on the material studied as well the type of characters sampled, recognition of two species will result in two weakly defined taxa. Clearly more collecting as well as use of other characters (flavonoids, chromosomes, etc.) will help to elucidate the taxonomy of P. corcovadensis. Piper anisum, on the other hand, appears to be more closely related to P. piliovarium than P. corcovadensis or P. miquelianum (Yuncker, 1973). Also, P. ottonoides and P. klotzchianum are unrelated to other species with sessile flowers and appear as a rather isolated group in a clade including otherwise all species with pedicellate flowers.

Outside clade D, other terminal groups as clade A and C concur with relationships postulated by previous students in the family. Clade B (P. darienense) seems to be an isolated taxon in subgen. Ottonia. This species overlaps in vegetative characters with species in clade B (i.e. P. piscatorum) and in seed characters with clade A (i.e. P. bartlingianum); however none of those similarities includes a clear synapomorphy. In

floral structure P. darienense is unusual among species occurring outside the southeastern Brazil forest, especially by the lack of fimbriate rachises and the presence of sessile floral bracts. Additionally, it is the only taxon in subgen. Ottonia occurring west of the Andes. Possible explanations for the present distribution of that species are examined in the following section.

Biogeography of Subgenus Ottonia

Based solely on the geographic distribution of species in subgen. Ottonia (Figs. 85-88), one may divide it into three major groups: 1) species restricted to the southeastern forests of Brazil, 2) species restricted to Amazonia, and 3) species (i.e. P. darienense) occurring west of the Andes. From the previous cladistic analysis it is clear that those groups do not conform to distinct clades. Rather the cladistics suggest that exchange of species has occurred amongst the three areas, especially between the southeastern Brazilian forest and Amazonia. Thus, there are two pairs of species which include taxa in Amazonia but with the sister species in the southeastern forest (i.e. P. piscatorum in Amazonia and P. hoffmannseggianum in SE Brazil (Fig. 86A), likewise P. otto-

noides and P. klotzchianum (Fig. 87B)). Distributions of species pairs in both regions is not uncommon and has been well documented by several authors in other groups of plants (Smith 1962; Soderstron & Calderón, 1974; Gentry, 1979; Mori et al. 1981; Prance, 1983; Steyermark, 1983) and animals as well (Brown, 1977, in butterflies; Haffer, 1982, and more recently Cracraft (unpublished data) in birds. Relationships between Amazonia and the forests of SE Brazil have been generally discussed within the context of the refuge theory (Andrade-Lima, 1982; Prance, 1982, and authors in previous references above). According to that theory forests of SE Brazil represent one of the areas of tropical forests where climatic conditions remained favorable during fluctuations of the Pleistocene (dry or humid climate periods as result of glaciations). Accordingly, continuous forest cover was disrupted and with it many organisms. Thus speciation followed isolation into separate populations. Unfortunately there is little data on the extent of forest cover as well as the splitting of it during the Pleistocene and therefore the sequence of disruptions between the areas is difficult to ascertain. At present Amazonia and the southeastern forest remain isolated (probably since late Tertiary, Prance (1983)). In any case, subgen. Ottonia seems to represent one of several groups in Piper (others including subgen. Isophyllum and subgen. Schilleria) with a major center of

diversity in southeastern Brazil. Indeed 16 of the 21 species in the subgenus are restricted to that region. The area surrounding Rio de Janeiro is conspicuous in its high number of endemics, and I believe this is not an artifact of collecting (as has been often suggested, Mori et al. (1984)).

From the previous paragraphs, it is clear that the present distribution of some species in subgen. Ottonia could be the result not only of dispersal, but also a vicariant event between the SE Brazil forests and Amazonia. The lack of resolution in the cladograms precludes any explicit hypothesis on the recent common ancestor of P. darienense, and therefore its position in subgen. Ottonia. This prohibits a more solid analysis (in the context of vicariance biogeography, see Nelson & Platnick, 1982)) on the relationships between the forests of SE Brazil, Amazonia, and the W Andes. Some hypotheses can be advanced however, judging from the distribution of P. darienense (Fig. 86B), its present range coinciding in N South America with refuge areas (i.e. Catatumbo, Magdalena, Sierra Nevada, and Chocó; Prance (1983)). Therefore it was more widespread before the Pleistocene, surviving today only in areas in which the forest cover did remain stable (distribution in Central America may be a secondary dispersal event from Chocó). This will coincide with an earlier isolation of this species by the uplift of the Andes (before the Pleistocene) from the rest of ottonias.

Fig. 85. Geographic distribution of subgen. Ottonia.

A. ● Piper francovilleianum; ☆ P. scutifolium; ▲ P.
ubatubensis. B. ● P. bartlingianum.

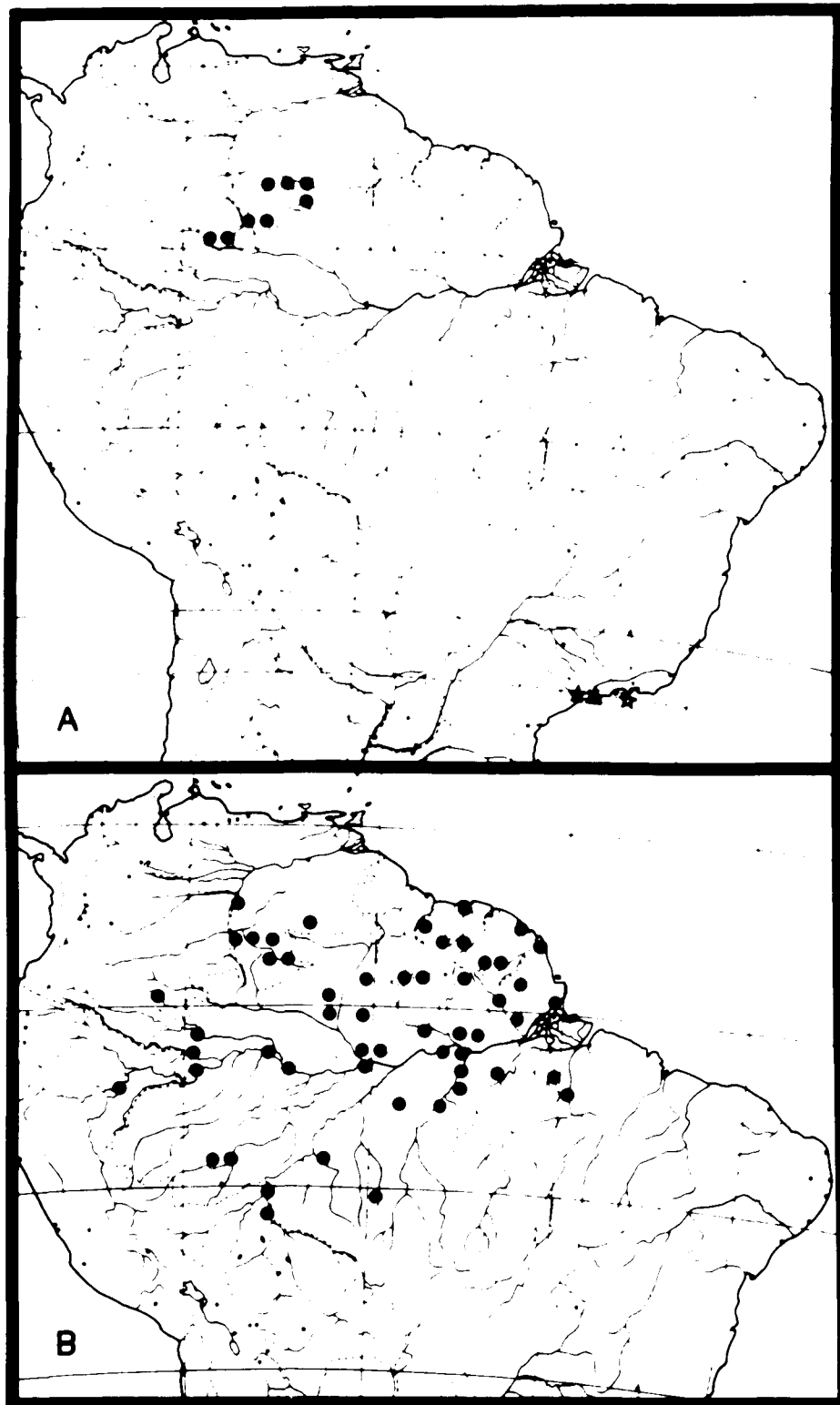


Fig. 86. Geographic distribution of subgen. Ottonia.

A. ◆ Piper alatabaccum; □ P. hoffmannseggianum var. hoffmannseggianum; ☆ P. hoffmannseggianum var. latifolium; ● P. piscatorum. B. ★ P. darienense.

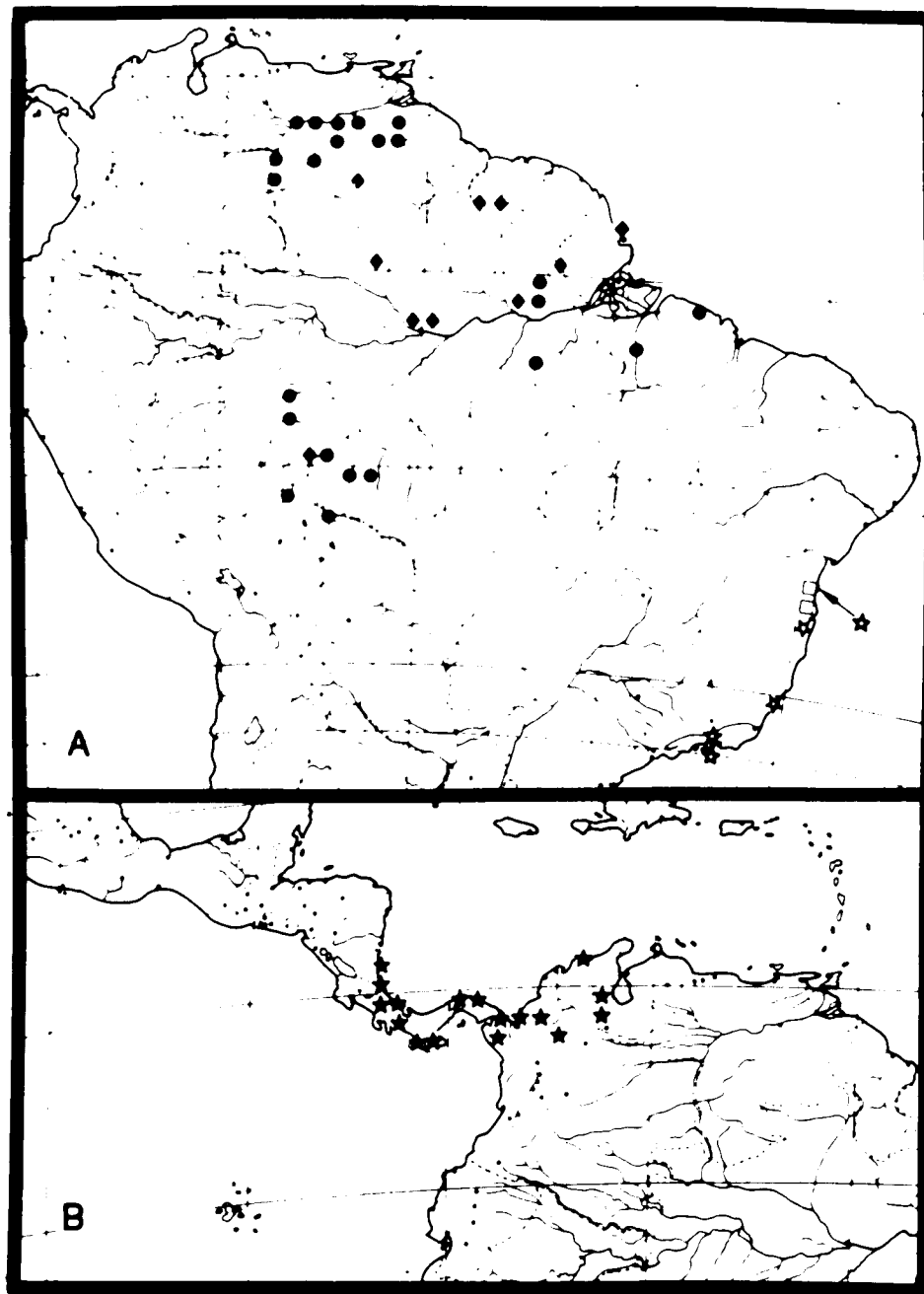


Fig. 87. Geographic distribution of subgen. Ottonia.

A. ★ Piper brevinodis; ★ P. guimaraesianum; ● P. klotszchianum; ■ P. ottonoides; ▲ P. villosobracteatum. B. ▲ P. eucalyptophyllum; ● P. hayneanum; ★ P. rizzinii.

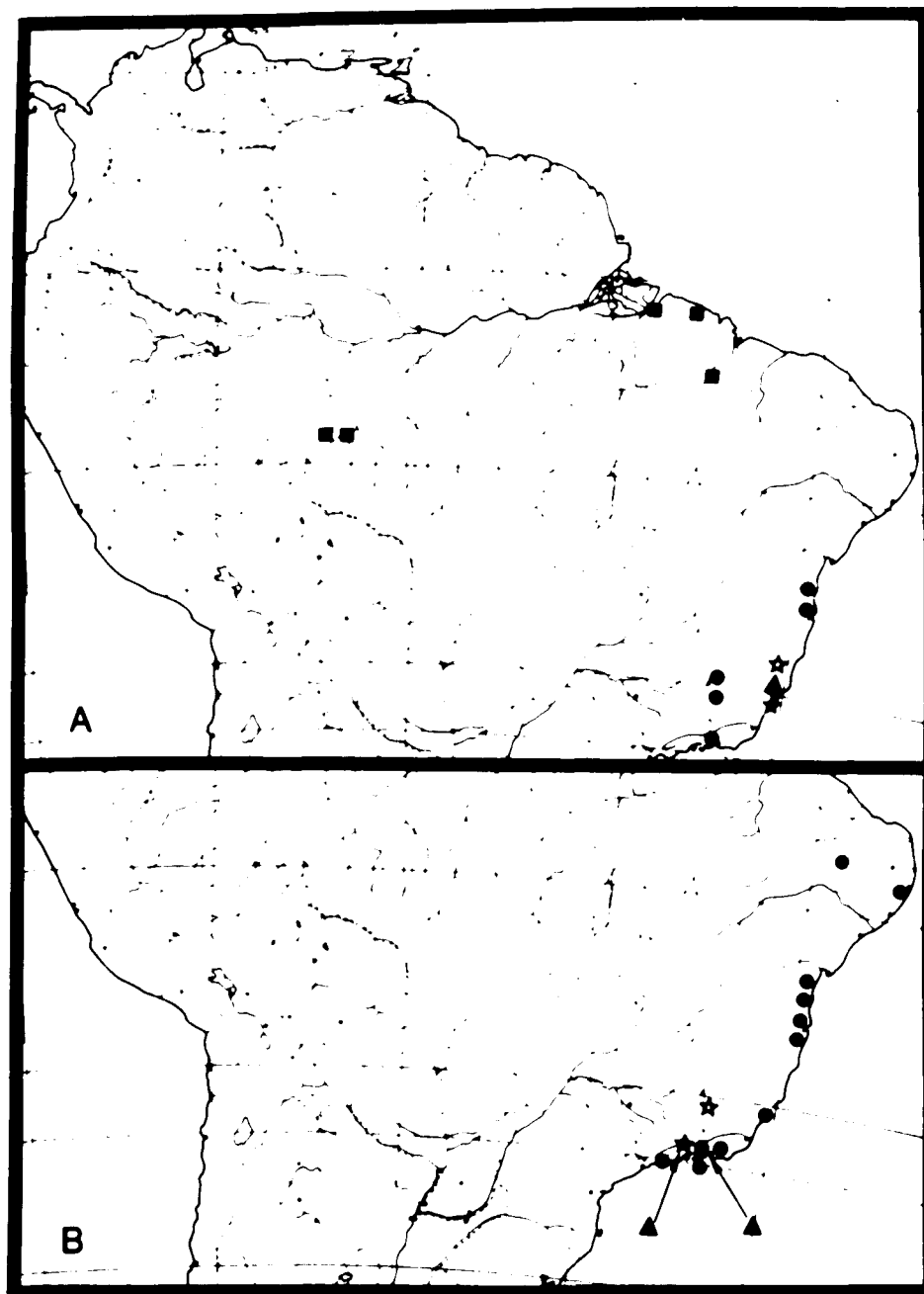
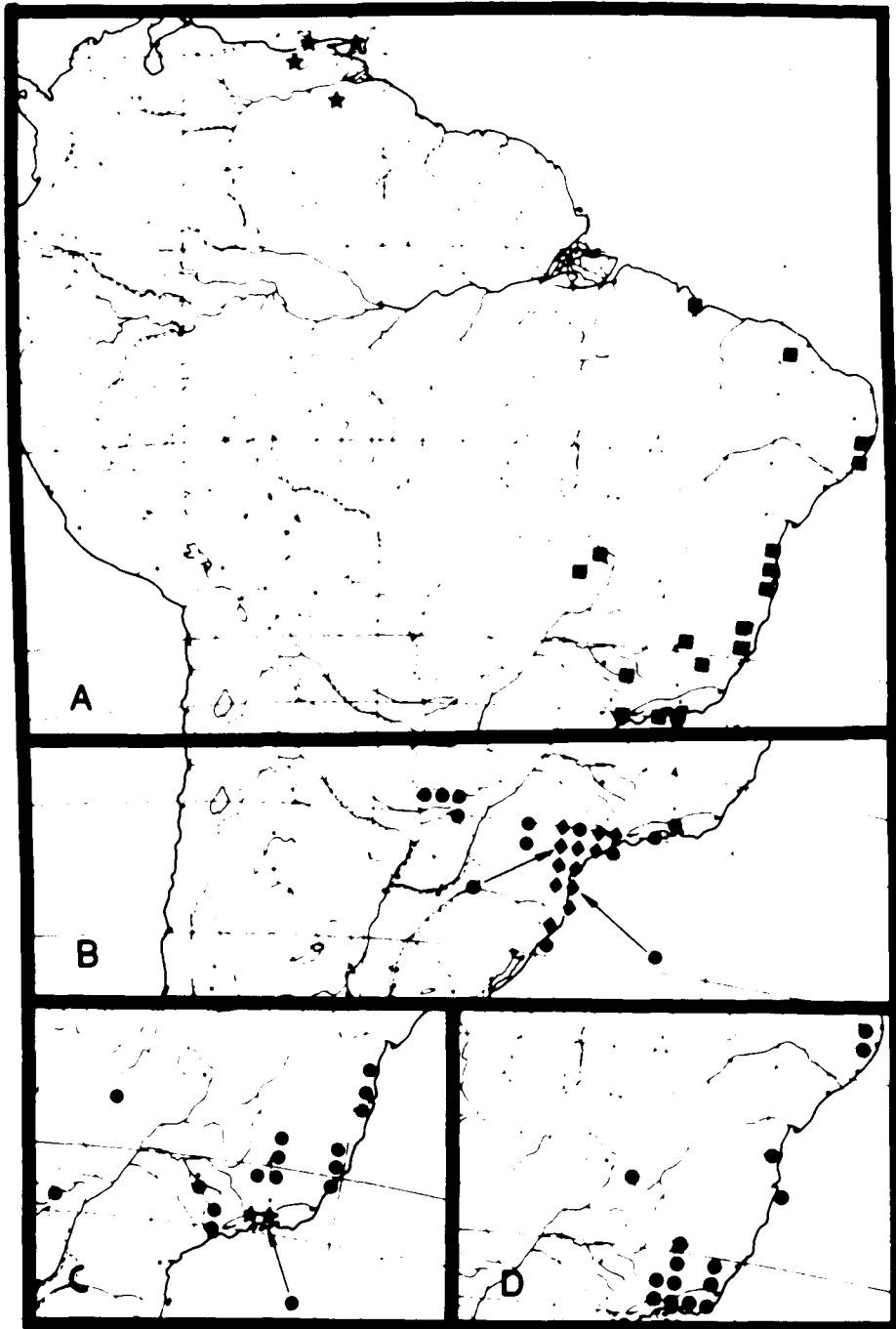


Fig. 88. Geographic distribution of subgen. Ottonia.

- A. ★ Piper ovatum var. ovatum; ■ Piper ovatum var. boucheanum; ● Piper piliovarium. B. ◆ Piper miquelianum var. miquelianum; ● Piper miquelianum var. hirtellum;
 C ★ Piper corcovadensis var. corcovadensis; ● Piper corcovadensis var. blanchetii. D. ● Piper anisum.



SYSTEMATIC TREATMENT

Piper subgenus Ottonia (Sprengel) C. de Candolle.

Ottonia Sprengel, Neue Entdeck. 1: 255. 1820;
 Gaudichaud ex Guillemin in B. de Lessert, Icon. Sel.
 pl. 3: 54, pl. 90. 1837 (as Serronia); Endlicher, Gen.
 pl. 1: 226. 1837; Miquel, Bull. Sci. phys. nat. Neerl.
 6: 452. 1839 (as Serronia); Kunth, Linnaea 13: 557-590.
 1839; Moricand, Pl. nouv. Amer. 6: 86-90. 1840;
 Miquel, Syst. piperac. 2: 535-548. 1844; Miquel,
 Linnaea 20: 175-182. 1847; Miquel, Nova Acta Acad.
 Caes. Leop. Catal. Nat. Cur. XXI suppl. 81-82. 1847;
 Presl, Epimel. bot. 264. 1849; Miquel in Martius, Fl.
 bras. 4(1): 62-71. 1852; Grisebach, Fl. Brit. W. I. 2:
 172 1859; C. de Candolle in A. P. de Candolle, Prodr.
 16(1): 252-256. 1869 (as Piper sect. Steffensia);
 Bentham & Hooker, Gen. pl. 3(1): 131. 1880 (as Piper
 subsect. Ottonia); Engler & Prantl, Die natürlichen
 Pflanzenfamilien III(1): 3-11. 1891 (as Piper sect.
Ottonia), C. de Candolle in Urban, Symbol. Antill. 3(3):
 174. 1903 (as Piper sect. Steffensia); C. de Candolle,
 Candollea 1: 71-74. 1923 (as Piper subgen. Ottonia);

- Trelease, Proc. Amer. Philos. Soc. 69: 309-327. 1930;
- Trelease, Proc. Amer. Philos. Soc. 75: 691-716. 1935;
- Trelease & Yuncker, Piperaceae Northern S. Amer. 1: 1-434. 1950 (Ottonia, p. 420); Yuncker, The Piperaceae of Trinidad & Tobago, Lilloa 26: 239-278. 1953 (Ottonia, p. 264); Angely, Piperaceae in Flora Analitica e Fitogeográfica do Estado de São Paulo 1: 154-166. 1969 (Ottonia, pp. 160-161); Yuncker, The Piperaceae of Brazil, pt. II. Hoehnea 3: 31-284. 1973 (Ottonia, pp. 121-144); Guimaraes et al., Piperaceae pt. I. in Flora Catarinense. 1-26. 1978 (Ottonia, pp. 4-16); Angely, Flora Descritiva do Paraná, 2. 1978 (as Ottonia on p. 377, and under Piper, pp. 387). Steyermark, Piperaceae in Flora de Venezuela, vol II. pt. 2: 1-619. 1984 (as Piper, p. 619); Guimaraes, Bol. Mus. Bot. Kuhlmann 7(3): 61-84. 1984. Type species. Ottonia anisum Sprengel. The genus honoring Friedrich C. Otto, German botanist and gardener at the Berlin Botanical Garden.
- Jaborandi Piso & Margrave, Historia naturalis Brasiliae. II, p. 69. 1648. An illustration and brief description are given, however both are too superficial to refer to a specific taxon. The name was never used by Linnaeus but is often synonymized under Ottonia.
- Suensonia Gaudichaud in Miquel, Syst. pipera. 2: 535.

1844. A name often found on labels of Gaudichaud collections; no type or description is known.

Serronia Gaudichaud ex Guillemín in B. de Lessert, Icon.

Sel. plant. 3: 54, pl. 90. 1837. Type. Serronia

jaborandi Gaudichaud ex Guillemín. Named after

Alvarez Serrão, Brazilian botanist at the Museum of Natural History in Rio de Janeiro.

Small to medium size, terrestrial shrubs, plants consisting of numerous monopodic stems originating from a sympodially branching collar; stems initially elongating horizontally and with reduced internodes later becoming erect; internodes between basal collar and first flowering branch nodes distinctly longer (6-8 times) than internodes in leafy branches, striated, covered by short, 1-2-celled, capitate hairs which in dry specimens are white and look like papillae; shoot apex emerging from within prophyll and free from leaf base at flowering nodes; prophyll thin-membranous. Leaves strongly dimorphic; young leaves (between basal collar and first flowering or branching nodes) reduced to a minute lamina becoming lanceolate and 3-4 times longer than wide and with a petiole having well developed stipule-like margins; adult leaves elliptic, ovate to wide ovate often lanceolate, glossy green above, light green beneath, pinnately-nerved, brochidromous with a well developed fimbriate vein, basally with

two callosities which are orange to reddish when dry.

Inflorescences erect, rarely pendulous, with sessile or pedicellate flowers loosely crowded, or the sessile flowers often tightly congested; rachis often visible; peduncle deeply grooved adaxially; floral bracts saccate-galeate, proximally with a white callous region, distally thin-membranous and translucent, pedicellate or sessile, densely papillate, not forming bands. Flowers bisexual, stamens 4 with the first pair in the frontal plane arising in a 3-9 position, distinctly larger than those in the sagittal plane; anthers latrorsely dehiscent; carpels 4, pistils conical and with 4 prominent stigmatic lobes, densely papillate at all stages. Fruit elliptic or globose when fresh, 4-ribbed when dry; seeds 4-ribbed and strongly sulcate.

A natural group of 21 species, with a major center of diversity in the southeastern coastal forests of Brazil (16 species). In addition, 5 species occur in the Amazon basin, and a single taxon in NE Colombia, Venezuela, and Central America (SE Nicaragua). Plants are found from sea level to 1500 m (normally between 50-400 m), in little disturbed lowland forests, often in sandy soils.

Notes on Keys and Species Descriptions

Because of the difficulties involved in recognizing certain floral characters in Piperaceae, an additional key for sterile material is here provided. This key will be particularly useful for those who are more interested in the medicinal properties of a species, collections of which often include sterile material. Species descriptions follow the order on which they appear in the key for flowering and/or fruiting material. Specific terminology for vesture, floral bracts, seeds, and fruits has been defined under MORPHOLOGY. Leaf measurements include only those at flowering nodes. Where leaf dimorphism is absent all leaves, regardless of the node, are measured. "Unbranched plants" refers to those species where branching is restricted to the basal portion of the corn or basal nodes of orthotropic shoots, thus distal branching is not present. Inflorescence measurements include only the flowering portion. The presence of vesture along the rachis is described only when inflorescences are fully expanded and mature. "Fimbriate rachises" refers to the presence of a distinct, continuous trichome zone along the ridges of the rachis. This character is otherwise present only in species with sessile and tightly congested flowers. Fruit and seed measurements are based on dry and fresh material. "Specimens examined" indicates that all collections seen are cited. In

description of localities, Rio de Janeiro, includes both Guanabara and Rio de Janeiro districts. Herbarium acronyms follow Holmgren et al. (1981).

Keys to the Species of Subgen. Ottonia

Key to Flowering and/or Fruiting Specimens

1. Flowers and fruits sessile (i.e. flowers not subtended by short or long pedicels or raised by the rachis ridges as to appear free from the rachis), or flowers at the base of the inflorescence pedicellate and gradually becoming sessile towards the apex.
2. Plants with dimorphic pubescence throughout, covered by long (10-25-celled) and short (5-8-celled) villous hairs; prophylls persistent at all nodes, apically attenuate; inflorescence pendulous at flower and fruit.
 1. P. francovilleanum.
2. Plants if pubescent with a single type of hair, then never long-villous, often sparsely short pubescent or glabrous throughout; prophylls caducous or if persistent only at upper nodes, apically short-acute; inflorescence erect at flower and fruit.
3. Midvein beneath densely short-pubescent; flowering portion curved.

4. Internodes glabrous throughout; leaves peltate;
stigmas sessile. 2. P. scutifolium.
4. Internodes densely short-pubescent throughout;
leaves not peltate; stigmas atop a long-terete
style. 3. P. ubatubensis.
3. Midvein beneath glabrous; flowering portion straight.
5. Rachis ridges densely fimbriate.
6. Leaves with the midvein impressed above,
throughout; rachis ridges covered by 2-3-celled
brownish hairs; floral bracts sessile in flower
and fruit, less than 0.2 mm distant from
rachis, 0.1-0.2 mm wide, 6-10 times shorter
than fruits.
4. P. bartlingianum.
6. Leaves with the midvein raised above, or if
impressed then with an intramarginal hirtellous
region beneath; rachis ridges covered by 6-10-
celled whitish hairs; floral bracts sessile in
flower, becoming pedicellate in fruit, 0.4-0.9
mm distant from rachis, 0.3-0.6 mm wide, as
long as or 2 times shorter than the fruit.
7. Plants glabrous throughout; leaves with
midvein raised above, the 6-10 secondary
veins widely spaced, basally long-acute,

decurrent with the petiole; seeds with distinct shoulders. 5. P. alatabaccum.

7. Plants locally short-pubescent, or if fully glabrous then with 15-19 narrowly-spaced secondary veins; midvein impressed above, leaves basally short-acute and not decurrent with the petiole; seeds without shoulders.

8. Upper internodes, petioles, and leaf base sparsely short-pubescent; leaves with an intramarginal hirtellous region beneath; seeds asymmetric; Amazon basin periphery, NE Colombia and Venezuela.

6. P. piscatorum.

8. Upper internodes, petioles, and leaf base glabrous; leaves with or without an intramarginal hirtellous region beneath; seeds bilaterally symmetrical; coastal forests of SE Brazil.

7. P. hoffmannseggianum.

5. Rachis ridges glabrous, sparsely pubescent, or papillate, never fimbriate.

9. Rachis ridges papillate; floral bracts 0.5-0.6 mm wide, sessile at all stages; fruits 1.5-2.5 mm long; NW Venezuela, Colombia, and Central America.

8. P. darienense.

9. Rachis ridges glabrous or short-pubescent;
floral bracts 0.2-0.3 mm wide, sessile at
anthesis but pedicellate in fruit, or if
sessile at all stages then proximally decurrent
with the rachis; fruits 0.8-1.2 mm long.
10. Leaves glandular dotted adaxially along
the midvein; rachis glabrous; floral
bracts sessile at all stages, proximally
decurrent with the rachis; Amazon basin
periphery. 9. P. ottonoides.
10. Leaves eglandular; rachis sparsely short-
pubescent; floral bracts sessile in flower
but short-pedicellate in fruit, proximally
not decurrent with the rachis; coastal
forest of SE Brazil.
10. P. klotzschianum.
1. Flowers and/or fruits pedicellate (i.e. flowers subtended
by short pedicels, then fruits appearing free from the
rachis), or only flowers at the base of inflorescence
pedicellate and then sessile toward the apex.
11. Plants long-villous throughout.
12. Leaves peltate. 11. P. guimaraesianum.
12. Leaves not peltate.
13. Proximal portion of floral bract long-villous.
12. P. villosobracteatum.

13. Proximal portion of floral bract glabrous.

13. P. brevinodis.

11. Plants not long-villous, either short-pubescent locally or glabrous throughout.

14. Leaves 11-17 times longer than wide; pedicels

longer than fruits.

14. P. rizzinii.

14. Leaves 1.5-8 times longer than wide; pedicels

longer or shorter than fruits.

15. Floral parts densely glandular dotted.

16. Leaves with an intramarginal hirtellous

region beneath; rachis sparsely pubescent;

floral bracts short-pedicellate, 0.3-0.5 mm

distant from rachis.

15. P. hayneanum.

16. Leaves glabrous throughout; rachis

glabrous; floral bracts long-pedicellate,

0.8-1 mm distant from rachis.

16. P. eucalyptophyllum.

15. Floral parts not glandular dotted.

17. Pedicels as long as or distinctly shorter than fruits.

18. Midvein beneath sparsely to densely

short-pubescent; rachis densely short-

pubescent; floral bracts distally and

fruits sparsely pubescent.

17. P. piliovarium.

18. Midvein beneath glabrous; rachis
sparsely pubescent; floral bracts and
fruits glabrous. 18. P. ovatum.
17. Pedicels longer than fruits.
19. Midvein beneath densely pubescent;
proximal portion of floral bracts,
pedicels, and fruits sparsely
pubescent. 19. P. anisum.
19. Midvein beneath glabrous or sparsely
pubescent; proximal portion of floral
bracts, pedicels, and fruits glabrous.
20. Midvein beneath sparsely pubescent,
rarely glabrous; leaf base obtuse
lobulate, asymmetric; infloresce-
nces often 1.5-3 cm long in flower
and fruit, or as long as or two ti-
mes longer than the leaves; fruits
2-4 mm long; Paraná, Sta. Catarina,
and São Paulo (Brazil) and NE
Paraguay. 20. P. miquelianum.
20. Midvein beneath always glabrous;
leaf base short-acute, often short-
peltate, or obtuse lobulate, then
mostly symmetric; inflorescences

6-10 cm long in flower becoming
10-13 cm long in fruit, shorter
than the leaves; fruits 1-1.5 mm
long; São Paulo, Minas Gerais, Rio
de Janeiro, and states in Brazil N
of Bahia along the SE Atlantic
coastal forest.

21. P. corcovadensis.

Key to Sterile Specimens

1. Plants long-villous throughout (sometimes also short-pubescent)
 2. Prophylls persistent at all nodes.
 3. Plants long-villous and short-pubescent throughout; prophylls apically long-attenuate.
 1. P. francovilleanum.
 3. Plants pubescence not dimorphic; prophylls apically short-acute.
 12. P. villosobracteatum.
 2. Prophylls persistent only at upper nodes.
 4. Leaves peltate.
 11. P. guimaraesianum.
 4. Leaves not peltate.
 13. P. brevinodis.
1. Plants sparsely or densely short-pubescent locally or throughout, or plants glabrous, never long-villous.

- 5. Internodes, petioles, and/or leaves densely glandular dotted, with reddish or dark orange glands.
- 6. Midvein beneath densely short-pubescent.
- 19. P. anisum.
- 6. Midvein beneath glabrous.
- 7. Leaves short-peltate. 21. P. corcovadensis.
- 7. Leaves not peltate.
- 8. Leaves with an intramarginal hirtellous region beneath.
- 9. Leaves with 18-23 narrowly spaced secondary veins.
- 7b. P. hoffmannseggianum var. latifolium.
- 9. Leaves with 10-14 widely spaced secondary veins.
- 15. P. hayneanum.
- 8. Leaves without an intramarginal hirtellous region beneath.
- 10. Prophylls and leaf base sparsely pubescent; Amazon basin (Pará). 9. P. ottonoides.
- 10. Prophylls and leaf base glabrous; SE Atlantic coastal forest (Brazil).
- 16. P. eucalyptophyllum.
- 5. Internodes, petioles, and/or leaves eglandular, or if glandular then glands white or yellowish translucent.
- 11. Midvein beneath glabrous.

12. Plants glabrous throughout; leaves never short-peltate.

13. Leaves 11-17 times longer than wide; Rio de Janeiro and Minas Gerais. 14. P. rizzinii.

13. Leaves 1.8-4.6 times longer than wide.

14. Leaves with edged areoles; Amazon basin and the Guianas.

15. Midrib raised above; leaf base acute decurrent with petiole; petioles stout leaving prominent scars.

5. P. alatabaccum.

15. Midrib impressed above; leaf base obtuse or if acute not decurrent with the petiole; petioles thin not leaving prominent scars.

4. P. bartlingianum.

14. Leaves without edged areoles; SE Atlantic coastal forests (Brazil).

16. Leaves drying brownish or dark green, often less than 3 times longer than wide.

21. P. corcovadensis.

16. Leaves drying light green or yellowish, often 3-4 times longer than wide.

7b. P. hoffmannseggianum var.

latifolium.

12. Plants locally pubescent at least with an intramarginal hirtellous region beneath, or if glabrous then leaves short-peltate.

17. Plants unbranched.

7a. P. hoffmannseggianum var.

hoffmannseggianum.

17. Plants distally branched.

18. Leaves short-peltate.

19. Leaves without an intramarginal hirtellous region beneath.

18. P. ovatum.

19. Leaves with an intramarginal hirtellous region beneath.

20. Leaves chartaceous, opaque.

18. P. ovatum.

20. Leaves thin membranous, translucent.

10. P. klotzschianum.

18. Leaves not peltate.

21. Midvein raised above; NE S America, C America, Trinidad, and Amazon basin.

22. Upper internodes, petioles, and
prophylls sparsely pubescent;
Amazon basin periphery.

6. P. piscatorum.

22. Upper internodes, petioles, and
prophylls glabrous; NE S America.
23. Leaves narrow ovate to lan-
ceolate, 2.5-3.5(-4) times
longer than wide; NE S
America & C America.

8. P. darienense.

23. Leaves ovate, wide ovate or
rarely narrow ovate, 2.2-2.6
times longer than wide;
Trinidad and NE Venezuela.

18. P. ovatum.

21. Midvein impressed above, or if
raised throughout then plants from
SE Atlantic forest (Brazil).
24. Leaves elliptic, basally acute;
midvein impressed.

21. P. corcovadensis.

24. Leaves ovate, basally obtuse;
midvein impressed or raised
throughout.

10. P. klotzschianum.

11. Midvein beneath sparsely to densely pubescent.

25. Plants densely short-pubescent throughout; leaves apically long-attenuate. 3. P. ubatubensis.

25. Plants sparsely pubescent locally; leaves short-acute to acuminate.

26. Leaves long-peltate; petioles inserted 0.7-1 cm above leaf base. 2. P. scutifolium.

26. Leaves short-peltate or not peltate; petioles inserted 0.3-0.5 mm above leaf base.

27. Upper internodes, petioles, prophylls, and midvein abaxially densely short-pubescent; leaves often thin-laminar and translucent, basally obtuse; secondary veins widely spaced. 19. P. anisum.

27. Upper internodes, petioles, and prophylls sparsely hirtellous or only midvein densely short-pubescent; leaves thick-chartaceous and opaque, rarely laminar and translucent, basally acute or obtuse; secondary veins narrowly spaced.

28. Leaves less than 3 times longer than wide, basally obtuse often with an intramarginal hirtellous region beneath.

29. Leaves with an intramarginal hirtellous region beneath.

20. P. miquelianum.

29. Leaves without an intramarginal hirtellous region beneath.

21. P. corcovadensis.

28. Leaves more than 3 times longer than wide, basally acute, obtuse or short-peltate, without an intramarginal hirtellous region beneath.

30. Leaf base obtuse.

17. P. piliovarium.

30. Leaf base acute or short-peltate.

21. P. corcovadensis.

1. Piper francovilleum C. de Candolle, J. bot. 4: 219.

1866. Type. Brazil. Amazonas: Rio Negro, nr. São Gabriel da Cachoeira, Jan-Aug 1852 (fr), Spruce 2362 (lectotype, G-DC, photo F neg. 7234; isoelectotypes, BM, NY, W.).

Piper perlongivillosum Yuncker, Fieldiana 28: 207. 1951.

Type. Venezuela. T. F. Amazonas: SE facing slopes along Caño Negro, tributary of Caño Iguapó, Cerro Duida, 305-1095 m, 25-26 Aug 1944 (fr), Steyermark 57953

(holotype, SGO; isotypes, F, NY).

Terrestrial shrub, 0.4-1 m tall, branching restricted to basal portion of plant, flowering branches orthotropic; internodes, terete, rugose or often striate, canaliculate, 2.5-4 cm long and 2-4 mm in diam., pubescence dimorphic, consisting of two distinct layers of trichomes, a lower layer with short 3-4-celled hairs which are erect, adpressed, or curved and somewhat moderately firm, and an upper villous layer with long 25-30-celled hairs which are spreading, soft, yellowish, translucent, becoming rigid and opaque in old internodes, often caducous. Leaves membranous, thin-translucent, or chartaceous and opaque, ovate to narrow ovate or lanceolate, (2-)2.3-2.8(-3.2) times longer than wide, lamina symmetric, often bullate above and pouched beneath, (11-)13-19(-22) x (4.3-)5-8(-9) cm, basally cordate to lobate, lobes sometimes continuous at the base, often one lobe harboring ants, apically short-acute to attenuate, glossy green above and sometimes variegated, light green beneath when living, olive-green above and yellowish-brown beneath when dry, long-villous and glabrescent above, long-villous and short-hirtellous beneath along the midvein and secondary venation, marginally villous; midvein and the 8-12 secondary veins impressed to sulcate above, raised beneath. Prophylls persistent at all flowering nodes, 1.3-2.5 cm long, tapering to a long-attenuate apex which is often terete and 3-4 mm long,

costally long-villous. Inflorescences pendulous, plants with a single inflorescence at any time, white in flower, dull green in fruit when living, brownish when dry; peduncles terete or finely striate, 2.7-3.3(-4) cm long, long-villous and hirtellous; flowering portion 7-11 cm long and 2-3 mm in diam.; rachis obscured at anthesis and then appearing smooth and glabrous, becoming fimbriate in fruit, covered by thin-translucent, soft 3-6-celled hairs, 0.5-0.8 mm long, yellow or whitish when dry; floral bracts 0.2-0.4 mm wide, saccate-galeate, distally sparsely pubescent, appearing sessile at anthesis becoming distinctly pedicellate at fruit, 2-3 mm distant from the rachis, densely pubescent at the base. Flowers sessile, tightly congested at all stages; anthers dehiscent laterally; stigmas sessile. Fruits 3-3.5 mm long, ovoid, 4-ribbed and slightly sulcate with four distinct pericarpous bulges; seeds wide ellipsoid, 0.6 x 0.5 mm, radially symmetric, 4-ribbed, ribs with distinct shoulders, strongly sulcate, glossy orange when dry.

Distribution. (Fig. 85A). Apparently restricted to the Rio Negro region (Imerí refuge of Prance, 1973; Río Negro refuge of Steyermark, 1982) in the NW Amazon basin periphery in Venezuela and Brazil. A very rare riparian species; 120-1400 m elev. Flowering material collected from Feb to May; fruiting from May through Aug.

Specimens examined. BRAZIL. Amazonas: Rio Negro, Vaupés, 1 May 1947 (fl), Pires 526 (IAN, NY). Roraima: Vic. of Auaris, foothills of Serra Parima, 900 m, 8 Feb 1969, Prance et al. 9732 (INPA, NY, US); Serra dos Surucucús, vic. of Posto Surucucú Mission, 19 Feb 1969 (fl), Prance et al. 10105 (INPA, K, NY, US); vic. of Uaica airstrip, Río Uraricoeira, 28 Feb 1971 (fl), Prance et al. 10779 (IAN, NY).

VENEZUELA. T. F. Amazonas: Between Shimada-Wochi and Upper Río Matacuní, 820-1000 m, 8 Nov 1983 (fr), Huber & Colchester 8383; Río Marawarimini, 2 km S of base camp of Cerro Neblina, 140 m, 5 Jul 1984 (fr), Liesner et al. 15672 (MO, NY, VEN); Sierra Parima, Venezuela-Brazil border, 45 km NE Río Orinoco, 1300 m, 18-23 May 1972 (fl,fr), Steysmark 106052 (NY, VEN); N slopes of Cerro Duida, SW of La Culebra, 800-900 m, 6 Feb 1982 (fl), Steysmark et al. 126156 (NY, VEN); Río Marawarimini, 2 Km S of base camp of Cerro Neblina, 140 m, 11 Apr 1984 (fr), Thomas et al. 3007 (NY); Río Siapa just below raudal Gallineta, 130 m, 21 Jul 1959 (fr), Wurdack & Adderley 43537 (NY, US).

The most derived taxon in subgen. Ottonia, P. francovilleum is easily recognized by its dimorphic pubescence, orthotropic flowering shoots, apically long-attenuate prophylls which are persistent at all flowering nodes, leaves with a

basal lobe often harboring ants, and pendulous inflorescences. These characters are all unique for subgen. Ottonia and of very restricted distribution in Piper. One of the most distinctive features of P. francovilleanum is the aerial branching system which consists only of orthotropic flowering shoots. Vegetative branches are restricted to the basal portion of the plant. In addition there is only one inflorescence per shoot instead of the presence of inflorescences at all flowering nodes along a branch, the case in most pipers. Thus it is possible that individuals of P. francovilleanum place more energy into the production of a single inflorescence per season with little biomass allocated to vegetative branching. Little or no variation is found in this species. Old specimens may become glabrescent, or some young leaves distinctly variegated.

Piper francovilleanum is most closely related to P. alatabaccum with which it shares all floral characters including: long-pedicellate bracts, fimbriate rachises, fruits with four prominent pericarpic bulges, wide elliptic seeds, ribs with shoulders, and V-shaped cell walls of the seed coat. The two taxa are allopatric (Fig. 85A, 86A) and apparently with very distinct ecological requirements, P. francovilleanum being a riparian taxon restricted to the forest understory while P. alatabaccum is common in campinaranas or in light gaps when

present in terra firme forests.

At the time Yuncker (1952) described P. perlongivillosum, he knew of P. francovilleanum, but had not seen the type; furthermore, the original description given by de Candolle was rather cryptic.

2. P. scutifolium Yuncker, Bol. Inst Bot. São Paulo 3: 123.

1966. Type. Brazil. Rio de Janeiro: Rio de Janeiro, fazenda Boa de Teresópolis, 11 Nov 1942 (fr), Emygdio 80 (holotype, R).

Terrestrial shrub 1.5 m tall, sparingly branched; internodes striate and finely canaliculate, (2.5-)3-4 cm long and 2-3 mm in diam., papillate, glabrous. Leaves chartaceous, opaque, narrow ovate to lanceolate, (2-)2.2-3(-4) times longer than wide, lamina symmetric to strongly asymmetric, (9-)15-20(-22) x (2.6-)5.5-7(-9) cm, basally long-peltate, oblique, apically short-acute to long-acuminate, light green above and beneath when living, grayish-green and often edged above and light green beneath when dry, glabrous above, pubescent beneath along the veins, with thin, white, 2-4-celled hairs; midvein and the 9-10 secondary veins impressed above, strongly raised beneath; petioles striate, 1.5-2 cm long, papillate, glabrous. Prophylls caducous, 1.5 cm long, apically acuminate, glabrous. Inflorescence curved, white in flower and

fruit when living, whitish to light orange when dry; peduncles striate, 7 mm long, glabrous; flowering portion 6-7(-10) cm long, and 2-3 mm in diam. in fruit; rachis ridges obscured at anthesis, appearing smooth and glabrous, then becoming fimbriate, covered by thin, erect, white translucent 5-7-celled hairs; floral bracts 0.7-0.9 mm wide, saccate-galeate, distally callous and densely hirtellous, obscurely glandular dotted, short-pedicellate, pubescent at the base. Flowers sessile, tightly congested at all stages; anthers dehiscing laterally; stigmas sessile. Fruits ovoid, 0.5-0.7 mm long, apiculate, 4-ribbed and sulcate; seeds narrow ellipsoid, 1 x 0.7 mm, radially symmetric, 4-ribbed and sulcate, blackish when dry.

Distribution. (Fig. 85A). Atlantic coastal forests of SE Brazil in the states of Rio de Janeiro and São Paulo. A rare understory species of little disturbed forests; 0-300 m elev. Flowering and fruiting material collected in Nov and Dec.

Specimens examined. BRAZIL. São Paulo: State Park of São Paulo, nr. Posso dos Urubús, 24 Nov 1947 (fl, fr), Hoehne 13489 (G, NY, RB, SPF), 280 m, 15 Dec 1983 (fr), Callejas et al. 2123, 2126, 2134 (HUA, NY, RB, SP, US).

This species is recognized by its abaxially pubescent leaves which are basally oblique and long-peltate, and the curved flowering portions. The type collection has lanceolate leaves which are 3-4 times longer than wide, while the other populations in São Paulo have narrow ovate leaves 2-2.2 times longer than wide.

Piper scutifolium is most closely related to P. ubatubensis. Both species have in common curved flowering portions, sessile and tightly congested flowers, floral bracts which are distally densely pubescent, and fimbriate rachises. The two taxa are easily distinguished by the long-stylose fruits and densely pubescent internodes and petioles of P. ubatubensis. The few collections of these species display wide variation in size and shape of the leaves.

3. Piper ubatubensis Callejas, sp. nov. Type. Brazil. São Paulo: Serra do Mar, above Ubatuba, 50-100 m, 21 Aug 1976 (fr), Davis et al. 59786 (holotype, F). Fig. 89.

A P. scutifolio Yuncker caulibus, petiolis, pedunculis dense hirtellis differt; foliorum laminis lanceolatis apice longe angusto-attenuatis, subtus in nervo venis dense hirtellis; pedunculis 1.3-1.5 cm longis; spicis arcuatis; floribus sessilibus; fructibus umbonatus, 0.8 mm; stylis teretibus, 1.4 mm longis.

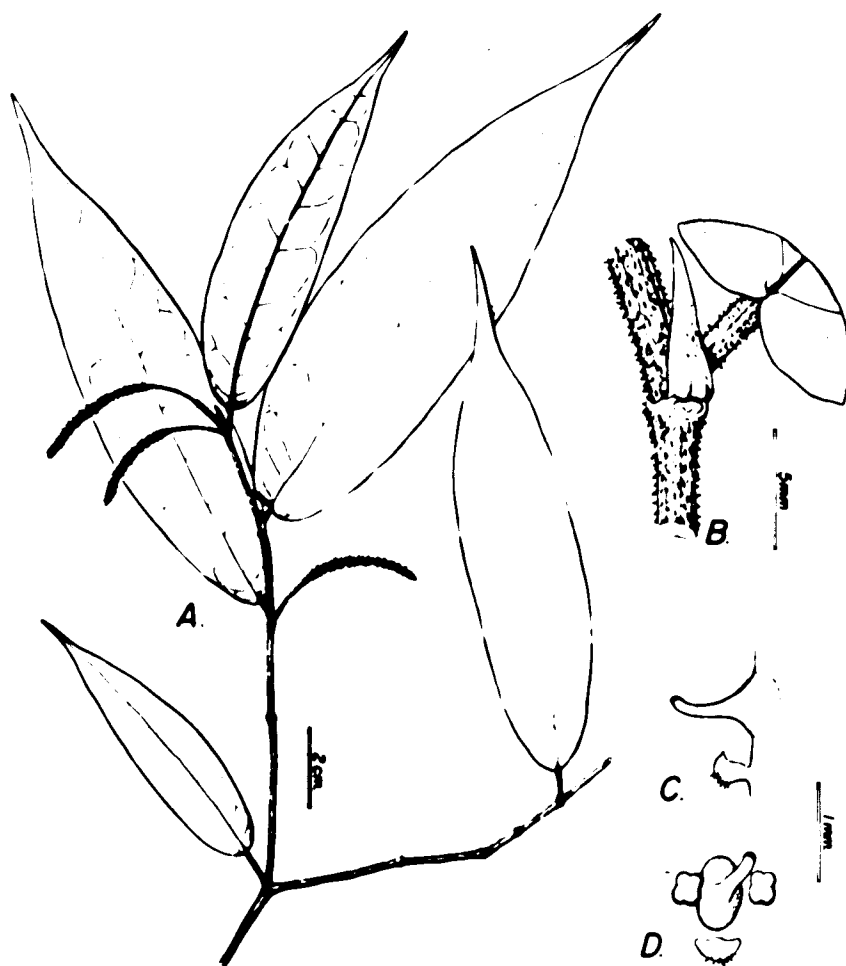
Terrestrial shrub 0.6 m tall, sparingly branched; inter-

nodes striate, canaliculate, 1.5-2 cm long and 2 mm in diam., densely pubescent, covered by thin, translucent 2-6-celled hairs. Leaves chartaceous and opaque, lanceolate, 3.4-4.2(-4.8) times longer than wide, lamina symmetric, 12-16 x 2.5-3.5(-3.8) cm, basally shortly lobate, lobes overlapping the petiole, apically-long attenuate, concolorous when living, but grayish-green and edged above, light green beneath when dry, glabrous above, densely pubescent and with an intramarginal hirtellous region beneath; petioles striate, grooved adaxially, 6 mm long, densely pubescent. Prophylls caducous, 4-5 mm long, apically short-acuminate, obscurely glandular dotted, costally sparsely pubescent. Inflorescence curved and white at all stages; flowering portion 2.1-3.5 cm long; rachis obscured at anthesis, appearing glabrous and smooth, then becoming fimbriate in fruit, covered by erect, thin, white translucent 5-6-celled hairs; floral bracts 1 mm wide, saccate-galeate, proximally densely pubescent, obscurely glandular dotted, short-pedicellate. Flowers sessile, tightly congested at anthesis and fruit; anthers dehiscing laterally; stigmas atop a 0.6 mm long terete style. Fruits narrow ellipsoid, umbonate, 0.8 mm long, 4-ribbed and strongly sulcate; seeds ellipsoid, 1 x 0.5 mm, radially symmetric, 4-ribbed and strongly sulcate, black when dry.

Fig. 89. Piper ubatubensis Callejas, sp. nov.

All from Davis et al. 59786.

A. Habit. B. Flowering nodes showing prophyll and leaf base. C. Close up of the long stylose fruit. D. Flower, upper view (the pair of stamens in the sagital plane are not shown).



Distribution. (Fig. 85A). Known from two collections. Apparently restricted to the mesic forests of Serra do Mar in the state of São Paulo, where it is very rare in the understory of little disturbed forests; 50-1180 m elev. Flowering and fruiting collections from Aug and Sep.

Specimens examined. BRAZIL: São Paulo, Cunha, 1180 m, 24 Sep 1980 (fr), Collares 39 (NY, RB).

This new species is recognized by apically long-attenuate, leaves, curved inflorescences, and densely pubescent vegetative parts. It also seems to occupy a wider altitudinal gradient, than most species in subgen. Ottonia. It is most closely related to P. scutifolium from which it differs by sessile stigmas and glabrous stems.

4. Piper bartlingianum (Miquel) C. de Candolle, Prodr.

16(1): 1869. Artanthe bartlingiana Miquel, Syst.

piperac. 2: 510. 1844. Type. French Guiana. Cayenne,

1819-1821 (fr), Poiteau s.n. (holotype, G, photo F

neg. 8405; isotype, U).

Fig. 90.

Artanthe warakabacoura Miquel, J. bot. 4: 469. 1845.

Ottonia warakabacoura (Miquel) Miquel, Linnaea 20: 180.

1847. Piper warakabacoura (Miquel) C. de Candolle, Prodr.

16(1): 257. 1869. Type. Guyana, without specific loca-

lity, no date, Parker s.n. (holotype, K).

Piper parimanum Trelease, Bull. Torr. Bot. Club 58: 354.

1931. Piper bartlingianum Miquel var. parimanum

(Trelease) Steyermark, Piperaceae. In: Flora de Venezuela, vol II. pt 2: 56. 1984. Type. Venezuela. T. F. Amazonas: Esmeraldas, middle camp, 98 m, 10 Nov 1928 (fr), Tate 370 (holotype, NY).

Terrestrial shrub, sometimes a treelet 6 m tall, sparingly to profusely branched, strongly nodose with petiole and inflorescence scars prominent; internodes terete, smooth or striate but not strongly canaliculate, (1.5-)2-4.5(-6.5) cm long and 2-5 mm in diam., papillate, glabrous. Leaves thick-chartaceous, opaque, wide ovate or ovate to narrow ovate or lanceolate, rarely elliptic to narrow elliptic (1.8)2-2.8(-4) times longer than wide, lamina symmetric (14-)15.6-21(-27) x (4.5-)5.5-9.5(-10.5) cm, basally acute, less often obtuse on one side, apically short-acute to long-acuminate, light green above and beneath when living, gray-green to brownish and edged above, brown to yellowish beneath when dry, glabrous on both sides; the 8-10 secondary veins impressed above, strongly raised beneath; petioles stout, terete, smooth or less often striate, 5-9 mm long, papillate, glabrous. Prophylls caducous, 0.5-1.5 cm long, apically long-acuminate, papillate, glabrous. Inflorescence erect, white in flower and green in fruit when living, brownish at all stages when dry; peduncles terete or

striate, 0.6-1 cm long, glabrous; flowering portion (4-)6-13(-14) cm long, rachis visible at all stages, ridges short-fimbriate, covered by 2-3-celled hairs, brown, ridges somewhat elevated above the pistils, then the flowering portion appearing distinctly zonated; floral bracts 0.1-0.2 mm wide, brownish short-pedicellate, glabrous. Flowers sessile, widely spaced at anthesis loosely congested in fruit; anthers with upwards dehiscence. Fruits obovoid, 2-3 mm long, 4-ribbed and slightly sulcate; seeds obovoid, 1.2 x 0.8 mm, radially symmetric, 4-ribbed, sulcate, black when dry.

Distribution. (Fig. 85B). Widespread in the Amazon basin in Bolivia (Beni, Pando), Colombia (Amazonas), Brazil (Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima), Perú (Loreto), Venezuela (T. F. Amazonas), and extending into Guyana. A species of the understory in forests of terra firme, campinaranas in poorly drained soils of little disturbed forests, along sandy banks of rivers or lakeshores in granitic soils, and in secondary vegetation in light gaps, less often as a riparian species; 100-1000 m elev. Flowering and fruiting throughout the year in the Amazon basin but with fruiting apparently more common from Oct to Dec in the NE range (Guyana, Surinam, French Guiana, and E Venezuela).

Fig. 90. Illustration of Ottonia warakabacoura (=Piper
bartlingianum. From Martius, Flora Brasiliensis, pl.
24. Vol. IV. 1856.

21



OTTONIA Warabacouria

Specimens examined. COLOMBIA. Amazonas: Río Caquetá, La Pedrera, 240 m, 1-4 Oct 1952 (fl), García-Barriga 14681 (COL).

VENEZUELA. T. F. Amazonas: Atabapo, upper portion of Caño Cname, 100 m, 3 May 1979 (fl, fr), Davidse et al. 17121 (MO, NY, VEN); Base Camani (SAS), 24 Apr 1971 (fr), Foldats 116A (US); Orinoco river below San Fernando de Atabapo, Caño Morocoto, 26 Mar 1974 (fr), Gentry et al. 10949 (MO, VEN), Steyermark et al. 103028 (VEN).

GUYANA. Basin of Essequibo river, nr. mouth of Onoro Creek, 15-24 Dec 1937 (fl, fr), L. B. Smith 2707 (NY), 2771 (NY); nr. mouth of Blackwater Creek, 29 Dec 1937 (fr), L. B. Smith 2826 (NY).

SURINAM. Trial Pakapaka to Ebba top, nr. km 22, 14 Feb 1951 (fr), Flürschütz 1399 (NY); Wilhelmina Gebergte, 3 km S of Juliana top, 12 km N of Lucie river 320 m, 6 Aug 1963 (early fl), Irwin et al. 54455 (NY), 44456 (NY); 9 km of Lucie river, 12 km W of Oost river, 275 m, 1 Aug 1963 (fr), Irwin et al. 54537 (NY, US); 2 km above confluence with Lucie river, 220-240 m, 19 Sep 1963 (fr), Irwin et al. 55868 (NY, US); Zuid river, nr. Kayser airstrip 45 km above confluence of Lucie river, 270 m, 27 Sep 1963 (early fl), Irwin et al. 57708 (NY); rd. Wia-wia bank, km 10.6, 25 Nov 1948 (fr), Lanjow et al. 1271 (NY); Tibiti savanna, Km 3, 10 Jan 1949 (fr), Lanjow et al. 1763 (NY); Nickerie river, area of Kabaledo dam project, 30-130 m, 23 Sep 1980 (fr), Lindeman et al. s.n. (NY, U); vic. of Moengo, Cottica river, on Begi Gado hill, 19 Mar 1955

(fl), Maguire 40817-A (NY, VEN); Wilhelmina Gebergte, Kayser airstrip, Zuid river, 25 km above confluence with Lucie river, 270 mn, 1 Jul 1963 (fr); Maguire et al. 53949 (NY, US); vic. of camp 11, 14 Jul 1963 (fr), Maguire et al. 54186 (NY, US); 3 km S of Julian top, 12 km N of Lucie river, 1000 m, 26 Jul 1963 (fr), Maguire et al. 54356 (NY); Brownsberg Nature Park, 90 km S of Paramaribo, Mazaroni Plateau, 23 Sep 1976 (fr), Mori et al. 8376 (NY, U, US); Raleighvallen-Voltzberg Nature Reserve on the Coopename river, 145 km SW of Paramaribo, 18 Nov 1976 (early fl), Mori et al. 8653 (NY, US); Yanamalie, 12 Jul 1939, Stahel 67 (NY); nr. Stondansi upper Nickerie river, 8 Dec 1962 (fl, fr), Wessels Boer 317 (NY, U); confluence of rivers Palomeu and Tapanahoni, 10 Apr 1963 (fr), Wessels Boer 1193 (NU, U).

FRENCH GUIANA: Sinnamary river, right margin, 8 km from river, 1 May 1969 (st), Granville 130 (NY, P); N slopes of Glabao Mountains 10 km WSW of Säul, 400 m, 2 May 1973 (fr), Granville B-4820 (CAY, NY, P); Säul, nr. geographic center of Dept. of French Guiana, junction of La Douana-Belvedere, 17 Dec 1976 (fl), Mori et al. 8787 (CAY, NY); Canopi river, Yanioe Mountain, 8 Feb 1968 (fr), Oldeman et al. 86 (NY, P); Lagon de la crique Paperoas, 10 Oct 1968 (st), Oldeman T-198 (NY, P); Iracouibo river, Saut Grand Franconie, 12 Aug 1966 (fl), Oldeman 2200 (NY, P); Arataje river, confluence of Approuague hills, nr. right margin, 8 Feb 1968 (st), Oldeman 2973 (NY,

P); Maroni, Anticum-Pata, nr. mouth of Maroni river, 20 Apr 1975 (fr), Sastre et al. 3841 (NY, P), Maroni, Anticum-Pata, nr. mouth of Maroni river, 20 Apr 1975 (fr), Sastre et al. 3841 (NY, P).

PERU. Loreto: Maynas, Negro Urco, Napo river, 160 m, 20 Jan 1983 (fr), Gentry et al. 39584 (MO, NY, US); Requena, Jenaro Herrera, 180 m, 3 Jul 19081 (fr), Vasquez et al. 2157 (MO, NY, VEN).

BRAZIL. Amapá: Araguari river, vic. camp 12, 28 Sep 1961 (fr, fl), Pires et al. 51281 (IAN, MG, NY, RB); rd. to Amapá, Agua Azul, km 134, 24 Jul 1962 (st), Pires et al. 52356 (IAN, MG, NY, US); Serra do Navio, Amapari river, 70-300 m, 17 Nov 1954 (fl), Cowan 38402 (NY, P, US); Oyapock airstrip, 4 Dec 1954 (fr), Cowan 38654 (NY, P, RB, US); 7 Dec 1954 (fr), Cowan 38697 (NY, P, RB, US); Oiapoque river, 4 km SW of Clevelândia, 24 Jul 1960 (fr), Irwin et al. 47148 (IAN, MG, NY), 47234 ; Jarí river, Aurucuopatari waterfalls 120 m, 17 Aug 1961 (fr), Egler et al. 46494 (IAN, MG, NY, RB). Amazonas: Along Río Negro, between Manaus and São Gabriel, Acãnga, 27 Jun 1979 (fr), Alencar 64 (INPA, MG, NY, RB); Altamira-Itaituba, km 115, 270 m, 18 Jan 1976 (fr), Bamps 5180 (LG, NY); 16 Feb 1976 (fr), Bamps 5392 (LG, NY); Manaus-Caracarái rd, km 146, 25 Sep 1973 (fl); Bisby et al. P-18069 (INPA, NY, U, US, VEN), P-18080 (INPA, K, MG, NY, U, US, VEN); vic. Uatamã river, Itapiranga,

in front of Igarapé Santa Luzia, 16 Aug 1979 (fl), Cid et al. 418 (INPA, MG, NY); vic. Uatumã in front of Pitinga river mouth, 27 Aug 1979 (fl); Cid et al. 866 (INPA, MG, NY, US); Mpio. Álvares, Igarapé Arua, 28 Nov 1982 (fl), Cid et al. 37941 (INPA, MG, NY); Mpio. Barba, Igarapé das Onças, 3 km N of Canumã, Canumã river, 30 Jan 1983 (fr), Cid 3961, 3964 (both nos. NY, MG, INPA, US); Mpio. Humaita, between Libramento and Ipixuna rivers, 7-18 Nov 1934 (fr), Krukoff 7219 (NY, US); Mpio. São Paulo de Olivença, Nov 1935 (fl), Krukoff 7546 (NY, US); Solimões and Javari rivers, Tefé lake, 13 Jul 1973 (fr), Lleras et al. P-16650 (INPA, MG, NY, U, UFMG, US, VEN); Solimões river, São Paulo de Olivença, 28 Feb 1977 (fl), Mori et al. 9166 (INPA, MG, NY, US); mouth of Içá river, 24 Feb 1977 (fr), Mori et al. 9083 (INPA, NY, USD); Mpio. Tefé, Tefé lake, NW shore, 10 Dec 1982 (fl), Plowman et al. 12435 (IAN, MG, NY, US); 11-14 Dec 1982 (fr), Plowman et al. 12524 (F, IAN, INPA, MG, NY); Mpio. of Manaus, Taruma, 14 km NW of Manaus, 19 Dec 1982 (fr), Plowman et al. 12640 (INPA, NY); along Rio Negro, between Manaus and São Gabriel, Acanga, across from Japo Island, 27 Jun 1979 (fr), Poole 1660 (INPA, MG, NY, RB, U, US, VEN); Acre and Purús rivers, mouth of Acre river, airstrip 20 Sep 1966 (fl), Prance et al. 2431 (IAN, INPA, MG, NY, RB); Mpio. Humaitá, Madeira river, rd Humaitá to Lábrea, km 42, 2 km W of Ipixuna river, 23 Nov 1966 (fl, fr), Prance et al. 3215 (IAN, INPA, NY, U); km 44, 29 Nov 1966 (st), Prance et al. 3462

(INPA, NY, US); Manaus vic. rd Manaus to Manacapuru, km 35, 5 Jan 1967 (fl), Prance et al. 3909 (INPA, NY, US, VEN); basin of Purús river, Mpio. Lábrea, margin of Lábrea airstrip, 5 Nov 1968 (fr), Prance et al. 8205 (INPA, NY, U), 28 Jun 1971 (fr), Prance et al. 13885 (INPA, K, MG, NY, P, R, RB, U, US, VEN); vic. of Totoboi mission, Yanomamo Indian village, tributary of Demeni river, 22 Aug 1975 (st), Prance & J. Ramos 23619 (INPA, MG, NY, R, RB, U, US, VEN); Manaus-Caracarí hwy., km 130, 22 Feb 1974 (fl), Steward et al. P-20426 (INPA, MG, NY, P, R, U, US); Mpio. Humaitá, rd Humaitá-Lábrea, km 64, 3 km N, 18 Jun 1982 (fr), Teixeira et al. 1017 (INPA, NY, US); rd. Humaitá-Porto Velho, km 60, 1 May 1982 (fr), Teixeira et al. 127 (INPA, NY, P, US); Humaitá-Lábrea, km 63, 5 Jun 1982 (fr), Teixeira et al. 946 (NY, U, US, VEN). Mato Grosso: Hill W side of Aripuana river, nr. base of Salto dos Dardanelos, 16 Oct 1973 (st), Berg P-18572 (A, F, INPA, MG, NY, R, U, US, VEN). Pará: Indigenous Park of Tumucumaque, Parú river, Tiriyo Mission, 9 Feb 1970 (fl, fr), Cavalcante 2323 (MG, NY); Mpio. Oriximiná, 200 m, from the left margin of the rd. Cachoeira-Porteira, parallel to Trombetas river, 18 Jun 1980 (fr), Cid & J. Ramos 1058 (INPA, NY); km 23, 27 Jun 1980 (fr), Cid & Mota 1125 (INPA, NY); Mapuera river, left margin, 28 Jun 1980 (fr), Cid & J. Ramos 1164 (INPA, NY); ca 45 km from Tucuruí, S SW on new BR-422, 3 Nov 1981 (fl), Daly & Callejas 1200, (all INPA, MG, NY, US); Mpio. Oriximiná, along

Trombetas river, ca 8-10 km SE from Cachoeira Porteira, 29 Jun 1980 (fr), Davidson & Martinelli 10586 (INPA, NY, US);

Oriximiná, Cachorro river, nr. barraca Ponto da Serra, 12 km NW de Cahoeira Porteira, 22 Jun 1980 (fr), Martinelli 7069 (INPA, NY, RB); BR-163, Cuiabá-Santarém hwy. 934, N of Para river, 13 Nov 1977 (fr), Prance et al. P-25354 (IAN, INPA, NY, RB, U, US); km 1004, 14 Nov 1977 (fr), Prance et al. P-25396 (INPA, MG, NY); BR-230, Transamazon hwy. 53 km NE of Itaituba, 28 Nov 1977 (fr), Prance et al. P-25830 (INPA, MG, NY, RB); basin of Xingú river, Gleba Bacaja, just below mouth of Bacaja river, 23 Nov 1980 (fl), Prance et al. P-26408 (MG, NY, RB, US);

Itaituba, km 60 of rd. Itaituba-Jacarecanga, National Park of Tapajós, 16 Nov 1978 (fl), M. G. Silva & C. Rosario 3758, 3987 (both INPA, MG, NY, US); Jarí river, Mounte dourado, Serrinha, 4 Dec 1968 (fl), N. T. Silva 1488 (IAN, NY); peak of Igarapé Pacaná, 11 Jun 1969 (fl, fr), N. T. Silva 1604, 1605 (both IAN, NY); rd to Munguba, 8 Feb 1969 (fr), N. T. Silva 1723 (INPA, MG, NY); S slopes of Akarai Mountains, in drainage of Mapuera river, 500-700 m, 18-20 Jan 1938 (fr), A. C. Smith 2955 (NY); vic Obidos, Dec 1849 (fl), Spruce 5 (NY). Rondônia:

Basin of Madeira river, margin of Mutumpurana airstrip, 25 Nov 1968 (fr), Prance et al. 8847 (INPA, MG, NY, U, US, VEN).

Roraima: Manaus-Caracará rd, km 346, Igarapé Jundia, 26 Nov 1976 (fl), Prance et al. 24322 (A, F, MG, NY, R, U, US); rd Mannaus-Caracará, k 329, army post N of Waimari Atoari Indian

reserve, 16 Nov 1977 (st), Steward et al. 31 (INPA, MG, NY, RB).

BOLIVIA. Beni: Junction of Beni and Madre de Dios rivers, Aug 1886 (fl), Rusby 2182 (NY); along rd from Guayaramerin to Cachuela Esperanza, 15 km on each side of Yata river, 26 Jan 1978 (fr), Anderson 11872 (MICH, NY); Prov. of Vaca Diez, 18.4 km E of Riberalta, 1 km NE to Cahuela Esperanza, 230 m, 26 May 1982 (fr), Solomon 7806 (MO, NY).

Local names and uses. Brazil: nhambi, paarimahasiko (Amazonas); joao-borandim, pimenta longa (Pará). Guyana: baluita, warakabacourrou, warakabacoura. Surinam: man-aneisiwiwirie, pete, warakabocourrou.

Leaves and roots of P. bartlingianum are used by the Tecuna Indians of Brazil (Amazonas) as components of the arrow poison, curare (fide Krukoff 7546). Stems and leaves are used for similar purposes in Guyana and Surinam as components of the Waiwai arrow poison, baluita (Guyana) and Ourali poison warakabacourrou (Surinam) (fide Parker s.n., as cited by Miquel, 1856). Prance 23619 reports the plants used as a tobacco substitute roots are mashed until soft, then beaten and rubbed in ash, and used in the mouth (Yanomamo Indians, Amazonas). Roots are also used as a cure for toothache in Pará (Brazil).

This most widespread species, P. bartlingianum, is recognized by fimbriate rachises covered by 2-3-celled hairs which are distinctly brownish when dry, pistils or immature fruits distinctly bordered by hairs, flowering portion appearing zonate, sessile and minute bracts, and obovoid seeds.

Although widespread, Piper bartlingianum is morphologically very uniform throughout its range. The type of P. warakabacoura has inflorescence both in flower and fruit, showing the rachis ridges character as well as fully developed fruits, characters otherwise obscured in the inflorescence of the type of P. bartlingianum. Piper parimanum includes populations which have leaves elliptic-lanceolate and 4-5 times longer than wide, as compared to those from E Guyana which are wide ovate and less than or three times longer than wide. Steyermark (1984) reduced this species to varietal status. However, he based his comparison on the material from E Guyana and the reduced material of Venezuela without mentioning variation of the species in the Amazon basin where the apparent discontinuities seen in Venezuela and Guyana break down completely.

It is closely related to P. alatabaccum, P. francovilleanum, and more distantly to P. darienense. With the former pair it has in common calcium oxalate crystals in the mesophyll (see Leaf Anatomy); with the latter obovoid fruits.

It occurs sympatrically and overlaps to large extent with P. alatabaccum. Both species are profusely branched, and have in common prominent petiole and inflorescence scars, and glabrous thick-chartaceous and adaxially edged leaves. Piper bartlingianum may be easily separated from P. alatabaccum in sterile condition by the following: in P. bartlingianum leaf venation is impressed above, and the base is short-acute or obtuse, whereas in P. alatabaccum venation is strongly raised above and the base is acute and decurrent with the petiole. Furthermore, P. bartlingianum is glabrous throughout and cannot be confused with P. francovilleianum which has dimorphic pubescence, or with P. darienense which has an intramarginal hirtellous leaf beneath.

5. Piper alatabaccum Trelease & Yuncker, Piperaceae of

Northern S. Amer. 1: 408. 1950. Type. Guyana.

Labbakabra Creek, Tiger Creek, Essequibo river, 24

Aug 1937 (fr), Sandwith 1191 (holotype, NY; isotype, U).

Terrestrial shrub 2.5 m tall, profusely branched, strongly nodose, petiole and inflorescence scars prominent; internodes terete, smooth, or often striate and canaliculate, 3-4.5 cm long and 5-6 mm in diam., glabrous. Leaves thick-chartaceous, opaque, ovate to wide ovate, less often lanceolate, (1.8-)2.1-2.9(-3.2) times longer than wide, lamina symmetric,

(13-)15-24(-29) x (4-)5-9.5(-10) cm, basally acute and decurrent with the petiole, apically acute to long-acuminate, light green above and beneath when living, yellowish or green-olive and edged above, yellowish to brownish beneath when dry, glabrous; the 5-10 secondary veins raised on both sides; petioles stout, terete, smooth, grooved adaxially, 0.7-1.2 cm long, glabrous. Prophylls caducous, 1-1.5 cm long, glabrous. Inflorescence erect, white at anthesis and green in fruit, brown to yellowish when dry; peduncle terete, smooth, 1 cm long, glabrous; flowering portion (4.5-)6-9(-11) cm long; rachis obscured at anthesis, appearing smooth and glabrous, becoming fimbriate, covered by erect, thin, white and translucent soft, 3-6-celled hairs, 0.6-0.8 mm long, yellowish when dry; floral bracts 0.2-0.3 mm wide, saccate-galeate, distally sparsely pubescent, sessile at anthesis, becoming pedicellate, 2 mm distant from the rachis, pubescent at the base. Flowers sessile, tightly congested at all stages; anthers dehiscing laterally; stigmas sessile. Fruits ellipsoid-obovoid, 2.3 mm long, 4-ribbed, obscurely sulcate and with four prominent pericarpic bulges at the top; seeds wide ellipsoid, 1.2 x 0.6 mm, radially symmetric, 4-ribbed, ribs with shoulders, strongly sulcate, glossy orange when dry.

Distribution. (Fig. 86A). Amazon basin in Brazil where it is more widespread in the northeastern periphery (Amazonas,

Amapá, Pará), but also known from the southeastern in the state of Rondônia; also in Surinam and Venezuela (Bolívar). In poor drainage soils of terra firme forests in the understory where it is common and often found as a riparian species, or in campinaranas in Brazil and Surinam. In Venezuela it is found on the wooded slopes of the Guiana Shield at the base of the sandstone bluffs; 80-625 m elev. Flowering and fruiting Apr through Dec.

Specimens examined. VENEZUELA. Bolívar: Sierra Ichún, along río Ichún, tributary of río Paragua, 500-625 m, 29 Dec 1961 (fr), Steiermark 90413 (NY, VEN).

SURINAM. Emmaketen Mountains, forest between camp 15 and main camp, 350 m, 19 Jul 1959 (fr), Daniëls & Jonker 778 (NY) Wilhelmina Gebergte, 9 km of Lucie river, 12 km W of Oörst river, 275 m, 1 Aug 1963 (fr), Irwin et al. 54549 (NY, US); Saramacca river, 1 Nov 1903 (fr), Pulle 1172 (U).

BRAZIL. Amapá: Jari river, nr. Cachoeiras das Guaribas, 160 m, 15 Aug 1961 (fr), Egler & Irwin 46422 (NY, US); rd. to Amapá, coastal region, km 134, Agua Azul, 24 Jul 1962 (fr), Pires & Cavalcante 52258 (IAN, MG, NY). Amazonas: Cuieiras river, 50 km upstream, farm of Sr. Caldez, 3 Apr 1974 (fl, fr), Campbell et al. P-21823 (INPA, MG, NY, US); Manaus, Tarauma Alta, 14 km NW of Manaus, 19 Dec 1982 (fl, fr), Plowman et al. 12641 (F, INPA, MG, NY); Urubú river, Serra da

Lua, between Cachoeira Iracema and Natal, 6 Jun 1968 (fr),
Prance et al. 5027 (INPA, MG, NY, RB, US). Pará: Oriximina,
 Cachorro river, barracao do Ponte da Serra, 12 km W of
 Cachoeira Porteira, 80 m, 21 Jan 1980 (fr), Martinelli 7106
 (INPA, NY, RB); Jari river, Mounte Dourado, Serrinha, 2 Dec
 1968 (fl), N. T. Silva 1485 (IAN, MG, NY), 14 Dec 1968 (fl),
N. T. Silva 1547 (IAN, NY), 1572 (IAN, NY), 18 May 1969 (fr),
N. T. Silva 1974 (INPA, MG, NY). Rondônia: 4 km ENE along rd.
 to São Sebastião off BR-364, 23 May 1984 (fr), Frame et al.
149 (MG, NY, RB, US).

Local names and uses. Brazil: jaborandy (Amapá). Surinam:
 malimbe-toko.

Piper alatabaccum is recognized by glabrous parts, stout
 petioles which leave prominent scars, leaves basally long-
 acute and deccurrent, venation raised on both sides, floral
 bracts long-pedicellate, fruits with four prominent pericarpic
 bulges at the top, wide ellipsoid seeds, and the V-shaped
 walls of the seed coat cell. Leaf shape as well as venation tend
 to display significant variation. Leaves can be ovate to
 widely ovate with 5-7 widely spaced secondary veins or lan-
 ceolate with 10-12 secondary veins which are narrowly spaced.
 Populations of the former type are common in campinarana
 forests but rare in terra firme forests; populations with lan-

ceolate leaves are only found in terra firme forests. These latter populations including specimens which overlap with P. bartlingianum.

The above fruit and floral characters are also common to P. francovilleanum and support their relationship (see CLADISTICS). The species are easily separated on other characters (see under P. francovilleanum). Yuncker (1972), in his treatment of the Brazilian Piperaceae, erroneously determined several specimens of P. alatabaccum as P. bartlingianum with the result that the former taxon was not mentioned for that country. Similarly, Steyermark (1984) cited one collection for Venezuela but included one specimen of P. alatabaccum (Steyermark 904123) in P. bartlingianum. Careful examination of specimens in both species disclose several important vegetative characters by which they can be easily separated in sterile condition (see under P. bartlingianum).

Fruits in several of the specimens examined contained insect larvae; however, no apparent damage was noticed in seeds or fruit development.

6. Piper piscatorum Trelease & Yuncker, Piperaceae of Northern S. Amer. 1: 395. 1950. Type. Venezuela. Bolívar: La Prisión, middle Caura river, 120 m, 3 Apr 1939 (fl), Ll. Williams 11685 (holotype, US; isotypes, F, ILL).

Terrestrial shrub, 1 m tall, sparingly branched; internodes striate, canaliculate, 2-3.4(-4) cm long, papillate, sparsely pubescent when young, glabrescent. Leaves chartaceous opaque, sometimes thin-membranous and translucent, narrow ovate to lanceolate 2-2.8(-3.3) times longer than wide, lamina symmetric to strongly asymmetric (8.5-)10-15(-18) x (2.1-)3.6-6.3(-7.5) cm, basally acute, sometimes obtuse on one side, apically short-acute to long-acuminate, glossy green above and light green beneath when living, olive or light green above and light green beneath when dry, sparsely hirtellous above at the base with an intramarginal hirtellous region beneath, midvein raised or impressed above in the distal half, the 9-13 secondary veins slightly raised above, venation raised beneath; petioles striate, canaliculate, 0.4-0.8 cm long, papillate, glabrous or sometimes sparsely hirtellous. Prophylls papillate, glabrous. Inflorescences erect, white in flowers and green in fruit when living, brown or blackish in fruit when dry; peduncles striate, 0.2-0.6 cm long, papillate, glabrous; flowering portion 2.6-4.1(-5.3) cm long; rachis ridges obscured at anthesis, appearing glabrous and smooth, becoming fimbriate at fruit, covered by thin, white translucent 6-10-celled hairs; floral bracts 0.2-0.5 mm wide, saccate-galeate, sessile at anthesis becoming pedicellate in fruit, 0.5-1 mm distant from the rachis, densely pubescent at the base. Flowers sessile, tightly congested at

anthesis, loosely crowded in fruit; anthers dehiscing laterally. Fruits wide obovoid, 1.7-2 mm long, 4-ribbed and slightly sulcate; seeds wide obovoid, 1.5 x 1 mm, asymmetric, 4-ribbed, slightly sulcate, blackish when dry.

Distribution. (Fig. 86A). Two apparent centers of dispersion occur north of the Amazon basin in Colombia (Vichada) and Venezuela (Bolívar) in the understory of gallery forests, and in the periphery of the Amazon basin at the edge of the Guiana and Brazilian Shields in Bolivia (Beni, Pando) and Brazil (W Amazonas, Maranhão, N SE Pará and Rondônia) where it grows in terra firme forests. It is normally found in little disturbed forests, less often in secondary vegetation. It is cultivated in W Amazonas (Brazil) and the state of Beni in Bolivia. It is rare in the southern portion of its range, otherwise apparently common and abundant at the gallery forests in Venezuela; 90-500 m elev. Flowering collections known from Jan to Apr in Colombia and Venezuela, and Aug to Oct from Bolivia and Brazil; fruiting collections are known from May through Dec.

Specimens examined. COLOMBIA. Vichada: Rd. between Pto. Carreño and Pto. Gaitán, El Delirio, 180 m, 21 Mar 1971 (fl), Pinto et al. 1477 (COL, P).

VENEZUELA. Bolívar: La Prisión on the Río Caura, 16 Dec 1901 (fl), André 3 (K); La Unión, basin of Río Caura, 90 m, 14 Feb 1939, Ll. Williams 11258 (US); El Morrocoy, Guayapo, basin of Río Caura, 200 m, 14 Apr 1939, Ll. Williams 11800 (US); 7 km NE of Ciudad Piar, 350-500 m, 10 Apr 1981 (fl), Liesner & González 11444 (MO, NY, VEN); El Dorado, Jun 1950 (fr), Curran A-2 (NY). T. F. Amazonas: Depto. Apures, rd. Pto. Ayacucho-Samaripo, km 22, from Pto. Ayacucho, Garcitas, 85 m, 6 Apr 1984 (fl), Plowman et al. 13514 (F, NY, VEN); lower and middle Caura, Oct 1960 (fr), Tamayo 4387 (VEN).

BRAZIL. Amazonas: Río Cunhua at Canaca, basin of Río Purús, 27 Nov 1971, Prance et al. 16387 (F, INPA, NY, U, US, VEN); vic. of Jamamadí Indian village, Río Apitua, trib. of Río Purús, 1 Jul 1971 (st), Prance et al. 13932 (ECON, INPA, NY, US). Maranhão: Rd. to Gurupy, region of Carutapera, 20 Jan 1933 (fl), Frões 2021 (NY). Pará: Tapajós region, Aramanahy, 6 Jan 1932 (fr), Monteiro da Costa 226 (F); Serra dos Carajás, Serra Norte, 15 km W of AMZA exploration camp, 400 m, 12 Oct 1977 (fr, fl), Berg et al. BG-478 (INPA, MG, NY), Lageira airstrip on Río Maicurú, 220 m, 19 Jul 1981 (fr), Strudwick et al. 3236 (MG, NY, US); 23 km upstream from Jagura airstrip, W bank of Río Micurú, 28 Jul 1981 (fr), Strudwick et al. 3650 (INPA, MG, NY); Sete Varas airstrip on Río Curuá, 5 Aug 1981 (fr), Strudwick et al. 4197 (MG, NY, US); Breu Branco, 40 km S of Tucuruí, 5 km W on old logging rd., 16 Nov 1981 (fr), Daly

& Callejas 1377 (INPA, MG, NY, US); 22 Nov 1981 (fr), Daly & Callejas 1540 (INPA, MG, NY, US). Rondônia: Pto. Velho to Cuiabá hwy., vic. of Jarú, 16 Aug 1968 (fl, fr), Forero & Wrigley 7132 (INPA, MG, NY, P, R, U, US); Mpio. Ariquemes, mining site, Mibrasa, upper Condeias, SE of Ariquemes, 15 May 1982 (fr), Teixeira et al. 477 (INPA, NY).

BOLIVIA. Beni: Pto. Itenez, region of Río Baures, 250 m, 20 Jan 1982 (fr), Chavez s.n. (LPB, NY); Prov. Vaca Díez, vic. Chácobo village, Alto Ivón, 200 m, 19 Nov 1983 (fr), Boom 4012 (NY); 16 km S of Riberalta, 31 Jul 1982 (fr), Daly et al. 2030 (LPB, NY). Pando: S of Río Abuna, 18 Jul 1968, Prance et al. 6150 (INPA, MG, NY, P, R, U, US, VEN).

Local names and uses. Bolivia: guatini, huatini, nibosa (Beni). Brazil: jaborandy, patsi, washi (Amazonas); jaborandy (Maranhão); jambú de mata, jambú de muela (Pará). Venezuela: manchauia, raíz de mato (Bolívar).

The anesthetic effects of the roots and stems are reported throughout its range. In Venezuela, the states of Maranhão and Pará in Brazil, and Beni in Bolivia, the roots are used for toothache. Additionally the roots are used as a fish poison in Venezuela (Ll. Williams 11258). Prance 13932 reports that the roots are chewed by the Jamamadí Indians

(Amazonas, Brazil) as a mild anesthetic producing a tingling sensation in the tongue and mouth. Boom 4012 observed among the Chácobo Indians (Beni, Bolivia) that "exudates from the stem are applied directly to the hurting tooth or even better a piece of root is chewed. A very strong numbing sensation is felt within 30 seconds." Monteiro da Costa 226 mentions the preparation of a tea made from stems as a diaphoretic; a similar use is reported by Fröes 2021 in Maranhão (Brazil). According to Prance and Boom (aforementioned collections) the species is cultivated by the Jamamadí and Chácobo Indians, respectively.

Piper piscatorum is recognized by sparsely pubescent young internodes, leaves sparsely pubescent at base and with an intramarginal hirtellous region beneath, floral bracts long-pedicellate, fruit obovoid, seeds asymmetric, and the omega-shaped walls of the seed coat. The asymmetric seeds are unique to the species.

In populations from the northern part of the P. piscatorum range (Venezuela and Colombia), with the exception of a single collection (Curran A-2), leaves are thin-membranous and translucent and with obtuse bases. On the other hand those populations in the periphery of the Amazon basin have chartaceous leaves with acute bases. These latter populations

overlap those of P. hoffmannseggianum var. latifolium from Rio de Janeiro, but are easily separated by the lack of an intramarginal hirtellous region on the leaf beneath (in var. latifolium).

Yuncker (1973) determined several specimens of P. piscatorum from Brazil as immature specimens of Ottonia sp., and therefore did not recognize the species for Brazil. Aside from the aforementioned variation, some specimens (Boom 4012) show flowering branches which abort, with a single inflorescence fully developed and appearing as emerging from the axil of the leaf.

Piper piscatorum is closely related to P. hoffmannseggianum. In both species the oil-containing idioblasts are in contact with tracheids which are oriented at right angles to the veinlets (Fig. 43). All floral characters, except for the seed shape and the seed coat of P. piscatorum are present in P. hoffmannseggianum.

7. P. hoffmannseggianum Roemer & Schultes, Mantissa 1: 242. 1822.

Terrestrial shrubs, sometimes scrambling and somewhat lianescent, or more rarely epiphytic, 0.4-3 m tall, sparingly to profusely branched; internodes terete or more commonly striate, canaliculate (2.5-)3-4(-5) cm long and 1-4 mm in diam., papillate, glabrous, rarely glandular dotted.

Leaves thick-chartaceous, opaque, less often thin-membranous and translucent, oblong, narrow oblong, more often elliptic or narrow elliptic to ovate, narrow ovate or lanceolate, (1.6-)2-4(-4.6) times longer than wide, lamina symmetric or rarely asymmetric, (8-)10-19(-27) x (2.5-)3.5-10(-11) cm, basally short-acute or obtuse on one or both sides, apically short-acute to acuminate, rarely mucronate, glossy green above and light green beneath when dry, glabrous above and often with an intramarginal hirtellous region beneath, occasionally the midrib sparsely hirtellous beneath distally, rarely glandular dotted throughout; midvein impressed or partially raised to fully raised above, the 6-16 secondary veins slightly raised to fully impressed above, venation strongly raised beneath; petioles thin or stout and then leaving prominent scars, striate, canaliculate, 0.6-1.5 cm long, papillate, glabrous, obscurely glandular dotted. Prophylls caducous, 0.8-1.2 cm long, apically short-acuminate, sparsely hirtellous when young, obscurely glandular dotted. Inflorescences erect, white in flower and green in fruit when living, white to orange when dry; peduncles thin or less often stout, striate canaliculate, 0.5-1.2 cm long, papillate, glabrous; flowering portion (3.5-)4-10(-12) cm long; rachis obscured at anthesis, appearing smooth and glabrous, becoming fimbriate, covered by thin, erect, white translucent 3-6-celled hairs, obscurely glandular dotted; floral bracts 0.4-0.7 mm wide, saccate-

galeate, obscurely glandular dotted, sessile at anthesis, becoming pedicellate at fruit, 1-2.1 mm distant from the rachis, densely pubescent at the base. Flowers sessile, tightly congested at all stages; anthers dehiscing laterally; stigmas sessile. Fruits wide ellipsoid, 2.8-4 mm long, 4-ribbed and slightly sulcate; seeds wide ellipsoid, 1.7 x 1.5 mm, bilaterally symmetrical, 4-ribbed, a pair of ribs in one plane distinctly massive and frontally sulcate, glossy orange when dry.

Distribution. (Fig. 86A). Occurring abundantly in the coastal forests of SE Brazil from Pernambuco to Rio de Janeiro as an understory shrub, and rarely in restinga areas in Bahia and Pernambuco.

Key to Varieties of Piper hoffmannseggianum

1. Flowering branches orthotropic; leaves oblong to narrow oblong, basally acute with 6-9 secondary veins equally spaced; forests bordering restingas or more commonly in restingas in Bahia, Pernambuco, and Pará (?).

7a. var. hoffmannseggianum.

1. Flowering branches plagiotropic; leaves ovate to wide

ovate or lanceolate, basally acute or obtuse with 10-16 secondary veins inaequilaterally spaced; forests in the interior or along the coasts of Bahia, Espírito Santo, Minas Gerais, Pará, and Rio de Janeiro.

7b. var. latifolium.

7a. Piper hoffmannseggianum var. hoffmannseggianum Roemer & Schultes.

Piper hoffmannseggianum Roemer & Schultes, Mantissa 1:

442. 1822. Type. Brazil. Pará (?), Sieber (?) s.n. in Hoffmannsegg's herbarium (holotype, B-Wildd. 646, IDC neg. 7440). As noticed by Hiepko (1972) the names of botanists appearing on the labels at the Willdenow herbarium are not always those who collected the plants. Von Hoffmannsegg, who never collected in South America (Cowan & Stafleau, 1979), has 470 specimens at that herbarium (Hiepko, 1972). According to Urban (1906) specimens in the Hoffmannsegg herbarium in B-Wildd. from Brazil were collected by F. W. Sieber. Sieber, a young servant of Hoffmannsegg, was trained by Link and travelled to Brazil where he collected (1801-1807) in the Amazon basin along the Tocantins river in Gametá, Gurupá, and the Amazonas in Santarém and Obidos. Besides specimens at B-Wildd., duplicates of Siebert collections were also deposited at HAL and/or were incorporated in Martius' herbarium (NY)

(Urban, 1906). I have not been able to locate any duplicate of Siebert in the aforementioned herbaria (except B-Willd.). The specimen at Berlin does not mention any collector, date or specific locality in Brazil. Thus the collector as well as the possible locality for the type collection follow Urban's information. As is mentioned in the discussion, the assumption that the type collection is from Pará involves significant implications on the species distribution (see discussion). Piper citrifolium Link, Bot. Jahrb. Syst. 3: 63. 1820, non Lamarck 1791. Ottonia laeta Kunth, Linnaea 13: 587. 1839, nom. superfl. Piper laetum (Kunth) C. de Candolle, Prodr. 16(1): 309. 1869, nom. superfl.

Piper regelii C. de Candolle, Prodr. 16(1): 309. 1869. Type. Brazil. Bahia: Ilhéus, Jun-Aug 1822 (fr), Riedel 79 (holotype, LE).

Piper quadratiovarium Yuncker, Bol. Inst. Bot. São Paulo. 3: 118. 1966. Type. Brazil. Pernambuco: Without specific locality, 25 Sep 1935 (fr), Pickel 4038 (holotype, IPA).

Terrestrial or less often epiphytic shrubs, 0.3-1 m tall, often flowering precociously, sparingly branched, flowering branches orthotropic; internodes stout, terete, smooth. Juvenile leaves often equal in size and shape to the adult ones, rigid, chartaceous, opaque, oblong to narrow oblong

(1.6-)2.1-2.6(-2.5) times longer than wide, lamina symmetric, basally short-acute on both sides, the 6-9 secondary veins with intercostal areas symmetrically spaced, glabrous above, with an intramarginal hirtellous region beneath; petioles stout, 1.2-1.5 cm long.

Distribution. (Fig. 86A). Known from the state of Bahia where it grows in the coastal forest at the edge of restinga areas or more commonly in disturbed restingas from Maraú to Una where it often grows as an epiphyte in the root system of cultivated palms (Attalea funifera), and from two collections in the state of Pernambuco; 0-30 m elev. Flowering and fruiting collections in Bahia from Jan to Jun, but apparently fruiting earlier (Sep) in Pernambuco. It probably also occurs in Pará (see under the type).

Specimens examined. BRAZIL. Bahia: Without specific locality, 1839 (fl, fr), Blanchet 238, 240 (both BM, G-DC); Igreja Velha, 1841 (fr), Blanchet 3232 (G-DC, P); Ilhéus, Ilha dos Amores, rd. Ilhéus-Itabuna, along Cachoeira & Fundão rivers, 13 May 1984 (fr), dos Santos 82, 85 (both CEPEC, NY); Pontal de Ilhéus, 23 Jun 1984 (fr), Carvalho 2088 (CEPEC, NY); Maraú, Campinho, 3 Oct 1983 (fr), Carvalho & Plowman 1448 (CEPEC); Una rd. Comandatuba-Piedras, km 8, 17 km S of Una, 13 Jan 1985 (fr), Mattos Silva 1812 (CEPEC, NY).

7b. Piper hoffmannseggianum Roemer & Scultes var. latifolium

(Kunth) Callejas, comb. nov.

Fig. 91.

Ottonia laeta Kunth var. latifolia Kunth, Linnaea 13: 587.

1839. Type. Brazil. Rio de Janeiro: Without specific locality, 1834 (fr), Gaudichaud 1113 (lectotype, here designated, G-DC). Kunth cited three collections (Sellow, Gaudichaud, and Luschnanth) without giving any numbers or specific localities. Nor did he indicate on which specimen he based his description. Miquel (1844) cited the same collectors but cited Gaudichaud's collection as Gaudichaud 1113. According to that author the collection was deposited in G, while the Sellow and Luschanth collections were deposited at B. I have not found any collection at Berlin or Paris (Sellow's collection) of any of the collectors mentioned by Kunth which correspond to P. hoffmannseggianum var. latifolium. Miquel's description (1844) is almost identical to that of Kunth, and is based on Gaudichaud 1113. It is difficult to determine whether or not Gaudichaud 1113 (of Miquel's description) and Gaudichaud s.n. (of Kunth's) represent the same collection or duplicates of it. I am here assuming they belong to the same collection or at least to material seen by both authors. The description of Kunth fits exactly Gaudichaud 1113. Thus I designate that collection as the lectotype.

Ottonia pohliana Miquel, Linnaea 20: 179. 1847. Type.

Brazil. Rio de Janeiro: Forests in Corafalga, Feb 1818 (fr), Pohl 5033 (holotype, W; isotypes, PRC, U). Piper pohlianum (Miquel) C. de Candolle, Prodr. 16(1): 256. 1869.

Artanthe divergens Presl, Epil. bot. 228. 1849. Type.

Brazil. Rio de Janeiro: Without specific locality, no date, Pohl s.n. (holotype, PRC). Piper divergens (Presl) C. de Candolle, Prodr. 16(1): 371. 1869.

Piper translucens Yuncker, Bol. Inst. Bot. São Paulo. 3: 130. 1966. Type. Brazil. Rio de Janeiro: Mount Corcovado, nr. Sebastianópolis, no date, Martius s.n. (holotype, M; isotype, M).

Terrestrial shrubs, sometimes scrambling, evoking a lianescent habit, 0.8-2.5 m tall, sparingly to profusely branched, flowering shoots orthotropic, internodes thin, striate, canaliculate. Juvenile leaves different in shape and size from adult ones, thick-chartaceous, opaque, less often thin-membranous and translucent, ovate to wide ovate often narrowly lanceolate, 1.2-3(-3.6) times longer than wide, lamina asymmetric then basally obtuse on one or both sides, or lamina symmetric and the leaf base acute on both sides, 10-16 secondary veins inaequilaterally spaced, glabrous on both sides or less often with an intramarginal hirtellous region beneath; petioles thin to stout 0.6-1.2 cm long.

Fig. 91. I. Illustration of Ottonia pohliana (= Piper hoffmann-
seggianum var. latifolium. From Martius Flora
Brasiliensis. pl. 23. Vol. IV. 1852.

27.



OTTONIA corrugata H. Pohlham.

Distribution. (Fig. 86A). Occurring in the coastal forests of SE Brazil in the states of Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro. Growing in the understory of wet forests, in little disturbed areas but more often in secondary vegetation where it is common; 0-960 m elev. Flowering and fruiting throughout the year, with most collections known from Sep to Jan.

Specimens examined. BRAZIL. Bahia: Rd. BR-5, 16 km S of Eunapólis, 28 Sep 1966 (fr), Belém & Pinheiro 2667 (CEPEC, NY); 2 km NW of Una, 22 Nov 1983 (fl), Callejas et al. 1779 (CEPEC, HUA, NY, RB); Itamarajú, fazenda Pau-Brazil, 5 km NW of Itamarajú, 30 Oct 1979 (fr), 160 m, 3 Nov 1983 (fl), Carvalho & Callejas 2021, 2047 (both CEPEC, HUA, NY, RB), 30 Oct 1979 (fr), Mattos Silva & Britto 663 (CEPEC); Urucuça, rd. to Taboquinha, 27 Apr 1971 (fr), Pinheiro 1241 (CEPEC). Espírito Santo: Engenheiro Reeve 500 m, 18 Feb 1903 (fr), Rober. s.n. (K). Minas Gerais: Mpio. Sete Lagoas, Jul 1937 (fr), Mertens 1749 (RBR). Rio de Janeiro: Without specific locality, no date, Burchell 4408 (K); Pedra da Gávea, 360 m, rd. to Iposeira, 13 Jan 1984 (fr), Callejas et al. 2023, 2025, 2039 (HUA, NY, RB, SP, U, US), 150 m, 27 Mar 1977 (fr), Carauta et al. 2394 (GUA, NY); Corcovado, no date, Cassareto 1701 (G-DC), Gardner 119 (BM, K, NY); no date, Gaudichaud

1111, 1118 (both G, P), Glaziou 4202 (C); Serra dos Orgãos,
 State Park, 1 Sep 1964 (fl), Hatschbach & E. Pereira 11470
 (MBM, NY); Pedra do Urubú, 8 Sep 1966 (fl), Ichaso 98 (NY,
 RB); forests of Pai Ricardo, 18 Sep 1946 (fl, fr), Occhioni
696 (NY, RB); forests of arboretum, 8 Jul 1954 (st), Pereira
734 (NY, RB); Botanical Garden, 16 Jan 1961, Pereira 5654
 (HB, IAN); Corcovado, Jan 1818 (fr), Pohl s.n. (PRC); Paqueta
 island, 20 May 1960, Scheinvar 105 (RB); Jacarepaguá, E of
 Pedra da Ituna, 30 Sep 1969 (fr), Sucre & Dun s.n. (NY, RB,
 US); Pedra da Gávea, 700-770 m, 4 Jan 1969 (fr), Sucre et al.
4273 (NY, RB); Forest Reserve of the Botanical Garden, 18 Jan
 1969 (fr), Sucre & Braga 4448 (NY, RB, RBR, US); NE slopes of
 Serra da Mendanha, 360-410 m, 13 Nov 1969 (fr), Sucre et al.
6276 (NY, RB); Jacarepaguá, 40 m, 20 Nov 1969 (fr), Sucre et
al. 6311 (NY, RB); Forest Reserve of Tijuca, 600 m, 25 Nov
 1969 (st), Sucre & Barroso 6340 (NY, RB); Serra da Mendanha,
 450 m, 27 Nov 1969 (fl, fr), Sucre et al. 6367 (NY, RB); 300
 m, 9 Apr 1970 (fr), Sucre 6563 (NY, RB), Taquara da Tijuca,
 sertão, 670 m, 20 Sep 1971 (fl), Sucre 7803 (NY, RB); Serra
 da Mendanha, 500 m, 19 Apr 1972 (fr), Sucre et al. 8856 (NY,
 RB). Without specific locality, no date, Miers 3075 (K);
Riedel 293 (LE, NY); Riedel & Langsdorff 102 (LE); 1816-1821
 (st), Saint-Hilaire 27 (K, NY, P); 20 Oct 1969 (fr), Sucre
6038 (NY, RB).

Local names and uses. Brazil: jaborandi, João-barandinho, João baradin (Bahía).

Used extensively in Bahia as a cure for tooth-ache and as a sudorific. Moura (1884) in his medical dissertation on the Brazilian sudorifics included extensive data on the uses and therapeutic effects of this species. His data was previously reviewed under Phytochemistry and Physiological Action and will not be repeated here.

Piper hoffmannseggianum is characterized by sessile and tightly congested flowers, pedicellate floral bracts, fimbriate rachises, and seeds with bilateral symmetry in which a pair of ribs is distinctly sulcate. Leaves in this species are generally obscurely glandular dotted. A single collection from Espírito Santo (Robert s.n.) has leaves glandular dotted, otherwise the collection matches in all other characters P. hoffmannseggianum.

As here recognized this species consists of two varieties, both of which include a habitat and to some extent a geographic component. In var. hoffmannseggianum individuals occupy transitional vegetation types between restingas and forests, thus one may find the species in fully exposed sandy dunes or in the understory of mesic forests. Regardless of the life zone, plants are generally poorly branched distally with

the aerial system of the plant consisting of orthotropic flowering shoots. When found in sandy dunes, plants of var. hoffmannseggianum are often found as epiphytes on the root system of palms. In such conditions plants rarely attain maturity and often flower precociously. Little or no variation is found in this variety. Piper regelii was erroneously described by C. de Candolle as having three carpels. The type of var. hoffmannseggianum was not examined by Yuncker (1973), a reason which may explain the description of P. quadratiovarium. Yuncker separated that species by the quadrate fruits, stout petioles and pedicels, and acute-based leaves. The fruit character is an artifact of drying and is more prominent in the immature stages of the fruit. Type collections of the aforementioned species are otherwise identical to that of var. hoffmannseggianum.

Piper hoffmannseggianum var. hoffmannseggianum is known from less than 10 collections. This could be a result of habitat destruction in the SE forests of Brazil, more specifically restingas (Mori & Boom, 1981), but also an artifact of poor collecting in the states north of Bahia.

P. hoffmannseggianum var. latifolium is very abundant. It displays wide range of variation in leaf characters, more particularly in shape, size and texture of the leaf, and to some extent in shape of the leaf base. Individuals are profusely branched, often treelets to 2.5 m tall. This variety grows in

the understory of the coastal forests, in little or heavily disturbed sites. In the southern portion of its range individuals have leaves thin-membranaceous, narrow lanceolate, and with acute bases, generally 3-3.6 times longer than wide. In the north leaves are thick-chartaceous, ovate to wide ovate, and with obtuse bases, generally 2.5 times longer than wide. Populations from the southern portion are mainly from Rio de Janeiro and constitutes 80% of the collections examined by Yuncker (1973). Not surprisingly the species concept has been strongly attached to those populations.

Both Ottonia pohliana and Arthante divergens have leaves wide ovate with inflorescences fully mature and in fruit. The latter taxon was described as a 3-carpellate taxon while O. pohliana was separated by its fruit shape, fimbriate rachises, and glabrous leaves. The two taxa were previously lumped by Yuncker (1973). That author, however, also described P. translucens, the type of which is hardly distinguishable from that of P. divergens. Yuncker relied too heavily on the fruit characters and described the new species by failing to recognize the immature stages of the fruit.

Piper hoffmannseggianum is one of two species (Piper ovatum being the other) of subgen. Ottonia in the forests of SE Brazil that extends into the Amazon basin. Collections from north of Pernambuco are known from few localities and may indicate either the extension of the southeastern forest (as to

be in contact with the Amazon basin) or a single dispersal event. Notice should be made that the areas where the species was supposedly collected by Sieber (type of the species) are otherwise heavily collected sites in Pará, (Prance, pers. comm.). Except from the type and the collection of Poisson (without specific locality), I have not seen a single specimen of P. hoffmannseggianum from the Amazon basin. Thus one should not preclude an artifact of collecting (from other areas outside of the Amazon basin).

The species is closely related to P. piscatorum from the Amazon basin. There are a series of vegetative characters on which both species can be separated (see under P. piscatorum). In the fertile condition these taxa are easily distinguished by the obovoid fruits and asymmetric seeds of P. piscatorum, compared to the wide ellipsoid fruits and bilaterally symmetric seeds of P. hoffmannseggianum.

8. Piper darienense C. de Candolle, Prodr. 16(1): 374. 1869.

Ottonia glaucescens Miquel, in Seem. Bot. Voy.

Herald 200. 1854, non Piper glaucescens Jacquin.

Type. Panamá. Veraguas: San Lorenzo, 1882 (fl),

Seeman 1218 (holotype, K; isotype, K).

Piper acuminatissimum C. de Candolle, Bot. Gaz.

(Crawfordsville) 70: 189. 1920. Type. Costa Rica. San

Carlos, no date, Pittier 16321 (holotype, US).

Piper laxispicum Trelease, Contr. U.S. Natl. Herb. 26: 24.

1927. Type. Panamá. Canal Zone: Gatún Lake, Barro Colorado Island, no date, Standley 31375 (holotype, US).

Piper laxispicum var. latifolium C. de Candolle ex

Trelease, Contr. U.S. Natl. Herb. 26: 24. 1927. Type. Panamá. Colón: Pto. Obaldía, San Blas coast, no date, Pittier 4288 (holotype, US).

Piper permarii Trelease, Ann. Missouri Bot. Gard. 27: 295.

1940. Type. Panamá. Bocas del Toro: Upper Changinola river, Feb 1939 (fr), Permar s.n. (holotype, MO).

Piper fagopyricarpum Trelease, Ann. Missouri Bot. Gard. 27:

295. 1940. Type. Panamá. Chiriquí: Vic. Puerto Armuelles, 0-75 m, 28-31 Jul 1940 (fr), Woodson & Schery 852 (holotype, US; isotypes, F, ILL n.v.).

Piper erythroxyloides R. E. Schultes & García-Barriga,

Rhodora 167: 77. 1975. Colombia. Santander del Norte: La Motilona, border of Colombia-Venezuela, mouth of Río de Oro, 40-50 m, 15-20 May 1965 (fr), García-Barriga & Lozano 18318 (holotype, COL; isotypes, ECON, US).

Terrestrial shrub to 1.5 m tall, sparingly branched; internodes terete or more often striate and canaliculate, 3.5-5 cm long and 3-4 mm in diam., papillate, glabrous. Leaves

chartaceous and opaque or less often thin-membranous, translucent, narrow ovate to lanceolate or elliptic 2.5-3.5(-4) times longer than wide, lamina asymmetric, (8.5-)10.5-19(-21) x (3.5-)4.5-8(-9.5) cm, basally short-acute or obtuse on one side, apically acute to long-acuminate, glossy green above and light green beneath when living, light green on both sides when dry, glabrous above and with an intramarginal hirtellous region beneath; the 7-10 secondary veins impressed above, strongly raised beneath; petioles striate, grooved adaxially, 0.8-1 cm long, papillate, glabrous. Prophylls caducous, 1-1.5 cm long, papillate, glabrous, obscurely glandular dotted. Inflorescence erect, white in flower and green in fruit when living, orange or olive-green when dry; peduncle terete or finely striate, 4-8 mm long, papillate, glabrous; flowering portion (1.5-)2.5-4.5(-5) cm long; rachis not obscured by the flowers, minutely fimbriate, covered by thin, white translucent 2-3-celled hairs, rarely glabrous, often glandular dotted; floral bracts 1-2 mm wide, saccate-galeate, sessile at all stages, obscurely glandular dotted, glabrous. Flowers sessile, widely spaced at anthesis, loosely congested in fruit; anthers dehiscing laterally; stigmas sessile. Fruits at immature stages often umbonate then becoming ovoid to ellipsoid, 3-3.5 mm long, 4-ribbed, slightly sulcate; seeds ovoid-ellipsoid, 2.1 x 1.7 mm, radially symmetric, 4-ribbed, glossy orange when dry.

Distribution. (Fig. 86B). Rather common from SE Nicaragua to Panamá and relatively infrequent in NE South America in Colombia (Antioquia, Bolívar, Chocó, Magdalena, and Santander del Norte) and Venezuela (Mérida, Zulia). It grows in the understory or often along streams, apparently preferring little disturbed forests; sea level to 300 m elev. Flowering Dec to Apr; fruiting from Mar to Apr.

Specimens examined: NICARAGUA. Zelaya: Rama, Nov 1911 (fl), Berger s.n. (US).

COSTA RICA. Alajuela: Above Río Peje, 2 km SE of Florencia, San Carlos, 300 m, 1 May 1972 (fr), Lent 2529 (F, NY); 8 km S of Canalete, 300 m, 2 Feb 1982 (fr), Utley & Utley 3967 (DUKE). Heredia: La Selva, OTS station on Río Pto. Viejo, E of its junction with Río Sarapiquí, 100 m, 21 May 1980 (fr), Grajam 2839 (DUKE); 27 May 1980 (fr), Grajam 2868 (DUKE); 100 m, 17 May 1980 (fr), Hammel 8687 (DUKE); 750 m, 16 Apr 1982 (fr), Hammel 11722 (DUKE); 25 May 1982 (fr), Hammel 12501 (DUKE); 10 May 1982 (fr), Hammel 12156 (DUKE).

PANAMA. Canal Zone: Barro Colorado Island, Dayton trail 370, 22 May 1968 (fr), Croat 5752 (MO, NY); W of clearing, 12 Sep 1970 (fr), Croat 12210 (DUKE, MO, NY); nr Zetek, 9 Jul 1969 (fr), Foster 1099 (DUKE); May 1970 (fr), Foster 1768 (DUKE); 25 m, 21 Sep 1944 (fr), Mexia 6551 (US). Darién:

Cuipó, forests, N of Santa Fé, 18-19 Jun 1967 (fr), Duke 12278 (ECON, MO); S of El Real, headwaters of Río Pirre at Dos Bocas, 100 m, 25 Sep 1969 (fr), Foster & Kennedy 1248 (DUKE); Mannene to the mouth of Río Coasi, 28 Jun 1968 (fr), Kirkbride & Bristan 1555 (NY). Veraguas: Golf of Montijo, Río Suay, 1948 (fl), Fabrega s.n. (MO, NY). Panamá: Torti, S of the Pan American hwy., 25 May 1980 (fl, fr), Folsom 7829 (NY, TEX).

COLOMBIA. Antioquia: Quebrada Guinea, 50 km S of Turbo, 80 m, 22 Apr 1945 (fl, fr), Haught 4587 (ILL, US); Mpio. de Tarazá, corregimiento El Doce, 210 km NE of Medellín, 200-350 m, 15 Dec 1977 (fl), Callejas 342 (COL, HUA). Bolívar: Frasuquillo on Río Sindú, 90-120 m, 5-6 Mar 1918 (fl, fr), Pennell 4603 (NY, US). Chocó: Darién, 1919 (fr), Dawe 886 (K, NY); upper Río Tigre, nr. base of Serranía del Darién, E of Unguía, 250-300 m, 18 Jul 1976 (fr), Gentry et al. 16753 (COL, MO, NY). Magdalena. Sta. Marta, nr. coast, Don Diego, 8 May 1899 (fl, fr), H. H. Smith 2666 (F, GH, MO, NY, PH, US); around Río Frío, between Ciénaga de Sta. Marta and foothills, 0-100 m, 22-30 Jan 1906 (fl), Pittier 1627 (US).

VENEZUELA. Mérida: No date, Carabot s.n. (US). Zulia: Dtto. Colón, Campo Rosario, 18 km E of Machiques-La Fría rd. nr. Ciénaga de Juan Manuel, 2 May 1979 (fr), Bunting et al. 7548 (NY, VEN); Sierra de Perijá, Nov-Dec 1944 (fl); without collector (VEN).

Local names and uses. Costa Rica: alcotán (Burger, 1971). Panamá: duerme boca (Canal Zone). Colombia: cordoncillo (Bolívar), dormidera (Chocó), achikaira, chankira, ishiraki-ra (Santander del Norte). Venezuela: ishi-raquia, sirankira (Zulia).

The leaves and roots are used in Costa Rica for treatment of toothache (Burger, 1971). In Panamá similar use is reported and additionally the plants are used as a fish poison (fide Mexia 6551). In Colombia, according to García-Barriga et al. 18318, as cited by Schultes (1975), the stems are chewed by the Motilones (Bari) Indians as a kind of narcotic which has local effects in the mouth that resemble those of coca leaves. Upon mastication the stems induce a strong burning sensation which is followed by numbness of the tongue and lips. In addition to this use, the plant is chewed in the belief that it prevents dental caries. In Venezuela the species is used to dull the appetite (Steyermark, 1984).

Piper darienense is recognized by sessile and loosely congested flowers, sessile bracts which are 1-2 mm wide, rachis densely short-fimbriate with 2-3-celled hairs, and large globose-ovoid seeds (2.1 x 1.7 mm). The size of the floral bracts (wider than in any other taxon) and the short white pubescence of the rachis distinguish Piper darienense

from other taxa in subgen. Ottonia. Although very distinctive it nevertheless displays wide extremes in fruit shape. Shortly after fertilization the stigmatic lobes are still straight and shortly decurrent to the ovary walls, and the immature fruit is thus described as umbonate. Often authors describe the fruit in this stage as being stylose, and fail to distinguish the stigmatic lobes from a true style. As maturation proceeds, the stigamtic lobes become fully decurrent throughout with the fruit walls, the mature fruit being shortly apiculate and globose to ovoid.

Types of P. permarii, P. fagopyricarpum, P. laxispicum, and P. erythroxyloides include specimens with immature fruits, the shape of which was used in each case as the diagnostic character for the species. Since the type collection includes immature young plants, the size of the leaf and to some extent its shape led de Candolle (1920) and Trelease (1927) to describe P. acuminatissimum (with narrow lanceolate and apically acuminate leaves) and P. laxispicum var. latifolium (wide ovate leaves), respectively.

Piper darienense overlaps in vegetative characters with P. ovatum, P. piscatorum, and P. bartlingianum, and sterile specimens of these latter taxa are not easy to separate (unless one relies on geographic distribution). The four species are otherwise easily distinguished by floral characters.

Piper darienense is closely related to P. bartlingianum

with which it has in common short-fimbriate pubescence along the rachis. It is distantly related to P. piscatorum, but not to P. klotzchianum as suggested by Guimarães and Ichaso (1969) (see under P. klotzchianum). It is significant that P. darienense occurs only west of the Andes, completely isolated from the rest of the species in subgen. Ottonia. Moreover its sister species, P. bartlingianum, is a widespread Amazonian-Guianan taxon and thus it is possible that the present distribution of P. darienense is the result of a vicariant event. In that case the ancestor of the two taxa may have attained a wider distribution into NE South America with populations isolated by uplift of the Andes in the Miocene/Pliocene period. The disjunct distribution of those two taxa is otherwise very illustrative of a pattern found for many other groups of plants (Gentry, 1982), with a Chocó-Guianan disjunction.

9. Piper ottonoides Yuncker, Bol. Inst. Bot. São Paulo 3:

109. 1966. Type. Brazil. Pará: Remansão, E of the Tocantins railroad, 1 Oct 1966 (fr), Fróes 23952 (holotype, IAN)

Terrestrial shrub, 1.5 m tall, sparingly branched; internodes striate, canaliculate, 2-3.5 cm long and 1-1.5 mm in diam., papillate, glabrous, obscurely glandular dotted. Leaves chartaceous, opaque, narrow ovate to lanceolate, exceptionally

wide ovate, (2.2-)2.6-3.9(-4.1) times longer than wide, lamina asymmetric, (9.5-)11-16(-18) x (3-)3.5-5(-8) cm, basally obtuse on both sides, often lobulate on one side and partially covering the petioles, rarely acute, apically short-acute to long-acuminate, glossy green above and light green beneath when living, olive-green above and brownish beneath when dry, glabrous, glandular dotted on both sides but more prominently above along the midvein; midvein and the 11-13 secondary veins raised on both sides; petioles striate, canaliculate, or rugose, 4-6 mm long, sparsely pubescent towards base, glabrescent. Prophylls caducous, 6 mm long, apically short-acute, sparsely pubescent, obscurely glandular dotted. Inflorescence erect, white at anthesis and greenish in fruit when living, brownish when dry; peduncles striate or rugose, 4-6 mm long, papillate, glabrous; flowering portion 3.5-7(-9) cm long; rachis not obscured at anthesis, weakly glandular dotted, glabrous; floral bracts 0.5-0.7 mm wide, saccate-galeate, distally long-decurrent with rachis (Fig. 9). Flowers sessile, widely spaced at all stages; anthers dehiscent laterally; stigmas sessile. Fruits umbonate, 0.6 mm long, 4-ribbed, slightly sulcate; seeds wide-ellipsoid, radially symmetric, 0.6 x 0.4 mm, 4-ribbed, strongly sulcate, blackish when dry.

Distribution. (Fig. 87A). Known only from the E Amazon basin in Brazil (Amazonas, Maranhão, Pará, and Rondônia). Rare but locally common in terra firme forests on lateritic soils where it grows in the understory; 50-100 m elev. Flowering collections known from May to Aug; fruiting collections from Sep to Dec.

Specimens examined. BRAZIL. Amazonas: Altamira on Rio Abuna, 5 Nov 1933 (fr), Krukoff 5831 (NY). Maranhão: Km 124 of BR-222, between Sta Inés and Açailândia, Belém-Brasília rd., 16 Dec 1978 (fr), N. Rosa et al. 3007 (MG, NY, US). Pará: Belém, 10 May 1948 (fl), Pires 1194 (IAN, US); km 64 on BR-22, 25 Aug 1964 (fl), Prance et al. PF-58876 (MG, NY); vic. of Piritoro, 5 Nov 1965 (fr), Prance et al. 1981 (MG, NY); Belém nr. Catú, 15 Sep 1942 (fr), N. T. Silva 70 (IAN, US). Rondônia: 4 km ENE along rd. to São Sebastião off BR-364, 23 May 1984 (fr), Frame et al. 147 (MG, NY).

Local names and uses. Brazil: jamborandi, jambú-assú, jamburana (Pará).

Collectors report that roots are chewed as cure for toothache. Prance et al. PF-58876 mentions that roots in Pará are used as a cure for rheumatism.

Piper ottonoides is characterized by leaves with the venation raised on both sides, glandular dotted leaves especially above along the midvein, sessile and widely spaced flowers at all stages, and sessile floral bracts the anterior portion of which is long-decurrent with the rachis. The collection from Rondônia (Frame et al. 148) has leaves ovate compared with all other specimens with leaves narrow ovate to lanceolate. The specimen agrees in all other characters.

In subgen. Ottonia the long-decurrent floral bracts are unique to P. ottonoides and separates it from its closest relative P. klotzschianum. These two taxa have in common sessile, widely-spaced flowers and straight cell walls in the upper and lower leaf epidermis. Piper ottonoides is easily distinguished in sterile condition from P. klotzschianum by its glandular dotted leaves and the raised venation on the adaxial side of the leaf. The two taxa also overlap in leaf shape, a reason for Yuncker (1972) to include several specimens of P. klotzschianum (Mexia 5332, Minas Gerais) under P. ottonoides. Specimens from Pará (Prance et al. 1981 and PF-58876) have ovate leaves very similar to those of specimens of P. piscatorum from Bolivia. Both taxa are separated by the presence of an intramarginal hirtellous region in P. piscatorum.

10. Piper klotzschianum (Kunth) C. de Candolle, Prodr. 16(1):

257. 1869. Type. Brazil. Bahia: Without specific

locality, no date (1835-1837 ?), Luschnath s.n.

(holotype, not found). Ottonia klotzschiana Kunth,

Linnaea 13: 589. 1839. Piper kunthianum Trelease,

Proc. Amer. Philos. Soc. 75: 716. 1935, nom. nudum.

For a discussion on the date of collecting see below
under Piper cosmianum.

Piper cosmianum C. de Candolle, Prodr. 16(1): 257. 1869.

Type. Brazil. Bahia: Bahia Cruz de Cosme, 23 Nov 1835

(fr), Luschnath s.n. (holotype, LE; isotypes, G, LE, W,

n.v). De Candolle does not mention any collector in the

original description. However, comparison of published

data on Luschnath's itinerary in Brazil (Urban, 1906) with

his collections in LE suggest the type of P. cosmianum was

indeed collected by Luschnath. Information on labels

attached to several collections of Piper collected by

Luschnath and included in Fischer's herbarium (date, loca-

lity data, handwriting, and accession numbers for Fischer's

herbarium) at LE, match exactly that of P. cosmianum.

Yuncker (1973) cited the type as collected in 1831 which

is erroneous since during that year Luschnath collected

only in Rio de Janeiro. Comparing the type collection of

P. cosmianum with the original description of P.

klotzschianum one is inclined to think that both names

could be based on the same specimen or at least on dupli-

cates of it. Furthermore, both species were collected by Luschnath. Thus the species may be nomenclatural synonyms rather than taxonomic ones. For the reasons given above I refrain from designating a neotype for P. klotzschianum.

Piper pseudottonia Guimarães & Ichäso, Rev. Brasil Biol.

34(2): 203. 1974. Type. Brazil. Rio de Janeiro: Forest Reserve of Tijuca, Grajau, 160-220 m, 25 Nov 1969 (fr), Sucre et al. 6365 (holotype, RB).

Terrestrial shrub, 1.5 m tall, sparingly branched; internodes striate, slightly canaliculate, 2-3.5 cm long and 3-4 mm in diam., papillate, glabrous, glandular dotted when young. Leaves chartaceous and opaque, ovate to wide ovate, rarely lanceolate, (1.8-)2.1-3.2 times longer than wide, lamina asymmetric, (8-)9.5-18(-19) x (3-)4.5-6.3(-8.5) cm, basally short-acute on one side and obtuse on the other, often shortly peltate and obtuse on both sides, apically short-acute to acuminate, glossy green above and pale green beneath when living, green opaque above and light green beneath when dry, glabrous above and often with an intramarginal hirtellous region beneath, sometimes glandular dotted above along midvein; midrib impressed or raised above, the 10-12 secondary veins impressed above and strongly raised beneath; petioles striate or rugose, 0.5-1 cm long, papillate, glabrous. Prophylls, caducous, 0.6-1 cm long, apically short-acute, obscurely glandular

dotted. Inflorescence erect, white at anthesis and green in fruit when living, brownish when dry; peduncles rugose, 0.7-1 cm long, papillate, glabrous; flowering portion 7-11 cm long, rachis partially obscured at anthesis, sparsely hirtellous to fully glabrous, often glandular dotted; floral bracts 0.3-0.5 mm wide, saccate-galeate, sessile at first, becoming pedicellate in fruit and 0.3-0.6 mm distant from the rachis, sparsely pubescent at base, glabrescent. Flowers sessile, loosely congested at anthesis, narrow to widely spaced in fruit; anthers dehiscent laterally; stigmas sessile. Fruit ovoid, 0.6-1.2 mm long, 4-ribbed, sulcate, obscurely glandular dotted; seeds ellipsoid, 1 x 0.7 mm, radially symmetric, 4-ribbed, strongly sulcate, blackish when dry.

Distribution. (Fig. 87B). Known from the Atlantic coastal forests of SE Brazil in the states of Bahia, Minas Geras, and Rio de Janeiro, where it is found in the understory of little disturbed forests or less often in secondary vegetation. It is a rare species but apparently abundant in the wooded slopes of gallery forests in Minas Gerais; 50-725 m elev. Flowering collections unknown; fruiting collections from Apr to Nov.

Specimens examined. BRAZIL: Bahia: Itabuna, rd. Itabuna-Ilheus 5 Apr 1965 (fr), Belém & Magalhaes 713 (CEPEC, NY, RB). Minas Gerais: Viçosa, fazenda José Alejandro, 725 m, 20 Nov

1930 (fr), Mexia 5332 (G, GH, MO, NY, S, US); Dionisio, State Park of Rio Doce, 23 Sep 1976 (fr), Heringer 16025 and 16041 (both IBGE, K, NY).

Piper klotzschianum is characterized by sessile and widely spaced flowers, pedicellate floral bracts, and sparsely pubescent rachis. Except for the type of P. pseudottonia, leaves on all specimens have an intramarginal hirtellous region beneath. Collections from Minas Gerais have leaves which are shortly peltate and lancolate compared to the not-peltate petiolate and wide ovate leaves from plantations in Bahia and Rio de Janeiro. Despite the fact that the descriptions of P. cosmianum and P. klotzschianum are very similar, Yuncker (1973), when lumping the first taxon under P. klotzschianum, did not give information on the type collection of P. klotzschianum or discuss reasons for synonymizing P. cosmianum. The same author suggested that P. klotzschianum was related to P. hoffmannseggianum (see that species). Guimarães and Ichaso discussed the relationships of P. pseudottonia with P. darienense and P. ottonoides. Those authors, by failing to distinguish the mature fruits of P. klotzschianum from those immature in the type of P. pseudottonia, segregated the new species on characters without diagnostic value. According to Guimarães and Ichaso P. pseudottonia was distinguished by its sessile flowers, short-apiculate, ovoid fruits which are den-

sely papillate, and presence of single unbranched veinlets in the marginal areoles of the leaves. Densely papillate fruits and the single unbranched veinlets are common to all species in subgen. Ottonia (see FRUIT and Leaf Histology). Short-apiculate fruits and sessile flowers, on the other hand, were found in all collections of P. klotzschianum here examined.

Piper klotzschianum is most closely related to P. ottonoides and those relationships are discussed under the latter species.

11. Piper guimaraesianum Callejas, nom. nov.

Ottonia peltata Guimarães & Ichaso, Arq. Jard. Bot. Rio de Janeiro 20: 355. 1977, non Piper peltatum Linnaeus. Type. Brazil. Espírito Santo: Mpio. Domingo Martins, Campinho, rd. to Chapeão, 15 Sep 1975 (fr), Carauta 1808 (holotype, RB).

Terrestrial, erect or scrambling shrub, sparingly branched, villous throughout, covered by thin-translucent, white, 15-20-celled hairs; internodes striate, canaliculate, 1.5-3 cm long, glabrescent. Leaves thick-chartaceous, opaque, less often thin-membranous and translucent, ovate to narrow ovate or elliptic, (1.8-)2-2.5 times longer than wide, lamina asymmetric, (9.5-)10-15.5 x (4-)5-7.7 cm, basally peltate,

apically acuminate, grayish-green on both sides when dry, glabrescent above, long-villous beneath especially along midvein, venation light green or whitish above when dry; midvein and the 8-10 secondary veins raised on both sides; petioles striate, canaliculate, 6-8 mm long, papillate, villous. Prophylls caducous, 6-8 mm long, apically long-acuminate, villous on the costa. Inflorescences erect, white at anthesis, brownish in flower and fruit when dry; peduncles striate, canaliculate, 4 mm long, papillate, villous; flowering portion 7-9 cm long; rachis not obscured by the flowers, sparsely hirtellous; floral bracts 0.3-0.4 mm wide, saccate-galeate, sessile at first but later becoming pedicellate and 0.6-0.7 mm distant from rachis. Flowers pedicellate, widely spaced; pedicels 2-4 mm long, glabrous, glandular dotted; anthers dehiscent laterally, densely glandular dotted; stigmas sessile. Fruits ovoid, 1 mm long, 4-ribbed, strongly sulcate; seeds ellipsoid, 1.3 x 1.2 mm, radially symmetric, 4-ribbed, strongly sulcate, blackish when dry.

Distribution. (Fig. 87A). Known only from two collections at the type locality in Espírito Santo (Brazil). It occurs in the understory of little disturbed forest at ca. 630 m elev. Flowering material is unknown; fruiting material has been collected in Jan and Nov.

Specimens examined. BRAZIL. Espírito Santo: Mpio. Domingo Martins, rd. to tower of radio station Campinho, 630 m, 18 Jan 1975 (fr), Peixoto et al. 438 (RB).

Among the species with pedicellate flowers in subgen. Ottonia, P. guimaraesianum is easily distinguished by long-villous parts and especially by its peltate leaves.

The relationships of this species are discussed under P. villosobracteatum. Although it is somewhat regrettable to create a new name for a species otherwise so distinct in subgen. Ottonia, the new name honors Dr. Elsie Guimarães from Rio de Janeiro who has long been a specialist in Piperaceae.

12. Piper villosobracteatum Callejas, nom. nov.

Ottonia villosa Yuncker, Bol. Inst. Bot. São Paulo. 3: 139.

1966, non Piper villosum C. de Candolle. Type. Brazil.

Espírito Santo: Nr. Sta. Thereza, 25 Nov 1953 (fl, fr),

Duarte 4012 (holotype, RB).

Terrestrial shrub, 0.8 m tall, sparingly branched, villous throughout, with thin-translucent or orange, 18-20-celled hairs; internodes striate, canaliculate, 2-3 cm long and 3-4 mm in diam., glabrescent, glandular dotted. Leaves thin, membranous and translucent, narrow ovate to elliptic, 2.2-2.5 times longer than wide, lamina strongly

asymmetric, (12-)15-17.5 x 5-7.5 cm, basally obtuse, lobulate, apically short-acute to long-acuminate, green opaque and with a silver stripe along midvein above, light green beneath when dry, glabrescent between the veins but with midvein long-villous above, densely long-villous beneath, marginally villous; the 10-12 secondary veins impressed above and strongly raised beneath; petioles striate, canaliculate, 0.6-0.9 cm long, papillate, villous. Prophylls persistent at all flowering nodes, apically long-acuminate, 0.8-1 cm long, long-villous. Inflorescences erect, white at anthesis but orange when dry; peduncles striate or rugose, 0.5-0.9 cm long, villous, glandular dotted; flowering portion 2-4 cm long; rachis not obscured by flowers, papillate, glandular dotted; floral bracts, 0.4 mm wide, saccate-galeate, distal laminar portion long-villous, pedicellate, 0.7 mm distant from the rachis, glandular dotted. Flowers pedicellate, loosely congested at anthesis but widely spaced in fruit; pedicels 1.5-2 mm long, glandular dotted; anthers dehiscing laterally, glandular dotted; stigmas sessile. Fruits immature, globose ovoid, 1.0 mm long, 4-ribbed, slightly sulcate, glandular dotted; seeds not seen.

Distribution. (Fig. 87A). Known only from the type locality, in the understory of secondary forests at 600 m elev. The type was collected with flowers and fruits in Nov.

Within the pedicellate-flowered species in subgen.

Ottonia, Piper villosobracteatum is recognized by long-villous parts, especially the villous distal portion of the floral bracts, villous midvein of the leaf above, persistent prophylls and glandular dotted parts. Villous bracts are rare in the genus Piper, otherwise known only from P. myrmecophyllum C. DC., a species with unisexual flowers from the Philippines.

Piper villosobracteatum is closely related to P. guimaraesianum also known from Espírito Santo. The taxa have in common wide ovate leaves, calcium oxalate crystals in the leaf mesophyll, and long-villous parts. They are easily distinguished however by the villous bracts of the former (glabrous in P. guimaraesianum) and peltate leaves of P. guimaraesianum (non-peltate in P. villosobracteatum).

The presence of villous hairs and pedicellate flowers is a rare combination of characters in subgen. Ottonia and otherwise occurs only in P. brevinodis. Piper brevinodis has a series of reduced internodes between each flowering node, a unique character in the subgenus. The presence of persistent prophylls, long-villous leaves, and a silver stripe in P. villosobracteatum is known also from the sessile-flowered taxon P. francovilleianum, from NE Amazonia. The two species are

otherwise only distantly related.

13. Piper brevinodis Callejas sp. nov. Type. Brazil. Minas

Gerais: Forest Reserve of Rio Doce, forests of Lagoa

Central, 190-200 m, 30 Aug 1973 (fr), Sucre et al.

10133 (holotype, RB; isotype, RB).

Fig. 92.

Frutex terrestris; ramulis gracilibus junioribus dense villosis patentibus 1-1.5 mm longis; internodis junioribus brevis; foliis membranaceis vel chartaceis, supra bullatis, subtus lacunosis, lanceolatis vel elliptico-oblanco-latis (9-)10.5-13 cm longis, 3-4.3 cm latis, basi aequalibus et cordatis vel lobatis, apice acutis vel longis attenuatis, supra glabris subtus in nervo et venis dense villosis; prophylliis persistentibus ad floriferis nodis, 1 cm longis costis densi longi villosis; pedunculis striatis, 7-9 cm longis, dense villosis; floribus pedicellatis, stigmatibus sessilibus.

Terrestrial shrub, 0.5 m tall, sparingly branched; first basal internodes between flowering nodes reduced, often 7-9, consisting of a single prophyll, this caducous but with a prominent clasping base persistent, normal elongated internodes striate, canaliculate, 2-3.5 cm long and 2 mm in diam., papillate, long-villous when young, with thin-translucent, 25-30-celled hairs, 1-1.5 mm long. Leaves membranous or less often chartaceous, bullate above, pouched beneath, lanceolate

or elliptic-oblongate, (2.5-)3-4(-4.3) times longer than wide, lamina symmetric, (9-)10.5-13 x 3-4.3 cm, basally equilaterally cordate or lobate, then lobes overlapping petioles, apically short-acute, less often attenuate, glossy green above when living, pale green or brownish on both sides when dry, glabrous above, long-villous beneath along the veins; the 10-12 secondary veins impressed above, strongly raised beneath; petioles striate, 3.5-7 mm long, villous. Prophylls caducous, 0.8-1 cm long, apically acuminate, long-villous on the costa. Inflorescence erect, white in flower, orange when dry; peduncles striate, 7-9 mm long, densely villous; flowering portion 1.5-2 cm long; rachis not obscured by the flowers, glabrous, obscurely glandular dotted; floral bracts 0.3-0.5 mm wide, proximally sparsely short-pubescent, obscurely glandular dotted, pedicellate 0.3 mm distant from the rachis. Flowers pedicellate, loosely congested; anthers 0.3 mm wide, dehiscing laterally; stigmas sessile. Fruits not seen.

Distribution. (Fig. 87A). Known only from the type in the understory of little disturbed primary forests; 190-200 m elev. Flowering in Aug; fruiting specimens unknown.

Piper brevinodis is characterized by numerous (7-9) reduced internodes in the flowering branches, each with the

persistent clasping base of the single prophyll, villous stems, petioles and leaves, bullate leaves, persistent prophylls, and pedicellate flowers.

The type specimen has the inflorescence in several stages. Flowers are fully developed and the pedicellate condition is evident, however there are no mature fruits and thus pedicel length (final length attained after fruits have already formed) can not be determined.

Piper brevinodis is related to P. guimaraesianum and P. villosobracteatum, with which it has in common long-villous hairs and pedicellate flowers. Piper brevinodis is easily separated by its reduced internodes and lanceolate to elliptic-oblongate bullate leaves. This taxon overlaps in leaf shape with some specimens of P. anisum, the leaves of which are not bullate.

14. Piper rizzinii Callejas, nom. nov.

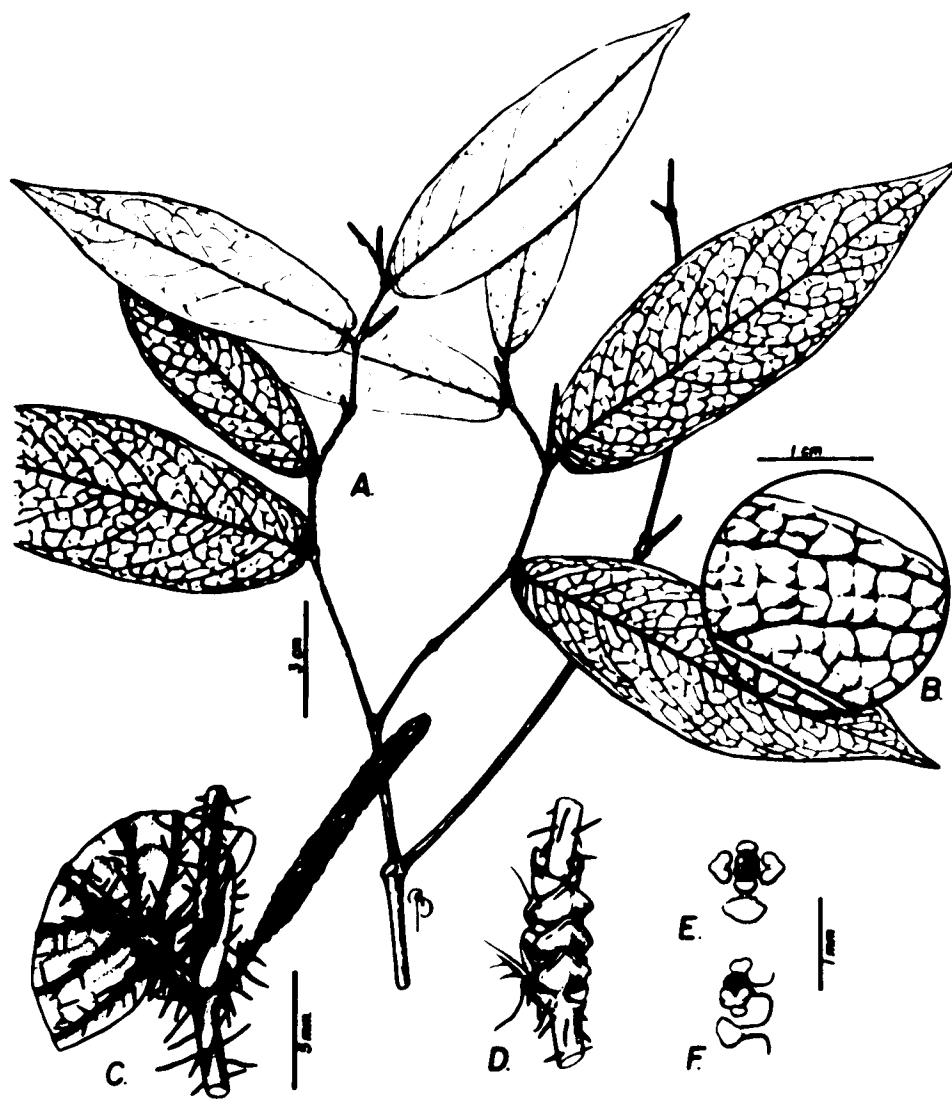
Ottonia angustifolia Rizzini, Dussenia 2: 265. 1952, non Piper angustifolium Lamarck. Type. Brazil. Rio de Janeiro: Rio de Janeiro, Itatiaia, Altamira, 24 Oct 1945 (fr), Walter 106 (holotype, RB).

Terrestrial shrub, 2 m tall, sparingly branched; internodes smooth, terete, sometimes striate and canaliculate, (1.5-)2-3.8(-5) cm long and 1-2 mm in diam., papillate,

Fig. 92. Illustration of Piper brevinodis Callejas, sp. nov.

All from Sucre et al. 10133

A. Habit, B. Close up of the adaxial bullate surface
of the leaf, C. Detail of the flowering node, D.
Flowering node showing the numerous scars of
prophylls, subtending reduced internodes, E.
Flower, upper view, F. Flower, lateral view.



glabrous. Leaves membranous, opaque or often chartaceous, lanceolate or narrow elliptic to very narrow elliptic, (5-)6.8-9.5(-11) times longer than wide, lamina symmetric, (13-)15-18.5(-20) x (1.3-)1.8-3.5(-5.2) cm, basally short-acute or obtuse on one side, apically short-acute to long-acuminate, light glossy green above and pale green beneath when living, olive-green or brownish above and light green beneath when dry, glabrous; the 17-26 secondary veins impressed above, venation strongly raised beneath; petioles terete or striate, then grooved adaxially, 0.8 cm long, glabrous. Prophylls caducous, thick, 2-2.5 cm long, apically short-acute, papillate glabrous. Inflorescence erect, white in flower and green in fruit when living, brown or orange when dry; peduncle finely striate, canaliculate, or sometimes terete and smooth, 0.7-1.5 cm long, glabrous; flowering portion (3-)5-6 cm long; rachis not obscured by the flowers, papillate; floral bracts 0.4-0.8 mm wide, saccate-glaucate, sessile at anthesis becoming pedicellate in fruit, 0.5 cm distant from the rachis, glabrous, obscurely glandular dotted. Flowers pedicellate, loosely spaced in flower, widely spaced in fruit; pedicels 1.5-1.8 mm long, glabrous; anthers 0.4 mm wide, dehiscing laterally; stigmas sessile. Fruits ovoid, 0.7 mm long, 4-ribbed, slightly sulcate; seeds ellipsoid, 1.9 x 1.5 mm, radially symmetric, 4-ribbed, strongly sulcate, glossy orange when dry.

Distribution. (Fig. 87B). SE Brazil where it is known from the states of Rio de Janeiro and SE Minas Gerais. The species is apparently rare, and restricted to the understory of wet forests; 50-450 m elev. Flowering collections unknown; fruiting in Sep-Jan.

Specimens examined. BRAZIL. Minas Gerais: Mpio. Santa Barabara, Serra do Caracá, rd. to Caphilina, 28 May 1983 (fr), Pirani & Yano 717 (NY, SPF). Rio de Janeiro: Rio de Janeiro, Itatiaia, plot 17, Sep 1934 (fr), Brade 14082 (RB); plot 21, 450 m, 28 Jan 1984 (fr).

Local names and uses. Brazil: jaborandy (Rio de Janeiro).

In subgen. Ottonia, Piper rizzinii is unique by its lanceolate to narrow elliptic leaves which are 5-11 times longer than wide, and the 17-24 secondary veins. In this species leaves have an upper hypodermis, and the oil containing idioblasts occur only along the venation, both characters otherwise present only in P. hayneanum and P. eucalyptophyllum, the sister group of P. rizzinii. Compared with the type, the collection from Minas Gerais (Pirani et al. 717) has leaves with obtuse bases and laminae which are thicker and more chartaceous.

15. Piper hayneanum C. de Candolle, Prodr. 16(1): 253. 1869.

Ottonia macrophylla Kunth, Linnaea 13: 583. 1839, non

Piper macrophyllum Humboldt, Bonpland & Kunth. Type.

Brazil. Rio de Janeiro: Without specific locality,

no date, Sellow s.n. (holotype, B; isotype, GH).

Fig. 7, 93.

Ottonia macrostachya Martius ex Miquel, Linnaea 20: 176.

1847. Piper sebastianopolitense C. de Candolle, Prodr.

16(1): 252. 1869, non Piper macrostachyum Vahl. Type.

Brazil. Rio de Janeiro: Sebastianópolis, in forest,

Aug-Nov (fr), Martius s.n. (holotype, M; isotype, U).

Piper hayneanum C. de Candolle var. macrophyllum C. de

Candolle, Prodr. 16(1): 253. 1869. Ottonia grandifolia

Trelease, Proc. Amer. Philos. Soc. 75: 705. 1935. Type.

Brazil. Minas Gerais: Without specific locality, in open

sunny places, no date, Martius s.n. (holotype, M; isotype,

U).

Ottonia mendonçae Trelease, Proc. Amer. Philos. Soc. 75:

708. 1935. Type. Brazil. Rio de Janeiro: Rio de Janeiro,

Mount Corcovado, no date, Mendonça 669 (holotype, B).

Terrestrial shrub or shrublet 1.5-2.5 m tall, sparingly
to profusely branched; internodes striate, canaliculate,
(2.5-)3-6.5(-7) cm long and 2.5-3 mm in diam., papillate,
glabrous, glandular dotted. Leaves chartaceous, opaque, or

often thin-membranous and translucent, sometimes bullate, narrow ovate to lanceolate, less often elliptic, (1.8-)2-3.2(3.9) times longer than wide, lamina symmetric, (11-)13-22(-25) x (4-)5-8(-10) cm, basally short-acute with one side distinctly longer or often equilaterally cordate to lobulate, apically short-acute to long-acuminate, glossy blue-green above and pale green beneath when living, grayish-green or dark green above and pale green beneath when dry, glabrous above, with an intramarginal hirtellous region beneath, glandular dotted throughout, rarely eglandular; the 10-15 secondary veins impressed above, strongly raised beneath; petioles striate, grooved abaxially, often stout, 0.7-1.1 cm long, papillate, glabrous. Prophylls caducous, 1-2 cm long, apically short-acute, papillate, glabrous, glandular dotted. Inflorescence erect, white in flower and glossy green in fruit when living, orange to brown when dry; peduncle terete, smooth, rarely striate, 0.7-1.4 cm long, papillate, glabrous, glandular dotted; flowering portion (3-)4-11(-14) cm long; rachis not obscured by the flowers, sparsely pubescent, with thin-translucent, 2-3-celled white hairs, rarely glabrous, glandular dotted; floral bracts 0.3-0.6 mm wide, saccate-galeate, glandular dotted, sessile at anthesis, remaining so in fruit but more often becoming distinctly pedicellate and 0.5 mm distant from the rachis, glabrous. Flowers pedicellate, loosely congested at anthesis, widely spaced in fruit; pedi-

Fig. 93. Illustration of Ottonia macrostachya (I) and O. macrophylla (II) (both= Piper hayneanum). From Martius' Flora Brasiliensis. pl. 22. Vol. IV. 1852.



OTTONIA macrostachya II macrophylla III Anisum

cels (0.5-)1.5-3(-4) mm long, glabrous, glandular dotted; anthers dehiscing laterally; stigmas sessile. Fruits ovoid-ellipsoid, 1-1.7(-2) mm long, 4-ribbed, sulcate, glandular dotted; seeds ellipsoid, 1.7 x 0.8 mm, radially symmetric, 4-ribbed, strongly sulcate, glossy black when dry.

Distribution. (Fig. 87B). Known from the forests of SE Brazil (Bahía, Espírito Santo, Minas Gerais, Paraíba, Pernambuco, Rio de Janeiro, São Paulo). It occurs in the understory of little disturbed forests, sometimes in secondary forests, or in abandoned fields of cocoa plantations (Bahía), rarely in open places; 30-1000 m elev. Flowering from Aug through Sep; fruiting Sep through Dec.

Specimens examined. BRAZIL. Bahía: Mpio. of Itamarajú, BR-500 rd., 15 km S of Itamarajú, 1 km from the entrance to Monte Pascoal National Park, 1 Nov 1983 (fr), Callejas et al. 1608, 1608b, 1678 (all CEPEC, NY, RB); Mpio. of Camacá, 2 km S of Camacá, rd. to Pau Brasil, 23 Apr 1983 (fr), Carvalho et al. 1894 (CEPEC); Mpio. Itamarajú, National Park of Monte Pascoal, NW side of Monte Pascoal, 100-200 m, 11 Jan 1977 (fl, fr), Harley et al. 17833 (CEPEC, K); Uruçuca, fazenda São Jorge, 7 Apr 1970 (fl, fr), T. S. Santos 637 (CEPEC, RB); Bahía Gandú, rd. to Algodão, 23 Oct 1970 (fl, fr), T. S. Santos 1183 (CEPEC, RB); Itabela on rd. to Guaratinga, 17 May 1970 (fr), T. S. Santos 1656 (CEPEC, RB); without specific locality, no date, Castellanos 24699 (CEPEC). Espírito Santo:

Mpio. Domingo Martins, Campinho, rd. to tower of Radio Campinho, 530 m, 13 Sep 1975 (fr), Martinelli 782 (RB). Minas Gerais: Without specific locality, no date, Martius s.n. (U). Paraíba: Serra do Araripe, Aug 1921 (fr), Luetzelburg 12532 (M, R, W). Pernambuco: Recife Mata de Dois Irmãos, 14 Oct 1960 (fr), Tavares 529 (CEPEC, US). Rio de Janeiro: Rio de Janeiro, Tijuca, Bico do Papagaio, 25 Oct 1938 (fr), Alston et al. 205 (U), 23 Aug 1976 (fr), Araujo 1150 (GUA); forest of Tijuca, rd. to camino das Almas, 27 Aug 1960 (fr), Atala 324 (GUA, RB), 16 Jul 1959 (fr), Carauta 63 (R); Chaminé dos Porcos, 13 Jan 1963 (fr), Carauta 161 (GUA, RB); Guanabara, Pedra Branca, 20 Sep 1964 (fl, fr), Carauta 228 (GUA, RP); Bico do Papagaio, 19 Nov 1946 (fr), Emygdio 504 (R); Pinta do Diabo, 1910 (fr), Luetzelburg 260 (M); forest of Tijuca, close to Gruta Paulo and Virginia, 31 Aug 1958 (fr), Pabst 4551 (HB, M, NY); Trilha do Bico do Papagaio, 800 m, 30 Nov 1983 (fr), Ribeiro 377 (RB); Castelnovo, Nov 1821 (fl, fr), Riedel 540 (LE); Mandioca, 4 Jan 1823 (fr), Riedel s.n. (LE), Oct 1823 (fr), Riedel s.n. (LE); National Park of Serra dos Orgãos, 1000 m, 26 Sep 1952 (fr), Rizzini 1105 (RB); rd. to Pau de Fome, Jacarepaguá, Pedra Branca, Reserve of IBDF, Rio Grande, 29 Aug 1977 (fr), I. A. Rodrigues et al. 130 (RB); rd. to Island of Jajoinha, no date, Satto & F. G. Silva s.n. (B); Matas da Lagoinha, 21 Aug 1968 (fr), Sucre 3673 (RB), 1 Jan

1969 (fl, fr), Sucre et al. 4408 (GUA, RB); Taquara da Tijuca, Sertão, 560-630 m, 29 Sep 1971 (fr), Sucre 7710 (RB), 20 Oct 1971 (fr), Sucre 7821 (RB); Mata Taquara da Tijuca, 22 Aug 1972 (fl), Sucre et al. 9517 (GUA, RB); Açude da Solidão, nr. Rio Sul, 14 Oct 1968 (fr), Vitória s.n. (GUA); without specific locality, 1876 (fr), Glaziou 8074 (G, K, P), 18 Oct 1936 (fl, fr), Hans s.n. (R), 1817 (fr), Langsdorff s.n. (LE), no date, Martius s.n. (M), 25 Oct 1874 (fl, fr), Mosén 2588 (C, M, R, S). São Paulo: Caraguatuba, 200 m, 26 Oct 1974 (fl, fr), Carauta 1746 (GUA, RB); São Sebastião Island, 27 Dec 1972 (fr), J. Mattos et al. 15676 (SP).

Local names and uses. Brazil: jaborandi (Bahia, Rio de Janeiro).

Roots and inflorescences are used to cure toothache in Bahia (Callejas et al. 1608b).

Piper hayneanum is characterized by elliptic to wide ovate leaves which are glandular dotted and with an intramarginal hirtellous region beneath, glandular dotted floral parts, and sparsely pubescent rachis.

A rather uniform species throughout its range with variation being almost restricted to the shape of the leaf base (see discussion below). Floral bracts in this species are

usually sessile, but some specimens (Riedel s.n.) have sessile and short- to long-pedicellate floral bracts in the same inflorescence.

Yuncker (1972) lumped all the species here cited without giving any reason. The type of Ottonia macrophylla has obtuse leaves and floral bracts which are short-pedicellate. Miquel (1847) distinguished Ottonia by leaves with acute bases, intramarginal hirtellous region beneath, and sessile floral bracts. The leaf base in P. hayneanum is apparently correlated with the nature of a particular node, the obtuse leaf bases are more often seen in branching than in flowering nodes with the result that specimens may then present leaves with two distinct base shapes. An intramarginal hirtellous region, on the other hand, is present in the type of O. macrophylla, but was apparently not seen by Miquel. Piper hayneanum var. macrophyllum was based on the presence of an intramarginal hirtellous region. Piper mendoncae was based on acute leaf bases and strongly glandular dotted leaves all characters present in the type of O. macrophylla.

Specimens collected from Monte Pascoal in (Bahia) have bullate leaves which are eglandular. In addition individuals are found growing in open sunny sites, unlike all other collections from the understory of wet forests. An examination of these specimens revealed the presence of a thick cuticle

which peels off in dry specimens but more often persists on leaves. Removal of this layer reveals the presence of numerous glandular dots. Leaf clearings of these specimens also disclosed that the oil-containing idioblasts are restricted to the veins, as is normally the case in O. macrophylla.

The species is closely related to P. rizzini and their relationships are discussed under the latter species. Piper hayneanum also overlaps with P. eucalyptophyllum in glandular dotted floral parts, dimensions and shape of leaves (sometimes elliptic and often 3 times longer than wide, as in P. eucalyptophyllum), and raised venation of the leaf above. Lack of an intramarginal hirtellous region distinguishes P. eucalyptophyllum.

16. Piper eucalyptophyllum C. de Candolle, Prodr. 16 (1):

252. 1869. Ottonia eucalyptifolia Kunth, Linnaea 13:
582 1839, non Piper eucalyptifolium Rudge. Type.
Brazil. Rio de Janeiro: Without specific locality,
1833 (fr), Gaudichaud 1100 (lectotype here
designated, G; isoelectotypes B, G-DC, P, photo F neg.
10954). Kunth's description is based on two collec-
tions, one by Luschnath from Macahé near Parahyba
(Rio de Janeiro) and a second one by Gaudichaud from
Rio de Janeiro. As was usually the case Kunth did not
mention any dates or collection numbers. That author

specifically stated however, that the description and measurements of the fruit were based on Gaudichaud's specimen while the rest of the protolog was based on Luschnath's collection. He further added that a copy of the original description is attached to the specimen collected by Luschnath (at that time deposited at Lucae's herbarium). Miquel (1844) cited both collections but without providing further data. He also mentioned that his (Miquel's) description is based and follows strictly that of Kunth. De Candolle (1869), in the Prodromus, does not mention Luschnath's collection but cites one of Gaudichaud as Gaudichaud 1100. This last specimen was later taken by Trelease (1935) to represent the holotype of Ottonia eucalyptifolia. His decision was followed by subsequent authors (Yuncker, 1972; Guimarães, 1984). Luschnath's collection, which ought to be chosen as the holotype, has never been found. Lucae's herbarium was integrated to KIEL and later destroyed (Stafleau, 1981). Duplicates of Luschnath collections at B, P, and W do not include any specimen of O. eucalyptifolia. Two specimens at C, without labels but with a handwritteng locality on the back of one sheet, are indicated as collected in Parahyba, Macahé. To what extent they represent duplicates of Luschnath's

collection is impossible to decide. In regards to Gaudichaud's collection the specimen cited by de Candolle (Gaudichaud 1100) bears Kunth's handwriting and thus may be a duplicate of the collections seen by that author. There are duplicates of this collection at B, G, G-DC, and P. The specimen at P differs from the rest of duplicates and represents another species, P. corcovadensis var. corcovadensis. That collection is otherwise identical to Gaudichaud 1101 and thus may represent a misnumbered collection. Based on a comparison of the protolog of Ottonia eucalyptifolia with Gaudichaud 1100, that collection is here taken to represent the original one seen by Kunth. The specimen at G is more complete than those in B and G-DC and is chosen as the lectotype.

Ottonia eucalyptifolia Kunth var. angustifolia Miquel in Martius Fl. bras. 4(1): 66. 1863. Type. Brazil. Rio de Janeiro: Without specific locality, no date, Houllet s.n. (holotype, U).

Piper janeiroensis C. de Candolle, Linnaea 37: 339. 1872. Ottonia janeiroensis (C. de Candolle) Trelease, Proc. Amer. Philos. Soc. 75: 706. 1935. Type. Brazil. Rio de Janeiro: Without specific locality, no date, Lund s.n. (lectotype, C; isoelectotypes, C, G).

Piper eucalyptophyllum C. de Candolle var. glaucescens C. de Candolle, Candollea 1: 247. 1923. Ottonia eucalypt-

tifolia Kunth var. glaucescens (C. de Candolle) Trelease,
Proc. Amer. Philos. Soc. 75: 703. 1935. Type. Brazil. Rio
de Janeiro: Without specific locality, no date, Glaziou
6805 (holotype, C; isotype, P n.v.).

Ottonia claussemi Trelease, Proc. Amer. Philos. Soc. 75:
699. 1935. Type. Brazil. Minas Gerais: Without specific
locality, 1840 (fr), Claussen s.n. (holotype, K).

Terrestrial shrub, 1.5 m tall, sparingly to profusely
branched; internodes striate, canaliculate, 1.5-3.5 cm long
and 1-1.5 mm in diam. Leaves thick-chartaceous or thin-membra-
nous, opaque, narrow ovate to lanceolate, (2.8-)3-4.4(-4.8)
times longer than wide, lamina asymmetric (8.5-)10-15(-17) x
(2.4-)2.9-4.6(-4.9) cm, basally acute or less often obtuse on
one side, apically long-acuminate, glossy green above and pale
green beneath when living and dry, glabrous, glandular dotted
throughout especially along midvein above; midvein and the
16-18 secondary veins raised on both sides; petioles striate,
canaliculate, 0.4-0.8 cm long, papillate, glabrous, glandular
dotted. Prophylls caducous, 0.5-0.8 cm long, apically short-
acute, papillate, glabrous, glandular dotted. Inflorescence
erect, white in flower and green in fruit when living, orange
or brownish when dry; peduncles striate, 0.5-1 cm long,
glabrous, glandular dotted; flowering portion
(2-)3.5-4.5(-5.6) cm long; rachis not obscured by the flowers,

sparsely pubescent, glabrescent, glandular dotted; floral bracts 0.3-0.7 mm wide, saccate-galeate, sessile at anthesis but becoming pedicellate in fruit, 0.7-1 mm distant from the rachis, sparsely pubescent at the base, glandular dotted. Flowers pedicellate, widely spaced at all stages; pedicels (2-)2.7-4.3(-5) cm long, glabrous, glandular dotted; anthers dehiscing laterally, glandular dotted; stigmas sessile. Fruits ovoid-ellipsoid, 2.1-3.5 mm long, 4-ribbed sulcate; seeds ellipsoid, 1.3 x 1 mm, radially symmetric, 4-ribbed, strongly sulcate, black or brownish when dry.

Distribution. (Fig. 87B). SE Brazil from the states of Rio de Janeiro and Minas Gerais. It is restricted to the understory of wet forest on slopes or as a riparian species, in primary or less often in secondary forests; 150-200 m elev. Flowering collections known from Aug through Oct; fruiting from Feb and Aug.

Specimens examined. BRAZIL. Rio de Janeiro: Mpio. Vassouras, trail Alferes Avelar, in arboretum Pau Grande, 28 Jan 1984 (fr), Callejas 2142, 2144 (both HUA, NY, RB, SP); nr. grupo Cumbuca, in arboretum, 22 Aug 1968 (fr), dos Santos s.n. (NY, RB); Mpio. Vassouras, trail Alferes Avelar, in arboretum Pau Grande, 20 Feb 1978 (fr), Ferreira et al. 239; National Park of Tijuca, arboretum, 14 Jul 1978 (fl), Lewiz & Brito 3 (RB); Mount Corcovado, between Paineiras and Botanical Garden,

250 m, 8 Oct 1977 (fl), Maas et al. 3119 (NY, U); base of Serra Carioca, Pedra do Bejo, 24 Aug 1975 (fl), M. C. Oliveira 6 (RB); E slope of Morro do Sumare, 8 Feb 1969 (fr), Sucre 4716 (NY, RB), 150-200 m, 23 Sep 1970 (fl), Sucre 7091 (RB); S facing slopes of Mount Corcovado along rd. Joana Angélica, 12 Sep 1972 (fl), Sucre et al. 9618 (NY, RB); without specific locality, 1839 (fl, fr) Guillemin 728 (G); 1825-1827 (fr), Lund s.n. (C); 1816-1821 (fl, fr), Saint-Hilaire 29 (P); no date, Pohl 420 (W); Riedel 43 (G).

Local names and uses. Brazil: jaborandi, jaborandi do mato, nhadú rasteiro, nhandú, timbo nhandú (Rio de Janeiro), (Guimarães, 1984).

Piper eucalyptophyllum is recognized by its glandular dotted leaves, stems and inflorescences, narrow ovate to lanceolate leaves, venation raised on both sides, and glabrous leaves and stems.

Leaf texture, leaf base, and color of the leaves when dry show variation interpreted by some authors as deserving specific status. The type of O. eucalyptifolia var. angustifolia (a Miquel variety completely ignored by other authors), for example, has leaves which are 15 x 2.4 cm with lamina thin and translucent; otherwise it does not differ from the type species. The types of P. janeiroensis and P. eucalyptophyllum

var. glauscegens have thick-chartaceous leaves which are opaque and light green to edged above (e.g. var. glauscegens), an artifact of drying. Neither collection no differs substantially from the type of P. eucalyptophyllum.

The relationships of P. eucalyptophyllum with P. rizinii and P. hayneanum are discussed under those species respectively.

17. Piper piliovarium Yuncker, Bol. Inst. Bot. São Paulo 3:

111. 1966. Type. Brazil. Rio de Janeiro: Without specific locality, 1838-1842 (fr), U.S. Exploring Expedition s.n. (holotype, GH).

Terrestrial shrub, 1 m tall, sparingly branched; internodes striate, canaliculate or less often terete and smooth, 1.5-3.5 cm long and 1-2 mm in diam., papillate, densely pubescent when young, obscurely glandular dotted. Leaves chartaceous, opaque or lamina thin and transluscent, lanceolate, (3-)3.5-4.2(-5.6) times longer than wide, lamina slightly asymmetric, (12.5-)13-15(-17) x (2.5-)3.5-4.2 cm, basally obtuse on both sides, apically short-acute to acuminate, blue-greenish above when living, grayish-green or olive-green above with the secondary veins drying pale green, light green beneath when dry, glabrous above, with the midvein densely to sparsely pubescent beneath; the 10-14 secondary veins

impressed above, strongly raised beneath; petioles striate or rugose, 5-7 mm long, papillate, sparsely pubescent, obscurely glandular dotted. Prophylls caducous, 0.8-1 cm long, papillate, sparsely to densely pubescent, obscurely glandular dotted. Inflorescence erect, brown or blackish in fruit when dry; peduncles striate, 5-6 mm long, papillate, glabrous. Flowering portion 6-8 cm long; rachis not obscured at any stage, densely pubescent, with thin-translucent 5-7-celled hairs, whitish when dry; floral bracts 0.2-0.3 mm wide, saccate-galeate, proximally densely short-pubescent, short-pedicellate, 0.2-0.4 mm distant from the rachis. Flowers pedicellate or sessile (with the pedicellate flowers occurring proximally, sessile distally), loosely to widely spaced in fruit; pedicels (when present) 0.2-0.3 mm long; anthers dehiscing laterally, stigmas sessile. Fruits globose-ovoid, 1-1.5 mm long, 4-ribbed, strongly sulcate, densely short-pubescent; seeds globose-ellipsoid, 1.6 x 0.8 mm, radially symmetric, 4-ribbed, strongly sulcate, black when dry.

Distribution. (Fig. 88A). Brazil. Known only from two collections in the state of Rio de Janeiro. Apparently rare, occurring in the understory of little disturbed wet forest; 150 m elev. Flowering collections unknown; fruiting collections known only from Mar.

Specimens examined: BRAZIL. Rio de Janeiro: Rio de Janeiro, Pedra da Gávea, nr. rd. Iposeira, 150 m, 27 Mar 1977 (fr), Carauta et al. 2394 (GUA, NY, RB).

This taxon is characterized by lanceolate leaves which are densely to sparsely pubescent beneath, densely pubescent rachis, and floral bracts which are proximally densely pubescent. It is also unusual in the presence of sessile and pedicellate flowers in the same inflorescence.

Unfortunately two collections are not sufficient to determine which floral condition (sessile vs. pedicellate flowers) is normal for the species. The distribution of the flowers in the inflorescence may suggests the presence of pedicels in the first developed flowers but its acropetal elimination as the inflorescence development continues. No examination of floral development was made on this species, however it is unlikely P. piliovarium will differ significantly from those observed in P. anisum and other members of the subgenus.

The species is closely related to P. anisum, both having in common the lower midvein sparsely pubescent, pubescent proximal portion of the floral bracts, sparsely pubescent rachis, and pubescent fruits.

Yuncker (1972), in the original description, suggested a relationship between P. piliovarium and P. hoffmannseggianum (here P. hoffmannseggianum var. latifolium) and more

distantly to P. ottonoides, both sessile-flowered taxa. Aside from the overlapping leaf shape (narrow lanceolate) there are no characters in subgen. Ottonia by which one can unite the three taxa. Yuncker's interpretation of P. piliovarium most probably shows that author lack's of knowledge of the pedicellate flowers in that species (Yuncker described it as a sessile-flowered taxon). Piper ottonoides has glabrous rachis and floral bracts which are also sessile and decurrent with the rachis. Similarly, Piper hoffmannseggianum has tightly congested flowers and fimbriate rachises, seeds with bilateral symmetry, and a quite distinct seed coat structure from that found in P. piliovarium.

18. Piper ovatum Vahl.

Terrestrial shrubs, erect or sometimes lianescent, 1-3.5 m tall, sparingly to profusely branched; internodes striate, canaliculate, (2-)2.8-4.5(-5.5) cm long and 1.5-4 mm in diam., papillate, glabrous, rarely glandular dotted. Leaves thin-membranous and translucent, but often thick-chartaceous and opaque, wide to narrow ovate or lanceolate, 2.2-3.4(-3.7) times longer than wide, lamina asymmetric, rarely symmetric, (8-)9.5-17.5(-21) x (3.2-)4-7.5(-8.5) cm, basally acute or obtuse on both sides or more often short-acute and obtuse, then partially covering the petioles, often short-peltate,

apically short-acute to long-acuminate, glossy green above and pale green beneath when living, pale or grayish-green above and pale green beneath when dry, venation often drying whitish or light green, glabrous above, often with an intramarginal hirtellous region beneath, rarely glandular dotted on both sides; midvein impressed to raised above, the 8-12 secondary veins slightly to strongly raised or fully impressed above, strongly raised beneath; petioles striate, often grooved adaxially, (3-)5-10 mm long, papillate, glabrous. Prophylls caducous, 0.5-1.2 cm long, apically short-acute, papillate, glabrous, rarely glandular dotted. Inflorescence erect, white in flower and olive-green in fruit when living, grayish or pale green when dry; peduncles striate or rugose, 0.3-0.9 cm long, papillate, glabrous, obscurely glandular dotted; flowering portion (3.5-)5-11(-13) cm long; rachis visible at all stages, rarely partially obscured in fruit, papillate and sparsely pubescent, glabrescent, obscurely glandular dotted; floral bracts 0.3-0.6 mm wide, saccate-galeate, papillate, glabrous; pedicel often glandular dotted, sessile at anthesis becoming distinctly pedicellate in fruit and 0.3-0.9 mm distant from the rachis. Flowers pedicellate, widely spaced at all stages or loosely congested in fruit, pedicels 0.1-0.7 mm long, often fully obscured by the fruits and then some fruits appearing fully sessile, glabrous, rarely glandular dotted;

anthers dehiscing laterally; stigmas sessile. Fruits narrow to wide ovoid, 1.2-2 mm long, papillate, glabrous, obscurely glandular dotted, 4-ribbed, strongly sulcate; seeds ellipsoid, 1.5-2.1 x 1-1.7 mm, radially symmetric, glossy orange or blackish when dry.

Distribution. (Fig. 88A). Widely distributed in SE Brazil with apparent disjunct populations in NE Venezuela and the Island of Trinidad; 0-1150 m elev

Key to the Varieties of Piper ovatum

1. Leaf base acute on one side, obtuse on the other, then with a small lobe which overlaps the petioles; veins impressed above; floral bract pedicel glandular dotted; fruits short-pedicellate, the pedicels 0.7-1.3 mm long; Trinidad and NE Venezuela. 17a. var. ovatum.
1. Leaf base acute or obtuse on both sides, often short-peltate; veins raised above; floral bract pedicel eglandular; fruits subsessile or sessile, less often short-pedicellate, then the pedicels 0.1-0.9 mm long; SE Brazil. 17b. var. boucheanum.

17a. Piper ovatum Vahl var. ovatum

Piper ovatum Vahl, Eclog. Am. 1: 3. 1796. Type. Trinidad.

Without specific locality, without date, Ryan s.n.

(holotype, C, isotype, C). Ottonia vahlii Kunth, Linnaea

13: 585. 1839, superf. comb. Ottonia ovata (Vahl)

Trelease, Proc. Amer. Philos. Soc. 75: 711. 1935.

Ottonia ovata (Vahl) Trelease var. stenostachya Trelease,

Proc. Amer. Philos. Soc. 75: 711. 1935. Type. Trinidad.

Without specific locality, 1877-1880 (fr), Fendler 669

(holotype, P; isotype, NY).

Leaves wide, rarely narrow ovate, 2.2-2.6 times longer than wide, basally asymmetric, short-acute and obtuse, then lobate and covering partially the petiole; the 8-12 secondary veins impressed above. Flowering portion 2-7 cm long; floral bract pedicel glandular dotted; flowers short-pedicellate at all stages, the pedicel 0.7-1.3 mm long. Fruits 1.1-1.3 mm long.

Distribution. (Fig. 88A). Known from Trinidad and NE Venezuela (Anzoátegui, Bolívar, and Sucre). Common and apparently locally abundant in Trinidad, but very rare in Venezuela and growing in the understory of wet forests, often along gallery forests; sea level to 100 m elev. in Trinidad, but reaching 1000 m in Venezuela. Flowering collections rare and only known from Jun; fruiting material collected from Oct to Jan.

Specimens examined. TRINIDAD. Chaguanas, Oct 1894 (fr),
Bourne 4334 (NY, TRIN); Cedros, S central rd., without date
Broadway 7165 (TRIN); Maracas, without date, Crueger s.n.
 (K); Guayaguayare rd., 17 Oct 1930 (fr), Marshall 12442 (NY);
 Arima, 1848 (fr), Purdie s.n. (K); Tucker valley, without
 date or collector (TRIN).

VENEZUELA. Anzóategui: Quebrada Bonita, draining towards
 Río Neverí, between Camelita and Río León, NE of Bergantín,
 800-1100 m, 18 Feb 1945 (st), Steyermark 60986 (F, NY, US).
 Bolívar: Campamentos El Paraíso-La Yagua, 48 km NE of Los
 Rosos, rd. Upata-San Félix, June 1966 (fl, fr), Blanco 530
 (NY). Sucre: Sitio Los Altos, 950 m, Jan 1942 (fr), Tamayo
2154 (G, US).

17b. Piper ovatum Vahl var. boucheanum (C. de Candolle)

Callejas, stat. nov.

Fig. 5, 95.

Piper boucheanum C. de Candolle, Prodr. 16(1): 254. 1869.

Type. Brazil. Without specific locality or date, Sellow
s.n. (holotype, B; isotype, K), non Piper leptostachyum

Richard. Ottonia leptostachya Kunth, Linnaea 13: 586.

1839.

Piper frutescens C. de Candolle, Linnaea 37: 337. 1872.

Type. Brazil. Minas Gerais: Lagoa Santa, Quebra, 14 Oct
 1863 (fl), Warming s.n. (holotype, C; isotype, G n.v).

Ottonia frutescens (C. de Candolle) Trelease, Proc. Amer.
 Philos. Soc. 75: 703. 1935.

Piper atosanguineum C. de Candolle, Linnaea 37: 338. 1872.

Type. Brazil. Minas Gerais: Lagoa Santa, 17 Nov 1863

(fl, fr), Warming s.n. (holotype, C). Ottonia atro-
sanguinea (C. de Candolle) Trelease, Proc. Amer.

Philos. Soc. 75: 698. 1935.

Piper brevistipitatum C. de Candolle, Linnaea. 37: 338.

1872. Type. Brazil. Minas Gerais: Lagoa Santa, Quebra,
14 Oct 1863 (fr), Warming s.n. (holotype, C, photo C, F,
NY, F neg. 21650; isotypes, C, LE). Yuncker (1972),
cited 24 Dec 1863 as the collection date; however, such
date refers only to the time at which Warming's collec-
tion was incorporated in C. A previous date in the
label, 14 Oct 1863, should be taken as the collection
date. Ottonia brevistipitata (C. de Candolle) Trelease,
Proc. Philos. Soc. Amer. 75: 698. 1935. Ottonia lep-
tostachya Kunth var. brevistipitata (C. de Candolle)
Guimarães, Bol. Mus. Bot. Kuhlmann 7(3): 70. 1984.

Ottonia mosenii Trelease, Proc. Amer. Philos. Soc. 75: 710.

1935. Type. Brazil. São Paulo: São Paulo, 20 Dec 1873,

Mosén 1689 (holotype, S).

Ottonia ludoviciana Miquel ex Trelease, Proc. Amer. Philos.

Soc. 75: 714. 1935. Type. Brazil. Maranhão: Sto.

Ludovicus Island, Jun (fr), without specific date,

Martius s.n. (holotype, M).

Ottonia leptostachya Kunth var. glandulosa Yuncker, Bol.

Inst. Bot. São Paulo 3: 135. 1966. Type. Espírito Santo:

Fazenda Salvador, Rio Doce, without date, Bueno et al.

181 (holotype, R).

Leaves wide to narrow ovate or more often lanceolate, 2.7-3.4(-3.7) times longer than wide, basally symmetric, short-acute on both sides, often shortly peltate, less often both sides obtuse, but then never lobate; the 10-12 secondary veins raised above, sometimes the midvein impressed proximally. Flowering portion 2-17.5 cm long; floral bract pedicel eglandular; flowers short-pedicellate in flower becoming subsessile to fully sessile in fruit, rarely short-pedicellate in fruit, the pedicel 0.1-0.5(-1) mm long. Fruits 0.8-1(-2) mm long.

Distribution. (Fig. 88A). SE Brazil in Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Minas Gerais, Pará, Paraíba, Pernambuco, Rio de Janeiro, and São Paulo. Almost restricted to the coastal Atlantic forests where it is common in Bahia and Espírito Santo but rare north or south of those states. Its northern range reaches into Maranhão and Pará where it is known from single collections. In Paraíba the species occurs on forested slopes of brejos in Areia. Isolated populations in the Planalto are known from Goiás and Distrito Federal. An understory shrub of little to severely disturbed

areas (cocoa plantations in Bahia), the species is often locally abundant; sea level to 1150 m. elev. Flowering and fruiting throughout the year.

Specimens examined. BRAZIL. Bahia: Ilhéus, CEPLAC-CEPEC, 31 Mar 1965 (fl), Belém & Magalhães 604 (CEPEC, NY); rd. Camacá-Canavieira, 4 Oct 1965 (fl, fr), Belém & Magalhães 741 (CEPEC, NY); rd. BR-5, 16 km S of Eunápolis, 22 Sep 1966 (fr), Belém & Pinheiro 2624 (CEPEC, NY); Mpio. of Una, km 9 on the rd. São José de Burarema-Una, 28 Oct 1983 (fr), Callejas et al. 1554, 1556 (CEPEC, HUA, NY, RB, SP, U, US); Itabuna, km 10 on the rd. Juacarí-Palmeira, Fazenda Sto. Antonio, 300 m, 28 Oct 1983 (fr), Callejas et al. 1569 (CEPEC, NY); Ubaitaba, km 5 of the rd. Aurelino Leal, Lajes, 21 Jan 1982 (fr), Carvalho et al. 1144 (CEPEC, NY, RB); Itamarajú, Fazenda Pau-Brazil, km 5 of the rd. Itamarajú-Eunápolis, 160 m, 3 Nov 1983 (fr), Carvalho & Callejas 2048 (CEPEC, HUA, NY, RB, SP, US); between São José dos Macucos and Itabuna, Nov 1942 (fr), R. L. Froese 20043 (NY); Ilhéus, area of CEPLAC-CEPEC, km 22 of the rd. Ilhéus-Itabuna, BR415, 50 m, 14 Oct 1981 (fl), Hage & Brito 1478 (CEPEC, NY, RB), 8 Dec 1981 (fr), Hage 1552 (CEPEC, NY, RB); rd. Banco Central Ubaitaba, 21 Apr 1971 (fl, fr), R. S. Pinheiro 1220 (CEPEC, RB); Banco Central de Ilhéus, 15 Mar 1971 (fl, fr), Pinheiro 1146 (CEPEC, RB); Almadinha, Serra da Pancadinha, Fazenda Beija-Flor, 3 Aug 1971 (fl, fr), R. S. Pinheiro 1535 (CEPEC, RB); km 10 of the rd. Guaratinga-São

Paulinho, 29 Mar 1973 (fl), R. S. Pinheiro 2050 (CEPEC, RB); Mpio. of Una, BR-101, km 9 on the rd. São José-Una, 20 Jan 1982 (fr), T. S. dos Santos & L. A. Silva 3715 (CEPEC, NY, RB). Ceará: Serra of Baturité, Caridade, Jul 1937 (fr), Eugenio 468 (RB). Distrito Federal: Municipal Park of Gama, 1150 m, 11 Nov 1965 (fr), Irwin et al. 10179 (IAN, NY, RB, UB); 25 km SW of Brasília, 1000 m, 20 Feb 1966 (fr), Irwin et al. 13069 (IAN, NY, RB, UB); nr. Papuda, 18 km SE of Brasília, 9 Nov 1976 (fr), Xavier s.n. (ECON, UB). Espírito Santo: Mpio. Serra, 1-2 km of Nova Almeida towards Santo Cruz, 19 Jul 1973 (fr), Araujo et al. 307 (NY, RB); Biological Reserve of Soretama, 1959 (fr), Decuassos s.n (RB); Mpio of Linhares, rd. of Brano Novo, 20 m, 13 May 1977 (fl), Martinelli et al. 2049 (NY, RB); km 8 of the rd. Linhares-Vitoria, 23 Nov 1973 (fr), R. S. Pinheiro & T. S. dos Santos 2270 (CEPEC, RB); reserve of Soretama, forest of Tabuleiro do Macuco, 17 Jul 1969 (fr), Sucre 5676 (RB); reserve of Linhares, 4 Feb 1972 (fr), Sucre 8462 (NY, RB). Goiás: Serra of Pirineus, 20 km E of Pirenópolis, 1000 m, 16 Jan 1972 (fr), Irwin et al. 34353 (IAN, NY, RB, UB); Mpio. Corumbo de Goiás, top of Serra of Pirineus, 6 km from Cocalzinho, 1380 m, 14 Jan 1981 (fr), Nogueira et al. 102 (NY); Mpio. of Anápolis, Experimental Station, 16 Oct 1956 (fl), L. B. Smith & Macedo 4751 (US); Silveira, 19 Oct 1956 (fl), L. B. Smith & Macedo 4830 (US).

Minas Gerais: Viçosa, State Agricultural School, 23 Feb 1959 (fr), Irwin 2706 (NY), 690 m, 11 Oct 1930 (fl), Mexia 5166 (G, NY, PH, US); Lagoa Santa, 28 Oct 1864 (fl), Warming s.n. (C), 2 Jan 1864 (fl, fr), Warming s.n. (C, US). Pará: Without specific locality, no date, Huber 240 (G, MG). Paraíba: Areia, 21 May 1978 (fr), Agra 11 (RB), 10 Jun 1953 (fr), Coelho dos Morães 985 (IAN, NY, US). Pernambuco: Recife, Mata de Dois Irmãos, 12 Jun 1950 (fr), 12 Jun 1950 (fr), Leal & O. A. da Silva 28 (IAN, NY, US). Rio de Janeiro: Mpio. of Mangaritiba, old rd. to Muriqui, 22 Sep 1975 (fl), Araujo et al. 799 (NY, RB). São Paulo: Mpio. of Campinas, Fazenda Sta. Genebra, 3 Jun 1977 (st), Kirszenzaft et al. 4974 (NY, UEC); Mpio. of São José do Rio Pardo, 18 Sep 1889 (st), Löfgren 1386 (C, P, SP).

Local names and uses. Brazil: jaborandi, joao-barandinho, joao-borandin (Bahia), jaborandi, joao-Barandinho (Espírito Santo), jaborandi, malvarisco (Paraíba). Venezuela: anisillo (Bolívar, Sucre), raíz de candela, raíz de muela (Anzóategui, Sucre).

Steyermark (1984) cited also "raíz de candil." That author reported that in Venezuela the roots and leaves when bitten and chewed cause the tongue and lips to sense a paralyzed biting feeling. Additionally the plant is used as "barbasco"

for fish poisoning. In Trinidad, Yuncker (1953) reported that the species is used as a remedy for snake bite. He also mentioned that "the smelling powers of a dog are said to be improved if its head is bathed in a decoction up to its nostrils." In Brazil the leaves and roots are chewed for the treatment of toothache (Bahía). In the Planalto, tea is made from leaves and fruits to induce sleep (Xavier s.n.). All parts of the plant, but particularly the fruits, have a strong taste of anis.

Piper ovatum is characterized by leaves with an intramarginal hirtellous region beneath, these often with short-suprapeltate bases, sparsely pubescent rachis, and pedicellate flowers in which the pedicels are equal to or shorter than the fruits, these often being subsessile to sessile but always distinctly free from the rachis. The species, as it is here interpreted, consists of two varieties, both of which can be recognized by the characters given in the key.

Piper ovatum var. ovatum displays little variation within and among populations, albeit collections include specimens from sea level to nearly 1100 m elevation. Most variation seems to be related to age of individuals and accounts for the description of P. ovata var. stenostachya. This variety was segregated by Trelease on length of the fruits and diameter of the inflorescence, both of which are larger than those found in the type collection (a young specimen with immature fruits).

Piper ovatum var. boucheanum displays wide variation, especially in pedicel length. Inflorescences may have short-pedicellate (0.7-1 mm long), subsessile (0.5-0.2 mm long), or sessile fruits. Thus pedicels do not elongate as fruit maturation proceeds which is the case in other species with pedicellate flowers (except for P. piliovarium). Populations with subsessile to sessile fruits are more common in the northern range (Paraíba, Pernambuco), while those with short-pedicellate fruits occur in the south (Bahía and Rio de Janeiro). This however breaks down in Minas Gerais. Regardless of actual pedicel length, it is always shorter than the total length of the fruit.

Discontinuities in the length of the pedicel and authors failing to understand it resulted in the description of P. brevistipitatum, O. mosennii and O. santa-ludoviciana. The type of the former species as that of var. bouchenaum have short-subpeltate leaves which are impossible to distinguish from those of O. frutescens and P. atrosanguineum with similar leaf bases, but otherwise short-pedicellate fruits. Subpeltate leaf base is a character which occurs in P. bartlingianum, P. anisum, P. corcovadensis, P. hoffmannseggianum, and P. klotzschianum. In some species (e.g. P. klotzschianum), subpeltate leaves are more commonly found in branching than in flowering nodes, or in all leaves along a single branch (P. corcovadensis), or in the first branching node alone (P.

bartlingianum). Thus variation of this character and its apparent correlation with particular node in some taxa makes it rather difficult to use at the species level.

Unfortunately Yuncker (1972) included under P. frutescens (subpeltate leaves) all specimens of Ottonia with pedicellate flowers and short-peltate leaves, thus making it a heterogeneous species and obscuring completely its real identity as a synonym of Piper ovatum var. boucheanum.

Guimarães (1984) reduced O. brevistipitata to a variety of O. leptostachya. She further considered the latter to consist of three varieties, the two aforementioned and a third one, var. glandulosa. According to that author, O. leptostachya var. leptostachya had pedicels longer than those of var. brevistipitata. Apparently Guimarães did not see the type of O. leptostachya or O. brevistipitata which reveals that the former has sessile fruits while the latter short-pedicellate to subsessile ones. Thus her interpretation of the species is entirely opposite to that of the types.

Ottonia brevistipitata var. glandulosa was distinguished by Yuncker (1966) as being densely glandular dotted. The type came from Rio Doce, (Espírito Santo). Collections of other taxa (e.g. P. hoffmannseggianum, P. villosobracteatum, P. corcovadensis) from that region are often found to be more densely glandular dotted than specimens outside that area.

Mere coincidence or not, the fact is that the same factor (environmental?) is somewhat affecting the distribution and development of oil-containing idioblasts in similar ways in different taxa. Therefore it seems rather artificial to segregate collections from that area as distinct varieties.

The type collection of O. brevistipitata var. glandulosa has fruits which are short-pedicellate as those of O. leptostachya (= P. boucheanum) and therefore it is here included under that species.

Within subgen. Ottonia, P. ovatum is the only species with pedicellate flowers occurring outside the coastal forests of Brazil. Although two revisionary studies on Ottonia (sensu Trelease (1935) and Yuncker (1972)) have been published, an explanation for the puzzling distribution of P. ovatum in Trinidad, and a discussion of its relationships in subgen. Ottonia has never been given. De Candolle (1903) thought that P. ovatum was closely related to populations of a pedicellate-flowered taxon in Paraguay, one he described as P. ovatum var. hirtellum. Trelease (1935) however, transferred that variety to his new species O. cordulatifolia. Based on my field collecting in Paraguay and neighboring Paraná (Brazil) it seems now populations in Paraguay are more closely related to Piper miquelianum from SE Brazil and represent a distinct variety within that taxon (see under P. miquelianum var. hirtellum).

Piper ovatum seems to be closely related to P. corcovadensis with which it often occurs sympatrically. Both species overlap in most vegetative characters. They may be separated however by floral characters, especially by the the longer pedicels in P. corcovadensis. Additionally in P. ovatum calcium oxalate crystals occur throughout the leaf mesophyll but are restricted to the midvein in P. corcovadensis. Albeit the similarities between the two taxa, no synapomorphy for both species seems to occur and the relationships of P. ovatum for the time being are not yet clear (see CLADISTICS).

19. Piper anisum (Sprengel) Angely, Flora Descritiva do

Paraná 2: 387. 1978. Type. Brazil. Rio de Janeiro:
Without specific locality, 1816 (fr), Kulenkamp s.n.
(lectotype, LE, here designated). Ottonia anisum
Sprengel, Neue Entdeck 1: 255. 1820. Sprengel (1820),
in the original description, mentioned one collection
from E Brazil sent to him by Mertens (without date,
collector, or specific locality). According to
Stafleau (1967) Sprengel's herbarium was dismembered
and sold in small portions to different individuals
and institutions. Large portions were sold in sets of
families or genera to specialists (not including
Piperaceae). Even after this rigorous expenditure a

considerable portion remained and was acquired by K. Müller in 1853 and later sold to Berlin (B) where it was destroyed during WWII. Two hundred forty specimens, however, are in the Willdenow Herbarium and another set of 200 at L. No specimens of Piperaceae are included in such collections. I received on loan from Merten's herbarium (LE) collections of P. anisum. One specimen has a printed label attached indicating its being collected from Rio de Janeiro but does not mention a date or collector. This sheet was designated by Yuncker (1973) as an isotype; however, he did not indicate the placement of the holotype or any knowledge of its existence. The second collection consists of a specimen with two handwritten labels, one of which indicates that the specimen was collected, in Rio de Janeiro (E Brazil) in 1816 by Kulenkamp. Additionally, a handwritten description of the genus Ottonia plus the last paragraph of the prolog of O. anisum is attached to this specimen and dated 1819. Since there is uncertainty as to the original collection cited by Sprengel and the lack of solid evidence by Yuncker for designating an isotype, I decided to select a lectotype. In doing this I am assuming that any specimen of O. anisum in Mertens' herbarium, collected in E Brazil and dated before

1820 may belong to the original material sent by Mertens to Sprengel. Kulenkamp's collection (LE) is here designated as the lectotype. It not only fits the original description better than the sheet chosen by Yuncker but includes more information from the protolog.

Serronia jaborandi Gaudichaud ex Guillemain in B. de Lessert, Icon. Sel. pl. 3: 54, pl. 90. 1837. Type. Brazil. Rio de Janeiro: Without specific locality, 1831-1833 (fr), Gaudichaud 1102 ter (lectotype, P, here designated; isoelectotypes, G (four sheets numbered 1102 bis, 1102 ter, and 1102), NY (one sheet numbered as 1102 and dated 1834)). Ottonia jaborandi (Gaudichaud ex Guillemain) Kunth, Linnaea 13: 579. 1839. Piper jaborandi Vellozo, C. de Candolle in Prodr. 16(1): 252. 1869. When transferring Ottonia to Piper C. de Candolle did not recognize O. anisum but Serronia jaborandi then having to use the Vellozo's name, otherwise a doubtful one.

Ottonia diversifolia Kunth, Linnaea 13: 578. 1839. Type. Brazil. Rio de Janeiro: Without specific locality, 1814-1818 (fr), Sellow s.n. (holotype, B; isotype, K), non Piper diversifolium Poir. Piper selloi C. de Candolle, Prodr. 16(1): 252. 1869.

Ottonia pteropoda Moricand, Pl. nouv. Amer. 88. 1840. Type.

Brazil. Bahia: Without specific locality or date,
Blanchet 1946 (lectotype, G, here designated; isolec-
 totype, G). Piper pteropodon (Moricand) C. de Candolle,
 Prodr. 16(1): 255. 1869.

Ottonia hookeriana Miquel, London J. bot. 4: 470. 1845.

Type. Brazil. Minas Gerais: Ouro Fino, Oct 1840 (fl, fr),
Gardner 5186 (holotype, K; isotype, BM), non Piper
hookerianum C. de Candolle. Piper gardnerii C. de
 Candolle, Prodr. 16(1): 254. 1869.

Ottonia carpinifolia Presl, Epil. bot. 229. 1849. Type.

Brazil. Rio de Janeiro: Without specific locality or
 date, Bescke s.n (holotype, PRC), Piper carpinifolium
 (Presl) C. de Candolle, Prodr. 16(1): 155. 1869.

Ottonia consanguinea Presl, Epil. bot. 230. 1849. Type.

Brazil. Rio de Janeiro: Corcovado, without date, Mikan
s.n. (holotype, PRC). non Piper consanguineum Kunth.
Piper punctatissimum C. de Candolle, Prodr. 16(1): 255.
 1869.

Ottonia anisum Sprengel f. glabrior Miquel, Linnaea 20:

175. 1847. Type. Brazil. Without specific locality, 1839
 (fr), Pohl s.n. (holotype, M).

Ottonia diversifolia Kunth var. grandifolia Miquel,

Martius, Fl. bras. 4(1): 63. 1868. Type. Brazil. Rio de
 Janeiro: Sebastianópolis, without date, Scouler s.n.
 (holotype, B).

Piper hirtellum C. de Candolle, Prodr. 16 (1): 254. 1869.

Type. Brazil. Without specific locality or date, Sellow 258 (holotype, B, n.v.).

Piper praecox C. de Candolle, Annuaire Conserv. Jard. Bot.

Geneve 2: 254. 1898. Type. Brazil. Minas Gerais: Without specific locality, 1844 (fr), Claussen & Weddell s.n.

(holotype, P). Ottonia praecox (C. de Candolle) Trelease, Proc. Amer. Philos. Soc. 75: 712. 1935.

Ottonia armondi Trelease, Proc. Amer. Philos. Soc. 75: 697.

1935. Type. Brazil. Rio de Janeiro: Mpio. of Carmo, without date, Armond 156 (holotype, R).

Ottonia glazioui Trelease, Proc. Amer. Philos. Soc. 75:

704. 1935. Type. Brazil. Rio de Janeiro: Serra of Estrella, 15 Dec 1872 (fr), Glaziou 6001 (holotype, P; isotypes, C).

Ottonia burchellii Trelease, Proc. Amer. Philos. Soc. 75:

699. 1935. Type. Brazil. Rio de Janeiro: Corcovado, without date, Burchell 1127 (holotype, K; isotypes, G, GH).

Ottonia mexiae Trelease, Proc. Amer. Philos. Soc. 75: 709.

1935. Type. Brazil. Minas Gerais: Viçosa, Agric. College lands, Barbado, 680 m, 9 Oct 1930 (fl, fr), Mexia 5160 (lectotype, ILL (designated by Jones, 1985), n.v.; isolecotypes, BM, F, GH, NY, S, US, U n.v., Z n.v.).

Ottonia mexiae Trelease var. fertilior Trelease, Proc.

Amer. Philos. Soc. 75: 709. 1935, pro part. synonym. Type.

Brazil. Minas Gerais: Viçosa, Agric. College lands,

Barbardo, 170 m, 9 Apr 1930 (fr), Mexia 4587 (lectotype,

ILL (designated by Jones, 1985); isoelectotypes, AA, BM,

F, G, GH, NY, PH, U, US). A specimen in Stockholm (S) with

the same label belongs to P. corcovadensis.

Ottonia santa-ritana Trelease, Proc. Amer. Philos. Soc. 75:

714. 1935. Type. Brazil. Minas Gerais: Santa Rita,

without date, Schwacke 11326 (holotype, G; isotype, B

n.v.).

Ottonia taperana Trelease, Proc. Amer. Philos. Soc. 75:

715. 1935. Type. Brazil. Pernambuco: Tapera, Palmares,

Oct 1931 (fr), Pickel 2789 (holotype, US).

Ottonia carpinifolia Presl f. hirtipedicellata Yuncker,

Bol. Inst. Bot. São Paulo 3: 134 1966. Type. Brazil. Rio

de Janeiro: Rio de Janeiro, Serra de los Orgãos, National

Park, 4 Apr 1953 (fr), Pereira 702 (holotype, RB).

Terrestrial shrub, sometimes a treelet, 0.7-2.5 m tall, sparingly to profusely branched; internodes striate, canaliculate, 1.8-3.5(-4.5) cm long and 2-4 mm in diam., papillate, densely short-pubescent, covered by thin, erect, white to brown or less often reddish 3-4(-8)-celled hairs, glabrescent, rarely glandular dotted. Leaves thin-membranous and translucent, or thick-chartaceous and opaque, wide to narrow

ovate or often lanceolate, (2-)2.4-3.8(-4.7) times longer than wide, lamina symmetric to strongly asymmetric, (6-)8.4-15(-18) x (2.8-)3.6-4.4(-5) cm, basally asymmetric, obtuse to symmetrically cordate, rarely short-acute, rarely short-peltate, apically short-acute to long-acuminate, glossy green above pale green beneath when living, grayish-green above or sometimes with venation drying light green or whitish and forming edged areoles above and pale green or brownish beneath when dry, glabrous above but sometimes sparsely pubescent at the base, densely short-pubescent beneath along the midvein and secondary veins or less often secondary veins glabrous, or glabrescent, rarely glandular dotted; midvein impressed above or raised only by proximally half of its length, the 8-12 secondary veins impressed above, venation strongly raised beneath; petioles striate. Prophylls caducous, 4-8(-10) mm, apically short-acute, papillate, glabrous, rarely densely short-pubescent, obscurely glandular dotted. Inflorescence erect, white in flower and green or purple in fruit when living, brownish or reddish in flower and fruit when dry; peduncles striate, rugose less often terete, (2.5-)4.7-7(-10) mm, papillate, densely short-pubescent, glabrescent, rarely glandular dotted; flowering portion (2-)3.5-11(-14) cm long; rachis visible at all stages, densely to sparsely pubescent, glabrescent, obscurely glandular dot-

ted; floral bracts 0.3-0.5 mm wide, saccate-galeate, proximally densely short-pubescent, obscurely glandular dotted, sessile in anthesis, becoming distinctly pedicellate, 0.6-0.8(-1.5) mm distant from the rachis, basally sparsely pubescent, glabrescent. Flowers pedicellate, loosely congested in anthesis and widely spaced in fruit; pedicels 1.5-4.2 mm long, sparsely pubescent, glabrescent, obscurely glandular dotted; anthers dehiscing laterally, obscurely glandular dotted; stigmas sessile. Fruits globose or ellipsoid-ovoid, 0.7-3 mm long, 4-ribbed, strongly sulcate, papillate, sparsely short-pubescent, glabrescent; seeds ellipsoid, 1.6-2.5 x 1-1.3 mm, radially symmetric, 4-ribbed, strongly sulcate, glossy orange or blackish when dry.

Distribution. (Fig. 88D). Coastal forest of SE Brazil in Bahia, Espírito Santo, Minas Gerais, Paraíba, Pernambuco, Rio de Janeiro, and São Paulo (known from a single collection). Growing in the understory of the forest in little to heavily disturbed vegetation; in Minas Gerais growing on steep slopes or shady cutovers in gallery forests surrounded by cerrado vegetation; relatively rare but locally abundant; 80-1000 m elev. Flowering and fruiting throughout the year.

Specimens examined. BRAZIL. Bahia: Km 14, rd. Porto Seguro-Eunápolis, 4 Nov 2983 (fr), Callejas et al. 1637 (CEPEC, NY, RB, US), 1637-B (CEPEC, NY), 1639 (CEPEC, NY, RB,

US), km 13, 2 Apr 1972 (fr), Eupunino 200 (CEPEC, RB); Sta. Cruz Cabralia, km 13 of rd. to Porto Seguro, 21 Sep 1972 (fr), Eupunino 288 (CEPEC, RB); Ilhéus, Castelo Novo, 9 Sep 1944, Velloso 1056 (R). Espírito Santo: Canaan, Sta. Tereza, 800-850 m, 2 Jan 1969 (fl), Sucre & Braga 4544 (RB); between Bananal and São João da Mata, 17 Oct 1924, Vidal s.n. (R). Minas Gerais: Belo Horizonte, Jardim Botânico, 10 May 1934 (fr), Barreto 306 (F); Sta. Rita de Jacutinga, Feb 1972 (fr), Braga & Marilene 2429 (NY, RB); Mpio. Coronel Pacheco, Coffe Experimental station, 6 Nov 1940 (fr), Heringer 409 (SP); Mpio. Dionisio, State Park of Rio Doce, 29 Nov 1976 (fr), Heringer 16010 (IBGE, MO, NY); 50 km SE of Belo Horizonte, Serra do Itabirito, 1500 m, 10 Feb 1968 (fr), Irwin et al. 19742 (IAN, NY, UB); Viçosa, Agric. college lands, N slope of Barbado, 710 m, 22 Apr 1930 (fr), Mexia 4619 (A, G, GH, NY, PH, US); State experimental station of Agua Limpa, 15 Oct 1965 (fl, fr), S. V. Monteiro 2646 (RB); nr. Belo Horizonte, 11 Nov 1940 (fr), Occhioni s.n. (R); forests nr. Prefeitura, 3 Jan 1979 (fr), Ramalho & G. Rodriguez 13520 (NY, RB). Paraíba: Fazenda do Sabral, without date, Saldanha s.n. (R). Pernambuco: Recife, Dois Irmãos, 12 Dec 1948 (fr), A. Lima 48-131 (RB). Rio de Janeiro: Parati, Parati-Mirim, 1 Dec 1976 (fr), Araujo 1387 (RB); Itatiaia, rd. to Maromba, km 3, 6 Oct 1945 (fr),

Barbosa et al. 101 (RB); Pirai, 1887 (fr), Bello 154 (R); Nova Friburgo, 5 Sep 1953 (fr), Capel s.n. (MA); Rio de Janeiro, Pedra da Gávea, rd. to Furnas, 400 m, 1 May 1977 (fr), Carauta & Kirkbride 2439 (GUA, RB); Nova Friburgo, Nov 1842 (fr), Claussen s.n. (NY); Rezende, National Park of Itatiaia, along Rio Campo Belo, 17 Oct 1977 (fr), Ferreira & Brolarijo 195 (RB); Rio de Janeiro, without date, Gaudichaud 83 (P); Petrópolis, Carangola, Dec 1943 (fr), Goes & D. Constantino 1014 (RB); Corcovado, 1839 (fr), Guillemin s.n. (G, P); Serra da Estrela, 22 Apr 1937 (fl, fr), Kuhlmann et al. 15744 (RB); Mount Corcovado, without date, Langsdorff s.n., 83 (LE); Nova Friburgo, Oct 1946 (fl, fr), Leite 4159 (F, MA, NY, US); Petrópolis, Serra da Estrela, base of the Serra, junction of rd Pedras-Vilha, 5 Sep 1977 (fl, fr), Mantone et al. 294 (RB); Vale Florido, 9 Nov 1977 (fr), Marquete et al. 158 (RB); Araras, Rio of Capoeirão, 1000 m, 17 Apr 1977 (fr), Martinelli 1634 (RB); Rio de Janeiro, Campo Grande, Serra da Mendanha, 600-700 m, 4 Apr 1978 (fr), Martinelli et al. 4131 (NY, RB); Sebastiãoopolis, Nov-Dec (fr), Martius 218 (?) (M); Rio de Janeiro, Mount Corcovado, between Paineiras and Jardim Botânico, 200 m, 8 Oct 1977 (fr), Maas et al. 3123 (NY, U); Terezópolis, National Park of Serra dos Orgãos, 300-400 m, 21 Oct 1977 (fr), Maas & Martinelli 3409 (NY, RB, U); Fazenda Sta. Mônica, 6 Nov 1948 (fl, fr), Occhioni 1184 (RB); Teresópolis, 3 May 1917 (fr), Sampaio 2451 (R); Serra do Monte

Verde, Tres Irmãos, 12 May 1919 (fl, fr), Sampaio 3198 (R); old rd. to Lagoinha, 4 Oct 1940 (fr), Satto et al. s.n. (RB); Palmeiras, Oct 1876 (fr), Schwacke 1062 (RB); Sobral, nr. Parnahyba do Sul, 1881 (fr), Schwacke 3349 (RB); Serra da Mendanha, 450 m, 27 Nov 1969 (fr), Sucre et al. 6370 (F, NY, RB), 400-500 m, 27 Oct 1969 (fr), Sucre et al. 6409 (F, NY, RB), 600-700 m, 9 Apr 1970 (fr), Sucre & Ichaso 576 (RB); second district of Rio das Flores, Fazenda Sta. Genoveva, 500-600 m, 7 Oct 1971 (fl), Sucre 7770 (NY, RB); Taquara da Tijuca, 620 m, 20 Oct 1971 (fl, fr), Sucre 7818 (NY, RB); Serra da Mendanha, 500 m, 19 Apr 1972 (fr), Sucre et al. 8849 (NY, RB); Nova Friburgo, Jan 1898 (fr), Ule 4597 (R); without specific locality, or date, Glaziou 1163 (C); Luschnath s.n. (LE); 1835 (fr), Luschnath s.n. (LE); Martius 1210 (G, LE, M); Martius s.n. (M); without date, Miers et al. 3409 (NY, RB, U); Peters s.n. (LE); Riedel 16 (LE); Riedel s.n. (C, GH); 1838-1842 (fr), U.S. Pacific Exp. s.n. (US); 1843 (st), Weddel s.n. (NY, P); 1944 (fl), Widgren s.n. (S).

Local names and uses. Brazil: jaborandy (Bahia, Rio de Janeiro), joão-barandi (Minas Gerais), joão borandinho (Bahia), joao-borandy (Minas Gerais, Rio de Janeiro); jaborandi de Minas (Minas Gerais), tremedor (Minas Gerais). Guimarães (1984) cites the following names: borandi, capoty, cataiguacie, cutia, jaborandi da mata virgen, nhamdu, yandi.

This species is used for the treatment of toothache, as a diuretic, sudorific, and aphrodisiac. Guimarães (1984) reported its use in religious ceremonies by the natives in Brazil in the so called "banhos de descarrego" and "defumadores de caboclo" for the purpose of avoiding misfortune and getting rid of bad spirits.

Although extensive literature on the medicinal uses of P. anisum is often cited, much of it is inaccurate or is based on different taxa to which the name O. anisum was often ascribed (e.g. Moura, 1884). To date no chemical analysis has been performed on this species, however, the Institute of Medicinal Plants of Bahia (?), as cited by Guimarães (1984) reported the presence of the following chemical compounds: pilocarpine, pilocarpidine, isopilocarpidine, carpine, pseudopilocarpine, jaborine, pseudojaborine, pilosine, and essential oils. All these compounds, are found in the genus Pilocarpus (Rutaceae), species of which are known in Brazil under the common name "jaborandi"!

Piper anisum is easily recognized by its sparsely to densely pubescent midvein beneath the leaf, proximal portion of the floral bracts, rachis, fruits and pedicels, these often 2-5 times longer than the subtending fruit.

Leaves are normally thin-membranous and translucent, or very rarely chartaceous. At flowering nodes they are commonly wide ovate and basally asymmetric in plants which are sparsely branched. On the other hand, in profusely branched individuals, there is a tendency towards narrow lanceolate leaves and symmetric bases in branches of 3-4 order. Less often all leaves on all branches have similar size. This last phenotype apparently is not correlated with ecology or geography. Floral organs and most vegetative parts are glabrescent. Not surprisingly a large number of collections include extremes between glabrous plants and densely pubescent ones with specimens often glabrous in floral parts and densely pubescent in vegetative organs. The densely pubescent midvein beneath the leaf as well as the sparsely to densely pubescent proximal portion of the floral bracts, however, tend to be less glabrescent than other parts of the plant.

The type collection from Rio de Janeiro corresponds to populations with wide ovate leaves which are chartaceous and opaque, with asymmetric leaf bases, and densely pubescent parts but glabrescent fruits. The type of O. consanguinea from Corcovado (Rio de Janeiro) is almost identical to the type O. anisum, except for the fact that fruits are still immature, leaves are thin-membranous and translucent, and the

inflorescences are shorter. According to Presl (1849) some fruits in that taxon are tricarpellate. I have not seen such fruits in the type collection, and Presl's observation is probably related to breaking or falling of stigmas in some fruits. The membranous leaves observed in O. consanguinea are rather common in the state of Bahia, however those leaves are somewhat narrow ovate to lanceolate instead of wide ovate. Some of those populations also have orange to reddish pubescence, but this is variable within single collections (Callejas 1637). Variation in the type described above may explain the descriptions of O. pteropoda and O. diversifolia var. grandifolia. While little emphasis was placed on variation of leaf size and shape, length of the pedicel and pubescence were thought to be worth recognition (e.g. see the discussion of Guimarães (1984) on O. hookeriana). Thus the type O. diversifolia corresponds to specimens with narrow ovate leaves which are chartaceous and with glabrous pedicels and fruits which are obscurely glandular dotted. This is similar to O. diversifolia. With more sparsely pubescent parts are the types of O. hookeriana, O. carpinifolia, and O. anisum var. glabrior. Specimens with immature fruits or pedicels which had not fully elongated correspond to the types of O. praecox, C. mexiae, and O. mexiae var. fertilior.

In P. anisum vegetative parts are for the most part eglandular or only obscurely glandular dotted. However two

specimens from Pernambuco are densely glandular dotted. These collections have floral bracts, pedicels, and rachises which are sparsely pubescent. Trelease (1935) segregated those individuals as O. taperana. Both Yuncker (1973) and Guimarães (1984) accepted the taxon and both agreed in its relationship to P. anisum. Except for the glandular dotted parts (leaves and rachises), I can not find any significant differences between the type of P. anisum and that of O. taperana.

Piper anisum is most closely related to P. piliovarium and their relationships are discussed under the later taxon.

The combination P. anisum (Sprengel) Angely, while perfectly valid, is nevertheless the result of careless taxonomy more than a detailed study of the relationships between Piper and Ottonia. In his "Flora Descritiva do Paraná", Angely listed all species of Piperaceae known to occur in that state, including those belonging to Ottonia. On page 377, he cited O. anisum as the type species of that genus and mentioned three species occurring in Paraná. On page 387, the author gave the species of the genus Piper for Paraná among which he included P. anisum (Sprengel) Angely; thus in the same work that author in effect accepted and rejected the genus Ottonia. Angely, however, did not offer any explanation for such a strange decision.

20. Piper miquelianum C. de Candolle

Terrestrial shrub, erect but sometimes lianescent, 0.8-3.5 m tall, sparsely to profusely branched; internodes striate, canaliculate, 1.5-5 cm long and 2-4 mm in diam., papillate, sparsely pubescent when young, glabrescent. Leaves chartaceous and opaque, less often thin-membranous and translucent wide to narrow ovate or oblong to wide oblong, (1.1-)1.4-2.7(-2.9) times longer than wide, lamina strongly asymmetric, (6-)7.5-19(-21) x (2.7-)3.5-9(-10) cm, basally obtuse, cordulate to lobulate, then with one lobule partially covering the petiole, rarely subpeltate, apically short-acute, glossy green above and pale green beneath when living, grayish-green or olive-green above and brownish beneath when dry, glabrous above, sparsely pubescent along the midvein and with an intramarginal hirtellous region beneath, with erect, thick, whitish 3-6-celled hairs, glabrescent, rarely fully glabrous, eglandular; midvein impressed above, rarely raised, then only the proximal half of its length, the 10-13 secondary veins impressed above and strongly raised beneath; petioles striate, (3-)5-12 mm long, papillate, sparsely pubescent when young. Prophylls caducous, apically long-acuminate, (5-)8-12 mm long, papillate, often sparsely pubescent, obscurely glandular dotted. Inflorescence erect at all stages, white in flower and green in fruit when living, black or brownish when dry;

peduncles striate or rugose, 4-10 mm long, sparsely pubescent; flowering portion (1.5-)3.5-14(-17) cm; rachis visible at all stages, sparsely to densely pubescent, rarely glabrous. Flowers pedicellate, loosely congested at anthesis, widely spaced in fruit; pedicels 0.6-3(-4) mm long, glabrous, obscurely glandular dotted; floral bracts, 0.4-0.5 mm wide, saccate-galeate, sessile in anthesis becoming pedicellate in fruit, 0.6-1 mm distant from the rachis, glabrous, obscurely glandular dotted; anthers dehiscing laterally, eglandular; stigmas sessile. Fruits narrow to wide ovoid, long-apiculate, 3-5 mm long, 4-ribbed, strongly sulcate; seeds ellipsoid, 2 x 1.6 mm, radially symmetric, 4-ribbed, strongly sulcate, black when dry.

Distribution. (Fig. 88B). Atlantic coastal forest of SE Brazil in the subtropical region from São Paulo to Rio Grande do Sul and in the Rio Paraná delta in Paraguay.

Key to Varieties of Piper miquelianum

1. Leaves oblong to wide oblong, (6-)7.5-16.5(-18) x (2.7-)3-5.8(-9.7) cm; inflorescence in fruit (1.5-)2.5-5 cm long. 20a. var. miquelianum.
1. Leaves ovate to wide ovate, 12-19(-21) x 6-7.5(-9) cm; inflorescence in fruit 7-14(-17) cm long. 20b. var. hirtellum.

- 20a. Piper miquelianum C. de Candolle var. miquelianum,
 Prodr. 16(1): 254. 1869, non Piper martianum Kunth.
Ottonia martiana Miquel, Linnaea 20: 178. 1847. Type.
 Brazil. Without specific locality or date, Martius
s.n. (holotype, U). Figs. 1,6.
- Ottonia duseni Trelease var. heterophylla Trelease, Proc.
 Amer. Philos. Soc. 75: 702. 1935. Type. Brazil. Paraná:
 Pinhaes, 12 Feb 1914 (fl), Dusén 14506 (holotype, S).
- Ottonia edwallii Trelease, Proc. Amer. Philos. Soc. 75:
 702. 1935. Type. Brazil. São Paulo: Rd. to Ipiranga, 29
 Oct 1894 (fr), Löfgren & Edwall 2814 (holotype, SP).
- Ottonia elocalis Trelease, Proc. Amer. Philos. Soc. 75:
 703. 1935. Type. Brazil. São Paulo: São Paulo, Ipiranga,
 Mar 1912 (fr), Luederwaldt s.n. (holotype, SP).
- Ottonia hammari Trelease, Proc. Amer. Philos. Soc. 75: 705.
 1935. Type. Brazil. São Paulo: Coafuerao, Cantareira, 4
 Apr 1901 (fr), Hammar 4551 (holotype, SP).
- Ottonia hoehnei Trelease, Proc. Amer. Philos. Soc. 75: 705.
 1935. Type. Brazil. São Paulo: São Paulo, Butantán, 14
 Oct 1918 (fl), Hoehne s.n. (holotype, SP).
- Ottonia palhosana Trelease, Proc. Amer. Philos. Soc. 75:
 712. 1935. Type. Brazil. Sta. Catarina: Florianópolis,
 Palhoca, 22 Oct 1929 (fr), Hoehne s.n. (holotype, SP).
- Ottonia peruibensis, Trelease, Proc. Amer. Philos. Soc. 75:
 712. 1935. Type. Brazil. São Paulo: Piriube, 30 Oct 1891

(fr), Loefgren & Edwall 1625 (holotype, SP; isotype, C).

Ottonia santa-annae Trelease, Proc. Amer. Philos. Soc. 75:

713. 1935. Type. Brazil. São Paulo: Sta. Anna, Nov 1912

(fr), Brade 5786 (holotype, SP).

Ottonia schwackeae Trelease, Proc. Amer. Philos. Soc. 75:

714. 1935. Type. Brazil. Sta. Catarina: Blumenau, 14 Sep

1884 (fr), Swacke 5038 (holotype, G-DC; isotype, RB).

Ottonia pickelii Yuncker, Bol. Inst. Bot. São Paulo. 3:

136. 1966. Type. Brazil. São Paulo: São Paulo, 6 Oct 1941

(fr), Pickel 5443 (holotype, US).

Leaves oblong to wide oblong, (1.4-)1.7-2.7(-2.9) times longer than wide, lamina (6-)7.5-16.5(-18) x (2.7-)3-5.8(-9.7) cm. Flowering portion 1-1.5 cm long at anthesis, becoming 2.5-5(-6) cm long in fruit.

Distribution. (Fig. 88B). Southeastern Brazil from the tropical to subtropical regions in the states of Paraná, Sta. Catarina, and São Paulo. A common shrub in the understory of disturbed forests, often dominant species; 0-860 m elev. Flowering and fruiting throughout the year but with a conspicuous season from Sep to Feb.

Specimens examined. BRAZIL. Paraná: Guaratuba, 10 m, 12 Jul 1971 (fr), Braga & Marilene 2319 (RB); Antonina, 6 km from the reserve of Sapitanduba, 20 m, 1 Dec 1983 (fr), Callejas et al. 1836 (HUA, MB, NY, RB, U, US); Paranaguá, 5 km N of Colony

María Luisa, 50 m, 1 Dec 1983 (fr), Callejas et al. 1844 (HUA, MB, NY, RB, U, US); Cerro Azul, old rd. Cerro Azul-Jaguarai-va, 12 km from Rio Ribeira, 7 Dec 1983 (fl, fr), Callejas et al. 1868, 1869, 1870, 1871 (all G, HUA, MB, NY, RB, U, US, W); Matinhos, 28 Oct 1975 (fl), Dombrowski 7048 (MB, RB); Alexandra, 15 Dec 1909 (fr), Dusén 8676 (S); Antonina, 27 Oct 1909 (fl), Dusén 8852 (G, NY, S); Jaguaraihyba, 19 Apr 1910 (fr), Dusén 9803 (S), 6 Jul 1910 (fr), Dusén 10059 (S); Guaratuba, 22 Nov 1912 (fr), Dusén 13778 (G, S); Marumby, 27 Apr 1912 (fr), Dusén 14901 (S); Serra da Preta, 20 Jul 1914 (fr), Dusén 15326 (S, US); Paranaguá, Rio Cachoeirinha, 27 Oct 1950 (fl, fr), Hatschbach 2018 (MB, US), Guaraqueçaba, Rio Acunguí, 20 m, 8 Oct 1970 (fl), Hatschbach 24911 (C, MB, US); Morretes, Anhaia, 23 Oct 1972 (fr), Hatschbach 30538 (MB, NY); Antonina, Saiva, 17 Oct 1974 (fl); Hatschbach & Kummrow 35235 (MB, NY, U); Rio Sapitanduva, 4 Oct 1981 (fl, fr), Hatschbach 44331 (MB, NY), Port of Cima, 18 Jun 1914 (fr), Joussau 524-A (S); Caioba, Morro do Boi, Matinhos, 1 Sep 1984 (fr), Kummrow 2457 (MB, NY). Santa Catarina: rd to Aloma, Joinville, 29 Sep 1879 (fl, fr), without collector (RB); Itajai, Cunhas, 10 m, 8 Feb 1955 (fr), Klein 1122 (US); Ressacada Hill, Itajaí, 100 m 31 Mar 1955 (fr), Klein 1255 (US); Garuva, Palmital, 30 Sep 1983 (fl), Kumrow & P. I. Oliveira 2329 (MB, NY); Azambuja,

Brusque, 50 m, 12 Nov 1947 (fr), Reitz C-1944 (US); fazenda's hill, Itajaí, 100 m, 23 Sep 1954 (fl, fr), Reitz & Klein 2081 (US); Ibirama, arboretum at INP, 300 m, 12 Oct 1956 (fr), Reitz & Klein 4019 (NY, US); Jacinto Machado, 200 m, 4 Sep 1959 (st), Reitz & Klein 9009 (US); Brusque, Forest of Malucher, 40-50 m, 23 Feb 1952 (fr), L. B. Smith 5789 (US); fazenda's hill, Itajaí, 50-100 m, 3 Nov 1956 (fr), L. B. Smith et al. 7279 (US). São Paulo: São Paulo, Villa Emma, Feb 1947 (fr), Brade 18177 (RB); Biological Reserve Fontes do Ipiranga, 80 m, 2 Jan 1984 (fr), Callejas et al. 2034, 2036, 2038 (HUA, NY, RB, SP), 14 Nov 1980 (fr) Chiea & Chiea 146 (SP); Area 18, 5 Apr 1974 (fr), Corrêa 21 (SP); Area 5, 14 Oct 1975 (fr), Corrêa 105 (SP), São Paulo, grounds of Instituto Botânico, 860 m, 21 Feb 1976 (fr), Davidse 10455 (MO, SP), 10 Aug 1967 (fr), Faria 32 (SP); Pirajussara, 2 Feb 1941 (fr), Gehrt s.n. (SP); São Paulo, Botanical Garden, 20 Oct 1940 (fr), Handro s.n. (SP); São Paulo, garden in the city, 2 Oct 1936 (fr), Hoehne s.n. (SP); São Paulo, Ipiranga, 6 Aug 1934 (fl), Kuhlmann s.n. (SP); Juquia, margin of Juquia river, 25 Jun 1941 (fr), Kuhlmann & Kuehn s.n. (SP); Botanical Garden, 4 Nov 1958 (fl, fr), Kuhlmann s.n. (SP); São Paulo, forest reserve of Ipiranga, 24 Oct 1977 (fl, fr), Makino 92 (SP); Moji-Guaçu, nr. Padua Sales, 2 Sep 1965 (fr), Mattos 12528 (SP); São Paulo, forest reserve of Ipiranga, 25 Feb 1981 (fr), Melo et al. 243 (SP); São Paulo, 21 Aug 1941 (fl), Pickel 5355 (SP); forest reserve of Botanical Institute, 14 Nov 1980 (fl, fr),

N. A. Rosa & Pires 3690 (MG, SP); 21 Nov 1969 (fr), Sendulsky 807 (SP); forest reserve of Ipiranga, 4 Oct 1975 (fr), J. S. Silva 393 (SP).

20b. Piper miquelianum C. de Candolle var. hirtellum (C. de Candolle) Callejas, comb. nov. Fig. 96.

Piper ovatum Vahl var. hirtellum C. de Candolle, Bull.

herb. Boiss. 4: 396. 1093. Type. Paraguay. Amambay:

Sierra Maracayú, 6 Nov 1898-1899 (fr), Hassler 5387

(lectotype, G, here designated; isoelectotypes, G, GH).

Ottonia cordulatifolia Trelease var. hirtella (C. de

Candolle) Trelease, Proc. Amer. Philos. Soc. 75: 701.

1935.

Ottonia apodostachya Trelease, Proc. Amer. Philos. Soc. 75:

697. 1935. Type. Brazil. Santa Catarina: Jaraguá, 11 Oct

1929 (fr), Hoehne s.n. (holotype, SP).

Ottonia apodostachya Trelease var. vidalii Trelease, Proc.

Amer. Philos. Soc. 75: 697. 1935. Type. Brazil. Espírito

Santo: Without specific locality or date, Vidal 138

(holotype, not found).

Ottonia cordulatifolia Trelease, Proc. Amer. Philos. Soc.

75: 700. 1935. Paraguay. Alto Paraná, 1909-1910 (fr),

Fiebrig 5625 (holotype, K; isotypes, G, GH).

Ottonia duseni Trelease Proc. Amer. Philos. Soc. 75: 702.

1935. Type. Brazil. Paraná: Jaguariahyva, 23 Oct 1910

(fr), Dusén 14506 (holotype, S).

Ottonia duseni Trelease var. variifolia Trelease, Proc.

Amer. Philos. Soc. 75: 702. 1935. Type. Brazil. Paraná:

Jaguariahyva, 16 Apr 1911 (fr), Dusén s.n. (holotype, S)

Ottonia loefgreni Trelease, Proc. Amer. Philos. Soc. 75:

707. 1935. Type. Brazil. São Paulo: Pirituba, 30 Dec 1893

(fr), Löfgren 1552 (holotype, SP; isotype, C).

Ottonia muelleri Trelease, Proc. Amer. Philos. Soc. 75:

710. 1935. Type. Brazil. Santa Catarina: Blumenau, without

date, Müeller 459 (holotype, B; isotype, G).

Ottonia rio-feioana Trelease, Proc. Amer. Philos. Soc. 75:

713. 1935. Type. Brazil. São Paulo: Rio Feio, without date,

Edwall s.n. (holotype, SP).

Ottonia martiana Miquel var. latifolia Yuncker, Inst. Bot.

São Paulo 3: 135. 1966. Type. Brazil. São Paulo: São

Paulo, Ipiranga, 28 Oct 1943 (fr), Pickel 287 (holotype,

NY).

Leaves ovate to wide ovate, (1.1-)1.4-2.3 times longer than wide, lamina 12-19(-21) x 6-7.5(-9) cm. Flowering portion 4.5-5 cm long in flower, becoming 7-14(-17) cm long in fruit.

Distribution. (Fig. 88B). Brazil in the states of Espírito Santo (a single collection), Matto Grosso do Sul (east), Paraná (Fig. 94), Rio de Janeiro (south), Rio Grande do Sul, and Santa Catarina, and in Paraguay in the state of Amambay.

Occurring in secondary forests in relatively dry understory, often found in light gaps. Mostly restricted to the subtropical region in Brazil, but rarely growing in understory of Araucaria forests in Paraná. A common element of the understory it may often be dominant; sea level to 800 m elev. Flowering and fruiting as the typical variety.

Specimens examined. BRAZIL. Matto Grosso do Sul: Amambai, rd. Amambai-Ponta Porã, 20 km NW of Amambay, 700 m, 14 Dec 1983 (fl, fr), Callejas et al. 1918 (G, HUA, MB, NY, RB, US), 650 m, 12 Feb 1983 (fr), Hatschbach 46152 (MB, NY, RB).
Paraná: Cerro Azul, old rd. Cerro Azul-Jaguariahyva, 12 km from bridge on Rio Ribeira, 450 m, 7 Dec 1983 (fr), Callejas et al. 1874 (HUA, MB, NY, RB, U, US); new rd. Cerro Azul-Jaguariahyva, 500 m, 8 Dec 1983 (fr), Callejas et al. 1895, 1897, 1899 (all G, HUA, MB, NY, RB, U, US); Rio Branco do Sul, 44 km along rd. to Curitiba, 600 m, 8 Dec 1983 (fr), Callejas et al. 1903 (MB, NY, RB); Antonina, 27 Oct 1909 (fl, fr), Dusén 8852 (G, S); Terezinha, 20 Jan 1911 (fr), Dusén 11182 (S); Jacarehy, 26 Sep 1915 (fr), Dusén 17208 (S); Itarare, 7 Nov 1910 (fr), Dusén s.n. (S); Jaguariahyva, 30 Dec 1914 (fr), Dusén s.n. (S); Patrimônio, 9 Mar 1915 (fr), Dusén s.n. (S); Adrianópolis, Paranai, 150 m, 26 Sep 1962 (fl, fr), Hatschbach 9291 (MB, U); Morretes, Jurapé, 8 Feb 1979 (fr), Hatschbach 41971 (MB, NY); Cerro Azul, Barra do Canha, 18 Feb 1981 (fr); Hatschbach 43607 (F, MB, NY); Sete Quedas, Guaira, 16 Sep 1981

(fr), Hatschbach 43981 (MB, NY, US); Rio Ivai, 30 km E of Cianorte, 250-300 m, 26 Mar 1966 (fr), Lindeman & J. de Haas 781 (NY, U, US); W of Matinhos, Morro do Tabaquara, 2 Jan 1967 (fl, fr), Lindeman & J. de Haas 3847 (NY, U); Rio Paraná, Barra da Felicidade, 20 Jun 1967 (dt), Lindeman & J. de Haas 5478 (U). Rio de Janeiro: Petrópolis, rd de Contorno, 650 m, 11 Feb 1968 (fr), Sucre 2364 (HB, FEEMA); Vale do Bonsucesso, 650 m, 11 Feb 1968 (fr), Sucre & Braga 2371 (RB); Mata do Judeu, 800 m, 25 Jan 1969 (fr), Sucre & Braga 4501 (RB). Rio Grande do Sul: Mount Sapucaia, nr. São Leopoldo, 10 Nov 1948, Rambo 37948 (PACA), 25 Jan 1933, Rambo 561 (LIL); without specific locality or date, Loefgren s.n. (RB). Santa Catarina: Brusque, mata da Azombuja, 19 Oct 1950 (fr), Klein 174 (US); Itajaí, Morro da Fazenda, 250 m, 7 Oct 1955 (fr), Klein 1651 (G, HBR, M), 27 Dec 1983 (fr), Callejas et al. 1965, 1969 (both HUA, HBR NY, U, US); Morro do Bau, Ilhota, 30 Jan 1964 (fr), Pereira 8765 (HBR, NY, RB); Ararangua, Turvo, 11 Nov 1943 (fr), Reitz C-179 (GH), 25 Mar 1944 (fr), Reitz 537 (SP); Garapuvú, Vista Alegre, 20 m, 12 Dec 1959 (fr), Reitz et al. 9412 (HBR, US); Itajaí, Morro da Fazenda, 5-100 m, 3 Nov 1965 (fr), L. B. Smith et al. 7279 (NY, US). São Paulo: Pinhal, Fazenda Sta. Tereza, 14 Nov 1947 (fr), Kuhlmann 1550 (SP).

PARAGUAY. Alto Paraná: Along Río Monday, 200 m, 26 May 1945 (fr), Bertoni 13764 (LILL, NY). Amambay: 40 km N of Ponta Porá, 350 m, 15 Dec 1983 (fr), Callejas et al. 1923, 1925 (both MB, NY, U, US); Pedro Juan Caballero, 370 m, 15 Dec 1983 (fl, fr), Callejas et al. 1957 (HUA, MB, NY, U, US); Sierra Maracayú, 1898-1899, Hassler 5103 (G, NY); Río Yhu, Sep 1905 (fr), Hassler s.n. (GH); Cerro Cuatia, 18 Km W of Cuatia, La Sirena, 30 Apr 1981 (fl), Soejarto 5692 (ECON, F, G, GH, K, P, S, US).

Local names and uses. Brazil: jaborandy, janguarandin (Matto Grosso do Sul, Paraná, Santa Catarina), João barandinho (Rio de Janeiro). Paraguay: anestesia (Amambay).

In Brazil the roots and leaves are used for treatment of toothache. Lindeman 5478 mentioned "the juice from roots and stems is pungent, like formic." Soejarto 5692 noted the numbing effects on the mouth parts by chewing roots and stems. According to the same collector the plant is widely used as a silagoge and toothache remedy, potions of which are used as gargle.

Piper miquelianum is characterized by leaves wide ovate, less than three times longer than wide, basally obtuse and with prominent lobes, sparse pubescence along the midvein beneath, long pedicels which are 2-4 times longer than the fruits which

are 3-5 mm long. Except for the rachis, which is sparsely pubescent, the floral parts are glabrous.

The species overlaps to a large extent with P. corcovadensis and especially with var. blanchetti. Both taxa have glabrous floral parts and pedicels which are longer than the fruits. In the latter taxon, leaves are narrow elliptic to lanceolate rarely ovate, but then glabrous along the midvein beneath. The two species often occur sympatrically especially in the coastal forest in Rio de Janeiro and in Santa Catarina. Compared with P. corcovadensis, P. miquelianum is more commonly found in subtropical regions rarely reaching beyond Rio de Janeiro into the tropics.

Piper miquelianum is here divided in two varieties. This interpretation of the species was suggested by Yuncker (1966) when he named O. martiana var. latifolia. The often small oblong leaves and short inflorescence of var. miquelianum (1-2.5 cm) are very distinctive and make it easy to separate from var. hirtellum. The fruits in the typical variety are often (but not always) larger than those in var. hirtellum. In both varieties inflorescences and fruits are commonly fasciated, so the former appear shorter (1-1.5 cm) and the latter abnormally larger (9-10 mm long).

The two varieties seem to occupy different habitats. The typical variety is more common in little disturbed areas where

it does not tolerate light gaps. By contrast populations of var. hirtellum often grow in open light conditions in disturbed vegetation. Both varieties branch profusely at the base with the branches evocating at first a plagiotropic orientation but soon becoming erect some distance from the parent plant, rooting and soon detaching from the parent plants to form new individuals.

Yuncker (1973) included large numbers of specimens of O. propinqua (=P. corcovadensis) under O. martiana (=P. miquelianum), and erroneously lumped several species described by Trelease under the latter taxon. These created a heterogeneous taxon in O. martiana (=P. miquelianum) and made rather ambiguous the differences by which Yuncker (1973) separated the taxa. The reason for this was the presence of glabrous leaves in some collections found in subtropical regions rarely reaching beyond Rio de Janeiro into the tropics; they include the types of O. edwallii, O. palhosana, O. peruibensis, and O. santa-annae.

Populations of the typical variety in Paraná and Sta. Catarina have leaves which are distinctly larger than those in São Paulo. As a result of this, differences in the shape and size between leaves on flowering and vegetative nodes are rather accentuated. The obvious and commonly present leaf dimorphism in this taxon was nevertheless, misinterpreted by

Trelease, who often used such dimorphism at the species level examples of which include O. duseni var. heterophylla and O. schwakeae.

Ottonia pickelii, here lumped under var. miquelianum, represents a collection with leaves smaller than the type, immature inflorescences, and glabrescent parts. Otherwise it agrees well with P. miquelianum.

Characters by which Trelease segregated many of his taxa, now in synonymy under P. miquelianum var. miquelianum, were certainly minor morphological discontinuities. In the synonymy of P. miquelianum var. hirtellum, on the other hand, taxa do not correspond to any obvious morphological variations (see below) but rather to the geographic distribution. Likewise O. duseni var. varifolia, O. apodostachya, and O. apodostachya var. vidalii were segregated on leaf dimorphisms, very much like species described under P. miquelianum var. miquelianum.

Piper miquelianum resembles P. guimaraesianum and P. bracteo-villosum in leaf shape and length of the pedicel. The relationships of the three taxa were previously discussed under the latter pair of species.

21. Piper corcovadensis (Miquel) C. de Candolle.

Terrestrial shrubs, erect or often lianescent, 0.7-2 m tall, profusely branched; internodes striate and canaliculate, sometimes terete and smooth, 2.5-4.5(-7) cm long and 2-3.5 mm

in diam., papillate, glabrous, rarely sparsely pubescent when young, eglandular. Leaves thick-chartaceous and opaque, rarely thin and membranous but not translucent, (1.8-)2.1-3.4(-3.7) times longer than wide, ovate to narrow ovate or lanceolate, often elliptic, lamina symmetric to strongly asymmetric, (7-)8.5-18(-20) x (2.5-)4-7.2(-8) cm, glossy green above and pale green beneath when living, grayish-pale green or brown to blackish above and pale green or light brown beneath when dry, basally short-acute or obtuse on both sides then not lobulate but often cordulate, less often wide obtuse at one side and short-acute on the other, apically short-acute to long-acuminate or sometimes attenuate; midvein and the 12-14 secondary veins raised on both sides, or impressed above and raised beneath, glabrous above, often with an intramarginal hirtellous region beneath, eglandular to sometimes obscurely glandular dotted above along the midvein, often pitted beneath; petioles striate, rugose, sometimes grooved adaxially, 5-12 mm long, papillate, glabrous. Prophylls caducous, 10-12 mm long, apically short-acute, papillate, glabrous, obscurely glandular dotted. Inflorescence erect, white in flower and greenish in fruit when living, brown, olive-green, or often dark brownish when dry; peduncles striate, rugose, 0.7-1 cm long, papillate; flowering portion (3-)4-9(-11) cm long; rachis not obscured in flower or fruit, papillate, glabrous or rarely sparsely pubescent, obscurely glandular dotted; floral bracts 0.2-0.4

mm wide, saccate-galeate, glabrous, sessile at anthesis, becoming pedicellate and 0.3-0.7 mm distant from the rachis. Flowers pedicellate, widely spaced at all stages; pedicels 0.6-2.0(-3.2) mm long, glabrous, obscurely glandular dotted; anthers dehiscing laterally, eglandular to glandular dotted; stigmas sessile. Fruits ellipsoid to wide ovoid, (0.6-)1.2-2.4(-2.7)mm long, 4-ribbed, strongly sulcate, papillate, glabrous, obscurely glandular dotted; seeds ellipsoid, 1.2 x 1.8 mm, radially symmetric, 4-ribbed, strongly sulcate, brown to blackish when dry.

Distribution. (Fig. 88C). Southeastern Brazil in the coastal forest from Bahia to Rio Grande do Sul with some isolated populations in Goiás; 400-1500 m elev.

Key to the Varieties of Piper corcovadensis

1. Internodes 5-7 cm long; leaves (8.5-)9-13(-14.5) x (2.5-)3-6 cm, drying rigid chartaceous, brown to blackish when dry, apically long-acuminate to attenuate; venation raised on both sides, glabrous; rachis glabrous stamens glandular dotted. 21a. var. corcovadensis.
1. Internodes 1.5-3.7 cm long; leaves (10.5-)17-19(-20) x (3-)5-8 cm, drying chartaceous but not rigid, pale green or greenish when dry, apically short-acute; venation impressed above, strongly raised beneath, often with an

intramarginal hirtellous region beneath; rachis sparsely hirtellous, rarely glabrous; stamens eglandular.

21b. var. blanchetii.

21a. Piper corcovadensis (Miquel) C. de Candolle var. corcovadensis, Prodr. 16(1): 255. 1869.

Ottonia propinqua Kunth, Linnaea 13: 583. 1839. Type.

Brazil. Without specific locality or date, Sellow s.n. (holotype, B; isotype, K. Specimen at K is mounted on the same sheet with a Blanchet s.n. collection of the same species), non Piper propinquum Kunth.

Ottonia padifolia Kunth, Linnaea 13: 580. 1839. Type. Brazil.

Without specific locality, no date, Sellow, s.n. (holotype, B, photo F neg. 1'09. Piper padifolium (Kunth) C. de Candolle, Prodr. 16(1): 253. 1869.

Ottonia corcovadensis Miquel, Linnaea 20: 175. 1847. Type.

Brazil. Rio de Janeiro: Rio de Janeiro, Corcovado, Feb (fr), without specific date, Pohl 4776 (lectotype, U, here designated). The type collection at U consists of portions of two specimens. According to the label (Miquel's handwriting) and Miquel's description, both specimens correspond to Pohl 4776 and 3030. The latter corresponds to Pohl's P. ovatum. There is no way, however, to determine which specimen corresponds to which number. Miquel's

description mentions characters from both specimens, but does not indicate which (the left or right hand specimen) he chose as the type. The specimen on the left hand of the sheet is in fruit and the leaves are obscurely glandular dotted beneath, two characters he mentioned in the diagnosis. The specimen on the right has immature inflorescences but is not glandular dotted. Even if both collections belong to the same species, one of them, the first one mentioned above (left hand specimen) better fits the original description, and is here chosen as the lectotype.

Piper corcovadensis (Miquel) C. de Candolle var. petiolatum

Miquel ex C. de Candolle, Prodr. 16(1): 255. 1869. Type.

Brazil. Rio de Janeiro: Without specific locality, 1833

(fr), Gaudichaud 1101 (holotype, G-DC; isotypes, G, U, P).

The specimen at P is labeled Gaudichaud 1100 and deter-

mined as O. eucalyptifolia Kunth. It was determined by

Yuncker (1973) as the isotype of that species. That collec-

tion, however, does not match duplicates of the same

collection at G. Furthermore, it does not fit the descrip-

tion of O. eucalyptifolia, but rather of P. corcovadensis

var. petiolatum. Thus, it probably represents a misnumbered collection.

Piper selloi C. de Candolle var. latilimbum C. de Candolle,

Notizbl. Bot Gart. Berlin-Dahlem 6: 464. 1917. Type.

Brazil. Without specific locality, 1892, Glaziou 19865

(holotype B; isotypes, C, K. The label at K indicates the collection is from Rio de Janeiro?). Ottonia latilimba (C. de Candolle) Trelease, Proc. Amer. Philos. Soc. Amer. 75: 706. 1935

Piper padifolium (Kunth) C. de Candolle var. corcovadensis Miquel ex C. de Candolle, Prodr. 16(1): 253. 1869, Type. Brazil. Rio de Janeiro: Rio de Janeiro, Corcovado, without date, Martius s.n. (holotype, M), non Piper corcovadensis (Miquel) C. de Candolle. Ottonia gibbimontis Trelease, Proc. Amer. Philos. Soc. 75: 704. 1935.

Ottonia colliculorum Trelease, Proc. Amer. Philos. Soc. 75: 699. 1935. Type. Brazil. Rio de Janeiro: Niteori, Morro de Cavalão, nr. Santa Rosa, without date, Schwacke s.n. (holotype, RB).

Piper riedelii Trelease, Proc. Amer. Philos. Soc. 75: 713. 1935. Type. Brazil. Without specific locality or date, Riedel s.n. (lectotype, ILL, designated by Jones (1985)). Internodes 5-7 cm long, terete and smooth, rarely striate and canaliculate. Leaves (8.5-)9-13(-14.5) x (2.5-)3-6 cm, drying rigid-chartaceous, brown to blackish when dry, apically long-acuminate to attenuate, venation raised on both sides, glabrous, eglandular or rarely obscurely glandular dotted, sometimes pouched beneath. Inflorescences 2.8-4 cm long; peduncle 0.9-1.2 cm long; rachis glabrous; floral bracts 0.5-0.7 mm distant from the rachis, stamens glandular dotted.

Distribution. (Fig. 88C). Restricted to the state of Rio de Janeiro, Brazil, where it grows in the understory of primary or more often secondary forests; 15-210 m elev. Flowering collections known from Aug to Sep; fruiting from Oct to Dec.

Specimens examined. BRAZIL. Rio de Janeiro: Petrópolis, rd. Petrópolis-Teresópolis, Pilares, 15 Nov 1969 (fl), Braga 1751 (NY, RB); Morro da Babylonia, Oct 1914 (fl) Hoehne s.n. (SP); Corcovado, 1835 (fl, fr), Luschnath s.n. (LE); Bahia of Sepetiba, Ilha Furtada, 4 Nov 1967 (fr), Sucre 1861 (RB); forest reserve of Grajaú, 100 m, 25 Nov 1969 (fl), Sucre 6356 (NY, RB); base of Serra da Piaba, S slope, 28 Oct 1971 (fl, fr), Sucre 7838 (NY, RB), 100-210 m, 29 Aug 1972 (fl), Sucre J. da Silva 9560 (NY, RB); Jacarepagua, rd. 9, 15-30 m, 5 Sep 1972 (fl), Sucre 9596 (RB). Without collector at Fischer's herbarium, 1842-1846 (fl), (G-DC, LE).

21b. Piper corcovadensis (Miquel) C. de Candolle var.

blanchetii (Moricand) Callejas, comb. nov. Fig. 97.

Ottonia blanchetii Moricand, Pl. nouv. Amer. 87. 1840.

Type. Brazil. Bahia: Without specific locality or date, Blanchet s.n. (holotype, G). This specimen matches exactly the illustration. The attached label further indicates it

as part of the Moricand's herbarium (donated to G in 1908) and being collected by Blanchet. No date, specific locality, or number are indicated however. Serronia acuminata Moricand, Pl. nouv. Amer. 87. 1840. Unaware at the time of the description of the generic name Ottonia, Moricand initially described the species using Gaudichaud's generic name Serronia. In the same publication Moricand indicated that he changed the species name to O. blanchetii once he knew of Kunth's revision of Ottonia (1839). Thus both names O. blanchetii and S. acuminata appeared in the same publication. Moricand did not use the epithet acuminata for the new name because he realized that the long-acuminate leaves of the species were not diagnostic to it, and were present in many taxa of Ottonia. Ottonia covadensis Miquel var. blanchetii (Moricand) Trelease, Proc. Amer. Philos. Soc. 75: 700. 1936, non Piper blanchetii (Miquel) C. de Candolle.

Piper baptisianum Miquel ex C. de Candolle, Prodr. 16(1):

253. 1869. Type. Brazil. Minas Gerais: São João

Batista, without date, Martius 434 (holotype, M). Ottonia baptisiana (Miquel ex C. de Candolle) Trelease, Proc.

Amer. Philos. Soc. 76: 698. 1935.

Piper machadoense C. de Candolle, Prodr. 16(1): 254. 1869.

Type. Brazil. Minas Gerais, Rio Machado, Caldas, Batista,

1854-1855 (fr), Lindberg s.n. (holotype, BR). Ottonia machadoensis (C. de Candolle) Trelease, Proc. Amer. Philos. Soc. 75: 701. 1935.

Piper corcovadensis (Miquel) C. de Candolle var. sessilifolium C. de Candolle, Prodr. 16(1): 255. 1869. Type. Brazil. Bahia: Without specific locality, 1834 (fr), Blanchet 1094 (holotype, G-DC).

Piper subglaucum C. de Candolle, Linnaea 37: 337. 1872. Type. Brazil. Without specific locality, 28 Feb 1864 (fr), Warming s.n. (holotype, C; isotype, G). Ottonia subglaucum (C. de Candolle) Trelease, Proc. Amer. Philos. Soc. 75: 715. 1935.

Piper frutescens C. de Candolle var. microcarpum C. de Candolle, Linnaea 37: 338. 1872. Type. Brazil. Minas Gerais, Lagoa Santa, 11 Nov 1864 (fr), Warming s.n. (holotype, C). Ottonia frutescens (C. de Candolle) Trelease var. microcarpa (C. de Candolle) Trelease, Proc. Amer. Philos. Soc. 75: 704. 1935.

Ottonia aguadana Trelease, Proc. Amer. Philos. Soc. 75: 696. 1935. Type. Brazil. Minas Gerais: Viçosa, fazenda de Aguada, 5 km beyond Yute, 700 m, 15 Oct 1930 (fl), Mexia 5178 (lectotype, ILL, designated by Jones (1985); isoelectotypes, BM, F, G, GH, NY, PH, S, U, US).

Ottonia lancifolia Trelease, Proc. Amer. Philos. Soc. 75:

1935. Type. Brazil. Minas. Gerais: Viçosa, Agricultural College lands, 700 m, 22 Mar 1930 (fr), Mexia 4499 (lectotype, here designated, NY; isoelectotypes, BM, G, GH, U). Trelease (1935), while using Mexia 4499 as the type collection of O. lancifolia, did include the same collection number as one of several syntypes of O. miguelitensis. Yuncker (1973) cited Mexia 4499 as the type of the aforementioned species. Jones (1985) designated Mexia 4564 as the lectotype of O. miguelitensis but still included Mexia 4499 as a paratype of that species.

Ottonia ituana Trelease, Proc. Amer. Philos. Soc. 75: 706.

1935. Type. Brazil. São Paulo: Itu, 25 Mar 1897 (fr), Russell 199 (holotype, SP).

Ottonia miguelitensis Trelease, Proc. Amer. Philos. Soc.

75: 709. 1935. Type. Brazil. Minas Gerais: Viçosa, rd. to São Miguel, 4 km from São Miguel, 690 m, 4 Apr 1930 (fr), Mexia 4564 (not 4964 fide Yuncker, 1973) (lectotype, US, designated by Jones (1985); isoelectotypes, BM, G, GH, ILL, NY, U).

Ottonia miguelitensis Trelease var. longipes Trelease,

Proc. Amer. Philos. Soc. 75: 710. 1935. Type. Brazil. Minas Gerais: Viçosa, fazenda de Grasiúma, 700 m, 15 May 1930 (fr), Mexia 4702 (lectotype, ILL, designated by Jones (1985); isoelectotypes, F, GH, NY, M, U, US). Mexia 4702

was erroneously cited by Trelease (1935) as a syntype of
var. miguelitensis and as a type of var. longipes.

Ottonia miguelitensis Trelease var. parcepilosa Trelease,
Proc. Amer. Philos. Soc. 75: 710. 1935. Type. Brazil.
Minas Gerais: Rd. Areponga-São Miguel, 850 m, 5 May 1930
(fr), Mexia 4676-b (lectotype, ILL).

Ottonia stationis Trelease, Proc. Amer. Philos. Soc. 75:
714. 1935. Type. Brazil. Bahia: Without specific locality
or date, Blanchet s.n. (holotype, P).

Ottonia usteri Trelease, Proc. Amer. Philos. Soc. 75: 716.
1935. Type. Brazil. São Paulo: São Caetano, 16 Nov 1907,
Usteri s.n. (holotype, SP; isotype, ILL n.v.).

Ottonia gibbimontis Trelease var. acuta Trelease, Proc.
Amer. Philos. Soc. 75: 704. 1935. Type. Brazil. Rio de
Janeiro: Rio de Janeiro, Corcovado, without date, Pohl
5030 (holotype, W).

Ottonia novaesii Trelease, Proc. Amer. Philos. Soc. 75:
711. 1935. Type. Brazil. São Paulo: Campinas, Oct 1900
(fr), Novaes 504 (holotype, US).

Ottonia propinqua Kunth f. longiracemosa Yuncker, Bol.
Inst. Bot. São Paulo 3: 137. 1966. Type. Brazil. São
Paulo: Jardinópolis, Rio Pardo, 20 Nov 1947 (fr), Kuhlmann
1603 (holotype, SP).

Internodes 1.5-3.7 cm long, striate to canaliculate, rarely terete and smooth. Leaves (10.5-)17-19(-20) x (3-)5-8 cm, drying chartaceous or sometimes thin-membranous, grayish above and pale green below, apically short-acute to long-acuminate, venation impressed above, raised beneath, glabrous or with an intramarginal hirtellous region beneath, eglandular. Inflorescences 3.6-11 cm long; peduncle 0.7-0.9 cm long; rachis sparsely pubescent; floral bracts 0.2-0.6 mm distant from the rachis, stamens eglandular.

Distribution. (Fig. 88C). Mostly restricted to the coastal forests of SE Brazil in Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, and São Paulo. Also within gallery forests surrounded by cerrado vegetation in Minas Gerais and Goiás. Occasional and locally common in disturbed vegetation, then sometimes occurring at the edge of the forests along the coasts; 600-1500 m elev. Flowering and fruiting with the typical variety.

Specimens examined: BRAZIL. Bahia: Jacobina, without date Blanchet s.n. (G, LE); Ilhéus, without date, Blanchet s.n. (C, LE); Moritiba, 1843 (fl, fr), Blanchet 3519 (G); Jacobina, 1843 (fr), Blanchet 3742 (G, NY); Uruçuca, km 35 of BR-5, Porto Seguro, 23 Nov 1983 (fr), Callejas et al. 1896, 1897, 1902 (all at CEPEC, HUA, NY, RB, US); fazenda São Jorge, Capoeira, 7 Apr 1970 (fr), dos Santos 637 (CEPEC); BR-101, Rio Mucuruí, 2 Apr

1971 (fr), dos Santos 1540 (CEPEC, RB); BR-5, km 18, Porto Seguro, 6 Sep 1961 (fr), Duarte 6149 (NY, RB); Mpio. São Paulinho, 10 Nov 1942 (fl), Krukoff 12676 (A, NY); Cruz de Cosme, 23 Nov 1831 (fl, fr), Luschnath 154 (LE); rd. to Porto Seguro-Eunápolis, 21 Jan 1972 (fr), Pinheiro 1744 (CEPEC); without specific locality, 1831 (fr), Blanchet 237 (G); no date, Blanchet 238 (NY); 240 (G); 719 (NY); 1839 (fr), Blanchet 1043 (BM, S); Wawra & Maly 146 (LE). Espírito Santo: Mpio. de Itaguaçu, Alto Limoeiro, 11 May 1946 (fr), Brade et al. 18148 (RB); Cachoeira de Itapemirim, Correjo de Ouro, 2 Sep 1948 (fr), Brade 19407 (RB); Serra dos Aymorés, Mpio. Nova Venécia, 15 Nov 1953 (st), Duarte & Gomes 3619 (NY, RB); Serra de Ciuva, 16 Nov 1953 (fr), Duarte 3997 (RB); Mpio. Ibatiba, Corrego Espirado, 4 Dec 1984 (fr), Hatschbach & J. M. Silva 48608 (MB, NY); Mpio. Castello, Fario, 1000-1700 m, 6 Dec 1956 (fr), Pereira 2110 (RB); forests on N slope of Forestal reserve of Sooretama, 2 Aug, 1969 (st), Sucre 5454 (NY, RB). Goiás: Serra do Caiapó, 66 km N of Jataí, 22 Oct 1964 (fr), Prance & N. T. Silva 9567 (NY, RB, U, US). Minas Gerais: Mpio. Diamantina, Giabeira-Merces, 26 Nov 1937 (fl, fr), Mello Barreto 10045 (F, SP); Mpio. Dionísio, State Park of Rio Doce, 23 Sep 1974 (fr), Heringer 16034 (NY), 23 Nov 1976 (fr), Heringer 16045 (F, NY, UB); Serra do Espinhaço, Itabirito, 50 km SE of Belo Horizonte, 1500 m, 10 Feb 1968 (fr), Irwin et al. 19742 (NY, RB, UB); 10

km NE of Francisco Sá, rd to Salinas, 1100 m, 12 Feb 1969 (fr),
Irwin et al. 23154 (NY, UB, US); Mpio. Viçosa, State
 Agricultural College, 23 Feb 1959 (fr), Irwin 2706 (TEX, US);
 SE of the College, 19 Dec 1929 (fr), Mexia 4137 (GH, U, US);
 hill NW of College's building, 690 m, Feb 20 1930 (fl), Mexia
4372-a (GH, NY, US); Barbado watershed, 710 m, 9 Apr 1930 (fr),
Mexia 4587 (S); N slope of Barbado, 710 m, April 22-30 (fr),
Mexia 4619 (ILL, PH, U, US); Viçosa, rd. Areponga-São Miguel,
 850 m, nr. bridge over Casca river, 6 May 1930 (fr), Mexia 4676
 (GH); Agricultural College lands, hill on SE boundary, 690 m,
 11 Oct 1930 (fl), Mexia 5166 (U). Paraná: Guaira, Barra do Rio
 Ivaí, 19 Aug 1982, Hatschbach 45235 (MB, RJ). Rio de Janeiro:
 Santa Maria Magdalena, forests of Derrubadinho, 24 Sep 1977
 (fr), Carauta et al. 2759 (GUA, NY, RB); Reserva Biológica Poço
 das Antas, 25 Oct 1979 (fr), Carauta & Maciel 3288 (FEEMA, RB);
 Petrópolis, rd. to Contorno, 650 m, 11 Feb 1968 (fr), Sucre &
Braga 2364 (RB); Vale Bonsucesso, 3 Oct 1968 (fl), Sucre 4060
 (RB). São Paulo: Indaiatuba, 25 Oct 1935 (fl, fr), do Amaral
s.n. (SP); Mogi-Guaçu, fazenda Campininha, 600 m, 24 Sep 1980
 (fl, fr), Custodio Filho 339 (SP); Botanical Garden, 15 Oct
 1940 (fl, fr), Handro s.n. (SP); Mogi-Guaçu, fazenda
 Campininha, 4 Oct 1977 (fl, fr), Yung et al. 82 (COL, SP).

Local names and uses. Brazil: jaborandi (Bahia), jaborandi
 miúdo (São Paulo), joão barandy (Minas Gerais). In Minas Gerais
 pieces of stem are used for toothache (Mexia 4137)

Piper-corcovadensis is characterized by narrow ovate to elliptic lanceolate leaves which are commonly glabrous throughout (with an intramarginal hirtellous region beneath), and basally acute or obtuse but then never lobulate, and by pedicellate flowers with pedicels 2-3 times longer than the fruits. The two varieties here recognized are separated by the characters given in the key.

Compared with other species in the subgen. Ottonia, P. corcovadensis does not display a distinct autapomorphy by which the species can be separated, rather a combination of characters seems to delimit the taxon. Consequently characters in this taxon are of widespread occurrence in other species of the subgenus. It is of no surprise that the species has been loosely defined by previous authors (Yuncker, 1973). Glabrescent specimens of P. miquelianum as well as immature ones of P. ovatum var. boucheanum were normally determined as P. corcovadensis. Yuncker (1973) placed several names under P. corcovadensis that in fact belonged to P. miquelianum (see P. miquelianum), thus making extremely difficult to determine or segregate both species. This situation has been perpetuated by botanists, uncritical of the taxonomic decisions of Yuncker. That author apparently did not examine all types of those species he placed in the synonymy of P. corcovadensis. Otherwise it is difficult to explain how he lumped P. corcovadensis var.

petiolatum while keeping O. latilimba distinct. The types of both taxa are virtually identical. Yuncker's decision to keep O. latilimba distinct probably relates to the fact that the leaf base in the type is obtuse, not acute, as in most specimens of P. corcovadensis. Examination of P. corcovadensis var. petiolatum, however, shows the character to be quite variable within a single individual. By the same token, O. colliculorum was maintained by Yuncker as distinct despite its type being very similar to that of O. latilimba. Although the type specimen of the latter taxon has shorter racemes and shorter pedicels than P. corcovadensis, they are not yet fully mature and therefore the discontinuities are an artifact.

Many of the synonyms under P. corcovadensis var. blanchettii were previously placed by Yuncker (1973) under O. propinqua which also included many species previously described by Trelease (1935). That author erroneously misinterpreted leaf variation in many species, in which apparently repeated reiteration in the branching nodes resulted in branches with numerous lanceolate leaves, narrower and acute based as compared to leaves in the flowering nodes. Thus based on that leaf variation he segregated O. miguelitensis, O. miguelitensis var. longipes, O. miguelitensis var. parcepilosa (with sparsely pubescent young branches), O. aguadana, and O. clauseni, all taxa from Minas Gerais.

- Fig. 94-97. 94. Habitat of Piper miquelianum var. miquelianum,
(Mpio. Cerro Azul, Paraná, Brazil).
95. Piper ovatum var. boucheanum (Callejas et al.
1954). Close up of infructescence. X 0.10.
96. Piper miquelianum var. hirtellum (Callejas et
al. 1918). Close up of flowering branches.
X 0.8.
97. Piper corcovadensis var. blanchetii (Callejas
et al. 1896). Habit X.0.15.



Yuncker seemed to understand the artifacts on which Trelease based his species, but he himself relied too heavily on leaf texture as well as shape of the base. Thus he kept O. subglauca and O. frutescens var. microcarpa as distinct species, both of which are not different from the types of the species described by Trelease and lumped by Yuncker under O. propinqua (= P. corcovadensis).

The type of O. baptisiana represented a collection with slightly obtuse leaf bases, but which is otherwise difficult to separate from other collections of P. corcovadensis. Yuncker (1973) suggested it as a "frank replacement of C. de Candolle for Ottonia propinqua." Curiously he maintained it as distinct. Guimaraes (1984) correctly lumped O. baptisiana under O. propinqua.

The types of O. machadoensis and O. lancifolia (both from Minas Gerais), O. ituana and O. usterii (from São Paulo), and O. gibbimontis and its variety acuta (from Rio de Janeiro) were segregated on the inflorescence length (as long as or shorter than the leaves), pedicel length (2-3 or 4 times longer than the fruit), and to lesser extent on the leaf color when dry (edged in the type of O. ituana). All these characters fall within the variation found in P. corcovadensis var. blanchettii.

Piper corcovadensis is more closely related to P. ovatum var. boucheanum with which it has in common sparsely pubescent, fimbriate veins on the leaf beneath, similar leaf shape, and

glabrous floral parts. The taxa are difficult to separate in the sterile condition. When fertile they are easily separated by the short-pedicellate, subsessile to sessile flowers of P. ovatum var. boucheanum compared to the long pedicellate flowers of P. corcovadensis.

DOUBTFUL OR EXCLUDED TAXA

Ottonia carpunya (Ruiz & Pavón) Miquel, Syst. piperac. 2:

547. 1844 = Piper carpunya Ruiz & Pavón.

Ottonia lessertiana Miquel, Syst. piperac. 2: 546. 1844 =

Piper lessertianum (Miquel) C. de Candolle.

Ottonia stipulacea (Opiz) Presl, Epimel. bot. 231. 1849 =

Piper stipulaceum Opiz.

Ottonia sphaerocarpa Grisebach, Pl. wright. 176. 1860

(includes Piper sphaerostachyum (Grisebach) C. de

Candolle, Prodr. 16(1): 326. 1869, nom. illeg. Ottonia sphaerostachya Grisebach, Prodr. 16(1): 326. 1869, pro syn. nom. illeg.) = Piper sphaerocarpum (Grisebach)

Wright.

Ottonia punctata Grisebach, Cat. pl. cub. 65. 1866 = Piper

leptostachyum A. C. Rich, La Sagra cub. 11: 228. 1850,

non Piper punctatum Ruiz & Pavón.

Ottonia striaticaulis Trelease, Proc. Amer. Phil. Soc.

75: 715. 1935. Type. Brazil. Without specific locality, Tunela, (Hb. Endlicher), without date or collector, (herbarium ?). Also Locaja, without date, Mikan s.n. (herbarium ?). Trelease's description reads "A shrub, somewhat velvety upwards; twigs sulcate, transversely striate; leaves narrow lanceolate, very gradually pointed from the petiole, 5 mm long; racemes 5 x 20 mm. (? or longer); peduncle 5 mm. long; pedicels about as long as the flowers." I have not been able to locate the type of this doubtful species, and the description is too incomplete to determine its identity. Yuncker (1973) placed this taxon as a dubious synonym of O. anisum (= P. anisum). The velvety pubescence upwards suggests that species or P. ovatum var. boucheanum.

Ottonia thimeana (Trelease) Yuncker, Ann. Missouri Bot.

Gard. 37(1): 71. 1950 = Piper thimeanum Trelease.

Ottonia corei Yuncker, Amer. J. Bot. 43(3): 166. 1956.

Type. Colombia. Chocó: Nr. Quebrada de Girardot, branch of Río Atrato, 1500-2000 m, 2 Mar 1944 (fr), Core 348 (holotype, US) = Piper corei (Yuncker) Callejas, comb. nov. This interesting species has pedicellate flowers which are 3-merous, the first pair of stamens in the frontal plane in the 5-7 position, the fruits 3-sided, angulate, and with a prominent terete style and leaves pinnately nerved but with only two pairs of secondary

veins arising from near the leaf base. The species is one of three taxa found along the Andean slopes in Colombia with sessile flowers (the others include P. peculiare and Trianaeopiper enckeaespicum (a species erroneously placed by Yuncker (1956) in that genus and eventually to be transferred to Piper). In this complex flowers are widely spaced and subtended by floral bracts which are triangular-subpeltate. Additionally this group is characterized by peduncles distinctly longer than the flowering portion. Finally all the taxa are sarmentose-lianescent. Yuncker mentioned that the leaf venation was intermediate between that of subgen. Arctottonia (palmately nerved leaves and pedicellate flowers) and Ottonia (pinnately nerved leaves, brochidodromous). Since the concept of Ottonia was strongly linked to those species with pedicellate flowers in South America, that author erroneously placed the new species under Ottonia. It is obvious from the numerous characters of this taxon and related species, that the pedicellate flowers have arisen independently from those in Ottonia or Arctottonia and are not homologous with it. Consequently the species is here transferred and excluded from subgen. Ottonia.

Ottonia cowanii Yuncker, Brittonia 8: 233. 1957 = Piper cowanii (Yuncker) Yuncker.

Ottonia maguirei Yuncker, Brittonia 8: 233. 1957 = Piper
chumboense Yuncker, Brittonia 14: 189. 1962, non Piper
maguirei Yuncker.

NUMERICAL LIST OF TAXA

1. Piper francovilleianum C. de Candolle
2. P. scutifolium Yuncker
3. P. ubatubensis Callejas
4. P. bartlingianum (Miquel) C. de Candolle
5. P. alatabaccum Trelease & Yuncker
6. P. piscatorum Trelease & Yuncker
7. P. hoffmannseggianum Roemer & Schultes
 - a. var. hoffmannseggianum
 - b. var. latifolium (Kunth) Callejas
8. P. darienense C. de Candolle
9. P. ottonoides Yuncker
10. P. klotzchianum (Kunth) C. de Candolle
11. P. guimaraesianum Callejas
12. P. villosobracteatum Callejas
13. P. brevinodis Callejas
14. P. rizzinii Callejas
15. P. hayneanum C. de Candolle
16. P. eucalyptophyllum C. de Candolle
17. P. piliovarium Yuncker
18. P. ovatum Vahl
 - a. var. ovatum
 - b. var. boucheanum (C. de Candolle) Callejas
19. P. anisum (Sprengel) Angely

20. P. miquelianuma. var. miquelianumb. var. hirtellum C. de Candolle21. P. corcovadensis (Miquel) C. de Candollea. var. corcovadensisb. var. blanchetii (Moriciand) Callejas

LIST OF EXSICCATAE

- Agra, M., 11 (18b)
Alencar, L., 64 (4)
Almeida C. de. et al., 229 (15)
Alston, A. et al., 205 (15)
Altamiro & Walter, 106 (14)
Amaral, E., s.n. (21b)
Amaral, I. L. et al., 788 (5)
Anderson, W., 11684 (15); 11872 (4)
André, E., 3 (6)
Araujo, D. & A. L. Peixoto, 307 (20b); 605 (18b)
Araujo, D. et al., 799 (18b); 1150 (15); 1387 (19)
Armond, N., 156 (19)
Atala, F., 324 (15)
Bamps, P., 5180, 5392 (4)
Barbosa Rodriguez, J. et al., 101 (19)
Barreto, M., 306 (19); 10045, s.n. (21b)
Belém, P. & M. Magalhães, 604 (18b); 713 (10); 741 (18b)
Belém, P. & R. S. Pinheiro, 2664 (18b); 2667 (7b)
Bello, W., 154 (19)
Berg, C., P-18572 (4)
Bertoni D., M., 1374 (20b)
Bery, D. et al., BE-478 (6)
Bescke, s.n. (RJ) (19)
Bisby, F., et al., P-18069, 18080 (4)

- Blanchet, J., 237 (21b); 238 (7a); 240, 719, 1043, 1094 (21b);
 1946 (19); 3232 (7a); 3519, 3742, s.n. (Ilheus) (21b);
 s.n. (19)
- Blanco, C., 530 (18a)
- Boom, B., 4012 (6); 4075, 4571 (4)
- Bourne, 4334 (18a)
- Brade, A. C., 5786 (21b); 14082 (14); 18177, 18717 (20a);
 19407 (21b)
- Brade, A. C. et al., 18148 (21b)
- Braga, P., 1751 (21b)
- Braga, P. & Marilene, 2319 (20a); 2429 (19)
- Broadway, 7165
- Bueno et al., 181 (18b)
- Bunting, G. et al., 7548 (8)
- Burchell, W., 1127 (19); 4408 (7b)
- Burger, Wm., s.n. (8)
- Centro de Pesquisas Forestais (CPF) (Manaus), 6143 (4)
- Callejas, R., 342 (8)
- Callejas, R. et al., 1111, 1113, 1118 (7b); 1554, 1556, 1569
 (18b); 1608, 1608b (15); 1637, 1637b (19); 1678 (15);
 1721 (18b); 1836, 1844, 1868, 1869, 1870, 1871 (20a);
 1874, 1895 (20b); 1896 (21b); 1897, 1899 (20b); 1902
 (21b); 1903, 1918, 1923, 1925, 1957, 1965, 1969 (20b);
 2023, 2025 (7b); 2034, 2036 2038 (20a); 2039 (7b); 2123,
 2126, 2134 (2); 2142, 2144 (16)

- Campbell, G. D. et al., P-21823 (5)
- Capech, s.n. (1953), (19)
- Carabot, C. A., s.n. (8)
- Carauta, P. J., 63, 161, 228, 1746 (19); 1808 (11); 2394 (7b)
- Carauta, P. J. & J. Kirkbride, 2439 (19)
- Carauta, P. J. & N. C. Maciel, 3258 (21b)
- Carauta, P. J. et al., 2394 (17); 2759 (21b)
- Carvalho, A. M., 2088 (7a)
- Carvalho, A. M. & R. Callejas, 2020 (19); 2021, 2047 (7b);
2048 (18b)
- Carvalho, A. M. & V. Hollowell, 1144 (18b)
- Carvalho, A. M. & T. Plowman, 1448 (7a)
- Carvalho, A. M. et al. 1894 (15)
- Cassareto, 1701 (7b)
- Castellanos, A., 26499 (15)
- Cavalcante, P. B., 2323 (4)
- Chávez, G., s.n. (6)
- Chiea, S. & A. C. Chiea, 146 (20a)
- Cid, C. A., 3961, 3964 (4)
- Cid, C. A. & J. Lima, 3794 (4)
- Cid, C. A. & C. Mota, 1125 (4)
- Cid, C. A. & J. Ramos, 1058, 1164 (4)
- Cid, C. A. et al. 418, 866 (4)
- Claussen, M., s.n. (1840) (16); s.n. (Nov 1842) (19); s.n.
(Apr-Aug) (21b)

- Claussen, M. & M. Weddell, s.n. (19)
- Collares, J., 39 (21a)
- Corrêa, J., 21, 105 (20a)
- Costa, E. et al., 82 (18b)
- Cowan, R. S., 38402, 38654, 38697 (4)
- Croat, T. B., 5752, 12210 (8)
- Curran, H., A-2, s.n. (6)
- Daly, D. & R. Callejas, 1200 (4); 1377, 1540 (6)
- Daly, D. et al., 2030 (6)
- Daniels, G. A. & P. Yonker, 778 (5)
- Davidse, G., 10455 (20a)
- Davidse, G. et al., 17121 (4)
- Davidson, C. & G. Martinelli, 10586 (4)
- Davis, H. P. et al., D-59786 (3)
- Dawe, T. W., 886 (8)
- Decuassos, J., s.n. (Soretama) (18b)
- Dombrowski, L., 7048 (20a)
- dos Santos, E., 82, 85 (7a)
- dos Santos, T., s.n. (Cumbaça) (16); s.n. (16)
- Duarte, A. P., 3997 (21b); 4012 (12); 6149 (21b)
- Duke, J., 12278 (8)
- Dusén, P., 8676, 8852, 9803, 10059 (20a); 11182 (20b); 13778,
14036, 14091 (20a); 14506 (20b); 15326 (20a); 17208, s.n.

(30 Oct 1914), s.n. (9 Apr 1915), s.n. (16 Apr 1917)

(20b)

Eddwall, G., s.n. (Rio Fñio) (20b)

Egler, A. W. & H. S. Irwin, 46422 (5); 46494 (4)

Emygdio, 80 (2); 504 (15)

Encarnación, F., 26106 (4)

Eriger, s.n. (18b)

Eugenio, J., 468 (18b)

Eupunino, A., 200, 288 (19)

Fabrega, C., s.n. (8)

Faria, G., 32 (20a)

Fendler, A., 669 (18a)

Ferreira, F. V. & Brolarijo, 195 (19)

Ferreira, F. V. et al., 239 (16); 436 (15)

Fiebrig, K., 5625 (20b)

Filho, A., 339 (21b)

Florschütz, J. & P. A. Florschütz, s.n. (4)

Foldats, E., 116-A (4)

Folson, J. P., 7829 (8)

Forero, E. & B. L. Wrigley, 7132 (6)

Foster, R., 1099, 1768 (8)

Foster, R. & H. Kennedy, 1248 (8)

Frame, D. et al., 147 (9)

Fróes, L., 12676/41 (21b)

Fróes, R., 2021 (6); 3952 (9); 20043 (18b)

- García-Barriga, H., 14681 (4)
- García-Barriga, H. & G. Lozano, 18318 (8)
- Gardner, G., 119 (7b); 5186 (19)
- Gaudichaud, B. C., 83, 1100 (in part at G) (16) (21a), 1101 (21a); 1102, 1102 bis, 1102 ter (19); s.n. (7b)
- Gehrt, A., s.n. (20a)
- Gentry, A. & L. Emmons, 39584 (4)
- Gentry, A. et al., 10949 (4); 16753 (8)
- Glaziou, A., 1163 (19); 4202 (7b); 6001 (19); 6604 (15); 6805 (16); 8074 (15); 15436 (21b); 19865 (21a)
- Goés, G. & D. Constantino, 1014 (19)
- Grajam, M., 2839, 2868 (8)
- Granville, J., 130, 339, 1620, 1669, B-4820 (4); 6489 (5)
- Guillemin, A., 728 (16); s.n. (Corcovado, 1839) (19)
- Hage, J. L., 1552 (18b)
- Hage, J. L. & H. S. Brito, 1478 (18b)
- Hammar, A., 4551 (20a)
- Hammel, B., 8687, 11722, 12501, 12156 (8)
- Handro, O., s.n. (Oct 1940) (20a); s.n. (15 Oct 1940) (21b)
- Hans, s.n. (18 Oct 1936) (15)
- Harley, M. R. et al., 17833 (15)
- Hassler, E., 5103, 5387, 9475 (20b)
- Hatschbach, G., 2018 (20a); 9291 (20b); 24911, 30538 (20a); 41971 (20b); 43607 (20b); 43981 (20b); 44331 (20a); 45235 (21b); 46152 (20b)

- Hatschbach, G. & J. Gomes, 3619 (21b)
- Hatschbach, G. & O. Guimarães, 46936 (18b)
- Hatschbach, G. & R. Kummrow, 35235 (20a)
- Hatschbach, G. & E. Pereira, 11470 (7b)
- Haught, O., 4587 (8)
- Heringer, P. E., 409, 16010 (19); 16025 (10); 16034, 16045
(21b)
- Hoehne, W., s.n. (Oct 1914) (21a); s.n. (Butantán, 1918)
(20a); s.n. (11 Oct 1929) (20b); s.n. (Palhoça, 1929),
s.n. (São Paulo, 2 Oct 1936) (20a); s.n. (2)
- Houllet, s.n. (Rio de Janeiro) (16)
- Huber, J., 240 (18b)
- Huber, O. & M. Colchester, 8383 (1)
- Ichaso, L. C. 98 (7b)
- Irwin, H. S., 2706 (21b)
- Irwin, H. S. et al., 10179, 13069 (18b); 19742 (19); 23154
(21b); 34353 (18b); 47148, 47234, 47568, 47625, 54455,
54456, 54537, 55868, 57664, 57708 (4); 54549 (5)
- Jangoux, J. & R. P. Bahia, 238-A (6)
- Joussau, G., 524-a (20)
- Jouvins, P., 509, 518 (15)
- Jung, S. et al., 170 (21b)
- Kirkbride, J. & N. Bristan, 1555 (8)

- Kirkenzaft et al., 4974 (18b)
- Klein, R., 174 (20b); 1122, 1255 (20a); 1651 (20b)
- Krukoff, B. A., 5831 (9); 7219, 7546 (4); 12676 (21b)
- Kuhlmann, M., 805, 1603, s.n. (21b); 1550 (20b); 3959, s.n. (6 Aug 1934), s.n. (4 Nov 1958) (20a)
- Kulenkamp, s.n. (Rio de Janeiro) (19)
- Kummrow, R., 2457 (20a)
- Kummrow, R. & P. I. Oliveira, 2329 (20a)
- Langsdorff, G., 83, s.n. (Corcovado) (19); s.n. (Jan 1823), s.n. (Oct 1823) (15)
- Lanjow, J. & J. C. Lindeman, 1271, 1763 (4)
- Leal, C. & O. A. da Silva, 28 (18b)
- Leite, J., 4159 (19)
- Lent, R. W., 2529 (8)
- Lewiz, A. & T. Brito, 3 (16)
- Liesner, R., 15672 (1)
- Liesner, R. & A. González, 11444 (6)
- Lima, A., 48-131 (19)
- Lindeman, C. J. & J. de Haas, 781, 3847, 5478 (20b)
- Lindeman, C. J. et al., 568, s.n. (4)
- Lindserg, s.n. (1854-1855, Batista) (21b)
- Lleras, E. et al., P-16650 (4)
- Löfgren, A., 136 (18b); 534 (21b); 1386 (18b); 1425 (21b); 1552 (20b)

- Löfgren, A. & G. Eddwall, 1625, 2814 (20a)
- Luederwaldt, s.n. (Ipiranga, 1912) (20a)
- Luetzelburg, Ph., 160, 12532 (15)
- Lund, P., s.n. (Rio de Janeiro), s.n. (1825-1828) (16)
- Luschnath, B., 153 (10); 154 (21b); s.n. (19); s.n.
(Corcovado, 1835) (21a); s.n. (Bahia, 1835-37), s.n. (Cruz
de Cosme) (10); s.n. (Rio de Janeiro), s.n. (1835) (19)
- Lütz, A., 205 (15)
- Maas, P. & P. J. Carauta, 3119 (16)
- Maas, P. & G. Martinelli, 3409 (19)
- Maguire, B., 40817-a (4)
- Maguire, B. et al., 53949, 54186, 54356, 61399 (4)
- Makino, H., 92 (20a)
- Mantone, L. et al., 294 (19)
- Marins, F., 9279 (21b)
- Marquete, M. et al., (158) (19)
- Martinelli, G., 782 (15); 7069 (4); 7106 (5)
- Martinelli, G. et al., 1634 (19); 2409 (18b); 2071 (20b); 4131
(19)
- Martius, K., 218 (19); 434 (21b); 1210 (19); 1212 (7b); s.n.
(Rio de Janeiro) (19); s.n. (Maranhão) (18b); s.n. (Rio
de Janeiro), s.n. (Minas Gerais) (15); s.n. (7b); s.n.
(Corcovado) (21a); s.n. (20a)
- Mattos, J., 12528 (20a)
- Mattos, L. et al., 15676 (15)

- Mattos-Silva, L. & H. Britto, 663 (7b)
- Mattos-Silva, L. et al., 1812 (7a)
- Melo, M. et al., 243 (20a)
- Mendes, O., s.n. (21b)
- Mendonça, 669 (15)
- Mertens, 1749 (7b)
- Mexia, Y., 4137, 4372-a, 4499, 4564, 4564-a, 4587 (p.p)
4619, 4676, 4702 (21b); 5160 (19); 5166, 5178 (21b); 5332
(10); 6551 (8)
- Miers, J., 3075 (7b)
- Mikan, J., s.n. (Corcovado) (19)
- Monteiro, S., 2646 (19)
- Moraes, J. C., 985 (18b)
- Mori, S. A. & A. Bolten, 8376, 8653 (4)
- Mori, S. A. & J. Granville, 8787 (4)
- Mori, S. A. et al., 8376, 9083, 9166 (4)
- Mosen, C., 2588 (15)
- Neuwied, F., s.n. (21a)
- Nogueira, E. et al., 102 (18b)
- Novaes, 504 (21b)
- Occhioni, P., 696 (7b); 1184, s.n. (Belo Horizonte) (19)
- Oldeman, R., FG-198, 2200, 2973 (4)
- Oldeman, R. & C. Sastre, 86 (4)
- Oliveira, M. C., 6 (16)
- Oliveira, J., 249 (21b)

- Pabst, G., 4551 (15)
- Parker, s.n. (4)
- Peixoto, A. I et al., 438 (11).
- Pennell, F. W., 4603 (8)
- Pereira, E., 702 (19); 734 (7b); 2110 (21b); 2328 (16); 5654
(7b); 8765 (20b)
- Pereira, 702 (19)
- Permar, s.n. (8)
- Peters, s.n. (19)
- Pickel, B., 287 (20b); 2789 (19); 4125 (15); 4038 (7a), 5355
(20a); 5443 (20a)
- Pinheiro, R. S., 1146, 1220 (15); 1241 (7b); 1535 (18b); 1744
(21b); 2050 (15)
- Pinheiro, R. S. & T. S. Santos, 2270 (18b)
- Pinto, P. et al., 1477 (6)
- Pirani, J. & O. Yano, 717 (14)
- Pires, J. M., 526 (1); 1194 (9)
- Pires, J. M. & P. B. Cavalcante, 52256 (4); 52258 (5)
- Pires, J. M. et al., 51281 (4)
- Pittier, H., 16321, 4288 (8)
- Plowman, T. et al., 12453, 12524, 12640 (4); 12641 (5); 13154
(6)
- Pohl, J., 420 (16); 4776 (21a); 5030 (21b); 5033 (7b); s.n.
(1839) (19); s.n. (16); s.n. (21a); s.n. (7b); s.n. (19)

- Poiteau, M., s.n. (4)
- Poole, J. M., 1660 (4)
- Porto, C., s.n. (19)
- Prance, G. T. et al., 1981 (9); 2431, 3215, 3462, 3909 (4);
5027 (5); 6150 (6); 8205, 8847 (4); 9732, 10105,
10779 (1); 13885 (4); 13932, 16387 (6); 24322, 25354,
25396, 25830, 26408 (4)
- Prance, G. T. & J. F. Ramos, 23619 (4)
- Prance, G. T. & N. T. Silva, 59567 (21b)
- Pulle, E., 1172 (5)
- Purdie, W., s.n. (Trinidad) (18a)
- Raimundo, S., 1146 (18b)
- Ramvalho, R. & G. Rodriguez, 1298 (21b); 1352 (19)
- Rambo, 561, 37948 (20b)
- Reitz, R., C-179, 537 (20b); C-1944 (20a)
- Reitz, R. & R. Klein, 2081, 4019, 9009 (20a); 9412 (20b)
- Ribeiro, R., 228, 377 (15)
- Ribeiro, R. & R. Callejas, 643 (15)
- Riedel, L., 16 (19); 41, 43 (15); 79 (7a); 293 (7b); 540 (15);
s.n. (Rio de Janeiro)
- Riedel, L. & B. Langsdorff, 102 (7b)
- Rizzini, C. T., 1105 (5)
- Robert, A., s.n. (7b)
- Rodriguez, A. I. et al., 130 (15)

- Rosa, N. & J. M. Pires, 3690 (20a)
- Rosa, N. et al., 3007 (4)
- Rusby, H. H., 2182 (4)
- Russell, A., 199 (21b)
- Ryan, s.n. (Trinidad) (18a)
- Saint-Hilaire, A., s.n. 27 (7b); 29 (21a)
- Saldanha, s.n. (Fazenda Sabral) (19)
- Sampaio, A. J., 2451, 3198 (19)
- Sandwith, 1191 (5)
- Santos, T. S., 637, 1183 (15); 1540 (21b); 1656, 1817 (15)
- Santos, T. S. & L. A. Silva, 3715 (18b)
- Sastre, C. et al., 3841 (4)
- Satto D. & F. G. Silva, s.n. (15)
- Satto et al., 3123, s.n. (4 Oct 1940) (19)
- Scheinvar, 105 (7b)
- Schwacke, A., 5038 (20a); 5157, s.n. (Niteroi) (21a)
- Schwacke, C., 1602, 3349, 11326 (19)
- Scouler, s.n. (Sebastianopolis) (19)
- Seeman, B., 1218 (8)
- Sellow, F., 258, s.n. (1814-1818), s.n. (19); s.n. (18b); s.n.
(Rio de Janeiro)
- Sendulsky, T., 807 (20a); 857 (21b)
- Sieber, s.n. (7a)
- Silva, M. G. & C. Rosario, 3578, 3987 (4)
- Silva, S. J., 393 (20a)

- Silva, N. T., 70 (9); 1485 (5); 1488 (4); 1547, 1572 (5);
 1604, 1605, 1723 (4); 1974 (5)
- Smith, H. H., 2666 (8)
- Smith, L. B., 5789 (20a)
- Smith, L. B. & R. Klein, 7279 (20b)
- Smith, A. C., 2707, 2771, 2826, 2955 (4)
- Smith, B. J. & A. Macedo, 4751, 4830 (18b)
- Soejarto, D. & E. Bordas, 5692 (20b)
- Solomon, J. C., 7806 (4)
- Solomon, J. C. et al., 6793 (20b)
- Spruce, R., 5 (4)
- Stahl, F., 67 (4)
- Standley, P., 31375 (8)
- Steward, Wm. C. et al., 31, P-20426 (4)
- Steyermack, J., 57953 (1); 60986 (18a); 90413 (5); 106052 (1)
- Steyermack, J. et al., 103028 (4); 126156 (1)
- Strudwick, J. et al., 3236, 3650, 4197 (6)
- Sucre, D., 1861 (21a); 2364 (20a); 3673 (15); 4060 (21b); 4716
 (16); 5454 (21b); 5676 (18b); 6038 (7b); 6356 (21a); 6563
 (7b); 7091 (16); 7710 (15); 7770 (19); 7803 (7b); 7818
 (19); 7821 (15); 7838 (21a); 8462 (18b); 9596 (21a); 9618
 (16)
- Sucre, D. & G. Barroso, 6340 (7b)
- Sucre, D. & P. Braga, 1227 (7b); 2364 (21b); 2371 (20b); 4448

- (7b); 4501 (20b); 4544 (19)
- Sucre, D. & D. Dun, s.n. (7b)
- Sucre, D. & C. L. Ichaso, 6576 (19)
- Sucre, D. & J. da Silva, 9560 (21a)
- Sucre, D. et al., 4273 (7b); 4408 (19); 6276, 6311 (7b); 6356
(21a); 6365 (10); 6367 (7b); 6370, 6409 (19); 8849 (19);
8856 (7b); 9517 (15); 10133 (13)
- Tamayo, F., 2154 (18a); 4387 (6)
- Tate, G., 370 (4)
- Tavares, S., 529 (15)
- Teixeira et al., 127 (4); 427 (6); 946, 1017 (4)
- Thomas, W. et al., 3007 (1)
- U.S. Pac. Expl., s.n. (17); s.n. (Rio de Janeiro) (19)
- Ulle, E., 4597 (19)
- Usteri, s.n. (Santa Catarina) (21b)
- Utley, J. & K. Utley, 3967 (8)
- Vasquez et al., 2157 (4)
- Vauthier, 547 (19)
- Velloso, H. P., 1056 (19)
- Vidal, s.n. (19)
- Vitória, H., s.n. (15)
- Warming, J., s.n. (19); s.n. (28 Feb 1864), s.n. (11 Nov 1864)
(21b); s.n. (14 Oct 1863), s.n. (2 Jan 1864), s.n. (28
Oct 1864) (18b)

- Wawra, H. & F. Maly, 146 (21b)
- Weddell, M., s.n. (1843) (19)
- Wessels Böer, J. G., 317, 1193 (4)
- Widgren, s.n. (S), (19)
- Williams, Ll., 11258, 11685, 11800 (6)
- Woodson, R. & R. Schery, 852 (8)
- Wurdack, J. & L. S. Adderley, 43537 (1)
- Xavier, M., s.n. (Papuda) (18b)

INDEX OF LOCAL NAMES

achikaira

alcotán

anestesia

anisillo

balauita

borandi

capoty

cataiguacie

chankira

cordoncillo

cutia

dormidera

duerme boca

guatini

huatini

ishi-raquia

ishiraki-ra

jaborandi

jaborandi de mata virgen

jaborandi de minas

jaborandi do mato

jaborandi miudo

jaborandinho

jaborandy

jamborandi

jambú

jambú-assú

jambú de mata

jambú de muela

jamburana

janguarandin

joão baradi

joão barandin

joão barandinho

joão borandinho

joão-barandi

joão-barandinho

joao-borandim

joao-borandin

joao-borandy

jondi

malimbe-toko

man-aneiseiwiwirie

manchauia

nhadú rateiro

nhambi

nhandú

nibosa

paarimahasiko

patsi

pete

pimenta longa

raíz de candela

raíz de candil

raíz de mato

raíz de muela

sirankira

timbo nhandú

tremedor

warakabacoura

warakabacourrou

washi

CLADISTIC ANALYSIS OF THE GENUS PIPER

The present cladistic analysis for the genus Piper is performed using the genus Peperomia and the Saururaceae as outgroups. Monophyly in the three groups has been rarely refuted. Only the sister group of the Piperales seems to be the major point of disagreement. Thus, some of the synapomorphies uniting Saururaceae with Piper and Peperomia may represent symplesiomorphies at a lower level. Synapomorphies for the Piperales include the zygomorphic flowers, exotegmic seeds with a well developed endotegmen, orthotropous ovules, single prophyll, seeds with abundant perisperm, little differentiated embryos, crystalloid proteins in the sieve cells, etc. Several of those character states may represent synapomorphies at a lower level with the Nymphaeaceae (e.g. crystalloid proteins in sieve cells and seeds with abundant perisperm) as suggested by Dahlgren (1984), or with Chloranthaceae (e.g. orthotropous ovules) as in the current system of classification of Cronquist (1982) (Fig. 98).

Regardless of the sister group considered for Piperales, the monophyly of the group still remains the same. Within the Piperales, Piper and Peperomia are united by the presence of single ovules, presence of papillate hairs, and the embryo type (e.g. the Piperad type, in which the first division in the

zygote occurs in a longitudinal plane rather than in a transversel one). Peperomia may represent the most derived group in the order, with synapomorphies of a rather restricted distribution in other flowering plants. These include the single integument, the embryo sac (with 16 nuclei), secondarily inaperturate pollen grains, and single carpel. Synapomorphies for Piper include the presence of vascular cambium (probably of secondary origin (see Carlquist, 1985)), presence of isobutyramides alkaloid-like compounds, stem endodermis, and presence of mucilage canals.

Aside from the cladistic analysis performed by Bornstein (1986, pers. comm.) for subgen. Arctottonia, no cladistic analysis for the entire genus Piper has yet been elaborated. The present one is hand generated, and it is likely that more parsimonious cladograms may be found. The resulting cladogram for Piper (see Fig. 99) is only a hypothesis, one to be tested, and which in the context of the present treatment serves only for generating the possible sister group for subgen. Ottonia.

Information for the cladistic analysis of Piper is based on the collecting of neotropical pipers, especially in Brazil, Colombia, and to less extent Paraguay. Also on a large number of herbarium specimens, collected in Perú, Bolivia, and Ecuador from the herbaria at NY, MO, F, US, and AAU.

Recent systematic revisions for the Piperaceae have also

been used, especially for little known taxa or species complices. I have relied heavily on the treatment of Burger (1981) for Costa Rica, and Steyermark (1984) for Venezuela . For the Old World Tropics, holdings of the Philippines collections in NY have been a very important resources, especially since this region may hold more Piperaceae than any other one in SE Asia. Additionally the excellent treatment of Quisumbing (1930) for the Philippines, Liu (1975) for Taiwan, and Chen (1982) for continental China have also been used as well. Representatives of Piper in Africa and Java have been studied to lessser extent and based on collections from NY and AAU.

I'm sympathetic with the reader if he/she is not optimistic regarding the attempts to provide a cladistic analysis for the genus Piper. There are nearly 1000 species in the genus, many of them surrounded by numerous nomenclatural problems, others poorly described, sometimes known only from leaf fragments (e.g. Trelease & Yuncker treatment for NE South America, 1950). Additionally several authors (de Candolle, 1869, 1923; Yuncker, 1973) had doubts on the reliability of a system of classification in Piper. Especially since there is widespread variation in most characters, floral or vegetative ones. Surprisingly, and after years of studying Piper in the field as well in the herbarium, one finally begins to recognize natural groupings in the genus Piper, many of which were previously proposed by Kunth (1839) and Miquel (1843-1844), and

later (but not recognized at any rank) by C. de Candolle (1923); Trelease (1936); Trelease & Yuncker (1950) and Yuncker (1973).

The present analysis does not claim that every terminal group is monophyletic, especially in view of the lack of representative collections for many species. However I believe that the portions of the cladogram for the Old World tropics and the basal groups for the Neotropics, do indeed conform to distinct natural units. The terminal more diverse groups in the Neotropics such as subgen. Steffensia will require much more study and better collecting. Solving the cladistic structure of this group will be a major step towards a infrageneric classification in the genus Piper.

Character-states

Characters are polarized using Peperomia and Saururaceae as outgroups. Many characters may represent transformation series, but they are coded in binary form. The derived condition preceeds the primitive one. A brief discussion on the distribution of several characters is given. The data matrix for Piper, and the resulting cladogram are presented in Table VI and Fig. 99 respectively.

1. Plants sarmentose, creeping on other plants by nodal roots=1

Shrubs, erect, sometimes caespitose or single stemmed, some branches may become lianescent in habit, but then nodal roots are absent=0

Sarmentose or vine-like plants are the widespread condition in the Old World tropics. Some exceptions exist however, as in subgen. Macropiper, and some members of subgen. Chavica. The habit is absent in the outgroups, and I believe is derived within Piper. In the Neotropics the shrubby condition is dominant in most groups with vines occurring only in subgen. Sarcorrhachis, the Piper politii group, subgen. Nematanthera, and one species in subgen. Isophyllon (i.e. Piper pseudo-acreanum).

2. Flowers unisexual=1

Flowers bisexual=0

Unisexual flowers are the dominant condition in the Paleotropics. Bisexual flowers on the other hand are rare in that region, but the only one in the Neotropics. Reports on the presence of unisexual flowers in the Neotropics are based on a misinterpretation of the floral structure of subgen. Nematanthera (C. de Candolle, 1923; Yuncker, 1973). In that group the single staminate flowers loose the stamen before the fruit is fully mature. At that stage only the base of the filament remains attached to the fruit wall. It was in this stage, that many specimens

in subgen. Nematanthera were determined as unisexual or sometimes as unisexual and/or bisexual. In the Paleotropics, the unisexual condition, in some species, is often found in taxa which may also have bisexual flowers.

3. Stamens arising from the upper distal portion of the floral bract=1

Stamens arising from the rachis of the inflorescence=0

The derived condition is present in subgen. Muldera. It resembles that observed in the flowers of Saururus cernuus. In this species the flower is attached along the mid-portion of the floral bract. Such condition is otherwise strongly correlated with common primordia (Tucker, 1983). Flowers are bisexual in Saururus but unisexual in Muldera.

4. Flower and floral bract arising from single and distinct primordia=1

Flowers arising from common primordia=0

5. Floral bracts adnate to the rachis=1

Floral bracts free from the rachis=0

Adnate floral bracts occur only in subgen. Piper where they are normally oblong and free at the apex.

6. Floral bract distal portion orbicular (in it the pedicel of the bract is attached to the center of the distal portion, i.e. peltiforme bracts)=1

Floral bracts distal portion triangular or quadrate (in it the pedicel is attached near the margin of the distal

portion, i.e. subpeltate bracts)=0

The plesiomorphic condition is found in Saururaceae and in most Neotropical pipers. Peltiforme bracts are restricted to most species in the Paleotropics and to the genus Peperomia. Where it occurs, it is strongly correlated with low number of stamens (2-3), lack of banded patterns in the inflorescence and anthers with upward dehiscence.

7. Fruits becoming pedicellate=1

Maturing fruits remaining sessile after ovary fertilization=0

The derived condition is present only in the Paleotropics, in both subgen. Cubeba and subgen. Piper. The condition is not to be confused with pedicellate flowers. In this last condition a pedicel develops before fertilization has occurred. In subgen. Cubeba the pedicellate fruits are correlated with sessile peltiforme bracts; in subgen. Piper with sessile adnate floral bracts.

8. Bract pedicel pubescent=1

Bract pedicel glabrous=0

9. Leaves with camptodromous venation.=1

Leaves with campylodromous venation=0

Camptodromous venation (pinnately nerved) is likely to be

derived in Piper. It has evolved independently in the Paleotropics and Neotropics. In the first region, camp-todromous leaves are present in subgen. Peltandron and few isolated species in subgen. Cubeba (P. nigrescens). Campylodromous venation is widesprad in Saururaceae (except in Anemopsis) and Peperomia. In the first group, and as compared with Piper and Peperomia, leaves lack a well developed fimbriate vein.

10. Connective distally covering the anthers=1

Connective protruding above the anthers but not covering them=0

The derived condition is restricted to subgen.

Peltandron. Only one species in this group, P. paucirameum, seems to lack covering connective.

11. Inflorescence axillar=1

Inflorescence terminal=0

Inflorescences in Piper are always terminal. The term axillar refers then to a single inflorescence subtended by a prophyll, not a well developed leaf, and therefore appear as being axillar. Reduction of number of parts in each module, or often reduction of modules in a single branch is commonly described. Where it occurs a species is described as having axillar inflorescences. A more restricted use, as well as better definition, should apply.

12. Flowers pedicellate=1

Flowers sessile=0

(See cladistic analysis of subgen. Ottonia).

13. Connective forming a laminar projection above the anthers=1

Connective not expanded as to form a lamina=0

The derived condition is known only from subgen.

Zippelia. The stamens resemble very much laminar stamens seen in some families in the Ranales. Lack of studies on flower development in this group (Piper) precludes any assessment on the level of homology of such a character.

14. Fruits glochidiate=1

Fruit outer wall smooth=0

Glochidiate fruits are unique to subgen. Zippelia, and not found elsewhere in the Magnoliidae. A similar but yet not homologous condition is found in some fruits in Peperomia. In this group the outer walls are covered by thin-translucent trichomes.

15. Leaves with two callosities at the base=1

Leaves without callosities at the base=0

Callosities at the leaf base are restricted to subgen. Enckea, Ottonia, Callianira, and Arctotonia. The callosities or thickenings result from folding of the leaf margins at the base.

16. Isobutyl amides of the piperovatine type=1

Isobutyl amides of the piperlonguminine type=0

(See chapter on Phytochemistry and Physiological action).

17. Leaf venation acrodromous basal=1

Leaf venation acrodromous suprabasal=0

18. Flowers 3-carpellate=1

Flowers 4-carpellate=0

(See discussion on flower development in subgen.

Ottonia).

19. Distal portion of floral bract with the anterior extreme lobulate=1

Distal portion of floral bract with the anterior portion entire=0

The outline of the floral bract distal portion in the anterior extreme results from the contact of the floral bract with the covering axillary flowers. Different outlines in this portion of the bract are prominent in the Neotropics, but absent in the Paleotropics.

20. Floral bracts saccate-galeate=1

Floral bracts without a galeate portion in the posterior extreme of the distal portion=0

Saccate-galeate bracts are restricted to subgen.

Ottonia.

21. First pair of stamen primordia in the frontal plane arising in a 3-9 position=1

First pair of stamen primordia in the frontal plane arising in a 5-7 position=0

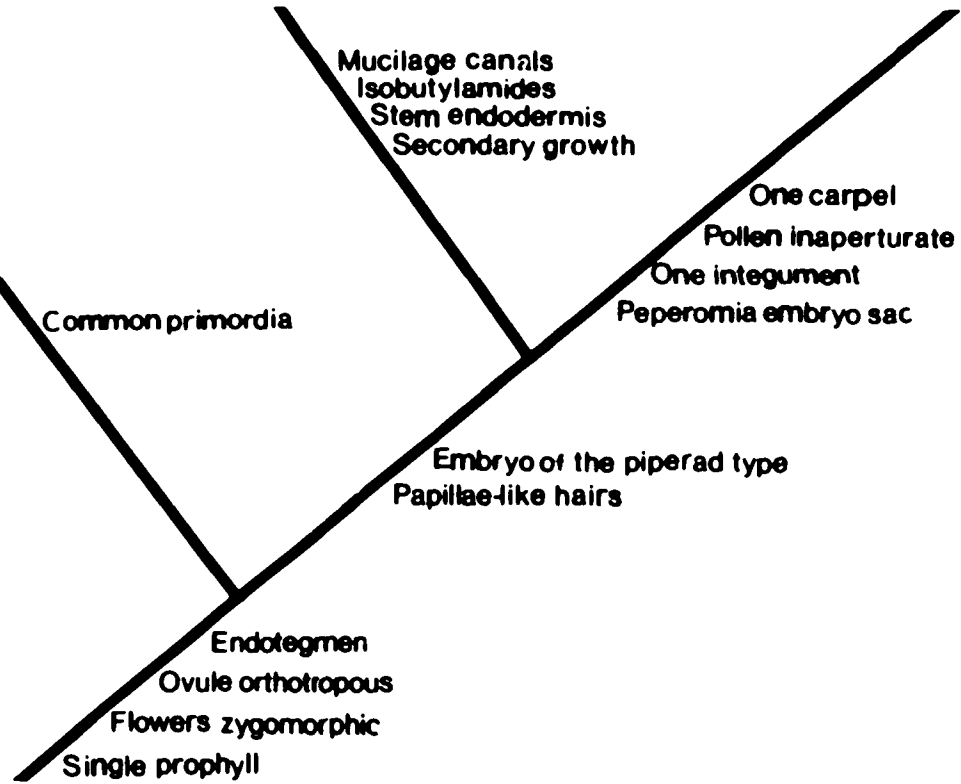
(See Flower Development in subgen. Ottonia).

Fig. 98. Cladogram for the Piperales.

SAURURACEAE

PIPER

PEPEROMIA



22. Carpels alternate with stamens=1

Carpels opposite to stamens=0

(See Flower development in subgen. Ottonia).

23. Seeds 4-ribbed and sulcate=1

Seeds angulate, not ribbed or sulcate=0

Seed shape outline is strongly correlated with number of carpels. Thus 4-ribbed seeds occur only in species with 4-carpellate flowers as in subgen. Enckea, Acrtotonia and Ottonia. Sulcate seeds, however, occur only in Ottonia.

24. Flowers in distinct banded patterns in the inflorescence=1

Flowers not forming banded patterns in the inflorescence=0

The derived condition is correlated with the outline of the distal portion in the floral bract, number of flower parts, and vestiture of floral bracts. Banded patterns are restricted to Piper in the Neotropics.

25. Fruits partially immersed (concrecent?) in the rachis=1

Fruits free from the rachis=0

Immersed fruits are present in the Saururaceae in a single species (i.e. Anemopsis californica); it is absent in Peperomia. It occurs elsewhere in many species of Piper in the Paleotropics as in most taxa of subgen. Coccobryon, several taxa in subgen. Macropiper (e.g. P. excelsum), and subgen. Chavica (e.g. P. betle and in P. firmolimbium, in this latter taxon fruits are fully immersed in the rachis). In the Neotropics the condition is seen in sub-

gen. Sarcorhachis and subgen. Isophyllon (P. glabrescens-group). It occurs also in an isolated taxon in subgen. Enckea (i.e. P. nudilimbum).

26. Mucilage canals forming discrete ring in the cortex=1
Mucilage canals not forming discrete rings in the cortex, absent from it or occurring scattered but without forming distinct patterns=0
27. Prophyll apex truncate=1
Prophyll apex acuminate=0
28. Shrubs lianescent=1
Shrubs not lianescent=0.
29. Anthers with dehiscence occurring in a horizontal plane=1
Anthers with dehiscence occurring in a vertical plane=0
Upwards dehiscence (i.e. in the horizontal plane) results from the overgrowth of the connective at the base of the anthers which are then pushed up changing the plane of dehiscence.
30. Inflorescence apex with a sterile terete rachis portion=1
Inflorescence apex without sterile terete rachis portion=0
The derived condition is probably related to the cessation on the activity of the inflorescence meristem.
31. Leaf base geniculate=1
Leaf base acute or lobulate, never geniculate=0
32. Floral bracts in the distal portion densely hirtellous throughout=1

Floral bracts in the distal portion locally pubescent
(along the margins or the posterior extreme of the
distal portion)=0

The former condition occurs only in subgen. Macrostachys.

33. Lobulate bracts with a central deltoid portion=1

Lobulate bracts continuous between the lobes=0

34. Flowers 1-staminate=1

Flowers with 2 or more stamens=0

One staminate flowers occur in subgen. Nematanthera and
a single species (P. korsthalsi) in subgen. Chavica.

35. Inflorescence obpyramidal=1

Inflorescence terete=0

36. Lobulate floral bracts marginally ciliate=1

Lobulate floral bracts marginally glabrous=0

Marginally ciliate bracts are restricted to Neotropical
Piper. Sparsely pilose bracts occur in few species in the
Palaotropics. They are otherwise absent from Peperomia and
Saururaceae.

37. Prophylls as long as the internodes=1

Prophylls shorter than the internodes=0

38. Prophylls more than 3 cm broad=1

Prophylls less than 1 cm broad=0

39. Leaves with raised oil cells=1

Leaves with impressed oil cells=0

The derived condition is widespread in the family as it

occurs in isolated taxa in several subgenera. It is prominent in subgen. Peltobryon but absent in Peperomia and Saururaceae.

40. Fruits densely pubescent=1

Fruits glabrous=0

41. Leaves with asymmetrically acute leaf base=1

Leaves with symmetrically acute leaf base.=0

42. Stem epidermis with a papillate layer covered by the cuticle=1

Stem epidermis without a papillate layer=0

A papillate layer is present in Piper aduncum, P. hispidum, and P. variegatum. I have not examined more species in subgen. Steffensia and the distribution of this character in that subgenus should be more carefully assessed.

43. Peltiforme bracts densely ciliate=1

Peltiforme bracts glabrous=0

44. Peltiforme bracts with raised oil cells=1

Peltiforme bracts with impressed oil cells=0

45. Fruit style with raised oil cells=1

Fruit style with impressed oil cells=0

46. Fimbriate lobulate bracts with a central thick glandular dotted region=1

Fimbriate lobulate bracts without a central thick glandular

dular dotted region=0

The derived condition is unique to subgen. Trianaeopiper.

47. Stamens uniseriate=1

Stamens in two planes=0

Uniseriate stamens occur only in subgen. Muldera. It is difficult to assert whether or not the condition results from tilting of the floral apex or if the arrangement is due to the emergence of stamens in a single plane.

48. Infructescence globose=1

Infructescence terete=0

Globose infructescence occurs in subgen. Coccobryon and is correlated with the immersed fruits in the rachis. In the Neotropics, globose infructescence are seen in P. nudilimbium and P. piluliferum.

49. Inflorescences axillar and terminal=1

All inflorescences on well developed branches or reduced branches, but never on both=0

The presence of axillar and opposite inflorescences occurs only in subgen. Sarcorrhachis.

50. Sarmentose, viny plants with leaf dimorphism=1

Sarmentose, viny plants without leaf dimorphism=0

51. Prophylls costally long-villous=1

Prophylls costally glabrous=0

52. Fruits longer than wide=1

Fruits as long as wide=0

53. Leaf base lobulate=1
 Leaf base acute=0
54. Stamen connective, at the top, with black oil cells=1
 Stamen connective, at the top, with reddish oil cells=0
55. Floral bracts at anthesis inflexed and covering the
 flower=1
 Floral bracts at anthesis not inflexed, lying above the
 flower=0
56. Leaves with stellate pubescence=1
 Leaves with simple trichomes=0.

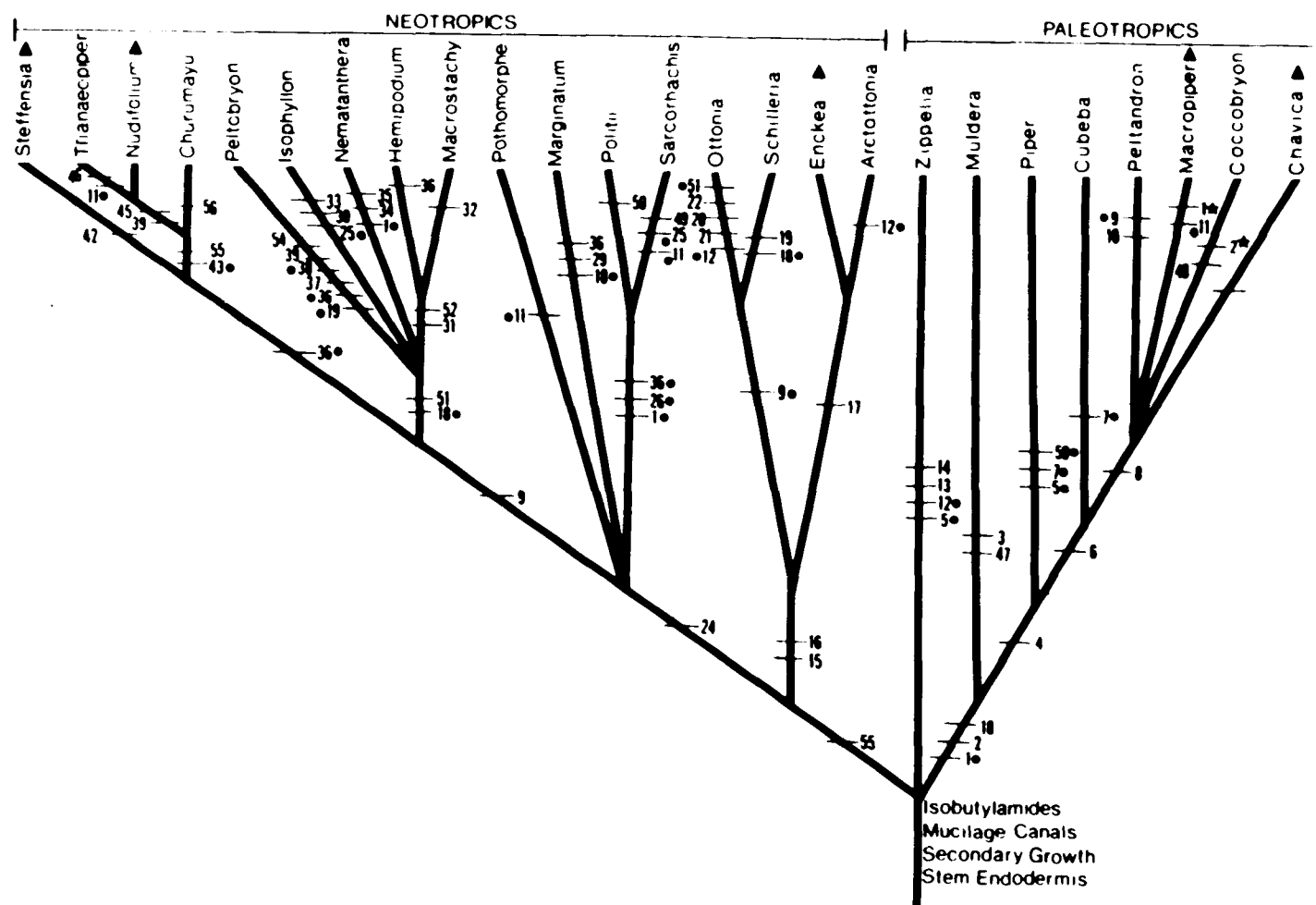
Description of Subgenera in Piper

1. Zippelia Blume in Roemer & Schultes, Syst. Veg. 7: 1614.
 1830.

Shrubs. Leaves palmately nerved (acrodromous), basally cordate to lobulate, long-petiolate, foliar dimorphism absent. Inflorescences terminal. Flowers bisexual, pedicellate, widely spaced; floral bracts sessile and partially adnate to the rachis; 6-staminate, connective expanded (?) beyond the thecae, laminar, filaments longer than the anthers, laterally dehiscent; 4-carpellate, stigmas sessile. Fruit rounded, glochidiate, pendulous.

Fig. 99. Cladogram for Piper

Triangle indicate paraphyletic groups, circles indicate multiple independent gains, and start indicate reversals.



One species, Piper begoniaefolium (Blume) Quisumbing.
Widespread in Indochina and Malaysia. Relationships uncertain.
The partially adnate floral bracts resemble those of subgen.
Piper. The species is unique in the Piperales by the glochidiate fruits and expanded laminar connectives. It is the only species of Piper in the Old World tropics with pedicellate bisexual flowers.

2. Muldera Miquel, Comm. Phyt. 34. 1840 (as a genus)

(=Schizonephos Griffin, Notulae 4: 383. 1854 as a genus).

Creeping vines. Leaves 5-7-plinerved, basally acute, short-petiolate, foliar dimorphism absent. Inflorescences terminal. Flowers dioecious, sessile, widely spaced at all stages; in staminate spikes the floral bracts are distinctly pedicellate, forming a cupular receptacle with 7-10 stamens sunken atop; in staminate flowers, 1-2 (?) floral bracts sessile, partially adnate to the rachis subtending a short pedicellate fruit; stamens uniseriate, anthers on short filaments, laterally dehiscent; 3-4-carpellate, stigmas sessile. Fruit rounded.

Nine to ten species. In SE India and Malaysia. A basal group to other subgenera in the Old World tropics. The staminate flowers suggest connation of parts. In Saururaceae such connation in floral structure is correlated with common primor-

dia (Tucker, 1975, 1976, 1985) consequently it is possible that such primordia are present in Muldera. The uniseriate, 7-10 stamens, borne on the bracts rather than on the rachis, are restricted to this subgenus. Floral ontogeny studies in this group should be undertaken in order to determine the level of homology of the floral parts.

3. Piper Linnaeus, Sp. pl. 28. 1753 (genus Piper sensu Miquel, Syst. piperac. 305. 1844).

Creeping vines. Leaves 3-5(-7)-plinerved, less often palmately nerved, basally obtuse or acute, long-petiolate, foliar dimorphism in many species apparent as display in the shape of leaf base. Inflorescences terminal. Flowers dioecious, monoecious or less often dioecious polygamous (e.g. Piper nigrum), widely spaced; floral bracts sessile adnate to the rachis with only the apex being free from the rachis; stamens 2-3(-4), filaments as long as or shorter than the anthers, anthers laterally less often upwardly dehiscent; 3-carpellate, stigmas sessile. Fruits pedicellate, the pedicels often shorter than the fruits, these then appearing subsessile.

30-40 species. Indochina, Africa, Pacific and Malaysia. Closely related to Muldera. The sister group of all other spe-

cies in the Old World tropics. The adnate floral bracts and the acrescentic fruits are derived in the group, but occur elsewhere in subgen. Cubeba (pedicellate fruits) and subgen. Muldera (adnate floral bracts in pistillate flowers).

4. Cubeba Miquel, Comm. Phyt. 33. 1840 (as a genus).

(=Cubeba Rafinesque, Sylva tellur. 84. 1838) (as a genus).

Creeeping vines, less often shrubs. Leaves 3-5(7)-pinnerved, acrodromous or rarely pinnately nerved throughout (e.g. Piper nigrescens), basally acute, obtuse and asymmetric or geniculate, foliar dimorphism absent. Inflorescences terminal. Flowers dioecious, widely spaced; floral bracts pedicellate (in staminate flowers) or sessile (in pistillate flowers), distally orbicular (i.e. the bracts then appearing centrally peltate); stamens 2-3(-4), laterally or upwardly dehiscent; 3-4-carpellate, stigmas sessile. Fruits short pedicellate, pedicels commonly longer than the fruits.

40-50 species. Widespread in the Old World tropics, but with most taxa in Malaysia. The pedicellate fruits are derived for the group.

5. Peltandron Miquel, Syst. piperac. 224: 1843-1844 (as a sect. of genus Chavica).

(=Penninervia Quisumbing, Philippine. J. Sci. 43(1): 177. 1930)

(as a section of subgen. Eupiper).

Creeping vines. Leaves pinnately nerved throughout, basally acute, foliar dimorphism absent (?). Inflorescences terminal. Flowers dioecious, loosely congested, floral bracts pedicellate, proximally densely pubescent, distally orbicular (e.g. peltiforme); stamens 2-3, filaments shorter than the anthers, laterally dehiscent, connective protruding above the anthers, fleshy and partially covering the anthers (except in Piper paucirameum); 3-4 carpellate, stigmas sessile. Fruits sessile, free, oblong, rounded.

5-7 species, endemic to Philippines. The pinnately nerved leaves and the fleshy connective are derived in the group. More closely related to subgen. Chavica.

6. Macropiper Miquel, Bull. Sci. Phys. Nat. Neerl. 447. 1839

(as a genus).

(=Andersoniopiper Trelease, Proc. Amer. Phylos. Soc. 73: 329. 1934 as a genus).

Shrubs or treelets, often lianescent sarmentose, rarely creeping vines. Leaves plinerved, palmately nerved, then acrodromous or campylodromous, foliar dimorphism present in some species. Inflorescences axillary, single but more often in

umbells. Flowers dioecious, less often monoecious, rarely staminate and pistillate flowers in the same spike, loosely to tightly congested, floral bracts short-pedicellate (pistillate flowers) to long-pedicellate (in staminate-flowers), proximally densely pubescent, distally orbicular (peltiforme), glabrous or sparsely pubescent; stamens 2-3, filaments shorter than the anthers, laterally dehiscent; 3-4 carpellate, stigmas sessile. Fruits sessile, free from the rachis, in one species (P. excelsum) partially concrescent with the rachis.

Nine species, limited to the Pacific. The axillary inflorescences are derived in the group. Closely related to Chavica.

7. Chavica Miquel, Syst. piperac. 222. 1843-1844 (as a genus).

(=Rhyncholepis Miquel, Syst. piperac. 282. 1843-1844, as a genus).

(=Sphaerostachyon Miquel, Syst. piperac. 375. 1843-1844 (as a genus)).

Creeping vines, rarely shrubs. Leaves plinerved, palmately nerved (acrodromous or campylodromous), rarely pinnately nerved, basally acute, obtuse and then often strongly lobulate, foliar dimorphism present or absent. Inflorescences terminal. Flowers dioecious, rarely monoecious, less often bisexual,

loosely to tightly congested, floral bracts pedicellate (in staminate or pistillate flowers) or subsessile (in pistillate flowers), proximally densely pubescent, distally orbicular (peltiforme), glabrous, rarely villous (e.g. Piper rhyncholepis); stamens (1-)2-3(-4), filaments as long as or, longer but more often shorter than the anthers, laterally or upwardly dehiscent; 3-4-carpellate, stigmas sessile, rarely on a style, free from the rachis, concrescent with the rachis to fully immersed in it, then inflorescences becoming globose.

100-150 species. Widespread in the old world tropics. More likely paraphyletic.

8. Coccobryon C. de Candolle, Prodr. 16(1): 336. 1869.

Vines, rarely shrubs. Leaves palmately nerved (acrodromous), rarely plinerved, leaf dimorphism absent (?), basally acute to obtuse, rarely cordate. Inflorescences terminal and opposite. Flowers bisexual, tightly congested, not forming banded patterns, floral bracts pedicellate, rarely sessile, peltate, distally orbicular, glabrous, but sometimes short-pubescent at the base; stamens 2-3 on filaments shorter than the anthers, upwardly dehiscent; 3-4-carpellate, stigmas sessile. Fruits free but often also concrescent or fully immersed in the rachis, rounded.

20-30 species. Restricted to the Old World tropics where it is common in China and India. With one species in Africa. The

group is unusual among the pipers in the Old World tropics by its bisexual flowers.

9. Enckea Kunth, Linnaea 13: 587. 1839 (as a genus).

(=Amalago Rafinesque, Silv. Tellur. 83. 1799).

(=Pleio-stachyopiper Killip, Smith & Trelease, Field. Mus.

Nat. Hist. Botany Publ. 13(2): 1936. (as a genus).

Shrubs, often treelets, rarely lianas. Leaves palmately nerved (acrodromous), leaf dimorphism basent, basally acute and with two callosities, rarely obtuse. Inflorescences terminal, opposite. Flowers bisexual, loosely to widely spaced, not forming banded patterns, floral bracts triangular-cucullate, subpeltate, glabrous or loosely pubescent at the base, stamens 3-4(-6), epigynous or hypogynous, filaments as long as or shorter than the anthers, laterally dehiscent; 3-4(-5) carpellate, stigmas sessile. Fruits free, in one species becoming partially immersed in the rachis (P. nudilimbum), then inflorescences becoming globose.

25-40 species. It includes Piper reticulatum and the P. amalago-complex of species. The palmately-nerved group of species of Trelease and Yuncker (1950), but excluding P. marginatum, P. niceforoi, and P. cinereum.

The acrodromous leaf venation is derived in the group. The subgenus is particularly rich in species in Central America

and the Caribbean. The sister group of subgen. Arctottonia.

10. Arctottonia Trelease, Proc. Amer. Philos. Soc. 69: 315.
1930 (as a genus).

As Enckea but the flowers pedicellate or subpedicellate, and always distant from the rachis, stamens often epigynous and hypogynous in the same inflorescence.

14-16 species confined to Central America with a widespread taxon (P. yucatanensis). The rest of the taxa are restricted to Mexico and NE Guatemala. Many species are semideciduous. The group has been recently revised by Bornstein. (pers. comm.), who reduced it to a subgenus of Piper).

11. Schilleria Kunth, Linnaea. 13: 609. 1839 (as a genus)
(=Carpunya Presl, Epimel bot. 228. 1850 (as a genus, but
excluding Piper klotszchianum and P. hoffmannseggianum).

Shrubs, sometimes sarmentose, not creeping, however, some species (P. carpunya and P. lenticelloseum) densely lenticellate. Leaves plinerved to pinnately nerved throughout, venation quite variable within a single plant (e.g. P. aequale), basally acute, decurrent with the petiole, or often the basally short-peltate, or leaves peltate at branching nodes (e.g. P. subscutatum), callosities present at the base. Inflorescences terminal. Flowers bisexual, loosely to tightly congested, not forming banded patterns, floral bracts pedi-

cellate, proximally glabrous to densely pubescent, distally sparsely pubescent, but never marginally ciliate, cucullate, and with the proximal extreme slightly lobulate; stamens 4, on filaments distinctly longer than the anthers, laterally or less often upwardly dehiscent; 3-carpellate, stigmas sessile, but often the stigmatic lobes long-decurrent, and the fruits long apiculate. Fruits free, trigonous, obovoid, laterally compressed.

20-35 species. It includes P. callosum, P. cinereum, P. aequale, P. sprengelianum, P. rivinoides, P. subscutatum, P. oxiphyllum, P. carrilloanum, P. lenticellosum, P. carpunya, P. concinum, etc. Most species are glabrous, when pubescent then never long-villous, oil cells are impressed, the inflorescences are less than 0.5 mm thick in diam. With many taxa in the SE forest of Brazil, a widespread taxon (P. aequale), 5-7 species in Chocó, and 7-10 species in Central America.

The sister group of subgen. Ottonia.

12. Ottonia Sprengel (see systematic treatment in the present work).

13. Sarcorhachis Trelease, Contrib. U.S. Natl. Herb. 26: 16. 1927 (as a genus).

Creeping vines, stem cortex with numerous mucilage canals

in the cortex. Leaves palmately nerved (campylodromous), rarely plinerved, leaf dimorphism absent, basally obtuse to cordate. Inflorescences terminal and axillar, in this case in branches of third order, the entire branch being reduced to a single inflorescence and a subtending prophyll, rarely the inflorescence subtended by a small reduced leaf. Flowers bisexual, tightly congested, forming banded patterns, floral bracts pedicellate, cucullate, distally orbicular and sub-peltate, marginally densely ciliate; stamens 4(-5) on filaments as long as the anthers, upwardly dehiscent; 4-5(-6)-carpellate, stigmas sessile. Fruits concrescent and immersed in the fleshy rachis, rounded or ellipsoid.

5 species. All taxa disjunct, a single species in SE Brazil, one in Chocó (Colombia and Ecuador), one in Central America, and two in Venezuela. The leaf shape (ovate), the creeping viney habit, lack of dimorphism and the fruits fully immersed in the rachis are reminiscent of the Old World pipers. The habit, infructescence, and the presence of terminal and axillar inflorescences are derived in the group. The presence of mucilage canals and the habit are synapomorphies shared with the Piper politii-complex.

14. Piper politii-complex.

Creeping vines, stem cortex with numerous mucilage canals

in the cortex. Leaves palmately nerved (campylodromous) and basally obtuse and cordate in orthotropic branches, plinerved to pinnately nerved (often quite variable in the same branch) and basally acute to slightly obtuse, but never cordate, in plagiotropic branches. Inflorescence terminal. Flowers bisexual, tightly congested, forming banded patterns, floral bracts pedicellate, distally cucullate, orbicular, and sub-peltate, marginally densely ciliate; stamens 4-5, filaments as long as or slightly longer than the anthers, laterally dehiscent; 4-6(-7(?))-carpellate, stigmas sessile or in a single species on a short style. Fruits partially concrescent but never fully immersed in the rachis, obovoid, rounded.

A group of 4 species including Piper politii, P. steyermarki, P. vitaceum, and P. dactylostigmum. It is restricted to Amazonia and the neighboring Guiana Shield. Leaf dimorphism, evident in all plants, seems to be strongly correlated with the variation in leaf venation and it is likely that P. vitaceum as well as several varieties of P. politii (Steyermark, 1984) should be synonymized as they are based on leaf venation and leaf shape.

15. Piper marginatum-complex.

(=Callianira Kunth, in part).

Shrubs, erect or sarmentose but never creeping vines.

Leaves palmately nerved (campylodromous), rarely with basally a pair of secondary veins departing from the midvein above the leaf base, basally obtuse, cordate, leaf dimorphism absent. Inflorescences terminal. Flowers bisexual, tightly congested, forming banded patterns, floral bracts cucullate, pedicellate, densely pubescent at the base, distally orbicular, subpeltate, marginally ciliate; stamens 4, filaments as long as the stamens, upwardly dehiscent, 3-carpellate, stigmas sessile. Fruits free, obovoid.

The complex includes Piper marginatum, P. cinereum, P. calceolarium, and P. caucaense all of which are shrubs. A second group is tentatively placed here (as based on leaf shape, venation and floral characters) and includes P. multiplinervium, P. schwackei, and P. poiteanum. The anthers with upward dehiscence, the 3-staminate bracts, and the banded pattern of flowers are derived in the group, but occur independently in many other species of Neotropical pipers.

16. Pothomorphe Miquel, Bull. Sci. Phys. Nat. Neer. 450. 1840.

(=Lepianthes Rafinesque, Silv. Tellur. 85. 1838, not Lepanthes Swartz, 1799).

(=Heckeria Kunth, Linnaea 13: 564. 1839 (as a genus).

(=Peperidia Kostal, Allg. Med. Pharm. Fl. 2: 455. 1831).

Shrubs, or often herbs. Leaves palmately nerved, basally

obtuse, cordate or rounded. Leaf dimorphism absent.

Inflorescences terminal in congested leafless axillar branches, in groups of 1 or 2 to 15 inflorescences (then appearing as umbells). Flowers bisexual, tightly congested, forming banded patterns, floral bracts peltoid, densely marginally long-ciliate, distally orbicular; stamens 2, filaments as long as the anthers, upwardly dehiscent, 3 carpellate, stigmas sessile. Fruits free, obovoid.

Two species. Widespread in the Neotropics at low elevations. Introduced in the Old World tropics. The 2-staminate flowers, orbicular peltate and marginally ciliate floral bracts, and axillar inflorescences appear to be derived in the group. The relationships of this group remains, however, obscure. Burger (1971) suggested it to be related to P. auritum.

17. Macrostachys Miquel, Syst. piperac. 378. 1843-1844 (as a section of genus Artanthe; the group of P. obliquum fide Kunth (1839) in the genus Steffensia).

Shrubs, often single stemmed. Leaves pinnately nerved, but rarely throughout, basally lobulate, symmetric or strongly asymmetric, lobes often overlapping and covering the petiole, rarely the leaf base not lobulate, then asymmetric (P. inaequale, P. begoniicolor); leaf dimorphism evident between plagiotropic and orthotropic branches. Inflorescences terminal

and often pendulous, normally as long as or longer than the leaves, attaining 20-60 cm long. Flowers bisexual, tightly congested, forming banded patterns or not, floral bracts cucullate, pedicellate, proximally densely pubescent, distally the proximal portion lunulate, lobulate, hirtellous at the center, rarely marginally ciliate (*P. auritum*); stamens 4, on filaments longer than the anthers, laterally dehiscent (exceptionally upwardly dehiscent; 3-carpellate, stigmas sessile, rarely on a style. Fruits free, rectangular, often densely hirtellous.

The group contains 30-40 species, including all taxa with large lobulate leaves and inflorescences which are distinctly as long as or longer than the leaves. The floral bracts, fruit shape, leaf base, and relative size between inflorescence and leaves are derived in the group. Based on leaf characters *P. auritum* is included here. This species seems however, to be anomalous by the marginally ciliate bracts. Burger (1971) suggested that based on floral characters and prophyll structure it is more closely related to *P. marginatum*. The group is more closely related to subgen. *Hemipodium*. It is a common element in the Andes and also has many taxa in the lowlands of South America, but is poorly represented in Central America.

18. *Hemipodium* Miquel, Syst. piperac. 490. 1844 (as a section of genus *Artanthe*).

(= Piper tuberculatum group of Kunth (1839) in the genus Steffensia).

Shrubs, often treelets, stems often with prominent lenticels (e.g. P. tuberculatum, P. swartzianum). Leaves pinnately nerved throughout, basally geniculate, leaf dimorphism absent. Inflorescences terminal. Flowers bisexual, tightly congested, forming banded patterns, floral bracts cucullate, pedicellate, proximally densely pubescent, distally cucullate, triangular to orbiculate and subpeltate, marginally ciliate; stamens 4, filaments as long as or longer than the anthers, upwardly dehiscent; 3-carpellate, stigmas sessile. Fruits rectangular.

7 species. The group includes P. arboreum, P. tuberculatum, P. savanense, P. holttonii, P. swartzianum, P. stamineum, and P. verrucosum. The first two taxa are widespread weeds. The last three are restricted to the Caribbean islands. The leaf base, fruit shape, marginally ciliate bracts, anther dehiscence, and leaf venation are derived for the group. Based on fruit shape the group is placed as sister group of subgen. Macrostachys.

19. Isophyllon Miquel, Syst. piperac. 501. 1843-1844 (as a section of genus Artanthe).

Shrubs, erect but sometimes sarmentose (e.g. P. viçosanum), rarely creeping vines (P. pseudoacreanum). Leaves pinnately nerved throughout, basally obtuse or acute, leaf dimorphism often present, the leaves on branching nodes narrow lanceolate and smaller than those in flowering nodes. Inflorescences terminal, with a sterile apical residuum. Flowers bisexual, tightly congested, not forming banded patterns, floral bracts cucullate, rarely in one species spatulate (P. brasiliense) pedicellate, proximally glabrous, distally narrowly obtriangular and long lobulate, glabrous; stamens 4, filaments as long as the anthers, laterally dehiscent; 3-carpellate, stigmas sessile. Fruits partially conrescent with the rachis, ellipsoid.

30-40 species. Species in the group includes P. anonifolium, P. amplum, P. ilheusense, P. rhododendron, P. piresii, P. glabrescens, P. viçosanum, P. plurinervosum, P. biolleyi, etc., all taxa with acute leaf bases. A second group includes P. demeraranum, P. concretiflorum, P. consanguineum, and relatives, all with obtuse and lobulate leaf bases. It is easily distinguished from other groups by the tightly congested and partially conrescent fruits (a derived feature), the inflorescences with an apicular sterile portion, and the pinnately nerved leaves. The group is prominent among the pipers in the coastal forests of SE Brazil. It reaches into Central

America where is represented by P. biolleyi, P. glabrescens, and its relatives (see Burger, 1971). A third group including P. hostamannianum, P. maguirei, P. citrifolium, and relatives could be included here, but the leaves are not pinnately nerved throughout, otherwise it agrees in other floral characters. This third group is in part of a polytomie in the cladogram, and its relationships await complete sampling of characters.

20. Peltobryon Klotzsch ex Miquel, Syst. piperac. 369. 1843-1844

(as a section of genus Artanthe).

(= Piper heterophyllum group of Kunth (1839) in the genus Steffensia).

Shrubs erect, rarely sarmentose (P. chavicoide), single to several stemmed. Leaves pinnately nerved throughout, often secondary veins not equally spaced and quite variable in number and angle of departure from the midvein (P. divaricatum, P. heterophyllum, P. dumosum), basally acute and slightly asymmetric, less often obtuse and cordate (P. pterocladon), dimorphism foliar often present, leaves densely glandular dotted (e.g. oil cells raised), marginally ciliate. Prophylls wide-laminar, costally long-villous, as long as the internodes, often persistent at all flowering nodes. Inflorescences terminal, but in one species axillary (Piper sp. nov. undescribed, J. Jaramillo 3046, NY, QCA). Flowers bisexual, not forming

banded patterns, floral bracts cucullate, pedicellate, basally densely pubescent, distally obtriangular and lobulate, marginally ciliate; stamens 4, filaments slightly longer than the anthers, laterally dehiscent, the connective apically black-glandular dotted; 3-carpellate, stigmas sessile or often on long styles (e.g. P. phytolaccaefolium). Pubescence of single trichomes, less often vestiture consisting of stellate trichomes (P. asterotrichum, P. permolle, P. tridentipilum and relatives).

40-60 species. Very distinct group in the Neotropics, it includes P. augustum, P. leticianum, P. casapiense, P. monozonensis, P. munchanum, P. heterophyllum, P. longestylosum, P. dumosum, etc.). The glandular dotted leaves, anthers with the glandular dotted connective, prophylls as long as the internodes, and the floral bracts are derived in the group. It also includes P. trigonum, P. adenandrum, and the P. lanceolatum-complex. Widespread in South America, poorly represented elsewhere. Most taxa are represented in Amazonia especially in Perú.

21. Nematanthera Miquel, Linnaea 18: 606. 1848 (as a genus).

Creeping vines. Leaves pinnately nerved in plagiotropic branches, palmately nerved to plinerved in orthotropic branches, basally acute (in the plagiotropic branches), obtuse

and then cordate (in orthotropic branches), leaves marginally ciliate. Inflorescences terminal, obpyramidal in flower, radial at anthesis; flowers bisexual, forming banded patterns in fruit, floral bracts cucullate, pedicellate, basally densely pubescent, distally, obtriangular and lobulate, marginally ciliate; stamen 1, filaments minute, shorter than the anthers, anthers ellipsoid-oblong, laterally dehiscent; 3-carpellate, stigams sessile. Fruits obpyramidal.

1-2 species. It includes Piper kegelii (erroneously described by Miquel as 4-staminate) and P. nematanthera. The two taxa differ in some vegetative characters, especially vesture and dimension of inflorescences; otherwise they may represent single species. The single staminate flowers, anther shape, inflorescence shape, and habit are derived in the group. Both C. de Candolle (1923) and Yuncker (1973) described several species in Piper (e.g. P. acreanum) as unisexual, or with inflorescences bisexual and unisexual on the same plant. Clearly those authors ignored the fact that stamens fall just after fruit fertilization. All fruits having thereafter the base of the filament attached to the base. The group is at present being revised by the author.

The reduced number of floral parts and the derived type of anther make it difficult to determine the relatives of this group. It resembles in floral bracts, leaf venation and vesture distribution to P. consanguineum in subgen. Isophyllon.

22. Churumayu Miquel, Syst. piperac. 407. 1843-1844 (as a genus).

(= P. crassinervium group of Kunth (1839) in the genus

Steffensia)

Shrubs caespitose. Leaves plinerved, basally acute to obtuse, often cordate, ovate, densely short-pubescent, in most taxa (except Piper subflavum) pubescence in the leaves is restricted to the abaxial side. Pubescence often consist of stellate trichomes. Inflorescences terminal. Flowers bisexual, tightly congested and forming banded patterns, floral bracts pedicellate, wide obtriangular, densely marginally long ciliate; stamens 4, filaments longer than the anthers, laterally dehiscent with the connective glandular dotted at the top; 3-carpellate, stigmas on a prominent style. Fruit obovate.

10-15 species. It includes P. crassinervium, P. subflavum, P. marequitense, P. psilophyllum, P. mite, P. dasypogon, and P. propinquum complex. With an apparent center of diversity in the Andes of Perú. The sister group of P. nudifolium complex.

23. P. nudifolium-complex.

As Churumayu but leaves densely glandular dotted, floral bracts narrowly obtriangular with a distinct central zone glandular dotted. Stellate pubescence otherwise absent.

It includes, P. nudifolium (Central America), P. cararense, P. yanaconense, and P. guapense. The densely glan-

dular dotted leaves and the foral bracts are synapomorphies shared with subgen. Trianeopiper. There is no synapomorphy for the group otherwise and it may be paraphyletic and it is not yet clear if this group simply represents a portion of Trianaeopiper. Aside from the axillary inflorescences in the latter group there is no difference by which they can be separated. The group is currently being revised by the author.

24. Trianaeopiper Trelease, Proc. Amer. Philos. Soc. 67: 50.
1936.

Shrubs, or terrestrial herbs, glandular dotted throughout. Leaves plinerved, rarely pinnately nerved throughout, basally obtuse, then cordate or distinctly lobulate, densely short-pubescent, in most taxa pubescence in the leaves restricted abaxially to the venation. Inflorescences axillar, the inflorescence subtended by a small prophyll, less often a reduced foliage leaf, normally one inflorescence at the axil of each leaf, sometimes (e.g. P. trianae), two to three inflorescences in a scape. Flowers bisexual, tightly congested, not forming banded patterns, floral bracts pedicellate, proximally densely pubescent, distally narrowly obtriangular, densely marginally ciliate, centrally with a distinct glandular dotted zone; stamens 3-4, filaments distinctly longer than the anthers, laterally dehiscent with the connective glandular

dotted at the top; 3-carpellate, stigmas on a prominent style, glandular dotted. Fruit obovate.

16-20 species. Including all species described by Trelease and Yuncker (1950) but excluding P. confertinodum, P. haughtii, P. contraverrugosum, and P. enckeaespicum. Including otherwise P. albozonatum and four new species yet to be described from Chocó. The position of the inflorescences has been repeatedly misunderstood by some authors and is now a heterogeneous taxon. The floral bracts, leaf glandular dotted, stylose fruits, and axillary inflorescences are derived for the group. None of these characters by themselves, however, are unique to the group, but the combination is unique. It is restricted to the Pacific coast of N South America in Chocó (Colombia, Ecuador) and Perú.

25. Steffensia Kunth, Linnaea 13: 609. 1839 (as a genus, in part).

(=Artanthe Miquel, Comm. Phyt. 40. 1840 (including sect. Radula).

Shrubs, often sarmentose but never creeping, stems epidermis with a distinct papillate-hairs layer bounded by a thick cuticle. Leaves plinerved, less often pinnately nerved throughout, often with strong foliar dimorphism, basally obtuse and then asymmetric, rarely acute, normally scabrous, bullate

or lacunose, hispidous to densely scabrous, rarely smooth. Inflorescences terminal, often curved at anthesis. Flowers bisexual, tightly congested, rarely loosely spaced, forming banded patterns, floral bracts cucullate, proximally densely pubescent, distally obtriangular or orbicular, marginally ciliate; (2-)3-4(-5)-staminate, filaments as long as the anthers, normally with upwards dehiscent, rarely laterally dehiscent; 3-carpellate, stigams sessile or on distinct styles.

300-350 species. A large diverse group as here interpreted, likely to be paraphyletic. It includes P. aduncum and P. hispidum-complex, P. brachypodon-complex, and the P. lacunosum group.

TABLE VI

CHARACTER DATA MATRIX FOR PIPER

[illegible]

[illegible]

-continued-

[illegible]

[illegible]

Trianae 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0

[illegible]

TABLE VI

-continued-

[illegible]

[illegible]

Trianae 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 1 0

Steffen 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0

LITERATURE CITED

- Andrade-Lima, D. 1977. Present-day refuges in northeastern Brazil. Pp. 245-251. In: G. T. Prance (ed.) Biological diversification in the tropics. Columbia Univ. Press, New York.
- Ax, P. 1985. Stem species and the stem lineage concept. *Cladistics* 1: 279-287.
- Bailey, I. W. & W. W. Tupper. 1918. Size variation in tracheary cells: I. A comparison between the secondary xylem of vascular cryptogams, gymnosperms and angiosperms. *Proc. Amer. Acad. Arts. Sci.* 54: 149-204.
- Balfour, E. 1958. The development of the vascular system of Macropiper excelsum Forster-II. The mature stem. *Phytomorphology* 8: 224-233.
- Barth, M. O. & A. F. Barbosa. 1975. Catalogo sistemático dos polens das plantas arboreas do Brazil meridional. X-Chloranthaceae e Piperaceae. *Mem. Inst. Oswaldo Cruz.* 73: 101-108.
- Barthlott, W. 1981. Epiderma! and seed surface characters of plant systematic applicability and some evolutionary aspects. *Nord. J. Bot.* 1: 345-355.
- Blanc, P. & K. Andraos. 1982. Etude microscopique des phénomènes de ramification chez Piper unguiculatum Ruiz et Pavón (Piperaceae). *Rev. gén. Bot.* 89: 193-211.
- _____. 1983. Remarques sur la dynamique de croissance dans le genre Piper L. (Piperaceae) et les genres affines. *Bull. Mus. natn. Hist. nt., Paris.* 4 ser, 5. section B, Adansonia 13: 259-282.
- Blaser, H. W. 1944. Studies on the morphology of the Cyperaceae II. The prophyll. *Amer. J. Bot.* 31: 53-64.
- Bond, G. 1931. The stem endodermis in the genus Piper. *Trans. Roy. Soc. Edinburg.* 56: 695-724.
- Brooks, D. R. & E. O. Wiley. 1985. Theories and methods in different approaches to phylogenetic systematics. *Cladistics* 1: 1-11.
- Brown, K. S., Jr. 1973. Centros de evolução, refúgios quaternários, e conservação de patrimônios na região neotropical: Padrões de diferenciação em Ithomiinae (Lepidoptera: Nymphalidae). *Acta Amazônica* 7: 75-137.

- Burger, Wm. C. 1971. Piperaceae. In: W. C. Burger (ed.), Flora Costaricensis. Fieldiana Bot. 24(3): 228-377.
- _____. 1972. Evolutionary trends in the Central American species of Piper (Piperaceae). Brittonia 24: 356-362.
- _____. 1977. The Piperales and the monocots. Alternative hypotheses for the origin of the monocotyledonous flowers. Bot. Rev. 43: 345-393.
- Calvet, J. 1877. These sobre o jaborandi. Faculdade de medicina de Rio de Janeiro. Rio de Janeiro.
- Camp, W. H. 1931. Rapidly ripened hematoxylin and its uses. Science 74: 661-662.
- Candolle, A. P. de & K. Sprengel. 1820. Grundzuge der Wissenschaftlichen Pflanzen Kunde, Leipzig.
- Candolle, C. de. 1866. Mémoire sur la famille des Pipéracées. Mem. Soc. Phys. Hist. Nat. Geneve. 18: 1-38.
- _____. 1869. Piperaceae. In: A. de Candolle, Prodromus 16(1): 235-471.
- _____. 1923. Piperacearum clavis analytica. Candollea 1: 65-415.
- Carlquist, S. 1962. A theory of paedomorphosis in dicotyledonous woods. Phytomorphology 12: 30-45.
- _____. 1975. Ecological strategies of xylem evolution. Univ. California Press, Berkeley.
- _____. 1985. Wood anatomy of Begoniaceae, with comments on raylessness, paedomorphosis, relationships, vessel diameter and ecology. Bull. Torr. Bot. Club 112: 59-69.
- Chen Pei-Shan, Tseng Yung-Chien & Zhu Pei-Zhi. 1982. Piperaceae. In: T. Yung-Chien (ed.) Flora reipublicae popularis Sinica 20(1): 11-77. Peking.
- Chibber, H. M. 1912. The morphology and histology of Piper betle Linn. J. Linn. Soc. Bot. 41: 357-383.
- Committee on Nomenclature-International Association of wood Anatomists. 1957. International glossary of terms used in wood anatomy. Tropical woods 107: 1-36.

- Côrrea, M. P. 1926. Dicionário das plantas úteis do Brazil e das exóticas cultivadas. Ministerio da Agricultura, Rio de Janeiro, Brazil.
- Cozzo, D. & L. Q. Cristiani. 1950. Los generos de fanerogamas argentinas con estructura leñosa estratificada. Rev. Ins. Nac. Invest. Ci. nat. Bernardino Rivadavia. Ci Bot. 1: 363-405.
- Criscy, J. V. & T. F. Steussy. 1980. Determining primitive character states for phylogenetic reconstruction. Syst. Bot. 5: 112-115.
- Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York.
- Dahlgren, R., H. T. Clifford & P. F. Yeo. 1985. The families of the monocotyledons: Structure, evolution and taxonomy. Springer Verlag, Berlin.
- Datta, C. P. & A. Dasgupta. 1979. Comparison of vegetative anatomy of Piperales III. Vascular supplies to leaves. Acta Bot. Indica 7: 39-46.
- Debray, F. 1885. Etude comparative des caractères anatomiques et du parcours des faisceaux fibro-vasculaires des Pipéracées. Thèse. Faculté des Sciences de Paris.
- Deferrari, A. M. 1977. Morfología foliar de especies argentinas del genero *Peperomia* Ruiz & Pavón (Piperaceae). Obra del Centenario del Museo de la Plata 3: 63-96.
- Donoghue, M. J. & P. D. Cantino. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Syst. Bot. 9: 192-202.
- Duke, J. A. 1965. Keys for the identification of seedlings of some prominent woody species in eight forest types in Puerto Rico. Ann. Missouri Bot. Gard 32: 314-350.
- _____. 1969. On tropical tree seedlings, systems, and systematics. Ann. Missouri Bot. Gard. 56: 125-161.
- Dunstan, W. R. & H. Garnett. 1895. The constituents of *Piper ovatum*. J. Chem. Soc. 67: 94-100.
- Éichler, A. W. 1875-1878. Blüthendiagramme. Pts. 1,2. Leipzig.
- Eldrege, N. & J. Cracraft. 1980. Phylogenetic patterns and the evolutionary process. Columbia Univ. Press, New York.

- Endress, P. K. 1975. Nachbarliche Formbeziehungen mit Hüllfunktion im Infloreszenz und Blütenbereich. Bot. Jahrb. Syst. 96: 1-14.
- Faegri, K. & L. van der Pijl. 1979. The principles of pollination ecology. 3 ed. Pergamon Press, London.
- Fahn, A. 1982. Plant anatomy. 3 ed. Pergamon Press, New York.
- Farris, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19: 83-92.
- _____. 1983. The logical basis of phylogenetic analysis. Pp. 7-36. In: N. I. Platnick & V. A. Funk. (eds.) Advances in cladistics: Proceedings of the second meeting of the Willi Hennig society. Columbia. Univ. Press, New York.
- Fisher, J. B. & D. E. Hibbs. 1982. Plasticity of tree architectures con estructura leñosa estratificada. Rev. Ins. Nac. Invest. Ci. nat. Bernardino Rivadavia. Ci Bot. 1: 363-405.
- Kluge, A. G. 1985. Ontogeny and phylogenetic systematics. Cladistics 1: 13-28.
- Konoshima, M. & T. Miyagawa. 1976. Pharmacological studies on the piperaceous plants: II. Studies on the crude drugs of stems. 2. On the genus Piper (Eupiper and Cubeba sections) and Peperomia. Soyoyakugaka Zasshi 30: 155-163.
- Kunth, K. 1839. Bemerkungen über die Familie der Piperaceen. Linnaea 13: 562-726.
- Lindley, J. 1848. Illustrated dictionary of botanical terms. London.
- Liu, Tang-Shui. 1975. Piperaceae. Pp. 556-555. In: Hui-Lin Li et al. (eds.). Flora of Taiwan. vol 2. Taipei.
- Maddison, W. P., M. J. Donoghue & D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83-103.
- Majumdar, G. P. & P. Pal. 1961. Developmental studies: VI. The morphology of the so-called stipule of Piper (from a comparative ontogenetical study of this structure) in P. betle, P. longum, P. nigrum, P. ornatum and two other species of Piper and the morphology of the leaf sheath of Scindapsis officinalis (Araceae) Proc. Natl. Inst. Sci. India. pt. B: Biol. Sci. 27: 26-39.

- Makapugay, H. C., D. D. Soejarto., A. D. Kinghorn & E. Bordas.
1983. Piperovatine, the tongue-numbing principle of Ottonia frutescens. Journal of Ethnopharmacology 7: 235-238.
- Maslim, T. P. 1952. Morphological criteria of phyletic relationships. Syst. Zool. 1: 49-70
- Matos Araujo, P. A. de, & A. de Mattos Filho. 1974. Estrutura das madeiras Brasileiras de angiospermas dicotiledôneas (IX). Piperaceae. (Piper aduncum L.). Rodriguésia 39: 85-93.
- Mayr, E. 1965. Classification and phylogeny. Amer. Zool. 5: 165-174
- _____. 1982. The growth of biological thought: Diversity, evolution and inheritance. Belknap, Cambridge.
- Metcalfe, C. & L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford.
- Miquel, F. A. W. 1839. Notes préliminaire sur les genres de la famille des Pipéracées. Bull. Sci. Phys. Nat. Néerl. 6: 447-454.
- _____. 1843-1844. Systema Piperacearum 1: 1-304. Rotterdam.
- _____. 1852. Piperaceae. In: Martius' Flora Brasiliensis 4: 1-76.
- Mohandas, K. K. & G. L. Shah. 1982. Structure and ontogeny of trichomes in some Piperaceae. Acta Botanica Indica 10: 92-95.
- Mori, S., B. Boom & G. T. Prance. 1981. Distribution patterns and conservation of eastern Brazilian coastal forest tree species. Brittonia 33: 233-245.
- Moricand, S. 1840. Plantes nouvelles ou rares d'Amérique 6. pl. 51-60. Genève.
- Moura, J. P. C. de. 1884. Sudoríficos brasileiros sua ação terapêutica. These apresentada a Faculdade de Medicina do Rio de Janeiro. Rio de Janeiro.
- Murty, Y. S. 1959. Studies in the order Piperales. V. A contribution to the study of floral morphology of some species of Piper. Proc. Indian Acad. Sci. 49: 52-65.

- Nelson, G. J. 1972. Comments on Hennig's "Phylogenetic systematics" and its influence on ichthyology. *Syst. Zool.* 21: 364-374.
- _____. 1985. Outgroups and ontogeny. *Cladistics* 1: 29-45.
- _____ & N. Platnick. 1981. Systematics and biogeography. Columbia Univ. Press, New York.
- Nikiticheva, Z. I. 1981. Embryological features of some Piperales. *Acta Soc. Bot. Poloniae.* 50: 329-332.
- Patel, R. N. & A. Bowles. 1980. Wood anatomy of the dicotyledons indigenous to New Zealand. *New Zealand J. Bot.* 18: 507-513.
- Payne, W. W. 1969. A quick method for clearing leaves. *Ward's Bulletin* 4-5.
- Piso, W. & G. Marcgrave. 1648. *Historia naturalis Brasiliae.* Amsterdam.
- Prakash, N. & Bak Heng Kin. 1982. Flower and fruit development in Piper nigrum L. cv. Kuching. *Malaysian J. Sci.* 7: 11-19.
- Prance, G. T. 1983. Forest refuges: evidence from woody-angiosperms. Pp. 137-157. In: G. T. Prance. (ed.). *Biological diversification in the tropics.* Columbia Univ. Press, New York.
- Price, S. J. & A. R. Pinder. 1970. Chemistry of Ottonia vahllei Kunth. II. Constitution of the nonvolatile component. *J. Org. Chemistry* 35: 2568-2571.
- Pring, B. G. 1982. Isolation and identification of amides from Piper callosum: Synthesis of pipercallosine and pipercallosidine. *J. Chem Soc. Perkins. Trans.* 10: 1493-1498.
- Quisumbing, E. 1930. Philippine Piperaceae. *Philipp. J. Sci.* 43: 1-246.
- Rafinesque, C. S. 1838. *Sylva Telluriana.* (pp. 84-85.)
- Raju, M. V. S. 1961. Morphology and anatomy of the Saururaceae. I. Floral anatomy and embryology. *Ann. Missouri Bot. Gard.* 48: 107-124.
- Remphrey, W. R., T. A. Steeves & B. R. Neal. 1983. The morphology and growth of Arctostaphylos uva-ursi (bearberry): an architectural analysis. *Canad. J. Bot.* 61: 2430-2450.

- Rizzini, C. T. 1952. De Piperaceis tribus, nova minusque cognitis, ad genus Ottoniam relatis. *Dusenian* 3: 263-266.
- Rousseau, D. 1927. Contribution à l'anatomie comparée des Piperacées. *Mem. Acad. R. Belg. Ser. 2.* 9: 1-45.
- Sabatino, A. & J. B. da Silva. 1975. Anatomia e óleo essencial das folhas de Piper regnellii (Miquel) C. DC. var. regnellii. *Bol. Bot. Univ. São Paulo.* 3: 95-106.
- Schaeffer, B., M. K. Hecht & N. Eldrege. 1972. Phylogeny and paleontology. *Evol. Biol.* 6: 31-46.
- Schmid, R. 1982. Sonication and other improvements on Jeffrey's technique for macerating wood. *Stain Technol.* 57: 293-299.
- Schmitz, F. 1872. Die Blüten-Entwicklungen der Piperaceen. *Bot. Abhandl. Geb. Morph. Physiol.* 2: 1-74.
- Schultes, R. E. 1975. De plantis toxicariis e mundo novo tropicale commentationes XII. Notes on biodynamic Piperaceous plants. *Rhodora* 77: 165-170.
- Semple, K. S. 1974. Pollination in Piperaceae. *Ann. Missouri Bot. Gard.* 61: 868-871.
- Smith, A. C. 1975. The genus Macropiper (Piperaceae). *Bot. J. Linn. Soc.* 71: 1-38.
- Snow, B. K. & D. W. Snow. 1971. The feeding ecology of rangers and honeycreepers in Trinidad. *Auk* 88: 291-322.
- Soares Costa, S. & W. B. Mors. 1981. Amides of Ottonia corcovadensis. *Phytochemistry* 20: 1305-1307.
- Soderstron, T. R. & C. E. Calderón. 1974. Primitive forests grasses and evolution of the Bambusoideae. *Biotropica* 6: 141-153.
- Sokolov, V. S. 1952. Alkaloid plants of the USSR. *Akademiia Nauk, Moscow.*
- Sprengel, K. 1820. Neue Entdeckungen im ganzen Umfang der Pflanzenkunde. Leipzig.
- Stafleau, F. A. & R. S. Cowan. 1979. Taxonomic Literature. vol. II: H-LE. Junk, The Hague.
- Stevens, P. F. 1980. Polarity of character states. *Annual Rev.*

- Ecol. Syst. 11: 333-358.
- Stevenson, D. W. 1980. Radial growth in the Cycadales. Amer. J. Bot. 67: 465-475.
- Steyermark, J. A. 1971. Notes on the genus Sarcorhachis Trel. (Piperaceae) Pittieria 3: 29-38.
- _____. 1984. Piperaceae. In: Flora de Venezuela. Inst. Nal. Parq. vol. II. 2nd pt. Editorial Fundación, Caracas.
- Swamy, B. G. L. 1944. A reinvestigation of the embryo sac of Piper betle L. Proc. nat. Acad. Sci. India 14: 109-113.
- Tomlinson, P. B. 1960. Seedling leaves in palms and their morphological significance. J. Arnold Arbor. 41: 414-428.
- Trelease, W. 1930. The geography of American peppers. Proc. Amer. Philos. Soc. 49: 309-325.
- _____. 1935. The pedicellate peppers of South America. Proc. Amer. Philos. Soc. 75: 691-716.
- _____. 1936. Piperaceae. Pp. 1-253. In: J. F. Macbride (ed.). Flora of Perú. Publ. Field. Mus. Bot. 13: 1-253.
- _____ & G. T. Yuncker. 1950. The Piperaceae of Northern South America. Univ. Illinois Press, Urbana.
- Tucker, S. C. 1962. The terminal idioblasts in Magnoliaceous leaves. Amer. J. Bot. 51: 1051-1062.
- _____. 1975. Floral development in Saururus cernuus. 1. Floral initiation and stamen development. Amer. J. Bot. 62: 993-1007.
- _____. 1976. Floral development in Saururus cernuus. 2. Carpel initiation and floral vasculature. Amer. J. Bot. 63: 289-301.
- _____. 1980. Inflorescence and flower development in the Piperaceae. I. Peperomia. Amer. J. Bot. 66: 227-236.
- _____. 1981. Inflorescence and floral development in Houttuynia cordata (Saururaceae). Amer. J. Bot. 68: 1017-1032.
- _____. 1982a. Inflorescence and flower development in the Piperaceae. II. Inflorescence and flower development of Piper. Amer. J. Bot. 69: 743-752.

- _____. 1982b. Inflorescence and flower development in the Piperaceae. III. Floral ontogeny of Piper. Amer. J. Bot. 69: 1489-1401.
- _____. 1985. Initiation and development of inflorescence and flower in Anemopsis californica (Saururaceae). Amer. J. Bot. 72: 20-31.
- Turpin, P. I. F. 1819. Mémoire sur l'inflorescence des Graminées et des Cyperées. Mem. Mus. Hist. Nat. Paris. 5. 426-492.
- Vahl, M. 1796. Piper. In: Eclogae Americanae 1:3-5.
- Vellozo, J. M. da Conceição. 1825. Flora fluminensis. Rio de Janeiro.
- Walker, J. W. & A. Doyle. 1975. Palynology. Pp. 664-723. In: The bases of Angiosperm phylogeny. J. W. Walker (ed.). Ann. Missouri Bot. Gard. 62: 615-834.
- Wathrous, L. E. & Q. D. Wheeler. 1981. The outgroup comparison method of character analysis. Syst. Zool. 30: 1-11.
- Wiley, E. O. 1981. Phylogenetics. John Wiley & Sons, New York.
- Yi-zhen, Xi. 1980. Studies of pollen morphology and its systematic position in the order Piperales. Acta Bot. Sinica 22: 323-333.
- Yoshida, O. 1960. Embryologische Studien über die Ordnung Piperales. IV: Embryologie von Piper futokazura Sieb. et Lucc. J. Coll. Arts. Sci. Chiba. 3: 155-162.
- Yuncker, G. T. 1951. Piperaceae. In: J. A. Steyermark, Botanical exploration in Venezuela. I. Fieldiana Bot. 18: 204-209.
- _____. 1956. South American Piperaceae: New species and nomenclatural notes on two previously published taxa. Amer. J. Bot. 43: 161-168.
- _____. 1972. The Piperaceae of Brazil. I. Piper-Group I, II, III and IV. Hoehnea 2: 19-366.
- _____. 1973. The Piperaceae of Brazil. II. Piper-Group V, Ottonia, Pothomorphe, Sarcorhachis. Hoehnea 3: 29-284.