GENERA ORCHIDACEARUM

Volume 5

Epidendroideae (Part Two)

GENERA ORCHIDACEARUM

Volume 5

Epidendroideae (Part Two)

Edited by

Alec M. Pridgeon, Phillip J. Cribb,
Mark W. Chase
Royal Botanic Gardens, Kew

and

Finn N. Rasmussen
Botanical Laboratory, University of Copenhagen

OXFORD
UNIVERSITY PRESS

OXFORD
UNIVERSITY PRESS
Great Clarendon Street, Oxford OX2 6DP
Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide in
Oxford New York
Auckland Cape Town Dar es Salaam Hong Kong Karachi
Kuala Lumpur Madrid Melbourne Mexico City Nairobi
New Delhi Shanghai Taipei Toronto
With offices in
Argentina Austria Brazil Chile Czech Republic France Greece
Guatemala Hungary Italy Japan Poland Portugal Singapore
South Korea Switzerland Thailand Turkey Ukraine Vietnam
Oxford is a registered trade mark of Oxford University Press
in the UK and in certain other countries
Published in the United States
by Oxford University Press Inc., New York

First published 2009

British Library Cataloguing in Publication Data
Data available
Library of Congress Cataloging in Publication Data
Data available
Typeset by Newgen Imaging Systems (P) Ltd., Chennai, India
Printed in Great Britain
on acid-free paper by
——————————
ISBN 978–0–19–850713–0
10 9 8 7 6 5 4 3 2 1

CONTRIBUTORS

DR FÁBIO DE BARROS (FB)
Instituto de Botânica, Av. Miguel Estéfano 3687, 04301-012 São Paulo, SP, Brasil

JOÃO A. N. BATISTA (JB)
Departamento de Botânica, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627 Pampulha, 31270-910—Belo Horizonte Minas Gerais, Brasil

LUCIANO B. BIANCHETTI (LB)
Embrapa, Recursos Genéticos e Biotecnologia, Parque Estação Biológica, P.O. Box 02372, Brasília, DF 70770-901, Brasil

MARIO BLANCO (MB)
Herbarium, Florida Museum of Natural History, University of Florida, 385 Dickinson Hall, PO Box 117800, Gainesville, Florida 32611-7800, USA

DR GERMÁN CARNEVALI FERNÁNDEZ-CONCHA (GC)
Herbarium CICY, Centro de Investigación Científica de Yucatán A. C. (CICY), Calle 43. No. 130. Col. Chuburná de Hidalgo, 97200 Mérida, Yucatán, México

PROF MARK W. CHASE (MC)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

DR PHILLIP J. CRIBB (PC)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

PROF CALAWAY H. DODSON (CD)
Marie Selby Botanical Gardens, 811S. Palm Avenue, Sarasota, Florida 34236, USA

DR ROBERT L. DRESSLER (RD)
Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166-0299, USA

DR GÜNTER GERLACH (GG)
Botanischer Garten München-Nymphenburg, Menzinger Str. 65, D-80638 München, Germany

DR RENÉE J. GRAYER (RG)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

JOHAN HERMANS (JH)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

BERT KLEIN (BK)
Botanischer Garten München-Nymphenburg, Menzinger Str. 65, D-80638 München, Germany

DR SAMANTHA KOEHLER (SK)
Departamento de Genética, Escola Superior de Agricultura 'Luiz de Queiróz'—USP, Caixa Postal 83, Piracicaba, SP, Brasil, 13400-970

DR HUBERT KURZWEIL (HK)
National Parks Board, 1 Cluny Road, Singapore 259569

PROF PETER LINDER (PL)
Bolus Herbarium, University of Cape Town, 7700 Rondebosch, South Africa

SILVANA HELENA MONTEIRO (SM)
Universidade Estadual de Feira de Santana—UEFS, BR 116, KM 03—Campus Universitário—LABIO, Programa de Pós-Graduação em Botânica, CEP 44.031-460—Feira de Santana—Bahia, Brasil

DR ISIDRO OJEDA (IO)
Herbarium CICY, Centro de Investigación Científica de Yucatán A. C. (CICY), Calle 43. No. 130. Col. Chuburná de Hidalgo, 97200 Mérida, Yucatán, México

DR ALEC M. PRIDGEON (AP)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

PROF FRANCO PUPULIN (FP)
Universidad de Costa Rica, Jardín Botánico Lankester, P.O. Box 1031-705, Cartago, Costa Rica

IVÓN M. RAMÍREZ (IR)
Herbarium CICY, Centro de Investigación Científica de Yucatán A. C. (CICY), Calle 43. No. 130. Col. Chuburná de Hidalgo, 97200 Mérida, Yucatán, México

DR GUSTAVO A. ROMERO-GONZÁLEZ (GR)
Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, USA

DR GERARDO A. SALAZAR (GS)
Herbario Nacional de México (MEXU), Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-367, 04510 México, D.F., Mexico

DR RODRIGO SINGER (RS)
Depto Botânica—Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, Bloco IV Prédio 43432 Sala 207, Bairro Agronomia, CEP 91501-970—Porto Alegre—RS, Brasil

DR A. L. V. TOSCANO DE BRITO (TB)
Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, BR 116, Km 3 Campus Universitário, CEP 44031-460 Feira de Santana, Bahia, Brasil

PROF CASSIO VAN DEN BERG (CvdB)
Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, BR 116, Km 3 Campus Universitário, CEP 44031-460 Feira de Santana, Bahia, Brasil

DR NIGEL C. VEITCH (NV)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

DR WILLIAM MARK WHITTEN (MW)
Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA

JEFFREY WOOD (JW)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

EPIDENDROIDEAE (Part Two)

Fig. 584.2. Distribution map of *Vargasiella*.

Romero, G. A. (2003). *Vargasiella*. In Orchidaceae (G. Carnevali *et al.,* ed.), *Flora of the Venezuelan Guayana VII* (ed. P. E. Berry *et al.*), pp. 612–13. Missouri Botanical Garden Press, St. Louis.
Schweinfurth, C. (1958). *Vargasiella venezuelana. Botanical Museum Leaflets (Harvard University)*, **18**, 219–23.

SUBTRIBE ZYGOPETALINAE

Zygopetalinae Schltr., *Orchideen*, 417 (1915). Type: *Zygopetalum* Hook.
Huntleyinae Schltr., *Orchideen*, 425 (1915). Type: *Huntleya* Bateman ex Lindl.
Dichaeinae Schltr., *Orchideen*, 532 (1915). Type: *Dichaea* Lindl.
Cryptarrheninae Dressler, *Phytologia,* **21**, 443 (1971). Type: *Cryptarrhena* R.Br.
Cryptarrheneae Dressler, *Orquídea (Méx.),* **7**, 288 (1980). Type: *Cryptarrhena* R.Br.
Warreinae Szlach., *Fragm. Fl. Geobot. Suppl.,* **3**, 96 (1995). Type: *Warrea* Lindl.

Description

Epiphytic, terrestrial or rarely lithophytic, caespitose or creeping *herbs*, with or without pseudobulbs. *Roots* produced from rhizome or cauline tissue. *Pseudobulb*, when present, homoblastic or heteroblastic, or *stem* abbreviated or rarely elongate, erect to pendent, cylindrical to flattened, mostly enclosed by imbricating, sometimes foliaceous sheaths, occasionally provided with hyaline-scarious margins. *Leaves* several, distichous, plicate or conduplicate, dorsiventrally flattened, articulated or not, membranaceous to coriaceous or fleshy, often distinctly petiolate, the petiole rarely articulate to the lamina. *Inflorescence* lateral, single- to many-flowered, mostly unbranched, peduncle and rachis terete, glabrous, provided with one or more conduplicate bracts; floral bracts often double, external larger, internal bractlet ligulate. *Flowers* resupinate or not, membranaceous to fleshy, often scented. *Sepals* free, rarely connate at base, basal margins often inrolled-folded, apex sometimes uncinate, sometimes decurrent on column foot. *Petals* free, sometimes decurrent on column foot. *Labellum* free, mostly articulate with column foot, entire to trilobed or anchor-shaped, disc mostly provided with a callus or keel. *Column* terete or semiterete, straight or arcuate, usually with a column foot, often provided with inconspicuous to large wings and a well-developed clinandrium; anther terminal, incumbent, rarely subdorsal, operculate, usually two-celled; pollinia four, dorsiventrally compressed, in two superposed pairs mostly different in size, with stipe and viscidium, sometimes scarcely distinct; stigma ventral, mostly transverse, narrow, rarely elliptic-suborbicular; rostellum mostly acicular, often flanked by small to prominent lobes. *Capsule* elliptic-globose, sometimes echinate, six-keeled; seeds *Maxillaria*-type or *Chondrorhyncha* variant (*sensu* Dressler 1993). **(FP)**

Distribution

Zygopetalinae species occur throughout the American tropics, from southern Mexico (North America) and the West Indies to Brazil, Paraguay, Bolivia, and northern Argentina (South America). The northernmost taxa are species of the genera *Kefersteinia* and *Stenotyla*. In South America, *Warrea warreana* (Lodd. ex Lindl.) C.Schweinf. and *Zygopetalum maxillare* Lodd. extend to Paraguay and Argentina. The highest diversity in Zygopetalinae, both in number of genera and species, is to be found along the Andean chain of northwestern South America. **(FP)**

Anatomy

Anatomy of Zygopetalinae was recently examined by Stern *et al.* (2004) in the framework of their systematic and comparative study of anatomy of Maxillarieae. The analysis concerned 27 genera included in Zygopetalinae, plus *Cryptarrhena*, treated as a monospecific member of subtribe Cryptarrheninae. Additional information on velamen (Porembski and Barthlott 1988) was published for *Aganisia* (as *Acacallis*), *Dichaea, Galeottia* (*as Mendoncella*), *Huntleya, Pescatoria, Promenaea, Stenia, Warczewiczella* (as *Chondrorhyncha*), *Zygopetalum*, and *Zygosepalum*. A summary of their observations follows.

Leaf

SURFACE

Hairs glandular, sunken, two-celled, on both surfaces. Stomata tetracytic, abaxial only.

TRANSVERSE SECTION

Epidermal cells of most taxa are isodiametric and periclinally oriented, but papillate in *Benzingia* (treated as *Ackermania*). Mesophyll includes plain-walled water-storage cells, but only those of *Promenaea* and isolated species of *Batemannia, Chaubardiella, Cryptarrhena*, and *Kefersteinia* have branched bars. Water-storage cells absent in *Aganisia*, *Kefersteinia*, *Neogardneria*, *Otostylis, Pabstia*, and *Warrea*. Fibre bundles absent in most taxa, but present in *Koellensteinia*, *Otostylis*, some species of *Zygopetalum,* and *Zygosepalum*.

Pseudobulb

TRANSVERSE SECTION

Hairs and stomata absent. Cuticle smooth. Epidermal cell walls (stem structure was not described for the genera with fan-shaped habit of the *Huntleya* clade) are thickened on the cuticle side, with the exceptions of *Dichaea* and *Warrea*, which have thin-walled cells. Ground tissue consisting of larger, water-storage cells surrounded by smaller assimilatory cells that may contain cruciate starch grains; fibre bundles scattered throughout in *Otostylis*. Vascular bundles collateral, scattered. Conical silica bodies in stegmata associated with fibre bundles and phloem sclerenchyma except in *Promenaea xanthina* (Lindl.) Lindl. The aerial stem of *Dichaea* structurally differs from other pseudobulbous stems.

Root

TRANSVERSE SECTION

Velamen mostly 2–5 cell layers wide (up to 15 in *Warrea*), the cells usually thin-walled, thickened in *Benzingia* and *Galeottia*. Spiral thickenings of velamen cell walls include branched bars in *Cryptarrhena*. Tilosomes absent. Cortical parenchyma with empty idioblasts having branched, thickened bands on cell walls in *Chaubardia, Koellensteinia*, *Neogardneria* (Stern *et al.* 2004), and also in *Galeottia, Huntleya*, *Promenaea*, and *Warczewiczella* (Porembski and Barthlott 1988). Endodermis uniseriate. Vascular cylinder 6–18-arch. Pith parenchymatous. **(FP)**

Palynology

Information on pollen ultrastructure is available for *Dichaea, Kefersteinia*, *Promenaea, and Warczewiczella* and is listed below by genus. **(AP)**

Cytogenetics

Chromosome counts have been published for *Dichaea, Koellensteinia, Promenaea, Warrea*, and *Zygopetalum* and are listed below by genus. **(AP)**

Phylogenetics

In creating subtribe Zygopetalinae, Schlechter (1915) mainly distinguished it from the closely related Huntleyinae Schltr. on the basis of leaf vernation, convolute in Zygopetalinae and conduplicate in Huntleyinae. Both subtribes in Schlechter's system included pseudobulbous genera as well as genera without pseudobulbs (i.e., *Promenaea* was a member of the mostly pseudobulbless Huntleyinae). Some genera presently included in Zygopetalinae were assigned by Schlechter to other, related subtribes, such as *Batemannia* to Lycastinae, *Warrea* to Cyrtopodiinae, *Cryptarrhena* to Ornithocephalinae, and *Dichaea* to Dichaeinae.

Dressler and Dodson (1960) subsumed Huntleyinae and Zygopetalinae in Maxillariinae, stating that traditional criteria used to separate the two subtribes (i.e. characters of leaf vernation) were inconsistent because both conduplicate and convolute vernation are present in young growths of *Zygopetalum* and *Cochleanthes*. They placed genera close to *Zygopetalum* into an informal *Zygopetalum* alliance and suggested *Eulophia*-like ancestors for it. *Dichaea* was placed as the monospecific member of its own alliance within Oncidiinae and considered closely related to the *Ornithocephalus* alliance, including *Cryptarrhena* among other genera.

Dressler (1981) assigned Zygopetalinae to Maxillarieae, with 26 genera grouped in four closely related alliances on the basis of characteristics of corms or pseudobulbs, leaf vernation, and inflorescence type. One of the alliances included only a genus of uncertain relationships, *Vargasiella*. The series with plicate leaves and homoblastic pseudobulbs (*Warrea* and its close relatives) was considered the primitive element of the subtribe. *Dichaea* was assigned to the monospecific subtribe Dichaeinae Schltr. (also included in the Maxillarieae), but a possible derivation of this anomalous genus from some Zygopetalinae-like ancestors was suggested for the first time. *Cryptarrhena* was placed in its own tribe, Cryptarrheneae, but the latter was ascribed to subfamily Epidendroideae rather than to Vandoideae.

In the last 15 years, several systems of classification of Maxillarieae were proposed, often disagreeing in the circumscription of Zygopetalinae. Senghas and Gerlach (1992–1993, 1993) mainly followed Schlechter in retaining Zygopetalinae, Huntleyinae, and Dichaeinae but mainly distinguished the first two subtribes by presence or absence of distinct pseudobulbs. In his later classification, Dressler (1993) broadened his previous concept of Zygopetalinae to include *Dichaea* and *Scuticaria*. *Cryptarrhena* was assigned to subtribe Cryptarrheninae Dressler, but on the basis of its seed structure the subtribe is now included in tribe Cymbidieae together with Zygopetalinae. *Vargasiella* was lumped into Zygopetalinae, but its phylogenetic position within Cymbidieae is now considered isolated, warranting a separate subtribe. In 1993, subtribe Vargasiellinae (originally proposed by Schweinfurth) was supported by evidence about the pollinarium structure of *Vargasiella* (Romero and Carnevali 1993).

Szlachetko (1995) split the genera of Zygopetalinae into three tribes and six subtribes. Dressler's alliances were formally recognized as subtribes Warreinae, Zygopetalinae, and Huntleyinae within tribe Zygopetaleae; *Cryptarrhena* was still the monospecific member of tribe Cryptarrheneae, subtribe Cryptarrheninae, and *Dichaea* and *Vargasiella* were monotypic genera of subtribes Dichaeinae and Vargasiellinae in tribe Dichaeae, also including subtribe Pachyphyllinae (with *Fernandezia* and *Pachyphyllum*).

The combined molecular analysis of Maxillarieae (Whitten *et al.* 2000), although mostly focused on the systematics of Stanhopeinae, indicated strong bootstrap support for a monophyletic Zygopetalinae, including the two morphologically

anomalous genera *Cryptarrhena* and *Dichaea*. The subtribe has traditionally been placed in Maxillarieae, but molecular data indicated that the tribe is sister to a paraphyletic grade of cymbidioid taxa, and Chase *et al.* (2003) lumped it with Cymbidiinae, Eulophiinae, Bromheadiinae, and Catasetinae into a broader, monophyletic Cymbidieae.

Phylogenetic relationships of the subtribe were recently evaluated using parsimony analysis of combined sequence data of nuclear and plastid DNA for 104 ingroup and two outgroup taxa (Whitten *et al.* 2005). The analysis confirmed the monophyly of Zygopetalinae, comprising a *Zygopetalum* grade/clade (genera with prominent, heteroblastic pseudobulbs and usually plicate, revolute leaves); a *Huntleya* clade (pseudobulbs mostly absent or reduced, leaves conduplicate), including the *Chondrorhyncha* complex plus *Dichaea* and a weakly supported *Cryptarrhena*; and a *Warrea* grade/clade (pseudobulbs homoblastic, leaves plicate). In spite of their placement on relatively long branches, sequence data from *matK, trnL-F*, and ITS (Whitten *et al.* 2000, 2005) as well as from *rbcL* (Cameron *et al.* 1999) support the inclusion of *Dichaea* and *Cryptarrhena* in Zygopetalinae.

The end result is a subtribe difficult to characterize in terms of morphological synapomorphies. Most genera in the subtribe have four superposed, dorsiventrally flattened pollinia; a transverse, narrow, slit-like stigma (with the notable exception of *Dichaea*); a column provided with a ventral keel; a tooth (often basal) or an infrastigmatic ligule; and a perianth variously spotted, blotched or flushed with violet, a colour rarely found in other Neotropical orchids. Among the genera of the *Huntleya* clade, an obvious synapomorphy is the presence of two floral bracts, greatly different in shape and size, the adaxial bract large and cucullate and the inner, apical bract, abaxial to the lip, smaller and ligulate. Ecologically, species of the subtribe exhibit a tendency to occupy shady, suboptimal niches in the forest canopy, sometimes associated with transformations in the epidermis (*Benzingia*, *Dichaea* spp.). The sampling of taxa for molecular analyses is more complete for the *Huntleya* clade (particularly in the so-called *Chondrorhyncha* complex), in which there have been several new genera erected and taxonomic transfers based on DNA evidence. Sampling within the *Zygopetalum* grade/clade is still sparse, and extractable material of a larger number of taxa is required to understand phylogenetic relationships among the basal nodes of the subtribe. Nevertheless, the cladograms presented by Whitten *et al.* (2005) revealed several inconsistencies in current generic concepts, such as polyphyly of *Koellensteinia*, *Zygopetalum,* and *Zygosepalum* as now circumscribed. **(FP)**

Ecology

Species are mainly inhabitants of constantly wet, temperate premontane forests at medium elevations, where they mostly grow as epiphytes in the shade of the lower canopy and main trunks of trees. Zygopetalinae are far less frequent in lowland seasonal forests. Among epiphytic species, a strong specificity in host relationship has been recorded for *Zygopetalum maxillare*, which grows almost exclusively on the stems of tree ferns. Relatively few species are obligatorily terrestrial. Some are restricted to particular kind of soils; *Zygosepalum tatei* Ames & C.Schweinf. is confined to the highly acidic soils of some Venezuelan tepuis. **(FP)**

Cultivation

Although species of Zygopetalinae range from near sea level to over 2500 m, most of the taxa can be grown in intermediate temperatures. With some exceptions, plants of Zygopetalinae are adapted to shaded, wet conditions of the lower canopy and main trunks of host trees, which are frequently covered with thick layers of mosses, and they should be accordingly cultivated in a shaded area, providing them with constant humidity and frequent watering year-round. **(FP)**

Taxonomic literature

Cameron, K. M., Chase, M. W., Whitten, W. M., Kores, P. J., Jarrell, D. C., Albert, V. A., Yukawa, T., Hills, H. G., and Goldman, D. H. (1999). A phylogenetic analysis of the Orchidaceae: evidence from *rbcL* nucleotide sequences. *American Journal of Botany*, **86,** 208–24.

Chase, M. W., Cameron, K. M., Barrett, R. L., and Freudenstein, J. V. (2003). DNA data and Orchidaceae systematics: a new phylogenetic classification. In *Orchid Conservation* (ed. K. W. Dixon, S. P. Kell, R. L. Barrett, and P. J. Cribb), pp. 69–89**.** Natural History Publications, Kota Kinabalu, Sabah, Malaysia.

Dressler, R. L. (1980). Orquídeas huérfanas II. *Cryptarrhena* – una nueva tribu, Cryptarrheneae. *Orquídea (México)*, **7**, 283–8.

Dressler, R. L. (1981). *The orchids: natural history and classification*. Harvard University Press.

Dressler, R. L. (1993). *Phylogeny and classfication in the orchid family*. Dioscorides Press, Portland, Oregon.

Dressler, R. L. and Dodson, C. H. (1960). Classification and phylogeny in the Orchidaceae. *Annals of the Missouri Botanical Garden*, **47**, 25–67.

Kränzlin, F. W. L. (1923). *Dichaea*. *In Das Pflanzenrreich* (ed. H. G. A. Engler), **4(50),** 33–64.

Pfitzer, E. H. H. (1887). *Entwurf einer natürlichen Anordnung der Orchideen*. Carl Winter's Universitätsbuchhandlung, Heidelberg.

Romero, G. A. and Carnevali, G. (1993). Reappraisal of subtribe Vargasiellinae (Maxillarieae, Orchidaceae). *Novon*, **3**, 79.

Schlechter, R. (1914–15). *Die Orchideen, ihre Beschreibung, Kultur und Züchtung*. Paul Parey, Berlin.

Senghas, K. and Gerlach, G. (1992–1993). Subtribus Huntleyinae. *In Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), pp. 1620–74. Paul Parey, Berlin.

Senghas, K. and Gerlach, G. (1993). Subtribus Zygopetalinae. *In Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), pp. 1674–1727. Paul Parey, Berlin.

Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.

Whitten, W. M., Williams, N. H., and Chase, M. W. (2000). Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. *American Journal of Botany,* **87**, 1842–55.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

Artificial key to the genera of Zygopetalinae (FP)

1. • Plants without pseudobulbs (or apparently so) 2
   • Plants with pseudobulbs 24
2. • Inflorescence few- to many-flowered 3
   • Inflorescence single-flowered. 4
3. • Inflorescence many-flowered (> 10); flowers < 1 cm wide; labellum 4-lobed . . . . . **595. *Cryptarrhena***
   • Inflorescence few-flowered (up to 5); flowers > 4 cm wide; labellum flabellate . . . . . **618. *Zygopetalum***
4. • Stem much longer than leaves; labellum mostly anchor-shaped; stigma elliptic-suborbicular, with a basal ligule. . . . . **597. *Dichaea***
   • Stem much shorter leaves; labellum never anchor-shaped; stigma slit-like, without ligule (*Chondrorhyncha* complex) 5
5. • Plants laxly pendent; leaves gray-green, minutely papillose . . . . . **588. *Benzingia***
   • Plants erect; leaves not papillose or gray-green 6
6. • Flowers non-resupinate 7
   • Flowers resupinate or pendent. 8
7. • Apex of labellum entire; viscidium of pollinarium curling after removal . . . . . **589. *Chaubardiella***
   • Apex of labellum erose; viscidium of pollinarium not curling after removal . . . . . **588. *Benzingia***
8. • Labellum deeply saccate 9
   • Labellum open or infundibuliform, not deeply saccate. 10
9. • Labellum distally closed; pollinarium with a distinct stipe . . . . . **612. *Stenia***
   • Labellum distally open; pollinarium with a small stipe . . . . . **588. *Benzingia***
10. • Callus basal. 11
    • Callus near or reaching the middle of labellum 13
11. • Callus laminar or umbonate, bilobed or with 2 or 4 teeth, without terminal bristles 12
    • Callus with more than 6 teeth, each one ending in an acuminate bristle . . . . . **602. *Huntleya***
12. • Callus raised, peltate or bilobed; column with a ventral tooth . . . . . **604. *Kefersteinia***
    • Callus flat, with 2 or 4 teeth; column without a ventral tooth . . . . . **613. *Stenotyla***
13. • Inflorescence slender; viscidium curling on removal; column with a ventral tooth . . . . . **604. *Kefersteinia***
    • Inflorescence stout; viscidium not curling on removal; column without a ventral tooth 14
14. • Flowers gullet-shaped; basal margins of the labellum upturned, surrounding column . . . . **614. *Warczewiczella***
    • Flowers patent; basal margins of labellum flat, not surrounding column 15
15. • Column with a ventral keel. . . . . **594. *Cochleanthes***
    • Column without ventral keel 16
16. • Callus semicircular, with raised, rounded keels. . . . . **610. *Pescatoria***
    • Callus flattened or bilobed, not semicircular 17
17. • Basal sheaths boldly spotted and blotched with purple; labellum callus broad and laminar, with many irregular teeth; stipe broad, shield-shaped . . . . . **599. *Euryblema***
    • Basal sheaths green; labellum callus narrow or triangular, with few teeth; stipe narrow near viscidium 18
18. • Labellum with a second thickening distal to bilobed callus; pollinarium with a distinct stipe . . . . **593. *Chondroscaphe***
    • Labellum without a distal thickening; pollinarium with a small, indistinct stipe. 19
19. • Labellum acuminate . . . . . **588. *Benzingia***
    • Labellum truncate, rounded or retuse 20
20. • Callus broad, bilobed, thick and fleshy . . . . **596. *Daiotyla***
    • Callus narrowing at apex, not thick and fleshy 21
21. • Ventral surface of column with globose, hairy appendages. . . . . **598. *Echinorhyncha***
    • Ventral surface of column without globose, hairy appendages. 22
22. • Labellum with a prominent keel below the bilobed callus; labellum blade pilose. . . . . **585. *Aetheorhyncha***
    • Labellum without keel below the bilobed callus; labellum blade glabrous 23
23. • Viscidium ovate; stipe indistinct . . . . . **603. *Ixyophora***
    • Viscidium subpandurate; stipe distinct . . . . . **592. *Chondrorhyncha***
24. • Pseudobulbs homoblastic. 25
    • Pseudobulbs heteroblastic 30
25. • Plant < 10 cm tall; flowers < 1 cm wide; callus of labellum with 4 lateral teeth and a central tooth produced by the distal extension of the basal keel . . . **591. *Cheiradenia***
    • Plant > 15 cm tall; flowers > 2 cm wide; callus of labellum different 26
26. • Flowers pendent, > 5 cm wide; callus a single, high, fleshy keel . . . . . **615. *Warrea***
    • Flowers patent, < 3 cm wide; callus many-ridged, flabellate-digitate or horseshoe-shaped 27
27. • Lateral sepals enrolled-folded at base; column provided with a prominent, ventral keel . . . . . **617. *Warreopsis***
    • Lateral sepals not folded at base; column without ventral keel 28
28. • Callus of disc composed of 3–5, longitudinal to radiating, apically digitate ridges . . . . . **616. *Warreella***
    • Callus of disc crenulate or transversely semicircular to W-shaped 29
29. • Column with subquadrate wings . . . . . **607. *Otostylis***
    • Column wingless . . . . . **609. *Paradisanthus***
30. • Apical leaf of pseudobulb vestigial, scale-like. 31
    • Apical leaf or leaves well developed 32
31. • Callus near middle of labellum, low, with 2 or 4 teeth. . . . . **613. *Stenotyla***

- Callus at base of labellum, high, many-ridged. . . . . **601. *Hoehneella***

32. • Inflorescence simultaneously many-flowered (>15 flowers); labellum anchor-shaped, 5-lobed. . . . . **595. *Cryptarrhena***
- Inflorescence single- to few-flowered (up to 10 flowers simultaneously open); labellum simple or trilobed, never anchor-shaped 33

33. • Flowers < 2.5 cm wide; callus bilobed, retrorse . . . . . **605. *Koellensteinia***
- Flowers > 3 cm wide; callus various, not retrorse 34

34. • Lateral sepals adnate to margins of column foot, forming a conspicuous chin 35
- Lateral sepals adnate to column foot near apex, without a chin or the chin inconspicuous 36

35. • Lateral sepals gibbose at base; lobes of labellum fimbriate; column with prominent auricles . . . . . **600. *Galeottia***
- Lateral sepals more or less concave at base but never gibbose; lateral lobes of labellum entire to erose, not fimbriate; column without prominent auricles . . . . . **587. *Batemannia***

36. • Anther with a prominent, fleshy, subulate apex . . . . . **619. *Zygosepalum***
- Anther without a prominent, fleshy, subulate apex 37

37. • Callus of labellum fan-shaped, composed of radiating ridges 38
- Callus of labellum not fan-shaped, nor composed of radiating ridges 40

38. • Inflorescence single-flowered. . . . . **589. *Chaubardia***
- Inflorescence with more than one flower 39

39. • Floral bracts cymbiform . . . . . **606. *Neogardneria***
- Floral bracts not cymbiform. . . . . **618. *Zygopetalum***

40. • Plants creeping. . . . . **586. *Aganisia***
- Plants caespitose 41

41. • Plant < 15 cm tall; inflorescence produced from mature pseudobulb; labellum subsessile, or the claw short . . . . . **611. *Promenaea***
- Plant > 25 cm tall; inflorescence produced from immature pseudobulb; labellum with a distinct claw. . . . . **608. *Pabstia***

585. AETHEORHYNCHA

Aetheorhyncha Dressler, *Lankesteriana*, **5,** 94 (2005). Type species: *Aetheorhyncha andreettae* (Jenny) Dressler (basionym: *Chondrorhyncha andreettae* Jenny)

Derivation of name

The name is derived from the Greek *aethes*, strange, different, and *rhynchos*, beak, snout, referring to the beak-like rostellum shared with *Chondrorhyncha*. **(FP)**

Description (Plate 190; Fig. 585.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from the rhizome. *Stem* abbreviated, enclosed by 7–9 imbricating, mostly foliaceous sheaths, provided with hyaline margins. *Leaves* conduplicate, articulate, membranaceous, oblanceolate to oblong-elliptic, acuminate, abaxially carinate, narrowed at base into an indistinct, conduplicate petiole. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths; peduncle terete, erect, provided at base with three conduplicate bracts; floral bract double, conduplicate, shorter than ovary, the external one widely ovate, loose, the subopposite internal bractlet ligulate. *Flowers* resupinate, with creamy white sepals, flushed yellow toward base, petals white, labellum white marked with a yellow blotch on disc, midlobe blotched and spotted with red. *Dorsal sepal* free, elliptic-lanceolate, acute, concave. *Lateral sepals* linear-lanceolate, acute, spreading-arcuate, inrolled-folded, overlapping at the base to form a funnel-shaped chamber, apex uncinate. *Petals* oblong-elliptic, obtuse, porrect, apically revolute. *Labellum* articulate with column foot, obovate to elliptic, trilobed, pubescent, base rounded, apex subacute, deflexed, lateral lobes rounded, erect, enfolding column, midlobe suborbicular, abruptly reflexed, distal margins crisped; disc with a distinct, longitudinal, median keel running from base to about the first third of labellum and a low, bilobed, truncate callus extending into centre of disc. *Column* straight, with a distinct foot, dilated at apex into inconspicuous stigmatic wings, sparsely pubescent adaxially; anther cap cucullate, ovate, flattened, two-celled, pollinia four, in two subequal pairs, on a broad stipe scarcely distinct from the rectangular-subtriangular, truncate, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 585.2)

A monospecific genus from southern Ecuador and possibly Peru (South America). The Peruvian record of *Chondrorhyncha andreettae* Jenny was given by Bennett and Christenson (1993) on the basis of a plant collected in the province of Huánuco, but the description and corresponding illustration differ from typical *A. andreettae* in plant habit, lip and callus shape, and pollinarium morphology. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Aetheorhyncha*. **(NV, RG)**

Phylogenetics

The only named species of *Aetheorhyncha* was originally described as a member of *Chondrorhyncha* Lindl. (Jenny 1989), a genus with which it shares a small, toothed callus in the centre of the disc. It is superficially similar to *Chondroscaphe*, but it lacks the second, distal callus on the lip that characterizes the latter. Studies based on DNA sequence data (Whitten *et al.* 2005) showed that *Aetheorhyncha* is sister to *Ixyophora* and *Chaubardiella* (in a weakly supported clade), but gross morphology of the flower and shape of the callus are different in the two groups. The pubescent

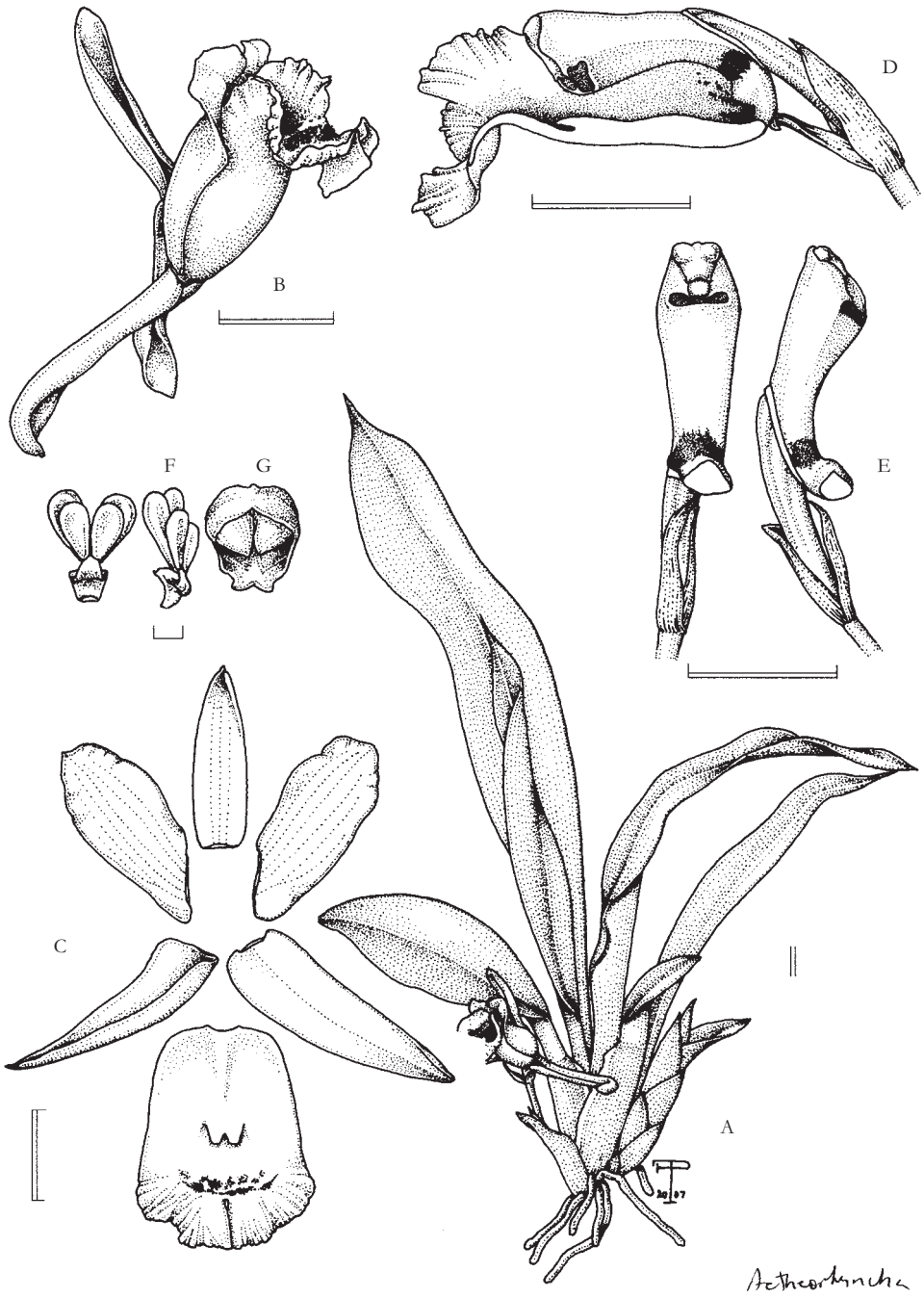


Fig. 585.1. *Aetheorhyncha andreettae* (Jenny) Dressler. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column and labellum, lateral view (the labellum in longitudinal section); E. Column, ventral and side views; F. Pollinarium (ventral and side views) and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 6609* (Ángel Andreetta Research Center on Andean Orchids Spirit Collection).

lamina of the lip, strong median keel basal to the bilobed callus, and narrow, truncate viscidium distinguish the genus among other relatives of the *Chondrorhyncha* complex. **(FP)**

Ecology

The species occurs as an epiphyte in evergreen, wet forests at around 900 m along the eastern Andean slopes of southern Ecuador. Flowering has been recorded in January in natural habitats and in July in plants cultivated in the Northern Hemisphere. **(FP)**

Pollination

Pollination vectors of *Aetheorhyncha* are unknown. **(FP)**

Uses

There are no known uses for the species. **(FP)**

Cultivation

Native to the premontane, wet forest of the Amazonian slopes of the Andes, plants of *Aetheorhyncha* should be grown in shade and

Fig. 585.2. Distribution map of *Aetheorhyncha.*

intermediate to warm temperatures with high levels of humidity and frequent watering year-round. **(FP)**

Taxonomic literature

Bennett, D. E. and Christenson, E. A. (1993). *Chondrorhyncha andreettae* Jenny. *Icones orchidacearum Peruvianum*, **1,** sub pl. 16.

Jenny, R. (1989). Zwei neu Arten aus der *Chondrorhyncha*—Verwandtschaft, *Chaubardiella pacuarensis* und *Chondrorhyncha andreettae*. *Orchidee (Hamburg)* **40**, 91–4.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

586. AGANISIA

Aganisia Lindl., *Edwards's Bot. Reg.*, **25** (Misc.), 45 (1839). Type species: *Aganisia pulchella* Lindl.

Acacallis Lindl., *Fol. Orch.*, **4,** 30 (1853). Type species: *Acacallis cyanea* Lindl.

Kochiophyton Schltr. ex Cogn., in C.F. P. von Martius (ed.), *Fl. Bras.*, **3(6),** 574 (1906). Type species: *Kochiophyton negrense* Schltr. ex Cogn.

Derivation of name

The name is derived from the Greek *aganos*, mild, desirable, in reference to the pleasing appearance of the plant. **(FP)**

Description (Plate 191; Fig. 586.1)

Epiphytic or terrestrial, pseudobulbous *herbs* with a creeping rhizome covered by fibrous sheaths. *Roots* terete, produced at intervals along rhizome or at nodes near pseudobulbs. *Pseudobulb* cylindric or oblong-conic to fusiform, often complanate to convex on one side, cryptic when young, enclosed by 2–9 imbricating, scarious, sometimes evanescent sheaths, unifoliate (rarely bifoliate). *Leaves* plicate, weakly coriaceous, elliptic to oblong, acute to acuminate, abaxially carinate along midnerve and one vein on either side, narrowed at base into a conduplicate, channeled petiole, clear to dark green, shiny on upper surface. *Inflorescences* lateral, a few(2)- to many(10)-flowered raceme produced laterally, shorter than or subequal to leaf; peduncle terete, erect to arching or laxly pendent, provided with 2–9, papery, conduplicate bracts; floral bracts lanceolate to triangular-ovate, conduplicate, shorter than ovary. *Flowers* resupinate, sepals white to pale blue-lavender or blue-mauve with adaxial surfaces flushed pink, petals white to pale blue-lavender or bluish mauve, pale pink-flushed white within; labellum white with yellow centre or blue-lavender with dark purple-lavender margins or gold-bronze with a mauve red or bluish purple centre; callus ivory white to yellow-cream or orange-pink, sometimes with brown on margins. *Dorsal sepal* free, elliptic-lanceolate to obovate, acute to abruptly subacuminate, usually concave, abaxially carinate. *Lateral sepals* lanceolate to oblong-obovate, acute to abruptly subacuminate, concave, abaxially carinate. *Petals* oblong-elliptic to suborbicular, acute to obtuse to rounded, apiculate. *Labellum* articulate with column foot, pandurate, trilobed, base with an obcuneate claw, apex subacute to rounded, apiculate, lateral lobes elliptic to obliquely triangular, midlobe ovate to flabellate or subcordate, concave, distal margins entire to undulate-serrate or long-fimbriate; disc with a fleshy, erect callus, apically provided with finger-like, fleshy projections, or a transverse, trilobed, thick ridge. *Column* straight to arcuate, with or without a distinct foot, winged from below middle, with prominent, oblong-falcate to subquadrate, rounded stigmatic wings; anther cap cucullate, ovate to obovate, flattened, two-celled, pollinia four, in two subequal pairs, on a laminar, narrowly elliptic to trapezoid or obovate stipe attached to an elliptical, hyaline viscidium; stigma transversely elliptic. **(FP)**

Distribution (Fig. 586.2)

Aganisia is a genus of four species from Trinidad and tropical South America, where it has been recorded from Venezuela to central Brazil, and from the Amazonian regions of Colombia, Ecuador, Peru, and Bolivia. **(FP)**

Phytochemistry

Lüning (1964) recorded that *A. cyanea* gave a positive result on screening for alkaloids. According to Kaiser (1993), the floral fragrance of this species comprises up to 80% myrcene together with 1,8-cineole, caryophyllene, ocimene, and *para*-cresol as minor components. Gerlach and Schill (1991) recorded only myrcene (91%) and 1,8-cineole (1%) as components. The floral fragrance of *A. pulchella* comprises geranylacetone as the major

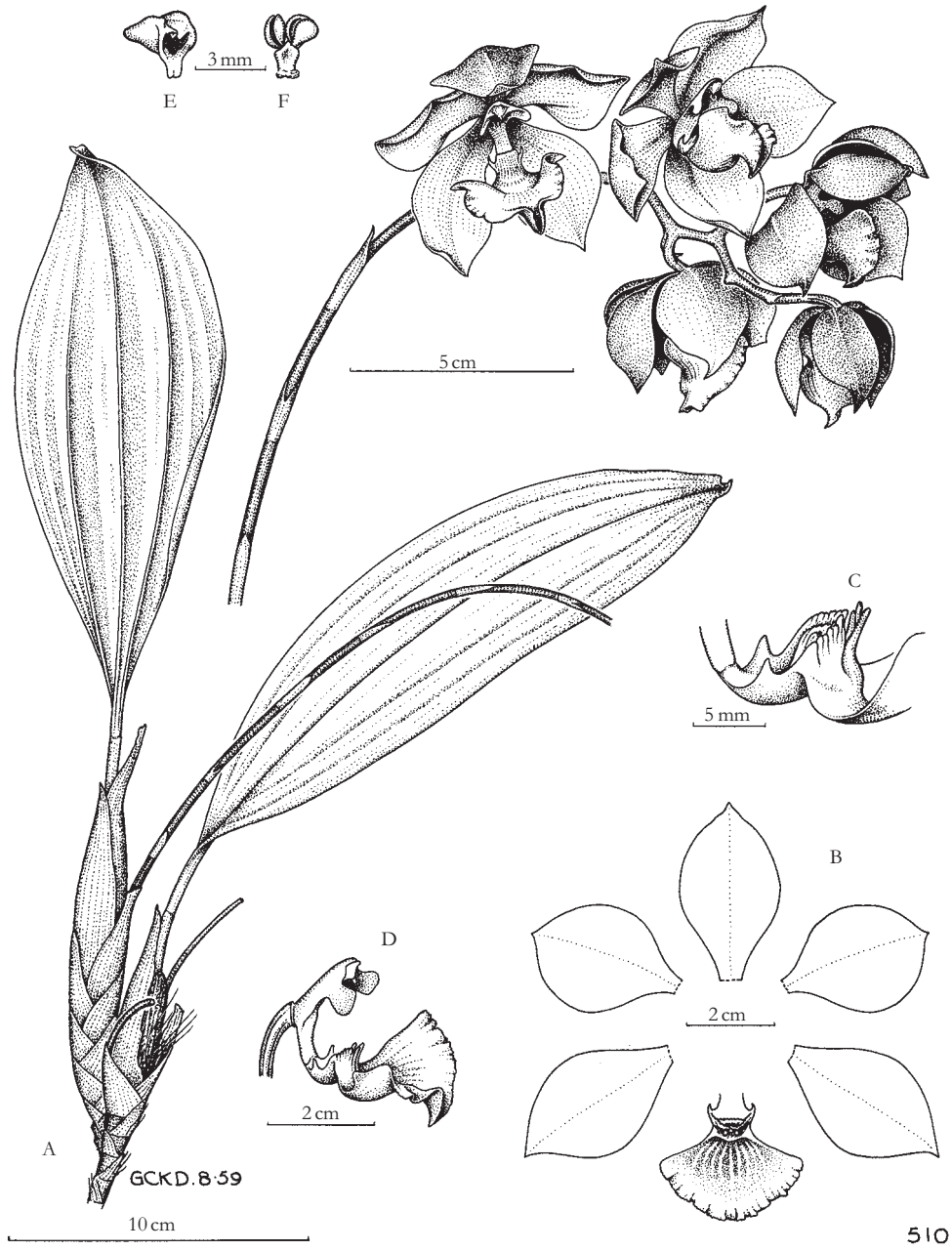


Fig. 586.1. *Aganisia cyanea* (Lindl.) Rchb.f. A. Habit, with inflorescence; B. Perianth, dissected; C. Labellum callus; D. Column and labellum, side view; E. Anther cap, ventral view; F. Pollinarium. Drawn by G.C.K. Dunsterville. Originally published as *Acacallis cyanea* Lindl. in *Venezuelan Orchids Illustrated,* **2**, 32 (1961). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

component together with smaller amounts of ionol and (*E*)-β-ocimene (Gerlach and Schill 1991). Many minor components of this scent remain unidentified. **(NV, RG)**

Phylogenetics

Garay (1973) and Senghas and Gerlach (1993) favoured recognition of *Acacallis* and *Aganisia* as distinct genera, mainly on the basis of plant habit (supposedly pendent in *Acacallis*, creeping to scandent in *Aganisia*), a column foot, one- versus three-toothed rostellum and shape of stipe (trapezoidal to obovate in *Acacallis* versus linear in *Aganisia*). On the basis of cladistic analysis of combined nuclear and plastid DNA sequence data (Whitten *et al.* 2005), the species pertaining to *Aganisia*/*Acacallis* form a weakly supported clade among the groups of genera related to *Zygopetalum* and allies, but this topology is weakly supported so relationships are best described as unclear. The *Aganisia*/*Acacallis* clade also includes a species originally described as a member of *Aganisia*, *A. boliviensis* Rolfe ex Rusby, and later transferred by Schlechter to the genus *Koellensteinia*. Molecular analyses confirmed the original placement of this taxon, although on a weakly supported branch, as a close relative of the remaining

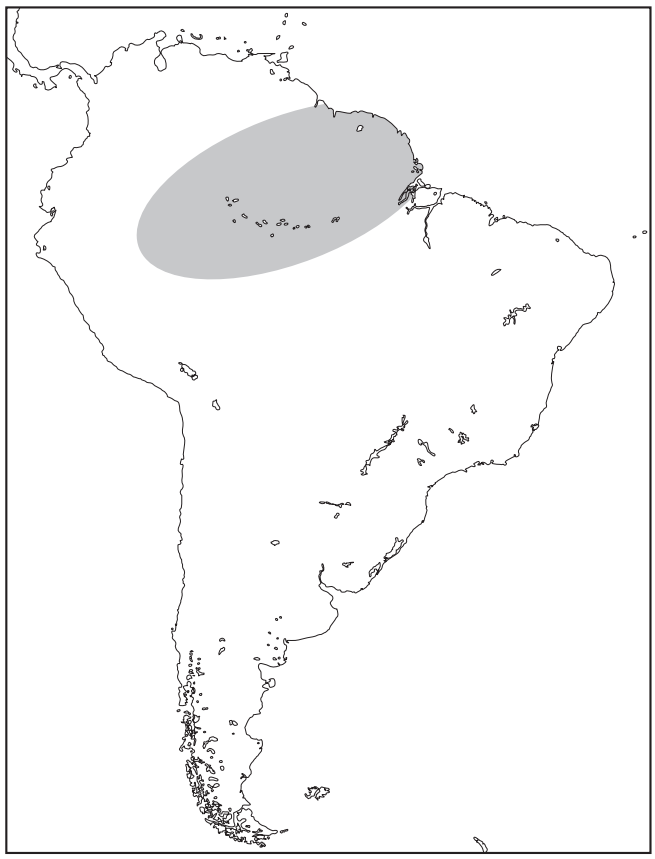


Fig. 586.2. Distribution map of *Aganisia*.

species of the *Aganisia/Acacallis* group. All species of the group already have validly published names under *Aganisia* (*A. boliviensis*, *A. cyanea* (Lindl.) Rchb.f., *A. fimbriata* Rchb.f., *A. pulchella* Lindl.), so no nomenclatural changes are required to reflect results of molecular analysis. The genus is characterized by a scrambling (rarely pendent) habit with distant, heteroblastic, narrowly conical-fusiform, one- (rarely two-) leaved pseudobulbs, plicate leaves, a widely ovate to flabellate or subcordate, concave lip, and basal, fleshy, erect, ridged callus, apically provided with finger-like, fleshy projections. **(FP)**

Ecology

Species of the genus occur as epiphytes in hot, tropical to premontane rain forests, usually at elevations of 100–500 m, rarely up to 1000 m. Flowering has been mostly recorded in natural habitats from January to August, but plants have also been sporadically found in flower in October; it is likely that they flower throughout the year on maturing growths. **(FP)**

Pollination

The pollinator of *Aganisia* is unknown, but like other species in the subtribe it is probably pollinated by *Eulaema* bees, which likely receive the pollinarium on the rear of the head. **(FP, GR)**

Uses

Other than as cultivated ornamentals, there are no known uses for the species. **(FP)**

Cultivation

With their characteristically creeping rhizome and distant pseudobulbs, plants of *Aganisia* should be grown in baskets or preferably mounted on large slabs. They require a constantly humid atmosphere and should be maintained in moderate shade with frequent watering throughout the year. **(FP)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–1727. Paul Parey, Berlin.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

587. BATEMANNIA

Batemannia Lindl., *Edwards's Bot. Reg.*, 20, t. 1714 (1834). Type species: *Batemannia colleyi* Lindl.

Petronia Barb.Rodr., *Gen. Sp. Orch.*, **1,** 106 (1877), *nom. illeg.* [*non Petronia* Jungh. 1845 (Asteraceae)]. Type species: *Petronia regia* Barb.Rodr.

Derivation of name

The name honours the British collector and orchid cultivator James Bateman (1811–1897), plant collector and author of the monumental *Orchids of Mexico and Guatemala*, *A Monograph of* Odontoglossum, and *A Second Century of Orchidaceous Plants*, published in London between 1837 and 1874. **(FP)**

Description (Plate 192; Fig. 587.1)

Epiphytic, caespitose *herbs*. *Roots* terete, flexuous, produced along rhizome near pseudobulbs. *Pseudobulb* heteroblastic, ovoid to oblong-ovoid, tetragonous, 1–3-leaved at apex, when young concealed by 3 or 4 scarious, eventually evanescent sheaths. *Leaves* subplicate-venose, membranaceous to subcoriaceous, lanceolate-elliptic to elliptic-oblong, acute, acuminate, abaxially obscurely carinate along nerves, narrowed at base into a conduplicate petiole, clear to dark green, shiny on upper surface. *Inflorescence* lateral, a 1–7-flowered raceme produced on an immature pseudobulb, emerging from axils of lower sheaths; peduncle terete, suberect to pendent, basally provided with 2–4, membranaceous, oblong-lanceolate, conduplicate, loose bracts, rachis sinuous to fractiflex; floral bracts widely ovate, conduplicate-cymbiform, loose, shorter than ovary. *Flowers* resupinate, sepals and petals greenish yellow or olive green, often suffused with brown, or with purple-brown blotches, labellum white

Fig. 587.1. *Batemannia colleyi* Lindl. A. Habit, with inflorescence; B. Perianth, dissected; C. Labellum, dorsal view; D. Labellum (sectioned), side view; E. Column, labellum, and lateral sepals, side view; F. Column, ventral view; G. Anther cap, ventral view; H. Pollinarium. Drawn by G.C.K. Dunsterville. Originally published in *Venezuelan Orchids Illustrated,* **1**, 48 (1959). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

or pale yellow, often finely spotted with purple, column white, spotted purple underneath. *Dorsal sepal* free, elliptic-lanceolate to widely elliptic, acute to acuminate, usually concave, often reclinate over the column. *Lateral sepals* narrowly linear-elliptic, subfalcate, curved, acute, inflexed-replicate toward base, apex revolute. *Petals* oblong-elliptic to lanceolate-oblong, subacute to obtuse or rounded, apiculate, sometimes porrect and flanking column. *Labellum* articulate with column foot, trilobed, subsessile or provided with an obcuneate claw, lateral lobes elliptic to semiobovate or subfalcate-oblong, rounded to subacute, erect, midlobe subspatulate-obovate to oblong, rounded to emarginate, reflexed, margins sometimes crenulate; disc with a fleshy, laminar, callus extending from the base to middle of the labellum, distal portion free, sometimes denticulate-ciliate. *Column* straight to arcuate, with a distinct foot, broadened toward apex, often provided with a prominent, irregularly erose clinandrium; anther cap cucullate, obovate, flattened, two-celled, pollinia four, in two pairs subequal or of different sizes, subsessile on a laminar, elliptic to trapezoid or obovate, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 587.2)

Batemannia is a genus of five species from tropical South America, ranging from Trinidad to northern Brazil, and from Venezuela to the Amazonian regions of Colombia, Ecuador, Peru, and Bolivia (South America). **(FP)**

Phytochemistry

A survey of alkaloid content in Orchidaceae recorded a negative result for *B. colleyi* (Lüning 1964). **(NV, RG)**

Phylogenetics

Fourteen species have been described in *Batemannia*, but after removal of species better assigned to *Huntleya* and *Galeottia*, only five taxa survive critical examination. Some species once assigned to *Batemannia* (i.e., *Galeottia fimbriata* (Linden & Rchb.f.) Schltr.) were moved among *Batemannia*, *Galeottia*, *Mendoncella*, *Zygosepalum,* and *Zygopetalum*, showing the inherent difficulty of assessing clear generic boundaries for this group of plants on the basis of morphological characters alone. Garay (1973) considered the genus easily separable from *Galeottia* by the lack of distinct auricles on the column and lateral sepals not gibbose at the base. *Batemannia* has been recently revised by Manara and Bergold (2004), who first recorded the presence of *B. armillata* Rchb.f. in Venezuela.

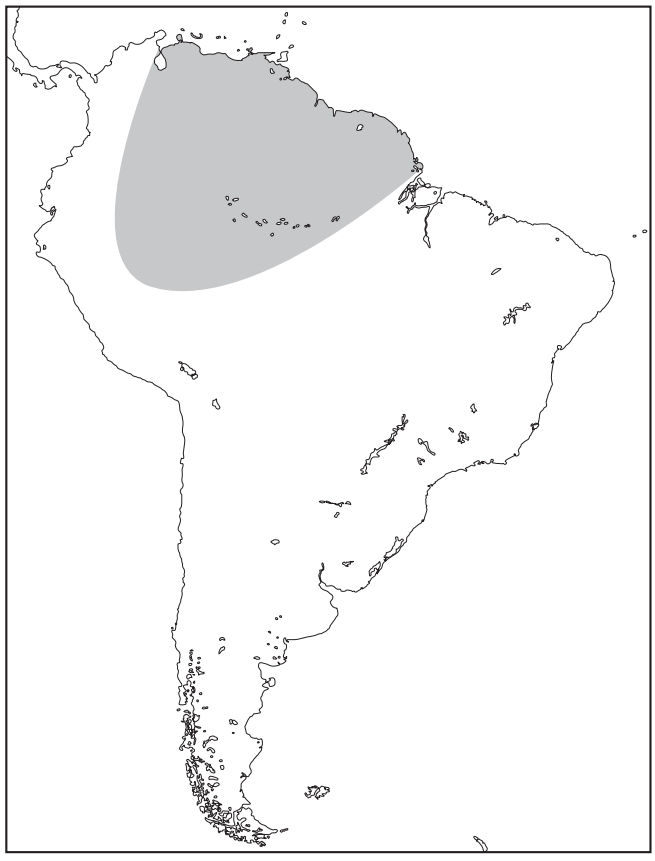


Fig. 587.2. Distribution map of *Batemannia.*

As presently circumscribed, the genus may be characterized by narrow lateral sepals inserted almost vertically at the apex of the column foot, lip with deflexed midlobe and low crest extending from the base to the middle of the lamina, and exauriculate column. However, in analyses of combined nuclear and plastid DNA data sets published by Whitten *et al.* (2005), *Batemannia* formed a strongly supported clade with *Zygosepalum labiosum* (Rich.) Garay; this pair was then strongly supported as members of a clade with all representatives of *Galeottia*. This clade is located within the larger *Zygopetalum* clade. Sequencing of additional taxa is required to understand more fully phylogenetic relationships and circumscription of these groups. **(FP)**

Ecology

Species of the genus occur as epiphytes in hot, tropical wet forests at elevations of 100–600 m. Flowering has been mostly recorded from March to June. **(FP)**

Pollination

Nothing is known about pollination in *Batemannia*. **(FP)**

Uses

Plants of *Batemannia* are occasionally cultivated. **(FP)**

Cultivation

According to the natural conditions of their native habitats, plants of *Batemannia* should be grown in a warm environment under moderate shade and constant humidity throughout the year. Due to the mainly pendent inflorescences, cultivated specimens are best suited to plaques, with some moisture-retaining medium such as *Sphagnum* moss around the roots to prevent excessive desiccation. **(FP)**

Taxonomic notes

Some authors have considered the double *n* in *Batemannia* as a typographical error by Lindley, but it is probably derived from the latinization of Bateman's name to 'Batemannius'. Duplication of the final consonant in a person's name was a common practice for keeping the preceding vowel short. Reichenbach was the first to modify the spelling to '*Batemania*', and both spellings have been used in the literature. However, *Batemania* should be regarded as an invalid orthographical variant (see Article 61 of the *Internation Code of Botanical Nomenclature*). **(MB)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Manara, B. and Bergold, G. (2004). El género *Batemania*, con énfasis sobre la *Batemania armillata*. *Orquideophilo*, **9**, 35–7.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

588. BENZINGIA

Benzingia Dodson ex Dodson, *Lindleyana*, **10,** 74 (1995). Type species: *Benzingia hirtzii* Dodson ex Dodson

Benzingia Dodson, *Icon. Pl. Trop.,* Ser. 2, **5,** t. 406 (1989), *nom. illeg.*

Ackermania Dodson & R.Escobar, *Orquideología*, **18,** 202 (1993), *nom. illeg.* Later homonym of *Ackermannia* Pat. (Fungi). Type species: *Ackermania cornuta* (Garay) Dodson & R.Escobar (basionym: *Chondrorhyncha cornuta* Garay)

Derivation of name

The genus was named to honour David Benzing (1937–), who participated in the first collection of the species. **(FP)**

Description (Plate 193; Fig. 588.1)

Epiphytic, caespitose, pendent *herbs* without pseudobulbs. *Roots* terete, filiform, produced from the rhizome. *Stem* abbreviated, enclosed by 5–10 imbricating sheaths, inflated toward base, provided with scarious, hyaline margins, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, irregularly wavy, lanceolate to elliptic-oblong, acute to acuminate, abaxially carinate, narrowed at base into a conduplicate petiole, grey-green, abaxial surface paler, adaxial surface papillose. *Inflorescences* lateral, one or two per shoot, single-flowered, produced from axils of lower sheaths; peduncle terete, suberect to pendent, provided with one or two distant, triangular-ovate, conduplicate bracts; floral bract double, conduplicate, shorter than ovary, external one widely ovate, often acuminate, loose, subopposite internal bractlet narrowly ligulate. *Flowers* resupinate or not, spreading to campanulate, sepals and petals white to clear orange-yellow, often tinged darker toward apex, rarely sparsely spotted with reddish brown, labellum whitish cream to pale orange, mostly spotted or blotched with reddish brown, usually solid orange-yellow apically, callus orange or red-purple. *Dorsal sepal* free, lanceolate-oblong to narrowly elliptic-ovate, obtuse to acute, often concave. *Lateral sepals* lanceolate to ovate, sometimes subfalcate, acute, lateral margins sometimes inrolled-folded toward the base. *Petals* oblong-elliptic to broadly elliptic, acute to subacuminate, apically revolute. *Labellum* articulate with column foot, concave, ovate to suborbicular, sometimes obscurely trilobed, base often deeply tubular-saccate, apex rounded to abruptly caudate, sometimes deflexed or with falcate, lateral teeth, distal margins entire to irregularly erose-crisped, proximal margins sometimes erect to flank the column; disc with a low, fleshy, longitudinal ridge from base to about middle of labellum, apically 2–4-toothed, or a fleshy, transverse, bilobed plate. *Column* straight to arched, with a distinct foot, usually dilated at apex into inconspicuous stigmatic wings, sometimes adaxially puberulent-pilose toward base; anther cap cucullate, ovate-elliptic, flattened, two-celled, pollinia four, in two subequal pairs, on a short stipe and a triangular-ovate, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 588.2)

Benzingia comprises eight species ranging from Central America (Costa Rica) to Andean South America, from Colombia to Peru. **(FP)**

Phytochemistry

The floral fragrance of the intensely scented *B. palorae* (Dodson & Hirtz) Dressler (cited as *Stenia palorae* Dodson) is dominated by methyl-(*E*)-cinnamate, which Gerlach and Schill (1991) recorded as constituting 98% of the volatile constituents. This compound attracts male euglossine bees, which are thought to pollinate the plant (Gerlach and Schill 1991). **(NV, RG)**

Phylogenetics

Species of *Benzingia* were previously assigned to *Ackermania*, *Chondrorhyncha,* and *Stenia.* The group is diverse in floral morphology. Flowers are patent or pendulous. Most of the species lack the false spur formed by reflexed, inrolled lateral sepals, but they are a characteristic feature of *B. reichenbachiana* (Schltr.) Dressler. Some species (previously assigned to *Ackermania* plus *Chondrorhyncha caudata*) have deeply saccate lips enfolding the column, whereas in others the lip is only slightly concave and column mostly exposed. These differences might indicate different systems of pollination or distinct sites of pollinarium deposition; the gullet-flower of *B. reichenbachiana* probably represents a nectar-deceit pollination syndrome, whereas the remaining species are likely pollinated by male euglossine bees attracted by fragrance rewards (Whitten *et al.* 2005).

When compared to the high diversity in floral patterns, similarities in vegetative architecture among the species of *Benzingia* are striking. Plants are usually pendent, and most possess narrow, fan-shaped growths with leaves that are distinctively glaucous grey-green. The upper surface of the leaves sparkle, accounted for by the papillose epidermal cells of the adaxial leaf blade (not papillose in any other genera of the *Huntleya* clade). These vegetative synapomorphies are supported by molecular analyses (Whitten *et al.* 2005), in which *Benzingia*, *Ackermania*, *Chondrorhyncha caudata* Ackerman, and *C. reichenbachiana* Schltr. form a well-supported clade, which is compatible with treating them as a single genus, in spite of their floral morphologies, which, depending on pollination systems, might be evolutionarily labile. In cladistic analyses of combined DNA sequence data, *Benzingia* is a member of a weakly supported clade containing *Euryblema* (to which species of *Benzingia* are similar in their wide, laminar callus), in a clade with *Stenia* and *Daiotyla.* **(FP)**

Ecology

Species of *Benzingia* occur as epiphytes in shady places, often on the trunks of trees, in premontane to cloud, evergreen, and extremely wet forests at 700–1500 m, along the Caribbean watershed of Central American mountain ranges and the eastern slopes of the Andes in South America. Flowering has been recorded for most of the year. **(FP)**

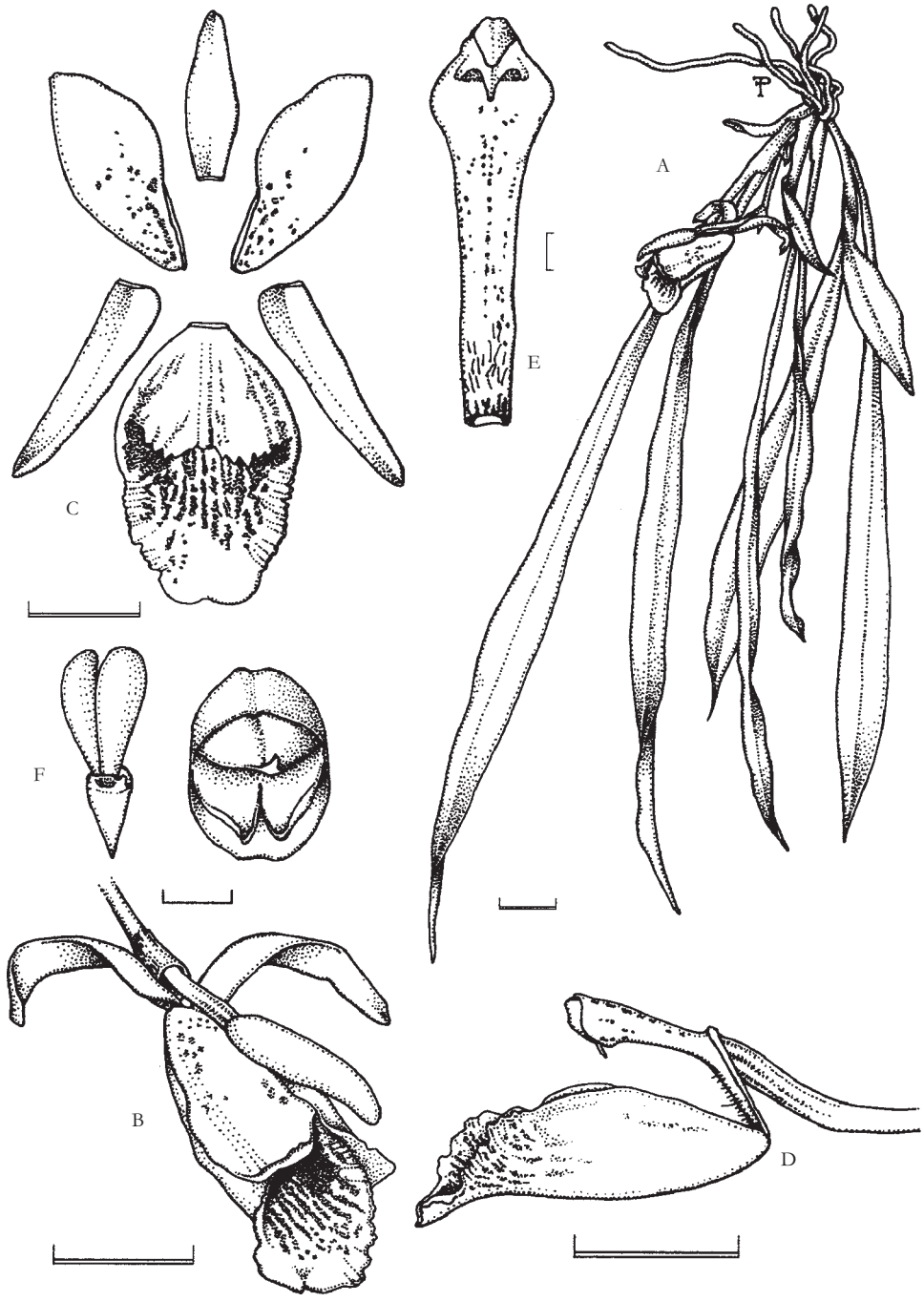


Fig. 588.1. *Benzingia reichenbachiana* (Schltr.) Dressler. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column and labellum, side view; E. Column, ventral view; F. Pollinarium and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin et al. 74* (USJ).

Pollination

Benzingia reichenbachiana (Schltr.) Dressler is pollinated by *Euglossa heterosticta* (Roubik and Hanson 2004), and other species of the genus are presumed also to be pollinated by male euglossine bees (Dodson and Escobar 1993). **(FP)**

Uses

There are no known uses of *Benzingia*, and it is rare in cultivation. **(FP)**

Cultivation

Plants of *Benzingia* are truly pendent, so they are best grown on slabs, which allow the new shoots to develop downward. The grey-green, glaucous leaves are intolerant of direct sun, and plants must be grown in medium to dark shade under intermediate to slightly cool temperatures. Humidity should be high and watering frequent throughout the year, taking care never to let plants dry out. Under proper cultural conditions, plants of *Benzingia* flower abundantly year round. **(FP)**

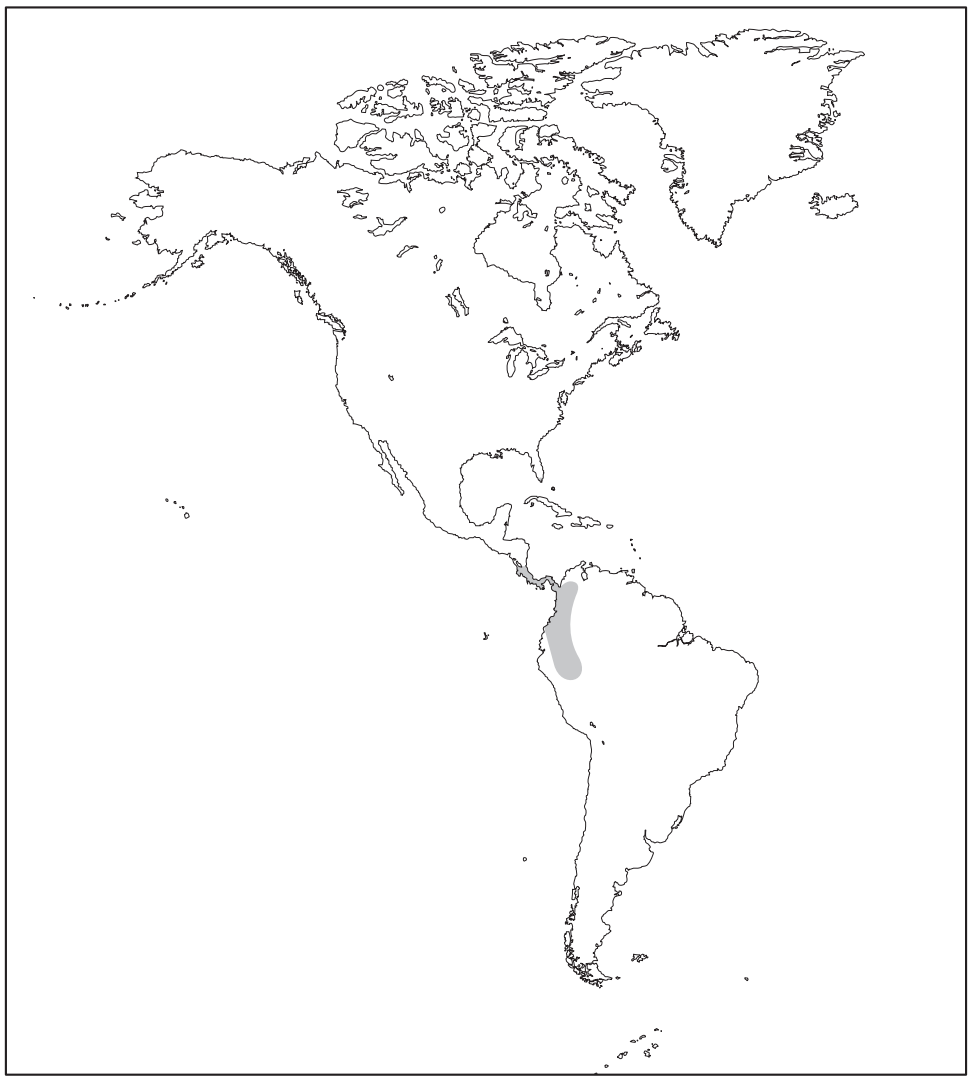


Fig. 588.2. Distribution map of *Benzingia*.

Taxonomic literature

Dodson, C. H. and Escobar, R. (1993). *Native Ecuadorian orchids, vol. 1*. Aa–Dracula. Editorial Colina, Médellin, Colombia.

Roubik, D. W. and Hanson, P. E. (2004). *Orchid bees of tropical America: biology and field guide*. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

589. CHAUBARDIA

Chaubardia Rchb.f., *Bot. Zeit.,* **10,** 671 (1852). Type species: *Chaubardia surinamensis* Rchb.f.

Derivation of name

The genus was named in honour of L. A. Chaubard (1785–1854), French botanist and student of the European flora. **(FP)**

Description (Plate 194; Fig. 589.1)

Epiphytic, caespitose, pseudobulbous *herbs*. *Roots* terete, produced from the rhizome. *Pseudobulb* elliptic to ovate, often cryptic, unifoliate or aphyllous, enclosed by 5–7 imbricating sheaths, upper ones foliaceous, margins sometimes hyaline-scarious. *Leaves* conduplicate, articulate, membranaceous, dark green, oblong-oblanceolate to elliptic, acute to acuminate, abaxially carinate, sometimes 3–5-nerved abaxially, narrowed at base into a conduplicate petiole. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths, peduncle terete, erect, provided with two or three scarious, ovate, conduplicate bracts, appressed to loose; floral bract double, conduplicate, shorter than or subequal to ovary, the external one widely ovate, loose, the subopposite internal bractlet narrowly ligulate. *Flowers* resupinate, with white or greenish yellow sepals and petals, sometimes longitudinally striped with reddish brown, labellum white, its apical lobe sometimes suffused with pink. *Dorsal sepal* free, lanceolate to elliptic-lanceolate, acute to acuminate, basal margins often reflexed, apex incurved. *Lateral sepals* lanceolate to

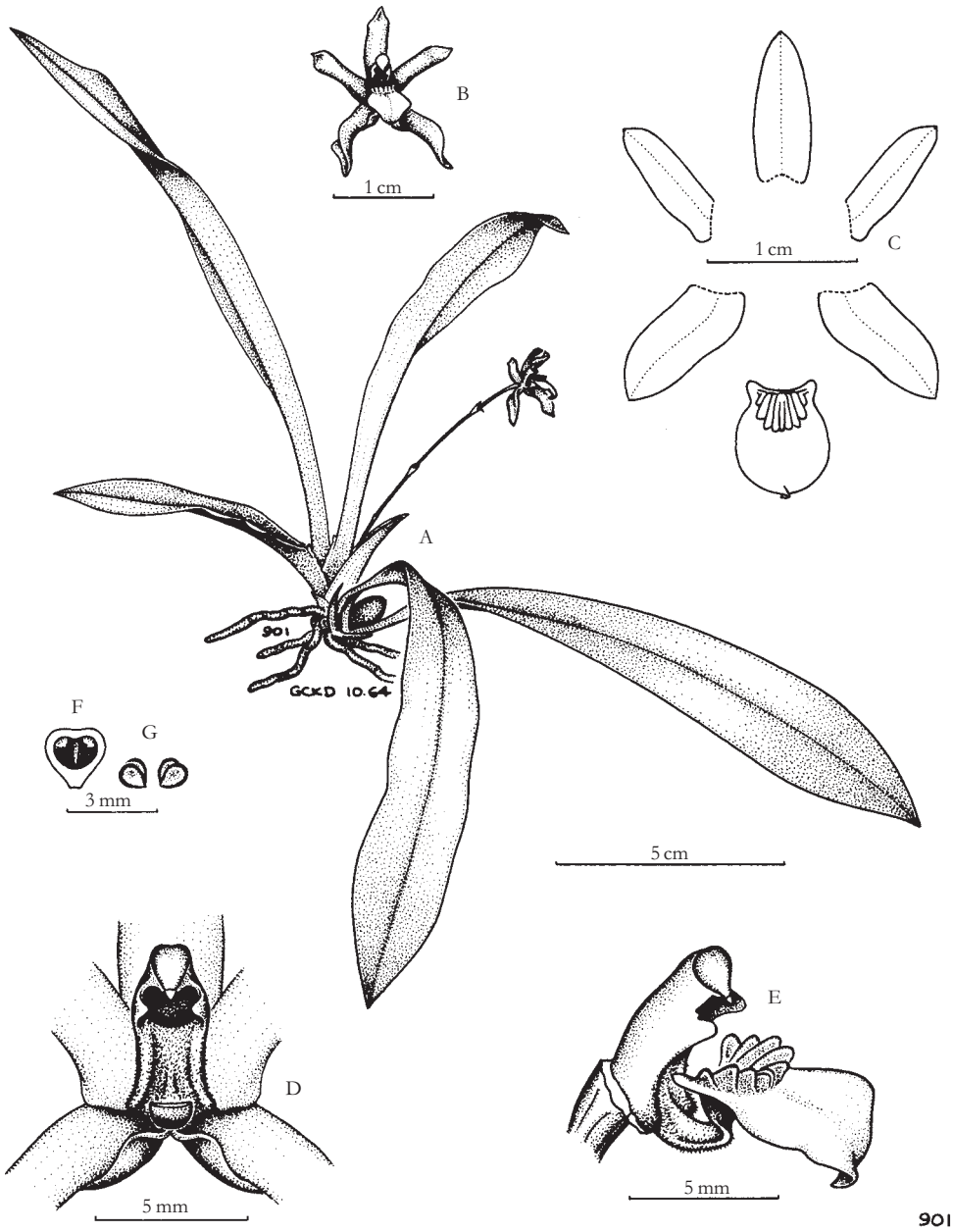


Fig. 589.1. *Chaubardia surinamensis* Rchb.f. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column, ventral view, with bases of sepals and petals (labellum removed); E. Column and labellum, oblique view; F. Anther cap, ventral view; G. Pollinia. Drawn by G.C.K. Dunsterville. Originally published in *Venezuelan Orchids Illustrated,* **4**, 50 (1966). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

lanceolate-elliptic, acute to acuminate, basal margins reflexed, usually abaxially carinate toward apex. *Petals* lanceolate to linear-lanceolate, acute to acuminate, concave apically. *Labellum* continuous or articulate with column foot, clawed, divided into a hypochile and epichile, hypochile conduplicate-concave or broadly cuneate, anterior margin digitate-fimbriate or composed of radiating, low keels, epichile lanceolate to ovate-suborbicular, acute, often conduplicate and reflexed, sometimes sparsely puberulent. *Column* straight or curved, with or without a distinct foot, dilated at the middle into prominent, triangular to triangular-falcate stigmatic wings, with a conspicuous clinandrium, often pubescent toward base, sometimes provided with a low, rounded, median keel; anther cap cucullate, triangular-ovate, flattened, two-celled, pollinia four, in two subequal pairs, attached to an obovate to rhombic stipe, sometimes provided with an abaxial, central, rounded keel, and an adaxial viscidium; stigma transverse or rounded. **(FP)**

Distribution (Fig. 589.2)

This genus of three to four species is native to Trinidad and South America, where they have been recorded to the east of the Andes from Venezuela to Guyana and Brazil and from Colombia to Bolivia. **(FP)**

Fig. 589.2. Distribution map of *Chaubardia.*

Phytochemistry

The floral fragrance of *C. heteroclita* (Poepp. & Endl.) Dodson & D.E.Benn. is composed mainly of monoterpenes, although one of two specimens analyzed by Gerlach and Schill (1991) also contained a simple aromatic compound (1,4-dimethoxybenzene) and aromatic ester (methyl salicylate). **(NV, RG)**

Phylogenetics

In the past, species of *Chaubardia* have been assigned to *Cochleanthes*, *Huntleya*, *Hoehneella*, *Maxillaria*, *Warczewiczella,* and *Zygopetalum*. However, according to recent analyses of combined DNA sequence data (Whitten *et al*. 2005), *Chaubardia* is strongly supported as monophyletic. The genus is morphologically characterized by heteroblastic pseudobulbs (obvious and leafless in one species, hidden by the imbricating sheaths and monophyllous in the others) and a lip composed of a large, callous, conduplicate-concave hypochile, digitate-fimbriate on the apical portion, and a lanceolate-rhombic epichile. Flowers of *Chaubardia* are similar to those of *Huntleya*, with a rhombic lip having conspicuously toothed calli at the base and a winged column marked by a well-developed clinandrium. *Huntleya* species, however, lack pseudobulbs. In spite of having distinct pseudobulbs, unusual in Zygopetalinae, *Chaubardia* is a member of the *Huntleya* clade according to DNA sequence analyses (Whitten *et al*. 2005) and strongly supported as sister to rest of the clade except for *Huntleya*. **(FP)**

Ecology

Species of the genus occur as epiphytes in evergreen, lowland, hot to submontane cloud forests from sea level to 1700 m. Flowering has been recorded from November to March, but species may well flower most of the year. **(FP)**

Pollination

Nothing is known about pollination biology of *Chaubardia*, but male euglossine bees are implicated (Dodson and Escobar 1993). **(FP)**

Uses

Apart from occasional cultivation, there are no known uses. **(FP)**

Cultivation

Plants of *Chaubardia* are shade-loving epiphytes and can be grown in pots or on plaques in subdued light. *Chaubardia surinamensis* Rchb.f. is a plant from hot, wet lowland forests and, accordingly, should be grown in a warm environment, with constant watering throughout the year. *Chaubardia heteroclita* and *C. klugii* (C.Schweinf.) Garay have been recorded as high as 1700 m and 1500 m, respectively, although in Peru the elevational range of the former species extends to the lowlands (100 m). Both should be cultivated under intermediate conditions with high levels of humidity and frequent watering year-round. **(FP)**

Taxonomic literature

Dodson, C. H. and Escobar, R. (1993). *Native Ecuadorian orchids, vol. 1*. Aa–Dracula. Editorial Colina, Médellin, Colombia.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

590. CHAUBARDIELLA

Chaubardiella Garay, *Orquideología*, **4,** 146 (1969). Type species: *Chaubardiella tigrina* (Garay & Dunst.) Garay (basionym: *Chaubardia tigrina* Garay & Dunst.)

Derivation of name

From *Chaubardia*, another genus in Zygopetalinae, and -ella, a Latin diminutive, in allusion to the affinities between the two genera and to the original generic placement of the type species. **(FP)**

Description (Plate 195; Fig. 590.1)

Epiphytic, caespitose *herbs* without pseudobulbs or rarely with pseudobulbs completely hidden by leaf bases. *Roots* terete, produced from the rhizome. *Stem* abbreviated, enclosed by 3–5 imbricating sheaths, the upper ones foliaceous. *Leaves* conduplicate,

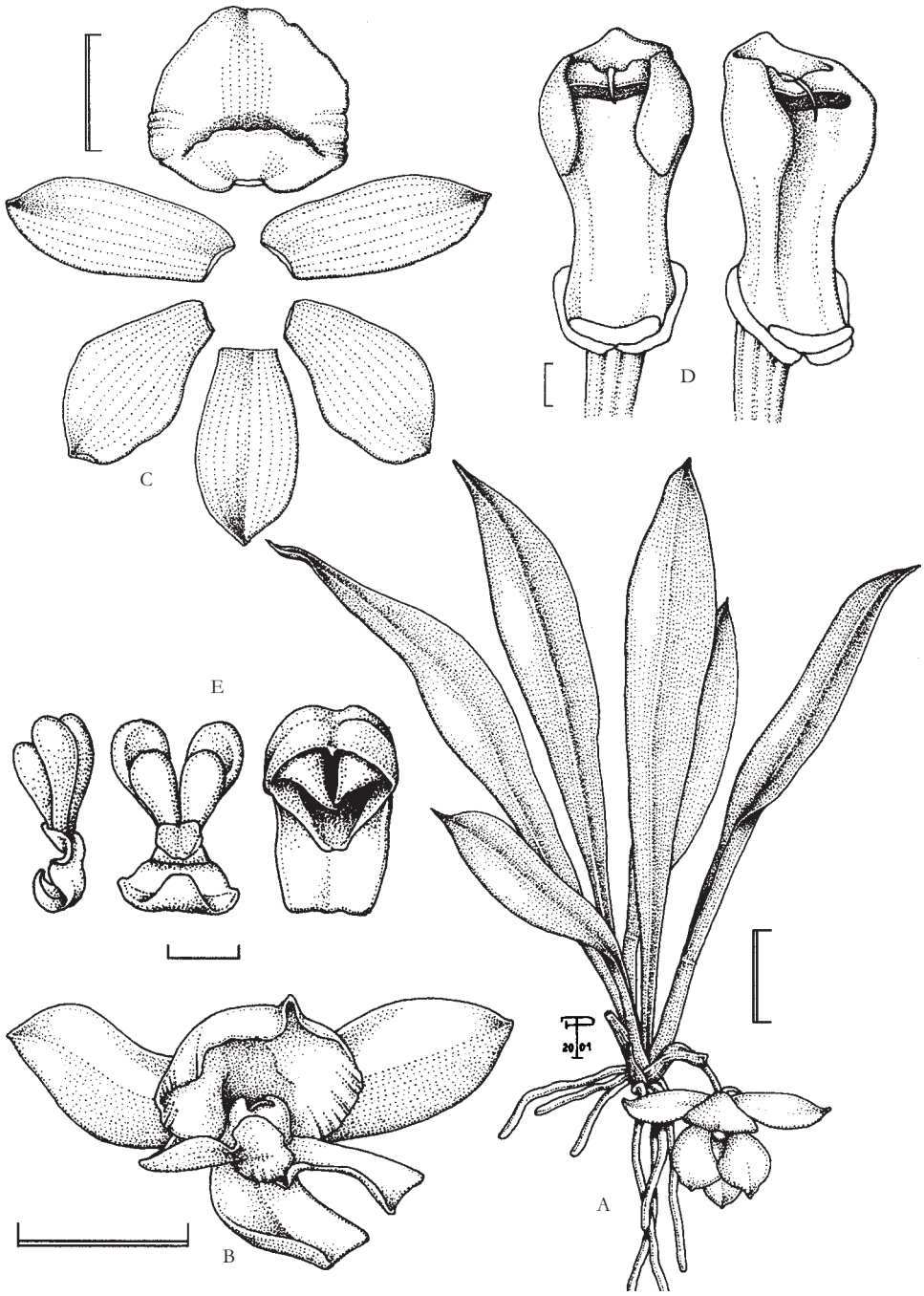


Fig. 590.1. *Chaubardiella pacuarensis* Jenny. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column, ventral and oblique views; E. Pollinarium (side and ventral views) and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 2583* (USJ).

articulate, membranaceous, elliptic-oblong to narrowly obovate, acute to subacuminate, abaxially carinate, narrowed at base into a conduplicate petiole, dark green, adaxial surface sometimes waxy. *Inflorescences* lateral, 1–3 per shoot, single-flowered, produced from axils of lower sheaths, peduncle terete, pendent, provided with one or two basal, tubular-imbricating, apically loose, scarious bracts; floral bract double, conduplicate, the external one widely ovate to suborbicular, scarious, loose, longer than ovary, the subopposite internal bractlet lanceolate, appressed to base of labellum. *Flowers* resupinate, spreading or campanulate, uniformly creamy white or yellow, yellowish tan to tan-brown or pale lavender to purple, often spotted or blotched dark brown or with transverse, dark purple markings or purple brown stripes, markings on the labellum usually darker. *Dorsal sepal* free, oblanceolate-elliptic to obovate, acute to acuminate, rarely apiculate. *Lateral sepals* lanceolate-elliptic to oblanceolate, sometimes subfalcate, obtuse to subacuminate, apically often reflexed. *Petals* spreading or variously porrect over column, oblanceolate to

Fig. 590.2. Distribution map of *Chaubardiella*.

broadly obovate-spatulate, acute to abruptly subacuminate, apically revolute. *Labellum* articulate with column foot, concave at base, distal portion of the blade usually flattened, subquadrate to ovate, rarely puberulent, base cuneate-rounded, sessile, apex acute to rounded-emarginate, distal margin entire to irregularly crenulate; disc with a fleshy, raised, fan-shaped or horseshoe-shaped, sometimes many-ridged, transverse plate, from base to about the middle of labellum. *Column* straight, with a foot, dilated at the apex into inconspicuous stigmatic wings, sometimes pubescent, provided with a low, rounded, median ridge below stigma; anther cap cucullate, ovate to subrectangular, flattened, two-celled, pollinia four, in two subequal pairs, on a quadrate stipe and an obovate-rhombic, curled, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 590.2)

Chaubardiella comprises eight or nine species ranging from Central America (Costa Rica) to Peru and Guyana in South America. **(FP)**

Phytochemistry

The main component of the floral fragrance of *C. tigrina* is the sesquiterpene β-farnesene (76%). In contrast, the monoterpene linalool and two unspecified γ-lactone derivatives comprise major scent components of *C. hirtzii* Dodson (Gerlach and Schill 1991). **(NV, RG)**

Phylogenetics

Before Garay established *Chaubardiella* in 1969, species of this genus were assigned to *Chaubardia*, *Kefersteinia* or *Stenia*. However, the true phylogenetic relationships of the genus were not immediately recognized, and the first synopsis of *Chaubardiella* (Garay 1969) included two species best assigned to *Stenia* on the basis of similar pollinarium morphology. As understood today, *Chaubardiella* is characterized by pendent flowers; a lip concave at the base with distal half flattened; laminar, transverse callus; abbreviated column provided with a foot; and a characteristic, hooked viscidium that curls after removal. In the

combined analysis of *matK/trnL-F/*ITS rDNA data set (Whitten *et al.* 2005), *Chaubardiella* was strongly supported as monophyletic. *Chaubardiella* fell within a clade including the strictly South American *Aetheorhyncha* and *Ixyophora* and was in a weakly supported polytomy with *Pescatoria* and *Warczewiczella*. **(FP)**

Ecology

Species occur as epiphytes in shady habitats, often growing on trunks and the oldest, mossy branches in warm tropical, premontane to cloud, evergreen, and extremely wet forests at elevations of 400–1800 m. Flowering has been recorded mostly from June to December. **(FP)**

Pollination

The only known pollinator of *Chaubardiella* is *Euglossa cibella* (Roubik and Hanson 2004), and presumably all species of the genus are similarly pollinated by male euglossine bees. The hook-shaped viscidium places the pollinarium at the base of one of the legs of the pollinator (Dodson 1990; Roubik and Hanson 2004; Whitten *et al.* 2005). **(FP)**

Uses

A few species are occasionally cultivated as ornamentals. **(FP)**

Cultivation

Because of their strictly pendent inflorescences, plants of *Chaubardiella* are best grown on slabs, but it is important to provide constant moisture to the fleshy roots. In their native habitats, *Chaubardiella* species do not experience a marked dry season, and the plants are usually found as epiphytes along shaded streams in mature vegetation. Cultivated specimens should be kept moist and shaded throughought the year. **(FP)**

Taxonomic literature

Dodson, C. H. and Escobar, R. (1993). *Native Ecuadorian orchids, vol. 1.* Aa–Dracula. Editorial Colina, Médellin, Colombia.

Garay, L. A. (1969). El complejo *Chondrorhyncha*. *Orquideología*, **4**, 139–52.

Roubik, D. W. and Hanson, P. E. (2004). *Orchid bees of tropical America: biology and field guide*. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

591. CHEIRADENIA

Cheiradenia Lindl., *Fol. Orch. Cheiradenia*, 1 (1853). Type species: *Cheiradenia cuspidata* Lindl.

Derivation of name

From the Greek *cheir*, hand, and *aden*, gland, in reference to the digitate callus on the apex of lip. **(FP)**

Description (Plate 196; Fig. 591.1)

Epiphytic, rarely lithophytic, caespitose, pseudobulbous *herbs*. *Roots* terete, filiform, produced at closely spaced intervals along rhizome. *Pseudobulb* homoblastic, ovoid, 1–3-leaved, oldest leaves covered by white sheaths. *Leaves* conduplicate, articulate, membranaceous, velvety green adaxially, paler abaxially, oblong-lanceolate to elliptic, acute to abruptly acuminate, sulcate-carinate, narrowed at base into an indistinct, conduplicate petiole. *Inflorescences* lateral, a 1–4-flowered raceme, rarely branching, produced from axils of the lower sheaths, peduncle terete, erect, provided with one or two acuminate, conduplicate bracts; floral bracts triangular-lanceolate, conduplicate, membranaceous, shorter than ovary, closely packed along rachis, seemingly spirally arranged to form a rosette on old inflorescences. *Flowers* resupinate, sepals white, petals white and sparsely dotted with purple-brown, labellum white with dark purple brown stripes and yellow callus. *Dorsal sepal* free, oblong to elliptic, obtuse, concave, reclinate over column. *Lateral sepals* elliptic-obovate, obtuse, concave toward base. *Petals* elliptic-suborbicular, obtuse to rounded, porrect, incurved. *Labellum* articulate with column foot, transversely elliptic, obscurely trilobed, cup-shaped in natural position, base rounded and contracted into a claw, apex rounded to truncate, basal margins erect; disc covered with a laminar, transverse plate extending to near the labellar apex, four-toothed in front, external teeth broader, and with a fleshy, median, longitudinal callus from base to apex of the plate, where it forms a fifth prominent tooth. *Column* suberect, straight, with a distinct foot, dilated at apex into inconspicuous, acute stigmatic wings; anther cap cucullate, transversely subrectangular, flattened, two-celled, pollinia four, in two subequal pairs, without a stipe, on a rhomboid-elliptic, hyaline viscidium; stigma rounded. **(FP)**

Distribution (Fig. 591.2)

Cheiradenia is a monospecific genus native to Venezuela and the Guyanas, perhaps ranging to northern Brazil (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Cheiradenia*. **(NV, RG)**

Phylogenetics

Material of *Cheiradenia* has not yet been available for molecular analysis, but on the basis of morphological characters, both vegetative and floral, it appears to be closely related to the *Zygopetalum* clade, including *Koellensteinia*, *Otostylis*, *Paradisanthus*, *Warrea*, *Warreella,* and *Warreopsis*. These genera and *Cheiradenia* share homoblastic pseudobulbs largely hidden by basal, imbricating sheaths. The lip of *Cheiradenia* is deeply cup-shaped, like that of *Koellensteinia* and *Otostylis*, and the digitate callus is structurally similar to that of *Koellensteinia*. According to Senghas and Gerlach (1993), the pollinarium of *Cheiradenia* lacks a stipe, a character also found in *Koellensteinia*. The genus may be recognized by

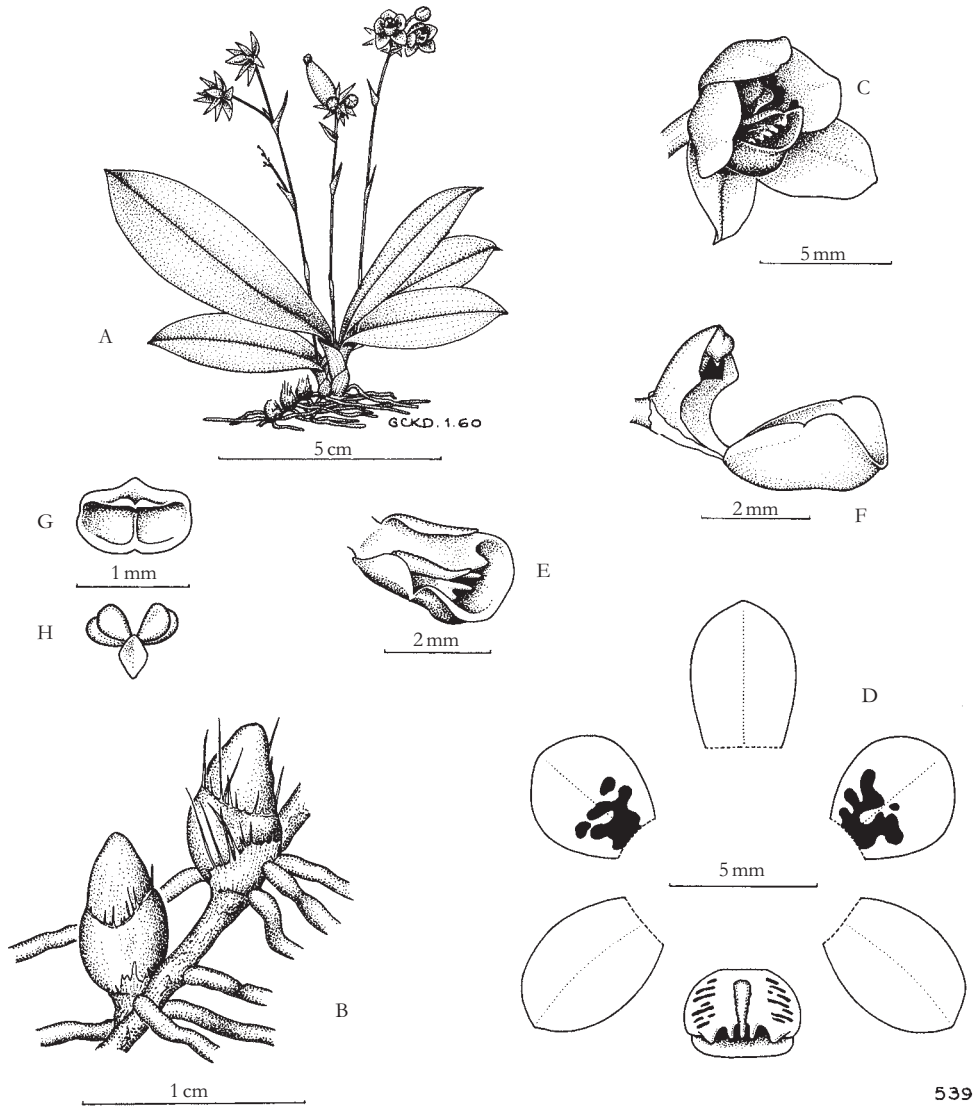


Fig. 591.1. *Cheiradenia cuspidata* Lindl. A. Habit, with inflorescences; B. Pseudobulbs, rhizome, and roots; C. Flower; D. Perianth, dissected; E. Labellum, dorsal view; F. Column and labellum, side view; G. Anther cap, ventral view; H. Pollinarium. Drawn by G.C.K. Dunsterville. Originally published as *Cheiradenia imthurnii* Cogn. in *Venezuelan Orchids Illustrated,* **2**, 74 (1961). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

homoblastic pseudobulbs, comparatively small size of the plant and flowers, and terminal callus of the lip composed of four lateral teeth and a central tooth produced by the distal extension of the basal keel. **(FP)**

Ecology

The species occurs as an epiphyte on mossy tree trunks and branches and sometimes as a lithophyte on mossy rocks, in evergreen, wet, tropical forests at 200–600 m, mostly along streams, in the Guyana Shield. Flowering has been recorded from November to February. **(FP)**

Pollination

The pollination biology of *Cheiradenia* is unknown. **(FP)**

Uses

There are no known uses of this species, although it occurs occasionally in specialist collections. **(FP)**

Cultivation

A plant native to the lowland forests of Guyana, *Cheiradenia* should be grown in shade and warm temperatures on plaques or in well-drained pots and provided with frequent watering and high levels of humidity year-round. **(FP)**

Taxonomic literature

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–1727. Paul Parey, Berlin.

Fig. 591.2. Distribution map of *Cheiradenia*.

592. CHONDRORHYNCHA

Chondrorhyncha Lindl., *Orch. Linden.*, 12 (1846). Type species: *Chondrorhyncha rosea* Lindl.

Derivation of name

From the Greek *chondros*, cartilage, and *rhynchos*, beak, snout, in allusion to the beak-like, long and narrow rostellum. **(FP)**

Description (Plate 197; Fig. 592.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, flexuous, produced from the rhizome. *Stem* abbreviated, enclosed by 5–9 imbricating sheaths, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, grass green, oblanceolate-ligulate to oblong-elliptic, acute to acuminate, carinate abaxially, subpetiolate at the conduplicate base. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths, peduncle terete, suberect to arching-pendent, provided with one or two conduplicate-clasping, lanceolate, acuminate bracts; floral bract double, conduplicate, shorter than ovary, the external one ovate to lanceolate, subacuminate, loose, the subopposite internal bractlet narrower, ligulate. *Flowers* resupinate, sepals pale green, yellowish green or creamy yellow, petals white to cream, sometimes spotted with red or brown, labellum white to cream or pink to solid dark red, often flushed and striped with red or spotted brown or spotted with rose and yellow, callus yellow to orange, often minutely spotted with red. *Dorsal sepal* free, lanceolate-elliptic to oblong, acute, concave, mostly deflexed over column, rarely suberect at apex. *Lateral sepals* oblong-elliptic to oblanceolate-oblong, acute, sometimes subfalcate, spreading-recurved to abruptly reflexed, concave, inrolled-folded toward base, apex sometimes subuncinate. *Petals* spatulate-obovate, rhombic-obovate or obovate, obtuse, apically recurved. *Labellum* articulate with column foot, obovate to elliptic-obovate, sometimes trilobed, base rounded-subsaccate, apex obtuse to emarginate or minutely bilobed, basal margins erect to flank the column, distal margin undulate, sometimes with verruculose veins, disc with or without longitudinal keels running from base to callus; callus in middle of blade, flat, pocket-like, 3–5-toothed. *Column* straight, with a distinct foot decurrent onto the ventral surface as a rounded, basal keel, dilated at apex into inconspicuous stigmatic wings; anther cap cucullate, elliptic-obovate, flattened, two-celled, pollinia four, in two subequal pairs, on an ovate to obtriangular-peltate, hyaline viscidium, without distinct stipe; stigma transverse. **(FP)**

Distribution (Fig. 592.2)

Chondrorhyncha, as redefined, is a genus of six or seven species native from the Andes of Venezuela and Colombia to Peru. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Chondrorhyncha*. **(NV, RG)**

Phylogenetics

Originally described to accommodate a species 'allied to *Helcia* and *Trichopilia*' (Lindley 1846), *Chondrorhyncha* was essentially defined by the oblique insertion of sepals and its long, cartilaginous, bristle-like rostellum, a condition likely plesiomorphic within the *Huntleya* clade. The genus traditionally embraced a vast array of different taxa, including species currently assigned to *Aetheorhyncha*, *Benzingia*, *Chondroscaphe*, *Cochleanthes*, *Daiotyla*, *Euryblema*, *Ixyophora*, *Kefersteinia*, *Stenia*, *Stenotyla*, and *Warczewiczella*. Dressler (2000) began to bring some degree of order into the *Chondrorhyncha* complex, indicating that *Chondrorhyncha s.s.* is a strictly South American genus, likely including only 8 to 10 species provided with a narrow, not fleshy callus near the middle of the lip that is wide basally and tapers to the apex. In describing *C. inedita*, Dressler and Dalström (2004) offered a first synopsis of *Chondrorhyncha s.s.*, reducing the genus to only five species. The cladistic analyses of a combined *matK/trnL-F/*ITS rDNA data set, performed by Whitten *et al.* (2005), unequivocally showed that *Chondrorhyncha*, as traditionally defined, is polyphyletic, the species previously placed in that genus being scattered in at least eight clades. In the cladogram, the type species of the genus (*C. rosea*) falls into a small, strongly supported clade, recognized as *Chondrorhyncha s.s.*, which is sister to rest of the *Huntleya* clade, excluding *Chaubardia* and *Huntleya*. **(FP)**

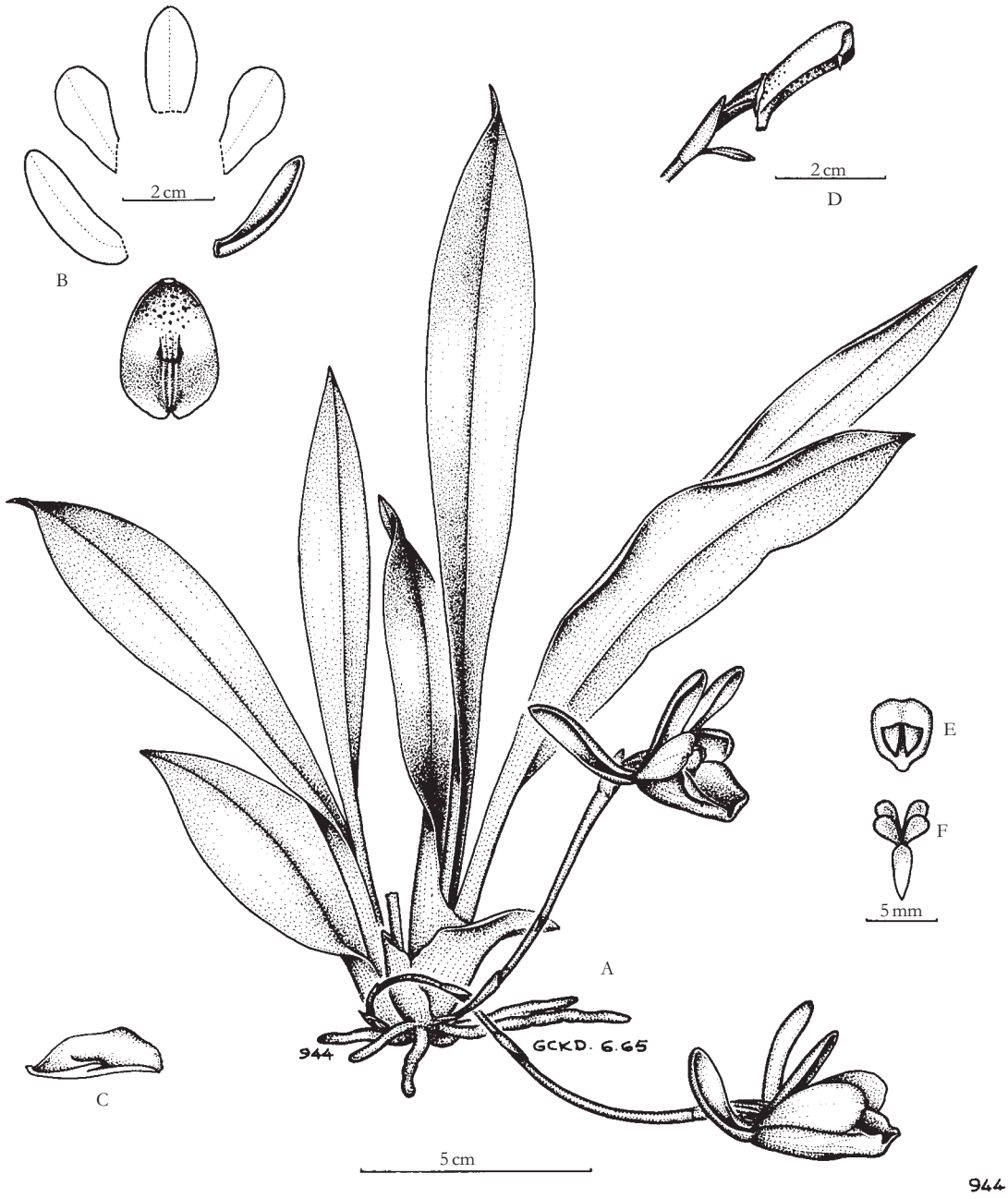


Fig. 592.1. *Chondrorhyncha rosea* Lindl. A. Habit, with inflorescences; B. Perianth, dissected; C. Labellum (sectioned), side view; D. Column, side view; E. Anther cap, ventral view; F. Pollinarium. Drawn by G.C.K. Dunsterville. Originally published in *Venezuelan Orchids Illustrated,* **4**, 52 (1966). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

Ecology

The species of *Chondrorhyncha* occur as epiphytes in evergreen, tropical to (mostly) premontane wet forests at 500–1800 m along the eastern slopes of the Andes. Flowering has been recorded throughout the year, peaking from January to July. **(FP)**

Pollination

Pollination vectors are unknown but presumed to be male euglossine bees. **(FP)**

Uses

There are no recorded uses of *Chondrorhyncha* except as horticultural ornamentals. **(FP)**

Cultivation

Mostly native to medium-elevation, wet forests of the Andes and Amazonian watershed, plants of *Chondrorhyncha* should be grown in a shaded area under intermediate temperatures with frequent watering and high levels of humidity year-round. To

Fig. 592.2. Distribution map of *Chondrorhyncha*.

date, *Chondrorhyncha suarezii* Dodson has been recorded only from lower elevations (450–500 m) and should be cultivated in the warm greenhouse. Due to their reduced size, plants of *Chondrorhyncha* can be grown on slabs or in pots as long as roots are never allowed taking to dry out completely. **(FP)**

Taxonomic literature

Dressler, R. L. (2000). Precursor to a revision of the *Chondrorhyncha* complex. *Orquideología,* **21,** 233–47.

Dressler, R. L. and Dalström, S. (2004). *Chondrorhyncha rosea*, una confusión centenaria, y una especie "nueva" de Colombia, *Chondrorhyncha inedita*. *Orquideología,* **23**, 79–82.

Lindley, J. (1846). *Orchidaceae Lindenianae*. Bradbury and Evans, London.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

593. CHONDROSCAPHE

Chondroscaphe (Dressler) Senghas & G.Gerlach in *R. Schlechter, Orchideen*, ed. 3, **1/B(27),** 1655 (1993). Type species: *Chondroscaphe flaveola* (Linden & Rchb.f.) Senghas & G.Gerlach (basionym: *Zygopetalum flaveolum* Linden & Rchb.f.)

Derivation of name

From the Greek *chondros*, cartilage, and *skyphos*, bowl, in reference to a second, membranaceous, laminar callus in front of the basal callus and originally alluding to a general similarity of *C.* sect. *Chondroscaphe* to the genus *Chondrorhyncha*. **(FP)**

Description (Plate 198; Fig. 593.1)

Epiphytic, caespitose *herbs* without pseudobulbs or occasionally with reduced pseudobulbs, completely hidden by leaf sheaths. *Roots* terete, flexuous, produced from the abbreviated rhizome. *Stem* completely enclosed by 5–8 imbricating sheaths provided with scarious margins, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, oblanceolate to narrowly oblanceolate-ligulate, acute to acuminate, abaxially carinate, narrowed at base into a conduplicate petiole, usually dark green. *Inflorescences* lateral, one or more per shoot, single-flowered, produced successively on a cincinnus partially or completely hidden within axils of lower sheaths, peduncle terete, suberect to arching-pendent, provided with one or two basal, tubular-infundibuliform, papery bracts; floral bract double, conduplicate, papyraceous, shorter than ovary, the external one elliptic-lanceolate to ovate, acute, clasping, the subopposite internal bractlet ligulate. *Flowers* resupinate, mostly subpendent, sepals and petals white or whitish cream to yellow, labellum white to yellow, often flushed yellow basally, sparsely spotted and blotched with purple at base up to distal thickening, basal callus white or yellow variously spotted with purple, distal callus usually spotted purple. *Dorsal sepal* free, lanceolate-elliptic to elliptic, acute to subacuminate, basally reclinate over column, distally erect usually, rarely concave-reclinate. *Lateral sepals* lanceolate-elliptic to elliptic, frequently asymmetrical-subfalcate, acute to acuminate, mostly reflexed, rarely spreading, inrolled-folded toward base, forming a chin with column foot. *Petals* inserted along margins of column foot, oblanceolate to obovate, subacute to obtuse, minutely apiculate, usually revolute at apex, apical margins undulate or crenulate to deeply lacerate. *Labellum* articulate with column foot, subsessile or with an inconspicuous claw, entire to trilobed, elliptic to obovate, base rounded, apex emarginate to retuse, deflexed, lateral lobes and proximal margins erect and flanking column, distal margins undulate-crisped, often fimbriate; disc with a basal, bilobed, laminar callus, and a distal, often rugose, callous thickening. *Column* straight, with a distinct foot, dilated toward the apex into protruding, rounded stigmatic wings, ventral surface plane; anther cap cucullate, obovate, flattened, two-celled, pollinia four, in two superposed pairs of different sizes, on an obovate or subquadrate stipe and an elliptic, hyaline viscidium; stigma transverse, acicular rostellum flanked by para-rostellar arms. **(FP)**

Distribution (Fig. 593.2)

Chondroscaphe is a genus of about 14 species ranging from Central America (Costa Rica and Panama) to Venezuela and from Colombia to Peru along the Andean regions (South America), reaching its highest diversity in Colombia and Ecuador (with seven and six recorded species, respectively) and Costa Rica with

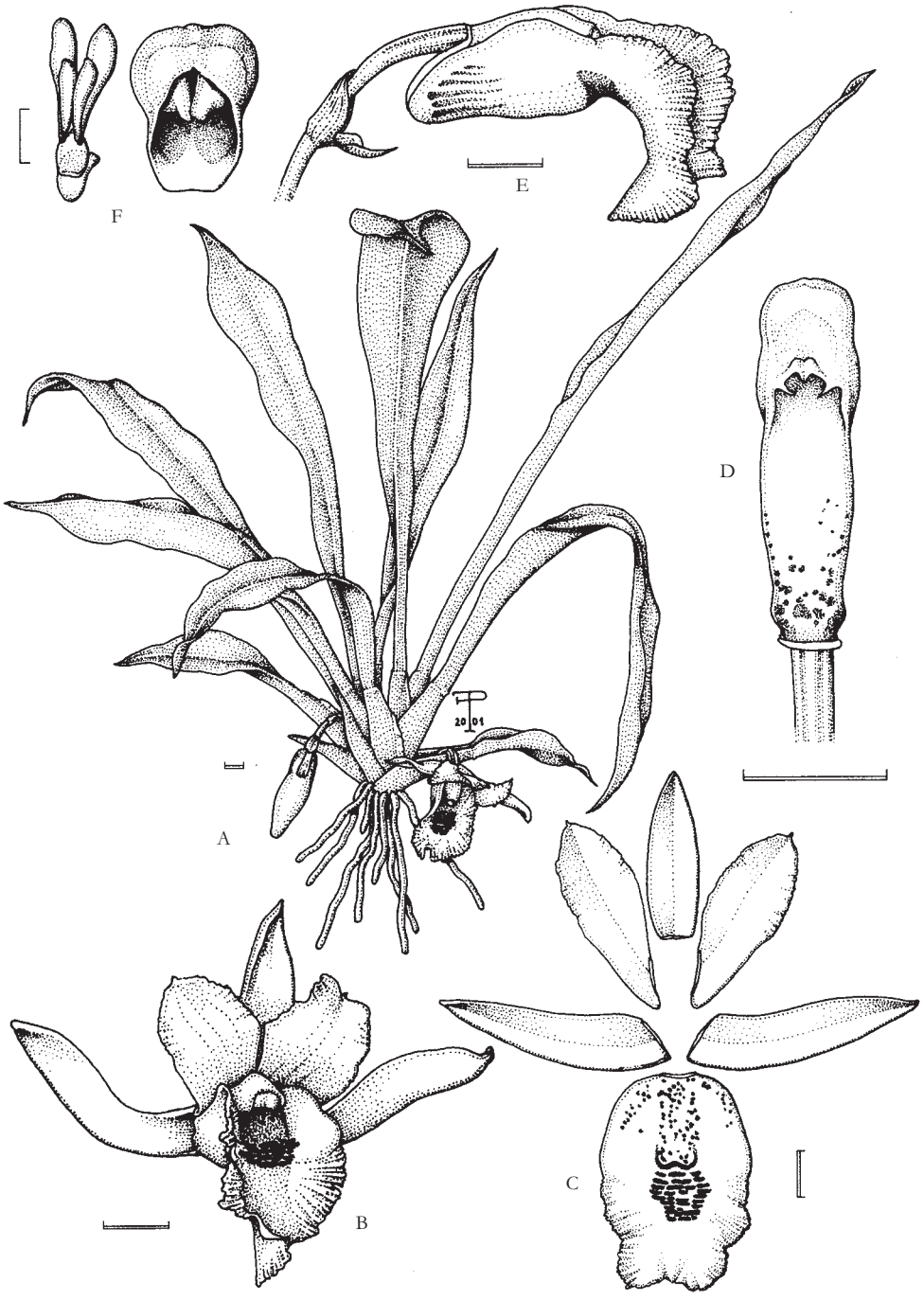


Fig. 593.1. *Chondroscaphe atrilinguis* Dressler. A. Habit, with inflorescences; B. Flower; C. Perianth, dissected; D. Column, ventral view; E. Column and labellum, side view; F. Pollinarium and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 2614* (USJ and Lankester Botanical Garden Spirit Collection).

five named species. Floral morphology in the taxa from southern Central America is largely uniform, and the number of names may exceed the actual number of species. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Chondroscaphe*. **(NV, RG)**

Phylogenetics

In creating *Chondrorhyncha* sect. *Chondroscaphe*, Dressler (1983) mentioned several features characteristic of the group, such as inflorescences borne successively on a comparatively long cincinnus, thick and rigid ventral throat of the flower, a second, distal callus on the lip, well-developed stipe of the pollinarium, stipe attached to the upper surface of viscidium, and para-rostellar

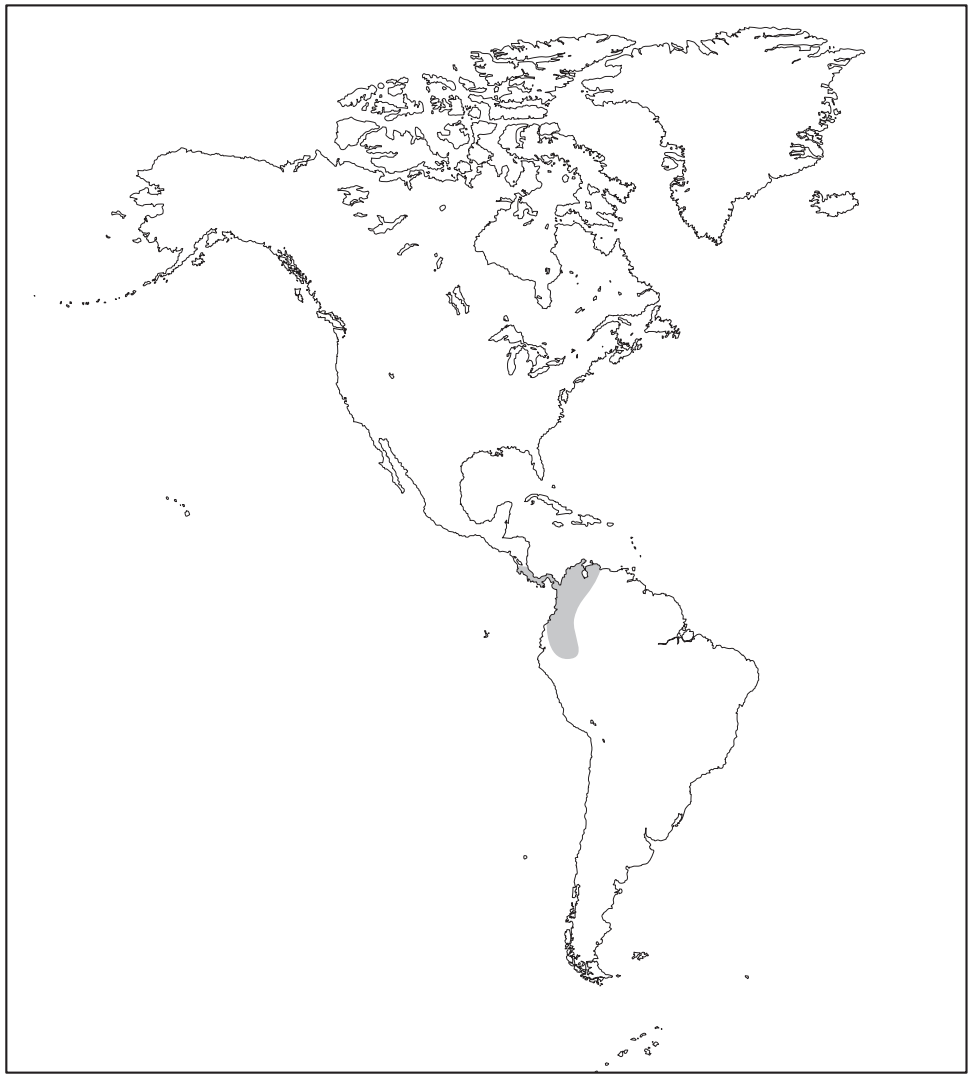


Fig. 593.2. Distribution map of *Chondroscaphe*.

teeth. According to these characters, *Chondroscaphe* (as a section of *Chondrorhyncha*), included both the fringed-lip species close to *Chondrorhyncha flaveola* Rchb.f. and the white-coloured species allied to *C. bicolor* Rolfe. In 1993, when Senghas and Gerlach elevated *C.* section *Chondroscaphe* to generic rank, they did include the mostly Central American species of the *C. bicolor* complex. In 2001, describing two new Central American species of *Chondroscaphe*, Dressler offered further morphological evidence supporting inclusion of the *C. bicolor* group in *Chondroscaphe*. The combined molecular analysis published by Whitten *et al.* (2005) strongly supported a broad circumscription of *Chondroscaphe* (including the *C. bicolor* group) which is weakly supported as sister to the clade comprising *Warczewiczella*, *Pescatoria*, *Chaubardiella*, *Ixyophora,* and *Aetheorhyncha*. **(FP)**

Ecology

Species of *Chondroscaphe* are shade-loving epiphytes of premontane wet and cloud forests, where they become established on large branches and trunks covered with mosses, mostly between 800 and 1500 m, although *C. plicata* (D.E.Benn. & Christenson) Dressler ranges to almost 2000 m. Successive flowering sporadically occurs throughout the year, with a peak during the rainy season. **(FP)**

Pollination

Pollination biology of *Chondroscaphe* is unknown, but species may be visited by euglossine bees, attracted by the false spur formed by swept-back lateral sepals that are revolute at the base. **(FP)**

Uses

Some species are cultivated ornamentals, but otherwise there are no known uses. **(FP)**

Cultivation

Plants of *Chondroscaphe* could be grown under intermediate conditions, and most of the species are tolerant of warmer temperatures. All species should be grown in a shaded area and protected from direct sun; most tolerate deep shade. Under

these conditions, high humidity and good air circulation should be provided to maintain plants in healthy condition. Specimens of *Chondroscaphe* can be grown on large plaques or in pots, with a moisture-retaining medium. Watering should be abundant year-round, and the medium should never be allowed to dry out completely. **(FP)**

Taxonomic literature

Dressler, R. L. (1983). Die Gattung *Chondrorhyncha* in Panama mit zwei neun Arten: *Chondrorhyncha crassa* und *Chondrorhyncha eburnea*. *Orchidee (Hamburg),* **34,** 220–6.

Dressler, R. L. (2001). Sobre el género *Chondroscaphe*, con dos especies nuevas de América Central, *Chondroscaphe atrilinguis* y *C. laevis*. *Orquideología,* **22**, 12–22.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), **1/B(27),** 1674–1727. Paul Parey, Berlin.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

594. COCHLEANTHES

Cochleanthes Raf., *Fl. Tell.*, **4,** 45 (1836). Type species: *Cochleanthes flabelliformis* (Sw.) R.E.Schult. & Garay (basionym: *Epidendrum flabelliforme* Sw.)

Derivation of name

From the Latin *cochlea*, snail-shell, and the Greek *anthos*, flower, in allusion to the cochleate lip and shell-shaped callus. **(FP)**

Description (Plate 199; Fig. 594.1)

Epiphytic, caespitose *herbs* without pseudobulbs, rarely with inconspicuous pseudobulbs completely hidden by leaf bases. *Roots* terete, produced from the rhizome. *Stem* enclosed by six or seven imbricating sheaths, provided with hyaline margins, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, oblanceolate to narrowly elliptic-obovate, acute to acuminate, abaxially carinate, narrowed at base into an indistinct, conduplicate petiole, grass green. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths; peduncle terete, spreading to suberect, provided with one or two conduplicate bracts; floral bract double, conduplicate, shorter than ovary, the external one loose, widely ovate, the subopposite internal bractlet narrowly lanceolate to ligulate. *Flowers* resupinate, usually strongly and sweetly scented (rarely unscented in autogamous populations), sepals and petals pale greenish cream to pale green, labellum whitish cream, with a violet-purple median band or basally veined with violet or purple, apically sometimes solidly violet, callus white or spotted purple-violet. *Dorsal sepal* free, lanceolate-elliptic, acute to acuminate, reflexed at base. *Lateral sepals* basally adnate to column foot, lanceolate-elliptic, acute to acuminate, inrolled-folded toward base. *Petals* oblanceolate to obovate, acute. *Labellum* with a claw, articulate with column foot, trilobed (sometimes obscurely), pandurate or suborbicular-flabellate, base cordiform, notched-bilobed and often reflexed at apex, apical margins undulate to crisped; disc with a semilunate, multiseriate callus, composed of many low, radiating, rounded ridges, protruding apically into rounded keels, central ones longer. *Column* curved, clavate to dilated at apex into rounded stigmatic wings, provided with a foot, the ventral surface basally provided with a low, rounded keel; anther cap cucullate, ovate to transversely elliptic, two-celled, pollinia four, in two subequal pairs, on a stipe scarcely distinct from triangular or elliptic-ovate, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 594.2)

Cochleanthes consists of two species, *C. flabelliformis* and *C. aromatica* (Rchb.f.) R.E.Schultes, collectively ranging from Mexico (North America) through Central America and the West Indies to northern South America. **(FP)**

Phytochemistry

Leaves of *C. flabelliformis* contain flavone *C*-glycosides (Williams 1979). This species also contains alkaloids (Lüning 1964; cited as *Warscewiczella flabelliformis* Cogn.). Kaiser (1993) noted that relative concentrations of constituents of the floral fragrance of *C. aromatica* vary with specimen and age of flower. However, the main components are the monoterpenes, geraniol, geraniol acetate, neral, and geranial. Minor components that make an important contribution to the scent include eugenol, indole, and vanillin. Gerlach and Schill (1991) reported a similar profile of monoterpene constituents for this species but did not record either indole or vanillin. **(NV, RG)**

Phylogenetics

Schultes and Garay (1954) assigned to *Cochleanthes* all the species previously described under *Warczewiczella*, but floral morphology is different in the two groups. The latter was revised in 1969 by Fowlie, who mainly distinguished it from *Cochleanthes* on the basis of the lip callus, free laterally and at the apex (versus solidly attached to the labellum at the base, anteriorly and laterally) and composed of radiating, digitate 'promontories' (versus a series of adjacent plates distally attached to the lip), and absence of a longitudinal, ventral keel on the column (prominent in *Cochleanthes*).

Studies based on DNA sequences (Whitten *et al.* 2005) showed that *Cochleanthes* is weakly supported as sister to the other species of the *Huntleya* clade provided with small pseudobulbs and included in *Stenotyla* and confirmed Fowlie's suggestion that the genus is only distantly related to *Warczewiczella*. *Cochleanthes* can be characterized by relatively large plants and flowers, plane or only slightly concave lip not enfolding the column, rounded and multiseriate callus laterally fused with the lip, and column with a ventral keel (Dressler 2000; Pupulin 2005; Whitten *et al.* 2005). **(FP)**

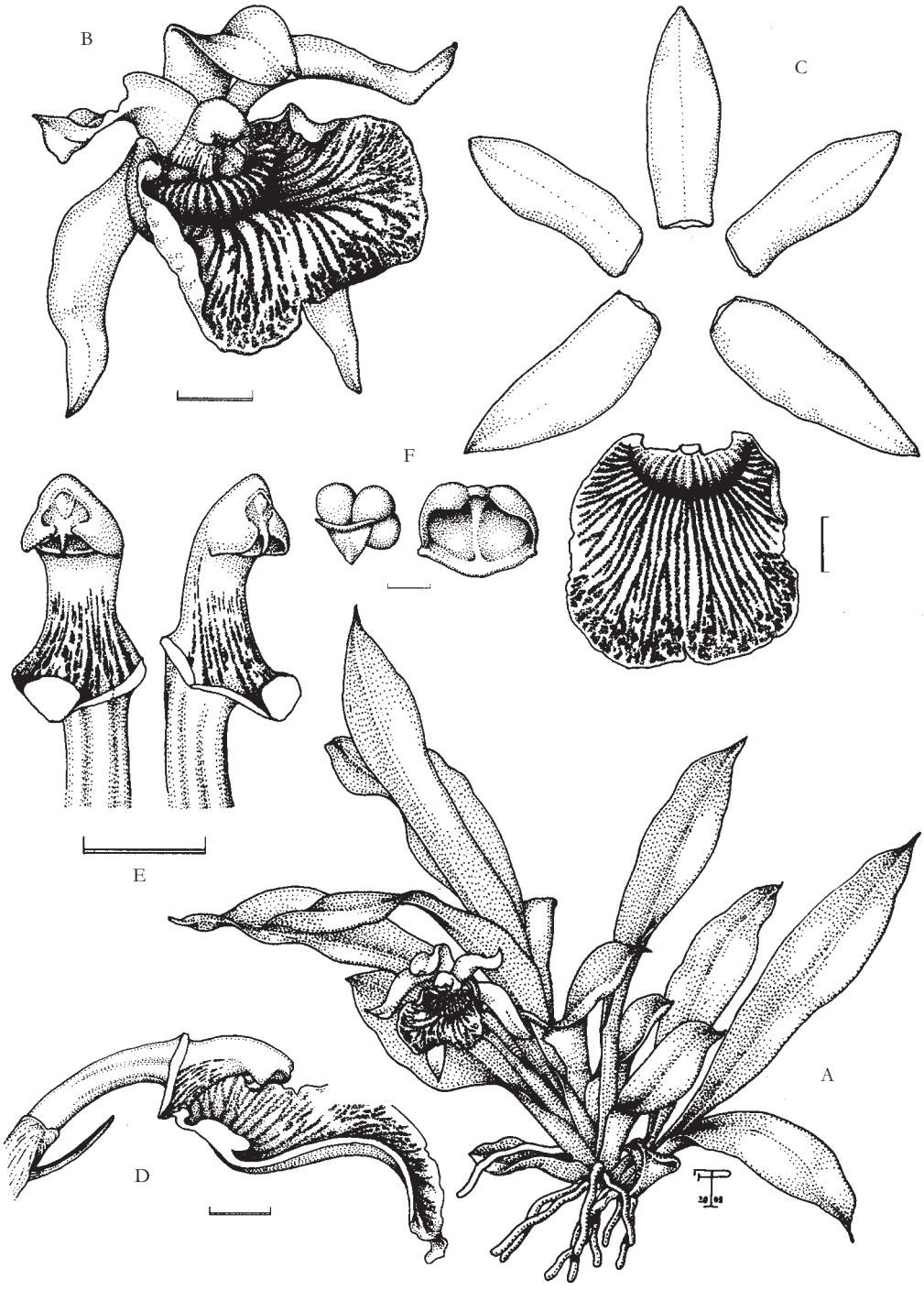


Fig. 594.1. *Cochleanthes flabelliformis* (Sw.) R.E.Schult. & Garay. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column and labellum, side view; E. Column, ventral and oblique views; F. Pollinarium and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 5725* (Lankester Botanical Garden Spirit Collection).

AQ: Is the reference to support distribution or the fact that most are unscented or both? If either of the latter two, the, reference should go at end of phrase, after West Indies.

Ecology

The species occur as epiphytes in shady sites in warm, tropical and premontane, evergreen wet forests at 200–1200 m. Plants mostly flower during the rainy season, often producing two or three flowers in succession. Self-pollinating forms, mostly with unscented flowers (Fowlie 1961; Ackerman 1995), are frequent in the West Indies, whereas in Central and South America the plants are usually allogamous. Where populations occur sympatrically in Costa Rica, the natural hybrid of *C. aromatica* with *Warczewiczella discolor* (Lindl.) Rchb.f. is infrequently found; the flowers of the hybrid have a widely opening lip, uniformly tinged with dark red or purple-red (Dressler 2003). **(FP)**

Fig. 594.2. Distribution map of *Cochleanthes*.

Pollination

Cochleanthes aromatica is pollinated by male euglossine bees of *Euglossa* and *Eulaema*. The pollinarium is deposited behind the bee's head (van der Pijl and Dodson 1966). **(FP)**

Uses

Cochleanthes species are occasionally cultivated, but there are no other known uses. **(FP)**

Cultivation

Both species occur in shady places in tropical and premontane, warm forests. Plants require a mild to slightly warm climate and should be maintained in open shade. They may be grown on slabs, but prefer pots with a coarse compost that allows the thick roots to receive adequate ventilation. Vigorous air circulation is essential to prevent fungal infections on the delicate foliage. Watering should be frequent to prevent desiccation. Large specimens should be disturbed as little as possible. **(FP)**

Taxonomic literature

Ackerman, J. D. (1995). An orchid flora of Puerto Rico and the Virgin Islands. Memoirs of the New York Botanical Garden, **73**, 1–203.

Dressler, R. L. (2000). Precursor to a revision of the *Chondrorhyncha* complex. *Orquideología,* **21,** 233–47.

Dressler, R. L. (2003). Orchidaceae. In *Manual de plantas de Costa Rica. Vol. 3.* (ed. B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora). Monographs in Systematic Botany, Vol. 83. Missouri Botanical Garden, St. Louis.

Fowlie, J. A. (1961). Ecology notes: Cochleanthes flabelliformis. American Orchid Society Bulletin, **30**, 797–9.

Fowlie, J. A. (1969). An annotated checklist of the genus *Warscewiczella. Orchid Digest*, **33,** 224–31.

Pupulin, F. (2005). *Cochleanthes* Raf. In *Vanishing beauty – native Costa Rican orchids, Vol. 1.* (ed. F. Pupulin), pp. 132–3. Editorial de la Universidad de Costa Rica, San José.

Pupulin, F. (2006). Genera zygopetalinarum. Part 2. The genus *Cochleanthes. Orchid Review*, **114,** 202–10.

Schultes, R. E. and Garay, L. A. (1954). On the validity of the generic name *Cochleanthes* Raf. *Botanical Museum Leaflets, Harvard University*, **18**, 321–7.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

595. CRYPTARRHENA R.Br.

Cryptarrhena R.Br., *Edwards's Bot. Reg.*, **2,** t. 153 (1816). Type species: *Cryptarrhena lunata* R.Br.

Clinhymenia A.Rich. & Galeotti, *Compt. Rend. Hebd. Séances Acad. Sci.*, **18,** 512 (1844). Type species: *Clinhymenia pallidiflora* A.Rich. & Galeotti

Orchidofunckia A.Rich. & Galeotti, *Ann. Sci. Nat., Bot.,* III, **3,** 24 (1845). Type species: *Orchidofunckia pallidiflora* A.Rich. & Galeotti

Derivation of name

From the Greek *kryptos*, hidden, and *harren*, stamen, in allusion to the hooded clinandrium that covers the anther. **(FP)**

Description (Plate 200; Fig. 595.1)

Epiphytic, caespitose *herbs* with a sometimes pseudobulbous stem. *Roots* terete, flexuous, produced at the base of new shoots or near pseudobulbs. *Pseudobulb*, when present, heteroblastic, ovoid, compressed, often cryptic, one or two-leaved at apex, concealed by few to numerous (up to 17) foliaceous sheaths. *Leaves* conduplicate, distichous, membranaceous to coriaceous, elliptic to elliptic-oblanceolate, subobtuse to acute, rarely acuminate, sometimes abaxially provided with a distinct keel along midvein, narrowed at base into an indistinct, conduplicate petiole, clear green. *Inflorescences* lateral, a many-flowered (up to 30) raceme produced from axils of the lower leaves or base of mature pseudobulb, usually longer than leaves, peduncle terete, arched to pendent, basally provided with 2–4, membranaceous, oblong-lanceolate, conduplicate, loose bracts; floral bracts narrowly lanceolate, acute to acuminate, shorter or subequal to ovary. *Flowers* resupinate, sepals and petals pale green to greenish yellow, labellum white or yellow. *Dorsal sepal* free, lanceolate-elliptic to elliptic-oblanceolate, acute to acuminate, usually concave, reclinate over the column. *Lateral sepals* lanceolate-elliptic to elliptic-oblanceolate, acute to acuminate, sometimes reflexed at base. *Petals* narrowly elliptic or lanceolate-elliptic to oblong-subspatulate, acuminate to rounded-apiculate, apex sometimes minutely and irregularly denticulate. *Labellum* adnate to base of column, trilobed, provided with a linear, laterally compressed, keeled claw; lateral lobes linear-falcate, acuminate, apex retrorse; midlobe subquadrate, apically bilobed, sometimes apiculate, distal lobes triangular or narrowly falcate, spreading. *Column* semiterete, arcuate, basally provided with a distinct, ventral tooth, apically dilated into a well-developed, hooded, irregularly crenulate clinandrium, provided with oblong, obtuse, porrect stigmatic wings and sometimes with a second pair of basal, triangular, acute arms; anther cap cucullate, obovate, geniculate, two-celled, pollinia four, flattened, in two subequal pairs on two cylindrical, partially joined caudicles, and an elliptic viscidium; stigma elliptic-ovate, protruding. **(FP)**

Distribution (Fig. 595.2)

The three or four species of *Cryptarrhena* are widespread in tropical America, ranging from Mexico (North America) through Central America, Jamaica, and Trinidad to Brazil, Peru, and Bolivia (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Cryptarrhena*. **(NV, RG)**

Phylogenetics

Nine species have been described in *Cryptarrhena*, but only three to four survived critical examination (Christenson 1993). The genus was originally assigned by Schlechter to Ornithocephalinae (now in Oncidiinae) on the basis of its four rounded pollinia, but in the genera related to *Ornithocephalus* these are borne on a long stipe, whereas in *Cryptarrhena* the 'stalks' are actually caudicles formed within the anther, joined before reaching the viscidium.

Dressler reassessed phylogenetic affinities of the genus in 1980. Although he noted the general resemblance of *Cryptarrhena* to Maxillarieae, he considered that details of the perianth (i.e. the anchor-shaped lip), column (hooded clinandrium), and pollinarium (no stipe) were so unlike other members of this tribe that it warranted tribal status as Cryptarrheneae (Dressler 1980, 1981). He later resurrected his subtribe Cryptarrheninae and included it within Maxillarieae, mostly on the basis of the *Maxillaria*-type seeds of *Cryptarrhena*, suggesting that the genus was probably derived from a primitive member of Maxillarieae (Dressler 1993).

The same phylogenetic placement was adopted by Szlachetko (1995), who included subtribe Cryptarrheninae in Maxillarieae. However, he noted that *Cryptarrhena* has several characteristics not found in other 'vandoid' orchids, arguing that floral morphology excluded a close relationship with Maxillarieae. In his scheme of possible relationships within subfamily Vandoideae, Cryptarrheninae are sister to the clade of Maxillarieae + Dichaeae + Oncidieae/Ornithocephaleae/Telipogoneae, and then sister to Zygopetaleae.

The combined molecular analysis of Maxillarieae carried out by Whitten *et al.* (2000) supported inclusion of the morphologically anomalous *Cryptarrhena* within a monophyletic Zygopetalinae. This conclusion was later confirmed by the evaluation of the phylogenetic relationships of Zygopetalinae by parsimony analysis of combined DNA sequence data (Whitten *et al.* 2005). In those studies, Zygopetalinae comprise two major clades: the predominantly pseudobulbous, plicate-leaved *Zygopetalum* clade and the mostly pseudobulbless, conduplicate-leaved *Huntleya* clade. In the combined analysis, *Cryptarrhena* is strongly supported as monophyletic, but its exact relationships to the two major clades is unclear. The sometimes pseudobulbous plants and long inflorescences with numerous, small flowers of *Cryptarrhena* seem out of place among the mostly single-flowered genera of the *Huntleya* clade (*Dichaea*, *Huntleya*, *Chaubardia,* and *Chondrorhyncha* complex). However, cryptic pseudobulbs are always present in *Stenotyla* and

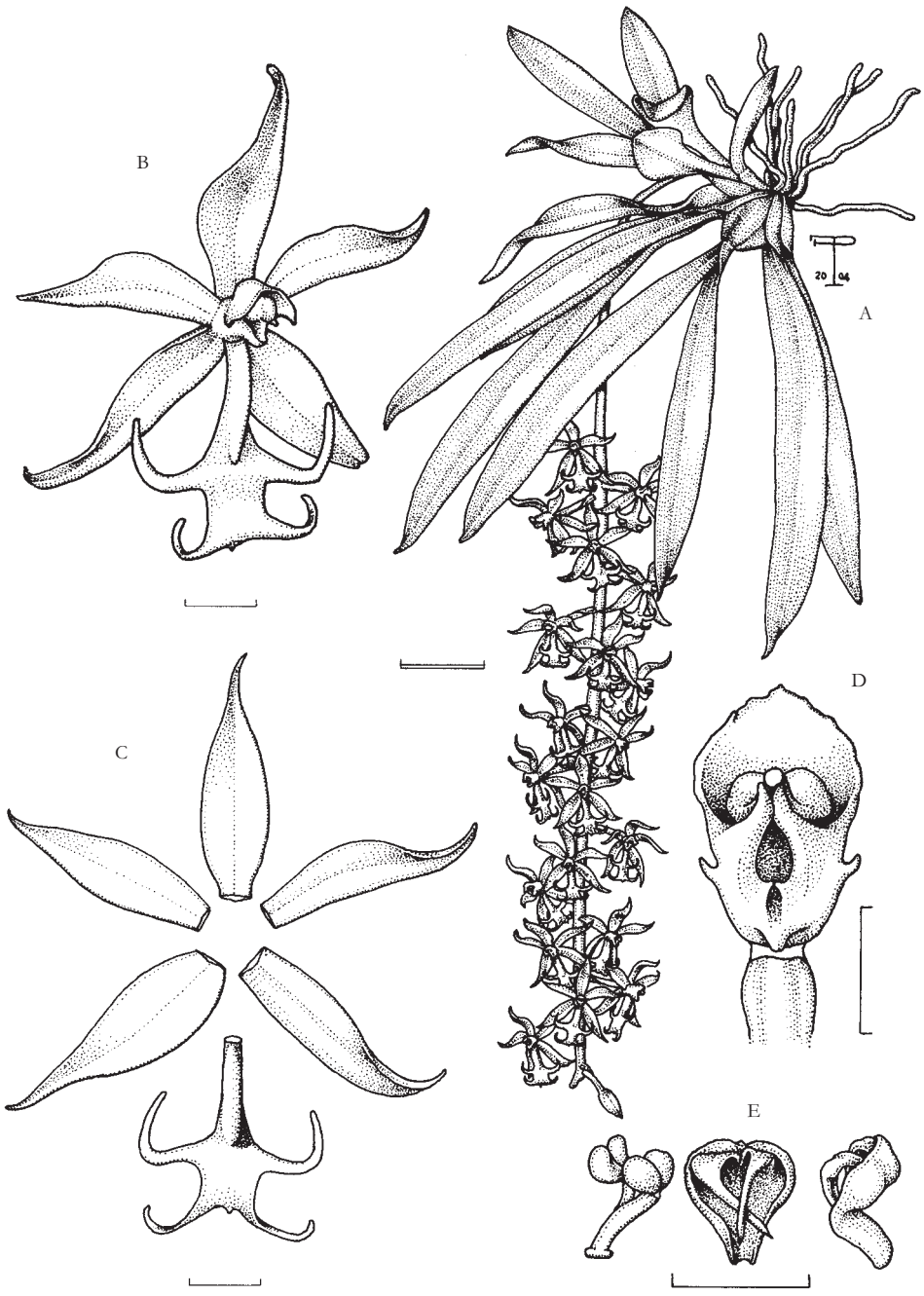


Fig. 595.1. *Cryptarrhena guatemalensis* Schltr. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column, ventral view; E. Pollinarium and anther cap (ventral and side views). Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 2957* (Lankester Botanical Garden Spirit Collection).

occasionally in *Chaubardiella* (both in the 'core' *Huntleya* clade), the lip shape is reminiscent of that of most *Dichaea* species, and the hooded apex of the column is similar to those of *Huntleya* and *Chaubardia*. **(FP)**

Ecology

Cryptarrhena species occur as epiphytes in warm, tropical to premontane wet forests, from sea level to about 1000 m. Flowering has been recorded mostly from January to May, but in Costa Rica *C. guatemalensis* Schltr. regularly flowers during the rainy season, from July to November. **(FP)**

Pollination

Pollination biology of the genus is unknown. **(FP)**

Uses

There are no known uses for any of the species. Some may be cultivated as curiosities. **(FP)**

Cultivation

Plants of *Cryptarrhena* are mostly found in warm, lowland to premontane, humid forests, usually in shaded spots in the lower

Fig. 595.2. Distribution map of *Cryptarrhena.*

portion of the canopy. They should be grown in a warm and shaded environment and provided with constant humidity and frequent watering throughout the year. Because of pendent inflorescences, plants should be mounted on plaques and disturbed as little as possible. **(FP)**

Taxonomic literature

Christenson, E. A. (1993). Mesoamerican orchid studies V: a synopsis of *Cryptarrhena* R. Br. *Lindleyana,* **8**, 163–5.

Dressler, R. L. (1980). Orphan orchids II. *Cryptarrhena* – a new tribe, Cryptarrheneae. *Orquídea* (*México*), **7**, 286–8.

Dressler, R. L. (1981). *The orchids: natural history and classification*. Harvard University Press.

Dressler, R. L. (1993). *Phylogeny and classification of the orchid family*. Dioscorides Press, Portland, Oregon.

Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum,* **3**, 1–152.

Whitten, W. M., Williams, N. H., and Chase, M. W. (2000). Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. *American Journal of Botany,* **87**, 1842–55.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

596. DAIOTYLA

Daiotyla Dressler, *Lankesteriana,* **5**, 92 (2005). Type species: *Daiotyla albicans* (Rolfe) Dressler (basionym: *Chondrorhyncha albicans* Rolfe)

Derivation of name

From the Greek *daio*, divide, and *tyle*, knot, in reference to the characteristic shape of the lip callus in the species. **(FP)**

Description (Plate 201; Fig. 596.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from rhizome. *Stem* abbreviated, enclosed by 4–6 imbricating sheaths, sometimes provided with hyaline margins,

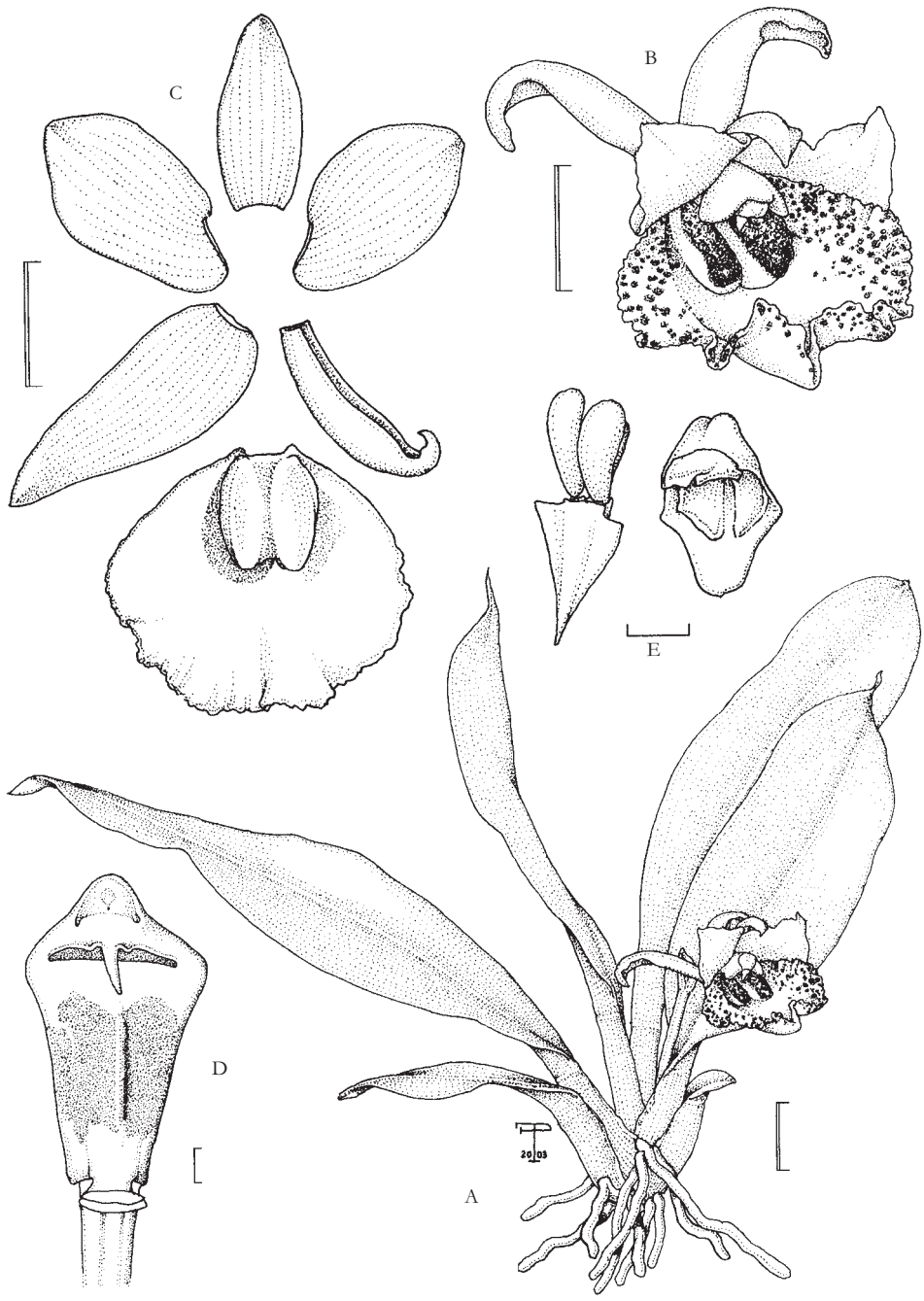


Fig. 596.1. *Daiotyla crassa* (Dressler) Dressler. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column, ventral view; E. Pollinarium and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 4204* (Lankester Botanical Garden Spirit Collection).

upper ones foliaceous. *Leaves* conduplicate, elliptic to oblanceolate, acute to acuminate, petiolate, abaxially carinate, dark green, adaxial surface shiny. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths, peduncle terete, suberect, provided with one or two conduplicate bracts; floral bract double, conduplicate, shorter than ovary, the external one ovate-elliptic to suborbicular, the subopposite internal bractlet narrowly elliptic to ligulate. *Flowers* resupinate, sepals and petals white to pale cream, labellum white or spotted with purple, callus tinged pale yellow or purple or spotted purple. *Dorsal sepal* lanceolate-elliptic, acute, conduplicate-folded, hooked at apex. *Lateral sepals* narrowly ovate-elliptic to elliptic-lanceolate, obtuse to subacute, reflexed, conduplicate-folded toward base, abaxially keeled, hooked at apex. *Petals* obovate to elliptic, rounded, sometimes apiculate. *Labellum* subrhombic to broadly obovate, rounded, emarginate-bilobed, apical margin undulate to finely crisped, sometimes infolded, basal margins erect, flanking column; disc with a transverse, thickened, bilamellate, rounded to emarginate, sometimes erose-undulate callus, median groove shallow. *Column* straight, subclavate to clavate, provided with a distinct foot, ventral surface plain; anther cap elliptic to ovate-rhombic, cucullate, two-celled, pollinia four, in two pairs of different sizes,

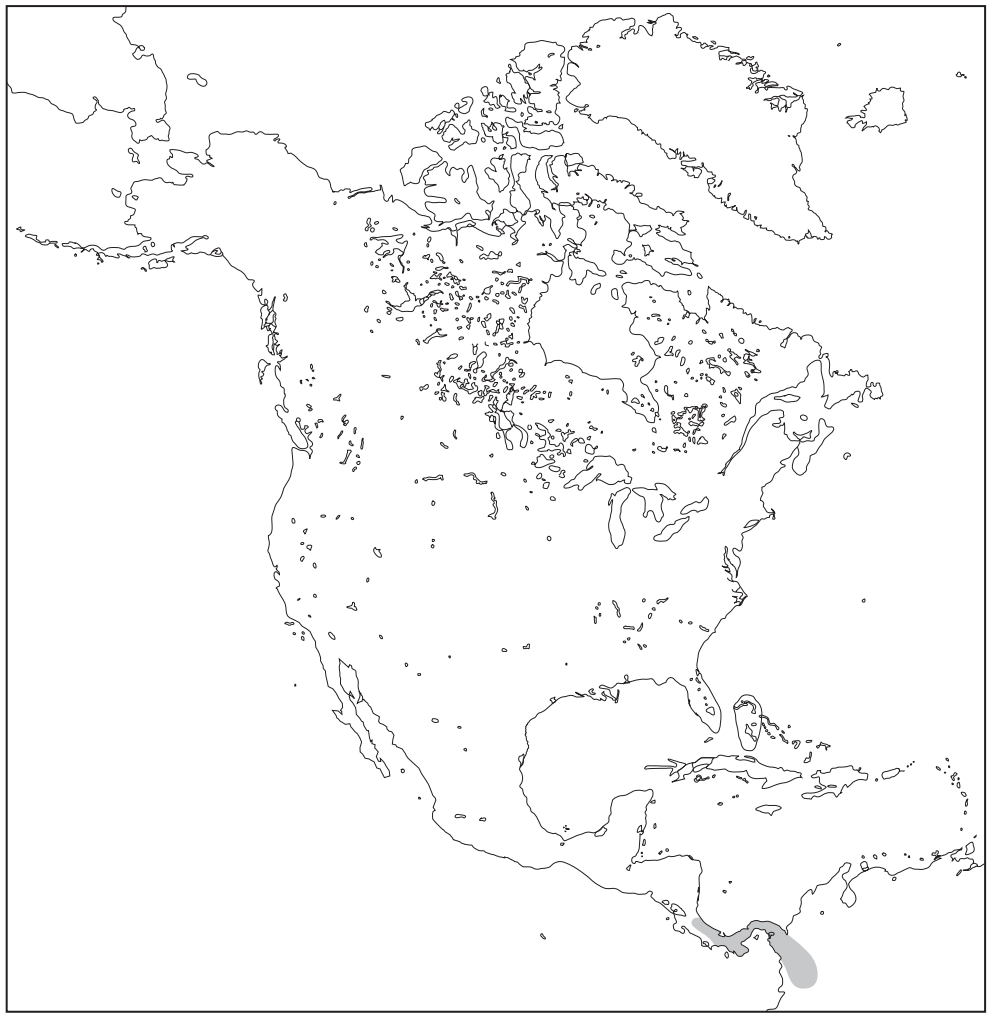


Fig. 596.2. Distribution map of *Daiotyla*.

on a stipe scarcely distinct from the triangular, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 596.2)

Daiotyla is a genus of three or four species distributed from Costa Rica (Central America) to Colombia (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Daiotyla*. **(NV, RG)**

Phylogenetics

Molecular analyses (Whitten *et al.* 2005) strongly supported *Daiotyla* as sister to *Stenia*, which the new genus resembles in having oblong to oblanceolate, dark green leaves. These both are members of the *Huntleya* clade. The shape of the lip, however, is different from that of *Stenia*. The genus mainly differs from *Chondrorhyncha* in the thick, two-parted callus at the base of the lip, which extends to about the middle of the blade. **(FP)**

Ecology

The species occur as epiphytes in shady sites in lowland to mid-montane, evergreen wet forests at 250–1800 m. Once the new growth is mature, plants flower in succession throughout the year. **(FP)**

Pollination

There is no information on pollination for the genus. **(FP)**

Uses

There are no known uses of any of the species. **(FP)**

Cultivation

Plants of this genus are shade-loving, and they can be satisfactorily grown in pots or on plaques of wood or tree fern, with frequent watering. Repotting after flowering is recommended every two years. Intermediate temperatures are appropriate for the species of *Daiotyla*, although plants can also tolerate warmer

temperatures. The delicate foliage is sensitive to excessive sunlight. **(FP)**

Taxonomic literature

Dressler, R. L. (1983). Die Gattung *Chondrorhyncha* in Panama mit zwei neuen Arten: *Chondrorhyncha crassa* und *Chondrorhyncha eburnea*. *Orchidee (Hamburg)*, **5**, 220–6.

Dressler, R. L. (2000). Precursor to a revision of the *Chondrorhyncha* complex. *Orquideología*, **21**, 233–55.

Fowlie, J. A. (1966). A revision of the Central American species of *Chondrorhyncha* and *Kefersteinia*, including the description of a new species from Costa Rica. *Orchid Digest*, **30**, 79–82.

Garay, L. A. (1961). Orquídeas Colombianas nuevas o críticas. Decena III. *Orquideología*, **4**, 153–61.

Pupulin, F. (2003). Die Orchideen flora Mittelamerika – Ergänzungen (Teil 1). Additamenta ad orchideologiam mesoamericanam, 1. *Orchidee (Hamburg)*, **54**, 467–77.

Pupulin, F. (2005). *Chondrorhyncha* Lindl. In *Vanishing beauty – native Costa Rican orchids, Vol. 1*. (ed. F. Pupulin), p. 100–9. Editorial de la Universidad de Costa Rica, San José.

Pupulin, F. (2006). Genera zygopetalinarum. Part 1. The genus *Daiotyla*. *Orchid Review*, **114,** 144–9.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

597. DICHAEA

Dichaea Lindl., *Gen. Sp. Orch. Pl.,* 208 (1833). Type species: *Dichaea echinocarpa* (Sw.) Lindl., *nom. illeg.* (= *Dichaea pendula* (Aubl.) Cogn.; basionym: *Limodorum pendulum* Aubl.)

Dichaeopsis Pfitzer, *in* Engler and Prantl, *Nat. Planzenfam. Orch.,* **2**(6), 206–7 (1889). Type species: not designated.

Derivation of name

From the Greek *di–*, two, and *keio*, to divide, in reference to the characteristic disposition of leaves in two rows along the stem. **(FP)**

Description (Plates 202–4; Fig. 597.1, 597.2)

Epiphytic, caespitose or scandent *herbs* without pseudobulbs. *Roots* terete, filiform to fleshy, rarely produced only at the base of the stem, commonly also cauline, rarely branching. *Stem* erect to arching or pendent, terete or dorsiventrally flattened, often freely branching, completely enclosed by persistent imbricating leaf-sheaths. *Leaves* distichous, articulate or not, simple, conduplicate, ovate to elliptic or lanceolate, rounded to acute, usually apiculate, abaxially carinate, margins entire or variously microciliate toward apex, sometimes evenly ciliate, medium to dark green or grey-green to brownish, sometimes glaucous on one or both surfaces. *Inflorescences* lateral, single-flowered, supra-axillary, produced sequentially or rarely simultaneously, emerging from axils of upper leaf-sheaths, peduncle terete, straight or geniculate, basally provided with two or three conduplicate bractlets; floral bract conduplicate, the external one larger, ovate, cucullate-funnelform, the subopposite internal bractlet narrowly lanceolate to ligulate. *Flowers* resupinate, ringent to spreading, often scented, sepals and petals ivory white to greenish white or orange-grey, sepals mostly flecked with purple-violet toward base, petals commonly heavily spotted or blotched with purple-violet, labellum white or spotted and blotched with violet, rarely solid purple, column greenish white, commonly tinged violet on foot and wings. *Dorsal sepal* ovate to elliptic-lanceolate, acute to subacuminate, concave toward base, abaxially smooth or variously tuberculate, erect above column. *Lateral sepals* obliquely ovate to elliptic-lanceolate, sometimes falcate, acute to subacuminate, concave toward base, smooth or tuberculate. *Petals* ovate to elliptic or obovate, acute to abruptly acuminate, frequently concave. *Labellum* distally trilobed to anchor-shaped, rarely subentire, variously clawed or infrequently sessile, usually conduplicate toward apex, acute to rounded or truncate, often apiculate, basal margins frequently ciliate, distal margins irregularly microserrate; disc mostly ecallose or with a central ridge or two basal knobs. *Column* erect or straight, subterete, provided with a foot, commonly with basal, ciliate wings; anther terminal, clinandrium shallow or hooded-petaloid, anther cap widely elliptic to ovate-rhombic, cucullate, flattened, two-celled, pollinia four, in two subequal pairs, rarely united in two heart-shaped pollinia, on a laminar, apically expanding stipe, continuous with the elliptic, sulcate, hyaline viscidium, stigma rounded, the lower rim commonly projecting into a variously shaped, frequently papillose-hirsute ligule. *Ovary* glabrous or variously muricate. **(FP)**

Distribution (Fig. 597.3)

Dichaea comprises about 110 species distributed from Mexico (North America) through Central America and the West Indies to Bolivia and Argentina (South America), with greatest diversity in Andean South America. **(FP)**

Infrageneric classification

Use of a limited number of morphological characters to assess phylogenetic affinities (in the case of *Dichaea* essentially restricted to characteristics of leaf articulation and ovary vestiture) has been a common approach to the taxonomy of the genus, resulting in several artificial schemes of infrageneric classification. In his treatment of the Monandrae-Dichaeinae orchids, Pfitzer (1888) characterized *Dichaea* by non-articulate leaves and verrucose to muricate fruits, segregating those species with articulate leaves and glabrous fruits *Dichaeopsis*, which was reduced to sectional rank by Kuntze in 1903. Cogniaux (1906) retained the broader concept of *Dichaea*, dividing it into four sections on the basis of leaf articulation and fruit vestiture. Among species with persistent leaves, he adopted a narrow circumscription of *D. sect. Dichaea* (then as *Eudichaea*) for the taxa with muricate fruits, creating *D.* sect. *Dichaestrum* for the species with glabrous fruits. He followed Kuntze in treating *Dichaeopsis* at sectional rank but considered it in the strict sense proposed by Pfitzer, encompassing only those species provided with articulate leaves and glabrous ovary, and grouped taxa with deciduous leaves and muricate ovary in *D.* sect. *Pseudodichaea*.

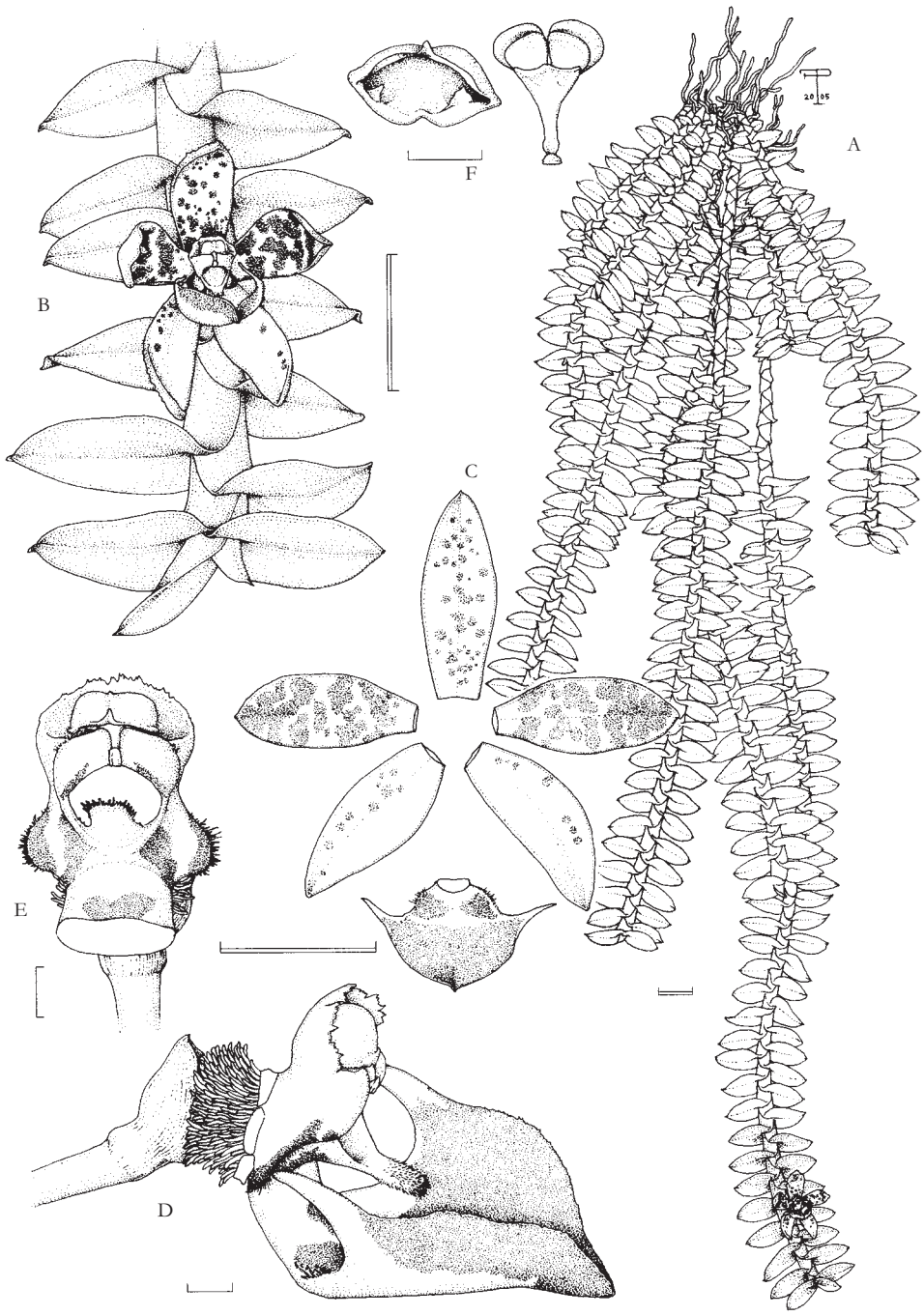


Fig. 597.1. *Dichaea poicillantha* Schltr. A. Habit, with inflorescence; B. Apex of stem and flower; C. Perianth, dissected; D. Column and labellum, side view; E. Column, ventral view; F. Anther cap and pollinarium. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 3420* (CR).

In the first synopsis of Dichaeinae, Schlechter (1914) accepted Pfitzer's view about the existence of two separate genera within the subtribe. He included in *Dichaea* all species with persistent leaf blades, maintaining Cogniaux's *D.* sect. *Dichaea* for species with muricate fruits and *D.* sect. *Dichaestrum* for those with smooth capsules and organizing *D.* sect. *Dichaea* into two series on the basis of the sessile or widely cuneiform vs. narrowly unguiculate base of the lip. For species with non-articulate leaves, Schlechter adopted the generic name *Epithecia* Knowles & Westc. over *Dichaeopsis* (he was mistaken over the nature of the type species of this name, which is a member of *Prosthechea*, Laeliinae). Nevertheless, his concept of *Epithecia* is more comprehensive than the genus *Dichaeopsis* as proposed by Pfitzer and adopted by Cogniaux for a section of *Dichaea*, comprising *D.* sects. *Dichaeopsis* and *Pseudodichaea*, i.e. all species with deciduous leaves, independent of the characteristic indumentum of the ovary and resulting fruit. *Dichaea* sect. *Dichaeopsis* was further subdivided into two series, according to proximal shape of the lip. After obtaining access to the original publication of *Epithecia* by Knowles and Westcott, Schlechter (1918) corrected his mistake, adopting *Dichaeopsis*. Nevertheless, in subsequent publications, he recognized the broader concept of *Dichaea*. In

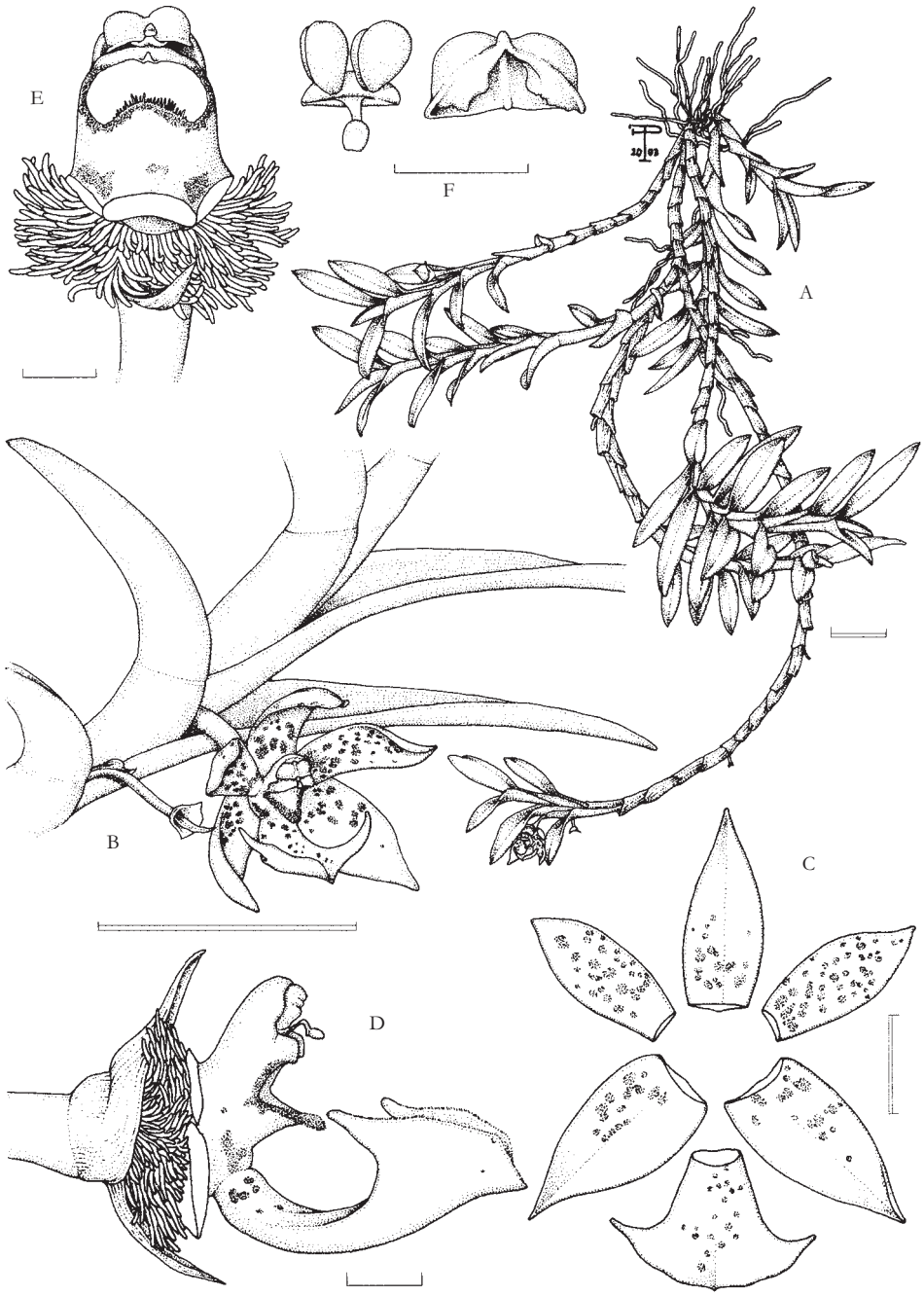


Fig. 597.2. *Dichaea elliptica* Dressler & Folsom. A. Habit, with inflorescence; B. Portion of the stem and flower; C. Perianth, dissected; D. Column and labellum, side view; E. Column, ventral view; F. Pollinarium and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin et al. 4945* (CR).

1923, Kränzlin published the first systematic monograph on *Dichaea*, accepting *D.* sects. *Dichaea* Cogn. (including *D.* sect. *Dichaeastrum*) and *Dichaeopsis* (Pfitzer) Cogn. and creating *D.* sect. *Maxillariopsis* for a group of species currently asssigned to *Maxillaria* or one of the closely related genera.

Folsom (1974) produced the first modern taxonomic revision of *D.* sect. *Dichaea*. Among species with persistent leaves, he circumscribed *D.* sect. *Dichaea* to include those taxa with a muricate ovary, implicitly accepting segregation of the species with smooth ovaries in *D.* sect. *Dichaeastrum*. He also excluded from his study species allied to *D. hystricina* Rchb.f., for which he suggested recognition at sectional level. On the other hand, he retained *D. camaridioides* Schltr. within the study group, but suggested the convenience of creating a monospecific section for this atypical species. In the generic treatment of Dichaeinae for the revised edition of Schlechter's *Die Orchideen*, Senghas accepted *Dichaea* with two subgenera and formally validated *D.* subgenus *Epithecia* (Senghas 1995) for those species with articulate, eventually deciduous leaf blades, perpetuating a misconception that had plagued the taxonomy of *Dichaea* for almost a century.

Recent studies by Neubig *et al.* (unpublished), based on DNA sequence data of nrITS as well as plastid *matK, trnL-F,* and *atpB-rbcL,* supported *Dichaea* as a monophyletic genus and showed that *D.* sect. *Pseudodichaea* is also monophyletic. However, *D.* sect.

Fig. 597.3. Distribution map of *Dichaea*.

Dichaeopsis is highly polyphyletic. *Dichaea* sects. *Dichaeastrum* and *Dichaea* together form a monophyletic group,but *D.* sect. *Dichaeastrum*, differentiated from *D.* sect. *Dichaea* primarily by a glabrous ovary, is potentially nonphyletic (Neubig 2005; Neubig *et al*. 2005). **(FP)**

Palynology

Schill and Pfeiffer (1977) described pollen of *D. trichocarpa* (Sw.) Lindl. as in convex tetrads with a laevigate-foveolate exine and rounded sexine. **(AP)**

Cytogenetics

Tanaka and Kamemoto (1974) listed a chromosome number of $2n = 52$ for *Dichaea muricata* (Sw.) Lindl. var. *neglecta* (Schltr.) Kränzl. (= *D. neglecta* Schltr.). **(AP)**

Phytochemistry

Leaves of *D. graminoides* Lindl. contain flavone *C*-glycosides (Williams 1979). Species recorded as giving a positive result in surveys for alkaloid content are *D. australis* Cogn., *D. cogniauxiana* Schltr., *D. muricata* Lindl., *D. pendula* (Aubl.) Cogn., and *D. trulla* Rchb.f. (Lüning 1964, 1967). The floral fragrance of *D. muricata* consists almost entirely of the aromatic ester benzyl acetate (Gerlach and Schill 1991). A detailed analysis (Kaiser 1993) of the corresponding fragrance of *D. rodriguesii* Pabst also revealed benzyl acetate as a major component (49.0%) together with anisyl acetate (32.5%). What is more striking from an olfactory point of view is several unsaturated C_{10}-lipid metabolites such as (*Z*)-4-decenal, (*E*,*Z*)-2,4-decadienal, and (*E*,*E*)-2,4-decadienal, compounds that are also found in the floral fragrance of *Pescatoria cerina* (Lindl.) Rchb.f. (see separate entry). **(NV, RG)**

Phylogenetics

Originally placed by Lindley in Vandeae, likely on the basis of the pollinarium provided with a caudicle united to a distinct viscidium, and then included among Brassidae close to *Fernandezia* Ruiz & Pav., *Dichaea* was assigned by Bentham (1881) to subtribe Maxillarieae (tribe Vandeae), a group of strictly American epiphytes characterized by mostly single-flowered inflorescences.

Pfitzer (1887) created tribe Dichaeae to group Neotropical species lacking pseudobulbs with two-ranked, duplicate leaves, single-flowered inflorescences, and four pollinia. In 1888 he included the genus *Dichaea* in the subtribe, creating *Dichaeopsis* for a distinct subset of species characterized by articulated leaves and glabrous ovaries (Pfitzer 1887, 1888). Kränzlin (1923) included *Dichaea* among pseudomonopodial, monandrous orchids, grouping it with *Centropetalum* Lindl., *Lockhartia* Hook., *Orchidotypus* Kränzl., *Pachyphyllum* Kunth, and *Pterostemma* Lehm. & Kränzl. on the basis of vegetative architecture (i.e. lacking pseudobulbs and having simple or few-branched stems, distichously arranged leaves, and mainly single-flowered inflorescences). Dressler and Dodson (1960) assigned *Dichaea* to the monogeneric *Dichaea* alliance, one of three alliances of Oncidiinae, distinguishing it within the subtribe by four pollinia, column with a short rostellum, and usually anchor-shaped lip. Dressler (1981) included *Dichaea* in the monogeneric subtribe Dichaeinae, but he noted a clear similarity of *Dichaea* with the *Chondrorhyncha* complex and suggested its possible derivation from Zygopetalinae-like ancestors. In 1993, he definitively placed *Dichaea* in subtribe Zygopetalinae (Dressler 1993). Szlachetko (1995) considered *Dichaea* the only member of a monogeneric subtribe Dichaeinae, one of three subtribes of 'monopodial' orchids in tribe Dichaeae Pfitzer (together with Vargasiellinae Romero & Carnevali and Pachyphyllinae Pfitzer), interpreted as an early and blind evolutionary offshoot of the oncidioid line. Nevertheless, he noted that velamen and seed morphology indicate that the probable ancestor of *Dichaea* should be found among the maxillarioid genera. Senghas (1995) accepted *Dichaea* as the monogeneric member of Dichaeinae, one of four subtribes comprising an informal *Subtribusgruppe* (or *tribella*) Tetrapolliniata, distinguished within the group by 'pseudomonopodial' habit and single-flowered inflorescence.

Although primarily focused on generic relationships of Stanhopeinae, the combined molecular analysis of Maxillarieae published by Whitten *et al.* (2000) indicated high bootstrap support for monophyly of Zygopetalinae (including *Dichaea*), confirming Dressler's view about inclusion of this morphologically anomalous genus in the subtribe. These preliminary findings were recently confirmed by work aimed to clarify generic relationships of Zygopetalinae through the analysis of combined nuclear and plastid DNA sequence data (Whitten *et al.* 2005). *Dichaea* was strongly supported as monophyletic and weakly supported as sister to the *Huntleya* clade (plants mostly without pseudobulbs and with conduplicate leaves). **(FP)**

Ecology

The species occur as epiphytes (rarely terrestrials), mostly restricted to shady places in the understorey of tropical to submontane, evergreen wet forests at 0–2500 m. With a few exceptions, species of *Dichaea* are shade-loving plants, invariably growing in subdued light on the main trunk (often near the soil) and large, shaded branches. Most species are not exposed to direct sunlight, and plants usually establish themselves among thick layers of mosses, which ultimately cover large portions of stems and leaves. **(FP)**

Pollination

Dichaea panamensis Lindl. is pollinated by male *Euglossa cordata* bees (Dressler 1968), and *D. potamophila* Folsom is pollinated by *Eulaema meriana* while scratching the base of the labellum in search of fragrances (Folsom 1987). The pollinarium is attached to the frons region of the insect head. **(FP)**

Uses

Ames and Correll (1953) recorded use of a poultice made by crushing and macerating the plant of *D. muricata* (= *D. muricatoides* Hamer & Garay) in Guatemala as a treatment for snakebite. Some species are culitvated as ornamentals. **(FP)**

Cultivation

With the exception of *D. glauca* (Sw.) Lindl., which is often found in exposed situations, plants of the genus are shade-loving epiphytes. The foliage is sensitive to excessive light and must be always protected from direct sun. *Dichaea* can be grown in pots with a medium to fine-grade, moisture-retaining medium and suspended under the bench or on plaques of wood or tree-fern, with frequent watering to prevent desiccation. Plants are sensitive to severe drought; high humidity must also be maintained. Depending on characteristics of the medium, repotting is recommended every three to four years, taking care not to damage filiform roots. Intermediate to slightly warm temperatures are optimal for growing *Dichaea*, although some species need cooler temperatures to flower. **(FP)**

Taxonomic literature

Bentham, G. (1881). Notes on Orchideae. *J. Linn. Soc. (Bot.),* **18**, 281–361.

Cogniaux, A. (1906). Orchidaceae III, *Dichaea*. In *Flora Brasiliensis* (ed. C. F. P. Martius), pp. 484–504. R. Oldenbourg, Monachii et Lipsiae.

Dressler, R. L. (1968). Observations on orchids and euglossine bees in Panama and Costa Rica. *Revista de Biología Tropical,* **15,** 143–83.

Dressler, R. L. (1981). *The orchids: natural history and classification*. Harvard University Press.

Dressler, R. L. (1993). *Phylogeny and classification of the orchid family*. Dioscorides Press, Portland, Oregon.

Dressler, R. L. and Dodson, C. H. (1960). Classification and phylogeny in the Orchidaceae. *Annals of the Missouri Botanical Garden,* **47**, 25–68.

Folsom, J. B. (1987). *A systematic monograph of* Dichaea *section* Dichaea *(Orchidaceae)*. Ph.D. thesis. University of Texas, Austin.

Kränzlin, F. W. L. (1923). *Dichaea*. In *Pflanzenreich* IV, 50 (ed. A. Engler), pp. 33–64.

Kuntze, C. E. O. (1903). Revision of *Dichaea*. In *Lexicon generum phanerogamarum* (ed. T. E. von Post), p. 171. Deutsche Verlag-Anstalt, Stuttgart.

Neubig, K. M. (2005). *Molecular systematics of the genus* Dichaea *(Zygopetalinae: Orchidaceae)*. Master's thesis. University of Florida, Gainesville.

Neubig, K. M., Williams, N. H., and Whitten, W. M. (2005). Molecular systematics of the genus *Dichaea* (Zygopetalinae:

Orchidaceae). First Scientific Conference on Andean Orchids, Gualaceo, Ecuador. Abstract.
Pfitzer, E. H. H. (1887). *Entwurf einer natürlichen Anordnung der Orchideen*. Carl Winter's Universitätsbuchhandlung, Heidelberg.
Pfitzer, E. H. H. (1889). Monandrae-Dichaeinae. In *Die natürlichen Pflanzenfamilien* (ed. H. G. A. Engler and K. A. E. Prantl), **2(6),** 206–7. Verlag von Wilhelm Engelmann, Leipzig.
Schlechter, R. (1914). Die Orchideen-Gruppe Dichaeinae Pfitzer. *Orchis,* **8**, 96–101.
Schlechter, R. (1926). Das System der Orchidaceen. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*, **9,** 563–91.
Senghas, K. (1995). *Dichaea*. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1854–61. Paul Parey, Berlin.
Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.
Whitten, W. M., Williams, N. H., and Chase, M. W. (2000). Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. *American Journal of Botany,* **87**, 1842–55.
Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G. and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbideae): combined molecular evidence. *Lankesteriana,* **5**, 87–107.

AQ: YZE/YSE words not found

598. ECHINORHYNCHA

Echinorhyncha Dressler, *Lankesteriana*, **5,** 94 (2005). Type species: *Echinorhyncha litensis* (Dodson) Dressler (basionym: *Chondrorhyncha litensis* Dodson)

Derivation of name

From the Greek *echinos*, sea urchin, hedgehog, and *rhynchos*, beak, in reference to the piliferous, hooked appendages under the column, characteristic of the genus. **(FP)**

Description (Plate 205; Fig. 598.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from the rhizome. *Stem* abbreviated, enclosed by 6–10 imbricating, mostly foliaceous sheaths, sometimes provided with scarious, hyaline margins. *Leaves* conduplicate, articulate, membranaceous, oblong-elliptic to narrowly ligulate-elliptic, acute to subacuminate, abaxially carinate, usually narrowed at base into a distinct, conduplicate petiole. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths, peduncle terete, suberect to arching or pendent, provided with 1–3 narrowly ovate, conduplicate, appressed bracts; floral bract double, conduplicate, shorter than ovary, the external one ovate, loose, the subopposite internal bractlet narrowly ligulate. *Flowers* resupinate, sepals and petals white to cream, labellum creamy white to yellow with red margins or apically suffused with wine-red or spotted and blotched red. *Dorsal sepal* free, lanceolate-elliptic to oblong-elliptic, acute to subacuminate, apex curved-reflexed. *Lateral sepals* lanceolate-elliptic to oblong-elliptic, rarely subfalcate, acute, reflexed, often inrolled-folded toward base. *Petals* lanceolate-elliptic to oblong-elliptic, acute, apically curved-revolute. *Labellum* articulate with the column foot, ovate to rhomboid to obovate-trullate, base rounded, apex obtuse to emarginate, usually deflexed, basal margins rounded, erect, distal margins sometimes dentate, wavy; disc with a longitudinal, central ridge running from the base to about the middle of labellum, terminating in 3–7 rounded teeth, lateral ones shorter. *Column* straight to arcuate, semiterete, ventrally flattened, with a distinct foot, expanded into apically indistinct or narrow, ovate wings above the middle, adaxially provided with 2–4 tuberous, pubescent-bristly, usually uncinate appendages under basal lobe of stigma; anther cap cucullate, ovate, flattened, two-celled, pollinia four, in two pairs similar in size, on a oblong-pandurate, basally narrowed stipe and a hyaline viscidium; stigma rounded. **(FP)**

Distribution (Fig. 598.2)

Four species of *Echinorhyncha* have been recorded from Colombia and Ecuador (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Echinorhyncha*. **(NV, RG)**

Phylogenetics

The close relationship among the species currently assigned to *Echinorhyncha* was first observed by Ortiz (1994), who noted that they all possess 2–4 piliferous glands on the ventral surface of the column. Flowers of *Echinorhyncha* resemble those of *Warczewizella* but may be distinguished by sea urchin-like, bristly appendages under the proximal margin of the stigma. The stipe is mostly pandurate, rarely narrowed basally, and the pollinia are almost equal in size. In recent cladistic analyses based on combined DNA sequences (Whitten *et al*. 2005), *Echinorhyncha* is weakly supported as sister to a clade including *Kefersteinia*, *Euryblema*, *Benzingia*, *Stenia,* and *Daiotyla*. **(FP)**

Ecology

Species are epiphytes in evergreen, submontane wet to montane cloud forests at 800–1800 m. In natural habitats, flowering has been recorded in July and October, but Dodson and Dodson (1989) reported that plants flower through most of the year. **(FP)**

Pollination

Pollinators of *Echinorhyncha* are unknown, but Ortiz (1994) suggested that piliferous glands on the underside of the column, present in all species of *Echinorhyncha*, probably have a role in attracting pollinators. **(FP)**

Uses

There are no known uses of any species, and they are rare in cultivation. **(FP)**

Fig. 598.1. *Echinorhyncha ecuadorensis* (Dodson) Dressler. A. Habit, with inflorescence; B. Flower, front view; C. Flower, side view; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum callus; I. Column, ventral view; J. Column, side view; K. Pollinarium. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone after drawing by Barbara N. Culbertson in Dodson, C. H. and Escobar, R. R. (1993). *Native Ecuadorian Orchids*, vol. 1. Hola Colina, Medellín, Colombia.

Cultivation

Native from the premontane and montane wet forest of the Andes, plants of *Echinorhyncha* should be grown in shade and intermediate to slightly cool temperatures with high levels of humidity and frequent watering year-round. The relatively large plants are probably best suited for cultivation in pots with a coarse compost that allows ample aeration around the thick roots. **(FP)**

Taxonomic literature

Dodson, C. H. and Dodson, P. M. (1989). Orchids of Ecuador. *Icones plantarum tropicarum,* ser. 2, fasc. 5–6. Missouri Botanical Garden, St. Louis.

Ortiz, V., P. (1994). Nuevas especies de Colombia. *Orquideología*, **19**, 13–19.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

599. EURYBLEMA

Euryblema Dressler, *Lankesteriana*, **5,** 94 (2005). Type species: *Euryblema anatomum* (Dressler) Dressler (basionym: *Cochleanthes anatona* Dressler)

Derivation of name

From the Greek *eurys*, broad, and *blema*, blanket or cover, in allusion to shape of the callus on the lip. **(FP)**

Fig. 598.2. Distribution map of *Echinorhyncha.*

Description (Plate 206; Fig. 599.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from rhizome. *Stem* abbreviated, enclosed by 4–6 imbricating sheaths, heavily spotted with red-purple or solid purple, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, oblanceolate to oblong-elliptic, acute to acuminate, abaxially carinate, narrowed at base into a indistinct, conduplicate petiole, grass green to dark green on upper surface, sometimes spotted with purple abaxially. *Inflorescences* lateral, stout, one or two per shoot, single-flowered, produced from axils of lower sheaths, peduncle terete, suberect to erect, provided with two or three narrow, conduplicate bracts; floral bract double, conduplicate, shorter than ovary, the external one narrowly deltoid, the subopposite internal bractlet ligulate. *Flowers* resupinate, scented, sepals greenish cream to yellowish green or yellow, dorsal sepal sometimes flushed with red-purple toward the apex, petals greenish cream to yellow, sometimes apically spotted with purple red, labellum whitish cream to pale orange, mostly spotted with purple-red, apically sometimes solid red with darker spots, callus yellow or red-purple. *Dorsal sepal* free, lanceolate-elliptic to oblong-elliptic, acute, apex revolute. *Lateral sepals* narrowly elliptic to oblong, acute, falcate, reflexed, apically erect, inrolled-folded toward base. *Petals* oblong-elliptic to narrowly elliptic, acute, apically arcuate-revolute. *Labellum* articulate with column foot, rhombic-ovate to elliptic, sometimes obscurely trilobed, base rounded-subcordiform, apex rounded to subacute, deflexed, distal margins undulate to crisped or irregularly lacerate, proximal margins erect, flanking column; disc with a low, longitudinal keel from base to about middle of labellum and a transverse, laminar, sometimes pilose callus extending over middle of blade, apically erose to irregularly toothed. *Column* straight, with a distinct foot, dilated at apex into inconspicuous stigmatic wings, adaxially pilose-hirsute toward base, ventral surface basally provided with a longitudinal, low keel; anther cap cucullate, widely ovate, flattened, two-celled, pollinia four, in two subequal pairs, on a stipe scarcely distinct from the peltate-oblong, apically truncate, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 599.2)

Euryblema is a genus of two or possibly three species ranging from Panama (Central America) to northern Colombia and perhaps Ecuador (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Euryblema*. **(NV, RG)**

Phylogenetics

The two named species of *Euryblema* were previously assigned to *Cochleanthes* (Dressler 1983) and *Chondrorhyncha* (Senghas 1990; Ortiz 1994), but they do not fit either group well. *Euryblema* resembles *Cochleanthes* and *Warczewiczella* in the short and rounded chin of the lip when observed from the side and shield-like viscidium, and the central position of the callus is reminiscent of *Chondrorhyncha*. Phylogenetic analyses based on DNA sequences unequivocally assigned *C. anatona* Dressler and *C. andreae* Ortíz to a clade with strong bootstrap support, and thus is compatible with generic recognition (Whitten *et al.* 2005). Among genera of the *Chondrorhyncha* complex, analyses of combined *matK/trnL-F/*ITS rDNA placed *Euryblema* in an unclear position in a well-supported larger clade comprisinig *Kefersteinia*, *Daiotyla*, *Benzingia,* and *Stenia* (Whitten *et al.* 2005). Vegetatively, the genus is characterized by having leaf sheath bases that are spotted to solid red-purple, a character unique within the *Huntleya* clade. Flowers of *Euryblema* are large compared to those of other genera of the *Chondrorhyncha* complex, and lateral sepals are falcate and reflexed, becoming erect apically. However, the callus is laminar and broad, covering the base of the lip up to the middle of the lamina, a character reminiscent of some species of *Benzingia*. **(FP)**

Ecology

The species occur as epiphytes in shady sites in evergreen, wet, premontane to cloud, forests at 700–1200 m. Flowering mostly occurs from July to December, roughly corresponding to the rainy season, but plants were collected in flower also in February. Each shoot produces two or three flowers in succession. **(FP)**

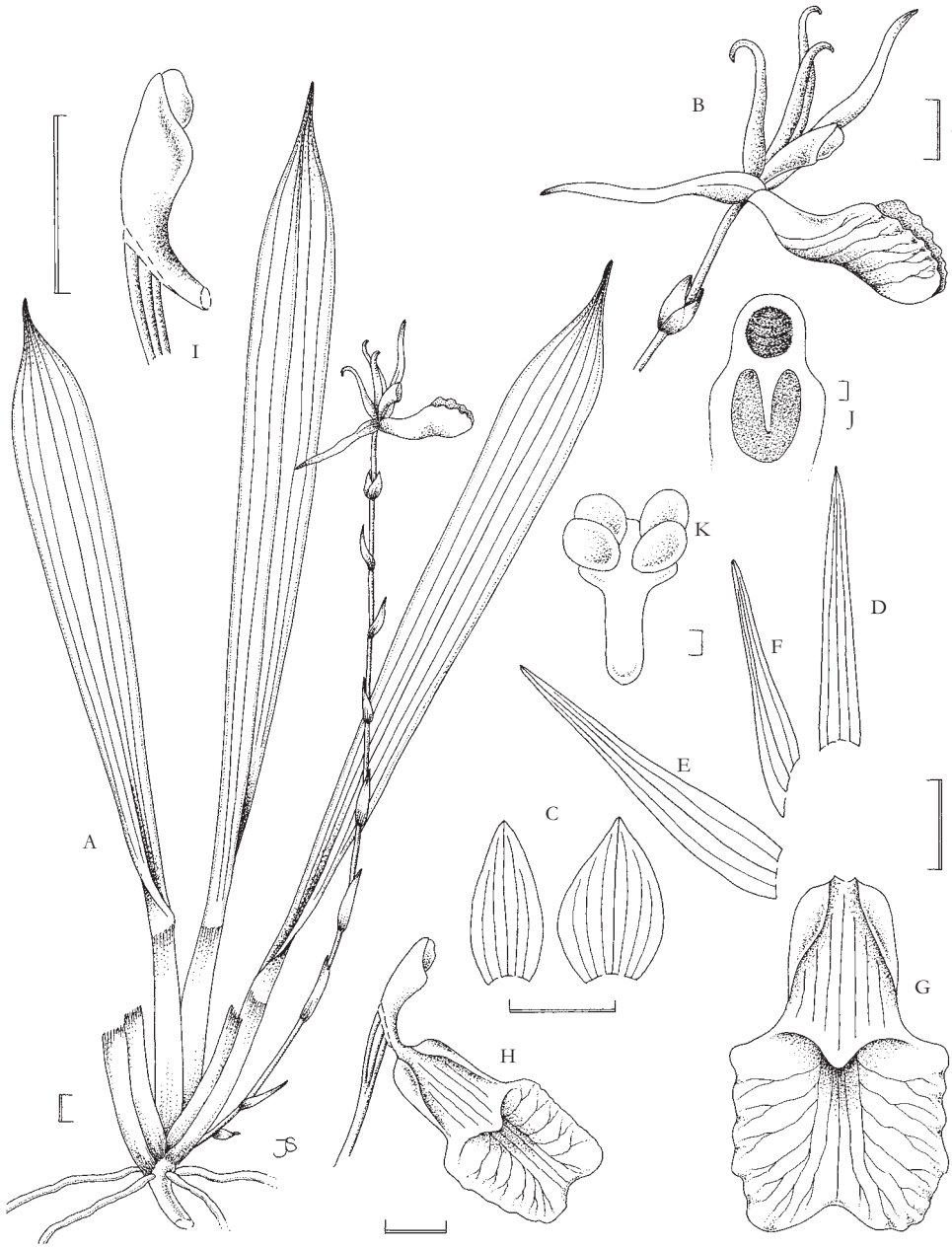


Fig. 599.1. *Euryblema andreae* (P.Ortiz) Dressler. A. Habit, with inflorescence; B. Flower, side view; C. Bracts; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Column and labellum, side view; I. Column, side view; J. Column apex, anther cap removed; K. Pollinarium. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Herbarium Lehmannianum Colombianum 10025* (K).

Pollination

The actual pollinator of *Euryblema* is unknown, but Dressler (1993) suggested that *E. anatonum* is pollinated the same way as *Cochleanthes*, with the pollinia placed behind the head rather than on the back of the pollinator. **(FP)**

Uses

Indigenous people from the Caribbean province of Bocas del Toro in western Panama collect wild specimens of *Euryblema anatonum* (Dressler) Dressler for the horticultural market. They call this plant *patirroja*, red-footed, in allusion to the purple pigmentation that covers the lowest portion of the leaf sheaths. **(FP)**

Cultivation

Plants of *Euryblema* should be grown in open shade and intermediate to slightly cool temperatures, maintaining high levels of humidity year-round. They may be grown on slabs, but cultivation in pots with a coarse compost provides more constant humidity around the roots. Watering should be frequent throughout the year. **(FP)**

Taxonomic literature

Dressler, R. L. (1983). Eine charakteristische neue *Cochleanthes* aus Panama: *Cochleanthes anatona*. *Orchidee (Hamburg)* **34**, 157–61.

Dressler, R. L. (1993). *Field guide to the orchids of Costa Rica and Panama*. Cornell University Press, Ithaca, New York.

Fig. 599.2. Distribution map of *Euryblema*.

Ortiz V., P. (1994). Nuevas especies de Colombia. *Orquideología*, **19**, 13–19.

Senghas, K. (1990). Die Gattung *Cochleanthes*, mit einer neuen Art, *C. palatina*. *Orchidee (Hamburg)*, **41**, 89–96.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

600. GALEOTTIA A.Rich.

Galeottia A.Rich., *Ann. Sci. Nat., Bot.,* **3(3),** 25 (1845). Type species: *Galeottia grandiflora* A.Rich.

Mendoncella A.D.Hawkes, Orquídea (Rio de Janeiro), **25,** 7 (1963), nom. superfl. illeg. Type species: Mendoncella grandiflora (A.Rich.) A.D.Hawkes

Derivation of name

The name honours Richard's colleague, the French botanist Henri Galeotti (1814–1858), who collected many orchid species in Mexico and Central America between 1835 and 1840. **(FP)**

Description (Plate 207; Fig. 600.1)

Epiphytic, pseudobulbous, caespitose *herbs*. *Roots* terete, thick, flexuous, produced along rhizome near pseudobulbs. *Pseudobulb* heteroblastic, approximate, rarely separated along the rhizome, ovoid to oblong-ovoid, sometimes ribbed, (1)2–3-leaved at apex, subtended by 4–7 membranaceous, eventually scarious-papery sheaths. *Leaves* subplicate-venose, membranaceous to subcoriaceous, lanceolate-elliptic to oblanceolate, acute, abruptly acuminate, abaxially obscurely carinate along nerves, narrowed at base into a distinct, conduplicate petiole, clear to dark green, shiny on upper surface. *Inflorescences* lateral, one or two per shoot, a 2–8-flowered raceme produced from base of the immature pseudobulb, emerging from axils of the lower sheaths, peduncle terete, erect to arching, provided with two or three, inflated, membranaceous, conduplicate, loose bracts, the rachis sinuous; floral bracts widely ovate, conduplicate-cymbiform, loose, shorter than ovary. *Flowers* showy, resupinate, sepals and petals yellowish green to cream, mostly longitudinally striped with reddish brown or with purple-brown stripes and blotches, rarely suffused with chestnut brown, labellum usually creamy white, rarely almost solid red or with yellow lateral lobes, midlobe often striped with purple, callus red or variously striped with purple, column white, striped purple on the underside. *Dorsal sepal* free, erect, ovate-lanceolate to broadly elliptic, acute to long-acuminate, rarely attenuate. *Lateral sepals* adnate to column foot to form a chin, narrowly ovate-elliptic to lanceolate, mostly asymmetrical, frequently incurved, acute to long-acuminate, rarely attenuate, inflexed-replicate toward the gibbose-subsaccate base, sometimes recurved at apex. *Petals* decurrent on column foot, spreading, oblong-elliptic to lanceolate, rarely falcate, acute to acuminate or attenuate. *Labellum* articulate with column foot, entire to distinctly trilobed, provided with a linear to obcuneate claw, lateral lobes trapezoidal to elliptic or broadly falcate, apically verrucose or crenulate to lacerate to long-fimbriate, mostly erect, midlobe mostly ovate or rhombic-ovate, less frequently linear, narrowly obovate, obovate or pandurate, usually acuminate, rarely subtruncate, but then provided with a distinct apicule, straight to deflexed at apex, margins entire, serrulate, lacerate or long-fimbriate; disc with a single, fleshy keel or with a high, plicate or lamellate crest, sometimes forming a shallow cup with lateral lobes, crest basal or extending to apex of hypochile, distal portion free, denticulate to digitate. *Column* arcuate-cymbiform with a distinct foot, broadened toward apex and provided with usually prominent, rounded to subquadrate, often irregularly erose wings and a broadly lobed clinandrium, anther cap cucullate, obovate, flattened, two-celled, pollinia four in two pairs, subequal or of different sizes, sessile on a laminar, obtriangular, shield-shaped, brown-hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 600.2)

Galeottia consists of 12 species ranging from southern Mexico (North America) through Central America to Peru and northern Atlantic Brazil (South America), with highest diversity on the western slopes of the Peruvian and Colombian Andes. **(FP)**

Phytochemistry

Floral fragrances of the strongly scented *G. ciliata* (Morel) Dressler & Christenson, *G. fimbriata* (Linden & Rchb.f.) Schltr.,

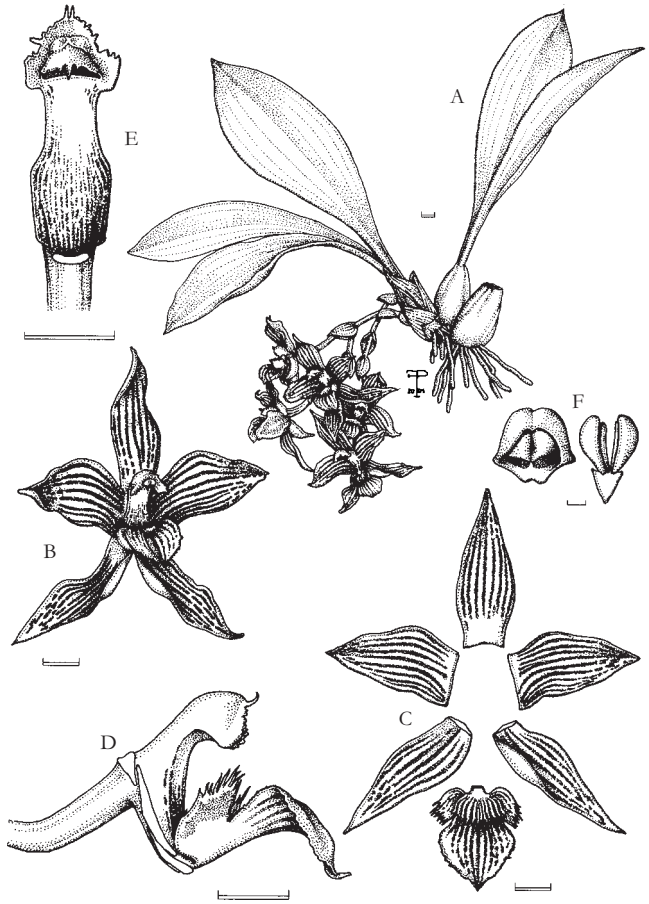


Fig. 600.1. *Galeottia grandiflora* A.Rich. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column and labellum, side view; E. Column, ventral view; F. Anther cap and pollinarium. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 3006* (Lankester Botanical Garden Spirit Collection).

and *G. negrensis* Schltr. are rich in monoterpenes. For example, that of *G. ciliata* contains 70% 1,8-cineole, whereas *G. fimbriata* is rich in α-pinene (45–76% of two specimens examined; Gerlach and Schill 1991). In contrast, *G. acuminata* (C.Schweinf.) Dressler & Christenson is only weakly scented, and contains the sesquiterpenes caryophyllene (69%) and germacrene D (7%). **(NV, RG)**

Phylogenetics

A synopsis of the genus (as *Mendoncella*) was offered by Garay (1973), who mainly distinguished *Galeottia* from other pseudobulbous Zygopetalinae by petals decurrent on the column foot and lateral sepals adnate to the column foot near the apex. He considered *Galeottia* close to *Batemannia*, from which it can be distinguished by well-developed auricles on the column, a corrugated or flabellate crest at the base of the hypochile, and lateral sepals inrolled-gibbose at the base. Species of *Galeottia* have been described in *Batemannia*, *Mendoncella*, *Zygopetalum,* and *Zygosepalum*, and many of them were moved among these genera because of the difficulty in assigning clear generic circumscriptions within the *Zygopetalum* complex on the sole basis of morphological features.

As here circumscribed, the prominent ribbed crest of the lip, the two-winged column, and distinctly saccate base of lateral sepals characterize the genus among the taxa of the *Zygopetalum* grade. In the combined analysis of nuclear and plastid DNA data sets published by Whitten *et al.* (2005), a strongly supported clade which includes *Galeottia*, *Batemannia,* and *Zygosepalum labiosum* (Rich.) Garay, is sister to the *Zygopetalum* clade. **(FP)**

Ecology

The species of the genus occur as epiphytes or terrestrials in tropical to montane wet forests at elevations of 150–2500 m in shady to partially exposed spots. Flowering occurs throughout the year but mostly during the rainy season, when immature pseudobulbs have completely developed new leaves. **(FP)**

Pollination

No records of natural pollination of *Galeottia* exist, but species of the genus are likely pollinated by male euglossine bees. **(FP)**

Uses

Apart from occasional cultivation as ornamentals, there are no known uses. **(FP)**

Cultivation

Given the usually large size of the plants, *Galeottia* species are best grown in pots, filled with a compost that retains moisture but allows ample air circulation around the thick roots. Plants should be maintained in partial shade, preventing exposure to direct sunlight and providing constant humidity throughout the year. Watering should be abundant during the growing season, with a partial rest after new pseudobulbs mature following flowering. Most species of *Galeottia* are native to temperate forests around 1000–1500 m, and they can be satisfactorily grown in intermediate temperatures. *Galeottia fimbriata* from the low, western slopes of the Colombian Andes, *G. negrensis* Schltr. from the Amazonian regions of Brazil, the widespread *G. grandiflora*, and *G. marginata* (Garay) Dressler & Christenson are warm climate plants and tolerate higher temperatures, whereas specimens of *G. acuminata* (C.Schweinf.) Dressler & Christenson*, G. colombiana* (Garay) Dressler & Christenson, and *G. burkei* (Rchb.f.) Dressler & Christenson come from higher elevations (up to 2500 m) and are best suited to cooler conditions. **(FP)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología,* **8**, 15–51.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

Fig. 600.2. Distribution map of *Galeottia.*

601. HOEHNEELLA

Hoehneella Ruschi, *Orquid. Nov. Estad. Espirito Santo*, 3 (1945). Type species: *Hoehneella gehrtiana* (Hoehne) Ruschi (basionym: *Warscewiczella gehrtiana* Hoehne)

Derivation of name

The generic name honours the Brazilian botanist Federico Carlos Hoehne (1882–1959), author of the orchid treatment for the *Flora Brasilica*. **(FP)**

Description (Fig. 601.1)

Epiphytic, caespitose, pseudobulbous *herbs*. *Roots* terete, produced along rhizome. *Pseudobulb* heteroblastic, ovoid, sometimes cryptic, apically provided with a scale-like, reduced leaf, concealed by 3–6 conduplicate, imbricating sheaths, upper ones foliaceous, margins sometimes hyaline-scarious. *Leaves* conduplicate, articulate, membranaceous, dark velvety green, paler abaxially, elliptic-oblong, acute to subacuminate, sulcate-carinate, narrowed at base into an indistinct, conduplicate petiole. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths, peduncle terete, suberect to erect, provided with one or two acuminate, conduplicate, papery bracts; floral bract widely ovate, conduplicate, loose, papery, shorter than ovary. *Flowers* resupinate, parts not completely spreading, sepals and petals greenish yellow, labellum white with a violet callus. *Dorsal sepal* free, narrowly lanceolate-elliptic, acute, apex recurved. *Lateral sepals* narrowly lanceolate-elliptic, acute, concave toward base. *Petals* narrowly lanceolate-elliptic, acute, porrect. *Labellum* sessile, articulate with the column foot, narrowly obovate, trilobed, flat in natural position, base rounded, apex rounded to emarginate, basal lobes rounded-elliptic, erect, midlobe elliptic or obovate, with irregularly crenulate margins; disc with a triangular-ovate, laminar, 3- to 9-ridged, puberulent callus, low keels terminating in teeth. *Column* straight, semiterete, flat on ventral side, with a foot, slightly dilated at apex into inconspicuous, rounded wings; anther cap cucullate, transversely subrectangular to obovate, flattened, two-celled, pollinia four, in two subequal pairs, without a stipe, on a transversely elliptic, hyaline viscidium; stigma transversely elliptic. **(FP)**

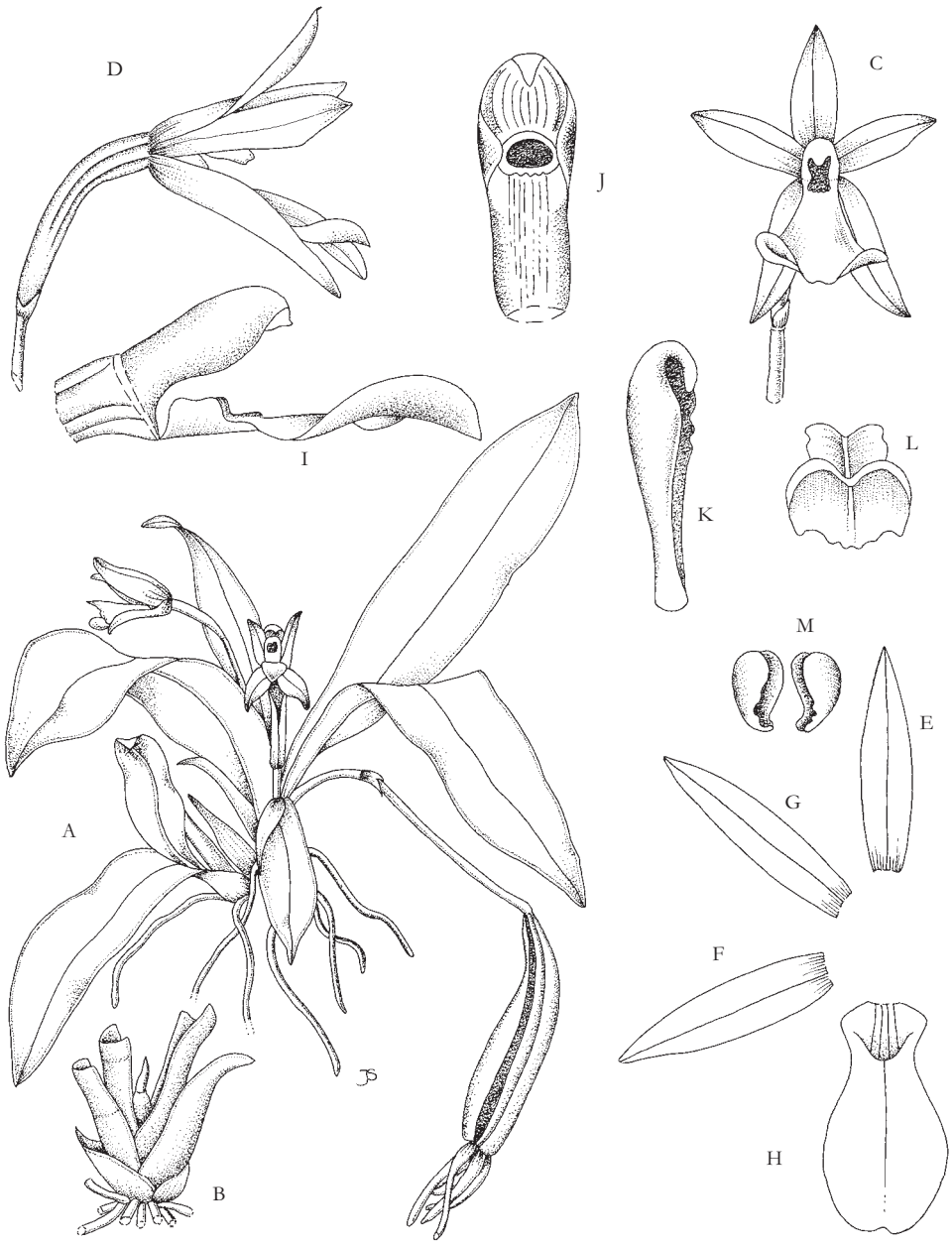


Fig. 601.1. *Hoehneella gehrtiana* (Hoehne) Ruschi. A. Habit, with inflorescences; B. Plant base; C. Flower, front view; D. Flower, side view; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Column and labellum, side view; J. Column, ventral view; K. Column, side view; L. Anther cap, ventral view; M. Pollinia. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone after drawing in Hoehne, F. C. (1949). *Iconografia de orchidaceas do Brasil.* Secretariea de Agricultura, São Paulo.

Distribution (Fig. 601.2)

Hoehneella is a genus of two species, endemic to the Atlantic regions of Brazil in the states of São Paulo and Espiritu Santo (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Hoehneella*. **(NV, RG)**

Phylogenetics

No material has been available for DNA sequencing. Flowers of *Hoehneella* are morphologically similar to those of *Huntleya* and particularly to *Chaubardia*. Vegetatively, the plants of *Hoehneella* resemble those of *Chaubardia*. However, *Hoeheneella* can be distinguished from the latter by lateral sepals (not gibbous at the base), sessile lip, column without stigmatic wings, conspicuously crested anther, and features of pollinarium (transversely elliptic viscidium, stipe absent; Garay 1973; Senghas and Gerlach 1993). **(FP)**

Ecology

Species occur as shade-epiphytes on mossy branches in evergreen, wet, premontane to cloud forests at 600–1100 m along the Atlantic portions of central and southern Brazil. Flowering has been recorded in January, but may occur at other times. **(FP)**

Pollination

Pollination biology of the genus is unknown. **(FP)**

Fig. 601.2. Distribution map of *Hoehnella*.

Uses

There are no known uses for either species. **(FP)**

Cultivation

Native to the tropical moist forests of the mountain range that runs along the the inland, coastal states of central and southern Brazil, plants of *Hoehneella* are adapted to a mild climate with high levels of annual rainfall. They should be grown in shade at intermediate to slightly warm temperatures, either on plaques or in well-drained pots. Plants need high humidty throughout the year and should be watered frequently. **(FP)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Senghas, K. and Gerlach, G. (1993). Subtribe Huntleyinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1620–74. Paul Parey, Berlin.

602. HUNTLEYA

Huntleya Bateman ex Lindl., *Edwards's Bot. Reg.*, **23,** t. 1991 (1837). Type species: *Huntleya meleagris* Lindl.

Derivation of name

John Lindley established the genus in honour of the Rev. J. T. Huntley, 'an ardent cultivator of Orchidaceous plants' of the early nineteenth century, apparently on the suggestion of James Bateman. **(FP)**

Description (Plate 208; Fig. 602.1)

Epiphytic, often large caespitose *herbs* without pseudobulbs. *Roots* terete, produced from rhizome. *Stem* enclosed by 7–16 imbricating sheaths, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous to coriaceous, oblanceolate to narrowly obovate, acute to acuminate, abaxially carinate, narrowed at base into an indistinct, conduplicate petiole, grass green to dark green. *Inflorescence* one or more per shoot, lateral, single-flowered, produced from axils of lower sheaths, peduncle terete, erect, provided with 1–3 conduplicate, clasping bracts; floral bract double, conduplicate, membranaceous, shorter than ovary, the external one loose, widely ovate, acute, the subopposite internal bractlet narrowly lanceolate to ligulate. *Flowers* resupinate, usually scented, sepals and petals glossy cream to yellow, frequently white in basal third, rarely concolorous, usually boldly blotched or barred with red-brown to almost solid red-brown, rarely covered with rounded, protruding osmophores (appearing tessellated), petals sometimes blotched with dark purple at base, labellum white to whitish cream or yellow, midlobe striped with purple or flushed purple apically to solid red-purple, callus white, with purple lacerate margins. *Dorsal sepal* free, erect, lanceolate-elliptic to ovate, acuminate to attenuate, concave. *Lateral sepals* basally adnate to column foot, narrowly triangular to lanceolate-elliptic or ovate, rarely subfalcate, acuminate to attenuate, concave toward apex. *Petals* narrowly ovate, rarely lanceolate, acuminate, usually with undulate margins. *Labellum* with a linear to obcuneate claw, articulate with column foot, simple or obscurely trilobed, ovate, acuminate, often convex and reflexed at apex, hypochile crested, erect, cupped, with a transverse, long-fimbriate callus sometimes extending to ventral surface of column. *Column* arcuate, sometimes dorsally subcarinate, dilated at crenulate to lacerate, broadly winged apex, provided with a distinct foot; anther cap cucullate, broadly ovate-subquadrate, flattened, two-celled, pollinia four, in two superposed pairs of different sizes, on a linear, basally acute stipe scarcely distinct from ventral, triangular, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 602.2)

The genus includes some 13 species, ranging from Belize (Central America) to Brazil, Bolivia (South America), and Trinidad, with a main centre of diversity in the northern Andean regions of Colombia and Ecuador, where seven and six *Huntleya* species have been recorded, respectively. Some of the species are remarkably similar in gross flower morphology and may not withstand critical examination at specific rank. **(FP)**

Phytochemistry

Two surveys of alkaloid content in Orchidaceae returned positive results for *H. meleagris*. (Lüning 1964, 1967). Kaiser (1993)

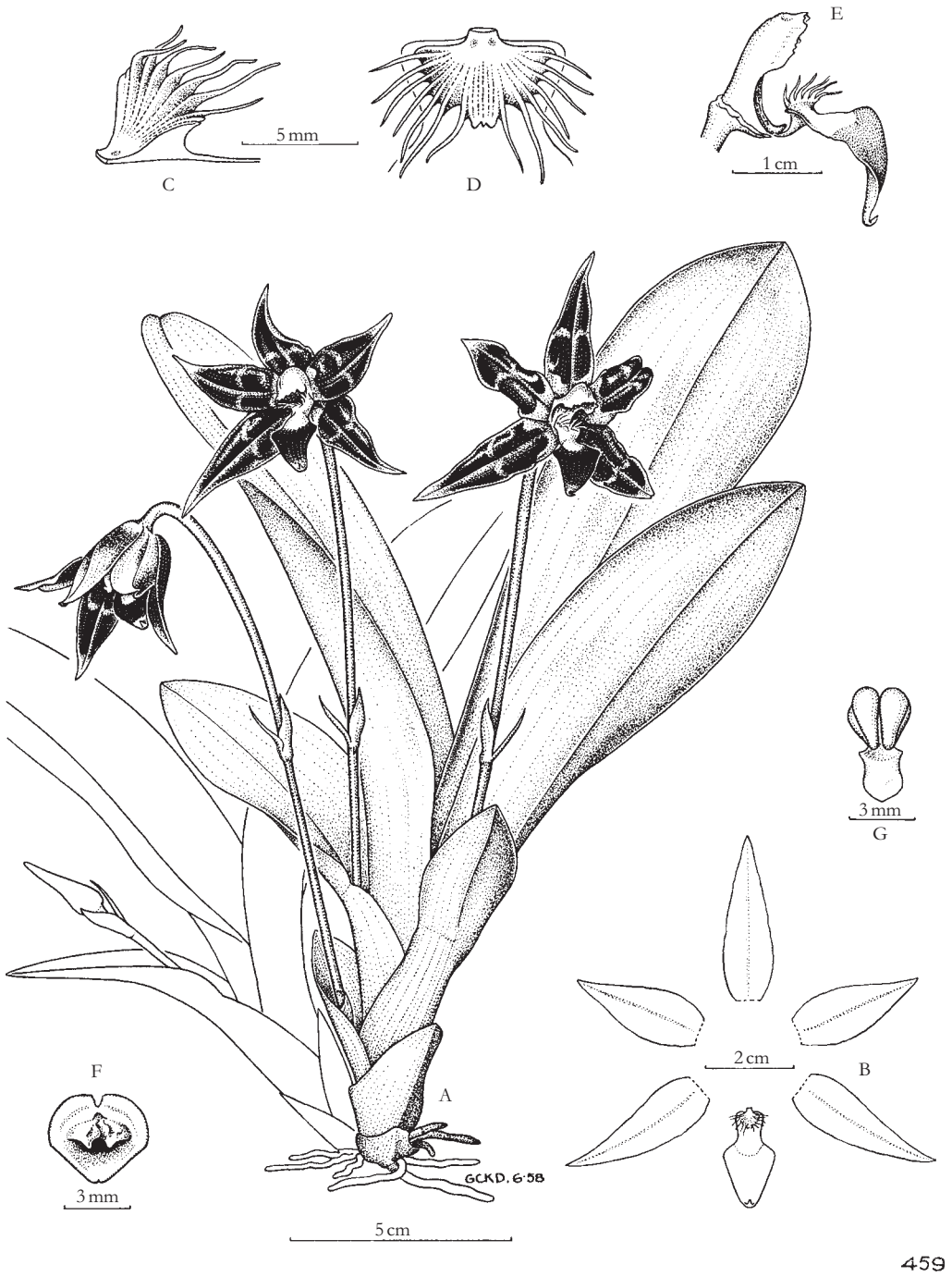


Fig. 602.1. *Huntleya lucida* (Rolfe) Rolfe. A. Habit, with inflorescences; B. Perianth, dissected; C. Labellum callus (sectioned), side view; D. Labellum callus, dorsal view; E. Column and labellum, side view; F. Anther cap; G. Pollinarium. Drawn by G.C.K. Dunsterville. Originally published in *Venezuelan Orchids Illustrated,* **1**, 172 (1959). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

has established that the main component of the floral fragrance of this species is *trans*-verbenol, although some variants have been described as scentless. The scent of *H. heteroclita* (Poepp. & Endl.) Garay is also dominated by monoterpenes, with geraniol, geranyl acetate, nerol, and neryl acetate present in similar proportions. Of particular interest as an additional scent constituent is the new natural product, 2(3)-epoxygeranyl acetate. The floral fragrance of *H. lucida* (Rolfe) Rolfe is completely different, consisting almost entirely of methyl salicylate (97%) according to Gerlach and Schill (1991). **(NV, RG)**

AQ: Will readers know why this is important? And what is a 'natural product'- do you mean new organic compound?

Phylogenetics

Many species of *Huntleya* were originally described as members of the genus *Batemannia*, from which *Huntleya* is mainly distinguished by absence of pseudobulbs and shape of callus. The

Fig. 602.2. Distribution map of *Huntleya*.

callus is long and deeply fimbriate in *Huntleya* versus fleshy, denticulate-ciliate in *Batemannia*. Synoptical views of the genus were offered by Rolfe (1900) and Fowlie (1967, 1984). Recent studies based on comparison of DNA sequences (Whitten *et al.* 2005) confirmed monophyly of *Huntleya* and showed that the genus is only distantly related to *Batemannia*. *Huntleya* is well supported as sister to the rest of the *Huntleya* clade. Large plants lacking pseudobulbs, often with long rhizomes separating fan-shaped growths bearing large, star-shaped, flat, glossy, and fragrant flowers distinguish the genus from its relatives in the *Huntleya* clade. **(FP)**

Ecology

Species of *Huntleya* are mostly restricted to extremely wet tropical and premontane forests, usually at medium and low elevations (from sea level to 800–1000 m). *Huntleya wallisii* (Rchb.f.) Rolfe and *H. gustavi* (Rchb.f.) Rolfe are recorded from higher regions, the latter ranging to 2000 m in Colombian Chocó. Plants of *Huntleya* mostly grow as large epiphytes on trunks and large branches, where the thick rhizome often assumes a creeping habit. The long-lasting flowers are usually produced at the beginning of the rainy season, but plants may flower sporadically throughout the year. **(FP)**

Pollination

Huntleya burtii is pollinated by *Eulaema meriana* (van der Pijl & Dodson 1966). Male euglossine bees in search of fragrance components probably pollinate other species of the genus. The pollinarium is placed behind the head of the bee. **(FP)**

Uses

Some species are cultivated as showy, fragrant ornamentals. **(FP)**

Cultivation

Inhabitants of shaded, wet places, mostly in tropical and premontane, warm forests, species of *Huntleya* should be grown in warm to intermediate temperatures and a shaded environment with high humidity year-round. Specimens of *H. wallisii*

and *H. gustavi* require cooler temperatures. Plants may be grown in baskets or on large slabs, but if on slabs, watering should be frequent. Cultivation in pots is not advisable, given the creeping habit. Large specimens should be disturbed as little as possible. **(FP)**

Taxonomic literature

Fowlie, J. A. (1967). Some observations on the genus *Huntleya* and related genera. *Orchid Digest,* **31**, 278–81.

Fowlie, J. A. (1984). A further contribution to an understanding of the genus *Huntleya*. *Orchid Digest,* **48**, 221–5.

Rolfe, R. A. (1900). The genus *Huntleya*. *Orchid Review*, **8**, 269–72; 302–303.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

603. IXYOPHORA

Ixyophora Dressler, *Lankesteriana*, **5,** 95 (2005). Type species: *Ixyophora viridisepala* (Senghas) Dressler (basionym: *Chondrorhyncha viridisepala* Senghas)

Derivation of name

From the Greek *ixys*, waist, and *phorein*, to bear, to carry, in reference to the narrow central portion (or the 'waist') of the stipe. **(FP)**

Description (Plate 209; Fig. 603.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from rhizome. *Stem* abbreviated, enclosed by 3–5 imbricating sheaths, upper ones foliaceous, sometimes provided with hyaline margins. *Leaves* conduplicate, articulate, membranaceous, grass green to dark green, oblanceolate to widely oblanceolate, acute to acuminate, abaxially carinate, narrowed at base into an indistinct conduplicate petiole. *Inflorescences* lateral, single-flowered, produced from axils of lower sheaths; peduncle terete, erect, arching or pendent, provided with two or three lanceolate, conduplicate bracts; floral bract double, conduplicate, shorter than ovary, the external one ovate, loose, the subopposite internal bractlet narrower. *Flowers* resupinate, with yellowish green or yellow sepals and petals; labellum greenish yellow, marked pale green or yellow, sometimes striped with orange. *Dorsal sepal* free, elliptic to oblong, obtuse to subacute, concave, sometimes pubescent toward base. *Lateral sepals* oblong-elliptic to oblanceolate, obtuse, sometimes thickened toward apex and adaxially pubescent, reflexed and incurved, concave to inrolled-folded toward base, apex sometimes uncinate. *Petals* elliptic or oblong, obtuse to truncate or emarginate, apically revolute. *Labellum* articulate with column foot, obovate to elliptic, sometimes obscurely trilobed, base rounded-subsaccate, apex obtuse or emarginate, basal margins erect to flank the column, distal margin undulate; disc with a callus of 2–5 raised keels running from base to first third or middle of the labellum, ending in prominent teeth. *Column* straight, with a distinct foot, dilated at apex into inconspicuous stigmatic wings, adaxially pubescent toward the base, sometimes provided with a puberulent, rounded, median keel; anther cap cucullate, elliptic or ovate, flattened, two-celled, pollinia four, in two subequal pairs, on a scutiform, basally narrowed stipe, and a triangular-peltate, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 603.2)

Ixyophora is a genus of three species native to the Amazonian watershed of the Andes from Colombia to Peru (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Ixyophora*. **(NV, RG)**

Phylogenetics

Originally described as members of *Chondrorhyncha* (Jenny 1989), the three species of *Ixyophora* are also superficially similar to *Warczewiczella*. *Ixyophora viridisepala* and *I. carinata* (Ortiz) Dressler share gross floral morphology, but flowers of *I. aurantiaca* Senghas & G.Gerlach have wider perianth parts and a lip with nectar guides. All species of *Ixyophora* have a narrow stipe. In the cladistic analysis of combined *matK/trnL-F/*ITS rDNA data set published by Whitten *et al.* (2005), *Ixyophora* is well supported as sister to *Chaubardiella* in the *Huntleya* clade. **(FP)**

Ecology

Species are epiphytes in evergreen and wet forests at 800–2000 m along the eastern slopes of the Andes. Flowering has been recorded in April and May. **(FP)**

Pollination

Pollination biology of the genus is unknown. **(FP)**

Uses

Thre are no known uses of the species, and they are rarely cultivated. **(FP)**

Cultivation

Plants of *Ixyophora* should be grown in shade and intermediate to cool temperatures, with frequent watering and high levels of humidity year-round. **(FP)**

Taxonomic literature

Senghas, K. (1989). Die Gattung *Chondrorhyncha*, mit einer neue Art, *Chondrorhyncha viridisepala*, aus Ekuador. *Orchidee (Hamburg),* **40**, 178–81.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

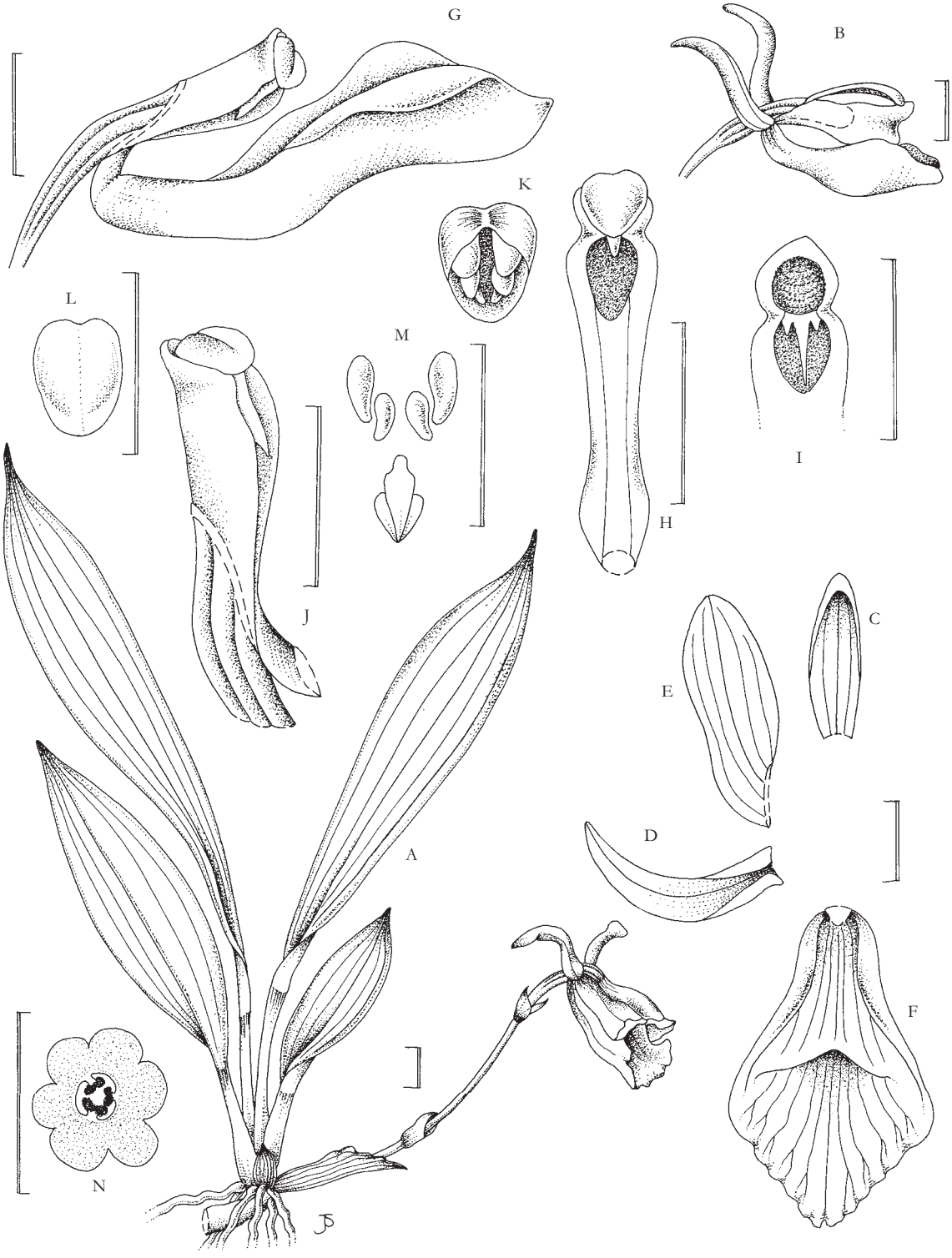


Fig. 603.1. *Ixyophora viridisepala* (Senghas) Dressler. A. Habit, with inflorescence; B. Flower, side view; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum; G. Column and labellum, side view; H. Column, ventral view; I. Column apex, anther cap removed; J. Column, side view; K. Anther cap with pollinia, ventral view; L. Anther cap, dorsal view; M. Pollinarium; N. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Herbarium Lehmannianum Colombianum 4542* (K).

Fig. 603.2. Distribution map of *Ixyophora.*

604. KEFERSTEINIA

Kefersteinia Rchb.f., *Bot. Zeit. (Berlin),* **10,** 633 (1852). Type species: *Kefersteinia graminea* (Lindl.) Rchb.f. (basionym: *Zygopetalum gramineum* Lindl.)

Senghasia Szlach., *J. Orchideenfreund,* **10,** 335 (2003). Type species: *Senghasia wercklei* (Schltr.) Szlach. (basionym: *Kefersteinia wercklei* Schltr.)

Derivation of name

The generic name honours Herr Keferstein of Kröllwitz, a German orchid grower active during the height of H. G. Reichenbach's botanical career. **(FP)**

Description (Plate 210; Fig. 604.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from rhizome. *Stem* abbreviated, enclosed by 3–6 imbricating sheaths, upper ones foliaceous, basal margins sometimes scarious. *Leaves* conduplicate, articulate, membranaceous, ligulate to oblong or narrowly obovate, acute to abruptly acuminate, abaxially carinate, narrowed at base into conduplicate petiole. *Inflorescences* lateral, 1–20 per shoot, single-flowered, produced from axils of lower sheaths, peduncle terete, arching or pendent, provided with one or two basal, triangular, membranaceous to scarious bracts; floral bract double, conduplicate, external one widely ovate-infundibuliform, scarious, loose, longer than ovary, the subopposite internal bractlet lanceolate, acuminate. *Flowers* resupinate, spreading or campanulate, sepals and petals pure white or yellow to cream white or pale green, rarely pale pink to pale purple, often spotted with purple to dark red-brown or tan- brown, heavily marked with orange-red or finely spotted purple toward base, rarely covered with large purple-brown blotches, labellum white or pinkish white to cream or yellow, spotted and flecked with purple to almost solid purple, rarely with a large, central, purple blotch, callus white to yellow, mostly finely spotted with purple, rarely solid purple or pink. *Dorsal sepal* free, linear-lanceolate to ovate-elliptic, erect to porrect over column, obtuse to acute, sometimes apiculate, mostly concave and dorsally carinate, sometimes reflexed at apex. *Lateral sepals* lanceolate-elliptic to ovate-oblong or ovate, sometimes subfalcate, mostly acute, spreading to distinctly reflexed, decurrent on column foot, basal margins sometimes involute. *Petals* spreading or variously porrect, flanking labellum and column, elliptic to lanceolate-elliptic to broadly ovate or oblanceolate, sometimes asymmetrical, broadly obovate-spatulate, acute to abruptly subacuminate, often revolute at apex. *Labellum* articulate with column foot, entire to trilobed, usually rounded, ovate to obovate, mostly concave at base, blade often folded back at middle, rarely puberulent to pubescent, base cuneate-rounded with a claw, apex emarginate to rounded or subacute, basal margins often erect, flanking the column, distal margin mostly crenulate to crisped, rarely long-fimbriate; disc with a basal, mostly bilobed callus, pedicellate and fleshy or sessile and laminar, transversely elliptic or semicircular-incurved. *Column* straight, semiterete, with a foot, dilated at apex from base into a ventral, fleshy plate, provided with a central keel basally protruding or not into one or more distinct teeth, sometimes with inconspicuous stigmatic wings; anther cap cucullate, subquadrate-rhombic to obtriangular-obovate, flattened, two-celled, pollinia four, in two pairs of different sizes, linear-oblong, subsigmoid to obovoid, on a linear to ovate or obpyriform, hyaline viscidium, basally rounded or attenuate, folded along margins, scarcely distinct from the rectangular stipe; rostellum tridentate; stigma transverse. **(FP)**

Distribution (Fig. 604.2)

Kefersteinia is a genus of about 60 species ranging from southern Mexico (North America) through Panama (Central America) and Venezuela and Colombia to Surinam and Bolivia in South America. The genus is most diverse along the Andes of Ecuador and Peru (with 19 and 16 species recorded, respectively), and it is particularly well represented in the mountainous areas of Central America up to Costa Rica, where ten species have been recorded so far. Species diversity rapidly diminishes toward the north, with a single species known from Guatemala and southern Mexico. **(FP)**

Infrageneric classification

Two main groups of species may be recognized on the basis of lip and callus morphology: in the mostly Andean group close

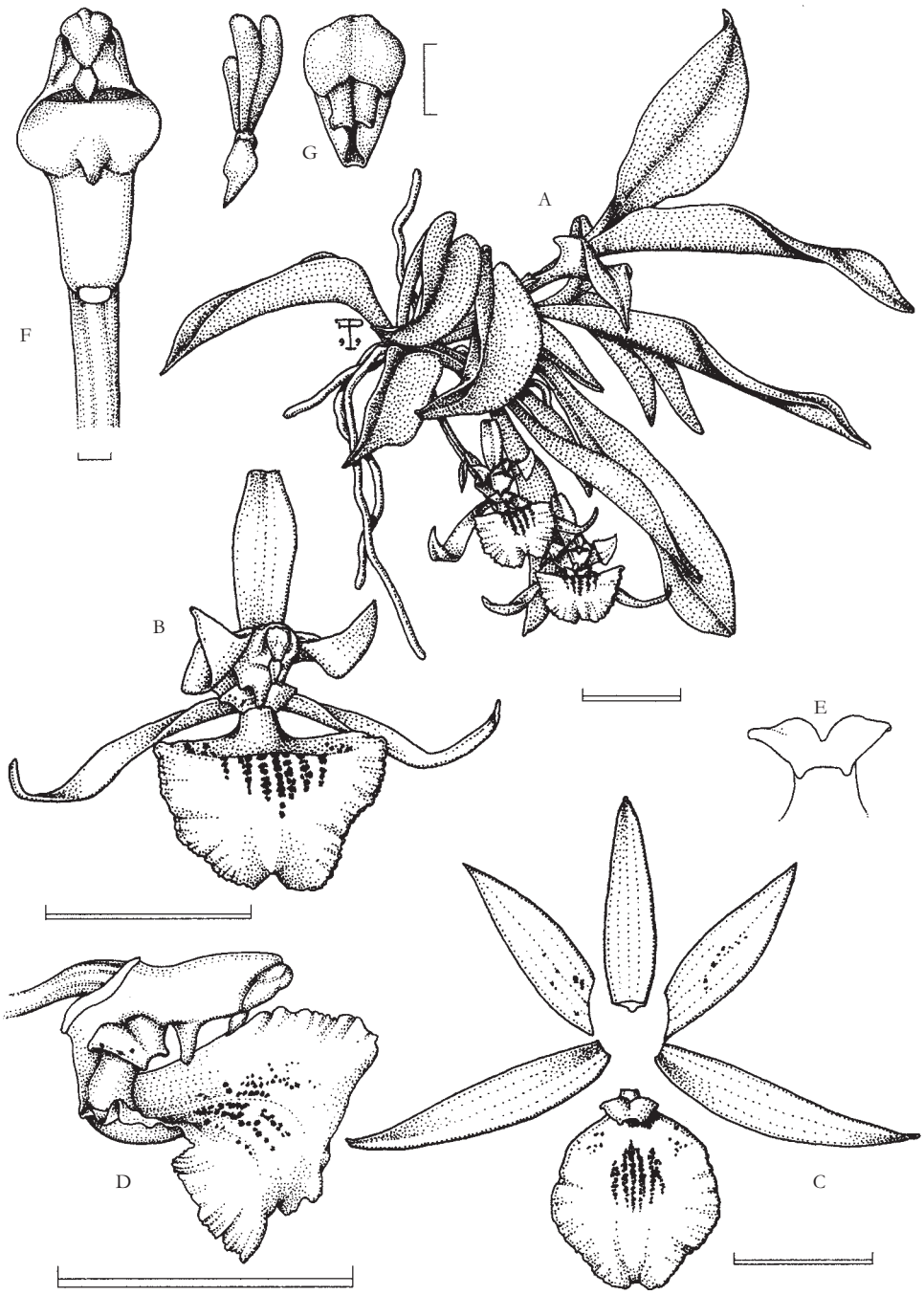


Fig. 604.1. *Kefersteinia orbicularis* Pupulin. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column and labellum, side view; E. Callus; F. Column, ventral view; G. Pollinarium and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin et al. 1170* (USJ).

to *K. graminea* (the type of the genus), the lip blade folds back abruptly at the middle and callus is sessile, low-laminar, whereas in species close to *K. wercklei* (mostly Central American in distribution) the lamina of the lip is straight, and the callus is supported by a distinct stalk. Senghas and Gerlach (1993) gave formal recognition to these groups creating *K.* sect. *Umbonatae* for those species with a solid, stalked callus.

In 2003, Szlachetko elevated *K.* section *Umbonatae* to generic rank with the name *Senghasia*, distinguishing the new genus from *Kefersteinia* by a large, umbonate callus at the base of the lip (Szlachetko 2003). However, it should be noted that in Central and South America the distinctiveness of the two groups (at whatever taxonomic rank) is often obscured by the presence of species with highly anomalous flower morphology—*K. endresii* Pupulin, *K. expansa* Rchb.f., *K. hirtzii* Dodson, *K. mystacina* (Rchb.f.) Rchb.f., *K. parvilabris* Schltr., *K. stevensonii* Dressler, among others—which precludes the use of sharply defined formal subgroupings. **(FP)**

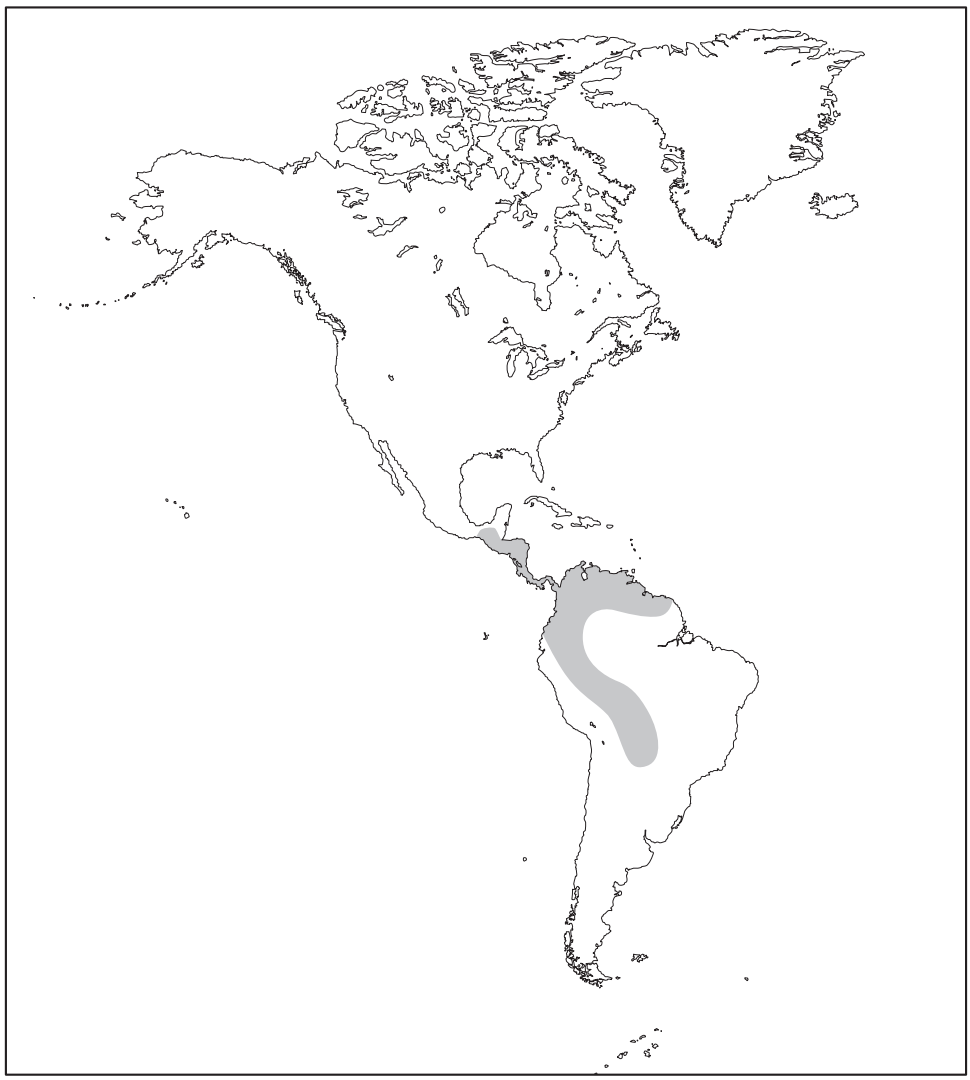


Fig. 604.2. Distribution map of *Kefersteinia.*

Palynology

Schill and Pfeiffer (1977) described pollen of *K. graminea* as convex tetrads with a laevigate exine and rounded sexine. **(AP)**

Phytochemistry

The floral fragrance of *K. auriculata* Dressler contains the sesquiterpene valencene (47%), a constituent of orange oil that is rarely encountered as a component of orchid flower scents. The aromatic compound 1,2-dimethoxybenzene was also reported from this species (Gerlach and Schill 1991). Gas chromatographic analysis (Gerlach and Schill 1991) of the corresponding fragrance of *K. pellita* Rchb.f. ex Dodson & D.E.Benn. failed to identify most scent components, with the exception of the minor constituent, methyl salicylate (3%). **(NV, RG)**

Phylogenetics

In creating *Kefersteinia*, Reichenbach defined it by the lip that continued onto the column foot, semiterete column winged at the distal margins, subulate rostellar tooth, and a keel extending from the lower margin of the stigma to the middle of the column. In his general realignment of *Zygopetalum* in 1861, he reduced *Kefersteinia* to sectional status, defined by the slender column, distally keeled under the stigma and the cucullate lip.

Fowlie (1966*a,b*) pointed out a close similarity between *Kefersteinia* and *Chondrorhyncha s.l.* on the basis of a set of common features (four pollinia in two unequal pairs, a bristle-like rostellum, flowers without a chin, an obscure to absent claw, similar callus structure, and transverse and slit-like stigma), which are distinctly different from the allied genera *Cochleanthes* and *Warczewiczella*. He mainly distinguished *Kefersteinia* from *Chondrorhyncha s.l.* by the presence of a short tooth on the anterior portion of the column in most species. In his fundamental revision of the *Chondrorhyncha* alliance, Garay (1969) distinguished *Kefersteinia* by the distinct vertical keel of the column and geniculate or replicate lip with a free, plate-like, basal callus.

As now circumscribed, *Kefersteinia* includes a large assemblage of species with varying floral morphology, but generally

characterized by one or more prominent teeth or a distinct infrastigmatic keel on the ventral surface of the column. Characters useful for identifying *Kefersteinia* are: usually small size; absence of pseudobulbs; slender, mostly pendent inflorescences; basal and mostly bilobed callus; and column provided with a ventral, laminar plate and a central keel, often extending to the rear into a tooth (Pupulin 2001). The pollinarium has four, ovoid to narrowly linear-sigmoid, pollinia connected to a rhombic to obtriangular-peltate viscidium through a reduced stipe.

In molecular analyses by Whitten *et al.* (2005), *Kefersteinia* formed a strongly supported group sister to *Euryblema*, *Stenia*, *Daiotyla,* and *Benzingia* (*Huntleya* clade). Molecular analyses from the sampled species do not support the distinctiveness of *Senghasia* and show that *K.* sects. *Kefersteinia* and *Umbonatae* are not monophyletic and therefore should not be recognized. **(FP)**

Ecology

Species of *Kefersteinia* occur as epiphytes in shady habitats, often growing on the trunks and mossy oldest branches of trees alongside streams. The habitat of *Kefersteinia* ranges from tropical warm to premontane and submontane temperate, cloud, evergreen and wet forests at elevations of 100–2500 m, although most species are found in premontane forests at mid-elevations (900–1500 m). Some species (namely *K. bengasahra* D.E.Benn. & Christenson, *K. expansa* Rchb.f., *K. retanae* G.Gerlach, *K. stevensonii* Dressler) are restricted to warm, tropical and premontane forests under 500 m, whereas *K. guacamayoana* Dodson & Hirtz, *K. aurorae* D.E.Benn. & Christenson, *K. pusilla* (C.Schweinf.) C.Schweinf., *K. pellita,* and *K. tolimensis* Schltr. have been exclusively recorded from montane forests at elevations of 1700–2500 m. Flowering has been recorded throughout the year, although some species seem to flower consistently during the dry season and others during the rainy months. **(FP)**

Pollination

Pollination of *Kefersteinia* is carried out by male euglossine bees of the genera *Euglossa* and *Eulaema* apparently attracted by floral scent (van der Pijl & Dodson 1966; Dressler 1968, 1983; Gerlach 1994), a syndrome shared with other members of Zygopetalinae. However, the method of pollinarium deposition in *Kefersteinia* is unique among euglossine-pollinated orchids: the prominently toothed ventral surface of the *Kefersteinia* column obliges the bee to twist its body so that the pollinarium is deposited on the basal segment of the antenna; the narrowly lanceolate to linear viscidium quickly curls after removal and wraps around and adheres to the bee's antenna. **(FP)**

Uses

There are no known uses of *Kefersteinia* except as cultivated ornamentals. **(FP)**

Cultivation

Culture of *Kefersteinia* species must take into account the habitat preferences of these delicate epiphytes. Plants mounted on slabs are less sensitive to bacterial and fungal rot, and their mostly arching to pendent inflorescences are better shown, but the higher humidity around the roots when potted seems to be beneficial for healthy growth. With the exception of a few species native to South American montane forests, the other taxa are warmth tolerant and seem best suited to the warm side of the intermediate greenhouse. In their native habitats, species of *Kefersteinia* do not have a marked dry season, and plants are usually found along streams in mature vegetation. Cultivated specimens should therefore be watered abundantly throughout the year, never allowing the roots to dry out. **(FP)**

Taxonomic literature

Dressler, R. L. (1968). Observations on orchids and euglossine bees in Panama and Costa Rica. *Revista de Biología Tropical,* **15,** 143–83.

Dressler, R. L. (1983). Two new *Kefersteinia* from Panama. *Orquideología,* **16**, 56–62.

Fowlie, J. A. (1966*a*). A revision of the Central American species of *Chondrorhyncha* and *Kefersteinia*, including the description of a new species from Costa Rica. Part I. Introduction and the genus *Chondrorhyncha. Orchid Digest,* **30**, 79–82.

Fowlie, J. A. (1966*b*). A revision of the Central American species of *Chondrorhyncha* and *Kefersteinia*, including the description of a new species from Costa Rica. Part II. *Orchid Digest,* **30**, 114–118.

Garay, L. A. (1969). El complejo *Chondrorhyncha*. *Orquideología,* **4**, 139–52.

Gerlach, G. (1994) [printed 1995]. *Kefersteinia retanae*, una nueva orquídea de Costa Rica. *Brenesia,* **41–42**, 99–106.

Pupulin, F. (2001). Contributions toward a reassessment of Costa Rican Zygopetalinae (Orchidaceae). The genus *Kefersteinia* Rchb.f. *Annalen des Naturhistorischen Museums in Wien,* **103B**, 525–555.

Reichenbach, H. G. (1861). Zygopetalum. Annales Botanicae Systematicae, **6**, 650–62.

Szlachetko, D. (2003). *Senghasia*, eine neue Gattung der Zygopetaleae. *Journal für den Orchideenfreund*, **10,** 335.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

605. KOELLENSTEINIA

Koellensteinia Rchb.f., *Bonpl.,* **2,** 17 (1854). Type species: *Koellensteinia kellneriana* Rchb.f.

Derivation of name

The generic name honours Austrian military Captain Kellner von Koellenstein, grower and collector of tropical plants during the 19th century. (FP)

Description (Plate 211; Fig. 605.1)

Terrestrial, rarely epiphytic, caespitose, mostly pseudobulbous *herbs*. *Roots* terete, produced on rhizome at base of pseudobulbs. *Pseudobulb* often rudimentary or cryptic, heteroblastic, narrowly

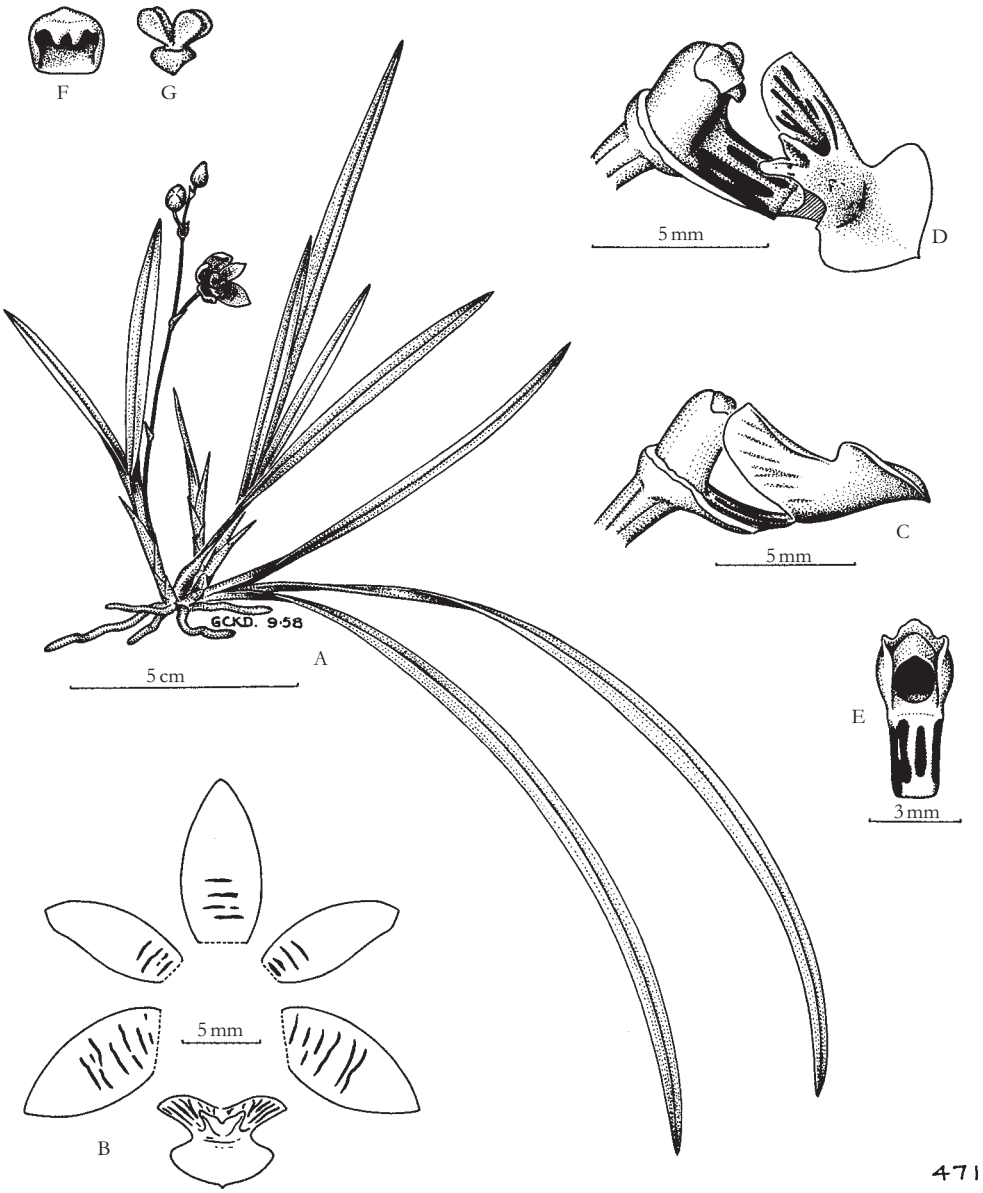


Fig. 605.1. *Koellensteinia graminea* (Lindl.) Rchb.f. A. Habit, with inflorescence; B. Perianth, dissected; C. Column and labellum, side view; D. Column and labellum (sectioned to show callus), side view; E. Column, ventral view; F. Anther cap, ventral view; G. Pollinarium. Drawn by G.C.K. Dunsterville. Originally published in *Venezuelan Orchids Illustrated,* **1**, 186 (1959). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

ovoid to oblong-cylindric or subterete, sometimes tetragonous or with a caulescent neck, 1–3 leaved at apex, when young completely concealed by three or four conduplicate, scarious, imbricating sheaths. *Leaves* plicate, membranaceous to subcoriaceous, dark green, linear-lanceolate to elliptic-lanceolate, acute to acuminate, veins abaxially ribbed, narrowed at base into a conduplicate petiole. *Inflorescence* a lateral, few-flowered, rarely branching raceme shorter than leaves, produced from base of pseudobulb or thickened stem, peduncle terete, erect, base clothed by three or four acuminate, conduplicate, scarious bracts, provided with 1–4 spreading to appressed, ovate, acuminate, papyraceous, remote bracts; floral bracts narrowly lanceolate, conduplicate, membranaceous, shorter than ovary. *Flowers* resupinate, sepals pale cream to pale green or clear light yellow, sometimes flushed with pink or transversely marked with rose, violet or red-brown toward base, petals pale cream to pale green or clear light yellow, sometimes sparsely dotted or transversely striped with purple, labellum white, mostly with transverse, purple stripes or with purple spots toward base, often flushed with yellow around callus. *Dorsal sepal* free, elliptic to elliptic-lanceolate or ovate, acute, mostly reclinate over column. *Lateral sepals* obliquely elliptic to elliptic-lanceolate or narrowly ovate, acute, concave toward base. *Petals* lanceolate to oblong, acute to subacuminate, rarely apiculate, sometimes porrect, concave. *Labellum* articulate with column foot, trilobed, flat to cup-shaped in natural position, base sometimes contracted into an

indistinct claw, apex widely obtuse to rounded or truncate, often apiculate, rarely emarginate, lateral lobes large, erect-patent to flank column, semiorbicular to obovate-reniform, midlobe usually larger lateral lobes, transversely elliptic to obreniform or semilunate; disc with an erect, mostly retrorse, bilobed callus, rarely with a third retrorse lobe. *Column* straight, with a distinct foot, terete or dilated at apex into conspicuous, elliptic, rounded stigmatic wings, clinandrium sometimes well developed; anther cap cucullate, obovate to transversely elliptic-subrectangular, flattened, two-celled, pollinia four, in two subequal pairs, on a stipe and a cordiform, grey to brownish cream viscidium; stigma transversely elliptic to rounded. (FP)

Distribution (Fig. 605.2)

Koellensteinia comprises some 18 species distributed in Puerto Rico and Trinidad, Central America (Belize and Panama), and tropical South America from Venezuela to Brazil and from Colombia to Peru and Bolivia along the Amazonian watershed of the Andes. The centre of diversity is northeastern Brazil. **(FP)**

Cytogenetics

Tanaka and Kamemoto (1984) reported a chromosome count of $2n$ = ca 48 for *K. graminea* (Lindl.) Rchb.f. **(AP)**

Fig. 605.2. Distribution map of *Koellensteinia.*

Phytochemistry

The leaves of *K. graminea* contain flavone *C*-glycosides (Williams 1979). **(NV, RG)**

Phylogenetics

Garay (1973) assigned *Koellensteinia* to the *Zygopetalum* complex, characterized by rhizomatous plants with heteroblastic pseudobulbs and an axillary inflorescence produced from the current season's growth together with the developing pseudobulbs. Within the complex, he included *Koellensteinia* among those genera with lateral sepals adnate to the column foot, the column without prominent auricles, small flower bracts, and small, numerous flowers. In this scheme, *Koellensteinia* appears closely related to *Paradisanthus*, from which it may be distinguished by the prominent, erect lateral lobes of the lip and the bilobed, retrorse callus. Senghas and Gerlach (1993) suggested that *Koellensteinia* is closely related to *Paradisanthus* and *Otostylis*, from which it can be distinguished mainly by the free callus, and to *Eriopsis* on the basis of the rounded rostellum.

Combined molecular evidence (Whitten *et al.* 2005) showed that the current generic concept of *Koellensteinia* is not monophyletic, the sampled species falling into two clades containing *Aganisia*, *Otostylis*, *Paradisanthus*, and *Zygopetalum*. *Koellesteinia bolivi-ensis* (Rolfe ex Rusby) Schltr. (originally described as a member of *Aganisia*) is sister to *Aganisia* in one strongly supported clade, but the other two study taxa of *Koellensteinia* are included in a strongly supported clade with *Otostylis* and *Paradisanthus*. Additional DNA sequencing is required to have a better understanding of the true affinities in the group. **(FP)**

Ecology

Species are terrestrials in humid soils and among mossy rocks on the floor of bright, open forests and grasslands and less frequently epiphytes on shaded tree trunks in evergreen cloud forests at 100–2300 m. Flowering has been mostly recorded from December to August. (FP)

Pollination

Pollinators are unknown but presumed to be male euglossine bees (Dodson 2001). (FP)

Uses

There are no known uses of *Koellensteinia* except as occasionally cultivated ornamentals. (FP)

Cultivation

Plants of *Koellensteinia* may be grown in well-drained baskets or pans under moderately shaded, humid conditions. The compost should be fine-graded to retain adequate moisture around the roots. Most of the species require constant watering throughout the year, and they should never be allowed to dry out. Under proper cultural conditions, plants of *Koellensteinia* may flower for several months at a time. (FP)

Taxonomic literature

Dodson, C. H. (2001). *Native Ecuadorian orchids, vol. 2*. Dresslerella-Lepanthes. Dodson Trust, Sarasota.

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

606. NEOGARDNERIA Schltr.

Neogardneria Schltr. ex Garay, *Orquideología*, **8,** 32 (1973). Type species: *Neogardneria murrayana* (Gardner ex Hook.) Schltr. ex Garay (basionym: *Zygopetalum murrayanum* Gardner ex Hook.)

Derivation of name

From the Greek *neos*, new, in reference to the second genus honouring the British plant collector George Gardner (1812–1849), who discovered the type species of the genus in the Organ Mountains, Brazil, and originally proposed the name *Zygopetalum murrayanum* for it. **(FP)**

Description (Plate 212; Fig. 606.1)

Epiphytic, caespitose, pseudobulbous *herbs*. *Roots* terete, produced along rhizome. *Pseudobulb* heteroblastic, ovoid, apically one- or two-leaved, concealed by 4–6 conduplicate, imbricating sheaths, lower ones scarious, upper ones foliaceous. *Leaves* plicate, articulate, membranaceous, elliptic, acute to subacuminate, narrowed at base into an indistinct, conduplicate petiole, medium to dark green, shiny on upper surface. *Inflorescences* lateral, one or two per shoot, a 2–6-flowered raceme produced from base of developing pseudobulb and emerging from axils of lower sheaths, peduncle terete, suberect to erect, rachis fractiflex; floral bracts lanceolate, conduplicate-cymbiform, loose, shorter than ovary. *Flowers* resupinate, spreading, greenish to light yellow, labellum white to greenish white, marked with red-purple freckles, callus and column yellow. *Dorsal sepal* free, lanceolate, acuminate, abaxially carinate, concave toward apex, margins revolute in distal half. *Lateral sepals* lanceolate, acuminate, abaxially carinate, concave. *Petals* lanceolate-elliptic, acute, abruptly acuminate, porrect-incurved. *Labellum* subsessile, articulate with column foot, trilobed, base cuneate into an indistinct claw, lateral lobes falcate, acute, erect, parallel to column, midlobe elliptic-oblong, acute, abruptly subacuminate, geniculate-deflexed, convex in natural position; disc with a flabelliform, erect-laminar, 7–9-ridged callus, low keels terminating in rounded teeths. *Column* straight to arched, semiterete, with a foot, dilated at apex into inconspicuous, rounded wings; anther cap cucullate, transversely subrectangular-elliptic, flattened, two-celled, pollinia four, in two subequal pairs, without a stipe, on an obtriangular-peltate, hyaline viscidium; stigma transverse, elliptic. **(FP)**

Distribution (Fig. 606.2)

This monospecific genus is endemic to southeastern Brazil (South America), recorded from Espírito Santo and Río de Janeiro states. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Neogardneria*. **(NV, RG)**

Phylogenetics

Originally proposed by Schlechter (*nomen nudum*), *Neogardneria* was validated by Garay (1973), who characterized it among genera of the *Zygopetalum* alliance by petals decurrent on the column foot and lateral sepals adnate to the column foot near the apex, column without distinct auricles, bracts and flowers large, lip sessile with a flabellate crest, and pollinia sessile on a short, broad viscidium. In Garay's treatment, *Neogardneria* is close to *Zygopetalum*, from which it can be distinguished by prominent, erect lateral lobes of the lip parallel with the column (versus the lip elobulate or with inconspicuous teeth of *Zygopetalum*) and midlobe deflexed (versus spreading-porrect) in front of the crest. In their key to genera of Zygopetalinae, Senghas and Gerlach (1993) suggested a close relationship of *Neogardneria* with *Pabstia* and *Batemannia* on the basis of the shared large, cymbiform floral bracts (versus small in *Zygopetalum*). Sequence data of ITS rDNA, as well as parsimony analyses of combined DNA nuclear and plastid data sets (Whitten *et al*. 2005) revealed *Neogardneria murrayana* within a weakly supported clade including *Pabstia* and several species of *Zygopetalum*. Once a better sampling of DNA sequences and taxa in the *Zygopetalum* clade becomes available, it is likely *Neogardneria* will be merged into a more broadly circumscribed genus, perhaps *Zygopetalum*. **(FP)**

Ecology

Species are epiphytes in the shade on mossy old tree trunks in evergreen cloud forests at 1200–1600 m, mostly along well-drained ridges of the Atlantic chains of central and southern Brazil. Flowering has been recorded from December through March. **(FP)**

Pollination

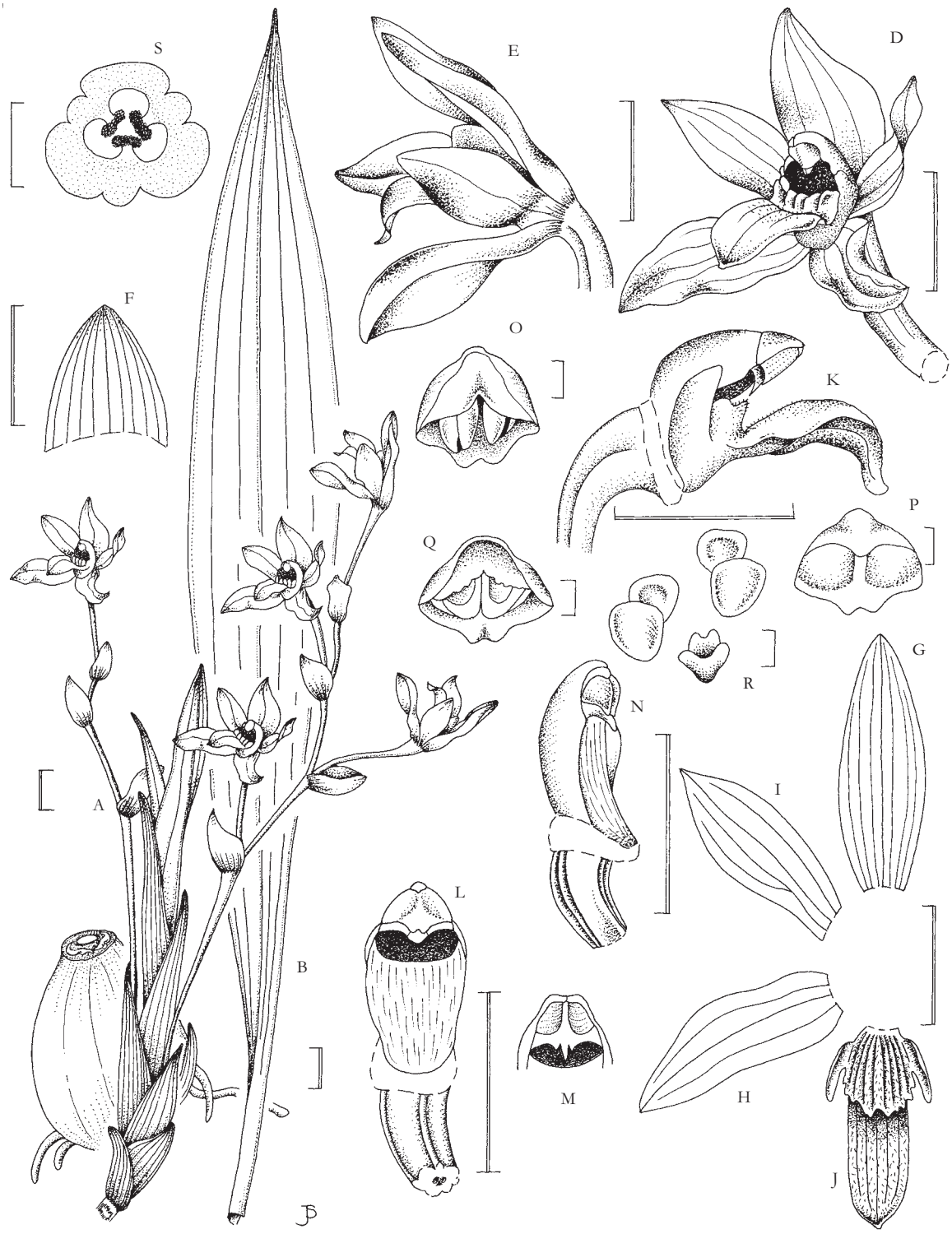
Pollination biology of *N. murrayana* is unknown. **(FP)**

Uses

There are no known uses. The species is rare in cultivation. **(FP)**

Cultivation

Cultivated specimens can be grown in pots or on plaques, in medium to deep shade at intermediate temperatures with frequent watering throughout the year. **(FP)**



AQ: Please note that label 'C' is missing in figure 606.1

Fig. 606.1. *Neogardneria murrayana* (Gardner ex Hook.) Schtr. ex Garay. A. Habit, with inflorescences; B. Leaf; C. Pseudobulb; D. Flower, front view; E. Flower, side view; F. Bract; G. Dorsal sepal; H. Lateral sepal; I. Petal; J. Labellum; K. Column and labellum, side view; L. Column, ventral view; M. Column apex, anther cap removed; N. Column, side view; O. Anther cap with pollinia, ventral view; P. Anther cap, dorsal view; Q. Anther cap, ventral view; R. Pollinarium; S. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Herbarium Hookerianum 635* (holotype, K), Kew Spirit Collection no. 50224, and drawing in Hoehne, F. C. (1949). *Iconografia de orchidaceas do Brasil*. Secretariea de Agricultura, São Paulo.

Fig. 606.2. Distribution map of *Neogardneria.*

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

607. OTOSTYLIS

Otostylis Schltr., *Orchis*, **12,** 38 (1918). Type species: *Otostylis brachystalix* (Rchb.f.) Schltr. (basionym: *Zygopetalum brachystalix* Rchb.f.)

Derivation of name

From the Greek *ous, otos*, ear, and *stylis*, column, in reference to auriculate wings of the column. **(FP)**

Description (Plate 213; Fig. 607.1)

Terrestrial, caespitose, pseudobulbous *herbs*. *Roots* terete, filiform, produced at intervals along rhizome. *Pseudobulb* homoblastic, ovoid to narrowly ovoid-fusiform, 1–3-leaved, cryptic when young among persistent, adpressed, basal leaf sheaths. *Leaves* subplicate to plicate, articulate, membranaceous, mid-green, narrowly lanceolate to linear-lanceolate, acute to subacuminate, abaxially sulcate-carinate, narrowed at base into a conduplicate petiole, often arching when mature. *Inflorescences* lateral, emerging from axils of lower sheaths, a successively flowered raceme, rarely branching at base, with 5–20 flowers open simultaneously, peduncle terete, erect, provided with 5–7 acute, triangular-conduplicate bracts; floral bracts triangular-ovate, acute, submembranaceous, shorter than ovary. *Flowers* resupinate, with sepals and petals white to pale cream, sometimes flushed with pale pink toward the apex, labellum white to pale cream, disc pale yellow to yellow, sometimes spotted purple toward base, column white, variously marked with purple-violet at base. *Dorsal sepal* free, elliptic to lanceolate-elliptic, acute, concave. *Lateral sepals* elliptic-ovate, acute to subobtuse, sometimes falcate. *Petals* elliptic-ovate to oblong, acute to obtuse and apiculate, rounded, porrect, smaller than sepals. *Labellum* sessile to clawed, articulate with base of column, entire to trilobed, widely elliptic to subrhombic, base rounded or biauriculate, apex obtuse to truncate, basal margins suberect; disc with a transverse, semicircular to W-shaped, apically undulate-toothed, verrucose ridge. *Column* straight, semiterete, with a foot, dilated at apex into elliptic to subquadrate, spreading, rounded to emarginate wings; anther cap cucullate, ovoid, ridged, two-celled, pollinia four, in two subequal pairs, on a ligulate-subrectangular stipe and rounded-elliptic viscidium; stigma transversely elliptic-subcircular. **(FP)**

Distribution (Fig. 607.2)

Otostylis is a genus of one to three species ranging from Trinidad to Venezuela and Brazil and from Colombia to Peru (South America), with most taxa recorded from the Guyana Shield and northern Brazil. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Otostylis*. **(NV, RG)**

Phylogenetics

In creating the new genus *Otostylis* in 1918 for three species previously described under *Zygopetalum* and *Aganisia*, Schlechter placed it between *Acacallis* (= *Aganisia*) and *Koellensteinia*, which it resembles in the partially cryptic pseudobulbs and floral morphology. Senghas and Gerlach (1993) placed *Otostylis* in the *Warrea* group on the basis of its homoblastic pseudobulbs, suggesting a close affinity with *Paradisanthus,* from which it can be distinguished by its toothed rostellum, winged column, and shape of the basal callus of the lip. Szlachetko (1995) gave the *Warrea* group formal recognition, creating subtribe Warreinae to group Zygopetalinae taxa provided with homoblastic pseudobulbs, plicate leaves, and a distinctly auriculate column, including *Otostylis*, *Warrea, Warreella,* and *Warreopsis*.

Cladistic analysis of combined DNA data sets (Whitten *et al.* 2005) placed *Otostylis* in a clade including members of *Koellensteinia*

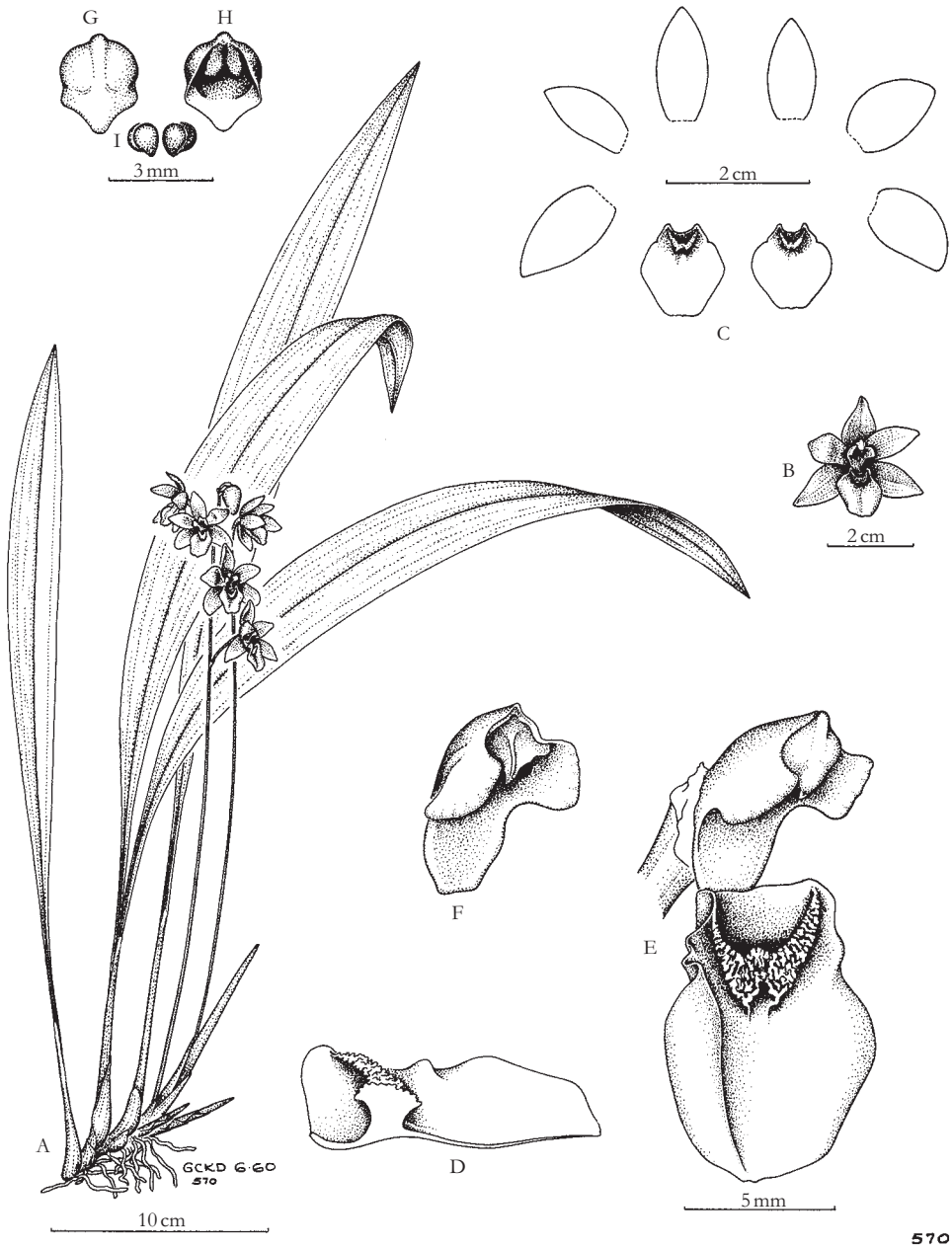


Fig. 607.1. *Otostylis lepida* (Linden & Rchb.f.) Schltr. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected, showing variation; D. Labellum (sectioned), side view; E. Column and labellum; F. Column, ventral view; G. Anther cap, dorsal view; H. Anther cap, ventral view; I. Pollinia. Drawn by G.C.K. Dunsterville. Originally published in *Venezuelan Orchids Illustrated,* **3**, 232 (1965). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

and *Paradisanthus* in the *Zygopetalum* clade, but this result is weakly supported. Nomenclatural consequences of this realignment have not been published yet, but molecular evidence indicates that structure of pseudobulbs, emphasized in previous phylogenetic schemes, is evolutionarily labile. Among primitive genera of Zygopetalinae, *Otostylis* may be recognized by homoblastic pseudobulbs; usually tall, erect inflorescences; ridge-shaped, verrucose callus of the lip; and prominently winged column. **(FP)**

Ecology

Species are terrestrial in moist and swampy peaty soils in open areas of evergreen, damp rain forests and semi-dwarf forests at 100–1700 m. Flowering has been recorded at least from April to June. **(FP)**

Pollination

Pollination biology of the genus is unknown. **(FP)**

Uses

There are no known uses of any of the species, which are also rare in cultivation. **(FP)**

Cultivation

Plants of *Otostylis* may be grown in pots with a moisture-retentive compost in bright light and intermediate to cool temperatures. Recorded from regions that experience a pronounced dry season, specimens of *Otosytlis* should receive abundant water with a short rest period after flowering. **(FP)**

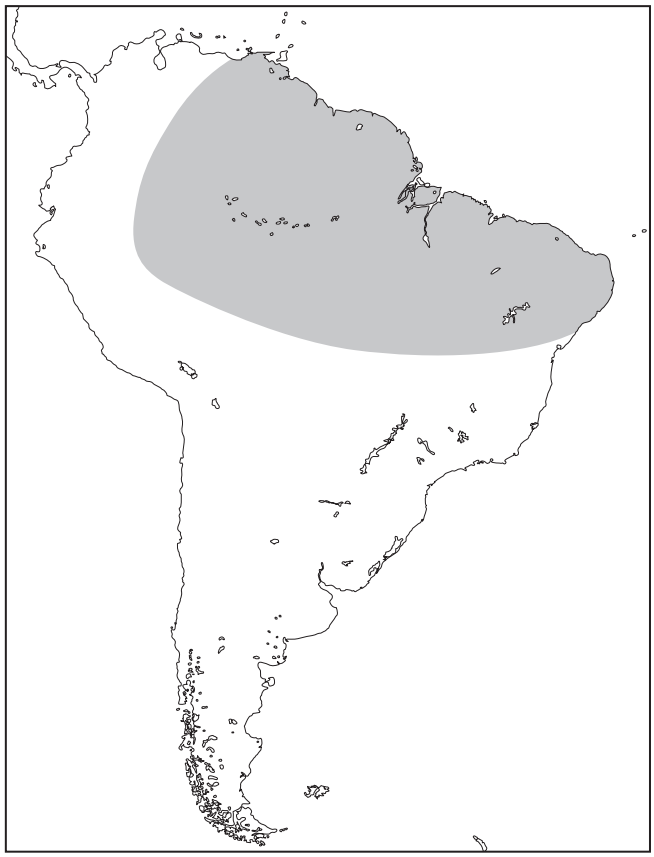


Fig. 607.2. Distribution map of *Otostylis*.

Taxonomic literature

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.

Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

608. PABSTIA

Pabstia Garay, *Bradea*, **1**, 306 (1973). Type species: *Pabstia viridis* (Lindl.) Garay (basionym: *Maxillaria viridis* Lindl.)

Colax Lindl., *Edwards's Bot. Reg.,* **29,** Misc., 50 (1843), *nom. illeg.*, *non* Lindl ex Spreng. (1826). Type species: *Colax viridis* (Lindl.) Lindl. (basionym: *Maxillaria viridis* Lindl.)

Derivation of name

Named in honour of Guido Frederico Joao Pabst (1914–1980), eminent Brazilian orchidologist and Director of the Herbarium Bradeanum in Río de Janeiro, co-author of *Orchidaceae Brasilienses* with Fritz Dungs. **(FP)**

Description (Plate 214; Fig. 608.1)

Epiphytic, lithophytic (occasionaly terrestrial), caespitose, pseudobulbous *herbs*. *Roots* terete, produced from rhizome. *Pseudobulb* narrowly ovoid to ovoid-oblong, compressed, ancipitous, rarely four-angled, sulcate, when young enclosed by two or three imbricating sheaths, upper ones foliaceous, apically one-two leaved. *Leaves* subplicate, articulate, subcoriaceous, oblong-lanceolate, acute to acuminate, abaxially sulcate-carinate, narrowed at base into a conduplicate petiole, medium to dark green, adaxially shiny/glossy-textured. *Inflorescences* lateral, 1–4 per shoot, one-few-flowered, produced from axils of lower sheaths of maturing pseudobulb, peduncle terete, spreading to arching, provided with one or two oblong-lanceolate, acute, conduplicate, loose, membranaceous bracts; floral bract oblong-lanceolate, loose to spreading, membranaceous, subequal to ovary, pale green. *Flowers* resupinate, subspreading to subglobose, scented, fleshy, sepals creamy white to green, rarely striped with red-brown, lateral sepals sometimes sparsely spotted with red-purple, petals creamy white to green, heavily spotted/blotched or striped with purple red, labellum white, blotched/striped with purple to solid violet apically, sometimes flushed with green toward apical margins, disc and callus greenish white to pale violet, column white flecked with purple to pale violet. *Dorsal sepal* free, erect to curved over column, obovate-oblong to broadly oblong, concave, obtuse to rounded. *Lateral sepals* broadly obovate-oblong, obtuse, concave, forming a mentum. *Petals* erect-spreading, elliptic-oblong to narrowly oblong-obovate, obtuse to subrounded. *Labellum* unguiculate, articulate with column foot, obovate to elliptic-oblong or subquadrate, trilobed, lateral lobes oblong-elliptic to triangular, obtuse to subacute, erect, margins undulate, midlobe suborbicular to transversely rhombic, broadly obtuse to rounded, convex, apically deflexed; disc furfuraceous-puberulent, provided with low, longitudinal keels running from base to insertion point of midlobe. *Column* semiterete, clavate, erect to arched, with a foot, apically puberulous and sometimes provided with indistinct auricles, ventral surface longitudinally bisulcate; anther cap cucullate, ovate, flattened, two-celled, pollinia four, in two subequal pairs, on a ligulate-triangular stipe scarcely distinct from ventral, ligulate, hyaline viscidium; stigma transversely, broadly elliptic. **(FP)**

Distribution (Fig. 608.2)

Pabstia is a genus of five or six species endemic to the tropical regions of coastal Brazil (Espírito Santo, Río de Janeiro, Santa Catarina) in South America. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Pabstia*. **(NV, RG)**

Phylogenetics

All recent schemes of phylogenetic relationships (Dressler 1981, 1993; Senghas and Gerlach 1993; Szlachetko 1995) agree

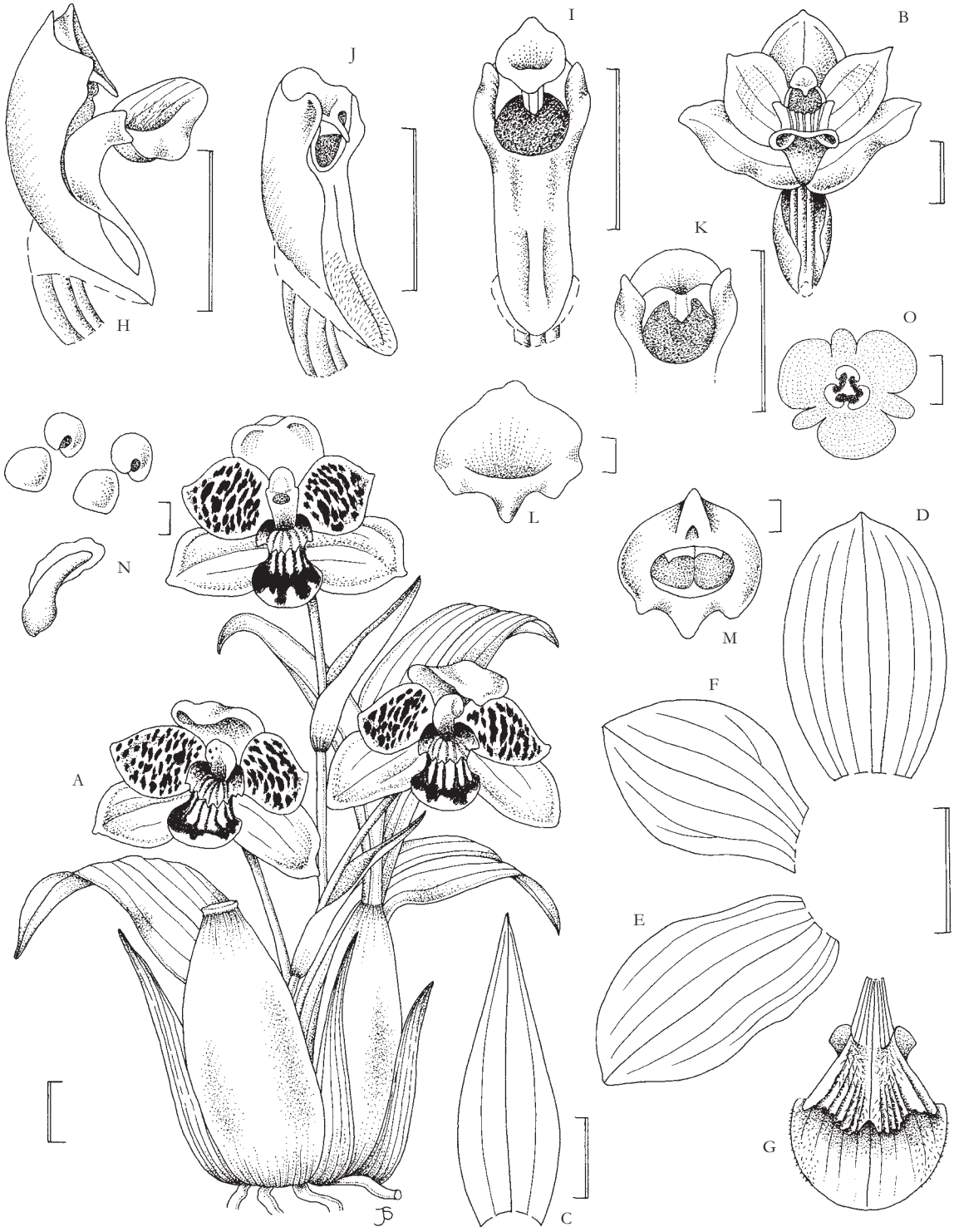


Fig. 608.1. *Pabstia jugosa* (Lindl.) Garay. A. Habit, with inflorescences; B. Flower; C. Bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Column and labellum, side view; I. Column, ventral view; J. Column, anther cap removed, side view; K. Column apex, anther cap removed; L. Anther cap, dorsal view; M. Anther cap, ventral view; N. Pollinarium; O. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from drawing by Pieter De Pannemaeker in *L'Illustration Horticole*, **18,** 96 (1872) and Kew Spirit Collection no. 36350.

about placement of *Pabstia* within the core of Zygopetalinae, together with *Galeottia, Neogardneria, Zygopetalum,* and *Zygosepalum* among others. Analyses of combined *matK/trnL-F/*ITS rDNA (Whitten *et al.* 2005) strongly supported monophyly of *Pabstia* in a clade including *Neogardneria* and various species of polyphyletic *Zygopetalum*. Among taxa of the *Zygopetalum* clade, *Pabstia* may be recognized by large, membranaceous floral bracts, trilobed lip, and exauriculate column. **(FP)**

Fig. 608.2. Distribution map of *Pabstia*.

Ecology

Species of *Pabstia* are epiphytes and lithophytes in shady and humid locations in rain forests or cloud forests along the coastal mountains of southeastern Brazil at 200–1500 m. Flowering occurs from July to December. **(FP)**

Pollination

Pollinators of *Pabstia* species are unknown. **(FP)**

Uses

The only uses of the genus are as cultivated ornamentals, which are occasionally in specialist collections and botanical gardens. **(FP)**

Cultivation

Plants of *Pabstia* should be grown in shade and intermediate to warm temperatures, maintaining high levels of humidity year-round. As they require a constantly moist compost, cultivation in pots with a medium-grade epiphyte mix is advisable. However, specimens may be also be grown on slabs with frequent watering. Water should be applied until the new pseudobulb matures, followed by a short rest period. **(FP)**

Taxonomic literature

Dressler, R. L. (1981). *The orchids: natural history and classification*. Harvard University Press.

Dressler, R. L. (1993). *Phylogeny and classification of the orchid family*. Dioscorides Press, Portland, Oregon.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.

Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.

Whitten, W. M., N. H. Williams, R. L. Dressler, G. Gerlach & F. Pupulin (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbideae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

609. PARADISANTHUS

Paradisanthus Rchb.f., *Bot. Zeitung (Berlin),* **10,** 930 (1852).
Type species: *Paradisanthus bahiensis* Rchb.f.

Derivation of name

From the Greek *paradeisos*, garden, paradise, and *anthos*, flower, alluding to the particular beauty of the flower. **(FP)**

Description (Plate 215; Fig. 609.1)

Terrestrial, caespitose, pseudobulbous *herbs*. *Roots* terete, flexuous, produced along rhizome at bases of developing pseudobulbs. *Pseudobulb* heteroblastic, ovoid-oblong, apically 1–2-leaved, when young completely hidden by the bases of 3–5 membranaceous, triangular, acute, evanescent sheaths. *Leaves* plicate, submembranaceous, medium to dark green, sometimes glaucous, abaxial surface paler, narrowly lanceolate to elliptic, acute to acuminate, sulcate-carinate, margins sometimes undulate, narrowed at base into a conduplicate petiole. *Inflorescences* lateral, a successively few-flowered, rarely branching raceme, produced from base of pseudobulb and emerging from axils of lower sheaths together with developing shoot, peduncle terete, erect, provided with two or three membranaceous, acuminate, clasping bracts; floral bracts narrowly triangular-lanceolate, conduplicate, acuminate, membranaceous, shorter than ovary. *Flowers* resupinate, with creamy white to pale green sepals and petals, mostly transversely striped with brownish red toward base, labellum white, sometimes spotted violet along margins of lateral lobes, column white, with ventral surface blotched red to dark purple-brown. *Dorsal sepal* free, ovate-elliptic, acute, concave. *Lateral sepals* widely ovate-elliptic, subacuminate, concave, abaxially carinate. *Petals* lanceolate, acute to acuminate. *Labellum* articulate with column foot, sessile to clawed, trilobed, base cuneate and sometimes contracted into a claw, lateral lobes triangular, subfalcate, erect, midlobe basally ligulate and abruptly expanding into a subcordiform, obtuse to retuse plate; callus antrorse, crenulate or digitate. *Column* curved, semiterete, with a foot, dilated at apex, sometimes forming inconspicuous, triangular, rounded stigmatic wings; anther cap cucullate, ovate, flattened, one-celled, pollinia

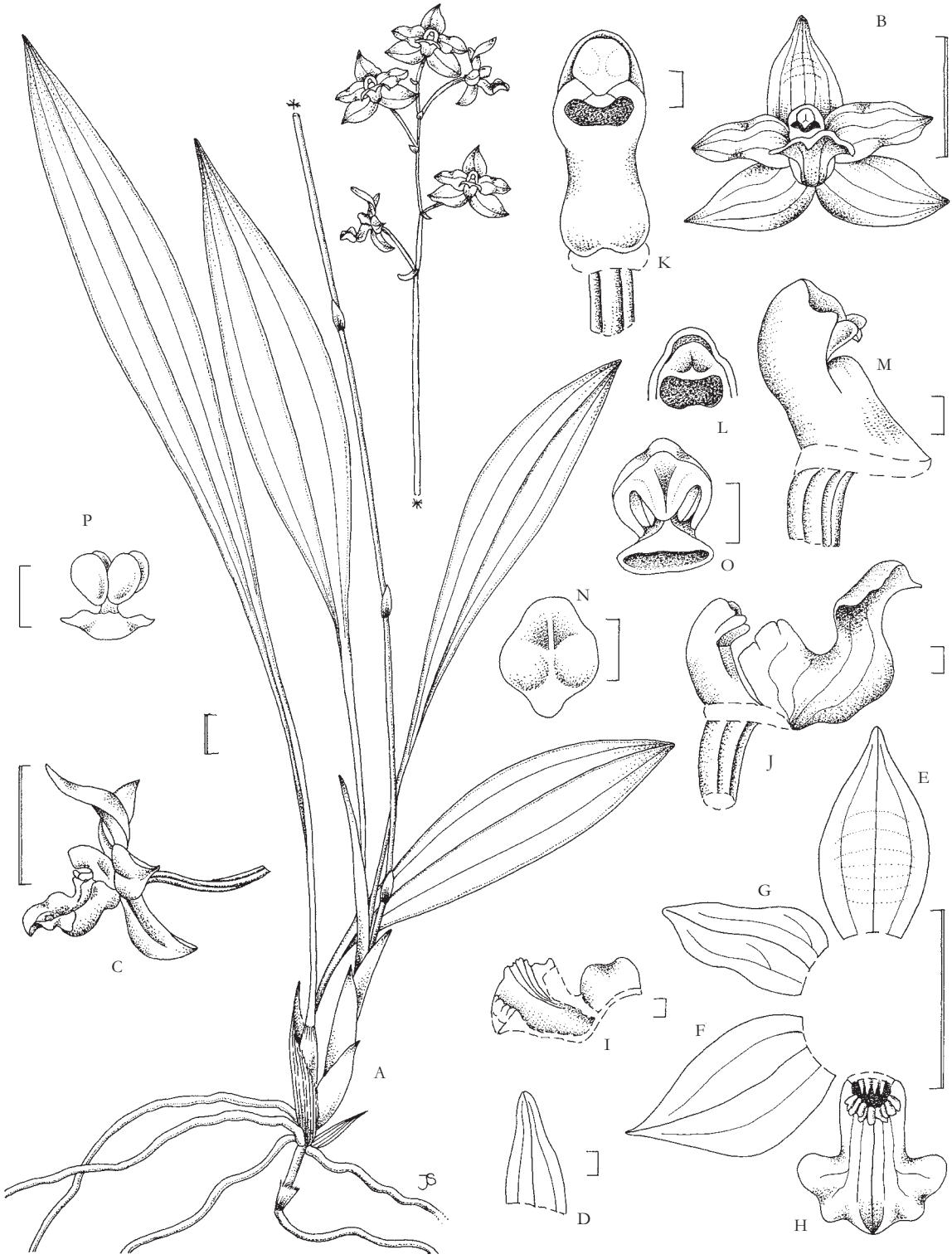


Fig. 609.1. *Paradisanthus micranthus* (Barb.Rodr.) Schltr. A. Habit, with inflorescence; B. Flower, front view; C. Flower, side view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum, longitudinal section; J. Column and labellum, side view; K. Column, ventral view; L. Column apex, anther cap removed; M. Column, side view; N. Anther cap, dorsal view; O. Anther cap with pollinia, ventral view; P. Pollinarium. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *G. Hatschbach 26253* (K) and Kew Spirit Collection no. 72024.

Fig. 609.2. Distribution map of *Paradisanthus.*

four, in two pairs of different sizes, without a stipe on a transversely triangular viscidium; stigma rounded. **(FP)**

Distribution (Fig. 609.2)

The four species of *Paradisanthus* are native to the coastal regions of central and southern Brazil (South America), where they have been recorded from the states of Bahia to Rio Grande do Sul. **(FP)**

Phytochemistry

Lüning (1964) reported that *P. micranthus* Schltr. gave a positive result in a survey of alkaloid content in Orchidaceae. **(NV, RG)**

Phylogenetics

In his revision of the *Zygopetalum* alliance, Garay (1973) characterized *Paradisanthus* by column without distinct auricles, small bracts, and inflorescence with numerous small, flowers, distinguishing it from the closely allied *Koellensteinia* by reduced lateral lobes of the lip (vs. prominent) and antrorse, crenulate-digitate callus of the lip (vs. retrorse, bilobed). Senghas and Gerlach (1993) placed *Paradisanthus* near *Cheiradenia*, *Otostylis*, *Warrea*, *Warreella,* and *Warreopsis* on the basis of the supposedly homoblastic pseudobulbs, distinguishing it from closely related *Otostylis* on the basis of the differently shaped rostellum, column provided with a distinct foot, and morphology of the callus.

In their cladistic analysis of combined DNA data sets, Whitten *et al.* (2005) showed that *Paradisanthus* belongs to a moderately supported clade with members of *Koellensteinia* and *Otostylis*. These clades of Zygopetalinae are weakly supported and require more study; they include genera with both homoblastic and heteroblastic pseudobulbs, and thus pseudobulb structure (i.e. number of internodes) would appear to be evolutionarily labile. **(FP)**

Ecology

Species of *Paradisanthus* are terrestrial plants in the open shade of tropical and subtropical, low-elevation rain forests, where they are usually found in dry soils with the roots growing among surface detritus. Flowering has been recorded from December to June. **(FP)**

Pollination

Pollination biology of the species is unknown. **(FP)**

Uses

There are no known uses, and plants are rare in cultivation. **(FP)**

Cultivation

Plants of *Paradisanthus* may be grown in large pots, with a coarse, well-drained compost in intermediate to warm conditions in bright light. Water should be provided frequently during each new vegetative cycle, with a short rest when new pseudobulbs and leaves are completely developed. **(FP)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

610. PESCATORIA

Pescatoria Rchb.f., *Bot. Zeitung (Berlin),* **10,** 667 (1852). Type species: *Pescatoria cerina* (Lindl. & Paxton) Rchb.f. (basionym: *Huntleya cerina* Lindl. & Paxton)

Bollea Rchb.f., *Bot. Zeitung (Berlin),* **10,** 667 (1852). Type species: *Bollea violacea* (Lindl.) Rchb.f. (basionym: *Huntleya violacea* Lindl.)

Derivation of name

The genus is dedicated to Jean Paul Pescatore (1793–1855), an eminent French horticulturist at Château Celle-St-Cloud near Paris, who supplied Reichenbach with a stream of rare orchid species imported from their native countries (see taxonomic notes). **(FP)**

Description (Plate 216; Fig. 610.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from rhizome. *Stem* enclosed by 7–12 imbricating, mostly foliaceous sheaths. *Leaves* conduplicate, articulate, membranaceous to coriaceous, erect to erect-spreading, narrowly ligulate to oblanceolate, obtuse to acute or acuminate, abaxially carinate, contracted at base into an indistinct, conduplicate petiole, grass green to dark green. *Inflorescences* one or more per shoot, lateral, single-flowered, produced from axils of lower, non-foliaceous sheaths, peduncle terete, arcuate or pendulous, provided with 1–3 conduplicate, loose, papery bracts; floral bract double, conduplicate, papery, shorter than ovary, external one loose, widely ovate, acute, subopposite internal bractlet narrowly lanceolate to ligulate. *Flowers* resupinate, fleshy, sepals and petals white to creamy yellow, greenish cream or pink to solid purple-violet, mostly flushed with lavender toward apex, rarely striped with lavender or purple in basal half, labellum white to pink or yellow, midlobe often flushed lavender or purple apically, rarely solid violet, callus yellow (rarely white) to dark purple, ribs of callus usually purple. *Dorsal sepal* free, erect to bent over column, elliptic to ovate-oblong to broadly obovate, obtuse to acute, mostly concave toward the apex. *Lateral sepals* basally adnate to column foot, forming a mentum, elliptic-lanceolate to widely ovate-oblong or obovate, obtuse to acute, concave toward apex, margins sometimes undulate to wavy and inner margins inrolled at base. *Petals* elliptic to obovate, obtuse to subacute, often with undulate and sometimes revolute margins. *Labellum* fleshy, contracted at base into a claw, articulate or adnate to column foot, entire or obscurely trilobed, ovate to obovate or sagittate, acute to retuse, usually convex and reflexed at apex, sometimes provided with warty asperities or bristles, lateral margins recurved, hypochile cupped, sometimes provided with lateral lobes resting against base of column, with an erect, semicircular, fleshy, plurisulcate callus, deeply grooved longitudinally into numerous, rounded ridges. *Column* arcuate, semiterete to navicular, dilated at apex, sometimes provided with swollen lobes, with a distinct foot; anther cap cucullate, ovate-subquadrate to transversely elliptic, flattened, two-celled, pollinia four, in two superposed pairs of different sizes, on a stipe and a flattened, cordiform, hyaline viscidium; stigma transverse. **(FP)**

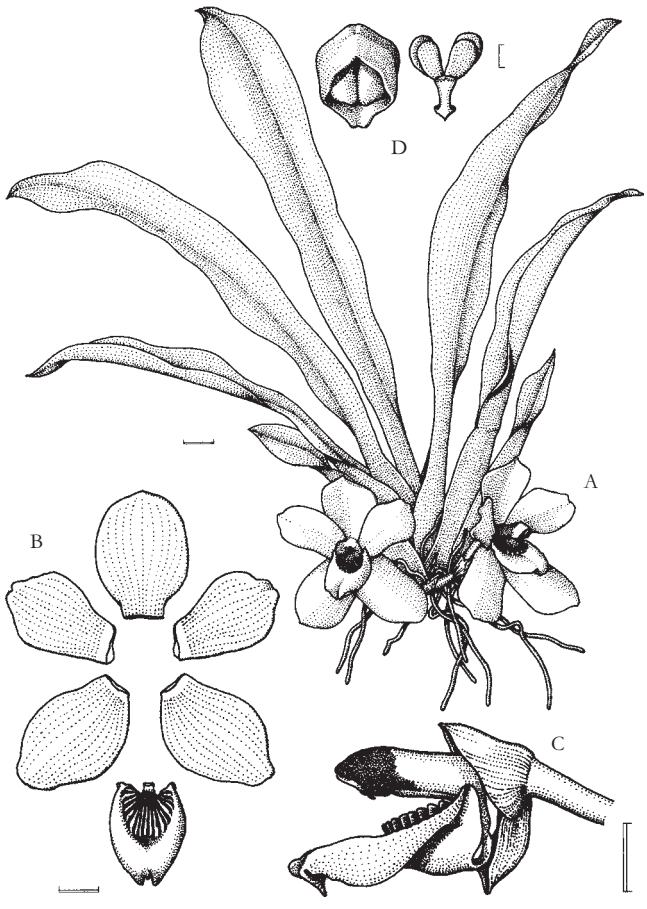


Fig. 610.1. *Pescatoria cerina* (Lindl. & Paxton) Rchb.f. A. Habit, with inflorescences; B. Perianth, dissected; C. Column and labellum, side view; D. Anther cap and pollinarium. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin et al. 2512* (voucher not preserved).

Distribution (Fig. 610.2)

Pescatoria is a genus of 22 species and two named natural hybrids, ranging from Costa Rica (Central America) to Brazil and Peru, centred in northwestern South America. *Pescatoria* is most diverse along the Andes of Colombia and Ecuador, with 16 and 9 species, respectively. Species diversity rapidly diminishes toward the north (a single species recorded for Costa Rica) as well as toward the southern end of the Andes (only one species in Peru) and in eastern South America. Two species are recorded from Venezuela and the Guyanas to northern Brazil. **(FP)**

Phytochemistry

Alkaloids were detected in *P. cerina* by Lüning (1967). The floral fragrance of this species is notable for its content of (*Z*)-4-decenal and two isomers of 2,4-decadienal, compounds that impart an unpleasant yeast-like scent to the flowers (see also *Stenotyla*; Kaiser 1993). The chemical profile of the scent of *P. coelestis* (Rchb.f.) Dressler (cited as *Bollea coelestis* Rchb.f.) is notable for its high content of caryophyll-5-en-2α-ol (Fig. 610.3, **3**), a compound that was not known previously either as a natural or a synthetic product (Kaiser 1993). Caryophyllene is the other major component, together with a small amount of caryophyllene epoxide (Fig. 610.3). The pleasant scent of *P. dayana* Rchb.f. is attributable mainly to a combination of benzyl acetate, geraniol, and cinnamic alcohol (Kaiser 1993). Some preliminary data are available on chemical composition of floral fragrances of *P. dayana var. rhodacra* Rchb.f., *P. klabochorum* Rchb.f., *P. lehmannii* Rchb.f., and *P. wallisii*

AQ: I did not get a copy of this figure.

Rchb.f. (Gerlach and Schill 1991). However, most constituents were not identified, with the exception of those present in the last species (mainly geraniol and nerol). **(NV, RG)**

Phylogenetics

Reichenbach originally described *Pescatoria* and *Bollea* in the same publication, distinguishing the latter mainly on the basis of broad lateral lobes of the column that protrude over the enlarged, semicircular callus. The two genera have been traditionally regarded as sister taxa, which primarily differ in the relative width of the column, and their close relationship was supported by putative intergeneric natural hybrids (*Pescatobollea*). Keys and annotated checklists of *Pescatoria* and *Bollea* were provided by Fowlie (1968, 1969), who informally divided *Pescatoria* into three groups on the basis of lip vestiture. In the cladistic analysis of combined DNA sequences by Whitten *et al.* (2005), the sampled species of *Pescatoria* and *Bollea* are intercalated and form a well-supported clade that is weakly supported to include *Warczewiczella*, *Chaubardiella*, *Ixyophora,* and *Aetheorhyncha*, among which relationships are unclear. **(FP)**

Ecology

Most species of *Pescatoria* are native to wet, premontane cloud forests at medium elevations (around 800–1500 m), but *P. hemixantha* (Rchb.f.) Dressler is found in the warmer forests of the tropical belt at 200–500 m. Plants of *Pescatoria* are large epiphytes, usually restricted to trunks and large branches of their hosts. The large and long-lasting flowers are generally produced during the rainy season, but some species of *Pescatoria* flower sporadically throughout the year. **(FP)**

Pollination

Male euglossine bees pollinate species of *Pescatoria*, and Dodson and Frymire (1961) recorded pollination of *P. wallisii* by *Eulaema polychroma*. Bees scratch at the base of the lip, and the pollinarium is attached to the thorax (Dodson 2003). **(FP)**

Uses

The only recorded use of *Pescatoria* species is as cultivated ornamentals. **(FP)**

Fig. 610.2. Distribution map of *Pescatoria.*

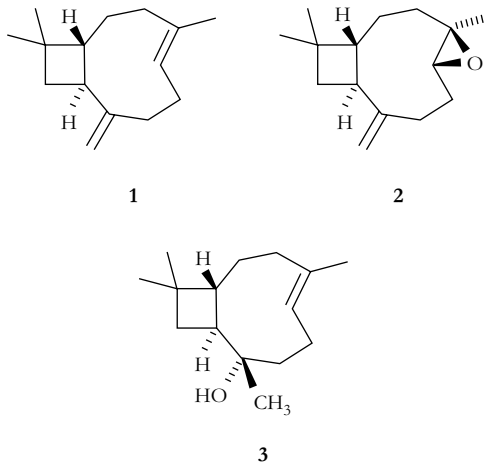


Fig. 610.3. Floral fragrance components of *Pescatoria coelestis*. (**1**) caryophyllene; (**2**) caryophyllene epoxide; (**3**) caryophyll-5-en-2α-ol.

Cultivation

Species can be grown in intermediate temperatures except for *P. pulvinaris* (Rchb.f.) Dressler and *P. wallisii*, which are from higher elevations and better suited to cooler temperatures. *Pescatoria* plants are usually large, and so they are best grown in baskets or in pots, watering them frequently and providing high humidity year-round. Large specimens should be disturbed as little as possible. **(FP)**

Taxonomic notes

Reichenbach adopted the spelling *Pescatoria* when he created the genus (using *Huntleya cerina* Lindl. & Paxton as the type) and in the second species he described (*P. triumphans* Rchb.f., in 1854); some consider this an intentional latinization of V. Pescatore's name. However, Reichenbach changed the spelling to '*Pescatorea*' in all subsequent publications (he described 12 additional species from 1869 to 1881), and other taxonomists have taken this as a sign that '*Pescatoria*' was an unintentional misspelling (e.g., Whitten *et al.* 2005). '*Pescatorea*' would have been a more conventional way of coining the generic name (e.g., Recommendation 60B of the *International Code of Botanical Nomenclature*). Both spellings have been used in the literature, but '*Pescatorea*' is far more common. We provisionally accept the spelling *Pescatoria*, but a proposal to the Committee on Spermatophyta could be submitted to adopt '*Pescatorea*' instead. (FP, MB)

Taxonomic literature

Dodson, C. H. (2003). *Native Ecuadorian orchids, vol. 4*. Oncidium-Restrepiopsis. Dodson Trust, Sarasota.

Dodson, C. H. and Frymire, G. P. (1961). Preliminary studies in the genus *Stanhopea*. *Annals of the Missouri Botanical Garden,* **48**, 137–72.

Fowlie, J. A. (1968). A key and annotated checklist to the genus *Pescatorea*. *Orchid Digest,* **32**, 86–91.

Fowlie, J. A. (1969). A key and annotated checklist to the genus *Bollea*. *Orchid Digest,* **33**, 100–3.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

611. PROMENAEA

Promenaea Lindl., *Edwards's Bot. Reg.*, **29,** Misc. 13 (1843).
Type species: *Promenaea lentiginosa* (Lindl.) Lindl.
(basionym: *Maxillaria lentiginosa* Lindl.)

Derivation of name

From the Greek *Promeneia*, a priestess at Dodona, mentioned by Herodotus in his chronicles. **(FP)**

Description (Plate 217; Fig. 611.1)

AQ: This looks awkward in the original form but I don't know the nomenclature well enough be certain of my revision. Previous chapters used one-two leaved, so maybe one-two-three leaved?

Epiphytic, caespitose, pseudobulbous *herbs*. *Roots* terete, produced from rhizome. *Pseudobulb* ovoid to ovoid-oblong, compressed, sometimes obscurely four-angled, sulcate, enclosed by 1–4 imbricating sheaths, upper ones foliaceous, apically 1–3 leaved. *Leaves* subplicate-venose, articulate, membranaceous, narrowly lanceolate to oblong-lanceolate, acute to acuminate, abaxially carinate, narrowed at base into a conduplicate petiole, grey-green to medium green, paler abaxially. *Inflorescences* lateral, 1–4 per shoot, 1-(rarely 2-)flowered, produced from axils of lower sheaths on mature pseudobulb, peduncle terete, suberect to arching, provided with one or two triangular-lanceolate, acute, conduplicate, clasping bracts; floral bract oblong-lanceolate, loose, membranaceous, shorter than ovary, pale greyish green. *Flowers* resupinate, large for plant, spreading, sepals and petals creamy white to pale greenish yellow to bright yellow, immaculate or variously spotted or transversely striped with red-purple to violet-brown, spots and blotches often concentrated on proximal half, labellum white to cream with yellow apex, greenish yellow to bright yellow, or solid black-purple, often heavily spotted with red purple, mostly in basal portion; disc and callus white to yellow, sometimes blotched with red-purple, column white to pale yellow, blotched with purple or solid dark purple toward base. *Dorsal sepal* free, erect to curved over column, narrowly oblong-lanceolate to ovate-lanceolate, concave, acute to acuminate, often apiculate. *Lateral sepals* narrowly oblong-lanceolate to ovate-lanceolate, obliquely inserted on column foot, concave, acute to acuminate, often apiculate, forming a mentum. *Petals* narrowly ovate to ovate, acute to acuminate. *Labellum* unguiculate, articulate to apex of column foot, elliptic-oblong to obovate, trilobed, lateral lobes oblong-subfalcate to linear-elliptic, rounded to subacute, erect, midlobe broadly elliptic to obovate-suborbicular, subacute to rounded or emarginate, concave to convex; disc provided with a prominent, trilobed, laminar crest, running from base to about the apex of side lobes. *Column* semiterete, clavate, arcuate, erect, with a foot, sometimes provided with indistinct stigmatic auricles; anther cap cucullate, elliptic-ovate, keeled, flattened, two-celled, pollinia four, in two pairs of different sizes, sessile on a triangular-elliptic to oblanceolate, hyaline viscidium; stigma transversely slit-like. **(FP)**

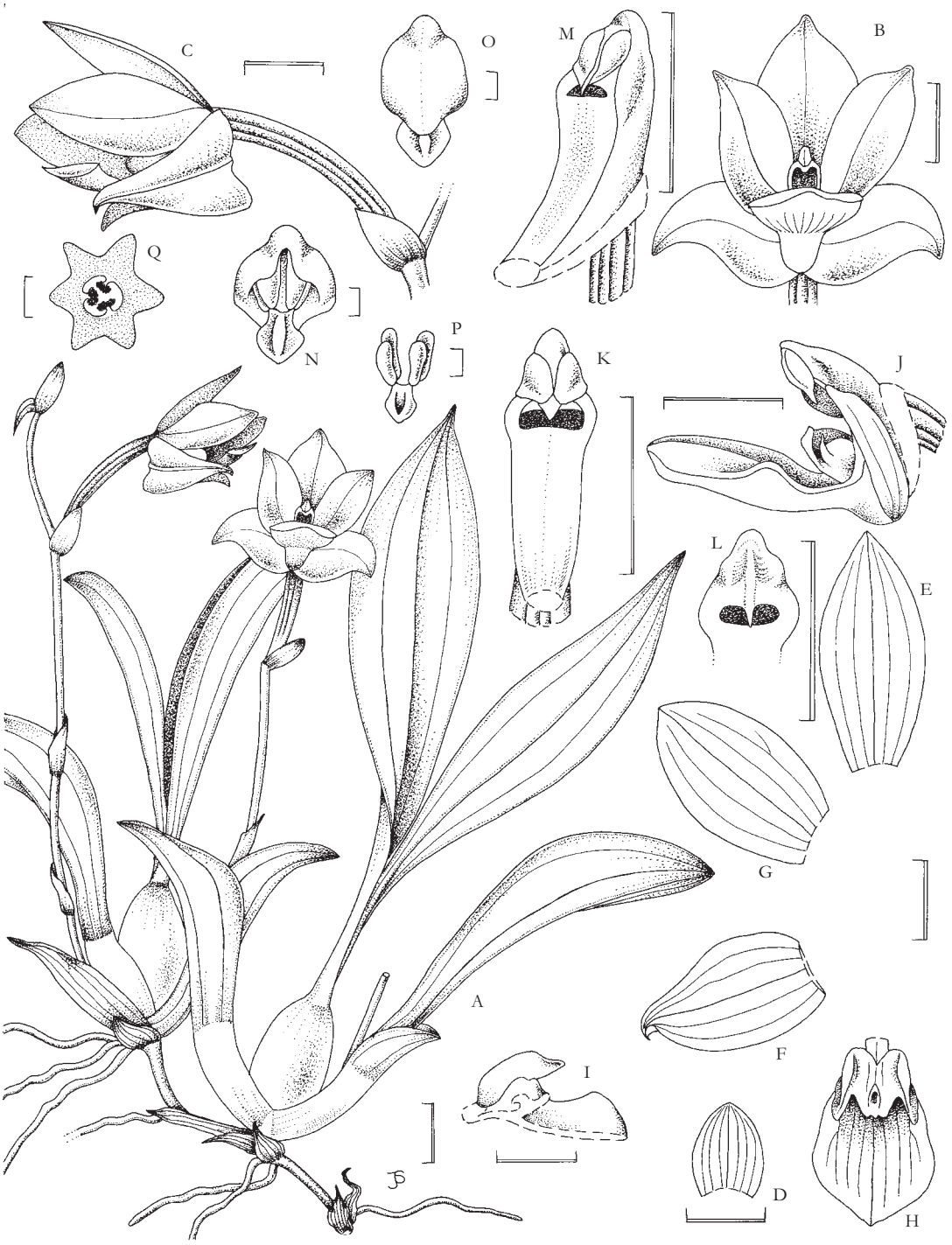


Fig. 611.1. *Promenaea xanthina* (Lindl.) Lindl. A. Habit, with inflorescences; B. Flower, front view; C. Flower, side view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum, longitudinal section; J. Column and labellum, side view; K. Column, ventral view; L. Column apex, anther cap removed; M. Column, side view; N. Anther cap with pollinia, ventral view; O. Anther cap, dorsal view; P. Pollinarium; Q. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *W. Ganev 1472* (K) and Kew Spirit Collection no. 13737.

Distribution (Fig. 611.2)

Promenaea comprises 20 species endemic to the tropical and subtropical regions of eastern Brazil (Bahia, Espírito Santo, Río de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul) in South America. **(FP)**

Palynology

Schill and Pfeiffer (1977) described pollen of *P. xanthina* (Lindl.) Lindl. as organized in convex tetrads with laevigate sculpturing (partly microfoveolate at the margins) and a rounded sexine. **(AP)**

Fig. 611.2. Distribution map of *Promenaea.*

Cytogenetics

Tanaka and Kamemoto (1984) reported a chromosome count of $2n = 46$ for the genus. (AP)

Phytochemistry

Lüning (1964, 1967) recorded that both *P. stapelioides* (Link & Otto) Lindl. and *P. xanthina* gave positive results on screening for alkaloids. **(NV, RG)**

Phylogenetics

Although sometimes considered a member of subtribe Gongorinae (i.e. Garay 1973; Pabst and Dungs 1977) on the basis of the inflorescence produced from the mature pseudobulb, most authors (Dressler 1993; Senghas and Gerlach 1993; Szlachetko 1995) agreed in placing *Promenaea* within core Zygopetalinae, together with *Galeottia, Neogardneria, Pabstia, Zygopetalum,* and *Zygosepalum*. Dressler (1993) noted that, with respect to the *Maxillaria* seed-type common in the *Zygopetalum* alliance, the *Chondrorhyncha* variant is also present in *Promenaea*, which does not fit the profile of the *Chondrorhyncha* alliance (i.e. lack of pseudobulbs and single-flowered inflorescences).

In the cladistic analysis based on combined *matK/trnL-F/*ITS rDNA data sets (Whitten *et al.* 2005), *Promenaea* was strongly supported, but its relationship to other members of the *Zygopetalum* clade were unclear. Pabst and Dungs (1977) proposed dividing *Promenaea* into three sections (*P.* sects. *Rollinsonii, Xanthina,* and *Stapelioides*) on the basis of features of the lip callus and flower colour. The sampling by Whitten *et al.* (2005) for the molecular study included two species in *P.* sect. *Xanthina* and one in *P.* sect. *Stapelioides*, and the results indicated that the sectional divisions proposed by Pabst and Dungs are not monophyletic. Among genera of the *Zygopetalum* clade, *Promenaea* can be recognized by single-flowered (rarely two-flowered) inflorescences; large, cymbiform bracts; relatively small flowers; lateral sepals connate with the column foot; and complex callus of the lip. **(FP)**

Ecology

The species of *Promenaea* are epiphytes in shady and humid locations in wet premontane forests, mostly along the Atlantic slopes of Serra do Mar in southeastern Brazil, at 1000–2000 m. Flowering occurs from September to May, with a peak from December through February. **(FP)**

Ecology

The species of *Promenaea* occur as epiphytes in shady and humid locations in wet premontane forests, mostly along the Atlantic slopes of Serra do Mar in southeastern Brazil, at 1000–2000 m. Flowering occurs from September to May, with a peak during the months of December through February. **(FP)**

Pollination

Pollinators are unknown. **(FP)**

Uses

The only use of the species is as cultivated ornamentals. **(FP)**

Cultivation

Plants of *Promenaea* are preferably grown in comparatively small pots or pans filled with a medium- or fine-grade compost that drains freely while retaining moisture around the slender roots. Repotting is recommended every two years. *Promenaea* species seem best suited to intermediate temperatures and shady conditions; if they receive too much light, the foliage quickly turns light grey. Plants should always be kept moist and never allowed to dry out completely, except for a short rest after flowering. Fertilizers may be applied—but at low concentrations (one fifth the recommended rate)—with every watering during active growth and every third day during the colder months after complete development of new pseudobulbs. Plants seem to be sensitive to a stagnant atmosphere, which favours rot of young growths, and require constant air movement for healthy growth. **(FP)**

Taxonomic literature

Dressler, R. L. (1993). *Phylogeny and classification of the orchid family*. Dioscorides Press, Portland, Oregon.

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Pabst, G. F. J. and Dungs, F. (1977). *Orchidaceae Brasilienses*, volume 2. Brücke-Verlag Schmersow, Hildesheim.
Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.
Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.
Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

612. STENIA

Stenia Lindl., *Edward's Bot. Reg.,* **23,** pl. 1991 (1837). Type species: *Stenia pallida* Lindl.
Stenopolen Raf., *Fl. Tellur.,* **4,** 49 (1838). Type species: not designated
Dodsonia Ackerman, *Selbyana,* **5,** 118 (1979). Type species: *Dodsonia saccata* (Garay) Ackerman (basionym: *Stenia saccata* Garay)

Derivation of name

From the Greek *stenos*, narrow, in reference to the long and narrow pollinia of the type species. **(FP)**

Description (Plate 218; Fig. 612.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, produced from rhizome. *Stem* abbreviated, enclosed by 3–5 imbricating sheaths, sometimes provided with scarious, hyaline margins, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, narrowly elliptic to broadly oblanceolate, acute to acuminate, abaxially carinate, narrowed at base into a distinct, conduplicate petiole, medium to dark green, abaxial surface usually paler. *Inflorescences* lateral, 1–3 per sympodium, single-flowered, produced from axils of lower sheaths, peduncle terete, pendent to suberect, basally provided with a tubular-imbricating, apically loose, papery bract; floral bract double, conduplicate, external one usually larger, widely ovate to suborbicular, acute, scarious, loose, longer than ovary, subopposite internal bractlet smaller, lanceolate, acute. *Flowers* spreading, sepals and petals white to creamy yellow, rarely spotted red-purple, labellum white to pale yellow, usually spotted with red-purple. *Dorsal sepal* free, lanceolate-elliptic to elliptic-suborbicular to obovate, obtuse-rounded to acute to abruptly acuminate, concave, abaxially carinate, sometimes reclinate over column. *Lateral sepals* obliquely and widely ovate to lanceolate-elliptic to oblong, obtuse-rounded, acute to subacuminate, often apiculate, concave toward base, abaxially carinate, rarely reflexed. *Petals* lanceolate-elliptic to suborbicular to widely oblanceolate, obtuse to acute to abruptly subacuminate, incurved to reflexed at apex. *Labellum* adnate to column foot, with a claw, trilobed, concave-saccate, subglobose at base, distal portion of blade often narrowed into an acuminate, sometimes deflexed tip, lateral lobes erect, not surrounding column, elliptic to broadly elliptic to falcate, rounded to serrate-lacerate, often closed toward apex, sometimes longer than midlobe, distal margins usually replicate, midlobe broadly triangular to narrowly triangular-ligulate, concave, acute, entire to denticulate, sometimes provided at base with two converging, transverse, papillose callosities; disc with a fleshy, broad, transverse, laminar callus consisting of 7–15 longitudinal, denticulate keels, from base to about middle of labellum. *Column* semiterete, straight or arcuate distally, provided with a distinct foot, dilated at apex into inconspicuous, rounded to triangular, obtuse stigmatic wings; anther cap cucullate, obovate to subrectangular, flattened, two-celled, pollinia four, in two pairs of different sizes, sublinear to pyriform, on a quadrate to narrowly linear-rectangular stipe and a cordiform, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 612.2)

Stenia is a genus of 21 species ranging from Trinidad throughout tropical South America from Venezuela to Brazil and from Colombia to Peru and Bolivia. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Stenia*. **(NV, RG)**

Phylogenetics

In his revision of the *Chondrorhyncha* alliance, Garay (1969) defined *Stenia* on the basis of the lip firmly adnate to and continuous with the column foot as well as the linear-oblong, unequal pollinia, the latter a character that is not consistent among the taxa of the genus. Ackerman (1979) created the genus *Dodsonia* for two species in the group, anomalous in that 1) conspicuous lateral lobes of the lip extend beyond the midlobe and 2) there are two converging, transverse, papillose callosities along the distal margin of the saccate base of the lip. However, in describing *Stenia glatzii*, Neudecker and Gerlach (2000) noted that this Ecuadorian species may be regarded as a connecting link between *Dodsonia* and *Stenia* and also suggested reducing *Dodsonia falcata* Ackerman to synonymy under *D. saccata*, making *Dodsonia* a monospecific genus. Comparison of the lip structure in the series *Stenia pallida* Lindl., *S. glatzii*, and *Dodsonia saccata* shows a clear tendency toward reduction of the central lobe and towards prolongation of the lateral lobes, with the resulting transformation of the lateral keels of the basal callus of *Stenia* into the lateral protuberances observed in the *Dodsonia* lip (Neudecker and Gerlach 2000).

These findings were confirmed by cladistic analyses of DNA sequence data reported by Whitten *et al.* (2005). In their reconstruction of the phylogenetic relationships of Zygopetalinae, *Stenia* including *Dodsonia* formed a strongly supported clade, which is strongly supported as sister to *Daiotyla*; the pair are then weakly supported as sister to *Benzingia* (*Huntleya* clade).

As presently understood, *Stenia* can be characterized by relatively small plants, pendent inflorescences, resupinate flowers with a rigid, deeply saccate and longitudinally folded lip, and prominent stipe of the pollinarium. Although *Stenia* is monophyletic in DNA sequence analyses, the pollinarium is variable within the genus (Whitten *et al.* 2005). The stipe is well developed and subquadrate in the type species and in most of the other taxa of

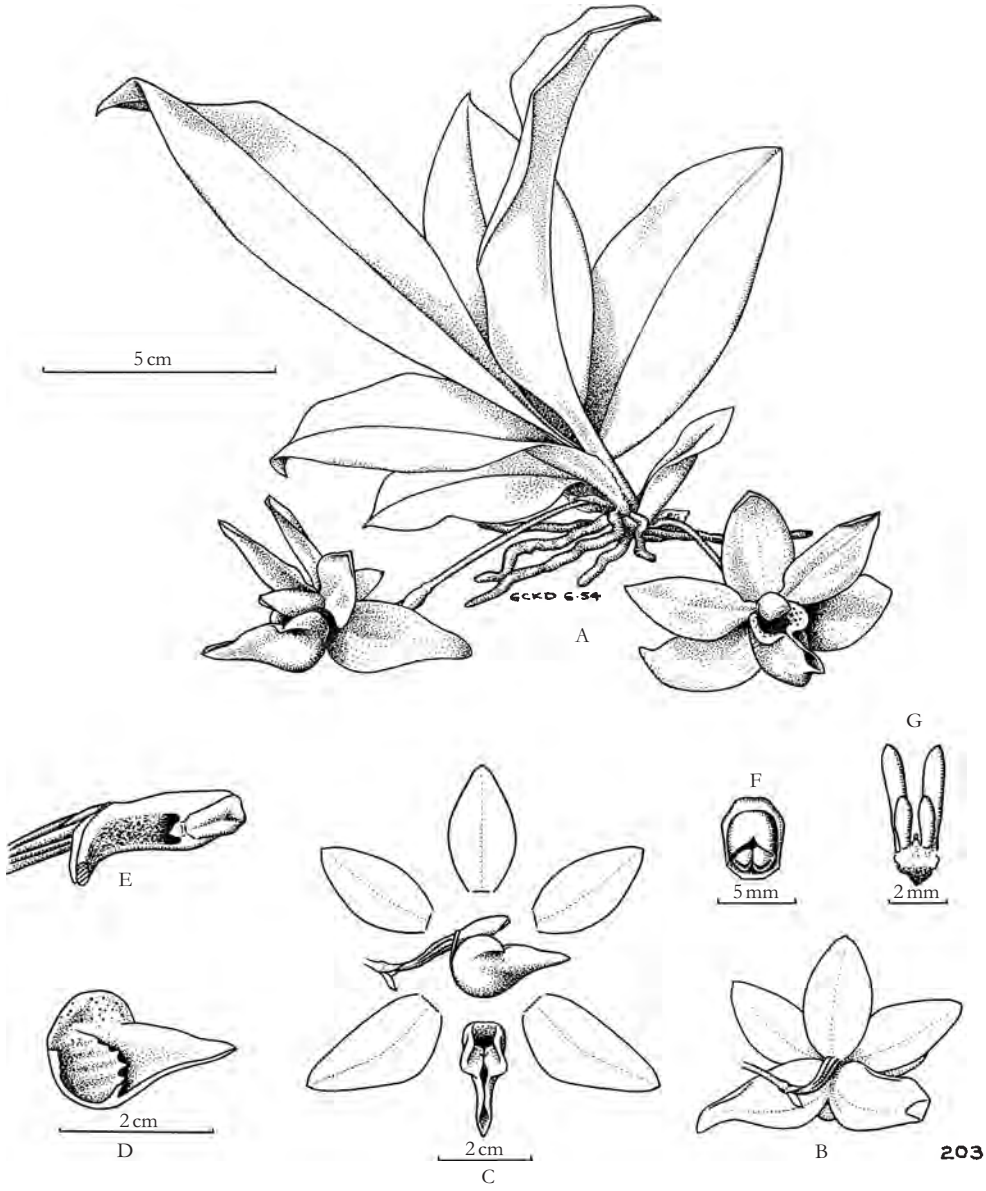


Fig. 612.1. *Stenia pallida* Lindl. A. Habit, with inflorescences; B. Flower, from behind; C. Perianth, dissected, with column and labellum in side view; D. Labellum (sectioned); E. Column, ventral view; F. Anther cap, ventral view; G. Pollinarium. Drawn by G.C.K. Dunsterville. Originally published in *Venezuelan Orchids Illustrated,* **1,** 422 (1959). Andre Deutsch, London. Reproduced with permission of the Oakes Ames Orchid Herbarium, Harvard University Herbaria.

the genus; however, the size of the stipe is considerably smaller in some species (i.e. *S. caudata* (Ackerman) Dodson & D.E.Benn.), and reduced to a ligulate to filiform strap, sometimes laterally fringed, in other species (i.e. *S. bismarckii* Dodson & D.E.Benn., *S. jarae* D.E.Benn., *S. pastorellii* D.E.Benn., and *S. stenioides* (Garay) Dodson). **(FP)**

Ecology

The species are epiphytes on shady trunks and mossy branches in tropical warm to montane cool, evergreen, wet forests at elevations of 500–2200 m. Flowering has been mostly recorded from December to August, but plants of *Stenia* probably flower sporadically throughout the year. **(FP)**

Pollination

Pollinators of *Stenia* are unknown, but they presumably are male euglossine bees (Dodson 2004). **(FP)**

Uses

There are no known uses, and species are rarely cultivated. **(FP)**

Cultivation

Because of their pendent inflorescences, plants of *Stenia* are best grown on slabs or in baskets with well-drained media, providing constant moisture to the relatively fleshy roots. They should be maintained in a shaded position with abundant watering

Fig. 612.2. Distribution map of *Stenia.*

throughout the year. Most species of *Stenia* can be grown under intermediate conditions, but *S. pallida* Lindl. prefers warmer temperatures, whereas *S. calceolaris* (Garay) Dodson & D.E.Benn., *S. guttata* Rchb.f., and *S. vasquezii* Dodson are best suited to cooler conditions. **(FP)**

Taxonomic literature

Ackerman, J. D. (1979). *Dodsonia*, a new Ecuadorian genus of the Zygopetalinae (Orchidaceae). *Selbyana*, **5**, 116–19.

Dodson, C. H. (2004). *Native Ecuadorian orchids, vol. 5*. Rodriguezia-Zygosepalum. Dodson Publishing, Sarasota.

Garay, L. A. (1969). El complejo *Chondrorhyncha*. *Orquideología*, **4**, 139–52.

Neudecker, T. and Gerlach, G. (2000). Rediscovery of the genus *Dodsonia*, and description of a new *Stenia* from Ecuador: *Stenia glatzii*. *Orquideología*, **21**, 256–21.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

613. STENOTYLA

Stenotyla Dressler, *Lankesteriana*, **5,** 96 (2005). Type species: *Stenotyla lendyana* (Rchb.f.) Dressler (basionym: *Chondrorhyncha lendyana* Rchb.f.)

Derivation of name

From the Greek *stenos*, narrow, and *tylo*, callus, alluding to shape of the lip callus. **(FP)**

Description (Plate 219; Fig. 613.1)

Epiphytic, caespitose *herbs*. *Roots* terete, produced from rhizome. *Pseudobulb* ovate-elliptic, laterally complanate, aphyllous or apically provided with a scale-like leaf, enclosed by 6–8 imbricating sheaths, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, narrowly elliptic to obovate, acute to acuminate, abaxially carinate, narrowed at base into a conduplicate petiole, pale to medium green. *Inflorescences* lateral, one or two per shoot, single-flowered, produced from axils of lower sheaths, peduncle terete, patent to erect, provided with two or three conduplicate, membranaceous bracts; floral bract double, conduplicate, shorter than ovary, the external one broadly ovate, obtuse to subacute, clasping, the subopposite internal bractlet ligulate. *Flowers* resupinate, sepals and petals white to yellowish cream, labellum white to cream, blotched at base with yellow or purple-red or striped with chestnut brown or dark purple, callus white or yellow. *Dorsal sepal* free, lanceolate-elliptic to elliptic, acute to subacuminate, porrect. *Lateral sepals* lanceolate-elliptic to elliptic, acute, sometimes falcate, spreading to reflex, sometimes becoming suberect, inrolled-folded toward base. *Petals* lanceolate-elliptic to narrowly obovate, acute to obtuse-rounded, usually revolute at apex. *Labellum* articulate with column foot, entire to obscurely trilobed, elliptic to obovate, rarely cymbiform, base cordate to form a chin, apex truncate to emarginate-retuse, deflexed, distal margins undulate, proximal margins erect, flanking column; callus laminar, in proximal third of blade, apically 2–4-toothed, sometimes provided with indistinct, low lateral keels. *Column* straight, with a distinct foot, dilated at apex, ventral surface plane; anther cap cucullate, elliptic-obovate to narrowly ovate, flattened, two-celled, pollinia four, in two pairs of different sizes, on an obtriangular-elliptic stipe scarcely distinct from ventral, ligulate, apically truncate, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 613.2)

Stenotyla is a genus of five, possibly six, species collectively ranging from southern Mexico to western Panama (Central America). **(FP)**

Phytochemistry

A detailed analysis of the floral fragrance of *S. lendyana* (cited as *Chondrorhyncha lendyana*) revealed that the major component is 3,5-dimethoxytoluene (Kaiser 1993). The characteristic scent, said to be reminiscent of an insect's defensive secretions with a hint of yeast, is due mainly to two isomers of 2,4-decadienal together with (*Z*)-4-decenol (see also *Pescatoria*; Kaiser 1993). **(NV, RG)**

Phylogenetics

The five named species referable to *Stenotyla* (one of which was described twice) were previously assigned to *Chondrorhyncha* and

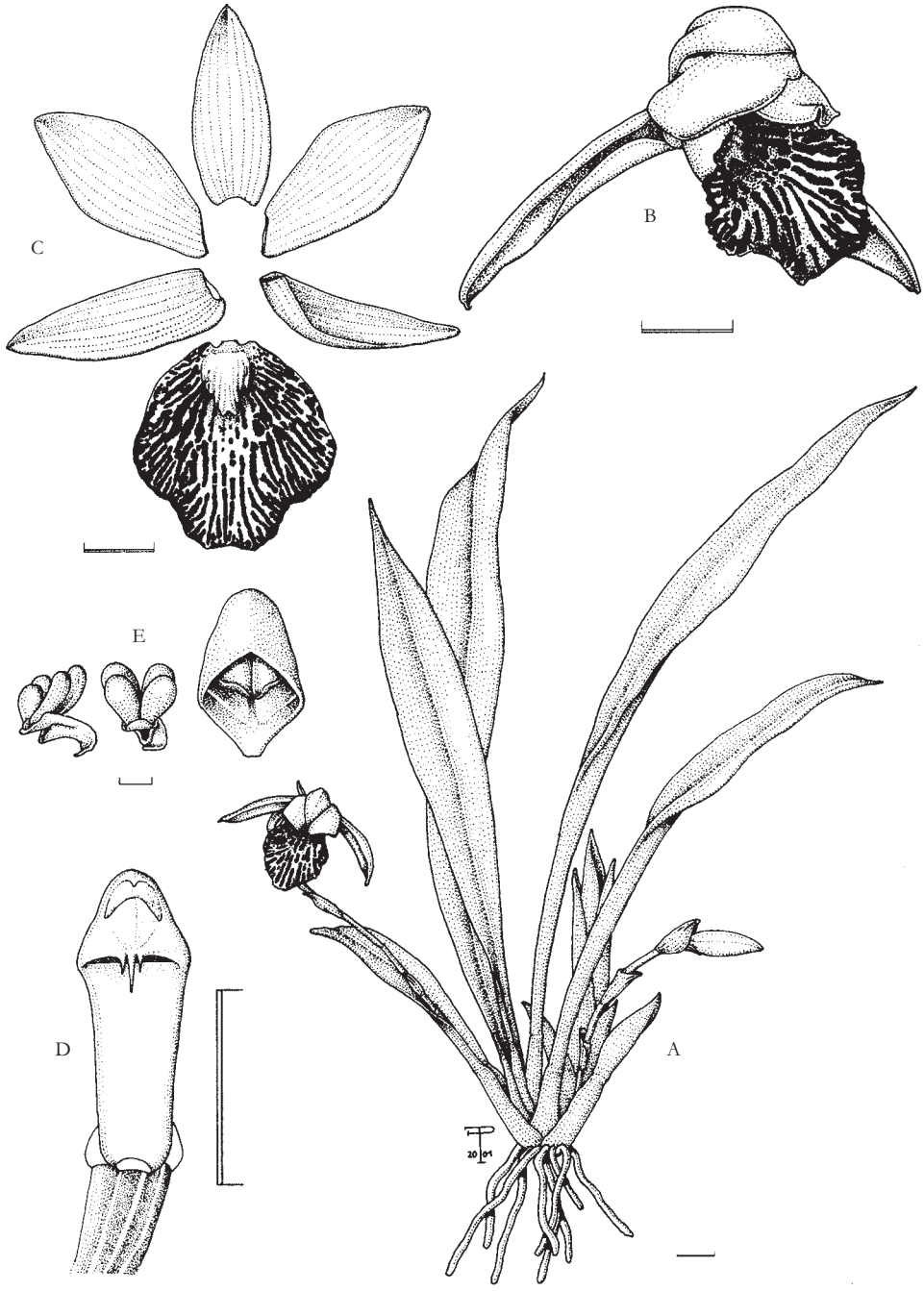


Fig. 613.1. *Stenotyla picta* (Rchb.f.) Dressler. A. Habit, with inflorescences; B. Flower; C. Perianth, dissected; D. Column, ventral view; E. Pollinarium (two views) and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin et al. 4072* (Lankester Botanical Garden Spirit Collection).

Warczewiczella, but they do not fit either group well. Vegetatively, *Stenotyla* resembles *Chondrorhyncha*, but all species of the genus have distinct, small pseudobulbs completely hidden by the leaf-sheaths, and they may be distinguished among other Zygopetalinae of the *Huntleya* clade by the narrow, laminar, basal callus and short chin at the base of the lip. The distinctiveness of the '*Chondrorhyncha*' species allied to *C. lendyana* was first noted by Dressler (2000), who keyed out the group on the basis of the column without wings and narrow, toothed callus. Phylogenetic analyses based on DNA sequences (Whitten *et al.* 2005) unequivocally placed *Stenotyla* species in a clade with strong bootstrap support, which has moderate support as sister to *Cochleanthes* (*Huntleya* clade). **(FP)**

Ecology

The species are epiphytes in sites in premontane to submontane, evergreen, wet and cloud forests at elevations of 1100–2100 m. Flowering mostly occurs from May to October, roughly corresponding to the rainy season, but once the new shoot matures flowers may be produced at any time of the year. **(FP)**

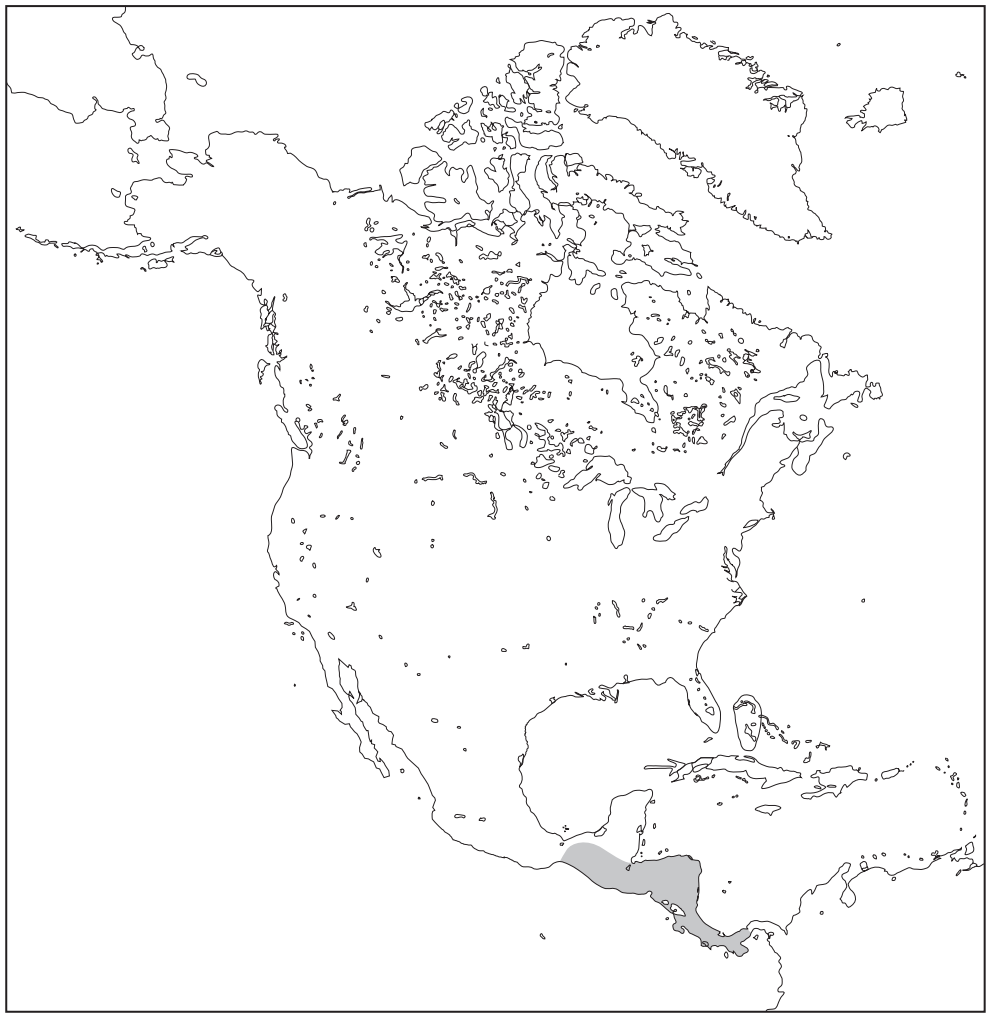


Fig. 613.2. Distribution map of *Stenotyla.*

Pollination

Pollinators of *Stenotyla* are unknown, but the shape of the pollinarium, with its stipe and viscidium that curl immediately after removal (F. Pupulin, personal observation), indicate that species of this group may be pollinated by euglossine bees in a way similar to that for *Kefersteinia* or *Chaubardiella*. **(FP)**

Uses

No uses are known, and species are rare in cultivation. **(FP)**

Cultivation

Plants of *Stenotyla* can be grown in shade in intermediate to cool temperatures, maintaining high levels of humidity year-round. All species should be grown in pots with an open compost to retain constant moisture around the roots. Watering should be frequent throughout the year, and the medium should never be allowed to dry out completely. **(FP)**

Taxonomic literature

Dressler, R. L. (2000). Precursor to a revision of the *Chondrorhyncha* complex. *Orquideología,* **21**, 233–47.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

614. WARCZEWICZELLA

Warczewiczella Rchb.f., *Bot. Zeitung (Berlin),* **10,** 636 (1852). Type species: *Warczewiczella discolor* (Lindl.) Rchb.f. (basionym: *Warrea discolor* Lindl.)

Derivation of name

The name honours the Polish explorer and erratic orchid collector Joseph von Rawicz Warszewicz (1812–1866), who corresponded with Reichenbach and discovered the type species of the genus. **(FP)**

Description (Plate 220; Fig. 614.1)

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, flexuous, produced from rhizome. *Stem* completely enclosed by 4–7 imbricating sheaths, upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, lanceolate to elliptic or oblanceolate, acute to acuminate, abaxially carinate, narrowed at base into a conduplicate petiole, medium to dark green. *Inflorescences* lateral, stout, one or two per shoot, single-flowered, produced from axils of lower sheaths, peduncle terete, erect to pendent, provided with one or two basal, tubular-infundibuliform, membranaceous to papery bracts; floral bract double, conduplicate, shorter than or equaling the ovary, the external one lanceolate to broadly ovate, obtuse to acute, clasping, the subopposite internal bractlet narrowly ligulate. *Flowers* resupinate, mostly scented, sepals white to yellowish cream or pale green, rarely suffused with pale violet, petals white to yellowish cream or pale green, sometimes flushed violet or with a large violet blotch toward apex, labellum white to cream, blotched at base with purple or

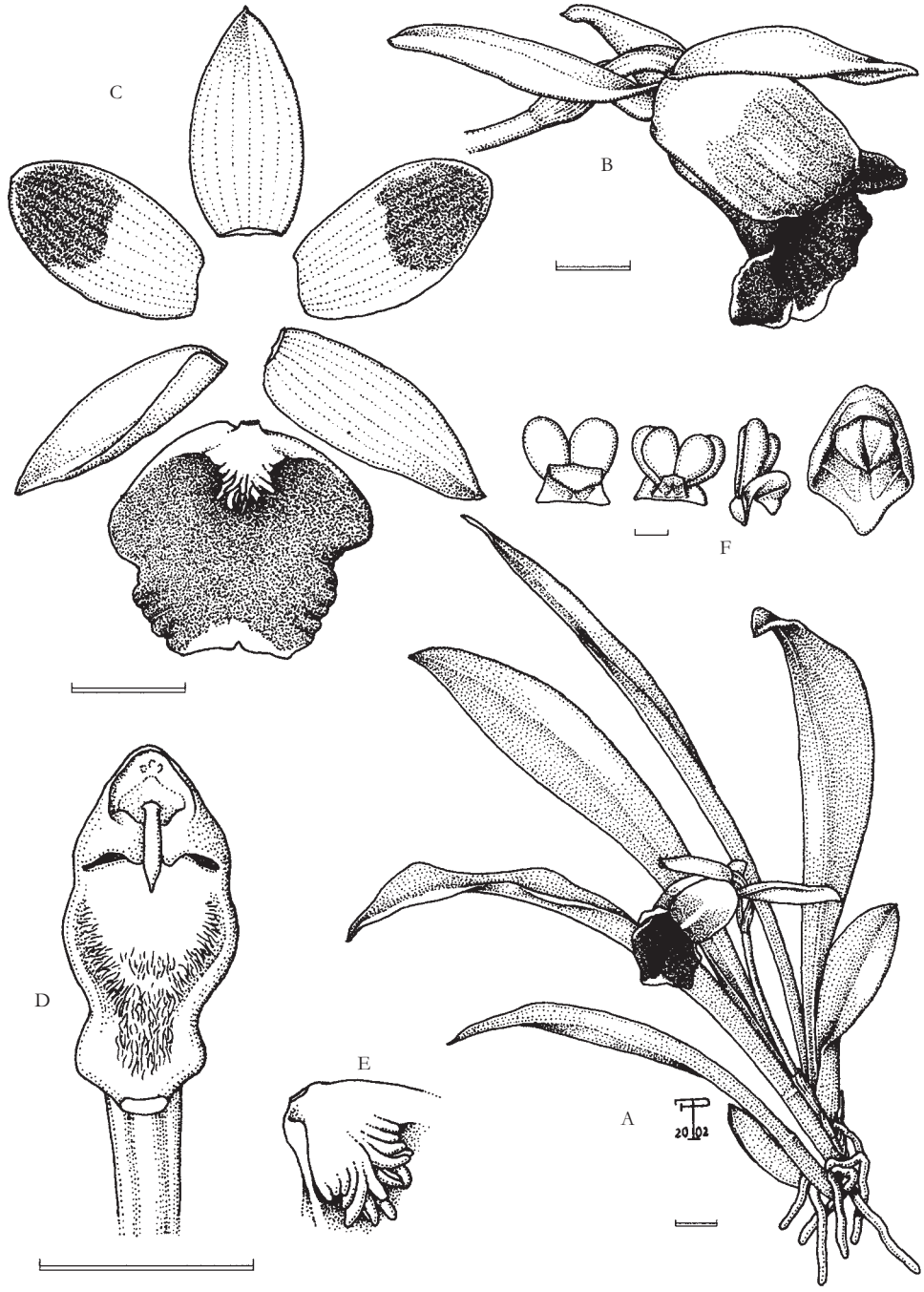


Fig. 614.1. *Warczewiczella discolor* (Rchb.f.) Dressler. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column, ventral view; E. Callus; F. Pollinarium (dorsal, front, and side views) and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 507* (Lankester Botanical Garden Spirit Collection).

yellow or striped with red to purple-violet or bluish violet, sometimes purple or violet toward the edge or flushed purple along midvein, callus white or yellow variously spotted or veined with purple. *Dorsal sepal* free, lanceolate-elliptic to elliptic or ovate, acute to subacuminate, mostly arched-reflexed. *Lateral sepals* lanceolate-elliptic to elliptic or ovate, acute, mostly abruptly reflexed, rarely spreading, inrolled-folded toward base. *Petals* lanceolate to elliptic, acute to obtuse-rounded, usually revolute at apex. *Labellum* articulate with column foot, unguiculate, entire to trilobed, ovate to broadly elliptic, base rounded to cordate, apex rounded to retuse or emarginate, deflexed, distal margins undulate, lateral lobes and proximal margins erect, enfolding column; disc with an hemicircular, multiseriate callus, composed of many distinct, radiating keels, sometimes of variable length, free at apex and laterally. *Column* straight or arched, with a distinct foot, dilated in central portion or toward apex, provided with rounded stigmatic wings, ventral surface plane, sometimes covered with hairs; anther cap cucullate, elliptic-obovate, flattened, two-celled, pollinia four, in two pairs of different sizes, on a wide, shield-shaped, ligular to obovate-elliptic or obpeltate stipe, indistinct from ventral, hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 614.2)

Warczewiczella comprises 10 species ranging from Honduras (Central America) to southern Brazil, Bolivia and Peru (South America), with the highest diversity along the Amazonian slopes of the Colombian Andes. **(FP)**

Palynology

Schill and Pfeiffer (1977) described pollen tetrads of *W. discolor* (as *Cochleanthes discolor*) as even to weakly convex with a laevigate exine and rounded sexine. Zavada (1990) noted for the same species (also as *Cochleanthes discolor*) that pollen grains peripheral in the pollinium have a tectate-granular exine, the granular layer resting on a bilayered intine; however, pollen grains on the interior lack an exine and are surrounded only by the bilayered intine. **(AP)**

Cytogenetics

A somatic number for *W. discolor* was reported as $2n = ca.$ 48 (Chardard 1963). **(FP)**

Fig. 614.2. Distribution map of *Warczewiczella.*

Phytochemistry

Acid-hydrolyzed extracts of leaves of *W. wendlandii* Hort. ex Nash contain *para*-coumaric, caffeic and ferulic acids, together with the flavonol kaempferol (Bate-Smith 1968). Alkaloids are present in *W. discolor* (Lindl.) Rchb.f. (cited as *Chondrorhyncha discolor* (Lindl.) P.H.Allen) and *W. wailesiana* (Lindl.) R.E.Schult. & Garay, according to surveys by Lüning (1964, 1967).

The floral fragrance of *W. discolor* (cited as *Cochleanthes discolor*) is dominated by sesquiterpenes, notably germacrene A (77.0%) and a ketone derivative tentatively identified as germacra-1(10),11-dien-5-one (Kaiser 1993). In contrast, that of *W. marginata* Rchb.f. (cited as *Cochleanthes marginata* (Rchb.f.) R.E.Schult. & Garay) comprises mainly methyl-(*E*)-cinnamate. Gerlach and Schill (1991) recorded that the floral fragrance of *W. aromatica* Rchb.f. & Warsz. (cited as *Cochleanthes amazonica* (Rchb.f. & Warsz.) R.E.Schult. & Garay) contains benzyl acetate and 1,4-dimethoxybenzene as major constituents together with terpinolene (tentative identification only). **(NV, RG)**

Phylogenetics

The original generic description of *Warczewiczella* by Reichenbach clearly stated the characteristic shape of the callus that distinguishes it from closely related taxa in the *Chondrorhyncha* complex. Although Schultes and Garay (1954) lumped the species of *Warczewiczella* with *Cochleanthes*, Fowlie (1969) was emphatic in separating the two genera on the basis of the different callus and column morphology.

Combined molecular analyses (Whitten *et al.* 2005) strongly supported separation of *Warczewiczella* from *Cochleanthes*. With the exception of *W. wailesiana* (on a long branch weakly supported as sister to the other species of *Warczewiczella* but morphologically similar to the other taxa of the clade), *Warczewiczella* forms a well-supported clade. It is part of a weakly supported clade containing *Pescatoria*, *Chaubardiella*, *Ixyophora,* and *Aetheorhyncha* and only distantly related to the clade containing *Cochleanthes* and *Stenotyla* (all *Huntleya* clade). Morphologically, the genus is characterized by relatively large plants and flowers, the base of the lip enfolding the column, and a basal, thick callus, free apically and laterally and composed of many ridges. **(FP)**

Ecology

Species of *Warczewiczella* are epiphytes or rarely terrestrials in open to dark shade, mostly on large branches covered with dense layers of mosses, in submontane wet forests and cloud forests. Most species grow in temperate regions of mid-elevation (700–1300 m), but *W. lipscombiae* (Rolfe) Fowlie grows near sea level, and *W. discolor* extends to over 2500 m. Flowering mostly occurs during the rainy season, but flowers are also sporadically produced following development of new shoots. **(FP)**

Pollination

In most species of *Warczewiczella,* lateral sepals are swept back and revolute to form a false spur, and the lip has a notch on either side of its base, allowing entrance to the tubular base of the sepals. These false nectaries, which mimic the floral arrangement of species of lianas in Bignoniaceae (Ackerman 1983), deceive euglossine bee pollinators. **(FP)**

Uses

Apart from cultivation in specialist collections, there are no known uses. **(FP)**

Cultivation

Most of the species of *Warczewiczella* could be grown under intermediate conditions and slightly warmer temperatures. *Warczewiczella lipscombiae* has been collected near sea level and could be maintained in the warm greenhouse. On the other hand, *W. discolor*, *W. marginata*, *W. palatina* (Senghas) Dressler, and *W. timbiensis* Ortiz occur in montane forests at higher elevations and are better suited to a cooler environment. All species thrive when protected from the direct rays of the sun, and most tolerate deep shade. Under these conditions, high humidity and good air circulation are essential to maintain the plants in healthy condition. Although they can be satisfactorily grown on large plaques, their extensive root system makes it advisable to cultivate plants of *Warczewiczella* in pots. When repotting, care must be taken not to damage roots. Watering should be abundant during development of new growth but reduced after the flowering season; however, even during the rest period, the medium should never be allowed to dry out completely. **(FP)**

Taxonomic literature

Fowlie, J. A. (1969). An annotated checklist of the genus *Warscewiczella*. *Orchid Digest* **33**, 224–31.

Schultes, R. E. and Garay, L. A. (1954). On the validity of the generic name *Cochleanthes* Raf. *Botanical Museum Leaflets, Harvard University*, **18**, 321–7.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

615. WARREA

Warrea Lindl., *Edwards's Bot. Reg.,* **29,** Misc. 14 (1843). Type species: *Warrea tricolor* Lindl. (= *Warrea warreana* (Lodd. ex Lindl.) C.Schweinf.)

Derivation of name

The name honours the explorer and collector Frederick Warre, who discovered the type species of the genus during his expedition to Brazil (c. 1820). **(FP)**

Description (Plate 221; Fig. 615.1)

Terrestrial, rarely epiphytic, caespitose, pseudobulbous *herbs*. *Roots* terete, produced along rhizome at base of pseudobulb. *Pseudobulb* homoblastic, fusiform-cylindric to elliptic-ovoid, usually cryptic

Fig. 615.1. *Warrea costaricensis* Schltr. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column, ventral view; E. Anther cap and pollinarium (side and ventral views). Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin 2952* (USJ and Lankester Botanical Garden Spirit Collection).

among bases of foliaceous sheaths, three-four-leaved, oldest ones exposed and covered with papery, lacerate, veined sheaths. *Leaves* plicate, articulate, membranaceous, linear-lanceolate to elliptic, acute to acuminate, narrowed at base into a conduplicate petiole. *Inflorescences* lateral, a 4–14-flowered raceme emerging from axils of lower sheaths from immature, developing pseudobulbs, peduncle terete, erect, provided with 3–6 ovate-triangular, acute, scarious, conduplicate, clasping bracts; floral bracts triangular-lanceolate, acute, conduplicate, membranaceous-scarious, shorter than ovary. *Flowers* resupinate, usually nodding, subglobose, sepals white to pale orange-yellow on inner surface, sometimes blotched with rose toward base, abaxially cream to orange, flushed purple, petals white to yellowish cream, often flecked with rose or pale purple, labellum white to yellow, with an orange to purple basal blotch or blotch restricted to disc, or flushed rose-purple and striped with purple at apex, the callus white to yellow, apically purple or solid purple. *Dorsal sepal* free, elliptic, acute, concave, usually reclinate over column. *Lateral sepals* widely elliptic, obtuse, sometimes apiculate, abaxially carinate, concave, inner margin replicate-folded toward base, forming a chin with column foot. *Petals* elliptic to lanceolate-elliptic, widely subacute to acute, porrect, incurved. *Labellum* articulate with column foot, elliptic-suborbicular, sometimes trilobed, cup-shaped in natural position, base cuneate and contracted into an indistinct claw, apex rounded-truncate, usually emarginate, basal lobes erect, clasping column, distal lobe often reflexed, with revolute, undulate-crisped margins; disc with a central, high, tuberculate, fleshy keel, extending from base to near half of lip. *Column* semiterete, curved, with a foot and inconspicuous stigmatic wings; anther cap cucullate, obovate, flattened, two-celled, pollinia four, in two subequal pairs, on a trapezoid or narrowly triangular stipe and a lanceolate-elliptic to triangular, hyaline viscidium; stigma transversely elliptic-rounded. **(FP)**

Distribution (Fig. 615.2)

Warrea consists of four or five species native from Mexico (Central America) to Venezuela, Brazil, Peru and Argentina (South America). **(FP)**

Cytogenetics

Aoyama (1989) reported a chromosome count of $2n = 52$. **(AP)**

Phytochemistry

Lüning (1964) noted that *W. tricolor* gave a positive result in a survey of alkaloid content in Orchidaceae. **(NV, RG)**

Phylogenetics

When Lindley described *Warrea* in 1843, he characterized the genus by subglobose flowers; entire lip provided with fleshy keels; pollinarium with four pollinia in two pairs; short, linear stipe; and a triangular viscidium. Because of the broad original circumscription, species currently assigned to such diverse genera as *Koellensteinia*, *Warreella,* and *Warczewiczella* were subsequently described as members of *Warrea*.

As presently understood, the genus can be easily recognized by the large plants with homoblastic pseudobulbs surrounded by bases of membranaceous, plicate leaves; lateral, erect inflorescences; large, subglobose and usually pendent flowers; and massive, basal callus of the lip. Szlachetko (1995) selected *Warrea* as the type of his new subtribe Warreinae, created to group those taxa having homoblastic pseudobulbs, plicate leaves, and auriculate column, including *Otostylis*, *Warreella,* and *Warreopsis*. In the cladistic analyses of DNA sequences carried out by Whitten *et al.* (2005), *Warrea* forms a moderately to well-supported clade together with *Warreopsis*, but their relationships to the other members of the *Zygopetalum* clade is unclear. **(FP)**

Ecology

Species of *Warrea* occur as terrestrials (rarely epiphytes) in decaying leaf matter, mostly in the shaded understorey of dense, wet forests and occasionally on drier slopes and in more exposed conditions. Records of *Warrea* distribution indicate that plants are mostly restricted to premontane forests, occasionally ranging

Fig. 615.2. Distribution map of *Warrea.*

to the tropical belt of moist to wet forests at 600–1500 m. In South America, flowering mostly occurs from February to July, but plants from the Mesoamerican region flower in September–October. **(FP)**

Pollination

Pollinators are unknown but are presumed to be male euglossine bees. **(FP)**

Uses

There are no known uses, and the species are rarely cultivated. **(FP)**

Cultivation

In cultivation, plants of *Warrea* should be provided with an intermediate to slightly warm climate and shaded conditions without direct exposure to the sun. Given the massive size of adult specimens and their strong, extensive root system, *Warrea* species are best grown in deep pots with excellent drainage and an open, moisture-retaining compost. Water should be supplied in abundance throughout the year. **(FP)**

Taxonomic literature

Pupulin, F. (2004). Zygopetalinae poco conocidas. El género *Warrea* Lindl. *Epidendrum,* **24,** 3–7.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.

Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

616. WARREELLA

Warreella Schltr., *Orchideen,* 424 (1914). Type species: *Warreella cyanea* (Lindl.) Schltr. (basionym: *Warrea cyanea* Lindl.)

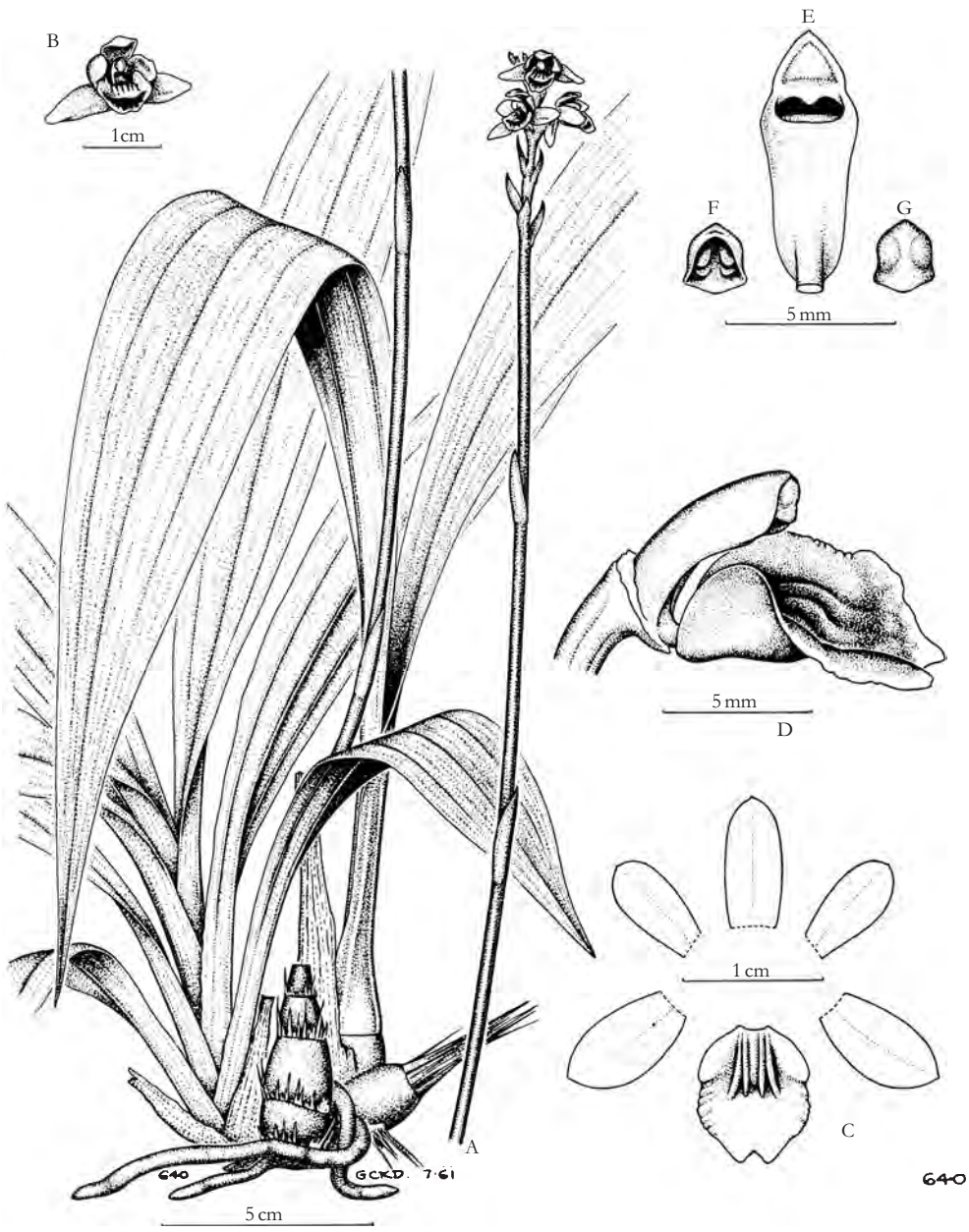


Fig. 616.1. *Warreella cyanea* (Lindl.) Schltr. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column and labellum, side view; E. Column, ventral view; F. Anther cap, ventral view; G. Anther cap, dorsal view. Drawn by G.C.K. Dunsterville, drawing donated to Royal Botanic Gardens, Kew. A similar illustration appears in *Venezuelan Orchids Illustrated,* **3**, 328 (1965). Andre Deutsch, London.

Derivation of name

From the generic name *Warrea* (Orchidaceae) and the Latin diminutive *–ella*, referring to similarity of the type species to *Warrea*, under which it was originally described. **(FP)**

Description (Plate 222; Fig. 616.1)

Terrestrial, caespitose, pseudobulbous *herbs*. *Roots* terete, produced along rhizome at base of pseudobulbs. *Pseudobulb* homoblastic, ovoid, cryptic among bases of foliaceous sheaths, three-four-leaved at nodes, when old fully exposed and covered with lacerate remains of sheaths. *Leaves* plicate, articulate, membranaceous, lanceolate to narrowly elliptic, acuminate, tapering at base into a conduplicate petiole. *Inflorescences* lateral, a successively flowered (3–7 flowers simultaneously open) raceme emerging from axils of lower sheaths of immature, developing pseudobulbs, peduncle terete, erect, provided with three or four lanceolate-elliptic, acute, clasping bracts; floral bracts narrowly triangular-lanceolate, acute, membranaceous, shorter than ovary. *Flowers* resupinate, spreading, inner surface of sepals and petals white to pink to pale violet (blue when newly opened), petals sometimes flushed with violet along midvein, sepals white or reddish brown abaxially, labellum white, flushed violet on inner surface toward solidly violet apex, lower surface much paler, callus white. *Dorsal sepal* free, elliptic-lanceolate to oblanceolate, acute to obtuse, reclinate over column. *Lateral sepals* widely elliptic,

Fig. 616.2. Distribution map of *Warreella.*

obtuse to rounded, abaxially carinate, concave, inner margin replicate-folded toward base. *Petals* oblanceolate to widely elliptic-obovate, subacute to obtuse-rounded. *Labellum* sessile, articulate with column foot, ovate to suborbicular, sometimes obscurely trilobed, apex obtuse-truncate, emarginate, basal margins erect, distal lobe reflexed, with undulate margins; disc with five longitudinal, subradiating, rounded ridges, extending from base to near half of lip. *Column* semiterete, curved, with a foot, dilated at apex; anther cap cucullate, obpeltate, flattened, two-celled, pollinia four, in two pairs of different sizes, on a triangular stipe and a triangular, curved, brownish viscidium; stigma transverse, narrowly elliptic. **(FP)**

Distribution (Fig. 616.2)

Warreella comprises two or three species native to northern South America, centred in Colombia and ranging to Venezuela. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Warreella*. **(NV, RG)**

Phylogenetics

The close relationship of *Warreella* with *Warrea* was originally suggested by Schlechter, but its position among those genera of Zygopetalinae with homoblastic pseudobulbs was not immediately understood. *Otostylis alba* (Ridl.) Summerh., once assigned to *Warreella*, was moved in and out of *Aganisia*, *Otostylis,* and *Zygopetalum*. In his introduction to the *Zygopetalum* alliance, Garay (1973) assigned *Warreella* to the *Warrea* complex on the basis of its pseudobulbs composed of many internodes. Szlachetko (1995) included *Warreella* in his subtribe Warreinae, created to group those taxa provided with homoblastic pseudobulbs, plicate leaves, and auriculate column. Among genera of this complex, *Warreella* can be distinguished by relatively large plants with small flowers, column with a short foot, and callus of the disc composed of many rounded ridges. To date, no material of *Warreella* has been available for molecular analysis, but on the basis of its vegetative architecture and floral characters, the genus is likely a close relative of the other taxa that form the sister group to the remainder of Zygopetalinae, i.e. *Koellensteinia*, *Otostylis*, *Paradisanthus*, *Warrea,* and *Warreopsis*. **(FP)**

Ecology

Species of *Warreella* are terrestrials in decaying leaf matter, mostly along well-drained slopes, in the open shade of premontane and montane wet forests, at 1600–2400 m. Flowering has been recorded from April to September, with a flowering peak in early fall. **(FP)**

Pollination

Pollination biology of the genus is unknown. **(FP)**

Uses

There are no known uses for the species. They are rare in cultivation. **(FP)**

Cultivation

Plants of *Warreella* are relatively frequent in the Colombian and Venezuelan Andes, and according to records of their native habitats, they should be grown in intermediate to cool conditions. Cultivated specimens can be maintained in pots with a coarse, moisture-retaining compost, diffuse light, and high levels of humidity throughout the year. To stimulate flowering, watering should be reduced after new leaves are completely developed. **(FP)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.

617. WARREOPSIS

Warreopsis Garay, *Orquideología*, **8**, 51 (1973). Type species: *Warreopsis pardina* (Rchb.f.) Garay (basionym: *Zygopetalum pardinum* Rchb.f.)

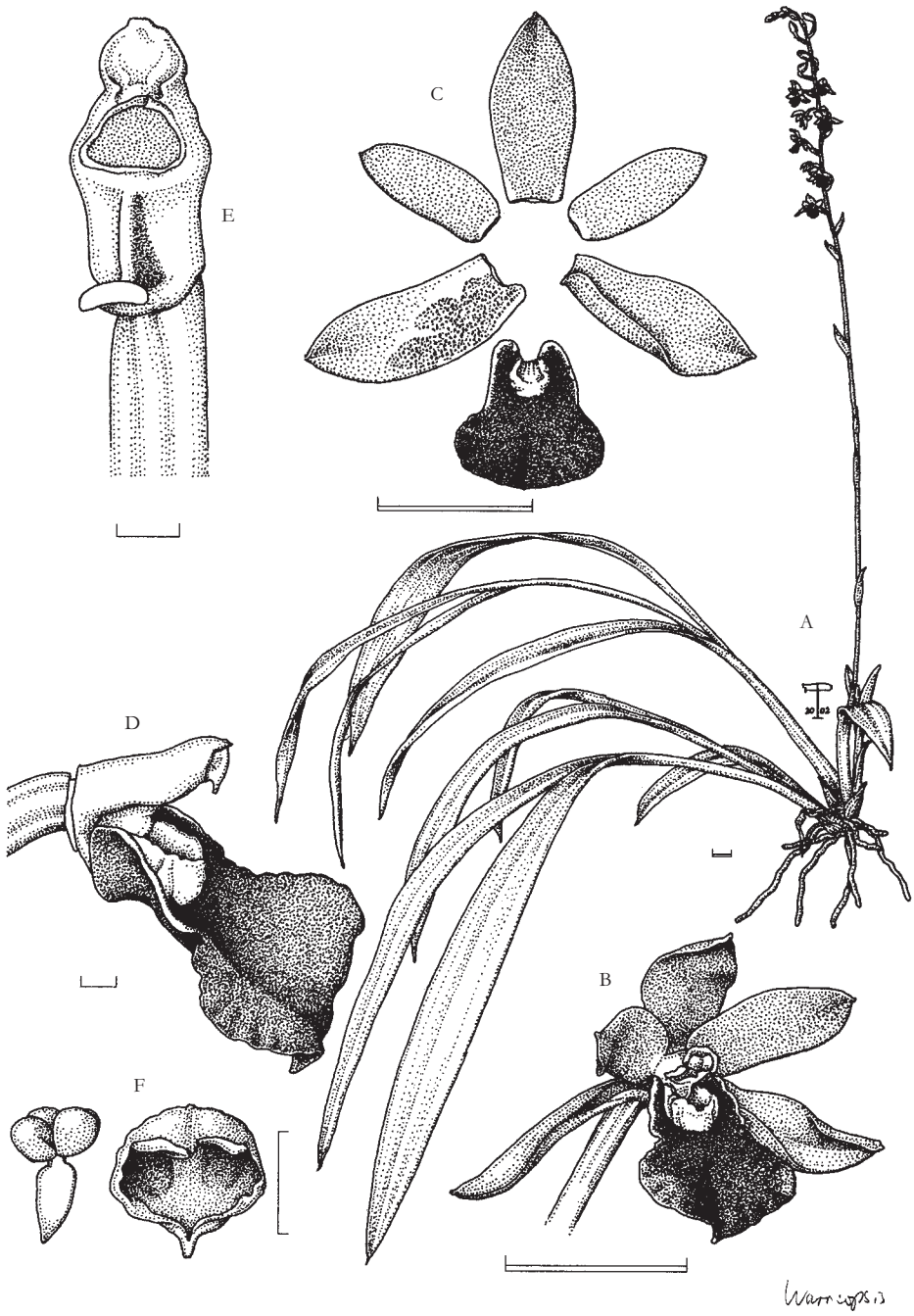


Fig. 617.1. *Warreopsis parviflora* (L.O.Williams) Garay. A. Habit, with inflorescence; B. Flower; C. Perianth, dissected; D. Column and labellum, side view; E. Column, ventral view; F. Pollinarium and anther cap. Single bar = 1 mm, double bar = 1 cm. Drawn by Franco Pupulin from *F. Pupulin et al. 3580* (USJ).

Derivation of name

From the orchid genus *Warrea*, and the Greek *opsis*, likeness, in allusion to the similarity of *Warreopsis* to *Warrea*. **(FP)**

Description (Plate 223; Fig. 617.1)

Terrestrial (rarely epiphytic), caespitose to repent, pseudobulbous *herbs*. *Roots* terete, produced along rhizome at base of pseudobulbs. *Pseudobulb* homoblastic, ellipsoid to subcylindric, cryptic among bases of sheaths and becoming increasingly foliaceous toward apex, 3–5-leaved at nodes, 1-leaved apically. *Leaves* articulate, membranaceous, abaxially plicate, lanceolate to narrowly elliptic, acuminate, narrowed at base into a conduplicate petiole. *Inflorescences* lateral, a successively flowered (3–8 flowers simultaneously open) raceme emerging from axils of lower sheaths of mature shoot, peduncle terete, erect, subequal to longer than leaves, provided with four or five lanceolate-elliptic, acute, clasping to loose bracts; floral bracts narrowly triangular-lanceolate, acute, membranaceous, subequal to ovary. *Flowers* resupinate, spreading, sepals and petals yellow to bronze-purple, sometimes spotted with purple-red or dorsally flushed with pink toward apex, labellum white to pinkish white, turning pale red to yellow with age, or solid violet, callus and column white. *Dorsal sepal* free, oblong to ovate-elliptic, acute to

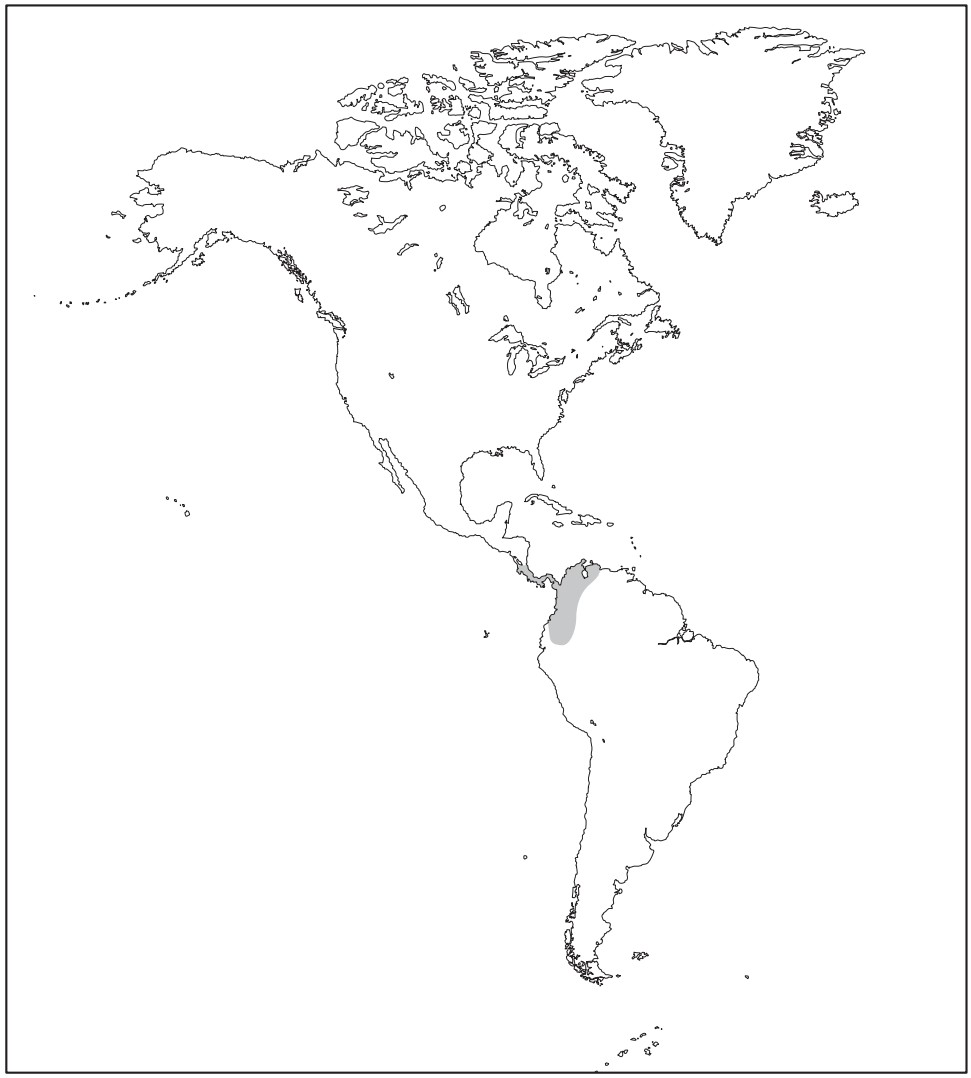


Fig. 617.2. Distribution map of *Warreopsis*.

acuminate, usually apiculate. *Lateral sepals* oblong to elliptic, acute to apiculate, abaxially carinate, concave, inner margin replicate-folded toward base. *Petals* obovate-oblong to elliptic-obovate, obtuse-rounded, apiculate. *Labellum* clawed, obovate to spathulate-oblong, sometimes obscurely trilobed, base cordate, apex rounded to truncate or emarginate, basal margins suberect to erect, distal lobe spreading, sometimes with undulate margins; disc with a ligulate to horsehoe-shaped, glabrous to verrucose callus. *Column* semiterete, straight, without a foot, dilated in central portion, provided with a prominent, longitudinal keel on ventral surface; anther cap cucullate, obovate to subreniform, flattened, two-celled, pollinia four, in two pairs subequal in size, on a ligulate-lanceolate, hyaline viscidium and a scarcely distinct stipe; stigma transversely elliptic. **(FP)**

Distribution (Fig. 617.2)

Warreopsis includes four species ranging from Costa Rica (Central America) to northern Venezuela and Ecuador (South America). **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Warreopsis*. **(NV, RG)**

Phylogenetics

Generic concepts for Zygopetalinae with many-noded pseudobulbs have been traditionally labile. With the exception of the recently described *W. purpurea* P.Ortiz, other species of *Warreopsis* were originally published as members of the polymorphic *Zygopetalum*, and *W. pardina* was described in 1984 as a species of *Ototstylis*. In his introduction to the *Zygopetalum* alliance, Garay (1973) assigned *Warreopsis* to the *Warrea* complex on the basis of its homoblastic pseudobulbs, placing the new genus close to *Warrea* and *Warreella*, from which it can be distinguished by a clawed lip and footless column. A similar view was adopted by Senghas and Gerlach in their key to genera of Zygopetalinae (1993) and also Szlachetko (1995), who created subtribe Warreinae for those taxa with homoblastic pseudobulbs, plicate leaves, and auriculate column.

In analysis of phylogenetic relationships of Zygopetalinae by Whitten *et al.* (2005), based on combined molecular evidence, *Warreopsis* belongs to a strongly supported clade with *Warrea*, but their relationship to the rest of the *Zygopetalum* clade is unclear. As presently understood, the genus may be recognized by the ellipsoid-subcylindric, homoblastic pseudobulbs enclosed by leaf bases; narrow and plicate leaves; erect, long, small-flowered inflorescence; lateral sepals with basal margins deeply inrolled; clawed lip; and column without a foot, provided with a prominent ventral keel. **(FP)**

Ecology

The species are terrestrials in well-drained, open soils in evergreen, wet cloud forests at 1500–2200 m. Flowering has been recorded most of the year. **(FP)**

Pollination

Pollinators are unknown but presumed to be fragrance-collecting bees. **(FP)**

Uses

There are no known uses of the species, and they are infrequently cultivated. **(FP)**

Cultivation

Warreopsis species should be grown in pots in a well-drained medium, with frequent watering and high levels of humidity year-round. The plants are best suited to shade, avoiding direct exposure of their delicate foliage to the sun. **(FP)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Senghas, K. and Gerlach, G. (1993). Subtribe Zygopetalinae. In *Rudolf Schlechter's Die Orchideen* (ed. F. G. Brieger, R. Maatsch, and K. Senghas), ed. 3, **1,** 1674–727. Paul Parey, Berlin.

Szlachetko, D. L. (1995). Systema orchidalium. *Fragmenta Floristica et Geobotanica Supplementum*, **3**, 1–152.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

618. ZYGOPETALUM

Zygopetalum Hook., *Bot. Mag.,* **54,** t. 2748 (1827). Type species: *Zygopetalum mackayi* Hook.

Zygopetalon Rchb., *Consp. Regn. Veg.,* 69 (1828), *orth. var.*

Derivation of name

From the Greek *zygon*, yoke, and *petalon*, petal, alluding to the thickened callus at the base of the lip, which seems to hold together (or yoke) the petals. **(FP)**

Description (Plate 224; Fig. 618.1)

Terrestrial, epiphytic or lithophytic, pseudobulbous (rarely without, in which case with a prostrate, indeterminate rhizome becoming erect apically), caespitose to scrambling *herbs*. *Roots* terete, flexuous, produced along rhizome near pseudobulbs. *Pseudobulbs* heteroblastic, approximate, rarely separated along rhizome or absent, elliptic to ovoid-oblong or conical, sometimes flattened and sulcate, 2–5-leaved at apex, subtended by 4–6 basal, mostly foliaceous sheaths, degenerating with age into fibres. *Leaves* plicate-venose, membranaceous to subcoriaceous, linear-lanceolate to lanceolate-elliptic or oblong-lanceolate, acute to acuminate, abaxially carinate along veins, narrowed at base into a conduplicate petiole, light to dark green, sometimes with an olive tinge. *Inflorescences* lateral, one or two per shoot, a 3–10-flowered raceme produced from base of immature pseudobulb, emerging from axils of sheaths, peduncle terete, erect to arching, exceeding leaves, provided with 3–5 membranaceous, tubular-infundibuliform to narrowly ovate, loose to inflated bracts; floral bracts prominent, widely ovate, conduplicate-cymbiform, loose. *Flowers* resupinate, showy, fragrant, sepals and petals yellowish green to green, heavily blotched or spotted with crimson or chestnut brown, rarely solid reddish brown, labellum white to purplish violet, heavily striped along veins with purple, violet or red, callus white to purple-violet, column white or yellow to green, variously spotted and flecked with purple, mostly on ventral surface. *Dorsal sepal* free, erect or reclined over column, ovate-lanceolate to broadly elliptic or elliptic-oblong, subobtuse to acute. *Lateral sepals* adnate to column foot to form a chin, ovate-elliptic to ovate, frequently asymmetrical, acute to acuminate, margins sometimes revolute. *Petals* spreading, narrowly oblong to lanceolate-elliptic, rarely subfalcate, obtuse to subacuminate, sometimes with revolute margins. *Labellum* articulate with apex of column foot, subentire to trilobed, sessile or provided with an obcuneate claw, lateral lobes spreading-auriculate, triangular to narrowly elliptic, midlobe spreading to convex, ovate to orbicular-ovate, less frequently obcordate, transversely elliptic or flabellate, rounded to truncate-retuse, often minutely emarginate, glabrous to villose, margins frequently undulate-crisped; disc with a basal, erect, fleshy, transverse, mostly bilobed, horseshoe-shaped to fan-shaped, low to high, plicate or lamellate, rarely tomentose crest, forming a shallow to deep cup beneath column base, distal portion sometimes denticulate. *Column* arcuate, with a distinct foot, ventral surface commonly tomentose to villose, broadened toward apex and provided with rounded to subquadrate wings and pointed clinandrium; anther cap cucullate, basally attenuate, obovate, flattened, two-celled, pollinia four, in two pairs subequal or of different sizes, on a rectangular-semicircular stipe and an elliptic-peltate, brown-hyaline viscidium; stigma transverse. **(FP)**

Distribution (Fig. 618.2)

Zygopetalum is a genus of 14 or 15 species and at least one natural hybrid centred in central and southern Atlantic Brazil, ranging to Paraguay, northern Argentina, Bolivia, and Peru (South America). All species currently assigned to *Zygopetalum* have been recorded from Brazil. **(FP)**

Fig. 618.1. *Zygopetalum mackayi* Hook. A. Habit, with inflorescence; B. Base of shoot showing pseudobulb; C. Flower, front view; D. Flower, side view; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum, longitudinal section; J. Column and labellum, side view; K. Column, ventral view; L. Column apex, anther cap removed; M. Column, side view; N. Anther cap with pollinia, ventral view; O. Anther cap, dorsal view; P. Pollinarium; Q. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *R.M. Hasley et al. H50662* (K), *R.M. Hasley 20915* (K), and Kew Spirit Collection no. 41060.

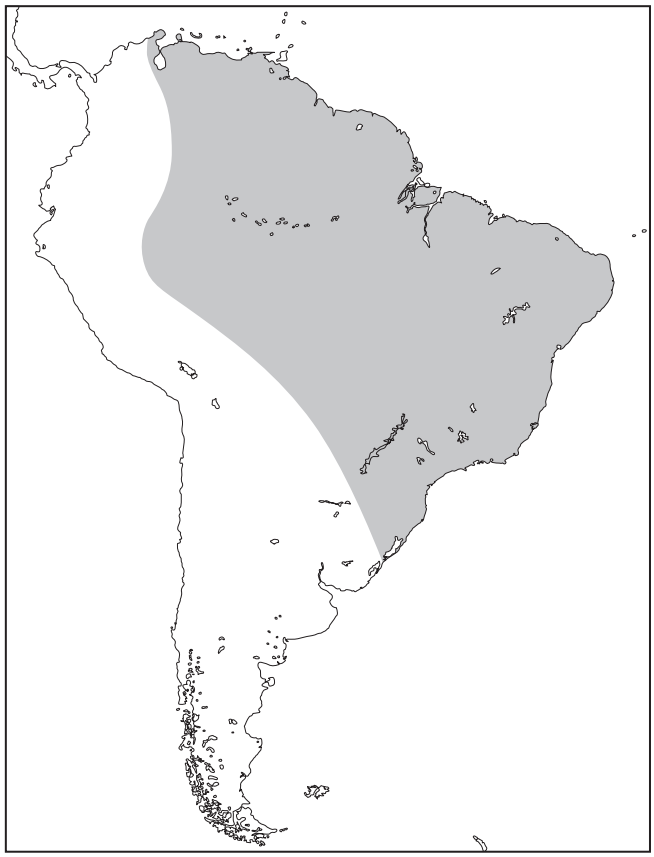


Fig. 618.2. Distribution map of *Zygopetalum*.

Cytogenetics

A somatic number of $2n = 96$ was reported by Tanaka (1964) for *Z. crinitum* Lodd. and *Z. mackayi*. Hoffmann (1930) and Blumenschein (1960) reported $2n = 48$ for *Z. mackayi* and *Z. maxillare* Lodd., and Sussenguth (1923) recorded $n = ca.$ 24 for *Z. mackayi*. Brandham (1999) suggested that the basic number might be either $x = 12$ or $x = 8$. **(FP)**

Phytochemistry

Surveys of alkaloid content in Orchidaceae indicate that these compounds are present in *Z. brachypetalum* Lindl., *Z. crinitum*, *Z. mackayi*, and *Z. maxillare* (Lüning 1964, 1967). Williams (1979) reported that leaves of *Zygopetalum* John Banks contain flavone *C*-glycosides.

Almost 40 components of the floral fragrance of *Z. crinitum* have been identified by gas chromatography coupled to mass spectrometry (Kaiser 1993). Those making an important contribution to the character of the scent include estragole (methylchavicol), eugenol, (*Z*,*E*)- and (*E*,*E*)-farnesal, geranial, geraniol, geraniol acetate, methyl anthranilate, and nerolidol (Kaiser 1993). The identity of 13 components of the corresponding fragrance of *Z. mackayi* was established using the same technique (Tatsuka *et al.* 1988). This species emits a strong fragrance at about 11:00 hours under greenhouse conditions. The most abundant components are the monoterpenes (*E*)-β-ocimene, and myrcene; however, the most important constituents from an olfactory point of view are probably 2-phenylethyl acetate, phenylacetaldehyde, and cinnamyl acetate (Tatsuka *et al.* 1988). **(NV, RG)**

Phylogenetics

Zygopetalum was originally described in 1827 to accommodate a species close to *Lycaste* and *Xylobium*, provided with a transverse callus or a flabellate crest at the base of the lip, but the circumscription of the genus rapidly grew to include members of only distantly related groups, including *Chondrorhyncha*, *Huntleya*, *Kefersteinia*, *Pescatorea*, and *Warczewiczella*. Garay (1973) proposed a review of the *Zygopetalum* alliance and considerably narrowed the limits of *Zygopetalum*, removing many species to the allied genera *Acacallis*, *Aganisia*, *Batemania*, *Koellensteinia*, *Mendoncella*, *Neogardneria*, *Pabstia*, *Paradisanthus*, and *Zygosepalum*, thus rendering *Zygopetalum* more homogenous. In its narrower circumscription, *Zygopetalum* includes species with heteroblastic pseudobulbs (exceptionally monopodial) with large flowers, without prominent lobes of the lip, and with the hypochile more or less cuneate and porrectly spreading.

However, the combined analysis of nuclear and plastid DNA data sets published by Whitten *et al.* (2005) revealed that *Zygopetalum* is polyphyletic even in the strict sense. *Zygopetalum maxillare* is sister to a clade including *Neogardneria murrayana*, *Pabstia*, and other species of *Zygopetalum*, which in turn is sister to *Promenaea* and successively sister to *Galeottia* + *Batemania* + *Zygosepalum labiosum*. A more complete species sampling is obviously required for a better understanding of the phylogenetic relationships among the genera of the *Zygopetalum* clade, and it is likely that *Zygopetalum* may need to be redefined in the future. **(FP)**

Ecology

Species of the genus are terrestrial or epiphytic (facultatively terrestrial and lithophytic) in submontane to montane wet forests, mostly at elevations of 1000–1800 m in shady to partially exposed situations. *Zygopetalum maxillare* is almost exclusively restricted to tree-ferns in wet and shady conditions. Plants of this species exhibit a dimorphic habit: they are rhizomatous-rambling until the growth reaches the tree-fern crown, where the pseudobulbs cluster and the habit becomes caespitose. *Zygopetalum pedicellatum* (Thunb.) Garay is a terrestrial, prostrate plant with a continuously growing rhizome several metres long; the roots anchor the plant to the leaf-litter substrate, and only the leafy, terminal part of the stem straddles the surrounding shrubs. Many species, such as *Z. brachypetalum* Lindl., *Z. mackayi,* and *Z. maculatum* (Kunth) Garay, are apparently obligate terrestrials and typical inhabitants of mountain slopes, ridge scrubs, and cleared roadside banks. Plants of *Zygopetalum* can flower from incipient pseudobulbs of immature growths in most months of the year, although some species exhibit a narrower flowering season. **(FP)**

Pollination

No records of natural pollination of *Zygopetalum* exist, but the strongly scented flowers are likely pollinated by male

euglossine bees. Dodson's (1965) record of the pollination of *Z. rhombilabium* C.Schweinf. actually refers to a species of *Chaubardia*. **(FP)**

Uses

Zygopetalum species and hybrids are among the most commonly cultivated plants of the subtribe. **(FP)**

Cultivation

Considering their size, the commonly terrestrial habit. and the erect inflorescences, plants of *Zygopetalum* are best grown in large pots, filled with a coarse, well-drained compost that allows air circulation around the thick roots. Plants should be maintained in filtered light, avoiding direct sunlight, and given constantly high humidity. Watering should be frequent during the growing season, with a partial rest after new pseudobulbs mature following flowering. Although they are known to be cool-growers, most species of *Zygopetalum* will grow well in intermediate to cool temperatures. *Zygopetalum triste* Barb.Rodr., from the montane forests of Minas Gerais, however, is best suited to cooler conditions. The rhizomatous plants of *Z. maxillare* are particularly sensitive to repotting and should be disturbed as little as possible. **(FP)**

Taxonomic literature

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología,* **8**, 15–51.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.

619. ZYGOSEPALUM

Zygosepalum Rchb.f., *Ned. Kruidk. Arch.*, 4, 330 (1859). Type species: *Zygosepalum kegelii* (Rchb.f.) Rchb.f. (basionym: *Zygopetalum kegelii* Rchb.f.)

Menadenium Raf., *Fl. Tellur.,* **4,** 45 (1838); Raf. ex Cogn. in Martius *Fl. Bras.*, **3(5),** 582 (1902). Type species: *Menadenium kegelii* (Rchb.f.) Cogn. (basionym: *Zygopetalum kegelii* Rchb.f.)

Derivation of name

From the Greek *zygon*, yoke, and *sepalon*, sepal, perhaps in reference to the connate lateral sepals or in allusion to similarity to *Zygopetalum*. **(FP)**

Description (Plate 225; Fig. 619.1)

Terrestrial or epiphytic, pseudobulbous, rhizomatous-creeping or caespitose *herbs*. *Roots* terete, flexuous, produced along rhizome. *Pseudobulbs* heteroblastic, separated along 'woody', often branching rhizome, rarely approximate, subcylindric to narrowly ovoid, laterally compressed, sulcate, 1–4-leaved at apex, subtended by 2–8 basal sheaths, upper ones sometimes foliaceous becoming brown to grey-scarious with age. *Leaves* plicate-venose to almost conduplicate, membranaceous to subcoriaceous, linear-lanceolate to oblanceolate-oblong, acute to acuminate, abaxially carinate along veins, narrowed at base into a conduplicate petiole, medium to dark green, sometimes shiny on upper surface. *Inflorescences* lateral, a 1–7-flowered raceme produced from base of immature or mature pseudobulb, mostly emerging from axils of foliaceous sheaths, peduncle terete, erect to arching toward apex, provided with 1–4, membranaceous to scarious, lanceolate to narrowly obovate, loose bracts; floral bracts prominent, lanceolate to widely ovate-lanceolate, conduplicate-cymbiform, scarious or membranaceous, acute to acuminate, shorter or subequal to ovary. *Flowers* resupinate, showy, sepals and petals pink or pale reddish brown to deep purple with cream margins, or yellowish green to green blotched with red-brown, labellum white to cream with a few purple lines at base to striped with purple-violet, or blotched purple at base, callus white striped purple to solid purple-violet, column white or yellowish to pale green, variously flecked with purple on ventral surface. *Dorsal sepal* free, erect or reclined over column, lanceolate to narrowly lanceolate, acute to subattenuate. *Lateral sepals* narrowly ovate-elliptic to lanceolate, sometimes asymmetrical, acute to subattenuate, concave, apex frequently reflexed. *Petals* spreading, lanceolate-elliptic to narrowly lanceolate, rarely subfalcate, acute to acuminate, sometimes apically reflexed. *Labellum* articulate with apex of column foot, sometimes forming a chin, entire to distinctly trilobed, sessile or provided with an obcuneate claw, sometimes divided into a basal hypochile, subparallel to column, and a distal, reflexed epichile, lateral lobes (when present) broadly elliptic, spreading, midlobe spreading to convex, cordate-ovate to suborbicular-ovate or transversely elliptic-reniform, acute to acuminate or apiculate, apex often abruptly deflexed, margins frequently undulate; disc with a basal, erect, fleshy, subquadrate to semicircular, fan-shaped callus, forming a cup beneath column base, distal margin entire to denticulate. *Column* arcuate, with a foot, broadened toward apex and provided with rounded to subquadrate, often erose wings and a pointed, sometimes fringed-lacerate clinandrium; anther cap cucullate, triangular, rostrate, two-celled, pollinia four, in two superposed pairs of different sizes, on a quadrate stipe with a ventral viscidium along basal margin or an ovate, acute viscidium, scarcely distinct from stipe; stigma transverse. **(FP)**

Distribution (Fig. 619.2)

Zygosepalum is a South American genus of six or seven species, mostly native to the Amazon and Orinoco basins and the Guyana shield, which range from Venezuela to northern Brazil and from Colombia to Ecuador in the Amazonian watershed of the Andes (South America). The distribution of *Zygosepalum* is centred in Venezuela, with five recorded species. **(FP)**

Phytochemistry

No reports have been found on phytochemistry of *Zygosepalum*. **(NV, RG)**

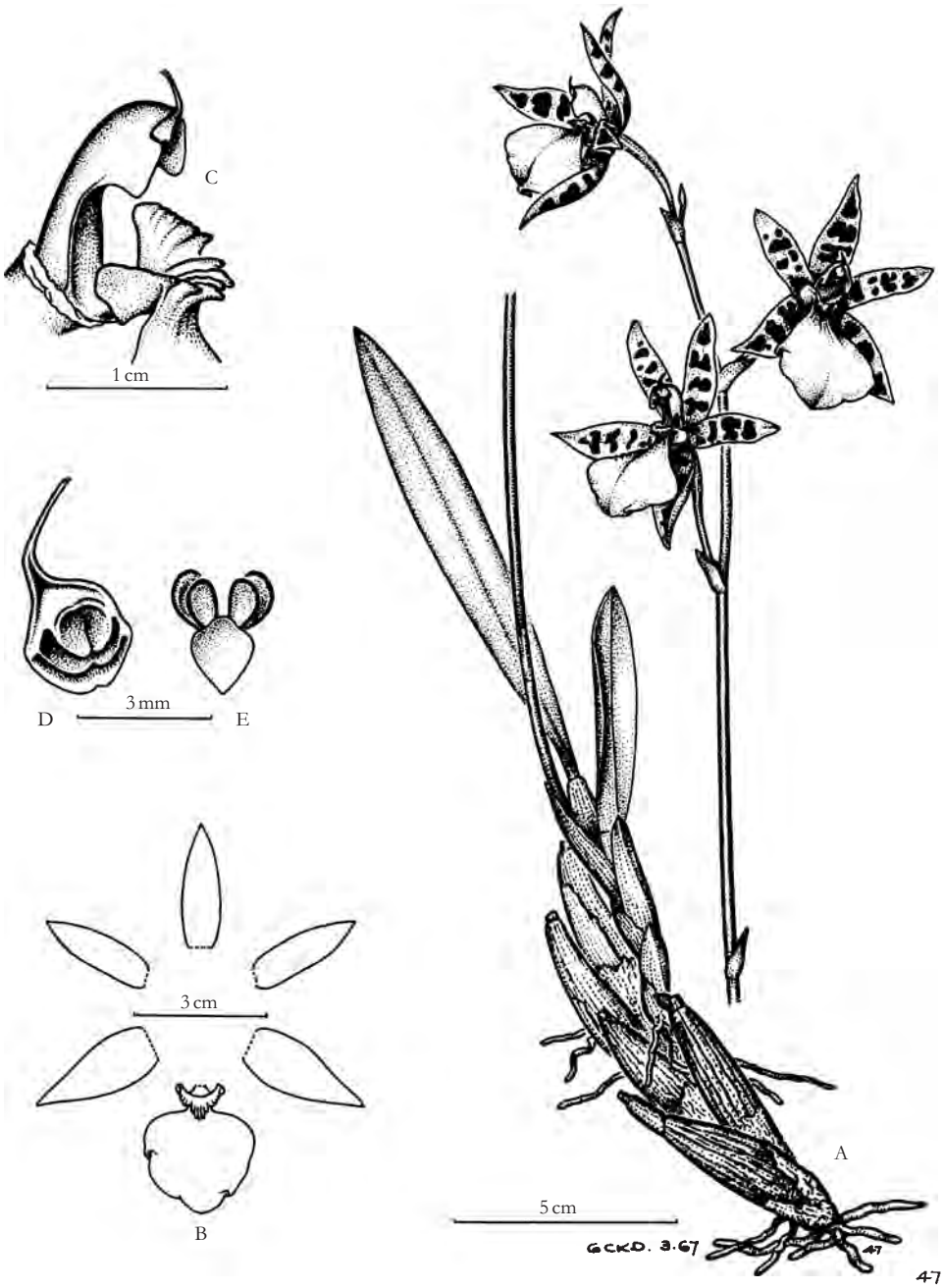


Fig. 619.1. *Zygosepalum tatei* (Ames & C.Schweinf.) Garay & Dunst. A. Habit, with inflorescence; B. Perianth, dissected; C. Column and labellum base, side view; D. Anther cap, ventral view; E. Pollinarium. Drawn by G.C.K. Dunsterville, drawing donated to Royal Botanic Gardens, Kew. A similar illustration appears in *Venezuelan Orchids Illustrated,* **5**, 318 (1972). Andre Deutsch, London.

Phylogenetics

Reichenbach originally proposed the genus *Zygosepalum* to accommodate those species of *Zygopetalum* with a hooded clinandrium and a cuspidate anther, i.e. *Z. rostratum* Hook. (= *Z. labiosum* (Rich.) C.Schweinf.) and *Z. kegelii* Rchb.f. Cogniaux (1902), and revived for this group of species the old name of *Menadenium*, mentioned but not formally published in 1838 by Rafinesque.

In 1967 Garay offered a first synopsis of the genus, only including in the genus those species close to *Z. labiosum* (namely, *Z. ballii* (Rolfe) Garay, *Z. kegelii,* and *Z. lindeniae* (Rolfe) Garay & Dunst.) and describing a new taxon later transferred to *Galeottia* A.Rich. In his revision of the *Zygopetalum* complex, Garay (1973) distinguished *Zygosepalum* by petals adnate to base of the column, lateral sepals adnate to sides of the column foot, and anther provided with a long, prominent, fleshy, subulate process. Here he explicitly included *Z. angustilabium* (C.Schweinf.) Garay, originally described as a variety of *Z. tatei* Ames & C.Schweinf., broadening the concept of *Zygosepalum* to include the highland species with many-flowered inflorescences.

As here circumscribed, the genus includes two groups of species that are both morphologically and ecologically distinct. The typical group, close to *Z. kegelii* (type of the genus), includes obligatory epiphytic, creeping plants with remote pseudobulbs and plicate, heavily veined, membranaceous leaves and upper

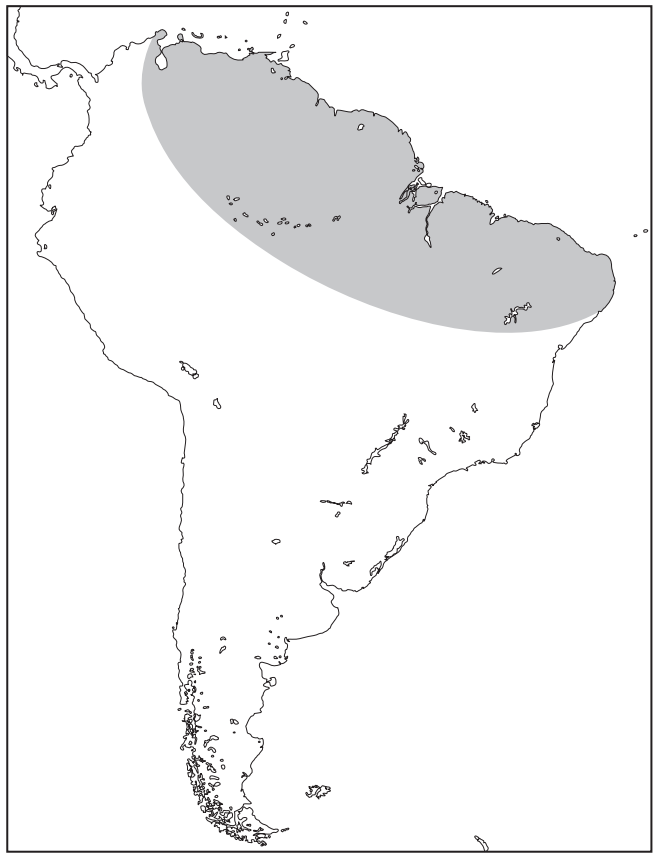


Fig. 619.2. Distribution map of *Zygosepalum*.

cataphylls mostly foliaceous. Inflorescences are few-flowered (1–3), shorter than leaves, with large, membranaceous floral bracts, and flowers have a large lip, striped with purple, that is rounded to cordate at the base. Pollinaria have a broad, hyaline white, subquadrate stipe with a distinct ventral viscidium along the basal margin. Plants of this group are typically inhabitants of the warm, lowland forests of the Amazon and Orinoco basins at elevations of 100–500 m, where they grow low on trees in shady sites close to the water.

In the second group, *Z. tatei* and closely related species are caespitose or shortly repent plants, mostly found growing in exposed positions on the ground or scrubby vegetation of high tepuis at elevations of 1600–2500 m. Leaves are subplicate-coriaceous (with only two lateral veins protruding), and the basal sheaths are strictly aphyllous. Inflorescences are frequently longer than leaves, many-flowered (up to seven), and have scarious, lanceolate floral bracts. The lip is divided into a hypochile subparallel to the column and a deflexed epichile. Pollinaria have a brown, ovate, acute viscidium, scarcely distinct from the stipe.

The phylogenetic analysis of combined DNA sequences published by Whitten *et al.* (2005) confirmed that *Zygosepalum*, as now defined, is polyphyletic. The two species included in the analysis fall into two different clades. *Zygosepalum labiosum* is sister to *Batemannia* in the *Galeottia-Batemannia* clade, whereas *Z. tatei* is sister to a clade including several species of *Zygopetalum, Neogardneria,* and *Pabstia*. *Zygosepalum* will need to be redefined in the future. **(FP)**

Ecology

Species of the genus are epiphytic or terrestrial (facultatively epiphytic) plants in tropical warm to montane wet forests at elevations of 200–2500 m in shady to partially exposed situations. *Zygosepalum labiosum* and closely related species are almost exclusively restricted to lower portions of trees, close to the water along streams and rivers in shady conditions. Species of tepuis, such as *Z. tatei* and *Z. angustilabium*, grow as terrestrials or epiphytes in dense, tangled, dwarf, wet forests, often in open conditions (Dunsterville 1979). Plants of *Zygosepalum* can flower most of the year from the incipient pseudobulbs of the immature growths or from mature pseudobulbs, mostly from October to March. **(FP)**

Pollination

Zygosepalum labiosum is pollinated by large bees of the genus *Eulaema*, and the pollinarium is placed behind the insect's head. **(FP, GR)**

Uses

Some species and hybrids of *Zygosepalum* are cultivated, but otherwise there are no known uses. **(FP)**

Cultivation

Species of *Zygosepalum* with a creeping habit are best suited to large plaques, on which elongate rhizomes can grow freely. Plants should be maintained in a shady, warm, and humid environment. Both *Z. labiosum* and *Z. lindeniae* have been recorded growing low on trunks of trees near the water's edge, where they may be flooded for short intervals at high-water, and they should be watered abundantly throughout the year. *Zygosepalum tatei* and *Z. angustilabium* can be grown in pots or shallow baskets in intermediate to cool conditions. In their natural habitat, plants of *Z. tatei* often root on highly acid soils, and these conditions should be in some way reproduced to maintain plants in captivity for long periods. Although they prefer shaded conditions, plants of *Z. tatei* and *Z. angustilabium* are more tolerant of light and can be grown in more exposed situations. **(FP)**

Taxonomic literature

Cogniaux, A. (1902). *Menadenium*. In *Flora Brasiliensis* (ed. C. F. P. Martius), **3(5),** 582. R. Oldenbourg, Monachii et Lipsiae.

Dunsterville, G. C. K. (1979). Zygosepalums of Venezuela. *American Orchid Society Bulletin,* **48**, 779–83.

Garay, L. A. (1967). Sinopsis del género *Zygosepalum* [*Zygopetalum, sphalm.*]. *Orquideología,* **3**, 5–9.

Garay, L. A. (1973). El complejo *Zygopetalum*. *Orquideología*, **8**, 15–51.

Whitten, W. M., Williams, N. H., Dressler, R. L., Gerlach, G., and Pupulin, F. (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana*, **5**, 87–107.