Keel, Shirley Hsiu-chun Kuo

A REVISION OF THE GENUS SALPICHROA (SOLANACEAE)

City University of New York PH.D. 1984

A REVISION OF THE GENUS SALPICHROA (SOLANACEAE)

by

SHIRLEY HSIU-CHUN KUO KEEL

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

1984

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

June 7, 1984

Date

Chairman of Examining Committee

15 June 1984

Date

Executive Officer

Dominick V. Basile, Ph.D.

Peter K. Nelson, Ph.D.

P. Richardson, Ph.D.

Dennis W. Stevenson, Ph.D.

Supervisory Committee

The City University of New York

ABSTRACT

A REVISION OF THE GENUS SALPICHROA (SOLANACEAE)

by

SHIRLEY HSIU-CHUN KUO KEEL

Adviser: Dr. Ghillean T. Prance

The genus Salpichroa (Solanaceae) contains fifteen species. Except for one cosmopolitan species, the genus is restricted to the Andes of South America. To a large degree the dissertation supports Simpson's (1975) phytogeographical hypothesis of the Andean flora. The study examines the data available from the investigations of external morphology, stem anatomy, palynology and seed coat morphology. A taxonomic revision, including keys, description, illustrations and discussion of the taxa are presented. The hypothetical relationships among the species of Salpichroa are summarized in a cladogram.

ACKNOWLEDGEMENTS

I am indebted to Dr. Ghillean T. Prance for his constant support, encouragement and guidance during my studies. I have benefited from the advice of Drs. James L. Luteyn and Scott A. Mori. I also wish to thank Drs. Rupert C. Barneby and Jacquelyn Kallunki who read the entire manuscript and helped me on innumerable occasions to clarify my thoughts.

I am also indebted to my advisory committee, Drs. Dominick V. Basile, Arthur Cronquist, Peter K. Nelson, P. Mick Richardson and Dennis W. Stevenson for critical review of this manuscript.

Field work for the study has been supported by a National Science Foundation Grant, No. WT 77-17704, which is gratefully acknowledged. I wish to express my gratitude to the individuals who collaborated with me during my field trip: Ing. Carlos Ochoa of the Centro Internacional de la Papa, Dr. Ramon Ferreyra and Ms. Graciela Vilcapoma of the Museo de Historia Natural "Javier Prado", Ing. Rene Chávez Alfaro, Dr. Efrain Carrillo and Dr. Cesar Vargas C. of the Universidad Nacional de San Antonio Abad del Cusco, Dr. Erika Geyger and Ms. Cecil Morales of the Universidad Mayor de San Andres, and Mr. Jaime Jaramillo of the Pontificia Universidad Católica del Ecuador.

I am grateful to my husband, Dr. Erich Keel, who helped me with my writing and encouraged my study. I thank Mr. Yung-Chau Huang and Ms. Aleka R. O'Connor for their help in the laboratory and the SEM work. I also thank Ms. Bobby Angell for her excellent illustration, and Dr. Lucia Atehortua, Ms. Lothian Lynas, Ms. Frances Maroncelli and Mr. Mark Wetter for their moral support and help.

Finally, I wish to express my gratitude to all the curators of the herbaria who made specimens available for this study: A, B, BM, BR, C, CORD, F, G, GB, GH, GOET, K, M, MICH, MO, NBV, NY, P, RB, S, U, UC, US, VEN, W, WIS.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

I. Introduction

Salpichroa (Solanaceae), contains 15 species of climbing shrubs and woody perennials. Except for one cosmopolitan species, S. origanifolia, the genus is restricted to the Andes of South America.

Salpichroa is characterized mainly by its ovate to cordate leaves, solitary flowers with valvate or induplicate aestivation, and tubular or urceolate corollas. Based on the shape and length of the corolla tube, Salpichroa can be divided into three groups: 1. taxa with long tubular corollas (8 spp.); 2. taxa with short tubular corollas (5 spp.); and 3. taxa with urceolate corollas (2 spp.).

In the past, some species of Salpichroa were referred to Physalis and Atropa, and species of Lycium, Juanulloa, Hawkesiophyton and Ectozoma were mistaken for Salpichroa. This confusion was largely the result of insufficient herbarium material and inconsistent generic concepts. Since Dunal (1852) last monographed the genus Salpichroa, 26 new species have been proposed, of which 18 so called "new species" are actually taxonomic synonyms. As more herbarium material has accumulated and new scientific methods have been introduced, it has become possible to reevaluate the genus Salpichroa.

The purpose of this monograph is to clarify the definition of Salpichroa and set forth a more precise and complete delineation of the species. About two thousand herbarium specimens have been examined. A three-month field trip to Ecuador, Peru and Bolivia was carried out and most of the known species of Salpichroa and one new species were collected and observed in the field. In addition to herbarium studies, literature research and field work, data from stem anatomy, palynology and seed coat morphology were used to make taxonomic decisions. Based on 19 selected characters, the relationships among the species of Salpichroa are discussed. Cytological studies were unsuccessful due to the difficulties in finding metaphase chromosomes in pollen of flower buds (solitary flower in Salpichroa) and the paucity of mature seeds for germination. However, the chromosome numbers of two species are known: S. hirsuta with N=12 (Heiser, 1963) and S. origanifolia with N=12 (Darlington & Wylie, 1961). Further cytological investigation and extensive breeding experiments should improve our understanding of the interrelationship among species.

II. Materials and Methods

On loan from twenty-six herbaria, about two thousand herbarium specimens of Salpichroa including all the

available types, have been studied. During a three-month field trip in South America, the plants were observed in natural habitats and specimens were collected for herbarium use. Stems, leaves and flowers were fixed in FAA (formalin, glacial acetic acid, and 50% alcohol in a ratio of 1:1:18), whereas flower buds were fixed in Newcomer's solution (isopropyl alcohol, dioxane, acetone, petroleum ether and propionic acid in a ratio of 6:1:1:1:3).

Herbarium specimens were examined under a dissecting microscope (10X-40X magnification). Cross-sections of the stem from pickled material were made on a sledge microtome at a thickness of 10-20μ, stained with 1% safranin (in 50% ethanol) and then counterstained with 0.5% fast green FCF. The stained sections were mounted in Canadian balsam and observed with a light microscope.

Wood shavings were dissociated in freshly made Jeffrey's solution (mixture of equal volume of 10% nitric acid and 10% chromic acid), stained in 1% safranin aqueous solution and dehydrated in alcohol-xylene series. Stained segments were separated into individual fibers or cells by teasing with a dissecting needle and were then mounted in Canadian balsam for observation.

To observe the shape of pores and furrows of pollen grains, anther samples from herbarium specimens were treated with 10% KOH aqueous solution and glacial acetic acid and

subjected to acetolysis with 1 part of concentrated sulfuric acid and 9 parts of acetic anhydride. Acetolyzed pollen was mounted in glycerine jelly and observed under a light microscope. To observe the exine sculpture and openings, pollen grains were mounted on standard aluminum SEM stubs using 2-faced sticky cellophane tape. The prepared stubs were vacuum-coated with gold palladium for 1-1.5 minutes at 10 milliamperes in a Hummer II. The coated pollen grains were viewed with a JEOL JSM-U3 SEM and pictures were taken at an acceleration voltage of 25KV (with the combination of condenser lens 11 and photomultiplier 3-4) using polaroid 4 x 5 land film (type 55/positive-negative film).

To observe the patterns of seed coats with a SEM, seeds were vacuum coated the same way as pollen grains, except that the coating time was twice as long, 2-3 minutes.

III. Taxonomic History

The first known species of Salpichroa was described by Lamarck (1793) as Physalis origanifolia. Lamarck mistook the Salpichroa for a Physalis, a genus characterized by fruits enclosed with inflated calyx, because he examined a type specimen which did not have any fruit. Subsequently, in Catalogus Plantarum Horti Regii Parisiensis, Desfontaines (1829) listed it under two names, Atropa origanifolia and Physalis origanifolia. He also provided an accurate

description of calyx and fruits. Between 1829 and 1837, four new species, subsequently referred to Salpichroa, were described as Atropa: A. rhomboidea Hooker (1829 [1830] = Salpichroa origanifolia), A. glandulosa Hooker (1831), A. hirsuta Meyen (1834) and A. dependens Hooker (1837).

In 1845 Miers removed several species from the ill-defined genus Atropa and proposed a new genus, Salpichroa, based on the following character differences: 1) calyx scarcely enlarged, not increasing much in size with the fruit; 2) corolla tubular, often constricted in the mouth, not companulate; 3) filaments inserted on the middle, not at the base, of the corolla tube; 4) anthers linear and erect, not oval and reflexed; 5) ovary deeply imbedded in a large, colored, fleshy disc, not wholly free or supported on a small 5-lobed ring; 6) stigma clavate, almost cup-shaped, not deeply sulcate, 2-lobed and reflexed; 7) berry bright scarlet, not greenish or black; 8) testa of the seed rugose and covered with rigid hairs, not smooth and reticulate. Although the latter three character differences do not always distinguish Salpichroa from Atropa today, the other characters mentioned above still do.

Miers divided Salpichroa into two sections: 1) Sect. Eusalpichroa with a long tubular corolla with an internally glabrous tube and 2) Sect. Perizoma with a short corolla tube, constricted in the middle and at the throat, and with

a thick woolly ring inside of the corolla tube. Section Eusalpichroa included three species removed from Atropa: Salpichroa glandulosa (Hooker) Miers, S. dependens (Mathews ex Hooker) Miers and S. hirsuta (Meyen) Miers, and one new species, S. ramosissima Miers. In section Perizoma he recognized two species: 1) Salpichroa rhomboidea, (Gillies et Hooker) Miers, formerly classified under Atropa, he further divided into two varieties, divaricata and pubescens and 2) Salpichroa ciliata (Schlechtendal) Miers, which he removed from Lycium because he believed that the dense villous ring above the base of the corolla tube resembles that of S. rhomboidea. Miers' observation of the villous ring in S. ciliata was a mistake. By 1852 Dunal had excluded the species from Salpichroa. In fact, most specimens I examined had hair only on the base of filaments instead of in a dense woolly ring on the inner surface of corolla tube. Moreover, the leaves and flowers of the so-called S. ciliata in general did not have the characters of Salpichroa.

The generic name Salpichroa was badly chosen because it refers only to the species with long tubular corollas. The word is derived from the Greek "salpinx" (a trumpet) and "chroa" (complexion or color) in allusion to the beautiful, trumpet-shaped flowers. Miers (1848) proposed the illegitimate name Salpichroma to replace Salpichroa to harmonize better with the names of the other two genera Iochroma and Poecilochroma. Despite the use of Salpichroma

by many botanists in succeeding years, Salpichroa is the legitimate name and must be used.

The section name Perizoma was made as a generic name by Lindley (1847) and Small (1903). Perizoma first appeared as a generic name in the list of genera of Solanaceae in Lindley's The Vegetable Kingdom (1847). Subsequently, in the third edition (1853), following comments by Miers, Perizoma was shown in italics as a synonym of Salpichroa. A more formal treatment of Perizoma as a genus is found in Small's Flora of the Southeastern United States (1903) and, later, in Small's Manual of the Southeastern Flora (1933).

Besides changing the spelling of the generic name, Miers (1848) also redefined the species concept of S. hirsuta, from which he separated two new species, S. diffusa and S. tristis, including them in Section Eusalpichroa. He published drawings of S. rhomboidea, S. hirsuta, S. tristis and S. diffusa in Illustrations of South American Plants (1850). Walpers, between 1847 and 1852, gradually published Miers' treatment of Salpichroa, and he used the name Salpichroa consistently.

Until 1848 only eight species of Salpichroa were recognized by Miers. Dunal (1852) expanded the genus and included species with racemose and corymbose inflorescences. He described one new variety, S. glandulosum var. longiflora Dunal, two new species, S. breviflorum Dunal and

S. cuspidatum Dunal, in Sect. Eusalpichroma, two new species, S.? urceolatum and S. parviflorum, in Sect. Perizoma and excluded S. ciliatum. In total, he recognized eleven species. This modification made Salpichroa a rather heterogeneous group because it included various species that were later determined to belong to other genera. Therefore his description of the genus is not very precise. In his generic description, he refers to anthers linear-oblong with 3 locules [a typographical error?], placenta central, stigma suppressed bilobed, berry red, all features which are not characteristic of Salpichroa. The mistakes were perpetuated by later taxonomists like Milne-Edwards (1864), Bentham and Hooker (1876), and Baillon (1888).

Bentham and Hooker (1876) described Salpichroa and related it to Nectouxia. They indicated that Salpichroa differs from Nectouxia by the corolla without a corona and the anthers without small appendages. The two genera also differ in their corolla shape-- salverform in Nectouxia, long-tubular or urceolate in Salpichroa. The two genera do share the following morphological characters: compressed seeds, curved embryo with incumbent cotyledons and abundant endosperm, dorsifixed anthers, ovate or cordate leaves, and a nectariferous disc around the ovary. However, a more detailed investigation is needed to see whether they are closely related phylogenetically.

Wettstein's (1891) generic description of Salpichroa largely followed that of Miers. He added S. wrightii, actually a Solanum, to the genus. In addition, he commented that Nectouxia, but not Salpichroa, has dilated connectives. In fact, this character cannot be used to distinguish the two genera, because dilated connectives are found in two species of Salpichroa (S. ramosissima and S. tristis).

In 1938, Benoist described eleven new species, many of which turned out to be taxonomic synonyms. He did not monograph Salpichroa, but he provided a key to distinguish seventeen species of the genus. Some of the characters used in his key, such as length and point of fusion of the sepals, number of corolla lobes (sensu lato, some of which should really be treated as teeth) are very useful. The most recent work, Macbride's (1962) monograph of Peruvian Solanaceae, recognized twelve species of Salpichroa. His description of the generic characters, "ovary free of fleshy disk,... berries typically scarlet or red" is contrary to previous work and my own field observations. Moreover, he repeats the mistakes of past botanists, such as capsular fruits in S. didierana, and dilated filaments in S. dilatata. Many specimens were misidentified because his definitions of the species are not very clear. Some characters he used in the key, such as the degree of pubescence and vegetative differences, were questioned even by himself.

In 1979, Hunziker modified Wettstein's system (1891) and published his synoptic survey of South American Solanaceae. He provided a key to the tribes and summarized distinctive characters and geographical distribution of all genera. Unlike earlier taxonomists, he put Salpichroa into the tribe of Jaboroseae instead of the tribe Solaneae. His Jaboroseae includes two other genera in South America, Jaborosa Jussieu and Trechonaetes Miers, and the monotypic genus Nectouxia in Mexico. It must be regretted that the relationship of Salpichroa to the other genera within the same tribe was not discussed by Hunziker (1979).

IV. Morphology and Anatomy

1. Habit and Branching System

The South American species of Salpichroa are mainly shrubs or subshrubs, rarely herbs. Differences in habit are not taxonomically significant because, depending on habitats, a given species can take the forms of a scandent shrub, a stunted, erect shrub, a hanging shrub or a procumbent shrub. The only species which does appear to be a perennial, decumbent herb is S. origanifolia, although it is frequently a subshrub.

The perennial rhizomes spread very extensively and send out lateral shoots which grow up through the soil. These new shoots can then develop leafy branches, bear flowers, and

eventually become a large plant. These new shoots in general have larger, glabrous leaves than main stems have.

Following Eichler and others, Wettstein (1891) described the branching system of Solanaceae in Natürlichen Pflanzenfamilien IV. However, he did not mention to which of his categories of branching system Salpichroa belongs. Child (1979), using Eichler's system, ascribed the branching system of Salpichroa to "difoliate sympodial units reduced to monochasial branching." Figure 1, taken from Pflanzenfamilien, demonstrates the branching system of Salpichroa. In the figure, the gross morphology of flower-bearing branches suggests a spiral main axis, lateral inflorescence and monopodial shoot system. The lateral branch II from the axil of bract b, carries two leaves, that is, α and β. Only the branch on the β side develops further and assumes the orthotropic position of the main axis, and the petiole of leaf β is fused with the axis of branch II. The leaf α remains at its point of origin, at the same level as bract b, and turns away from b at 90°. Therefore, leaves α and β (which is the bract of consecutive branch = bract of branch III) are geminate, which is also true for α' and β', and α'' and β''. Owing to epipodal suppression, the terminal flower of each branch appears at the level of the leaf cluster and is displaced laterally. Therefore, they are falsely axillary. As Child (1979) states well, "The cincinnus (monochasial sympodial unit) is betrayed by the

somewhat zig-zag line of the total axis and the deflected nature of the inflorescence axis (peduncle)". As a result, this kind of branching system forms an unbranched main axis in the floral region, a false axillary inflorescence, and paired unequal leaves.

The stunted, erect or hanging shrubs in open or exposed sites often develop more branches than the climbing shrubs in semi-shaded areas. In Salpichroa the young branches are often slender, spreading or drooping. Sometimes they assume the function of tendrils. Old woody branches and sometimes young branches are flexuous and bear corky wings. Stems of both prostrate herbs or hanging shrubs frequently develop adventitious roots which serve to anchor the plant in rock crevices.

Dammer (in Herzog, 1916, p.27) noted that the winged branches of Salpichroa alata (= S. tristis var. tristis) follow a simple pattern, that is, "one wing is added in every internode," i.e., if one branch has two internodes, the second internode has two wings. Furthermore, the wing of the mother branch continues and it is indistinguishable from that of daughter branches. Dammer's observation was based only on fragments of one specimen and after examing hundreds of specimens, I am unable to confirm his description of the pattern of winged branches.

2. Stem Anatomy

The stem of Salpichroa has bicollateral vascular bundles (Fig. 2). The variation among species occurs in quantitative changes in 1) the secondary xylem, 2) the layers of ray parenchyma (Fig. 3a & 3b), and 3) the cells (Fig. 4a), crystal-sand (Fig. 4b) and fibers (Fig. 4c) of the external phloem.

The epidermis consists of a unicellular layer of irregular, square or elongated, rectangular cells and 3-10 layers of hypodermis. The epidermal layer is forced outwards to form the wings on the stem and longitudinal cracks sometimes occur in the epidermal layer. The average size of epidermal cells is 25 X 74 μ.

The cortex consists of 5 to 6 layers of round, oval or rectangular parenchyma or collenchyma with rather small intercellular spaces. The cell size is about 35-74 X 35-40 μ. In some cells crystal-sand is present. The endodermis has a distinctive casparian strip (Fig. 4b) with cells about 49 X 25 μ.

External and internal phloem consists of sieve tubes, companion cells, phloem fibers and parenchymatous cells. External phloem is separated from the endodermis by parenchymatous cells which are irregular in size and occasionally contains crystal-sand (abundant in S. weberbaueri). Groups of internal phloem are separated from each other by rather large parenchymatous cells.

Lignified secondary xylem forms a cylinder inside the cambium. Cells dissociated by Jeffrey's solution are vessels (30-99 x 200-850 μ) which have simple perforation plates and alternately arranged bordered pits on the cell walls (Fig. 5a); tracheids (12-49 x 370-600 μ) which have tapered or round ends with scattered simple pits to alternately bordered pits on the walls (Fig. 5b & 5c); libriform fibers (12-20 x 600-1450 μ) which have tapered ends and scattered simple pits (Fig. 5d & 5e), and ray cells (19-30 x 50-60 μ) (Fig. 5f). Solereder (in Metcalfe & Chalk, 1948) refers to delicate septa in wood fibers of Salpichroa. However, I am unable to confirm this. The cross section of the stem shows multiseriate rays (up to 10 cells wide) in mature secondary xylem. Parenchymatous cells are scanty in the vascular bundle, but tyloses are sometimes found in vessels, Pith contains parenchyma, idioblasts (with crystal-sand) (Fig. 6a) and sclereids (with simple pits), 50-130 X 50-130 μ (Fig. 6b).

Some of the characters from the stem anatomy of S. origanifolia which have been used for numerical classification of the Solanaceae by Al-Nowaihi & Khalifa (1974) are inaccurate. They state that idioblasts and hypodermis are absent and pith is homogeneously thin. Metcalf and Chalk (1948) and my present observations show that idioblasts with crystal-sand and hypodermis are present and pith is heterogeneous with idioblasts and sclereids.

The qualitative anatomical characters of the stem are rather uniform among species. They are not very useful taxonomically, because the quantitative variation of these characters occurring within and between species probably is related to different ecological conditions.

3. Trichomes

The terminology used in this revision to describe trichomes follows Lawrence (1951). Salpichroa has two basic types of trichomes: eglandular and glandular; their structure can be either unicellular, simple or uniseriate, septate. Purple pigments, which are probably anthocyanins, often accumulate in the septa of uniseriate trichomes. Eglandular trichomes occur in various pubescence types: pilose, puberulous, villous, hirsute, occasionally stellate, velutinous or sericeous. Within one species, several types of pubescence can be found on any particular organ. Therefore pubescence types in Salpichroa, with a few exceptions, are of little taxonomic significance. The glandular trichomes, which are distributed randomly over the plant, have a simple structure. The basal portion resembles that of the non-glandular trichomes, but the apex is enlarged into a spherical or cylindrical secretory tip (Fig. 7). Sometimes this gland is completely filled with purple pigments. As indicated in Metcalfe & Chalk (1948), glandular

trichomes are widely distributed in the Solanaceae. In some instances, the trichome constituents seem to act as deterrents against aphids (Harborne, in press). In some plants of S. glandulosa subsp. glandulosa, S. gayi and S. tristis var. tristis, the secretion from glandular trichomes is so dense that plants become glutinous or viscous. However the function and composition of this glandular secretion are uncertain.

In Salpichroa, the most common types of pubescence are pilose and puberulose, including their glandular derivatives. In a few species of Salpichroa, the major types of pubescence are of diagnostic value. For example, hirsute pubescence is typical of S. hirsuta ;stellate or branched trichomes are found only on the branches, leaf blades and petioles of S. scandens and floccose pubescence on leaf buds and tips of young branches is characteristic of S. scandens and S. micrantha.

In some species, e.g., S. didierana, S. glandulosa, S. hirsuta, S. weberbaueri and S. origanifolia etc., the degree of pubescence varies from very dense to almost none. Whether this variation is related to specific ecological factors is still uncertain.

4. Leaves

The leaves of Salpichroa fall off in the dry season. Juvenile foliage of the rainy season is yellowish-green or bright green and often has purple veins which may be the results of anthocyanin deposition. The leaves turn dull or dark green when mature, and leaf texture is generally chartaceous. The stomata on leaves are anomocytic (Fig. 8). In Salpichroa origanifolia, crystal-sand has been found in the epidermis (Metcalfe & Chalk, 1948).

The leaves range from mainly ovate to sometimes elliptic or lanceolate, to rarely rhombate and deltoid. This variation may occur within the same plant and same species. All leaves of Salpichroa have entire margins. The principle venation is "brochidodromous" (Hickey, 1973) with random reticulate venation in the intercostal area. Leaf size varies greatly within the same plant. The leaves of suckers are usually larger, and some are slightly bullate. Given this variation, the size and shape of the leaves of Salpichroa have little diagnostic value. The developmental basis for geminate or unequal, opposite leaves in Salpichroa has been discussed in the section on the "branching system" (p. 10).

In the Neotropics, the leaves of many Solanaceous plants are food for the larvae of the Ithomiinae (Lepidoptera: Nymphalidae). This close association between plants and herbivores has been documented in ca. 450 species of

Ithomiinae and ca. 3000 species of Solanaceae (Drummond, in press). During my field trip, I have observed that leaves of Salpichroa show signs of damage but did not see any herbivores. Because Ithomiine butterflies are distributed between sea level and 2500 m elevation (Drummond, pers. comm.) and Salpichroa grows mainly between 2000 and 4000 m elevation, the possibility of Ithomiinae being the herbivores of Salpichroa is very slight. There may be other insects which can tolerate solanaceous alkaloids. Evans et al. (1972) isolated the alkaloids cuscohygrine, ψ-tropine, tropine, hyoscyamine and hygrine from the roots of S. origanifolia. Though alkaloids have been documented in only one species of Salpichroa, it is plausible that the other species of Salpichroa also contain solanaceous alkaloids in both roots and leaves. Future research on the isolation of solanaceous alkaloids from Salpichroa and the search for herbivores capable of tolerating these toxic alkaloids should be of great interest to students working on biochemical coevolution between host plants and herbivores.

5. Inflorescence and Floral Structures

The inflorescence of Salpichroa is a single flower, pseudo-axillary on mature branches but terminal on the new growth. The developmental basis for a pseudo-axillary flower have been discussed in the section on "branching system" (p.

11). The flowers of Salpichroa are pendent because the filiform pedicels are incapable of supporting the flowers in an erect position. During anthesis the pedicel elongates considerably and its length is not a useful taxonomic character, because it is extremely variable.

The calyx of Salpichroa, with a few exceptions, consists of five equally to subequally divided lobes connate only at the base. The lobes with valvate aestivation are usually linear, sometimes lanceolate or triangular-lanceolate. Two species form incomplete calyx tubes: (1) the calyx lobes of S. dependens are connate for ca. 1/3-1/2 of their length, but with one slit down to the calyx base (Fig. 9a); (2) those of S. microphylla are connate unevenly for more than 1/2 of their length (Fig. 9b). The division of calyx lobes is a very constant character within a given species and therefore is useful for the distinction of S. dependens and S. microphylla from other species.

In Salpichroa, the calyx is persistent and usually does not enlarge after fruiting. However, a slightly accrescent calyx is found in S. dependens ;while an abnormal swelling of the calyx is sometimes found in S. glandulosa subsp. glandulosa. The calyx of S. didierana and S. glandulosa subsp. glandulosa is sometimes heavily suffused with purple, while that of S. proboscidea turns completely dark-purple during fruiting. The evolutionary significance of

this coloration is difficult to assess, but in the case of S. proboscidea the purple calyx may attract animals for fruit dispersal.

The corollas of most species of Salpichroa are elongate-tubular, but in some are urceolate (S. origanifolia), or elongate-urceolate with the basal half slightly inflated (S. ramosissima), or infundibular and inflated on the upper part of the tube (S. hirsuta). The corolla shape and the constriction pattern of the tube are of diagnostic value. The corolla tubes of tubular flowers usually expand distally, with a few exceptions such as S. scandens, S. micrantha, and S. microloba. The corolla tube of S. scandens is constricted at the throat and at the middle or the upper one third; that of S. micrantha is constricted at the throat and at the middle; and that of S. microloba is constricted only at the throat. Inside the corolla tube, only S. origanifolia has a woolly band (Fig. 10), the other species are glabrous.

In Salpichroa the color of the corolla tube is usually yellow to yellowish-green except in S. origanifolia, which has white to greenish-white flowers, and in S. proboscidea, which has a salmon-pink corolla tube. Purple veins or dark lines on the corolla tube, which may serve as nectar guides, are found in S. didierana, S. diffusa, S. weberbaueri and S. proboscidea. Though yellow is not the coloration preferred

by hummingbirds, field observations by Dr. James L. Luteyn (pers. comm.) have revealed that hummingbirds do visit long-tubular yellow Salpichroa flowers. Grant & Grant (1968) also indicated that red is not required for pollination by tropical American hummingbirds. In the case of the species with a short-tubular corolla, bees may be the pollinators. However, more field work is needed to elucidate the pollinators of Salpichroa.

The color of the corolla lobes is not always the same as that of the corolla tube. For instance, S. proboscidea has yellow corolla lobes and a salmon-pink tube; S. diffusa has greenish-yellow lobes with deep yellow margins and a yellowish-green to pale green tube; S. scandens has pale yellow lobes and a yellowish-green tube; and S. micrantha has greenish-yellow lobes and a yellowish-green to pale green tube. The color differences or the same color with different tones between the corolla tube and lobes is probably connected with pollinator attraction. The shape of the corolla lobes varies from triangular to lanceolate, ovate-lanceolate, linear (S. gayi), or semicircular with an apiculate apex (S. hirsuta, see Fig. 11). In some species, there are furrows (S. gayi, S. weberbaueri, and S. tristis var. lehmanni) or green veins (S. micrantha) on each lobe, or teeth between the lobes (S. microphylla and S. glandulosa subsp. glandulosa) (Fig. 9b & 13a). At anthesis, the lobes spread horizontally or reflex at angles from 120° to 180°. The

reflection angle of the lobes (Fig. 12) and the shape of the teeth between the lobes are useful taxonomic characters. The texture of the corolla is usually slightly fleshy but is chartaceous in S. glandulosa subsp. glandulosa and membranous in S. scandens.

The corolla length ranges from 3.5 mm to 12.5 cm, and shows considerable infraspecific variation. However, it is taxonomically useful in combination with other characters. In general, the characters of the corolla are very useful for the separation of species.

Salpichroa has five equal to subequal stamens inserted on the upper 1/2 to 1/5 of corolla tube (in all species with long-tubular corollas except S. weberbaueri and in one short-tubular species, S. origanifolia) or inserted near the throat (in all species with short-tubular corollas except S. origanifolia and in one long-tubular species, S. weberbaueri). In long-tubular species such as S. didierana, S. microphylla, S. glandulosa and S. dependens, the stamens at anthesis are exserted beyond the corolla tubes; while in S. proboscidea, S. hirsuta and in short-tubular S. origanifolia, the stamens are equal in length to the corolla tube. The stamens of the other short-tubular species and of most S. weberbaueri are included. The anther sacs dehisce introrsely with elongate slits along their entire length. The stamens turn black and fall with the corolla tube after anthesis.

The filament is dorsifixed, extending into a connective (Fig. 13b) which is dilated only in S. ramosissima and S. tristis (Fig. 13c). The dilated connective was once used as a character to distinguish Salpichroa from a closely related monotypic genus Nectouxia (Wettstein, 1891). However, this character is found in some Salpichroa and in Nectouxia. It apparently does not have diagnostic value at the generic level.

The superior ovary has two locules and each locule contains numerous ovules which have placentae arising from the central column of the ovary tissue, a typical axile placentation. The nectariferous disc surrounding the base of the ovary is thick-tissued, annular, with five clear-cut glands. The nectary disc is found throughout the genus with the exception of S. microphylla. The color of the nectary varies: orange in S. weberbaueri, orange-red in S. diffusa, brick-red in S. origanifolia and yellowish-green in all other species.

The corolla tube and the adnate stamens arise from the base of ovary. The style extends from the tip of ovary and terminates in a capitate or subcapitate stigma which is not subdivided into lobes. The style is mostly glabrous except in S. gayi, S. origanifolia and S. weberbaueri in which it is sparsely pubescent. Heterostyly probably occurs in S. weberbaueri. Further observations and breeding experiments are needed to confirm this speculation.

6. Fruits and Seeds

Salpichroa has juicy, many-seeded berries which at maturity turn blue-black, dark purple, red? (in S. ramosissima according to Miers' type description), yellowish-green (S. scandens), white or pale yellow (S. origanifolia). The seeds are small, 1.5-4 X 1.5-3 mm, reniform, light brown or yellow.

Because only a limited number of seeds was available for the present investigation, the stage of maturity of the seeds examined was not determined. Only larger seeds were chosen for SEM studies. The seed coat patterns can exhibit geographical and intraspecific variation and can be affected also by drying conditions, photoperiod, and the position of the seeds inside the ovary (Brisson & Peterson, 1976), and the seed coat information offered here is only preliminary. Therefore, the list of seed coat characters is not meant to be a key for identification. Species not mentioned in this list are those of which immature or no seeds are available.

A detailed account of light-microscopic studies of seeds of S. origanifolia is given in USDA Technical Bulletin No. 1471. Under the SEM, I have observed that the testa surface of Salpichroa displays either a polyhedral or a rugulate

pattern.[1] The species exhibiting these two patterns can be further distinguished by the characters listed below:

1. Polyhedral pattern with undulating costae
   a. glabrous ... S. dependens (Keel & Centeno 384) (Fig. 14a).
   b. glabrous with thin transverse banding... S. weberbaueri (Keel 502) (Fig. 14b).
   c. hairy along costae... S. glandulosa subsp. glandulosa (Macbride 3050, Keel & Quéspe 467, Keel 418) (Fig. 15a & 15b); S. gayi (Keel 423).
2. Rugulate pattern
   a. glabrous with transverse banding at the edge of the seeds... S. micrantha (Keel 433) (Fig. 16a & 16b); S. tristis var. tristis (Luteyn et al. 6169).
   b. glabrous with costae topped with rope-like structure... S. diffusa (Keel 500, Prance 26597) (Fig. 18a).
   c. glabrous without transverse banding or rope-like structure... S. ramosissima (Keel 492) (Fig. 18b).
   d. hairy with costae covered with tiny papillae... S. scandens (Keel 415) (Fig. 19a).
   e. hairy without papillae... S. tristis var. tristis (Keel et al. 480, Mandon 434, Fiebrig 2625) (Fig. 19b); S. tristis var. lehmanii (Ellenberg

---

[1]Terminology used here is adapted from Hill (1976).

450, Rose et al. 22945) (Fig. 20a); S. hirsuta (Keel 453); S. origanifolia (Alvarez 582) (Fig. 20b); S. proboscidea (Keel 438).

Among the above species, S. origanifolia has the densest hair which covers the entire seed (Fig. 21). Nectouxia formosa (Gentry et al. 20249) (Fig. 17a & 17b) has the same pattern as S. micrantha, an additional character useful for indicating the relationship between Nectouxia and Salpichroa.

7. Pollen[2]

Salpichroa is characterized by spherical or subspherical monad, isopolar, radially symmetric, tricolporate pollen grain (Fig. 22a, 22b & 22c). The pollen size ranges from 45 to 118 μ at the polar axis and from 46 to 105 μ at the equatorial axis. The P/E ratio varies from 1.04 to 1.20 (see Table I). The amb type is circulaperturate. The only exception is S. didierana, in which a small portion of the pollen grains are subprolate (P/E=1.3), isopolar and bilateral (Fig. 23b). The same type of dimorphic pollen grains is also found in Nectouxia formosa (Fig. 24a & 24b). This unusual pollen type provides further evidence to support the affinity between Salpichroa and Nectouxia.

---

[2]The terminology here follows Walker & Doyle (1975).

The pattern of exine sculpture varies within the genus and can be divided into three subtypes:

1. Psilate:

S. didierana (Keel & Andrade 442) (Fig. 23a & 23b).

S. microphylla (Keel et al. 386) (Fig. 25a).

S. dependens (Keel 384).

2. Foveolate:

S. weberbaueri (Keel & Carrillo 444, Keel 502) (Fig. 25b).

S. origanifolia (Fiebrig 2144, Aguilar 319, Plowman 2720).

S. ramosissima (Keel & Vilcapoma 389, Keel 492).

S. gayi (Keel 423) (Fig. 26a).

S. micrantha (Keel 447, Keel 433).

S. diffusa (Keel 500).

S. tristis var. tristis (Luteyn et al. 6184, Linden 780, Fosberg 22062, Keel & Jaramillo 501, Keel 383, Keel et al. 480, Fiebrig 2625, Sleumer 290, Cabrera 7825).

S. tristis var. lehmanni (Boeke 467, Fernández 1066, Vilcapoma 128, André 4451, Buchtien 773).

The pattern of exine sculpture of Nectouxia formosa (Ball 4434, Fig. 26b) also belongs to this group, but whether this character indicates a relationship between Nectouxia and Salpichroa is unclear.

3a. Fossulate:

S. proboscidea (Keel 438) (Fig. 27a).

S. hirsuta (Keel 487, Luteyn & Lebrón-Luteyn 6467).

S. microloba (Keel & Vilcapoma 390) (Fig. 27b).

S. glandulosa subsp. glandulosa (Keel 418, Luteyn & Lebrón-Luteyn 6371) (Fig. 28a).

S. glandulosa subsp. weddellii (Brook 6096, Davidson 3718, Weberbauer 2936) (Fig. 28b).

A constriction on both sides of the pore and at a right angle to each colpus is found only in the two subspecies of S. glandulosa. This character strongly supports the affinity between the two subspecies of S. glandulosa.

3b. Fossulate & echinate:

S. scandens (Keel 415) (Fig. 29).

In Salpichroa only the pollen of S. glandulosa subsp. glandulosa from Bolivia has been investigated (Heusser, 1971). Erdtman (1971) indicated that the taxonomic significance of pollen morphology in Solanaceae is rather obscure. However, Gentry (in press) examined 15 genera and 26 species of Solanaceae, and said that exine sculpturing may prove to be a valuable taxonomic character in some genera. Moreover,the division of Salpichroa into groups based on the patterns of exine sculpture partially corresponds with that shown in the cladogram (Fig. 34). The evolutionary trend of pollen characters of Salpichroa is

difficult to assess. A clearer picture may appear as the pollen of more genera within the family is investigated.

V. Geographical Distribution and Habitats

All species of Salpichroa, except for S. origanifolia, indigenous to southern regions of South America but introduced to regions with a Mediterranean climate, are endemic to the Andean region of South America. They are distributed from Venezuela along the Andean chain southward through Colombia, Ecuador, Peru and Bolivia to Argentina in latitude 10° N to 42° S (Fig. 30). Southern Peru is the center of diversity, 14 out of 15 species being found there. The number of species tapers off quickly from there to the north and to the south.

Salpichroa is part of the highland vegetation, growing mostly between 2400 and 4700 m, except for S. origanifolia, which descends to sea level. From Peru northward, species of Salpichroa occur on both eastern and western mountain ranges. However, from Bolivia southward, Salpichroa is found only along the eastern Andean ranges. Except for one specimen of S. origanifolia (Fig. 31) of dubious origin which was collected in coastal Chile (Valparaíso), no Salpichroa has ever been found in the Chilean Andes. The desert areas extending more than two thousand miles from northern Peru to Copiapo (27° S, 71° W) in Chile may act as a

barrier which effectively blocks the migration of Salpichroa into the Andean region of Chile.

Two species are widespread along the Andean chain: S. tristis (Fig. 32) from Venezuela to Argentina and S. scandens (Fig. 31) from Peru to Argentina. The other species have relatively restricted distributions. Six of the fifteen taxa of Salpichroa are endemic to Peru. Salpichroa didierana (Fig. 33) grows only in the cloud forests of the Ayacucho-Cuzco area; S. microphylla (Fig. 33) is endemic to the subpuna of central Peru; while S. dependens (Fig. 32) is restricted to the NW part of southern Peru, and S. proboscidea (Fig. 33) to a single locality in cloud forest near Abra Acanacu National Park. Salpichroa gayi (Fig. 32) and S. micrantha (Fig. 31) are both endemic to the Cuzco region. Salpichroa ramosissima (Fig. 31) and S. microloba, (Fig. 33) which show disjunct distributions, grow mainly on the Pacific-facing slope of the Cordillera Occidental in Peru. The former has additional isolated populations in southern Bolivia and northern Argentina, while the latter has disjunct populations in Ecuador. These distribution patterns represent the result either of long-distance dispersal or of Pleistocene climatic changes which caused range expansion during glacial periods when vegetation zones were lowered and subsequent isolation during interglacial periods.

The distribution patterns of many species of Salpichroa add more evidence to support the hypothesis which Simpson (1975) proposed in her phytogeographical study of the Andean flora. In the northern Andes, S. diffusa (Fig. 33) is the only species endemic to Ecuador. The Huancabamba Deflection in northern Peru probably determines the distribution limit of S. diffusa and blocks its migration southward. According to Simpson (1975), species which occur on both Pacific-facing slopes and eastern slopes of the Cordillera Oriental almost always occur N of 8° S and often into Ecuador. This is evident in the distribution pattern of S. weberbaueri. (Fig. 32).

Simpson (1975) also suggested that the Titicaca Lake system and the extensive glaciation of the Cordillera Real east of La Paz in the Pleistocene effectively blocked north-south biotic migrations around the eastern edge of the present lake and, therefore, separated plant populations to the north and south. This is exemplified by the distribution pattern of S. hirsuta (Fig. 32) which has several populations on the north, south and west sides but none on the east side of Lake Titicaca. The two subspecies of S. glandulosa (glandulosa and weddellii) are separated by Cordillera Tres Cruces (Fig. 33).

Salpichroa origanifolia (Fig. 31) occurs mainly in southern South America, along the coast as well as inland.

However, south of Buenos Aires, few specimens have been collected in the coastal area and none inland. Because the climate of southern Argentina below the province of Buenos Aires is very arid (Smith, 1962), S. origanifolia probably originated in the NW part of the country. It may have migrated across the northern part to the coastal area, from where it further spread to other parts of the world.

The distribution of Salpichroa is also profoundly influenced by human activities, as shown by its ecology. Many short-tubular species occur in areas disturbed by man. Even the cloud forest species are frequent at the edges of secondary forests in exposed sites. Although the ranges of many species overlap, no hybridization has been detected in the field.

VI. Infrageneric Relationships

So far no phylogenetic analysis of Salpichroa has been published. The following discussion of the relationships within Salpichroa is a phyletic analysis based on the Groundplan-divergence Method (Wagner, 1980). Although speculation on phylogenetic relationships may never be proven, the phyletic analysis does offer an overview of the genus and may be refined as more data become available.

For this analysis, 19 characters from 16 taxa were studied. and the trend for each was determined (Table II) by using the criteria suggested by Crisci & Stuessy (1980). The character state for each taxon is listed in Table III. The hypothetical relationships among species of Salpichroa are presented in a cladogram (Fig. 34).

The Groundplan-divergence Method requires the designation of a recent common ancestor for the group analyzed. Since no extant taxon possesses all the character states of the hypothetical ancestor, some guiding principles have to be observed for the determination of the ancestral or divergent state of each character. Characters widespread in other genera of the tribe Solaneae, or within the genus Salpichroa are considered to be ancestral. On the other hand, characters which occur infrequently within the genus are considered to be divergent. In some cases, the divergent states of characters involve progressive fusion or specialization.

Because vegetative characters are rather uniform within Salpichroa, evolutionary trends in the group have been extrapolated mainly from floral characters. Some advanced character states mark particular taxa rather than exhibit a general trend.

The character states which are very common within the tribe Solanae and thus referred to as "ancestral" are the

following: 1) calyx accrescent after fruiting (B in Table II), and 2) pollen grains with sculptured exine (M).

Characters which occur infrequently within the genus and the tribe Solanae and are designated "divergent" include: 1) urceolate corolla (E), 2) woolly ring inside of corolla tube (I), 3) constriction on both sides of the colpus of pollen grain (N), and 4) dilated connectives (S). Character states which occur infrequently within the genus and are designated divergent are 1) membraneous texture of corolla tube (R), 2) furrows on the surface of corolla lobes (Q), 3) styles not exceeding stamens at anthesis (L), 4) different color patterns of corolla tube and its lobes (C), 5) salmon-pink corolla tube (D), and 6) short, constricted corolla tubes (F, G, H). The last three characters (4, 5, 6) may be related to the mode of pollination. Character state 5 occurs in a species with long corolla tube and with exserted style which exceeds stamens. It is no doubt a specialization for bird pollination. Character state 6 occurs in species with yellow or greenish-yellow corolla and with exserted style which exceeds stamens. I believe that it is a specialization for insect pollination.

Divergent character states which involve fusion are exemplified by 1) partially fused calyx lobes (A) and 2) teeth on the sinuses of corolla lobes which may lead to the fusion of lobes (J). One character state, stamens exserted

at anthesis (K), was designated as divergent on the basis of its co-occurrence with other characters. In Salpichroa, all taxa with exserted stamens have styles exceeding stamens. This syndrome is no doubt a specialization towards outcrossing. Even taxa with included stamens are frequently characterized by styles which exceed stamens. There are two exceptions: S. micrantha and S. gayi have styles which do not exceed included stamens. Therefore, it can be observed that cross pollination in Salpichroa is the rule. Character state K is considered to be divergent, because out-crossing represents an evolutionary specialization. Flowers with exserted stamens and spreading corolla lobes with a reflection angle $< 180^{\circ}$ (O) are more visible to pollinators. Therefore, these two character states (K, O) are viewed as "divergent". In terms of habitat (P), the cloud forests represent more stable, ancestral habitats than weedy places.

The species on the cladogram (Fig. 34) largely fall into two groups. Species on the left side of cladogram, including S.didierana, S. dependens, S. microphylla, S.glandulosa, and S. proboscidea, are less advanced. The habitats occupied by these species are wet cloud forests, edges of secondary forests, and semi-moist woodlands. The taxa are characterized by elongate, straight corolla tubes and exserted stamens. The following trends can be noted in this group: i) calyx lobes from deeply divided to partially fused with one slit open to the base to unequally fused with no

slit to the base (see Fig. 13a, 9a & 9b); 2) teeth in sinuses of corolla lobes from none to unequal to subequal or equal teeth (see Fig. 9a, 9b & 13a). Three taxa, S. didierana, S. dependens, and S. microphylla, have pollen grains with smooth exine. The color of corolla tube in this group is yellow except salmon-pink in S. proboscidea.

The right side of the cladogram consists of three subgroups of weedy species. Subgroup I, including S. microloba, S. ramosissima and S. origanifolia, is characterized by urceolate corollas or by corollas with the tube constricted at the throat and lobes reflected by 180 at anthesis. No trends can be observed in this group. However, one character state, a woolly ring inside of the corolla tube, occurs only in S. origanifolia. Subgroup II, including S. tristis, S. gayi, S. micrantha and S. scandens, is characterized by short-tubular corollas with partially constricted tubes and lobes reflected $< 180^{\circ}$, and by stamens included at anthesis. There are two cases of parallelism and one general tendency in this subgroup. The occasionally dilated connectives found in both varieties of S. tristis occur also in S. ramosissima of Subgroup I. The furrowed surface of the corolla lobes characteristic of S. gayi and S. tristis var. lehmanni is found also in S. weberbaueri of Subgroup III. A general tendency is manifested in this group-- the style at anthesis from exceeding to not exceeding the stamens. An infrequent character state,

membranous corolla tube occurs in S. scandens. Subgroup III, consisting of left-overs, S. diffusa, S. weberbaueri and S. hirsuta, is heterogeneous. The length of corolla tubes ranges from long to medium-long to short. The only common characters are the corolla tube never constricted at the throat and the calyx never accrescent after fruiting. Salpichroa hirsuta is the only long-tubular species and with anthers partially exserted at anthesis growing in a dry, weedy habitat. Salpichroa weberbaueri has a medium-long corolla tube with the styles at anthesis ranging from exceeding to not exceeding the stamens. The collections of S. weberbaueri do not as yet show heterostyly occurring in a given population. The relationship of members of Subgroup III to other taxa will be better revealed when more information is available.

VII. Systematic Treatment

Salpichroa Miers, London J. Bot. 4: 321. 1845; Miers, l. c. 7: 333. 1848 (as Salpichroma) Sendtner, Mart. Fl. Bras. 10: 149. 1846-1856; Walpers, Repertorium Botanices Systematicae 6: 612. 1847; Miers, Illustrations of South American Plants 1: p. 1 & p. 133. 1850 (as Salpichroma) Dunal, in de Candolle, Prodr. 13(1): 471. 1852 (as Salpichroma) Weddell, Chloris Andina 2: 97. 1859 (as Salpichroma) Milne-Edwards, De la Famille des Solanacees p. 59. 1864 (as Salpichroma) Baillon, Histoire des

Plantes p. 337. 1888; Bentham & Hooker, Genera Plantarum 2(2): 899. 1876; Wettstein, in Engler & Prantl, Nat. Pflanzenfamilien 4(3b): 25. 1897; Cabrera, Manual de la Flora de los alrededores de Buenos Aires p. 414. 1953; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 59. 1962; Cabrera, Flora de la Provincia de Buenos Aires 5: 220. 1965; Cabrera, Bol. Soc. Argent. Bot. 13(4): 328. 1971; Benítez de Rojas, Revista Fac. Agron. (Maracay) 7(3): 77. 1974; Hunziker, South American Solanaceae: a synoptic survey, in Hawkes et al., The Biology and Taxonomy of the Solanaceae p. 60. 1979.

Busbeckia Martius, in Schrank & Martius, Hortus Regius Monacensis p. 69. 1829, non Busbeckea Endlicher (= Capparis L.), nom. nud.

Perizoma Miers ex Lindley, Vegetable Kingdom p. 622. 1847, nom. nud.

Deciduous, scandent or pendent or stunted shrubs, spreading by suckers, the young stems hairy, but glabrate at maturity. Leaves geminate, simple, estipulate, basally obtuse to oblique or truncate to cordate, marginally entire, apically acute or obtuse, the midrib and lateral nerves plane and sometimes obscure on upper surface, slightly raised and more conspicuous on lower surface, the veinlets obscure. Flowers solitary, falsely axillary and pendulous;

pedicels filiform; calyx equally or unequally divided, 5-lobed, the lobes valvate, persistent, sometimes accrescent after fruiting; corolla elongate tubular, infundibular or urceolate, 5-lobed, the lobes valvate to induplicate, equal to subequal, reflexed or spreading at anthesis; stamens 5, alternate with corolla lobes, exserted to included, equal or subequal, the filaments glabrous, filiform, partially adnate to corolla tube, the anthers dorsifixed, sagittate, 2-celled, dehiscent longitudinally; ovary superior, glabrous, 2-locular, with axile placentas, the fleshy disc nectariferous (with the exception of S. microphylla), style filiform, straight, exserted, usually glabrous, usually exceeding stamens, the stigma usually capitate to subcapitate, the surface glabrous. Fruit a juicy, many-seeded, oblong to obovoid glabrous berry; seeds compressed, rugulose.

Lectotype species: S. glandulosa (Hooker) Miers. Miers did not designate a Salpichroa as the type species for this genus and when Cabrera so designated it in 1953, he did not give any reasons. Moreover, the identity of the type specimen of S. glandulosa is uncertain. The reason for choosing lectotype of S. glandulosa is discussed under S. glandulosa. The chosen lectotype, Cruckshanks s.n., will also be the generitype.

Key to the species of Salpichroa

1. Calyx equally and relatively deeply divided, lobes connate only at the base

2.Corolla tube 10-12.5 cm long..... 1. S. didierana

2. Corolla tube < 9 cm long

3. Style exceeding stamens, reaching more than 2/3 length of corolla tube

4. Stamens exserted at anthesis or only anthers partially exserted at anthesis

5. Corolla infundibular or elongate tubular, yellowish or pinkish, the tube > 1 cm long, internally glabrous

6. Corolla infundibular, the tube 2.8-4 cm long, the lobes semicircular with apiculate apex..... 6. S. hirsuta

6. Corolla elongate tubular, the lobes triangular or ovate-triangular to lanceolate with acute or acuminate to cuspidate apex

7. Sinuses of corolla lobes with 5 equal or subequal retuse teeth, corolla tube (3.3-)3.8-6.5(-) cm long .. 3a. S. glandulosa subsp. glandulosa

7. Sinuses of corolla lobes without teeth

8. Corolla tube and lobes yellow to greenish yellow, the tube (3.6-)5-7 cm long. Distributed on the SE side of Cordillera Tres Cruces in Bolivia ..... 3b. S. glandulosa subsp. weddellii

8. Corolla tube salmon-pink except ca. 1/5 of the basal part nearly white, 6-8(-8.5) cm long, the lobes yellow. Endemic to montane cloud forests between Paucartambo and Abra Acanacu, Dept. of Cuzco, Peru.. 5. S. proboscidea

5. Corolla urceolate, white to greenish white, the tube < 1 cm long, internally with a densely woolly band..... 8. S. origanifolia

4. Stamens included at anthesis

9. Corolla tube > 2 cm

10. Corolla tube upper 1/3 gradually widened, externally pubescent, the lobes triangular-lanceolate, 3-6 X 1-2 mm, horizontally spreading to reflexed by 135° at anthesis ..... 7. S. weberbaueri

10. Corolla tube constricted at throat, externally puberulous or glabrous, the lobes triangular or ovate-triangular, 2-3 X 1.5-3 mm, reflexed by 180 at anthesis..... 15. S. microloba

9. Corolla tube < 2 cm

11. Corolla tube not constricted, or constricted only at throat, lobes reflexed by 180° at anthesis, calyx never villous

12. Corolla elongate-urceolate, slightly succulent, the tube slightly inflated at lower

half, glabrous or sparsely puberulous, the tube and lobes yellowish-green or greenish-white; style included but exceeding stamens..... 10. S. ramosissima

12. Corolla tubular, not succulent, the tube straight, glabrous in lower 1/3, the rest pilose, yellowish-green to light green, the lobes greenish-yellow with deep yellow margins; Style exserted and exceeding stamens..... 13. S. diffusa

11. Part of corolla tube constricted, if tube straight then the calyx villous, the lobes spreading horizontally or reflexed by 120°-135° at anthesis

13. Corolla tube glabrous or very sparsely pubescent externally

14. Corolla membranous and frequently appearing transparent in the dry state, constricted at throat and in the middle or 1/3 of the tube both in bud and when mature, glabrous, the lobes reflexed by 135° at anthesis; berry yellow-green ..... 9. S. scandens

14. Corolla not membranous, the tube constricted in the middle, or the tube straight with villous calyx, glabrous, rarely

sparsely pubescent, the lobes spreading or reflexed by 120° at anthesis; berry purple-black to blue-black ..... 14a. S. tristis var. tristis

13. Corolla tube pubescent externally, constricted or slightly constricted in the middle, the lobes horizontally spreading at anthesis; berry black ..... 14b. S. tristis var. lehmanni

3. Style short, included, not exceeding stamens, only reaching to 1/2 length of corolla tube

15. Corolla tube 10-15 X 2-3 mm, puberulous or pilose externally; corolla lobes linear, each lobe with two unequal furrows, 3-4 X 0.5-1 mm, puberulous or puberulous-glandular. Plant glutinous and aromatic..... 12. S. gayi

15. Corolla tube 7-9 X 1.5-2 mm, glabrous externally; corolla lobes triangular-ovate, without furrows, 1-1.5 X 0.5-1 mm, ciliate. Plant not glutinous or aromatic..... 11. S. micrantha

1. Calyx unequally divided, the lobes connate for more than 1/3 length of calyx

16. Calyx lobes connate for more than 1/2 length of calyx, not accrescent after anthesis; sinuses of corolla lobes provided with 5 unequal obtuse or acute teeth, the lobes

induplicate, both lobes and teeth reflexed by 180° at anthesis..... 2. S. microphylla

16. Calyx lobes connate for 1/3 to 1/2 length of calyx, accrescent after anthesis and with one slit open to nearly the base of calyx; sinuses of corolla lobes without teeth the lobes valvate, spreading at anthesis.... 4. S. dependens

1. Salpichroa didierana Jaubert, Bull. Soc. Bot. France 8: 117. 1861; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 61. 1962. Type. Peru. Cuzco: San-Quentino, valley between country estate Totora and quebrada of Mollepata, 120 km from Cuzco, 4300 m, 13 Sep 1858 (fl, fr), Grandidier & Grandidier s.n. (holotype not found at P, presumably lost).

Scandent shrubs to 5 m tall, the young stems, leaves, pedicels and calyx villous with spreading, sometimes partly gland-tipped trichomes, but the leaves sometimes glabrous above. Branches and twigs terete or winged, with wings on 1 or 2 sides; bark ribbed. Leaf blades lanceolate, elliptic, or ovate, 2-5 x 1-4.5 cm, dull green when fresh, brown or black when dry; petioles subfiliform, 0.8-1 cm x 0.5 mm. Pedicels 0.8-2.4 cm long; calyx equally or unequally divided, the lobes linear, equal or subequal, 3.3-5.2 x 0.3 cm, apex attenuate; corolla elongate tubular slightly wider at throat, greenish-yellow, the tube straight, 10-12.5 x

0.5-0.9 cm, glabrous externally and internally, the lobes valvate, lanceolate to triangular, subequal, 1.3-1.7 x 0.5-0.6 cm, glabrous or villous, apex attenuate, reflexed at anthesis; stamens exserted, subequal, the filaments adnate to corolla tube for ca. 3/4 length, the free portion 4.5-4.7 cm long, light green, the anthers 7.5 mm long, light brown; style exceeding stamens, 13-15 cm long. Berry not seen.

Distribution. Montane cloud forest, 3100-3900 m, occasionally among the Inca ruins; south-central Peru. Flowering in the rainy season, September-February.

Specimens examined. PERU. Without locality: 27 Dec 1878 (fl), Martinet 1605 (P). Ayacucho: Nr. Cusimachay, ca. 25 km NE of Tambo, 3600 m, 28 Jul 1970 (fl), Madison 10367-70 (F); vic. of Pantes, 33-36 km NNE of Tambo, 3353 m, 2 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6348 (BM, G, K, LPB, MO, NY, P, US, USM). Cuzco: Cordillera Veronica, 3900 m, 27 Sep 1957 (fl), Rauh-Hirsch P1013 (F); Mollepata, Inca ruins above Hacienda Pincopata, 3400 m, 27 Jan 1976 (fl), Bishop 2929 (US), 3536 m, 26 Feb 1979 (fl), Keel & Andrade 442 (NY, USM); between Ollantaytambo and Alfamayo, 58-67 km NW of Ollantaytambo, 3415-3110 m, 11 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6447 (MO, NY, US, USM); between Ollantaytambo and Chaullay, km marker 144, 3500 m, 17 Jan 1975 (fl), Plowman & Davis 4746 (F, GH, K).

Salpichroa didierana is easily recognized by its strikingly long corolla tubes. The degree of pubescence on the stems, leaves, and calyx varies considerably within this species. Specimens from the Mollepata region are nearly glabrous, whereas those from the Tambo region are villous and those from the Cuzco area are moderately villous. One collection (Luteyn & Lebrón-Luteyn 6348) from the vicinity of Pentes is densely villous- even the corolla tube, which is totally glabrous in all other specimens seen, is covered with hairs. In addition, the calyx of that collection is heavily suffused with purple and the corolla has purple veins. Further investigation may reveal that this color pattern is related to the mode of pollination. The collections of Madison 10367-70 and Luteyn & Lebrón-Luteyn 6447 have conspicuous purplish veins on the lower leaf surface.

Jaubert (1861) named didierana to commemorate Ernest and Alfred Grandidier. In his description, he described the fruit as a capsule, and Macbride (1962), in his Flora of Peru, followed suit. I have not seen the type (presumably lost), and there are no fruits on any of the specimens examined. However, because all related Peruvian species with long-tubular corollas have baccate fruits, I believe that the fruit of S. didierana is probably baccate as well. Nevertheless, further field work is needed to confirm this.

Although Grandidier's collection from Madagascar is at P, I was unable to locate Grandidier's South American collections, in spite of the assistance of Drs. Heine, Jolinon and Lourteiq during my visit at P. However, because the type still may be relocated, a neotype is not designated here.

Local name. Peru: Jácapaillo (Keel & Andrade 442).

2. Salpichroa microphylla (Dunal) Keel, comb. nov.
Juanulloa microphylla Dunal, in de Candolle, Prodr. 13(1): 531. 1852; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 85. 1962. Type. PERU. Junín: Huasahuasi, 5-12 Dec 1779 (fl), Pavón s.n. (holotype, G).
Salpichroa longiflora Benoist, Bull. Soc. Bot. France 85: 408. 1938. Type. Peru. Junín: Huasahuasi, Oct-Dec 1779 (fl), Dombey s.n. (holotype, P).

Scandent shrubs to 3 m tall, the young stems, leaves and pedicels puberulous or villous, sometimes with gland-tipped trichomes, but the pedicels sometimes glabrous. Branches and twigs flexuous, terete or winged, with wings on 1 to 4 sides, each node sometimes with 2 to 4 semicircular scales. Leaf blades elliptic or ovate, 1.8-4 x 1.3-2.5 cm; petiole subfiliform, 10-15 x 0.5-1 mm. Pedicels 0.8-2 cm long; calyx unequally divided, connate for more than 1/2 its length, the tube 0.7-1.7 x 0.6-1 cm, glabrous or villous, the lobes triangular-lanceolate, subequal, ciliate or

occasionally gland-tipped, 8-13 X 3-3 mm, apex acute to acuminate; corolla elongate-tubular, yellow, the tube straight, 55-65 x 5-8 mm, externally glabrous to sparsely appressed puberulous on upper 1/3 to 1/2, internally glabrous, the lobes induplicate, narrowly triangular, equal, with well developed venation, 11-20 x 5-6 mm, apex attenuate, glabrous to puberulous, the margins ciliate, villous or glandular-villous, the sinuses with 5 unequal obtuse or acute teeth ca. 1-2 mm long, glabrous or ciliate, both lobes and teeth reflexed by 180° at anthesis; stamens exserted, equal, the filaments adnate to corolla tube for ca. 2/3 length, the free portion 2-2.6 cm long, the anthers 5-7 mm long; style exceeding stamens, (5.7-)7-8 cm long. Berry (immature) oblong, 3.5 x 1.2 cm.

Distribution. Semi-moist shrubby woodland within sub-puna, 3500-4000 m, frequent along small mountain paths climbing on Berberis sp.; central Peru. Flowering October-January, and sometimes in June.

Specimens examined. PERU. Without locality: 27 Dec 1878 (fl), Martinet 1317, 1618 (P), without date (fl), Maclean s.n. (K). Huánuco: Tambo de Vacas, 3960 m, 10-24 Jun 1923 (fl), Macbride 4419 (F). Junín: between Bella Vista and Marainico, ca. 1 hr. car ride from Palca, 3780 m, 27 Jan 1979 (fl, fr), Keel et al. 386 (BM, G, GOET, K, LPB, MO, NY, P, S, U, US, USM).

Morphologically, Salpichroa microphylla resembles the Bolivian population of S. glandulosa. However, although the two species have corolla tubes of similar lengths and corolla lobes with similar teeth in the sinuses, they differ in growth habit, habitat preference, and the morphological characteristics given in Table IV. Salpichroa microphylla is a tall climbing shrub of semi-moist woodland, whereas the Bolivian population of S glandulosa is a small, weak-stemmed shrub pendent from rock crevices near stream banks.

Macbride (1962) has treated Juanulloa microphylla Dunal as a synonym of Salpichroa dependens. However, in his description of J. microphylla (p. 85), he states "...in habit and foliage it [J. microphylla] suggests Salpichroa it may, when flowers are discovered, be found to be Iochroma." Apparently, he was uncertain as to which genus J. microphylla belongs.

A close examination of the type of J. microphylla (Pavón s.n.), however, revealed that it is similar to the type of S. longiflora (Dombey s.n.). Because the handwriting on the labels of both specimens is identical, I believe that both were collected in 1779 on Dombey's, Pavon's and Ruiz's expedition through South America (Ruiz, 1940). Although the fertile parts of the type specimen of J. microphylla that I examined consist only of a calyx tube and an ovary, its vegetative parts are clearly similar to that of Dombey's

collection. Dunal described the leaves of J. microphylla as mucronate and Macbride followed suit. To me, these few "mucros" are merely dried leaf tips.

Macbride 4419 was incorrectly cited in the Flora of Peru as S. dependens. Although the calyx of S. microphylla resembles that of S. dependens, the characters of corolla, including the presence or absence of teeth between lobes, the spreading or reflexed position of the lobes at anthesis, in addition to the presence or absence of a nectariferous disc distinquish these two taxa (see Key on p. 43 & 44).

3. Salpichroa glandulosa (Hooker) Miers

Scandent shrubs to 3 m tall or gnarled shrubs to 0.5 m tall or pendent shrubs to 1 m tall, the young stems, leaves, pedicels and calyx puberulous, hirsute or pilose, rarely villous with partly gland-tipped trichomes, but the calyx lobes sometimes ciliate, the leaves and pedicels sometimes glabrous. Branches and twigs rarely flexuous, terete or winged, with wings on 1 or 2 sides, mature branches sometimes with adventitious roots. Leaf blades ovate to elliptic or lanceolate, 1.2-4(-5.4) x 0.7-3(-3.5) cm; petioles subfiliform, 7-25(-40) x 0.5-1 mm. Pedicels 0.7-2.5(-4) cm; calyx equally divided, the lobes linear, subequal or unequal, 0.8-2.5 X 0.1-0.3 cm, connate only at the base, this sometimes swollen after fruiting, apex attenuate; corolla elongate tubular, greenish-yellow to

sulphur-yellow, sometimes golden-yellow to pale yellow, the tube slightly wider distally, (3.3-)3.8-6.5(-7) x 0.3-0.9 cm, externally pilose or puberulous and often with gland-tipped trichomes, rarely glabrous, internally glabrous, the lobes induplicate to valvate, triangular or ovate-triangular to lanceolate, equal, with well developed venation, (2-)5-15(-20) x (2-)3.5-8 mm, apex acute or acuminate to cuspidate, the sinuses often, but not always, provided with 5 equal or subequal retuse teeth, 2.5-3 x (0.5)1-5.5 mm, glabrous or ciliate or with same types of pubescence as corolla tube, both lobes and teeth reflexed by 180° at anthesis; stamens equal or subequal, the filaments included to exserted, adnate to corolla tube for ca. 2/3-3/4 length, the free portion 0.6-2.5 cm long, the anthers partially to completely exserted, 3-5 mm long; style exceeding stamens, 3.4-7 cm long. Berry black with dull sheen when mature, immature green, elliptic-oblong, 2.8 x 1-1.6 cm.

Key to the subspecies of Salpichroa glandulosa

1. Pedicels 0.7-2.5 cm long; calyx base sometimes swollen after fruiting; corolla lobes induplicate, triangular, the sinuses with 5 equal or subequal retuse teeth. Distributed in Peru and on the NW side of Cordillera Tres Cruces in Bolivia ..... 3a. subsp. glandulosa.
1. Pedicels 1.5-4 cm long; calyx base not swollen after fruiting; corolla lobes valvate-induplicate, ovate-triangular to lanceolate, the sinuses without teeth.

Distributed on the SE side of Cordillera Tres Cruces in Bolivia ..... 3b. subsp. weddellii.

3a. Salpichroa glandulosa (Hooker) Miers Subsp. glandulosa London J. Bot. 4: 325. 1845; Walpers, Repertorium Botanices Systematicae 6: 613. 1847; Miers, Illustrations of South American Plants 1: 5. 1850; Dunal, in de Candolle, Prodr. 13(1): 472. 1852; Weddell, Chloris Andina 2: 98. 1859; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1):63. 1962. Atropa glandulosa Hooker, Bot. Misc. 2: 230. 1831; Hooker's Icon Pl. 2: tab. 106. 1837. Type. PERU. Pasco: Huaylluay, near Pasco, 24 Jul 1830 (fl), Cruckshanks s.n. (lectotype, K, here designated).

Salpichroa glandulosa (Hooker) Miers var. longiflora Dunal, in de Candolle, Prodr. 13(1): 472. 1852. Type. PERU (see discussion). without locality, without date, Pavón s.n. or Ruiz & Pavón s.n. (holotype, G; isotype, BM).

Salpichroa amoena Benoist, Bull. Soc. Bot. France 85: 409. 1938. Type. BOLIVIA. La Paz: nr. Sorata, between Laripata and Iiconquaya, Paracollo, 3300-3600 m, Aug-Jan 1898 (fl, fr), Mandon 438 (holotype, P; isotypes, BM, G, GH, K, NY, P-3 sheets, S, W-2 sheets).

Leaf blades 1.2-4(-5.4) cm long ; petioles 0.7-2.5 (-3.3) cm long, glabrous or puberulous or glandular-puberulous. Pedicels 0.7-2.5 cm long; calyx green or tinged with purple-

bronze, the lobes 0.8-2.5 cm x 1-2 mm; corolla greenish-yellow to golden-yellow, the tube with green nerves, the nerves sometimes tinged with purple, (3.3-)3.8-6.5 x 0.3-0.8 cm in diam., the lobes induplicate, triangular, (0.2-)0.5-1.3 cm long; the sinuses with 5 equal or subequal retuse teeth.

Distribution. Mainly in puna, sub-puna, and montane cloud forests, among rocks or in rock crevices nr. streams or lakes but also occurring in scrublands, roadsides, grass-steppe areas or agricultural fields, 3050-4700 m; most common in the western and southern part of central Peru, extending into the NW side of Cordillera Tres Cruces, Bolivia. Flowering October-April, fruiting December onwards.

Specimens examined. COLOMBIA(?). Without locality, without date (fl), Lobb 291 (K). PERU. La Libertad: S of Huamachuco, on eastern base of Cerro Huaylillas, 3900 m, 27 Nov 1936 (fl), West 8127 (GH, UC). Ancash: Cordillera Blanca, 4300 m, 12 Aug 1957 (fl), Rauh-Hirsch P1941 (F); Huarás, 4100 m, without date, 1906 (fl, fr), Weberbauer 2936 (G). Pasco: nr. Pasco(=Cerro de Pasco), without date, 1834 (fl), Mathews 667 (BM), Jul 1835 (fl), M'Lindley 667 (G); on road 24.4 km from Huayllay to Santo Domingo, 4230-4610 m, 6 Mar 1977 (fl), Boeke 1134 (NY). Lima: Río Blanco, 4570 m, 20-25 Mar 1923 (fl), Macbride 3050 (F, NY, US); between San Mateo & Casapalca, above Chicla, 3800-3900 m, 27 Jan 1950

(fl), Ferreyra 6540 (US); on highway Lima-Chicla, 1/2 mile before Chicla, 4328 m, 24 Feb 1963 (fl, fr), Saunders 817 (K); Lima, without date (fl), Maclean s.n. (K). Junín: nr. Sacsacancha(=Casacancha), without date (fl), Maclean s.n. (K); between Acopalca & Pariahuanca, 4400 m, 16 Mar 1939 (fl), Stork 10932 (F, UC); between Huancayo and Acopalca, Feb 1948 (fl), Soukup 3688 (F, US); nr. Huancayo, Mount La Juntay, 4700 m, 27 Apr 1929 (fl, fr), Killip & Smith 22073 (F, MO). Huancavelica: 13 miles SW of Huancavelica, nr. Huama, 4000 m, 28 Dec 1974 (fl, fr), Plowman & Davis 4645 (F, GH, S, U); Patacancha, 4000 m, 8 Apr 1961 (fl), Tovar 3179 (US); vic. of Pucayaco, 70 km NW of Huanta, 3720 m, 1 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6332 (NY, US, USM). Ayacucho: half way from Quinua to Tambo, 3900 m, 10 Feb 1979 (fl, fr), Keel 413 (NY, USM); between Quinua & Tambo, Laguna de Apacheta, 4000 m, 13 Feb 1979 (fl, fr), Keel 418 (BM, G, K, MO, NY, P, U, US, USM); 14 km NE of Quinua, 3690 m, 2 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6336 (B, BM, BR, CORD, F, G, GOET, K, LPB, MO, P, NY, S, U, US, USM, VEN); on road between Huanta & Ayacucho, ca. 15 km before Ayacucho, ca. 3050 m, 1 Jan 1962 (fl), Saunders 726 (NY). Apurimac: Quebrada of Juccuchic-Chupan on trail Chincheros-Andahuaylas, 4200 m, 3 Nov 1935 (fl), West 3719 (GH, MO, UC); Andahualas-Abancay road, km 98, ca. 100 km W of Abancay, 3900 m, 4 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6371 (G, K, MO, NY, P, US, USM); ca. 160 km from Chalhuanca

to Puquio, 4110 m, 6 Jan 1962 (fl), Saunders 777 (NY). Cuzco: on road between Ollantaytambo and Alfamayo, 22 km NW of Ollantaytambo, 3600 m, 11 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6445 (NY, US, USM); Chincheros, nr. the community of Taucca, 13° 25′ S, 72° W, 4050-4250 m, 14 Jan 1982 (fl), Davis et al. 1554 (F, NY), summit of Antakillqa, 13° 23′ S, 72° 2′ W, 4500 m, 20 Jan 1982 (fl), Davis et al. 1707 (F, US); Prov. Paucartambo, Hacienda Churu, 3500 m, Jan 1926 (fl), Herrera s.n. (US); Chectacuchu, nr. Marcapata, 4100 m, 11 Dec 1943 (fl), Vargas 3752 (F). BOLIVIA. La Paz: 2 km S of Ambana, 3500 m, 19 Dec 1980 (fl), Beck 4164 (NY); top of the pass on the Tipuani-Ancoma-Sorata trail down to Sorata, 4250 m, 30 Apr 1926 (fl), Tate 824 (NY); Luipichi, nr. Laripata, 3960 m, 27 Sep 1920 (fl), Williams 1547 (NY, US); Sorata, 4500 m, Dec 1919 (fl), Günther 5831 (US); Cordillera Pakollu, between Sorata and Achacachi, 4100 m, 12 Apr 1939 (fl), Balls 6468 (BM, K, UC, US), 3750 m, 15 Mar 1979 (fl, fr), Keel & Quéspe 467 (NY, US); Valle de Zongo, 4050 m, 12 Jan 1980 (fl, fr), Beck 2772 (NY), 4125 m, 1 Feb 1981 (fl), Beck 6099 (NY), 4090 m, 12 Dec 1973 (fl), Graf 303 (NY); La Fabulosa, tin mine at the head of the Challana valley, 4570 m, 1 May 1950 (fl), Brooke 6368 (BM, F); road to Peñas, 47 km from Mina Fabulosa, 4500 m, 18 Feb 1980 (fl), Beck 2891 (NY); between La Cumbre & Unduavi, 3650 m, 21 Feb 1975 (fl, fr), Plowman & Davis 5138 (F, GH, K, MO, U); Unduavi, 3048 m, Oct 1885 (fl), Rusby 1935 (F, GH ,NY, US).

There are some doubts about the type collections of Atropa glandulosa. A single sheet from K, which originally belonged to the Hooker Herbarium, has three mounted specimens. On top is a small branch of S. microphylla with a signature by Maclean underneath (probably collected by Maclean). At the bottom of the sheet is a branch of S. glandulosa, with the signature of Lobb, and the word Colombia. This latter specimen represents the only S. glandulosa from Colombia. Because this species occurs neither in northern Peru, nor in Ecuador and because recent collectors have never found S. glandulosa in Colombia, I question the accuracy of the locality indicated by Lobb. In the center of the sheet is a specimen of S. glandulosa bearing a label with the locality Huaylluay, near Pasco. However, no collector is indicated. Because the handwriting on this label matches well Hooker's handwriting (Burdet, 1975), I suspect that the specimen on this central portion of the sheet was collected by Cruckshanks and used by Hooker for his description. Thus, I here designate it as lectotype. In Hooker's Icones Plantarum (1837), the drawing of S. glandulosa shows well the characters of the type specimen, but it fails to show the typical character of the species- teeth in the sinuses of the corolla lobes.

Macbride (1962) cited the type locality of Atropa glandulosa as Obrajillo, valley of Canta. Although Cruckshanks collected in Obrajillo during his journey to

Pasco (=Cerro de Pasco), the type of A. glandulosa was actually collected in Huayllay (Cruckshanks, 1831). Hooker in his type description also indicated that the plant was from Huayllay, near Pasco. Macbride's type citation is obviously a copying mistake, because A. glandulosa is described on a page which also gives a description of A. biflora, whose type specimen was collected in Obrajillo, valley of Canta.

The type of S. glandulosa var. longiflora from G has a label which mentions Pavón as the collector and Nueva Espana (=Mexico) as the collection locality. However, an identical specimen from BM has a label indicating that it was collected in Peru by Ruiz and Pavón. It is well known that the South American collection of Ruiz and Pavón has been confused with the Mexican collection of Sessé and Mociño (Colmeiro, 1858). Because Pavón never collected in Mexico and because no species of Salpichroa has been found in Mexico, I believe that the locality mentioned on the label at G is wrong. According to the species description given here, this collection is morphologically identical to specimens of S. glandulosa collected in Peru, and, therefore, var. longiflora is not recognized here .

Salpichroa glandulosa, a widespread species, exhibits considerable morphological variation, probably resulting from its adaptation to various habitats. The glandular

pubescence, from which the specific epithet is derived, occurred frequently in the collections studied. However, the specimens from the Department of Junín and Huancavelica are only hirsute, and two collections, Saunders 726 and West 3719, are nearly glabrous. In the Peruvian specimens, the staminal filaments are included at anthesis, except for three collections (Luteyn & Lebrón-Luteyn 6371 & 6445, and Vargas 3752) that contain some flowers with exserted filaments. Two of these three collections are from the Cuzco region (Luteyn & Lebrón-Luteyn 6445, Vargas 3752). They have flowers with included stamens and with exserted stamens on the same plant. In all flowers, the styles exceed the stamens in length, but they differ in exceeding or not exceeding the corolla tubes. The length of the corolla tubes and the size of teeth in the sinuses of the corolla lobes also show quantitative variation in some plants. Specimens of West 8127, from the Department of La Libertad, and those of Luteyn & Lebrón-Luteyn 6332, collected near an agricultural field, have the shortest corolla tubes (3-3.5 cm). The Cuzco and La Libertad collections are on the periphery of the geographical range of S. glandulosa. It is not unusual to find character deviation in the peripheral populations of a taxon.

The Bolivian collections of S. glandulosa from the puna or sub-puna regions and the Bolivian collections from montane cloud forests show character differences, though

they all occupy the same habitat, namely rock crevices. The puna or sub-puna collections are more similar to the Peruvian collections with which they share glandular pubescence, shorter corolla tubes, included filaments and triangular corolla lobes, whereas the cloud forest collections have eglandular pubescence, longer corollas with well exserted filaments and styles, and the shape of corolla lobes approaching cuspidate. Gene exchange between the Bolivian populations in these two habitats is indicated by the presence of intermediate forms.

The Bolivian collections from montane cloud forests differ conspicuously from the other collections of subsp. glandulosa in the relative size of corolla tube and length of stamens and styles. The largest corolla observed in collections from the Bolivian cloud forest is about twice the size of the smallest corolla in the Peruvian collections. In most plants of S. glandulosa the anthers are not completely exserted; moreover the styles exceed the stamens only slightly (three exceptions from the Peruvian collections are mentioned above). In contrast, in plants from Bolivian cloud forest, the anthers and filaments are all far exserted and styles exceed the tip of the anthers by about 3-5 mm at anthesis. These character differences suggest that these populations have different pollination mechanisms. If the plants are self-compatible, those of the Bolivian cloud forest population will be less likely to

self-pollinate. If they are self-incompatible, the flowers with corolla tubes of different lengths may require different pollinators. The specimen label of Luteyn & Lebrón-Luteyn 6336 states that this population of S. glandulosa was visited by hummingbirds (species unknown). However, members of this genus propagate naturally by suckers. Pollinators may not be obligatory for the survival of this species, but they do contribute to the diversification of reproductive strategies and the enrichment of genetic composition. Further field work is needed to confirm the pollination mechanism of this species.

Fruits of S. glandulosa are edible, long distance dispersal by animals or even by man is facilitated and further contributes to the wide occurrence of this species.

Local names and uses. PERU: pepino silvestre (Luteyn & Lebrón-Luteyn 6336), aqha aqha (Davis et al. 1554), pires pires (Davis et al. 1707), fruit edible (Davis et al. 1707). "Plants aromatic" was indicated on 2 collections, Boeke 1134 and Keel 418, leaves and branches grazed by sheep (Mathews in Hooker, 1837).

3b. Salpichroa glandulosa (Hooker) Miers subsp. weddellii (Benoist) Keel, stat. nov. Salpichroa weddellii Benoist, Bull. Soc. Bot. France 85: 408. 1938. Type. Bolivia. Cochabamba: between Llave and Morochata, Dec 1846 (fl), Weddell 4116 (holotype, P; isotypes, P-2 sheets).

Leaf blades (0.9-)2.5-4(-5) cm long ; petioles (0.3-)0.8-1.5(-4) cm long, pilose, never glabrous. Pedicels (0.3-)1.5-4 cm long; calyx lobes (0.7-)1.2-2 x 0.1-0.3 cm; corolla greenish-yellow to pale yellow, the tube (33-)50-70 x (2.5-)5-8.5 mm, the lobes valvate-induplicate, ovate-triangular to lanceolate, (0.6-)1.2-1.5(-2) cm long; the sinuses without teeth.

Distribution. In montane cloud forests, on dry slopes or near snow line, most frequently in wet rock-crevices, 3000-4050 m; in the Department of Cochabamba, on the SE side of Cordillera Tres Cruces, Bolivia. Flowering November-February, fruiting January onwards.

Specimens examined. BOLIVIA. Cochabamba: km 69, on the way to Chaparé, 3000 m, Nov 1964 (fl), Cárdenas 6147 (US); Choro, above the Cocapata river ca. 100 miles NW of Cochabamba, across the Tunari range, 66°30'W, 17°N, 3050-3950 m, 22 Jan 1950 (fl, fr), Brooke 6040 (BM, F, NY, U), 3350-4050 m, 3 Feb 1950 (fl), Brooke 6096 (BM, F); Cordillera Chimoré, 3800 m, 2 Nov 1937 (fl), Cárdenas 2068 (US); vic. of Cochabamba, Mt. Tunari, nr. snow-line, 1891 (fl), Bang 1048 (BM, F, GH, MO, NY, US); ca. 1 km E of Challa on Carretera Fundamental 4 to Cochabamba, 4100 m, 3 Dec 1975 (fl), Davidson 3718 (NY).

Benoist (1938b) separated the Bolivian population of S. glandulosa subsp. glandulosa (=S. amoena, sensu Benoist)

from S. weddellii by the shape of the corolla lobes and the presence or absence of teeth (=smaller lobes, sensu Benoist) in the sinuses of the corolla lobes. After close examination of all available specimens, I have concluded that these two taxa (sensu Benoist) are similar in growth habit, habitat preference and all aspects of morphology (including pollen morphology) except pedicel length and presence or absence of teeth between corolla lobes. They represent two populations, separated geographically by the Cordillera Tres Cruces, which are best treated as vicariant geographic subspecies.

There is little morphological and habitat variation within this subspecies. Bang 1048 is the only collection of the subsp. weddellii with consistently though sparsely pubescent corolla tubes and lobes. Because the type of hair and degree of pubescence are highly variable within the species of S. glandulosa, they are not of diagnostic value. Cárdenas 2068, collected from a dry slope instead of wet rock-crevices (the usual habitat), does not exhibit any morphological differences except for shorter pedicels. "Herb prostrate" is indicated on the label, and adventitious roots occur on the stem of this specimen. These probably are the result of an adaptation to dry habitats.

Davidson 3718, an unicate collection, is a miniature form of this subspecies. The length of its corolla tube, 3-3.7 cm x 2.5-3.5 mm, is approximately half of the average

corolla length of subsp. weddellii. The leaves are correspondingly smaller, but except for size, there are no other distinctive characters. On his label, Davidson indicated that this plant was common in crevices of cliffs and on steep slopes-- the same kind of habitats from which the other collections come. Therefore, the smaller size of this plant may not be the result of ecological variation and the quantitative difference raises two questions: 1. Is this subsp. a polyploid complex? 2. Are the collections of this subsp. insufficient to exhibit the range of morphological variation? Because there is only one specimen available of this miniature form, I tentatively include it in the subsp. weddellii. Material for chromosome study of this species is needed.

The Bolivian populations of S. glandulosa, which include both subsp. glandulosa and weddellii, appear similar in their gross morphology to S. microphylla. The differences are discussed under the latter taxon.

4. Salpichroa dependens (Mathews ex Hooker) Miers, Lond. J. Bot. 4: 325. 1845; Walpers, Repertorium Botanices Systematicae 6: 613. 1847; Miers, Illustration of South American Plants 1: 5. 1850; Dunal, in de Candolle, Prodr. 13(1): 472. 1852; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 60. 1962. Atropa dependens Mathews ex Hooker, in Hooker's Icon. Pl. 2: tab. 107. 1837. Type. PERU. Eastern side of

the Cordillera of Peru, without date (fl, fr in figure), Mathews 829 (holotype, BM; isotype, K).

Scandent shrubs to 3 m tall, the young stems, leaves, pedicels and calyx villous, pilose or puberulous, sometimes with gland-tipped trichomes, but the vesture variable in density, the leaf blades sometimes glabrous on lower surface and the pedicels sometimes nearly glabrous. Branches and twigs occasionally flexuous, terete or winged, with wings on 1 side, each node sometimes with 1 to 4 semicircular scales. Leaf blades ovate or elliptic, 2-4.5 x 1.3-3(-3.5) cm; petioles subfiliform, 8-20 x 0.5-1 mm. Pedicels 0.5-1.6(-3) cm long; calyx unequally divided, connate for 1/3 to 1/2 its length, accrescent after anthesis and with one slit open to nearly the base, the lobes linear to lanceolate, equal or unequal, 1-1.5(-2) x 0.1-0.3(-0.4) cm before fruiting, (1.2-)1.8-2 x 0.4-0.5 cm after fruiting (measurement made at the stage of young fruits), apex attenuate; corolla elongate-tubular, greenish-yellow, the tube straight, (4.5-)5-6.5 x 0.5-0.8 cm, externally glabrous, pilose or glandular-pilose, pubescence increasing gradually from basal 1/3 of the tube to corolla lobes, internally glabrous, the lobes valvate, lanceolate to triangular, equal to subequal, with well developed venation, 0.8-1.5 x 0.4-0.5 cm, pilose or glandular-pilose or villous, spreading at anthesis, apex attenuate; stamens exserted, equal; filaments adnate to corolla tube for ca. 1/2 length, the free portion 2.7-3.5 cm

long, greenish-yellow; the anthers 4.5-5.5 mm long, brown; style exceeding stamens, (5.5-)7-8(-8.5) cm long. Berry (immature) elliptic-angular, 4.4 x 1 cm.

Distribution. Montane cloud forests or shrubby woods near moist ravines, 3200-3780 m; in NW of southern Peru. Flowering and fruiting January onwards.

Specimens examined. PERU. Junín: Comas, 3500-3600 m, without date, 1909-1914 (fl), Weberbauer 6603 (F, GH, US); Pahval, 65 km from Huancayo, 3597 m, 24 Jan 1979 (fl, fr), Keel & Centeno 384 (BM, G, GOET, K, LPB, MO, NY, P, S, U, US, USM); Pariahuanca, 3400-3500 m, without date, 1909-1914 (fl), Weberbauer 6596 (F, GH, US). Huancavelica: 3 km N of Salcabamba village, 3500 m, 9 Jan 1939 (fl), Stork & Horton 10332 (F, G, GH, UC); on the road between Colcabamba & Pampas, 3780 m, 25 Jan 1979 (fl, fr), Keel & Centeno 385 (BM, G, GOET, K, LPB, MO, NY, P, S, U, US, USM). Ayacucho: mountains NE of Huanta, 3200 m, 1-10 Feb 1926 (fl), Weberbauer 7515 (F).

Salpichroa dependens is probably related to S. didierana, because their floral morphology is similar except for the obvious differences in the division of the calyx and the length of the corolla tube.

5. Salpichroa proboscidea Benoist, Bull. Soc. Bot. France 85: 409. 1938. Type. PERU. without locality, without date, 1839-1840 (fl), Gay 1061 (holotype, P).

Scandent shrubs to 5 m tall, the young stems, leaves and pedicels pilose or villous, but the pedicels sometimes nearly glabrous. Branches and twigs flexuous, terete or winged, with wings on 1 to 4 sides, each node sometimes with 2 semicircular scales, mature branches occasionally with adventitious roots. Leaf blades ovate to ovate-lanceolate, 1.5-4(-6) x 1.2-3.5(-4) cm; petioles subfiliform, 8-20(-30) x 0.5-1 mm. Pedicels 0.8-2(-2.5) cm long; calyx deeply divided, the lobes linear, equal to subequal, green tinged with purple, moderately to sparsely villous, 12-20 x 1-1.5 mm, connate only at the base, apex attenuate; corolla elongate tubular, the tube 6-8(-8.5) cm long, upper 2/3 gradually widened, 3-5 mm wide at base, 0.8-1.3 cm wide near throat, salmon-pink except basal 1/5 nearly white, glabrous externally and internally, the lobes triangular, equal, yellow, induplicate to valvate, with well developed venation, 5-8 x 5-7 mm, ciliate, apex acuminate, reflexed by 180° at anthesis, 10 dark lines running from the sinuses and the middle of the lobes to the base of the tube; stamens with anthers partially exserted, equal, the filaments adnate to corolla tube for ca. 4/5 length, the free portion 0.8-1.2 cm long, the anthers 3-4 mm long; style exceeding stamens, (6-)6.5-8(-8.5) cm long, the stigma clavate to subcapitate. Berry (immature) 1.8 x 0.9 cm, pale-green tinged with red purple bands.

Distribution. This species is known only from one locality in southern Peru, near Abra Acanacu National Park, a reserve of montane cloud forest. It occurs in secondary growth along roadside slopes and often near small creeks, 2990-3320 m. Flowering December-February, fruiting February onwards.

Specimens examined. PERU. Cuzco: above Paucartambo on road to Abra Acanacu, 2987 m, 3 Feb 1975 (fl), Plowman & Davis 4924 (F, K), 16-17 kms NE of Paucartambo, 3170 m, 9 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6441 (B, BM, BR, C, COL, CORD, F, G, GB, GOET, K, LPB, MICH, MO, NY, NBV, P, S, U, UC, US, USM, VEN), 20 kms NE of Paucartambo, 3320 m, 24 Feb 1979 (fl, fr), Keel 438 (BM, G, K, LPB, MO, NY, P, S, US, USM).

The dominant flower color of Salpichroa is yellow; its spectrum ranges from greenish-yellow through pale yellow to sulfur yellow. Therefore the color pattern found in S. proboscidea merits special attention. Its corolla lobes are, as expected, yellow, but the corolla tube is salmon-pink with ten dark lines running from the sinuses and the middle of the corolla lobes to the base of the tube. Because it has been observed that some species of Salpichroa are visited by hummingbirds, this salmon-pink coloration could be the result of evolutionary specialization towards bird pollination.

Although it probably does not play a role in pollination, the color change in the calyx is quite interesting. During flowering, the calyx is mostly green tinged with purple or dark red, but it turns dark purple in fruit.

Local names and uses. PERU. Nustos (Luteyn & Lebrón-Luteyn 6441), fruits not eaten locally.

6. Salpichroa hirsuta (Meyen) Miers, London J. Bot. 4: 325. 1845; Walpers, Repertorium Botanices Systematicae 6: 613. 1847; Miers, l.c. 7: 334. 1848; Miers, Illustrations of South American Plants 1: p.6, 133 & Plate 28A. 1850; Dunal, in de Candolle, Prodr. 13(1): 472. 1852; Walpers, Ann. Bot. Syst. 3: 169. 1852; Weddell, Chloris Andina 2: 97. 1859; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 63. 1962. Atropa hirsuta Meyen, Reise um die Erde 1: 466. 1834; Meyen, Nov. Actorum Acad. Caes. Leop. - Carol. Nat. Cur. 19 (suppl. 1): 389. 1843. Type. Peru. Puno: Pizacoma, 4580 m, Apr 1836 (fl), Meyen s.n. (holotype, B, n.v., presumably destroyed; lectotype, K, here designated).

Stunted shrubs to 2 m tall, the young stems, leaves, pedicels and calyx hirsute, pilose or sometimes with gland-tipped trichomes, but the vesture variable in density, the leaf blades sometimes nearly glabrous. Branches and twigs terete or rarely winged, with wings on 1 or 2 sides. Leaf

blades ovate to elliptic, (1-)1.5-3.6(-7) x 0.8-2.5(-5.5) cm; petioles filiform to flattened, (5-)10-25(-30) x 0.5-1(-2) mm. Pedicels (0.5-)1-2.2 cm long; calyx deeply divided, the lobes linear, subequal, 0.5-1.5 x 0.1-0.2 cm, connate only at the base, apex attenuate; corolla pale yellow to greenish-yellow, infundibular, the tube gradually wider or inflated on upper ca. 2/3 length, 2.8-4 x 0.5-1 cm at inflated part, 1-5 mm wide at constricted part, externally hirsute or nearly glabrous or rarely glandular-pilose on inflated part, the rest glabrous, internally glabrous, the lobes valvate, semicircular, with apiculate apex, subequal, 3-7 x 3-8 mm, hirsute or glandular-hirsute or rarely ciliate, reflexed by 180° at anthesis; stamens with anthers partially exserted, equal, the filaments adnate to corolla tube for ca. 2/3 length, the free portion 0.6-1 cm long, the anthers 3-4 mm long; style exceeding or not exceeding stamens, 2.8-4.2 cm long. Berry obovoid, minutely beaked, the beak ca. 1 mm long, dark purple, 3.1 x 1.5 cm.

Distribution. In puna or dry regions, between 3000 and 4580 m, in rocky places, rock crevices, and occasionally among the Inca ruins; in southern Peru, the Department of Puno, and along Lake Titicaca and the Andes, extending to west-central Bolivia. Flowering November-May, mature fruits found in March.

Specimens examined. PERU. Puno: vic. of Lake Titicaca, Occa Pampa (Ocopamba?), 3965 m, 10 Dec 1919 (fl), Shepard 76 (GH); Puno-Juliaca highway km 7, 3350 m, 23 Apr 1977 (fl), Boeke & Rossel 1564 (NY); ruins of Sillustani, 32 km NW of Puno, 3900 m, 25 Mar 1979 (fl), Keel 487 (MO, NY, US, USM); nr. Puno, Granja de Salcedo, 3835 m, 23 Nov 1935 (fl), Mexia 7779 (BM, F, G, GB, K, NY, S, U, UC, US), Mexia 04198 (GH, MO, UC), 3860 m, 16 Nov 1938 (fl), Vargas 1274 (F, MO), rocky hill 1 km beyond Granja de Salcedo, 3962 m, 8 Mar 1979 (fl, fr), Keel 453 (BR, F, G, MO, NY, US, USM, VEN); nr. Puno, 4000 m, without date, 1935 (fl), Soukup 88 (F), Puno, Nov 1937 (fl), Soukup 88 (GH); Juliaca-Arequipa road, km 101-102, ca. 39 km S of Santa Lucia, 4025 m, 11 Dec 1978 (fl), Luteyn & Lebrón-Luteyn 6467 (G, K, MO, NY, P, US, USM); San Antonio de Esquilache, 3810 m, 24 May 1937 (fl), Stafford 767 (BM, F). BOLIVIA. La Paz: nr. Lake Titicaca, Guaqui, Jan-Mar 1903 (fl, fr), Hill 352 (K), 3900 m, Nov 1911 (fl), Herzog 2507 (NBV, S, W); nr. Querqueta, 5-10 Mar 1934 (fl), Hammarlund 240 (S); Comanche, 3500 m, 16 Nov 1974 (fl), Keel 134 (NY), 4000 m, 8 Dec 1980 (fl), Beck 4078 (NY). Cochabamba: Tunari slopes, 3000 m, Mar 1939 (fl), Cárdenas 2294 (US).

When Miers first separated the genus Salpichroa from Atropa in 1845, his species delimitation of S. hirsuta was not clearly made. In addition to Meyen's type collection, he cited many other specimens, such as Jameson 32, 125 &

301, Hartweg 1311, and Goudot s.n. I have not seen Jameson 301, but Jameson 32 & Hartweg 1311 are in fact S. diffusa, while Jameson 125 & Goudot s.n. belong to S. tristis var. tristis. Therefore, the various characters which he pointed out in his description are not typical of S. hirsuta. He stated, for example, incorrectly:"...the corolla [is] about ten lines long, ...having oblong obtuse lobes, ...the oval berry is terminated by the persistent glabrous style." Moreover, the description of the crenate leaf margin based on the collection of Maclean s.n. does not occur in any known species of Salpichroa and not even in the Maclean specimen studied by Miers! Miers in 1848 redefined S. hirsuta, referring only to Meyen's collection, and placed all the rest-- Jameson 32 & 301, Goudot s.n. and Maclean s.n. -- under the new name S. diffusa. (Maclean s.n. is herein identified as S. tristis var. tristis.) In this revision, the species concept of S. hirsuta is identical to that of Miers' publication in 1848, although this name was first published in 1845.

Salpichroa hirsuta is easily recognized by its mature flowers with partially inflated corolla tubes and short apiculate apices on semi-circular corolla lobes. Within the species, the basic type of pubescence is hirsute, but slight variation exists. The glandular-hirsute type of trichome is found in the following collections: Luteyn & Lebrón-Luteyn 6467, Stafford 767, Hill 352, Herzog 2507, and Beck 4078.

The entire plant is usually very hairy except for the glabrous turions (Keel 453) and the corolla tube in the collection of Beck 4078. Meyen's type specimen has a very small branch with one immature flower. Without the hirsute pubescence on the vegetative parts, this specimen would be rather difficult to identify.

Macbride(1962) doubted whether S. hirsuta extends to Colombia. According to current information, this species is not found there.

Local names and uses. Peru. Llungullungu (Shepard 76); Llautia (Keel 487); Yuncu-yuncu (Keel 453). Mature fruits edible and leaves grazed by llamas (Keel 453).

7. Salpichroa weberbaueri Dammer, Bot. Jahrb. Syst. 37: 640. 1906; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 66. 1962. Type. Peru. Ancash: nr. Ocros, 3500-3700 m, 28 Mar 1903 (fl), Weberbauer 2693 (holotype, +B = photo F neg. 2945, photos, F, GH, NY; fragments, F; isotype, G).

   Salpichroa diffusa Miers var. longiflora Hicken, Apuntes Hist. Nat. 1: 175. 1909 [1913]. Type. Peru. Cuzco: Sicuani, 3551 m, 6 Mar 1903 (fl), Hicken 42 (lectotype, S).

   Salpichroa tenuiflora Benoist, Bull. Soc. Bot. France 85: 54. 1938. Type. Ecuador. Tungurahua: Baños, 2134 m, Sep 1857 (fl, fr), Spruce 5057 (holotype, P; isotypes,

BM, C, G, GH, GOET, K, NY, W-3 sheets). (The above information is based on the sheet at K. In the original description the collection number was wrongly printed as 5054.)

Scandent or pendent shrubs to 2 m tall, the young stems, leaves, pedicels, calyx and corolla puberulous, pilose or sometimes with gland-tipped trichomes, but the leaf blades sometimes glabrous or ciliate along the margin and major veins, the calyx and corolla lobes sometimes ciliate. Branches and twigs rarely flexuous, terete or winged, with wings on 1 or 2, rarely 4 sides, each node sometimes with 2 (rarely more than 3) semicircular scales. Leaf blades ovate to ovate-elliptic, (1-)1.5-4-(-6) x (0.7-)1-3.5(-5.3) cm; petioles subfiliform to flattened, 5-15(-20) x 0.5-1 mm. Pedicels 0.4-1.5 cm long; calyx deeply divided, the lobes linear, equal to subequal, 0.5-1.3 x 0.1 cm, connate only at the base, apex attenuate; corolla elongate-tubular, the tube yellow to greenish-yellow or orange-yellow, 2.2-2.8(-3.2) cm long, upper 1/3 gradually widened, 1.5-3(-4) mm wide at base, 3-5.5(-6.5) mm wide near throat, glabrous internally, the lobes triangular-lanceolate, yellow, equal or subequal, valvate to induplicate, with 2 furrows on the lower half, 3-6 x 1-2 mm, glabrous internally, apex acute, horizontally spreading to reflexed by 135° at anthesis; stamens included, equal, the filaments almost completely adnate to corolla tube, the free portion 1-1.5(-2.5) mm long, the anthers

1.5-2.5 mm long; style nearly equal to the throat of corolla tube or slightly exserted, exceeding stamens, 2-3 cm long, glabrous or sparsely ciliate or sericeous. Berry (immature) ovoid, 1.2 x 0.7 cm.

Distribution. Grass pastures, hedge-rows near agricultural fields, stone walls in ruins, stream banks or shelters of earthy banks, 2100-4100 m; in central Ecuador, west-central and southern Peru. Flowering December-April, fruiting December onwards in Peru, September in Ecuador.

Specimens examined. ECUADOR. Cotopaxi: nr. Pilaló, between Latacunga and Quevedo, 2590 m, 9 Apr 1979 (fl, fr), Keel 502 (B, BM, BR, CORD, F, G, GOET, K, LPB, MICH, MO, NY, P, S, U, UC, US, USM, VEN). PERU. Without locality: without date 1869 (fl), Whiteley s.n. (BM). Ayacucho: valley Puquio, between Lucanas and Puquio, 3400 m, 14 Mar 1957 (fl, fr), Rauh-Hirsch P463 (F). Apurimac: between Cotaruse and Colca, ca. 15 km S. of Chalhuance, 3000-3100 m, 16 Dec 1962 (fl, fr), Iltis et al. s.n. (K, UC). Cuzco: Calca, Juchuy Cuzco above Hacienda Venero, 3719 m, 4 Mar 1979 (fl, fr), Keel & Carrillo 444 (B, BM, BR, COL, CORD, F, G, GB, GOET, K, LPB, MICH, MO, NY, P, S, U, UC, US, USM, VEN), above Hacienda Paucartica, 3600 m, 8 Jan 1937 (fl, fr), Vargas 157 (F, P); Pisaq, ruins above town, 3500 m, 27 Jan 1975 (fl), Plowman & Davis 4894 (K); Oropesa, Tipon ruins above town, 3475 m, 6 Mar 1979 (fl), Keel & Andrade 450 (NY, US, USM);

on road to Acomayo, 3900 m, 8 Jan 1939 (fl), Vargas 9753 (F, G, UC); Sicuani, 3600 m, 8 Apr 1915 (fl), Cook & Gilbert 92 (US), 4100 m, 18 Feb 1937 (fl), Stafford 524 (BM, K); along road to La Raya Pass, ca. 5 km SE of Sicuani, 3600 m, 8 Jan 1963 (fl, fr), Iltis & Ugent 1226 (GH, K, U, UC); halfway between Sicuani and La Raya Pass, ESE of Marangani, ca. 8 km WNW of Ocobamba, 8 Jan 1963 (fl), Iltis & Ugent 1240 (K). Moquequa: Carumas, 3100 m, 21 Feb-6 Mar 1925 (fl), Weberbauer 7260 (F).

Except for the area around Cuzco, S. weberbaueri has a rather scattered distribution. Because its fruits are edible and its habitats are disturbed in areas such as ruins and agricultural fields, the distribution pattern of this species may reflect long distance dispersal by man.

The collections from Ecuador, all from lower elevations, display only two morphological differences: the corolla lobes are relatively fleshy in texture and lack furrows, and pubescence varies from glabrous to puberulous. These differences do not warrant the establishment of a subspecies, despite the spatial separation between the Peruvian and Ecuadorian populations. Within this species, the style varies from 2/3 length of corolla tube to equal or longer than it. The possibility of heterostyly in this species should be explored.

In Flora of Peru, Weberbauer 2936 is cited under S. weberbaueri. Although it was collected in the Department of Ancash, the same general area as the type locality of S. weberbaueri, its corolla tube is 5.5 cm long, its corolla lobes are not triangular-lanceolate, and the plant is not puberulous. In my opinion, this collection belongs to S. glandulosa. Because it is from the periphery of the geographic range of S. glandulosa, its gross morphology does not match exactly that of the central populations of S. glandulosa from the Departments of Junín, Huancavelica and Ayacucho. However, Weberbauer 2936 has retuse teeth in the sinuses of the corolla lobes and the length of corolla tube and the pubescence of the plant are within the range of variation in S. glandulosa. Therefore, in this revision, Weberbauer 2936 is identified as S. glandulosa subsp. glandulosa.

Pennell 13266 cited as 3266. It is probably due to a printing error in Flora of Peru. The flower color (rich orange) noted on the label of Iltis & Ugent 1226 may be incorrect.

Local names and uses. Peru: Aja-Aja (Keel & Carrillo 444), Quitung-quitung or Nuño-nuño (Cook & Gilbert 92); fruit edible, plant aromatic, leaves oily when crushed.

8. Salpichroa origanifolia (Lamarck) Baillon, Histoire des

Plantes 9: 288 & Fig. 363. 1888. Physalis origanifolia Lamarck, Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature, Botanique 2: 28. 1793. Type. Argentina & Uruguay, Buenos Aires & Montevideo, without date (fl), Commerson s.n. (holotype, P, n.v., photo F neg. 39393, photo, GH; lectotype, P, here designated; isotypes, P-2 sheets). Atropa origanifolia (Lamarck) Desfontaines, Catalogus Plantarum Horti Regii Parisiensis p. 396. 1829. Withania origanifolia Paillieux, Bull. Soc. Natl. Acclim. France 4(1): 667. 1884. in syn. Salpichroa origanifolia (Lamarck) Thellung, Mém. Soc. Sci. Nat. Cherbourg 38(4): 452. 1912; Cabrera, Manual de la Flora de los alrededores de Buenos Aires p. 414. & Fig. 152 B-D. 1953; Cabrera, Flora de la Provincia de Buenos Aires 5: p. 220. & Fig. 75. 1965; Burkart, Flora Illustrada de Entre Ríos (Argentina) p. 397. & Fig. 191. 1979.

Busbeckia radicans Martius, in Schrank & Martius, Hortus Regius Monacensis p. 69. 1829. nom. nud.

Atropa rhomboidea Gillies et Hooker, Bot. Misc. 1: p. 135 & tab. 37. 1829 [1830]. Type. Argentina. Buenos Aires: nr. Buenos Aires, without date, 1825 (fl, fr), Gillies s.n. (holotype, K). Salpichroa rhomboidea (Gillies et Hooker) Miers, London J. Bot. 4: 326. 1845; Walpers, Repertorium Botanices Systematicae 6:

613. 1847; Miers, Illustration of South American Plants 1: p. 7 & Plate 1. 1850; Miers, loc. cit. 1: 133. 1850 (as Salpichroma); Sendtner, Mart. Fl. Bras. 10: 150. 1846. Hicken, Chloris Platensis Argentina p. 212. 1910. Perizoma rhomboidea (Gillies et Hooker) Miers, London J. Bot. 4: 327. 1845. in syn. Perizoma rhomboidea (Gillies et Hooker) Small, Flora of the Southeastern United States p. 991. 1903.

Salpichroa rhomboidea (Gillies et Hooker) Miers var. divaricata Miers, London J. Bot. 4: 328. 1845. Type. Argentina. Córdoba: Portezuelo, from Esquina de Medrano to Frayle Muerto, without date (fl, fr), Miers s.n. (holotype, BM).

Salpichroa rhomboidea (Gillies et Hooker) Miers var. pubescens Miers, London J. Bot. 4: 329. 1845. Type. Argentina. San Luis: Between San Luis & Río Quinto, without date (fr), Miers s.n. (holotype, BM).

Salpichroma rhomboidea Dunal var. mollis Dammer, Bot. Jahrb. Syst. 37: 640. 1906. Type. Bolivia. Huayavilla, 2500 m, 20 Nov 1903 (fl, fr), Fiebrig 2144 (holotype, B, n.v., presumably destroyed; lectotype, K, here designated; isotypes, BM, G, GH-2 sheets, GOET, M, NBV, P, S, U, US, W).

Salpichroma parviflorum Dunal, in de Candolle, Prodr. 13(1): 476. 1852. Type. Brazil. São Paulo: without locality, without date, 1833 (fl), Gaudichaud s.n. (holotype, P).

Planchonia arbutiflora Dunal, in de Candolle, Prodr. 13(1) 475. 1852, in syn.

Decumbent perennial herbs forming rhizomatous clumps to 1/2 m or climbing shrubs to 2 m tall, the young stems, leaves, pedicels and calyx pilose or puberulous, rarely hirsute, sometimes with gland-tipped trichomes, but the leaves sometimes nearly glabrous, the calyx lobes sometimes ciliate. Branches and twigs rarely flexuous, terete or rarely winged, with wings on 1 or 2 sides. Leaf blades ovate to elliptic or rhombate, (0.7-)1-3.5(-6.2) x (0.5-)0.7-3.5(-5) cm; petioles subfiliform to flattened, (3-)5-20(-23) x 0.5-1 mm. Pedicels 0.3-1.4(-2) cm long; calyx deeply divided, the lobes linear, equal to subequal, 2-3(-5) x 0.5-1 mm before fruiting, 4-6(-8) x 1-2 mm after fruiting, connate only at the base, apex attenuate; corolla urceolate, white or greenish-white, the tube sometimes slightly gibbous basally, (3.5-)5-8 x (2-)4-6 mm, externally glabrous, internally with a densely woolly band occupying the second 1/4 from base, glabrous above and below, the lobes triangular to triangular-lanceolate, equal, valvate, (1-)2-3 x (0.5-)1-1.5 mm, glabrous or ciliate, sometimes ciliate-glandular, apex acute, reflexed by 180° at anthesis; stamens with anthers slightly exserted, equal, the filaments adnate to corolla tube for ca. 2/3 to 1/2 length, the free portion (1-)1.5-2.5 mm long, the anthers pale yellow, (1-)1.5-2 mm long; styles exceeding stamens, (3-)5-8 mm

long, upper 1/2 glabrous, lower 1/2 sericeous, rarely totally glabrous; ovary with a deep brick-red nectariferous disc. Berry white or pale yellow, with strong disagreeable smell, ovoid, 1-1.7 x 0.8-1.2 cm.

Distribution. A weedy species growing mainly on roadsides, waste grounds around towns, buildings, cultivated lands, lawns, terraces, grassy plains, hedgerows, gravels or stone walls of ruins, also in dry stony stream beds, on river banks, beaches, sand dunes, heavy alluvium, at edge of woods, or in thickets, 0-2000(-2900) m; in Chile (one collection only ?), Peru (two collections only), central part of southern Bolivia, Paraguay, Uruguay, southern Brazil, Argentina, and naturalized in southern U.S.A., England and southern Europe (France, Spain, Portugal, Italy), Africa (Algeria and Egypt), and Australia. In South America flowering around the year with its peak in the rainy season, September-March, fruiting September onwards.

Representative specimens. CHILE. Valparaíso: Valparaíso, Oct 1928 (fl), Günther (?) & Buchtien s.n. (NBV). PERU. Without locality: without date (fl), Mann 49 (MO, W). Cuzco: Prov. Acomayo, nr. Mayu Huillca, 2900 m, Feb 1937 (fl, fr), Vargas 255 (F, MO). Bolivia. Cochabamba: Mizque, on the road Villa Eufronio Viscarra to Station Cruz, 2030 m, 21 Dec 1949 (fl, fr), Brooke 5895 (F, NY). Santa Cruz: Comarapa, Valle Grande, 2100 m, Nov 1947 (fl, fr), Cárdenas 4002 (F, US);

Valley of Comarapa, 2000 m, 26 Oct 1928 (fl, fr), Steinbach 8571 (G, GH, MO, NY, S); Samaipata, 1500 m, 21 Mar 1920 (fl, fr), Steinbach 3798 (GH, NY, US). Chuquisaca: Serrano, 2100 m, Feb 1949 (fl, fr), Cárdenas 4130 (US). Tarija: Narváez, 1700 m, 5 Feb 1937 (fl, fr), West 8248 (GH, MO, UC); Tarija, 11 Feb 1938 (fl, fr), Blood & Tremelling 321 (NY), Mar 1864 (fl), Pearce s.n. (GH). PARAGUAY. Without locality: Sep 1875 (fl), Balansa 2124 (BM, BR, G, GOET, K, S). Amambay: Sierras de Amambay, without date, 1912-1913 (fl), Hassler 11445 (G, MO, NY, S, UC). Central: Between Tacuaral (?) and Pirayu, 1 June 1874 (fl, fr), Balansa 2124a (G); nr. Asunción, May 1889 (fl), Morong 707 (MO, NY). BRAZIL. Without locality: without date (fl, fr), Sellow s.n. (BM, BR, G, GOET, K, S, W). Guanabara: Rio de Janeiro, 1851 (fl), Andersson s.n. (S). Paraná: without locality, without date, 1858 (fl, fr), Gibert 32 (K). Santa Catarina: without locality, without date, 1816-1821 (fl, fr), Saint-Hilaire 1792 (P); Cabecuda, 26 Jun 1909 (fl), Dusén 8409 (GH, S). Río Grande do Sul: without locality, without date, 1833 (fl), Gaudichaud s.n. (P), without date, 1816-1821 (fl), Saint-Hilaire 1873 (B, P); Cristal, nr. Pôrto Alegre, 31 Mar 1949 (fl, fr), Rambo 40732 (BR, G, MO). URUGUAY. Salto: Vera, 19 Dec 1898 (fl, fr), Berro 128 (G). Río Negro: Nr. Concepción del Uruguay, Apr 1875 (fl, fr), Lorentz 76 (GOET, W). Soriano: Juan Jackson, Estancia Monzón-Heber, Nov 1941 (fl, fr), Gallinal et al. PE-4811 (U). Colonia: Colonia

Valdense, Estate of Galland, Feb 1955 (fl, fr), Dubuqnon 10 (G). Canelones: Santa Lucía, 6 Mar 1910 (fl, fr), Herter 280f (S). Montevideo: Miguelete, 40 m, Mar 1928 (fl, fr), Herter 280 b (GOET, NY, S, U, US). Maldonado: Punta Ballena, 1 Sep 1841 (fl), Descole 145 (GH). ARGENTINA. Without locality: without date (fr), Gonnot s.n. (P). Jujuy: on road from El Fuerte to Palma Sola, 20 Feb 1972 (fl), Cabrera et al. 22245 (K). Salta: Campo Quijano, 1200 m, 28 Jan 1941 (fl), Meyer 3653 (F, GH, NY, UC). Formosa: outskirts of Formosa, ca. 60 m, 5 Mar 1937 (fl), West 8484 (MO, UC). Chaco: Margarita Belén, 10 Feb 1945 (fl), Aquilar 319 (A, S). Corrientes: village of Guacara, without date (fl), D'Orbigny 73 (P); Estancia "Santa Teresa", 17 Sep 1951 (fl, fr), Pedersen 1189 (A, BR, C, G, MO, NY, P, S, U, US). Tucumán: Villa Luján, 460 m, 25 Dec 1918 (fl), Venturi 82 (A, S, UC). Catamarca: Belén, 6 Mar 1929 (fl), Cabrera 1188 (NY). Santiago del Estero: Ojo de Agua, 15 Apr 1945 (fl), Garcia 877 (A). La Rioja: La Hoyada, Dept. Chilecito, ca. 2500 m, 31 Jan 1908 (fl, fr), Kurtz 15064 (S, CORD). Córdoba: Córdoba, Dec 1878 (fr), Grisebach s.n. (K), 10 Oct 1877 (fl, fr), Hieronymus 25714 (BR, G, UC, US). Santa Fé: San José del Rincón, 5 Oct 1946 (fl), Alvarez 852 (MO). Entre Ríos: 63 km from Paraná on road to Villaguay, 60 m, 17 Jan 1966 (fr), Hawkes et al. 3249 (C). Buenos Aires: Buenos Aires, without date, 1884 (fl), Lefebvre s.n. (BR, P); Pereyra, 14 Mar 1932 (fl, fr), Cabrera 2066 (F, NY, S, US);

10 km N of Mar del Plata, road to Balcarce, 50 m, 11 Dec 1938 (fl, fr), Everdam et al. 23627 (G, GH, UC). Río Negro: Viedma, 2 Dec 1944 (fl), Meyer 7243 (A). Patagon (=Patagonia ?): Without locality, Apr 1882 (fl), Moreno & Tonini 274 (NY).

Both localities, Buenos Aires and Montevideo, are shown on the label of one single type specimen (collected by Commerson) at P. In his type description, however, Lamarck indicated that this species came from "Magellania." The curator of South American plants at P, Dr. Lourteig, has added a note on one of the isotypes, "The locality Magellan is an error. Must be Buenos Aires." According to the present distribution, S. origanifolia has never been collected near the Straits of Magellan and the majority of collections come from southern Uruguay and north-central Argentina. Therefore, there are equal possibilities that the type could have come from either Montevideo or Buenos Aires, and I have listed both as type localities.

One single collection from Chile, Günther (?) & Buchtien s.n., is of dubious origin. It has no duplicates and it is the only specimen of S. origanifolia collected in Chile. Moreover, this sheet has been passed to Herbarium Alleizette and could well be mislabeled.

Lamarck was uncertain whether or not this species was identical with Physalis curassavica L. The type of P.

curassavica is not in the Catalogue of the Linnaeus Herbarium (Savage, 1945); furthermore the description of P. origanifolia by Lamarck and that of P. curassavica by Linnaeus in Species Plantarum (1753) are too brief to distinguish these two taxa. In Hortus Cliffortianus, Linnaeus (1737) however gave a more detailed description of P. curassavica: "flore viete sulphureo, fundo purpureo". Salpichroa origanifolia, however, has white flowers. Moreover, the type of P. curassavica is, according to the Kew Index, from Curaçao or Venezuela. I have not seen a single specimen of S. origanifolia from the Caribbean or Venezuela. Therefore, though I have not seen the type of P. curassavica, I believe that these two taxa cannot be identical. The nomenclatural confusion of S. origanifolia has been discussed extensively, though not completely, by Shinners (1962).

Miers (1845) added two varieties to this species: var. divaricata with a spreading branching habit and smaller leaves, and var. pubescens with small, densely pubescent leaves and longer, slender petioles. Dammer (1906) added var. mollis, distinguished by the dense, minute, white pubescence on the leaves. Having examined hundreds of specimens, I concluded that these vegetative characters are quantitatively variable and the variation is continuous within the species. Moreover, in the same plant the new shoots produced from rhizomes usually bear larger and less

hairy leaves. The degree of pubescence and the size of leaves are apparently not very good characters for the separation of varieties. Therefore, in this revision, these varieties are not recognized.

Salpichroa parviflorum of Dunal (1852) was based on an artificial character. He described the leaf margin as "subrepandis", probably because his specimen was withered before pressing or simply not well pressed. A close examination of the type (Gaudichaud s.n.) shows that the leaf margin is in fact not wavy or uneven. Except for its smaller overall size, S. parviflorum does not differ qualitatively from S. origanifolia. Considering the size variation in many species of Salpichroa, it is doubtful whether the mere difference in size is an adequate basis to separate a species. There is one other collection (D'Orbigny 73) of plants of reduced size. These small plants could be genetic mutants or ecotypic variants.

Salpichroa origanifolia is the only Salpichroa that grows in the Southern United States. Gray (1878) described a Solanum as Salpichroa wrightii. Since then, specimens of S. origanifolia have been occasionally identified as S. wrightii. In this revision, S. wrightii is listed under the "Excluded Names". During my search to verify the type of S. wrightii, a few errors were found in both the type description and type specimen. According to the protologue

of S. wrightii, the type is Wright 1692, collected in Arizona on the Sonoita. However, the specimen designated as the holotype of S. wrightii at GH is Wright 1592 collected in New Mexico between 1851-52. The characters mentioned in the protologue apply to Wright 1592. According to Elizabeth Shaw (pers. com.) bibliographer and research taxonomist at GH, Wright 1592 is the type of S. wrightii and is from Arizona, whereas Wright 1692 is an Asclepias collected in Western Texas. This confusion probably arose because Gray cited his own distribution number rather than Wright's collection number. Thus, the type of S. wrightii should be Wright 1592 instead of Wright 1692 as cited in the type description, and the locality and date indicated on the specimen of Wright 1592 should read: "on the Sonoita in Arizona on 17 Sep 1851" instead of "New Mexico between 1851-52".

Salpichroa origanifolia is distinguished from all other members of the genus by its short, white, urceolate corolla and the woolly band inside the corolla tube. It is also the only species of Salpichroa occurring at lower altitudes, including the coastal area. Hooker (1829) originally placed it in Atropa and mentioned that it resembles A. biflora from Peru. Miers (1845) was correct in transferring this species to Salpichroa because of the general resemblance of calyx, fruits, all vegetative aspects and growth habits.

Salpichroa origanifolia is probably self-incompatible, because I have made several unsuccessful attempts to pollinate my greenhouse plants. In October, 1981, during my short stay at the Paris Botanical Garden, I observed cultivated S. origanifolia being visited by bumble bees. The dense, woolly band inside of corolla tube conceals the brick-red nectary, an arrangement which may act to prevent the drying of nectar or to exclude unwanted pollinators.

Miers (1845) described the berry as bright scarlet. This does not correspond to the fieldnotes on the specimens examined or to various other descriptions (Desfontaines, 1829; Macbride, 1962; Cabrera, 1965; Burkart, 1979) which state that the berry is white or pale yellow. The fruit color given by Miers must be an error.

Salpichroa origanifolia is a widely distributed weedy species. Originating in South America, it has been naturalized in southern United States (West, 1952) and the Mediterranean region of Europe and Africa where it has become an aggressive, pestilent weed.

Local names and uses. Argentina. Huevo de Gallo (Eyerdam et al. 23627), Huevito de Gallo (Hawkes et al. 3249, Lefebvre s.n.), Uvilla, Uva del Campo (Hieronymus, 1882), Canambú (in Dept. Mburucuyá of Prov. Corrientes, Pedersen 1189). Uruguay. Congona (Herter, 1937). Bolivia. Pacpacha (Blood & Tremelling 321). U.S.A. Lily-of-the-valley Vine, (

Thorne 39311); fruits edible and used for jam (Paillieux & Bois , 1884), with medicinal properties- diuretic or use for curing skin scab (Hieronymus, 1882).

9. Salpichroa scandens Dammer, Bot. Jahrb. Syst. 37: 641. 1906 (as Salpichroma); Cabrera, Bol. Soc. Argent. Bot. 13(4): p. 330. & Fig. 2D. 1971. Type. Bolivia. Cochabamba: Padcaya, 2000 m, 19 Dec 1903 (fl, fr), Fiebrig 2590 (holotype, +B = photo F neg. 2943, photos, F, GH, NY; fragments, F; isotypes, A, BM, F, G, GH, GOET, K, M, NBV, P, S, U, US, W).

Scandent or stunted shrubs to 3 m tall, the young stems, leaves, pedicels and calyx pilose, floccose, puberulous or sometimes with gland-tipped trichomes, the young stems and petioles sometimes stellate, the calyx sometimes ciliate, but the vesture variable in density, the leaves and peduncles sometimes nearly glabrous, trichomes sometimes densely tufted at axils between branches and petioles or peduncles. Branches and twigs rarely flexuous, terete or rarely winged on 1 or 2 sides. Leaf blades ovate to ovate-elliptic, (1.8-)2-4(-4.2) x (0.8-)1-2.5(-2.7) cm; petioles subfiliform, 5-18(-22) x 0.5 mm. Pedicels (0.5-)0.7-1.1 cm long. calyx deeply divided, the lobes linear, equal to subequal, 2-4 x 0.5-1 mm, connate only at the base, apex attenuate; corolla elongate-tubular, membranous, yellowish-green, the tube constricted at throat and in the middle or upper 1/3 of the tube, inflated above the constriction,

12-20 x (1-)2-3 mm in the constricted part, glabrous externally and internally, rarely glandular-pilose externally, the lobes ovate-triangular, pale yellow, equal to subequal, induplicate, 1.5-2.5 x 1 mm, ciliate, apex acute, reflexed by 135° at anthesis; stamens included, equal, the filaments almost completely adnate to corolla tube, the free portion 0.7-1.2 mm long, the anthers reaching the throat, 1.5-2 mm long; style slightly exserted, exceeding stamens, 1.3-1.8 cm long, glabrous. Berry yellow-green, ovoid, 1.6 x 0.9 cm.

Distribution. On rock walls, rocky slopes, in dry siliceous places, sandy gravelly soil, or on river banks, 1200-3500 m; in the southern part of central Peru, and from western Bolivia into NW Argentina. Flowering November-March, fruiting December-April.

Specimens examined. PERU. Ayacucho: city limit of Ayacucho, along Río Alameda, 2761 m, 12 Feb 1979 (fl, fr), Keel 415 (BM, G, GOET, K, LPB, MO, NY, P, U, US, USM); Ayacucho, 2407 m, Mar 1951 (fl, fr), Soukup 4022 (F, US); 1 km W of Ayacucho, 2800 m, 5 Mar 1939 (fl, fr), Stork & Horton 10804 (F, G, GH, UC); BOLIVIA. La Paz: Cotaña, 2500 m, Nov 1911 (fl), Buchtien 3261 (MO, NY, US). Cochabamba: Puente San Miguel, above Liriuni on the Cochabamba-Vizcachas road, ca. 25 km NNW of Cochabamba, 9 Apr 1963 (fr), Ugent 4758 (UC); Parotani, 2440 m, 30 Dec 1948 (fl), Brooke 5019

(BM, F, NY). Chuquisaca: Without locality, without date (fl), D'Orbigny 1166 (P); nr. Pomabamba, Dec 1845-Jan 1846 (fl), Weddell 3807 (P). Potosí: San Antonio, Dec 1931 (fl), Cárdenas 41 (A). ARGENTINA. Salta: Santa Victoria, 2385 m, 29 Jan 1943 (fl, fr), Meyer 4897 (UC). Jujuy: La Quiaca, 3450 m, 17 Feb 1940 (fl, fr), Meyer 33399 (F, GH, UC, NY); nr. Yavi, 3550 m, 30 Jan 1953 (fl), Sleumer 3606 (S); Volcán, 1 Mar 1971 (fl), Cabrera et al. 21758 (C). Tucumán: Sara, 1200 m, 10 Feb 1912 (fl), Rodríguez 376 (UC). Catamarca: Quebrada Choya, Feb 1873 (fl), Kendantz 212 (GOET, K); Pozo de Piedra, ca. 1900 m, 25-31 Jan 1952 (fl), Sleumer & Vervoorst 2378 (G, US); Las Blancas, 2200 m, Mar 1938 (fl), Schreiter 10513 (UC); El Candado, 2700 m, 2 Feb 1916 (fl, fr), Jörgensen s.n. (ex Herb. Corn. Osten. 11401) (G); La Playa, 2900 m, 6 Feb 1917 (fl, fr), Jörgensen 1073 (US).

A constricted corolla throat is present in all the following species, S. gayi, S. diffusa and S. tristis; it is not unique to S. scandens. In my opinion the most distinctive characters of S. scandens are the position of the constriction and the membranous texture of the corolla. The corolla tube both in buds and mature flowers is constricted at the throat and at the middle or at upper 1/3 of the tube . The membranous texture frequently makes the corolla look transparent when dry. Therefore, it is easy to identify S. scandens when corollas are present. In addition,

the mature, yellow-green fruits of S. scandens are easily distinguishable from the purple-black fruits of S. diffusa or S. tristis. Salpichroa scandens differs from S. gayi not only in the size and the texture of the corolla but also in the length of the style which, in S. gayi, never exceeds the stamens.

Local names and uses. Peru: Pepino Silvestre (Keel 415); fruits edible.

10. Salpichroa ramosissima Miers, London J. Bot. 4: 326. 1845; Walpers, Repertorium Botanices Systematicae 6: 613. 1847; Miers, Illustration of South American Plants p. 6. 1850; Dunal, in de Candolle, Prodr. 13(1): 473. 1852; Macbride, Field Mus. Nat. Hist. Bot. Ser. 13(5B)(1): 64. 1962. Type. Peru. Lima: Purruchuco, without date, Apr 1830-1841 (fl, fr), Mathews 1053 (holotype, K). Atropa ramosissima Mathews, London. J. Bot. 4: 326. 1845, in syn.

Salpichroma dilatata Dammer, Bot. Jahrb. Syst. 37: 639. 1906; Macbride, Field Mus. Nat. Hist. Bot. Ser. 13(5B)(1): 62. 1962 (as Salpichroa). Type. Peru. Ancash: nr. Ocros, 3200-3400 m, 27 Mar 1903 (fl), Weberbauer 2679 (holotype, +B = photo F neg. 2940, photos, F, G, GH, NY; fragments, F).

Salpichroa uncu Benoist, Bull. Soc. Bot. France 85: 55. 1938; Macbride, Field Mus. Nat. Hist. Bot. Ser. 13(5B)(1): 65. 1965. Type. Peru. Lima: Acotama, 22

July - 22 Oct 1778 (fl, fr), Dombey s.n. (lectotype, P, here designated; isotype, P-3 sheets).

Straggling, prostrate or scandent shrubs to 1 m tall, the young stems, leaves, pedicels and calyx glabrous, puberulous, pilose, sometimes villous or with gland-tipped trichomes, the calyx sometimes ciliate, the leaf blades sometimes floccose or appressed-pilose, but the vesture variable in density, the leaves glabrate at maturity. Branches and twigs sometimes flexuous, terete or occasionally winged on 1 to 4 sides, each node sometimes with 2 to 4 semicircular scales. Leaf blades ovate or deltoid, (0.9-)1.5-3(-3.8) x (0.7-)1-2.5(-3.7) cm; petioles subfiliform to flattened, 6-15(-20) x 0.5-1 mm. Pedicels 3-7 mm long; calyx deeply divided, the lobes linear, equal to subequal, 2.5-6 x 1 mm, connate only at the base, apex attenuate; corolla elongate-urceolate, slightly succulent, the tube slightly inflated in lower half, yellowish-green or greenish-white, 9-15 x 3-5 mm, glabrous or sparsely puberulous externally, glabrous internally, the lobes ovate-lanceolate, yellow, equal to subequal, valvate to induplicate, 2-3 x 1-1.5 mm, glabrous or ciliate, rarely glandular-ciliate, apex acute, reflexed by 180° at anthesis; stamens included, equal, inserted at top 1/3 of the tube, the filaments almost completely adnate to corolla tube, the free portion (0.5-)1-2 mm long, sometimes dilated, especially at attachment to the anthers, these (1.5-)2.5-3

mm long; style included, exceeding stamens, 0.7-1.2 cm long, glabrous. Berry (immature) ovoid, 1.5-1.7 x 1.2-1.4 cm.

Distribution. In rock crevices, hedgerows, grass steppes, argillaceous slopes, desert hills or sandy loams, 305 m (one collection), 2500-4572 m; mainly in the western part of central and southern Peru, also in southern Bolivia and NW Argentina. Flowering November-June and September, fruiting December onwards.

Specimens examined. PERU. Ancash: Tallenga, 3400-3600 m, 17 May 1950 (fl, fr), Ferreyra 7485 (US). Lima: Río Blanco, 4572 m, 20-25 Mar 1923 (fl, fr), Macbride 3041 (F); Pariamarca, few km from Canta on the way to Lachaqui, 3048 m, 1 Feb 1979 (fl, fr), Keel & Vilcapoma 389 (G, K, MO, NY, P, US, USM); Lachaqui, on the road to Arahuay, 3300 m, 28 Dec 1972 (fl, fr) Vilcapoma 129 (US); highway Lima-Chicla, half mile before Chicla, 3597 m, 24 Feb 1963 (fl, fr), Saunders 818 (K); Matucana, high on mountain, 2438 m, 14-18 Mar 1923 (fl), Macbride 2945 (F), mountain SW of Matucana, 3000 m, without date (fr), Weberbauer 186 (G), Matucana, Valley Rimac, 2500 m, 18 Feb 1954 (fl, fr), Rauh-Hirsch P177 (F); Cerro Ghuryúrume, above the town of Matucana, 2682 m, 31 Mar 1979 (fl, fr), Keel 492 (BM, G, K, MO, NY, P, U, US, USM). Ayacucho: Marcahuasi, above Puquio, 3300-3400 m, 23 Apr 1950 (fl, fr), Ferreyra 7209 (US). Arequipa: Mollendo, desert hill, 17 Nov 1923 (fl), Hitchcock 22392 (US), sandy

loam, open hillside, 305 m, 16 Sep 1937 (fl), Stafford 890 (BM, K). Bolivia. Potosí: nr. Chorolque, 3600 m, Dec 1932 (fl), Cárdenas 303 (US). ARGENTINA. Jujuy: Yavi, 3000-4000 m, 1 Jan 1901 (fl, fr), Fries 951a (S); Alfarcito, nr. Salinas Grandes, ca. 3500 m, 27 Dec 1901 (fl, fr), Fries 951 (P, S).

Salpichroa ramosissima, a subglabrous plant, is very distinct in its urceolate corolla. In leaf shape it sometimes resembles Nectouxia formosa, a closely related Mexican monospecific genus. This is well exemplified by Hitchcock 22392. Miers (1845) described the berry as red, but his observation cannot be corroborated at this time because the labels of the specimens studied do not state the fruit color and because I myself have seen only immature fruits in the field. However, if the type description is correct, the red berry would be another distinctive character for this species.

The length of the corolla tube and the width of the filaments show variation within this species. The collection Fries 951 from Argentina has the shortest corolla tubes and leaves that are in general smaller than those of other collections. This is probably related to the habitat in which it grew, rock crevices. Dilated filaments are found in Vilcapoma 129, Keel & Vilcapoma 389 (both from Canta Province in Peru) and Fries 951. Dammer (1906) named S.

dilatata with reference to its dilated filaments. The characters mentioned in the type description of S. dilatata and those shown on the photo of the type correspond well with those of S. ramosissima. Without seeing the original type specimen, I believe that S. dilatata is identical with S. ramosissima.

Judging from both type specimens and description, I believe that S. uncu Benoist is the same as S. ramosissima. A specimen of Herbarium Drake & Herbarium Richard, now at P, is accompanied by a label that furnishes no information but the names of the herbaria to which it previously belonged. However, I am sure it belongs to Dombey's collection, and it is here treated as one of the isotypes of S. uncu.

Macbride (1962) recognized S. ramosissima, S. dilatata and S. uncu as three distinct species. He identified the collections of López 1025, Stork & Horton 10804 and Soukup 4022, as S. dilatata. I have not seen the specimens of López 1025, but contrary to Macbride's species description, the specimens of Stork & Horton 10804 and Soukup 4022 do not have dilated filaments. They are S. scandens, a species occurring in Peru but not mentioned in Flora of Peru.

One of the 3 sheets of Fries 951a has a label indicating a locality and a date of collection which corresponds to the data given by Fries 951. When carefully examined the 3 specimens of Fries 951a are identical. I believe that the

label of Fries 951a repeating the information on the label of Fries 951 is wrong, and its locality and date of collection should therefore be corrected.

Local names and uses. Peru: Callalluma (Vilcapoma 129, Keel & Vilcapoma 389), Callayuma (Keel 492), uncu (in Benoist's type description of S. uncu) ;fruit edible.

11. Salpichroa micrantha Benoist, Bull. Soc. Bot. France 85: 55. 1938; Macbride, Field Mus. Nat. Hist. Bot. Ser. 13(5B)(1): 64. 1962. Type. Peru. Without locality, without date, 1839-1840 (fl), Gay 1973 (holotype, P; isotype, P).

Scandent or pendent shrubs to 3 m tall, the young stems, leaves and pedicels mostly glabrous, sometimes pilose, floccose or puberulous. Branches and twigs terete, flexuous, sometimes winged on 1 to 4 sides, each node occasionally with 1 to 4 semicircular scales. Leaf blades ovate or elliptic, 1-3(-3.5) x (0.6-)1-2.2(-2.7) cm; petioles subfiliform, 0.5-1 cm. Pedicels 1-2 mm long; calyx deeply divided, the lobes linear, equal to subequal, ciliate or rarely pilose, 1.5-3 x 0.5-1 mm, connate only at the base, apex attenuate; corolla tubular, slightly constricted at throat and at middle of the tube, the tube yellowish-green or pale yellow, 7-9 x 1.5-2 mm, externally and internally glabrous, the lobes triangular-ovate, greenish-yellow, equal to subequal, valvate, each lobe with 1 green vein, 1-1.5 x

0.5-1 mm, ciliate, horizontally spreading at anthesis; stamens included, nearly reaching the throat, equal, inserted ca. 3 mm below the throat, the filaments almost completely adnate to corolla tube, the free portion 0.5-1 mm long, the anthers 1.5-2 mm long; style included, not exceeding stamens, reaching ca. 1/2 length of corolla tube, 3-4 mm, glabrous, the stigma glabrous. Berry immature green, ca. 2 x 0.7 cm.

Distribution. In rock crevices, in hedgerows among shrubs, in Inca ruins or in cloudy, humid subtropical rain forests, 2400-3600 m; in the Urubamba valley of Department Cuzco, Peru. Flowering November-March, fruiting December onwards.

Specimens examined. PERU. Without locality, without date, 1869 (fl), Whiteley s.n. (BM). Cusco: Ollataytambo, 2900 m, 1 Mar 1979 (fl, fr), Keel 447 (NY, US, USM); Cusichaca, 2550 m, 17 Mar 1979 (fl), Chávez BB (NY, USM); Corihuayra China, 2400 m, 17 Mar 1979 (fl), Chávez CC (NY); Yucay, Dec 1937 (fl, fr), Soukup 750 (F); Calca, Hacienda Paucartica, 3600 m, 8 Jan 1937 (fl, fr), Vargas 157 (MO), on the road between Hacienda Venero and Hacienda Paucartica, 2950 m, 21 Feb 1979 (fl, fr), Keel 433 (BM, G, K, LPB, MO, NY, P, U, US, USM); on road to Calca, ca. 2800 m, 5 Jan 1963 (fl), Iltis & Ugent 1158 (K); Pisaq Inca ruins, 3500 m, 27 Jan 1975 (fl), Plowman & Davis 4897 (GH, K), 3048-3150 m, 18 Feb 1979 (fl,

fr), Keel 426 (BM, G, GOET, K, LPB, MO, NY, P, U, US, USM); Kayra, 3350 m, 2 Mar 1979 (fl), Chávez AA (NY, USM); nr. Oropesa, 3095 m, 28 Feb 1963 (fl, fr), Ugent 3994 (K, UC); ruins of Tipon, above the town of Oropesa, 3475 m, 6 Mar 1979 (fl, fr), Keel 451 (NY); between Urcos and Quiquijana, 6 km SSE of the village of Acopata, 3189 m, 7 Jan 1963 (fl, fr), Iltis & Ugent 1218 (NY, UC).

Salpichroa micrantha and S. gayi are the only species with a style that does not exceed the stamens. They both occur in the Department of Cuzco, though S. micrantha is more widespread than S. gayi. The morphological differences of these two species are listed in Table V.

Macbride (1962) mentioned that the sepals of S. micrantha are connate through the lower third of the calyx tube. Examining all the available specimens, I observed that the sepals are connate only at the base.

Local names and uses. Chinriques (Iltis & Ugent 1158).

12. Salpichroa gayi Benoist, Bull. Soc. Bot. France 85: 54. 1938; Macbride, Field Mus. Nat. Hist. Bot. Ser. 13(5B)(1): 62. 1962. Type. Peru. Without locality, without date, 1839-1840 (fl), Gay 2308 (holotype, P; isotype, P).

Scandent or pendent shrubs to 40 cm tall, the young stems, leaves, pedicels and calyx pilose, puberulous or

sometimes with gland-tipped trichomes. Branches and twigs terete or winged on 1 to 4 sides. Leaf blades ovate, 0.8-1.5(-2.3) x 0.6-1.2(-2.3) cm; petioles subfiliform, 0.4-1.2 cm. Pedicels 2-4 mm long; calyx deeply divided, the lobes linear, equal to subequal, 3-4 x 0.5-1 mm, connate only at the base, apex attenuate; corolla tubular, occasionally the middle of the tube slightly constricted, the tube yellowish-green or greenish, 10-15 x 2-3 mm, puberulous or pilose externally, glabrous internally, the lobes linear, greenish-yellow, equal to subequal, induplicate, each lobe with 2 unequal furrows, 3-4 x 0.5-1 mm, puberulous or glandular-puberulous, horizontally spreading at anthesis; stamens included, equal, the filaments almost completely adnate to corolla tube, the free portion 1-1.5 mm, the anthers white, 2-2.5 mm long; style included, only reaching ca. 1/2 length of corolla tube, 4-5 mm, puberulous on lower half and sparsely so above, the stigma ciliate or glabrous. Berry (immature) green, ca. 2.2 x 1 cm.

Distribution. In crevices of megalithic Inca walls, 3400-3575 m. Two collections are from the Urubamba region near Cusco. All others are from the ruins of Sacsahuaman and Kenco, near the city of Cusco, Department of Cusco, Peru. Flowering November-February, fruits collected once in February.

Specimens examined. PERU. Cuzco: trail from Chinchero plaza to Antakillqa hillside, about 13° 24′ S, 72° 3′ W, 3600 m, 13 Jan 1982 (fl, fr), Davis et al. 1420 (F, NY); Llamaponqa, El Chaccan, 7 Dec 1972 (fl), Brunel 136 (MO); Sacsahuaman ruins, 3400-3500 m, 16 Nov 1947 (fl), Ferreyra 2630 (US), 3550 m, 16 Feb 1979 (fl, fr), Keel 423 (B, BM, BR, COL, CORD, F, G, GB, GOET, K, LPB, MICH, MO, NBV, NY, P, S, U, UC, US, USM, VEN, W), Jan 1975 (fl, fr), Plowman & Davis 4739 (GH), Cerro sape, in front of Sacsahuaman ruins, 3400 m, 17 Nov 1947 (fl), Ferreyra 2652 (US), ruins of Kenco, Sacsahuaman hill, 3550 m, 13 Nov 1935 (fl), West 3853 (GH, UC).

Macbride (1962) cited Vargas 255 under S. qayi with a question mark. In fact, this collection is S. origanifolia and is one of the two known collections of that species from Peru. The morpholoqical differences between S. qayi and S. micrantha are discussed under the latter.

The external floral morphology of S. qayi is similar to that of the Bolivian population of S. tristis var. lehmannii. The only distinction is the length of the style. Because these two species do not occur in the same area, the possibility of heterostyly is ruled out in this case. It seems to me more plausible to treat them as distinct species.

Local names and uses. Peru: Pinku-Pinku (Brunel 136), Pires (Davis et al. 1420), Rocotitos, Pepino silvestre (Keel 423), Ccapapuno (West 3853); plant glutinous and aromatic, fruit edible (Davis et al. 1420).

13. Salpichroa diffusa Miers, London J. Bot. 7: 335. 1848; Miers, Illustration of South American Plants 1: p. 134. 1850; Dunal, in de Candolle, Prodr. 13(1): 473. 1852; Walpers, Ann. Bot. Syst. 3: 169. 1852; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 61. 1962. Type. Ecuador. Pichincha: the middle region of Pichincha, without date (fl), Jameson 32 (lectotype, K, here designated).

Salpichroa quitensis Benoist, Bull. Soc. Bot. France 85: 54. 1938. Type. Ecuador. Pichincha: slope of Pichincha above Rumipampa, 30 Mar 1930 (fl), Benoist 2319 (holotype, P).

Scandent shrubs to 3 m tall, the young stems, leaves, pedicels and calyx pilose or rarely glandular-pilose, the calyx sometimes ciliate or glandular-ciliate. Branches and twigs terete, occasionally alate. Leaf blades ovate, 1.3-2.5(-3.2) x 0.9-2(-2.8) cm; petioles subfiliform to flattened, 0.4-1(-1.5) cm. Pedicels 3-6 mm long; calyx deeply divided, the lobes linear, equal to subequal, 5-9 x 1-1.5 mm before fruiting, 10-13 x 1-3 mm after fruiting, connate only at the base, apex attenuate; corolla straight, tubular, the tube yellowish-green to pale green, 10-16 x 2-6

mm, lower 1/3 of the tube glabrous and the upper 2/3 pilose externally, glabrous or sparsely pilose internally, the lobes triangular-lanceolate, greenish-yellow with deep yellow margins, equal to subequal, induplicate, 3-5 x 1-3 mm, pilose, ciliate or rarely glandular-ciliate, apex acute, reflexed by 180° at anthesis; stamens included, equal to subequal, the filaments almost completely adnate to corolla tube, the free portion 1-2 mm, the anthers 2.5 mm long; style exserted, exceeding stamens, 0.9-1.3 cm long, glabrous. Nectary disc orange-red. Berry ovoid, dark-purple to black, ca. 1.5 x 2.4 cm.

Distribution. Roadside scrub, hedgerows, sub-páramo, upland cattle pastures, montane forests with pastures in clearings or among bushes, 2900-3630 m, in Colombia (one collection) and along the Andean chain of central Ecuador south to the Province of Azuay. Flowering December-September, fruiting January onwards.

Specimens examined. COLOMBIA. Hacienda de Pianstevea, without date (fl, fr), Hartweg 1311 (K). ECUADOR. Carchi: SE slopes of Volcán de Chiles, nr. Tufiño, 3250 m, 17 Aug 1944 (fl), Higgins 10643 (US). Imbabura: Lago San Marcos, Cayambe, 3414 m, 3 Dec 1961 (fl), Cazalet & Pennington 5497 (NY, US). Pichincha: open mountains E. of Nono, between Cotocollao and Nono, 3200-3300 m, 29 Jan 1974 (fl, fr), Harling & Andersson 11648 (GB, MO); Tuquerres, 15 May 1876

(fl), André 3177 (K, NY); Andes of Quito, 3048 m, without date, 1849 (fl), Jameson 754 (BM, G, K); slope of Volcán Pichincha, 12 Mar 1931 (fl), Benoist 4043 (P), above Quito, 3385 m, 25 Feb 1945 (fl), Fosberg 23237 (NY, US), along the path between Hacienda Mi Cielo and the peak, 3320-3630 m, 5 Apr 1979 (fl, fr), Keel 500 (F, G, K, MO, NY, P, US), punto Zotoras, 3500 m, 21 Apr 1927 (fl), Firmin 16 (US); Pumachaqui (=Pumachaca?), 3353 m, Sep 1859 (fl), Spruce 6064 (BM, G, GH, K, NY, P, W). Napo: Between Quito and Baeza, W of the Laguna de Papallacta, 3350 m, 17 Jul 1976 (fl), Øllgaard & Balslev 8019 (NY), nr. Papallacta, 12 Jan 1981 (fl, fr), D'Arcy 14086 (NY), 10 Jan 1981 (fl), Prance 26597 (K, MO, NY, P, US), 3000 m, 15-16 Jun 1968 (fl, fr), Harling et al. 10317 (GB, MO), 24.6 km W of Papallacta, 3480 m, 26 Mar 1972 (fl), MacBryde & Dwyer 1171 (MO); Antisana, Apr 1952 (fl, fr), Universidad Central Gabinete de Botánica 2220 (M). Bolívar: Hacienda Talahua, 3200 m, 1 May 1939 (fl, fr), Penland & Summers 592 (F, GH, US). Tungurahua: Carguairago (=Carihuairazo?), Jun 1858 (fl), Spruce 5451 (C, GOET, K, W). Chimborazo: El Retén, 20 km S of Cebadas, ca. 3200 m, 31 Jan 1968 (fl, fr), Harling et al. 6788 (GB, MO). Cañar: N of Biblían, 2900-3200 m, 6 Apr 1974 (fl), Harling & Andersson 13265 (GB, MO). Azuay: Sayausi, on the trail toward Cajas, 3100 m, 20 Jul 1939 (fl, fr), Penland & Summers 1081 (F, GH, US); Cumbe, 2900 m, 22-24 Apr 1968 (fl), Harling et al. 8605 (GB, MO).

Miers' S. diffusa actually consists of two different species: S. diffusa and S. tristis. Of the three collections mentioned by him, Jameson 32 corresponds best to his type description, and therefore I have chosen it as the lectotype. The other two collections, Maclean s.n. and Goudot s.n., are here listed under S. tristis var. tristis. The Plate 28C in Illustration of South American Plants claims to show S. diffusa, but it is obviously a drawing of Goudot s.n. which is not S. diffusa. Therefore, in the bibliographic citation of the basionym, I have only given the page number of the description and not the plate number.

It is sometimes difficult to distinguish S. diffusa from S. tristis in the dry state, but in the field the color patterns of the corolla, the patterns of the pubescence on the corolla tube, and the angles of reflexion of the corolla lobes at anthesis are very different. Salpichroa diffusa has a basically yellow-green corolla with deep-yellow margins on the lobes, and sometimes with purple lines running from the sinuses of the lobes to the base of the tube, with pubescence restricted to the upper 2/3 of the tube, and with lobes reflexed approximately 180° at anthesis. In contrast, S. tristis has a rather uniform yellowish-green corolla with yellow lobes, with a pubescence absent or evenly distributed on the tube, and with lobes which may be reflexed from 90° to 120° at anthesis. In dry specimens, two characters are rather consistent and useful for

identification: firstly, the above mentioned pattern of pubescence on the corolla tube, and secondly the straight corolla tube of S. diffusa which contrasts sharply with that of S. tristis, which is medially constricted. Distribution is another criterion to differentiate between the two species, because S. diffusa does not occur further south than Peru. Collections of S. tristis var. tristis from Sorata, Bolivia are an exception in that the corolla tube is straight. Neverthless, it can be separated easily from S. diffusa on the basis of geographical distribution and other characters such as pubescence.

Benítez de Rojas (1974) indicated that S. diffusa is the only species of the genus Salpichroa found in the Andean region of Venezuela. Actually, the species that occurs in Venezuela is S. tristis and not S. diffusa, and the collection he cited, Aristeguieta & Medina 3584, is here listed under S. tristis var. tristis.

Local names and uses. Ecuador: Cherche (André 3177) fruit edible, and used in ice cream (Raimondi, cited in Macride 1962).

14. Salpichroa tristis Miers, London J. Bot. 7: 335. 1848; Miers, Illustration of South American Plants 1: p. 134 & Plate 28B. 1850; Dunal, in de Candolle, Prodr. 13(1): 473. 1852; Walpers, Ann. Bot. Syst. 3: 170. 1852; Weddell, Chloris Andina 2: 98. 1859;

Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5B)(1): 61. 1962. Type. Ecuador. Andes of Quito, without date (fl), Jameson 125 (lectotype, K, here designated).

Salpichroma mandonianum Weddell, Chloris Andina 2: p. 98. 1859. Type. Bolivia. La Paz: vic. of Sorata, 3000 m, Nov 1857 (fl, fr), Mandon 437 (lectotype, P, designated by Grisebach in 1874; isotypes, BM, F- 2 sheets, G, GH, GOET, K, NY- 2 sheets, P, S, W).

Salpichroa mandoniana Weddell var. tucumanensis Grisebach, Plantae Lorentzianae p. 170. 1874. Type. Argentina. Tucumán: nr. Tafí, 1 Jan 1872 (fl), Lorentz 369 (lectotype, GOET; isotype, K).

Salpichroma foetida Dammer, Bot. Jahrb. Syst. 37: 639. 1906; Cabrera, Bol. Soc. Argent. Bot. 13(4): p. 328 & Fig. 2A-C. 1971. Type. Bolivia. Tarija: Puna Patanca, 3800 m, 9 Jan 1904 (fl, fr), Fiebrig 2625 (holotype, +B = photo F neg. 2941, photos F, GH, NY; fragments, F; isotypes, A, BM, G, GH, GOET, K, M, NBV, P, S, U).

Salpichroma alata Dammer, Meded. Rijks-Herb. 28: 26. 1916. Type. Bolivia. La Paz: Quebrada de Araca, 3700 m, Oct 1911 (fl), Herzog 2435 (holotype, B, n.v., presumably destroyed, photo F neg. 2939, photos, G, GH, NY; lectotype, NBV, here designated; isotypes, S, W).

Salpichroa colubrina Benoist, Bull. Soc. Bot. France 85:

53. 1938. Type. Ecuador. Pichincha: Cotocollao, on the way from Pamasqui, 5 Feb 1931 (fl, fr), Benoist 3799 (holotype, P; isotypes, P- 2 sheets).

Scandent shrubs to 3 or 4 m tall, the young stems, leaves, pedicels and calyx glabrous, pilose, puberulous, villous or sometimes with gland-tipped trichomes, rarely velutinous or glandular-hirsute, but the calyx lobes mostly ciliate or glandular-ciliate. Branches and twigs terete or alate on 1 to 4 sides. Leaf blades ovate or ellptic; petioles subfiliform to flattened. Pedicels 2-10 mm long; calyx deeply divided, the lobes linear, equal to subequal, connate only at the base, apex attenuate; corolla tubular, yellowish-green to pale green, internally glabrous, the lobes triangular or triangular-lanceolate, yellow to greenish-yellow, equal to subequal, induplicate, apex acute; stamens included, equal to subequal, inserted on upper 1/3 to 1/4 of the tube, the filaments almost completely adnate to corolla tube, the free portion 1-2 mm long; style glabrous.

Key to the varieties of S. tristis

1. Corolla tube glabrous, rarely sparsely minutely pilose or glandular-pilose, the lobes spreading or reflexed by 120 at anthesis; seeds glabrous or minutely hispidulous on the periphery. Distributed from Venezuela to Argentina..... 14a. var. tristis.
1. Corolla tube pilose, sometimes pilose-glandular or

villous, the lobes horizontally spreading at anthesis; seeds totally hispidulous. Distributed from Colombia to Bolivia..... 14b. var. lehmanni.

14a. Salpichroa tristis var. tristis

Branches and twigs frequently flexuous, sometimes with adventitious roots. Leaf blades ovate or elliptic, (1.2-)1.5-3.5(-5) x 0.7-2(-3.1) cm, petioles 0.4-1.5(-2.5) cm long. Calyx lobes 2-6 x 0.5-1 mm; corolla tube almost always constricted in the middle, 10-15(-18) mm long, 1.5-3.5(-5) mm wide at the middle of the tube, externally glabrous, rarely sparsely minutely pilose or glandular-pilose, the lobes 1.5-4 x 1 mm, ciliate or ciliate-glandular, spreading or reflexed by 120° at anthesis; anthers 1.5-2 mm long, the connectives sometimes dilated and thickened; style included to slightly exserted, exceeding stamens, 0.8-1.5 cm long. Berry ovoid, purple-black to blue-black, ca. 2 x 1.8 cm.

Distribution. Roadside scrubs, borders of agricultural fields, stream banks, among bushes, in thickets, on ruin walls or rocky ledges along hillsides, in open savana, sub-páramo, páramo, puna, (431-)1500-4000 m; along the Andean chain from north-central Venezuela and central Colombia south through Ecuador, western Peru and western Bolivia to northern Argentina. Flowering January-December, fruiting January-May and July-December.

Representative Specimens. VENEZUELA. Páramo de El Banco, 3450 m, 17 May 1944 (fl), Badillo 824 (VEN). Trujillo: Guiriqay, La Peña Blanca, 3300 m, Aug 1958 (fr), Aristeguieta & Medina 3584 (NY, VEN). Mérida: Páramo del Chorro, Hacienda de Cacute, nr. Mucurubá, 2000-2800 m, Aug 1958 (fl), Aristeguieta 3283 (NY, VEN); vic. of El Royal, nr. La Toma, ca. 2440 m, 4 Nov 1978 (fl, fr), Luteyn et al. 6184 (BM, G, K, LPB, MO, NY, US, VEN). Táchira: Bailladores-La Grita road, Páramo de Portachuelo, 1 km before turn-off to La Grita at the Liceo Militar "Jauregui", 2925 m, 17 Oct 1978 (fl, fr), Luteyn et al. 5875 (BM, G, GOET, K, LPB, MO, NY, P, S, U, US). COLOMBIA. Santander: nr. Páramo de Santurbán, 3000 m, 27 Aug 1948 (fl), Barkley & Araque 18S063 (US), 27 Aug 1948 (fr), Barkley & Araque 18S167 (US). Boyacá: Sierra Nevada del Cocuy, 26 Jul 1957 (fl, fr), Grubb et al. 67 (K, US); SW of Valle del Cocuy, 2780-3000 m, 15 Sep 1938 (fl), Cuatrecasas 1746 (F, US). Cundinamarca: Páramo de la Siberia, road to Guasca, nr. Hacienda El Salitre, 2700 m, 25 Oct 1952 (fl), Humbert et al. 26926 (P); Cerro de Suba, 2700 m, 6 Mar 1946 (fl, fr), Duque-Jaramillo 2773 (NY); Valle de Sopó, Santa Isabel, 2650 m, Jul 1953 (fl, fr), Fernández 3260 (US); Bogotá, 2650 m, without date, 1844 (fl), Goudot s.n. (F, G, K, P). Meta: Río Cabuyaro, Feb 1937 (fl), García-B 5145 (US). Tolima: Murillo, 2000-2300 m, 18 Dec 1917 (fl), Pennell 3184 (GH, NY); Cordillera Central, Mermillón to La Lora, new Quindío trail,

14 Aug 1922 (fl), Killip 9760 (GH, NY, US). Del Valle: western slope of Cordillera Central, above La Quebrada de Los Osos, towards Los Chuchos, 3000 m, 21 Apr 1946 (fl, fr), Cuatrecasas 20957 (F). Cauca: Canaan, Purace Mountain, bank of Río Aquablanca, 2900-3100 m, 11-16 Jun 1922 (fl), Killip 6747 (GH, US). ECUADOR. Without locality, without date (fl), Sodiro 114/93 (F, photos, G, GH, NY). Pichincha: small hill nr. the town of Calacali, 2865 m, 7 Apr 1979 (fl), Keel & Jaramillo 501 (BM, CORD, G, GOET, K, LPB, MO, NY, P, S, U, US, VEN); vic. of San Antonio & Pomasqui, 29 Oct 1918 (fl, fr), J. N. Rose & G. Rose 23568 (GH, NY, US). Napo: Misahuallí, 431 m, 17 Mar 1978 (fl), Jaramillo 100 (NY). Chimborazo: Quinia, nr. mount Condorazo, Jan 1859 (fl), Spruce 5847 (BM, G, K, NY, P, W); E of Riobamba, side valley of Río Chambo, 2900 m, 17 Mar 1934 (fl), Schimpff 835 (A, G). Azuay: Sayausí, 3100-3300 m, 16 Apr 1968 (fl), Harling et al. 8402 (GB, MO). PERU. Without locality, Andes of Peru, without date (fl), Maclean s.n. (K), collector unknown, probably Maclean s.n. (K). La Libertad: vic. of Agallpampa, 3000 m, 12 Feb 1954 (fl), Miranda 1025 (US); Canramaca, between Santiago de Chuco & Cachicadán, 2950 m, 9 Jun 1953 (fl), Miranda 1003 (US). Ancash: Chachapoyas, without date, 1846 (fl), Mathews s.n. (G). Junín: bottom of valley of Río Quishuarcancha, below Hacienda Casa Blanca, 3600 m, 28 Nov 1962 (fl), Iltis et al. 141 (K, UC); Acolla, nr. Jauja, 3414 m, 8 Feb 1979 (fl, fr), Keel 400 (G, MO, NY, US); ruins on

Cerro de Hudnacas, above Jauja, 3420 m, 23 Jan 1979 (fl, fr), Keel 383 (BM, G, K, LPB, MO, NY, P, US). Cusco: Urcos, 3048-3658 m, May 1932 (fl), Stafford 21 (K). Ayacucho: between Chaviña & Coracora, 3200-3300 m, May 1911 (fl, fr), Weberbauer 5785 (F, GH, US). BOLIVIA. La Paz: 1 km before the town of Laripata, 3109 m, 14 Mar 1979 (fl, fr), Keel 459 (BM, G, GOET, K, LPB, P, MO, NY, US); Ovejuyo, between La Paz and Calacoto, ca. 5 km towards Palca, 3800 m, 16 Dec 1979 (fl, fr), Beck 2403 (NY). Cochabamba: vic. of Cochabamba, Cerro above the Cevercería Taquiña, 3048 m, 20 Mar 1979 (fl, fr), Keel et al. 480 (G, K, LPB, MO, NY, US); Colomi, 3400 m, without date (fl), Cárdenas 4096 (US). Potosí: Laqunillas, 3800 m, Mar 1933 (fl, fr), Cárdenas 374 (US). ARGENTINA. Jujuy: Santa Catalina, puna region, 3400-4300 m, 9-14 Jan 1901 (fl), Claren 11404 (S); Quebrada de Cajas, 4000 m, 1 Feb 1942 (fl, fr), Cabrera 7825 (F, GH). Salta: Salta, Dec 1973 (fl), Rodríguez 1265 (UC); pasture at the foot of Nevado del Castillo, 25 Mar 1873 (fr), Lorentz & Hieronymus 187 (BM, GH, MO, NY, S, US). Tucumán: Las Palomas, 20 Dec 1913 (fl), Castillón 3134 (UC); Quebrada Honda, 83 km from Tucumán, 3000-3300 m, 19 Jan 1956 (fl), Böcher et al. 2393 (C); La Ciénaga, Sierra de Tucumán, 10-17 Jan 1874 (fl, fr), Lorentz & Hieronymus 709 (F, G, GOET, NY, US), 2500 m, 13 Jan 1905 (fl, fr), Lillo 4004 (A), Jan 1943 (fr), Descole 1531 (G); Las Pavas, 2200 m, 13 Dec 1925 (fl, fr), Venturi 4006 (A, F, GH, UC, US). Catamarca: El

Candado, 2700 m, 10 Feb 1916 (fl, fr), Jörgensen 1073 (GH, MO, UC); eastern slope of Sierra de Ambato, nr. Casa de Cubas, 3000 m, 28-30 Jan 1968 (fl), Hunziker & Fulvio 19844 (NY).

The collection of Maclean s.n. from the Peruvian Andes was cited in Miers' type descriptions of S. diffusa and S. tristis. There are two sheets of Maclean s.n. in the Hooker Herbarium (now in K). One sheet consists of 3 collections: Jameson 125, 754 and Maclean s.n. Miers (1848) classified the latter Maclean s.n. as S. diffusa, but the specimen's characters correspond better to my newly defined S. tristis. The other sheet does not give the collector's name but has a label that says "Andes P" and refers to some morphological characters. The handwriting on this label matches well that of Maclean on the previously mentioned sheet. Furthermore, the morphology of this plant resembles that of Jameson 125, a specimen that Miers cited with his type description of S. tristis. I believe the sheet without a collector's name is a syntype of S. tristis and was collected by Maclean in the Peruvian Andes. Jameson 125 and the newly designated Maclean s.n. are both stout miniature plants, probably an ecotype collected from rock crevices or some such unfavorable environment. Because Miers cited Quito as type locality, and this is the locality indicated on Jameson 125, I here designate this collection as the lectotype despite the fact that its morphology is not very typical for the species.

Weddell (1859) in his description of Salpichroma mandonianum did not mention the collection number of the type. Mandon 437 was later designated by Grisebach in 1874 when he published the var. tucumanensis. The labels on all specimens of Mandon 437 mention Nov. 1897 as the collection date with the exception of one sheet which indicates Nov. 1857. Because Mandon was in Bolivia for six years, between 1854 and 1860 (Weddell, 1867) and described S. mandonianum in 1859, the collection date of Mandon 437 must be 1857 and not 1897.

Bolivia's Sorata population of S. tristis, previously named Salpichroma mandonianum, exhibits a character, a straight corolla tube, which differs from the other populations of S. tristis. Grisebach (1874) named the plants from Argentina S. mandoniana var. tucumanensis, based on the constricted corolla tube, but there is no other character that can be used to support the recognition of this variety. In addition, S. tristis var. lehmanni has corolla tubes the outlines of which vary from slightly constricted to obviously constricted. If one used the form of corolla tube as the only criterion to separate the varieties of S. tristis, the Sorata population with straight corolla tubes would form a single group separated from the northern and southern populations with constricted corolla tubes. In view of the north-south axis of the Andean chain, the isolation of the Sorata population from the rest of S.

tristis does not make sense, unless unexpected ecological factors are involved. Therefore, the var. tucumanensis is not recognized here.

Salpichroa tristis occupies a wide range of habitats and covers the Andean chain from Venezuela to Argentina. Unlike S. origanifolia, which shows no morphlogical variation, S. tristis shows considerable quantitative variation in characters which are discussed in Fig. 35. In this revision, the distinction of var. tristis from var. lehmanni is based on the presence or absence of pubescence on the corolla tube which is quite a clear-cut character. Only a few plants of var. tristis have sparsely pubescent corolla tube. The population analysis based on three corolla characters reveals geographical variation in both varieties. Exserted styles occur much more frequently in var. lehmanni than in var. tristis. This character may indicate an important reproductive isolating mechanism between these two varieties. In var. tristis, the Colombian and Argentinian collections consist entirely of flowers with included styles; while the other collections have less than 40% flowers with exserted styles. However, in all flowers the styles exceed the stamens. The factors selecting these different character states are not known. The second character, the ratio of the width of the widest part to the constricted part of the corolla tube $\geq$ 1.5, measures the frequency of flowers with constricted corolla tubes. This

character shows considerable geographical variation in both varieties. Though the absolute values differ, the frequency of this character shows parallel changes from Ecuador, Peru to Bolivia in both varieties. Among all the specimens examined, the Bolivian collections (both varieties) include mainly flowers with straight or nearly straight corolla tubes. The adaptive advantage, if any, of a constricted or straight corolla tube is unclear. It may have some bearing on the accessibility of the nectary ring surrounding the ovary to pollinators. The third character, the ratio of the connective width to anther width $\geq$ 0.7, is used to detect the frequency of dilated connective. Dilated connectives were once used as a character to distinguish Salpichroa from a closely related monotypic genus Nectouxia growing in Mexico (Wettstein, 1891). However, after examining hundreds of specimens, I have concluded that dilated connectives are found in some Salpichroa and in Nectouxia and, thus, this is not a useful character to separate these two genera. From Fig. 35, one can see that the dilated connective is more typical of the collections of var. tristis. As to var. tristis, the Venezuelan collections have flowers whose connectives are always dilated, but the frequency of dilation declines slightly in Colombia and Ecuador, then drops significantly towards the South. In the Argentinian population this character reappears with increased frequency. As to var. lehmanni, both the Peruvian and

Bolivian collections are characterized by the absence of dilated connectives. The over-all higher frequency in the northern populations may indicate a relationship with Nectouxia. The function of the dilated connective is obscure.

Though var. tristis and var. lehmanni do occur side by side, var. tristis has a wider distribution. Besides Ecuador, Peru and Bolivia where var. lehmanni is found, var. tristis is also found in Venezuela, Colombia and Argentina. The survey of data on herbarium labels shows that there is no direct correlation between the flowering time of S. tristis and the elevation it occupies. Instead, the flowering time changes according to latitude, beginning in the north and ending in the south-- Venezuela (August), Ecuador (September or October), Peru and Bolivia (November or December), and Argentina (December).

Herzog 2435 is the only collection which has glandular-pilose hairs on the corolla tubes of immature flowers. However, the corolla tubes of mature flowers are nearly glabrous, and the collection is therefore listed under var. tristis. Spruce 5847 is another collection in which the corolla tubes are slightly more pubescent, but in every other aspect it is closer to var. tristis than to var. lehmanni. Miers (1848) described the stigma of Jameson 125 as having an obsoletely bilobed margin. I have been unable to confirm this observation.

The collection of Sodiro 114/93, was originally in the Berlin type herbarium. Now it only exists as a type photograph collection (photo neg. 2944) and a few fragments at F. However the epithet has never been published. Between 1898 and 1908, Sodiro's Ecuadorean collection was published in 5 parts in Bot. Jahrb. Syst. His Solanaceous collections were described by Dammer (in Sodiro, 1905) in Bot. Jahrb. Syst. vol. 36: 384-388. However, I have not found the epithet, sodiroi, in this publication. Dammer in 1905 and 1906 again published many new species of South American Solanaceae (in vol. 37: 167-171 & 636-642). Though many species of Salpichroa were included (in Vol. 37: 639-641), I was again unable to find "sodiroi". Because this epithet is neither in Kew Index, in Gray Cards, nor in any issue of Bot. Jahrb. Syst. between 1890-1915, the epithet sodiroi cannot be accepted, in spite of the extant type photo collection at F.

The work of Ruthsatz (1974) revealed that S. tristis var. tristis, a moderately branching shrub under 20 cm, is a rare species in the vegetation composition of the puna region, displaying a low value as a forage plant.

Local names and uses. Colombia: Rejalgar (Duque-Jaramillo 2773). Peru: Cuytulume (Miranda 1025). Argentina: Uva, Uvilla de la Sierra (Hieronymus, 1882); fruit edible, plant aromatic, clammy, and with minor forage importance (Ruthsatz, 1974).

14b. Salpichroa tristis Miers var. lehmanni (Dammer) Keel, stat. nov. Salpichroma lehmanni Dammer, Bot. Jahrb. Syst. 37: 640. 1906. Type. Ecuador. Azuay: Cuenca, 2500-2800 m, Nov-Dec 1880 (fl), Lehmann 5555 (holotype, B, n.v., presumably destroyed, photo F neg. 2942, photos, G, GH, NY; lectotype, K, here designated; isotypes, GH).

Salpichroa sarmentosa Benoist, Bull. Soc. Bot. France 85: 55. 1938. Type. Bolivia. La Paz: vic. of La Paz, 3700 m, Dec 1856 (fl), Mandon 436 (holotype, P; isotypes, F, G- 2 sheets).

Leaf blades ovate, (0.5-)1-3.5(-4) x (0.6-)1-2(-2.5) cm; petioles 0.4-2(-2.5) cm long. Calyx lobes 4-9 x 1-1.5 mm, corolla tube constricted or slightly constricted in the middle, the upper half slightly wider (with 10 prominent green veins in La Paz population), 8-18 mm long, 1.5-4 mm wide at the middle of the tube, externally pilose, sometimes glandular-pilose or villous, the lobes 2-7 x 1-2 mm, sometimes each lobe with 2 equal furrows, ciliate or pilose, sometimes with gland-tipped trichomes, horizontally spreading at anthesis; the anthers 1.5-2.5 mm long, the connectives frequently dilated and thickened in Ecuadorean collection; style reaching the throat to exserted, 1-1.4 cm. Berry mature black, obovoid, 1-1.5 x 1-1.2 cm.

Distribution. Hedgerows, roadside scrubs, on rocky cliffs or stone walls, in thickets, forests or semi-deserts, 2450-4050 m; in SW Colombia, central and southern Ecuador, western and southern Peru, west-central Bolivia, and northern tip of Argentina. Flowering September-April and June, fruiting September onwards.

Specimens examined. Without locality: without date 1804 (fl), Pavón 497 (G), without date 1828-1890 (fl), Triana 2275 (BM). COLOMBIA. Nariño: horse path between the town of Cumbal and the Lake of Cumbal, 3030-3200 m, 7 Jan 1952 (fl), Fernández et al. 1066 (NY). ECUADOR. Pichincha: old highway between Quito and Santo Domingo (via Chiriboga), km 12.9, 3050 m, 15 Dec 1976 (fl), Boeke 467 (NY). Chimborazo: Andean forest of Cubillín. Cordillera Oriental 3300-3400 m, 1 Mar 1944 (fl, fr), Acosta-Solís 7583 (F). Cañar: Parish Luis Cordero, along the trail between Azogues and San Marcos, 2900-3048 m, 28 Jan 1945 (fl, fr), Prieto P-173 (NY). Azuay: vic. of Cuenca, 17-24 Sep 1918 (fl, fr), Rose et al. 22945 (GH, NY, US), a few km W of Cuenca, 2500 m, 1-2 Feb 1945 (fl, fr), Giler 27 (NY, P, US), along the river Targui, 4-18 km S of Cuenca, 2500-2750 m, 26 Feb 1945 (fl, fr), Camp E-1896 (NY). Loja: Chuquiribamba, 16 Nov 1876 (fl), André 4451 (F, K, NY); Loja, Nov 1876 (fl) André K710 (F, NY). PERU. Tuapata, 3800 m, without date, 1916 (fl), Watkins s.n. (US). Cajamarca: between Guzmango and Cruz Grande, 2700 m, 18 Apr 1967 (fl, fr), Sagástegui et al. 6373 (US). Lima:

Lachaqui, 4000 m, 28 Dec 1972 (fl), Vilcapoma 128 (US). Huancavelica: Pana, below Conaica, 3350-3370 m, 16 Mar 1951 (fl), Tovar 207 (US). Ayacucho: Prov. Lucanas, 3250 m, 14 Dec 1962 (fl), Iltis & Ugent 453 (MO); between Puquio and Nazca, 3300 m, 20 Mar 1949 (fl), Ferreyra 5512 (G, US). Puno: Without locality, among rocks, 3658 m, Jan 1934 (fl), Stafford 255 (K); Checayane, 3980 m, 27 Mar 1957 (fr), Ellenberg 450 (U); Puno, 4000 m, without date 1937 (fl), Soukup 445 (F, GH, US); Ocopampa, vic. of Lake Titicaca, 3965 m, 10 Dec 1919 (fl), Shepard 77 (GH). Arequipa: above Chuquibamba, 3500 m, Mar-Apr 1914 (fl), Weberbauer 6848 (F, US); Nevado de Chachani, 3400-3700 m, 14 Apr 1925 (fl), Pennell 13266 (F, GH, NY, US), 3250 m, 14 Mar 1957 (fl), Ellenberg 102 (U). BOLIVIA. Without locality: Andes of Bolivia and Peru, 1 Mar 1903 (fl), Hill 353 (K). La Paz: 16° N, 68° W, dry bank nr. the railway, 3840 m, 13 Dec 1948 (fl), Brooke 5012 (BM, F); vic. of La Paz, 3048 m, without date 1889 (fl, fr), Bang 50 (A, BM, F, G, GH, MICH, MO, NY, US, W); 3750 m, 18 Jan 1907 (fl, fr), Buchtien 773 (B, F, G, GH, M, NBV, S, US, W), 3700 m, Jan 1910 (fl, fr), Buchtien 91 (F, G, GH, NBV, NY), 3650 m, 28 Feb 1912 (fl), Buchtien s.n. (BM, K), 3700 m, Mar 1913 (fl), Buchtien s.n. (C, S), 3700 m, Jan 1919 (fl), Buchtien 91 (?) (GH), below Obrajes, 3200 m, 2 Jun 1919 (fl), Buchtien 4700 (US), 3600 m, 21 Dec 1930 (fl), Buchtien 8518 (US), 3850 m, 12 Feb 1931 (fl, fr), Buchtien 8656 (BR, M), Apr 1919 (fl), Claude-Joseph 1114

(US), 3850 m, 29 Nov 1973 (fl), Graf 268 (NY), 11-12 Sep 1864 (fl), Pearce s.n. (K), 3048 m, Apr 1885 (fl, fr), Rusby 830 (BM, F, G, GH, NY, P, US); Yungas, 1829 m, without date 1885 (fl, fr), Rusby 830 (?) (NY); La Paz-Calacoto, 39 km to the east, road via Lambate, 4050 m, 31 Dec 1980 (fl), Beck 3961 (NY); Calacoto, above Instituto Bíblico Nazareno, 3320 m, 17 Mar 1979 (fl, fr), Keel 474 (LPB, NY); La Paz-Palca-Illimani, 3600-4800 m, Jan 1906 (fl), Hauthal 237 (GOET); Palca, 3400 m, 4 Nov 1926 (fl), Troll 2851 (M); 75 km S of La Paz and 27 km detour towards Sapahaqui, 3450-3650 m, 18 Jan 1981 (fl), Beck 6029 (NY); Cordillera Tres Cruces, descending from Quime, 3900 m, 24 Dec 1978 (fl), Beck 200 (NY). ARGENTINA. Jujuy: between La Quiaca & Villazón, 3442 m, 24 Jan 1940 (fl), Schreiter 11197 (GH).

Though var. lehmanni occurs in similar habitats as var. tristis, it prefers higher elevations. Except in a small area of Ecuador they are generally allopatric. This spatial separation probably limits the gene exchange between these two varieties and keeps some characters distinct.

Salpichroa tristis var. lehmanni is distributed along the north-south axis of the Andes. The corolla morphology varies among populations, though not as much as does the corolla morphology of var. tristis, in which the length of corolla tube and length of corolla lobes differs considerably. In northern populations of both varieties, the

connectives are dilated, which may indicate that a certain amount of gene exchange takes place between the two varieties.

Local names and uses. Ecuador: Shulala (Acosta-Solís 7583), Zhululaq (Prieto P173), Shulalaq (Rose et al. 22945). Peru: Chishinshique (Sagástegui et al. 6373), Callalluma (Vilcapoma 128), Uchu-uchu (Ellenberg 102).

15. Salpichroa microloba Keel, sp. nov.

Type. Peru. Lima: Arquircancha, nr. Lachaqui, 3658 m, 2 Feb 1979 (fl, fr), Keel & Vilcapoma 397 (holotype, NY; isotypes, MO, USM) (Fig. 36 & 37).

Frutices penduli vel effusi ad 1 m alti. Rami et ramuli interdum flexuosi, teretes longitrorsus 1-3-alati, in quoque nodo interdum squamis 2-4 semicircularibus vel circularibus obsiti puberuli vel puberulo-glandulosi, interdum glabri vel pilosi, glabrescentes sub maturitatem. Folia ovata vel elliptica, (1-)1.5-2.8(-3.6) x (0.6-)1-2.1(-3) cm, utrinque puberula, pilosa vel glabra, interdum puberulo-glandulosa; petioli subfiliformes vel complanati, 0.6-1.8 cm longi, pubescentes ut folia. Flores flavi vel viridi-flavescentes. Pedicelli filiformes, 0.5-1.5 cm longi, pilosi, puberuli, puberulo-glandulosi vel glabri. Calyx profunde 5-partitus, lobis linearibus, 5-13 x 0.5-2.5 mm, apice acutis vel attenuatis, connatis solum basi, inter se subaequalibus, ciliatis, dorso pilosis, puberulis vel glabris. Corolla

5-lobata, tubulosa, tubo recto vel apicem versus leviter dilatato, sed constricto ad faucem, 22-34 x 3-7 mm, extus puberulo vel glabro, intus glabro, lobis aestivatione valvatis, triangulatis vel ovato-triangulatis, 2-3 x 1.5-3 mm, apice acutis, inter se aequalibus vel subaequalibus, ciliatis, sub anthesi per 180° reflexis. Stamina inter se aequalia vel subaequalia, tubo aequalia, prope tubi apicem inserta, filamento glabro, 0.5-1.5 mm longo, anthera 2.5-4 mm longa. Stylus glaber, leviter exsertus vel tubum aequans, stamina excedens, 2-3 cm longus, stigmate subcapitato vel capitato. Bacca cyanea vel purpurea, 3 cm longa.

Distribution. Sub-puna or montane cloud forest, near creeks, in agricultural fields, hedgerows, on roadsides, grass steppes, or on stone walls, rock crevices; 2438-3800 m; in the Department of Cotopaxi, central Ecuador (one collection only) and west-central Peru. Flowering December-May, fruits found in Feburary.

Specimens examined. ECUADOR. Cotopaxi: road Quevedo-Latacunga, above Pilaló, ca. 2900 m, 3 May 1968 (fl), Harling et al. 8993 (GB, MO). PERU. Lima: Baños, on the way to Cerro de Pasco, 21-22 May 1839 (fl) [the collecting date based on Wilkes, 1845], Wilkes s.n. (US); Lachaqui, 3800 m, 28 Dec 1972 (fl), Vilcapoma 129 (US), 3400 m, 29 Dec 1972 (fl), Vilcapoma 130 (US), Pirocancha, on the way to Lachaqui, 3440 m, 1 Feb 1979 (fl, fr), Keel & Vilcapoma 390

(MO, NY, US, USM), Achaca, few km beyond Lachaqui, 3658 m, 2 Feb 1979 (fl, fr), Keel & Vilcapoma 396 (NY, USM); Matucana, 2438 m, 14-18 Mar 1923 (fl), Macbride 2946 (F); vic. of Huarochirí, western cordillera, 2100-3000 m, Feb 1913 (fl), Hrdlicka s.n. (US); vic. of Santiago, 3600-3700 m, 15 May 1953 (fl), Cerrate & Tovar 1909 (US).

Salpichroa microloba shows slight variation in degree of pubescence and size of leaves. Cerrate & Tovar 1909 is exceptional for its larger, glabrous leaves and wider corolla tubes. Salpichroa microloba and S. weberbaueri have nearly the same corolla length, but the shapes of corolla tube and lobes are very different. In the field, one can easily separate them by the shape of corolla and the degree of reflection of the corolla lobes at anthesis. The specific epithet, microloba, refers to the relatively small size of the corolla lobes.

Salpichroa microloba is probably related to S. ramosissima. Although the length of corolla tube of these two species is quite different (S. microloba 2.2-3.4 cm long, and S. ramosissima 0.9-1.5 cm), the shape of corolla and the reflection angle of lobes at anthesis are similar. Moreover, the distribution range of the two species overlaps in Lachaqui, Peru.

Local names and uses. Peru. Ayanata (Keel & Vilcapoma 397, Vilcapoma 129), Callalluma (Vilcapoma 130), Shuculumpa (Cerrate & Tovar 1909).

Excluded Species

Salpichroa ciliata (Schlechtendal) Miers, London J. Bot. 4: 329. 1845.= Lycium ciliatum Schlechtendal, Linnaea 7: 69. 1832, fide Dunal, in de Candolle, Prodr. 13(1): 476. 1852.

Salpichroma breviflorum Dunal, in de Candolle, Prodr. 13(1): 474. 1852.= Schopfia flexuosa (R. et P.) R. et S. (Olacaceae), in A. T. Hunziker, Kurtziana 11: 117. 1978.

Salpichroma cuspidatum Dunal, in de Candolle, Prodr. 13(1): 474. 1852. = Ectozoma pavonii Miers, Ann. Nat. Hist. Ser. II, 4(21): 185. 1849, fide A. T. Hunziker, Kurtziana 10: 31. 1977.

Macbride (1962) described S. breviflorum Dunal and S. cuspidatum Dunal under the genus Juanulloa, but he did not make any transfer. He noted that the characters of S. breviflorum were doubtfully those of Salpichroa, more probably of Juanulloa, but both species are equally aberrant under Juanulloa.

Salpichroma urceolatum Dunal, in de Candolle, Prodr. 13 (1): 475. 1852.

Salpichroa wrightii A. Gray, Synoptical Flora of North America 2 (1): 231. 1878. (see text p. 85 & 86).

Table I

Pollen size in the species of *Salpichroa*

Taxon	Pollen size (microns)				Voucher
	P		E	P/E*	
S. didierana	86	x	66	1.30	Keel & Andrade 442
S. microphylla	83	x	77	1.08	Keel et al. 386
S. glandulosa	90	x	81	1.11	Keel 418
S. dependens	94	x	82	1.15	Keel 384
S. proboscidea	96	x	89	1.08	Keel 438
S. hirsuta	88	x	74	1.20	Keel 453
S. weberbaueri	75	x	71	1.05	Keel 502
S. origanifolia	66	x	60	1.11	Fiebrig 2144
S. scandens	52	x	50	1.04	Keel 415
S. ramosissima	70	x	65	1.07	Keel & Vilcapoma 389
S. micrantha	59	x	55	1.06	Keel 433
S. diffusa	79	x	73	1.08	Keel 500
S. gayi	66	x	64	1.04	Keel 423
S. tristis	68	x	62	1.08	Keel 383
S. microloba	82	x	74	1.10	Keel & Vilcapoma 390

* The size of pollen was measured at polar axis (P) and equatorial axis (E). All measurements were based on 30 counts per species.

Table II

Characters used as basic data for the GROUNDPLAN-DIVERGENCE cladogram

	Character	Ancestral state (0)	Divergent state (1)
A	Sepal connation	free	partially fused
B	Calyx accrescent after fruiting	accrescent	not accrescent
C	Color patterns of corolla tube & its lobes	same	different
D	Color of corolla tube	yellowish or greenish	salmon pink
E	Corolla shape	tubular	urceolate
F	Shape of corolla tube	straight	constricted
G	Relative length of corolla tube	long	short
H	Opening of corolla tube	not constricted	constricted
I	Inner surface of corolla tube	glabrous	with woolly ring
J	Sinuses of corolla lobes	without teeth	with teeth
K	Length of stamens relative to corolla tube at anthesis	included 1/2: partially exserted	exserted
L	Length of style relative to that of stamens at anthesis	exceeded 1/2: equal	not exceeded
M	Pollen exine sculpture	not smooth	smooth
N	Constriction on both sides of the pore of pollen grain	without	with
O	Reflection angle of corolla lobes	180°	<180°
P	Habitat	cloud forests	weedy places
Q	Surface of corolla lobes	without furrows	with furrows
R	Texture of corolla tube	not membranous	membranous
S	Connectives	not dilated	sometimes dilated

Table III

Character states of Salpichroa

Taxon	Character States[a]																		Divergence Formula[b]	Divergence Level[c]
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	
didierana	1	1									1		1							ABKM	4
microphylla	1	1								1	1		1			1				ABJKMP	6
glandulosa subsp. glandulosa										1	1/2			1						J(K/2)N	21/2
glandulosa subsp. weddellii		1									1/2			1						B(K/2)N	21/2
dependens	1										1		1		1					AKMO	4
proboscidea		1	1	1							1/2									BCD(K/2)	31/2
hirsuta		1				1					1/2					1				BF(K/2)P	31/2
weberbaueri		1										1/2			1	1	1			B(L/2)OPQ	41/2
origanifolia		1			1		1	1	1		1/2					1				BEGHI(K/2)P	61/2
scandens		1				1	1	1							1	1		1		BFGHOPR	7
ramosissima		1			1		1	1								1			1	BEGHPS	6
micrantha		1				1	1	1				1			1	1				BFGHLOP	7
gayi		1				1	1					1			1	1	1			BFGLOPQ	7
diffusa		1					1									1				BGP	3
tristis		1				1	1								1	1			1	BFGOPS	6
microloba		1						1								1				BHP	3

a. 1 = divergent state.
b. The capital letter indicates the divergent state of each character occurring in each taxon.
c. Total number of changes of character states in each taxon.

Table IV

The major morphological differences between *S. microphylla* and Bolivian population of *S. glandulosa*

Characters	*S. microphylla*	*S. glandulosa*
Branches	Flexuous	Not flexuous
Calyx	Unequally divided, the lobes connate more than 1/2 length of calyx	Deeply divided, the lobes connate only at the base
Calyx lobes (shape & size)	Triangular-lanceolate, 0.8-1.3 x 0.3-0.5 cm.	Linear, 0.8-2.5 x 0.1-0.3 cm
Corolla texture	Fleshy	Chartaceous (subsp. *weddellii* not seen in vivo)
Sinuses of corolla lobes	Unequal teeth with obtuse or acute tip.	5 equal or subequal teeth with retuse tip present in subsp. *glandulosa*, or teeth absent in subsp. *weddellii*
Nectary	Absent	Present

Table V

The morphological differences of *S. micrantha* and *S. gayi*

Characters	*S. micrantha*	*S. gayi*
Leave blades & petioles	Mostly glabrous	Pubescent
Pedicels	Mostly glabrous, pilose or puberulous	Pilose, glandular-pilose, or puberulous
Calyx	Ciliate or rarely pilose; lobes 1.5–3 x 0.5–1 mm	Pilose, glandular-pilose, glandular-puberulous; lobes 3–4 x 0.5–1 mm
Corolla tube	Slightly constricted at throat & the middle of the tube, 7–9 x 1.5–2 mm, glabrous externally & internally	Occasionally slightly constricted at the middle of the tube, 10–15 x 2–3 mm, puberulous or pilose externally, glabrous internally
Corolla lobes	Triangular-ovate, each lobe with 1 green vein, 1–1.5 x 0.5–1 mm, ciliate	Linear, each lobe with 2 unequal furrows, 3–4 x 0.5–1 mm puberulous or glandular-puberulous
Free portion of filaments	0.5–1 mm long	1–1.5 mm long
Anthers	1.5–2 mm	2–2.5 mm
Style	3–4 mm, glabrous	4–5 mm, puberulous on lower half, and sparsely puberulous above
Stigma	Glabrous	Ciliate or glabrous

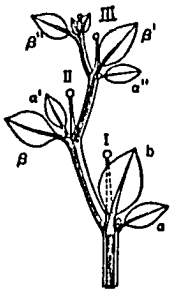


Fig. 1. The branching system of Salpichroa

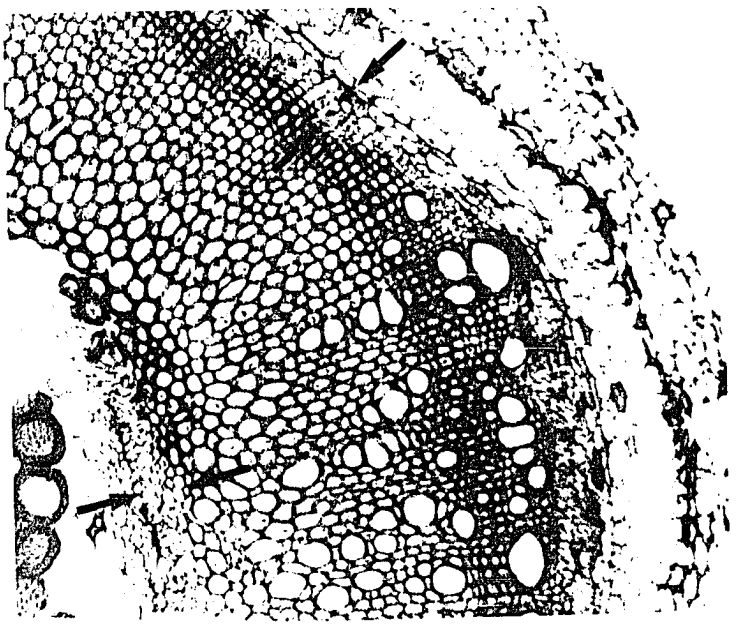


Fig. 2. Cross-section of the stem showing the bicollateral vascular bundle

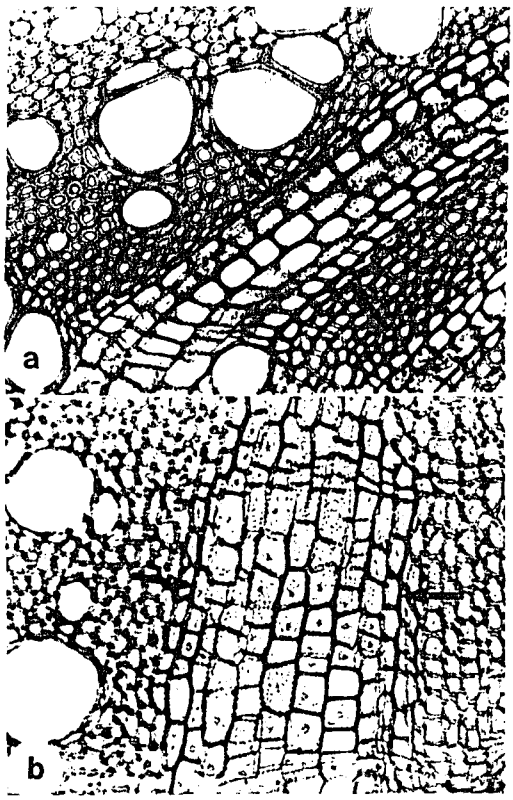


Fig. 3. Anatomy of the stem (I) showing the variation in the layers of ray parenchyma in Salpichroa: a. Cross-section of S. proboscidea; b. Cross-section of S. glandulosa subsp. glandulosa.

Fig. 4. Anatomy of the stem (II): a. Cross-section of S. diffusa showing the layer of external phloem; b. Cross-section of S. microloba showing 1) crystal-sand in the cells of external phloem 2) casparian strip; c. Cross-section of S. scandens showing phloem fibers.

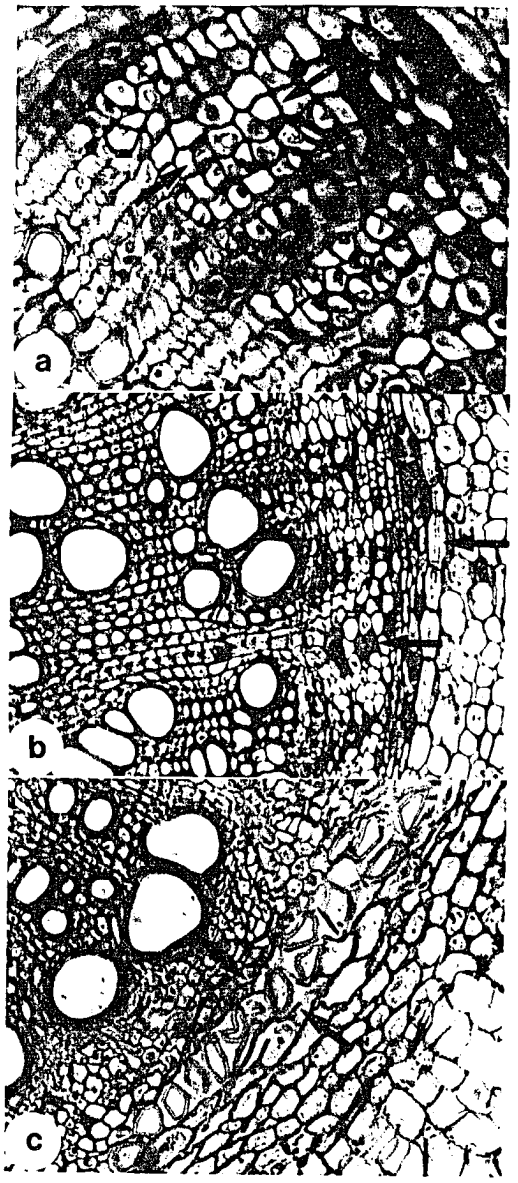


Figure 4

Fig. 5. Dissociated wood elements of Salpichroa: a. Vessel; b. Tracheid with tapered ends; c. Tracheid with alternately bordered pits; d. Libriform fibers; e. Fiber with tapered ends and scattered simple pits; f. Ray cells.

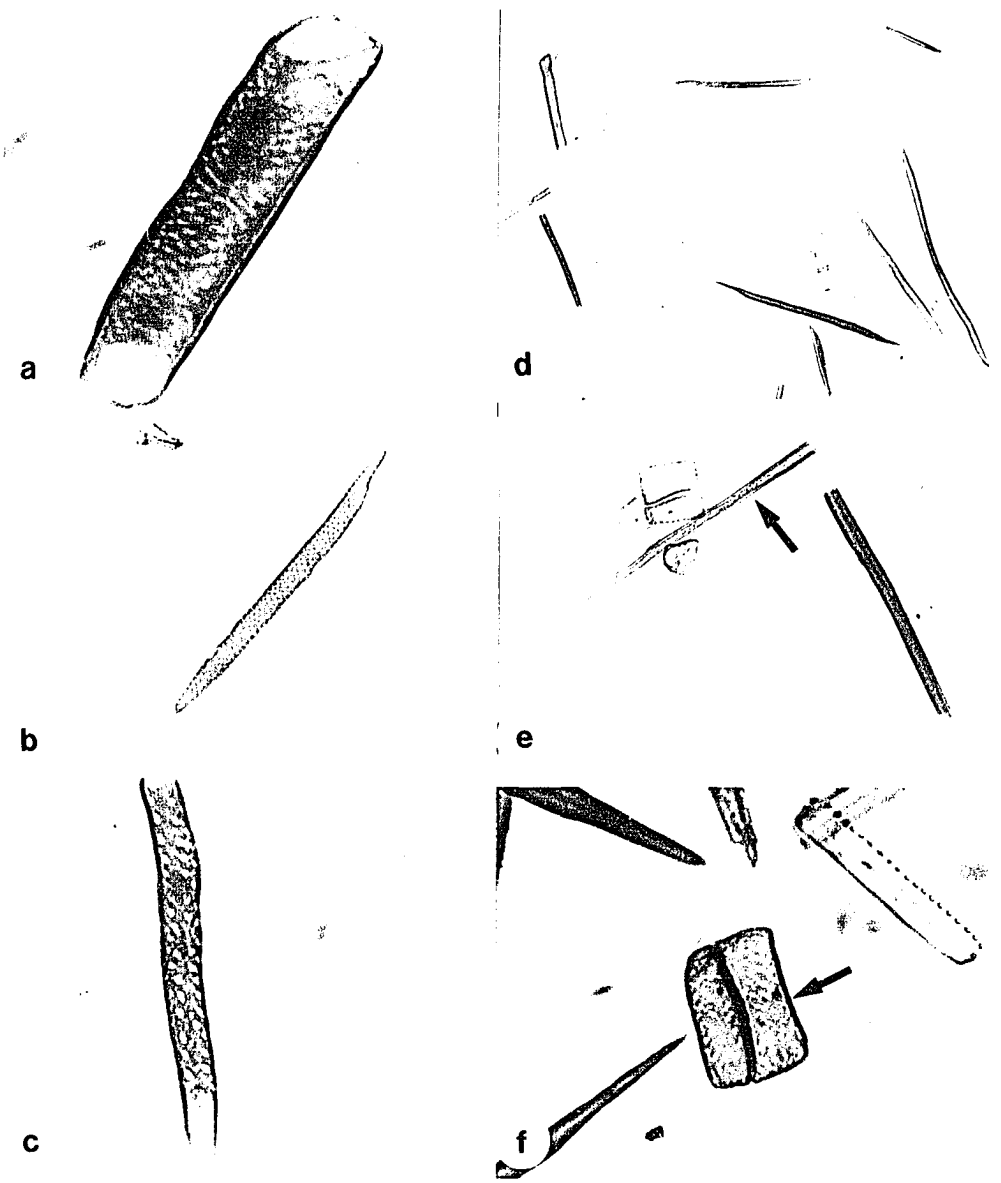


Figure 5

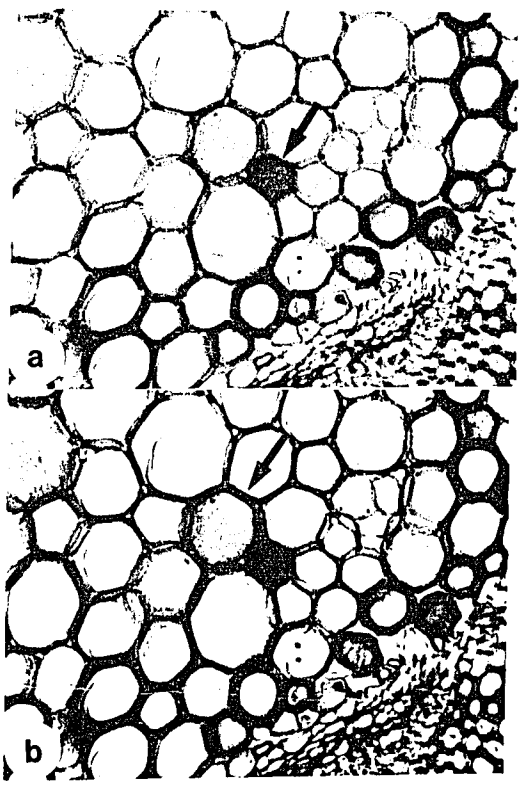


Fig. 6. Anatomy of the stem (III): cross-section of the pith of S. ramosissima. a. The idioblast with crystal-sand; b. Sclereids with simple pits.

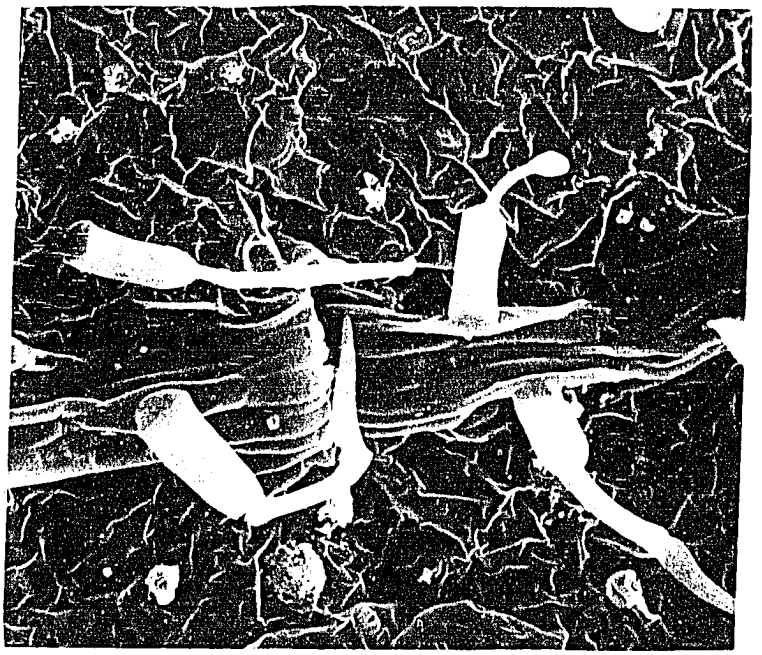


Fig. 7. Glandular trichomes of S. scandens (100x)

Fig. 8. Anomocytic stomata of Salpichroa (2000x)

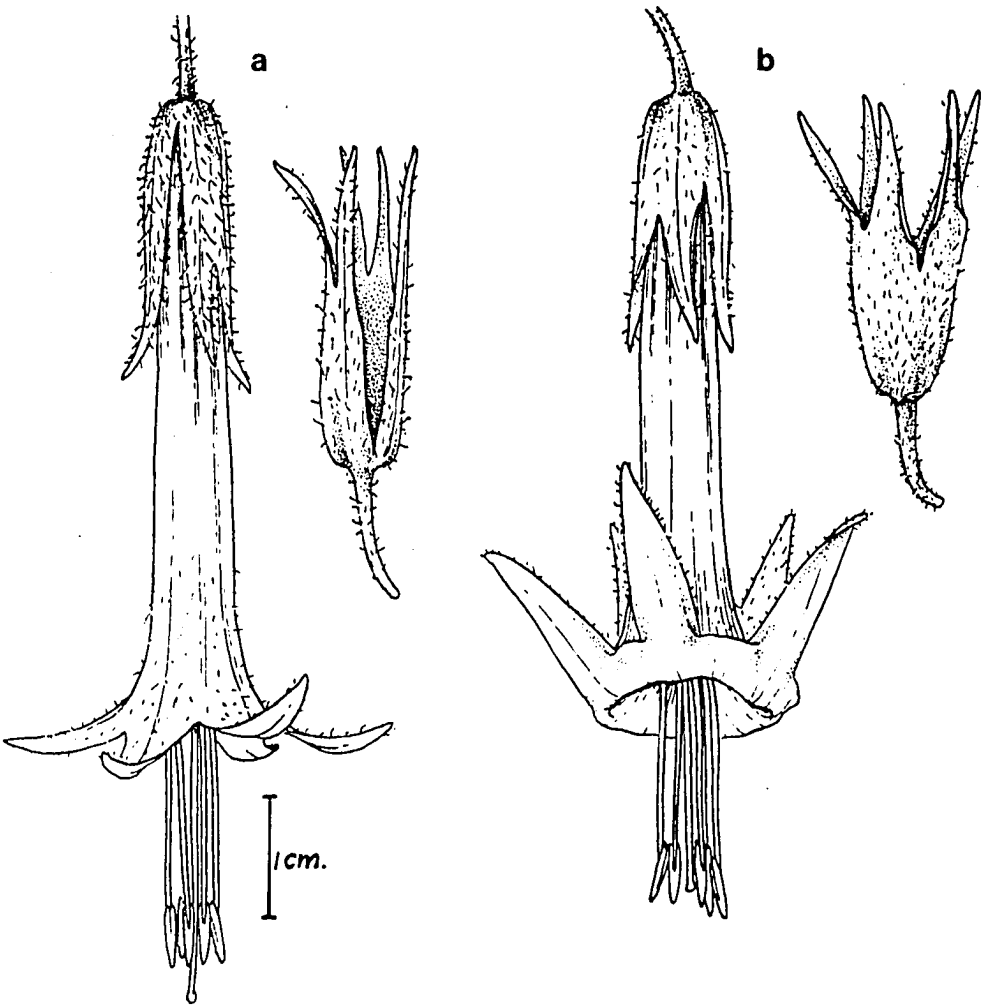
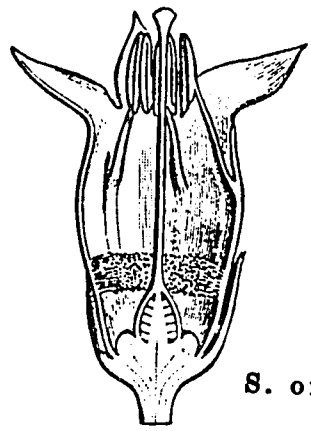


Fig. 9. Comparison of the connate lobes of calyx:
a. S. dependens; b. S. microphylla.

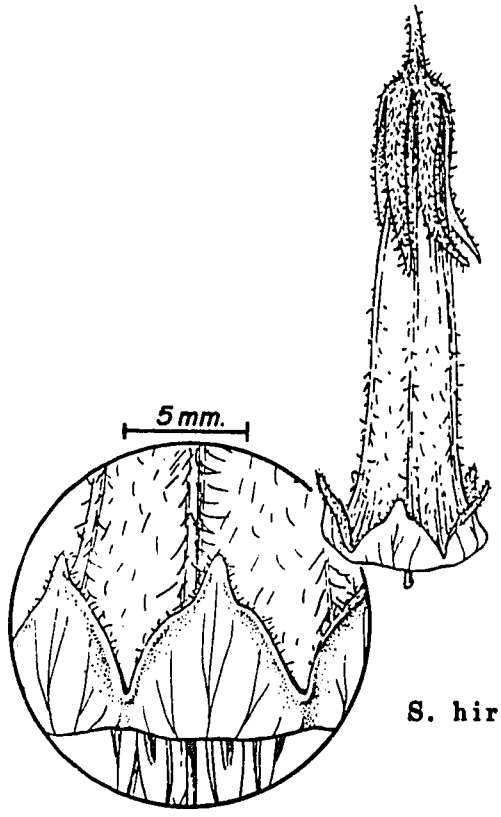
Fig. 10. The woolly band inside of the corolla tube of S. origanifolia (adapted from Baillon, 1888. Histoire des Plantes. Fig. 363)

Fig. 11. Corolla lobes of S. hirsuta



S. origanifolia

Figure 10



S. hirsuta

Figure 11

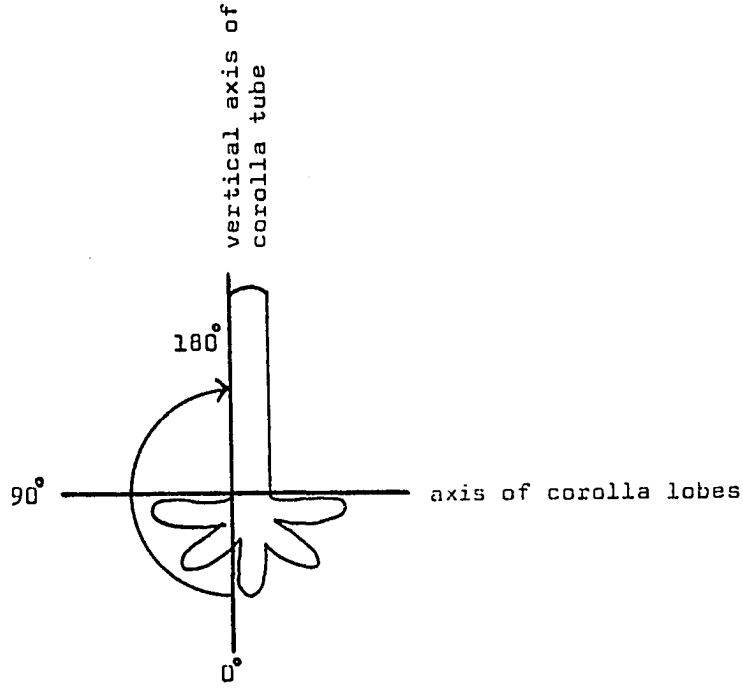
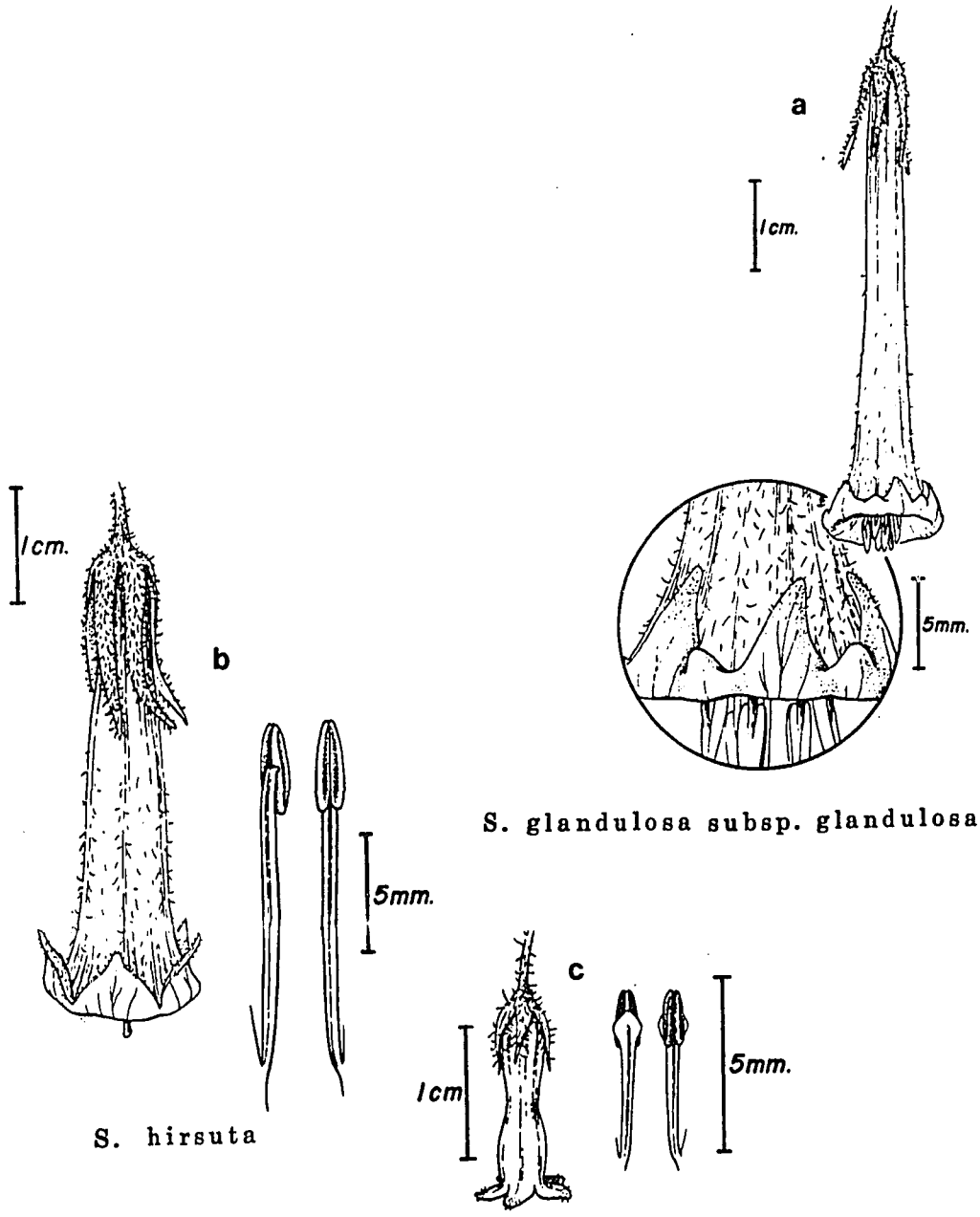


Fig. 12. The reflection angle of the corolla lobe is defined as the space between the vertical axis of the corolla tube and the axis formed by the corolla lobes.

Fig. 13. Corolla lobes and stamens: a. Teeth at the sinuses of the corolla lobes of S. glandulosa subsp. glandulosa; b. Connectives of S. hirsuta; c. Dilated connectives of S. tristis var. tristis.



S. glandulosa subsp. glandulosa

S. hirsuta

S. tristis var. tristis

Figure 13

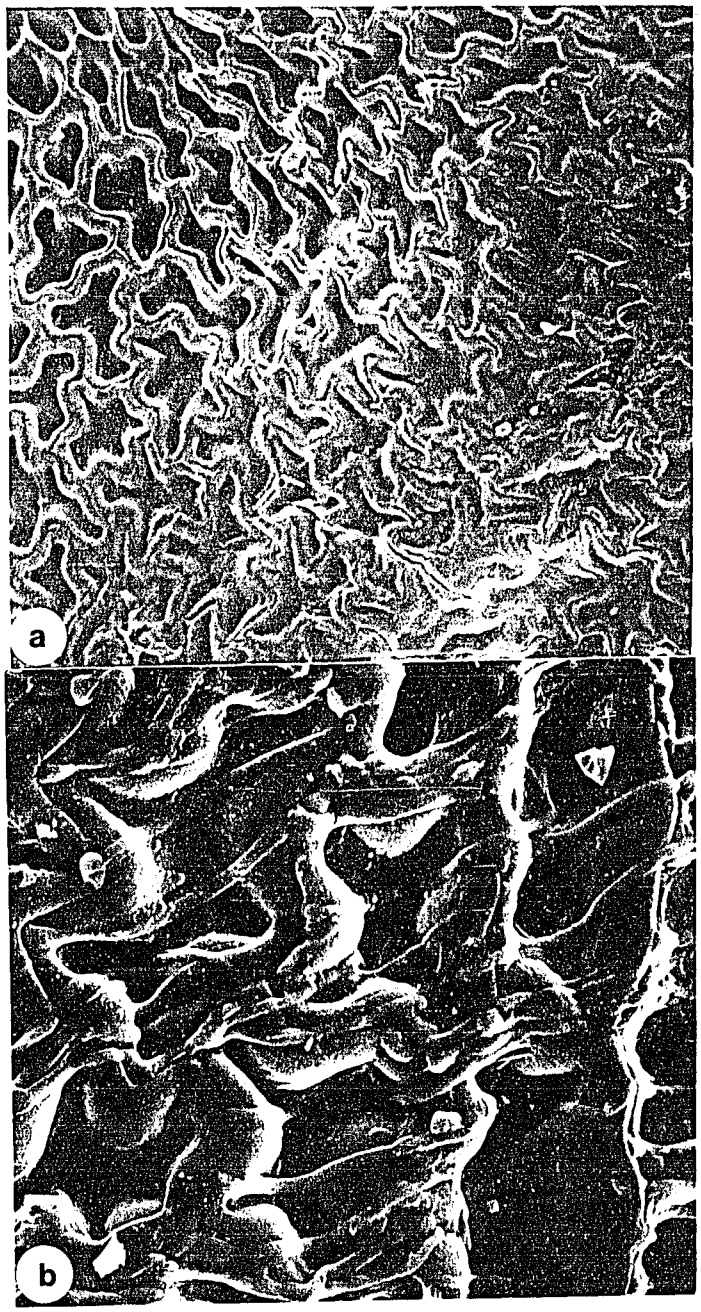


Fig. 14. Seed coats (I): a. S. dependens (100x);

b. S. weberbaueri (300x).

Fig. 15. Seed coats (II): a. S. glandulosa var. glandulosa (100x); b. S. glandulosa var. glandulosa (400x) showing the base of broken hair.

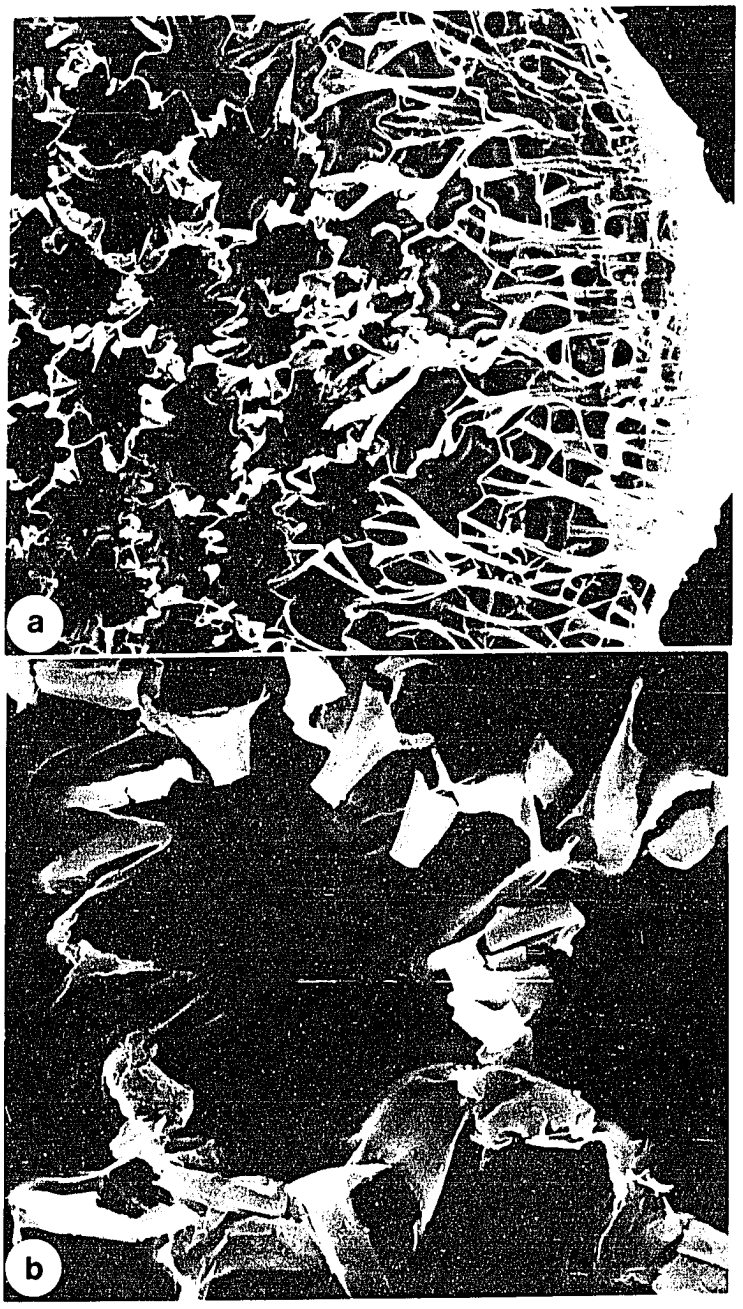


Figure 15

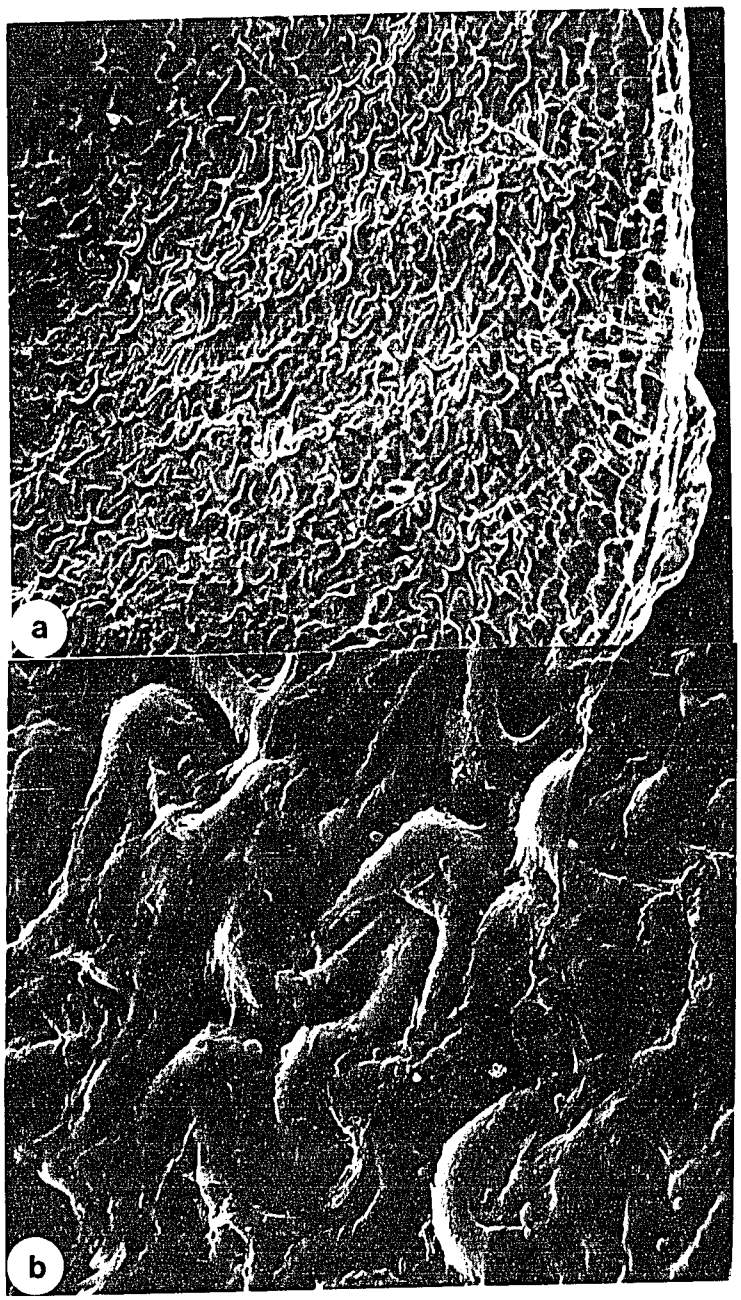


Fig. 16. Seed coats (III): a. S. micrantha (100x);
b. S. micrantha (600x).

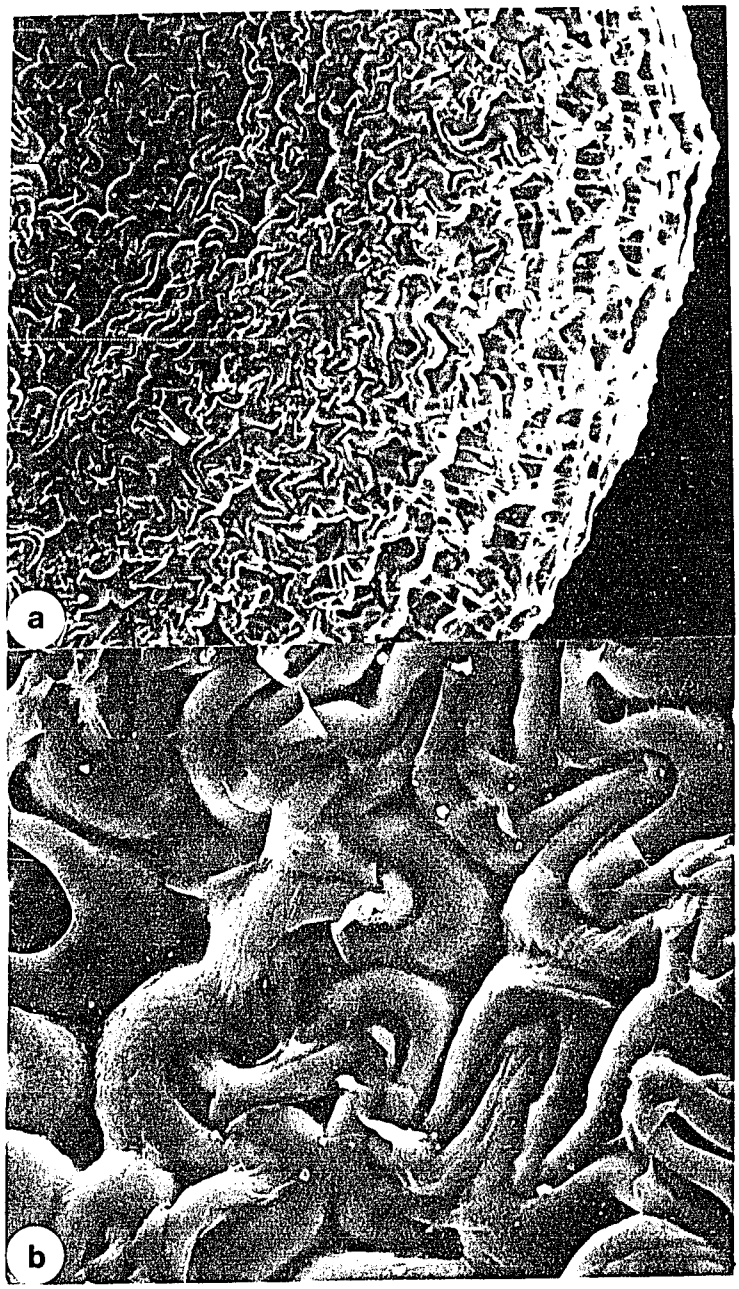


Fig. 17. Seed coats (IV): a. Nectouxia formosa (100x);

b. Nectouxia formosa (500x).

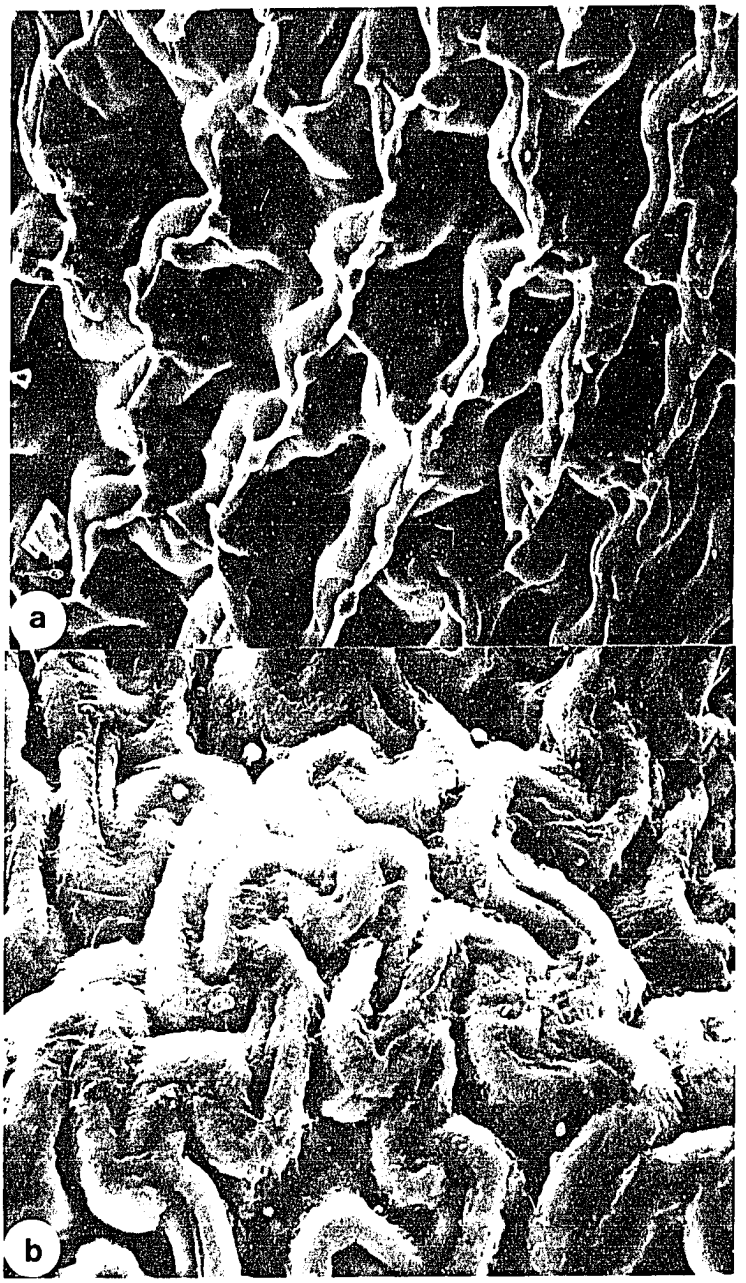


Fig. 18. Seed coats (V): a. S. diffusa (250x);

b. S. ramosissima (500x).

Fig. 19. Seed coats (VI): a. S. scandens (600x);

b. S. tristis var. tristis (300x).

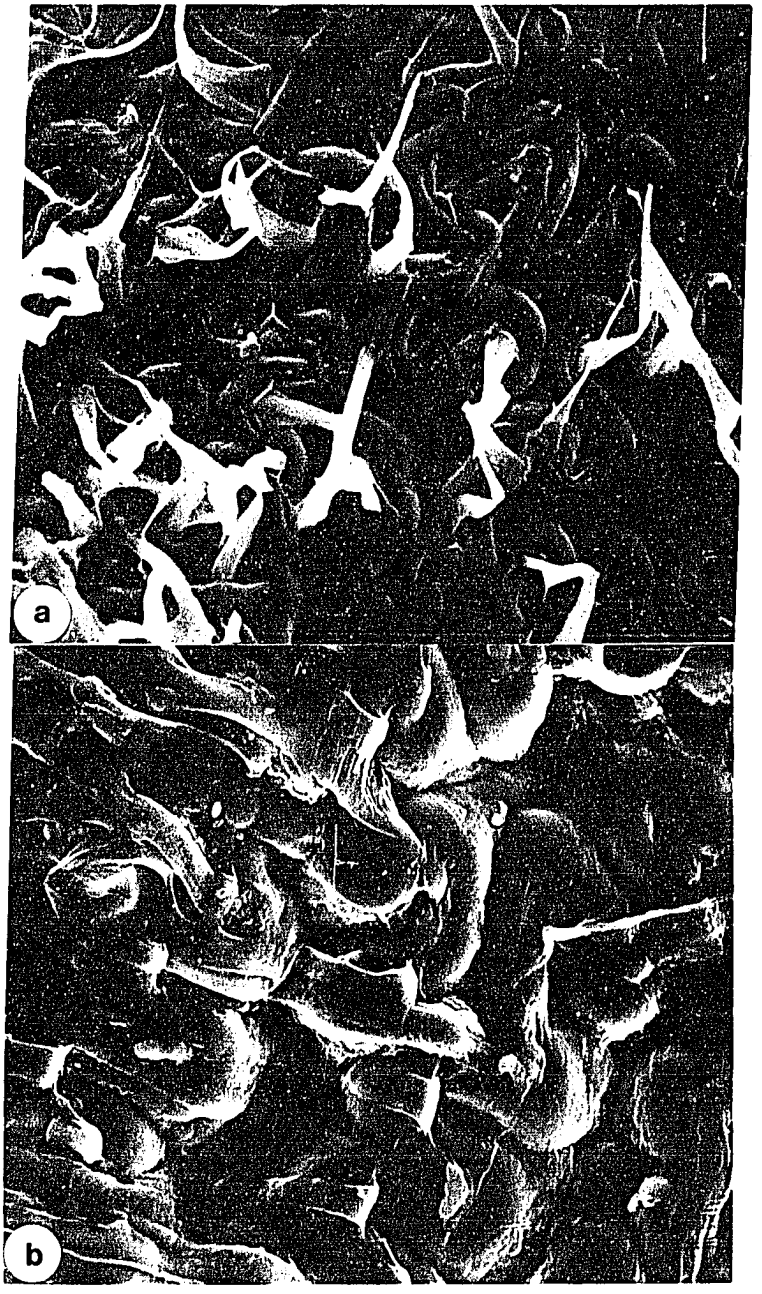


Fig. 20. Seed coats (VII): a. S. tristis var. lehmanni (300x); b. S. origanifolia (500x).

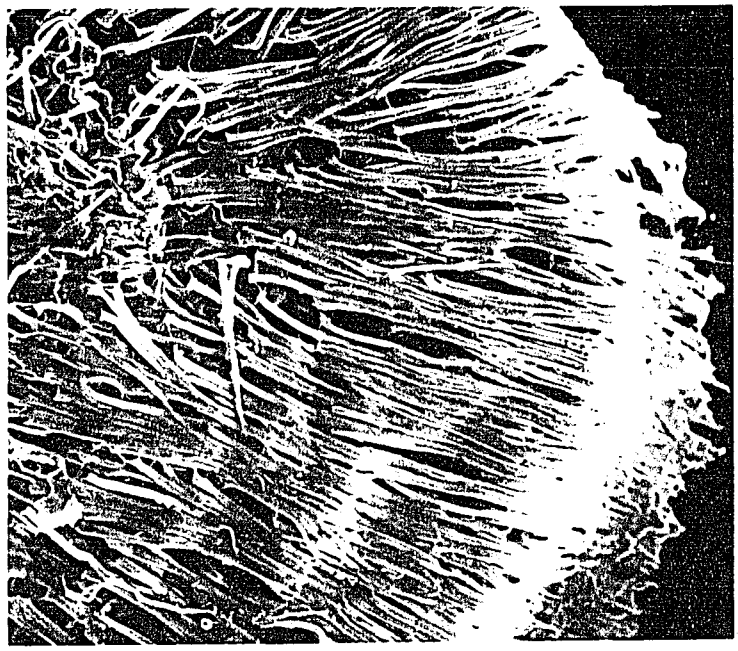


Fig. 21. Seed coats (VIII) of S. origanifolia (100x)

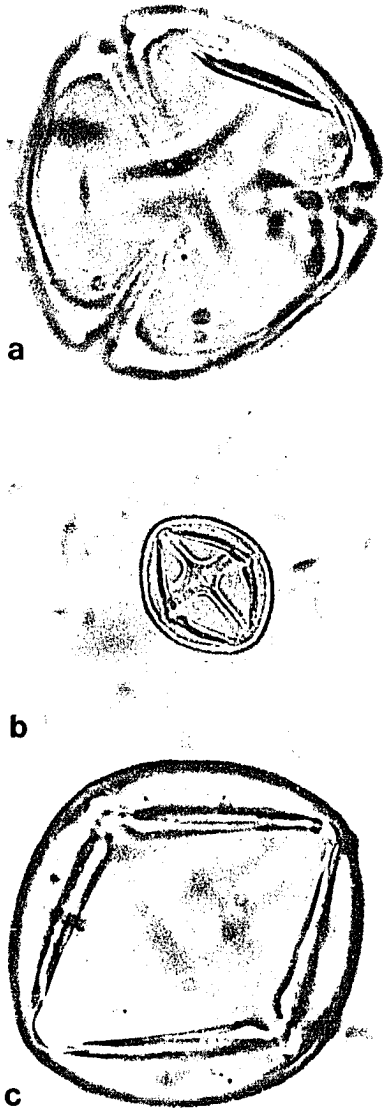


Fig. 22. Pollen of Salpichroa under light microscope: a. S. microphylla, polar view (1000x); b. S. weberbaueri, equatorial view (400x); c. S. microphylla, equatorial view (1000x).

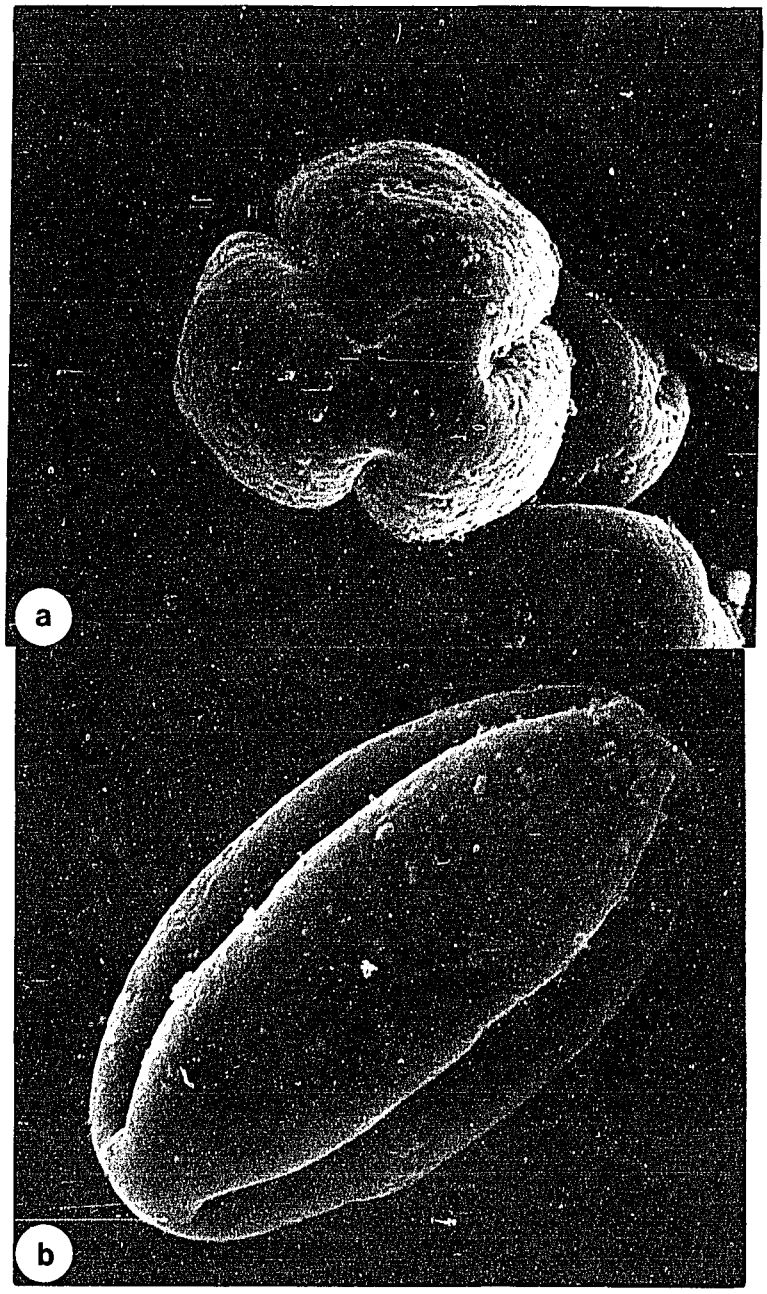


Fig. 23. Exine sculpture (I): a. S. didierana, polar view (2000x); b. S. didierana, equatorial view (2000x).

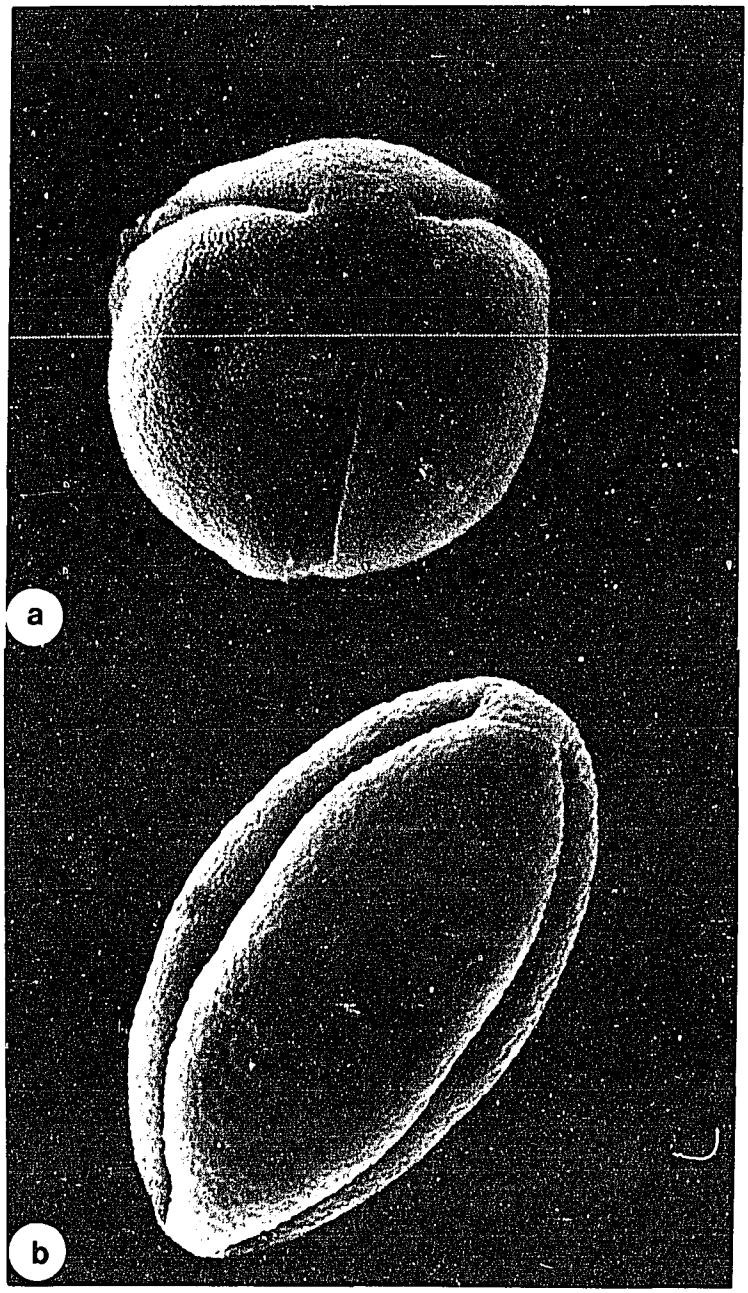


Fig. 24. Exine sculpture (II): a. Nectouxia formosa, polar view (2000x); b. Nectouxia formosa, equatorial view (2000x).

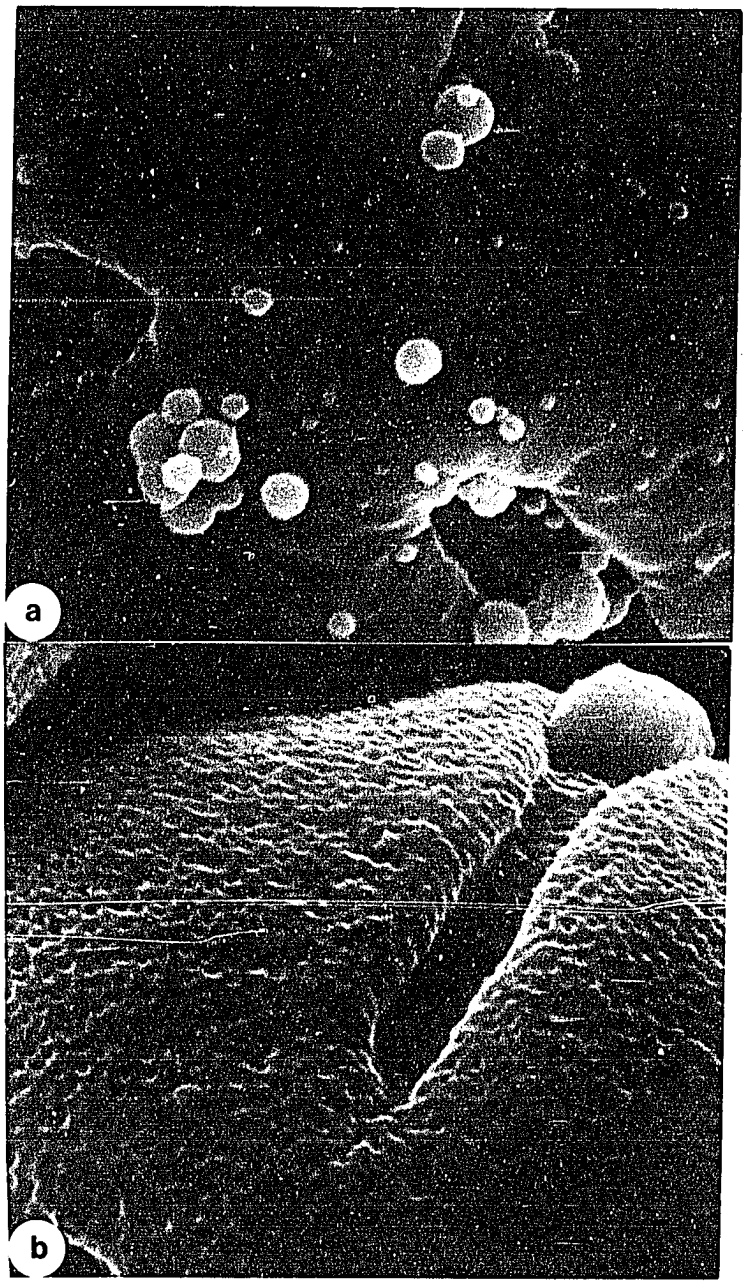


Fig. 25. Exine sculpture (III): a. S. microphylla (6000x); b. S. weberbaueri (6000x).

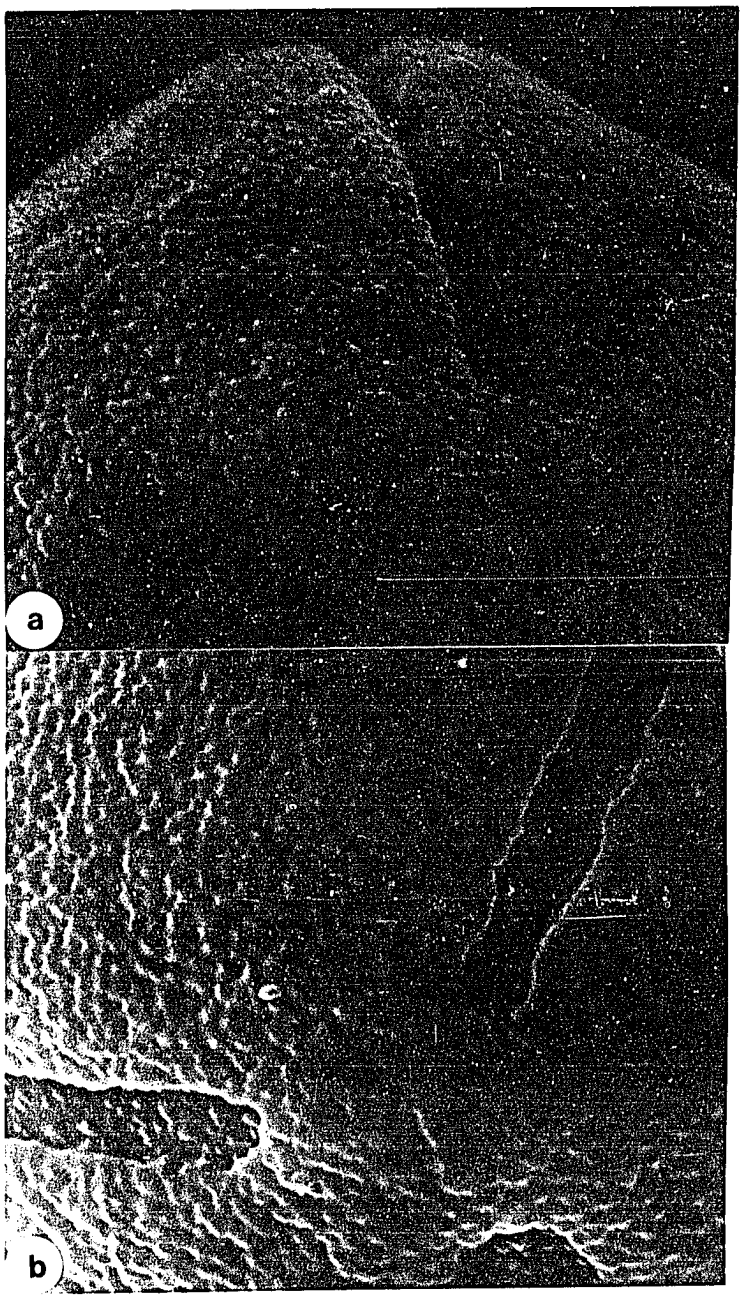


Fig. 26. Exine sculpture (IV): a. S. gayi (6000x);

b. Nectouxia formosa (6000x).

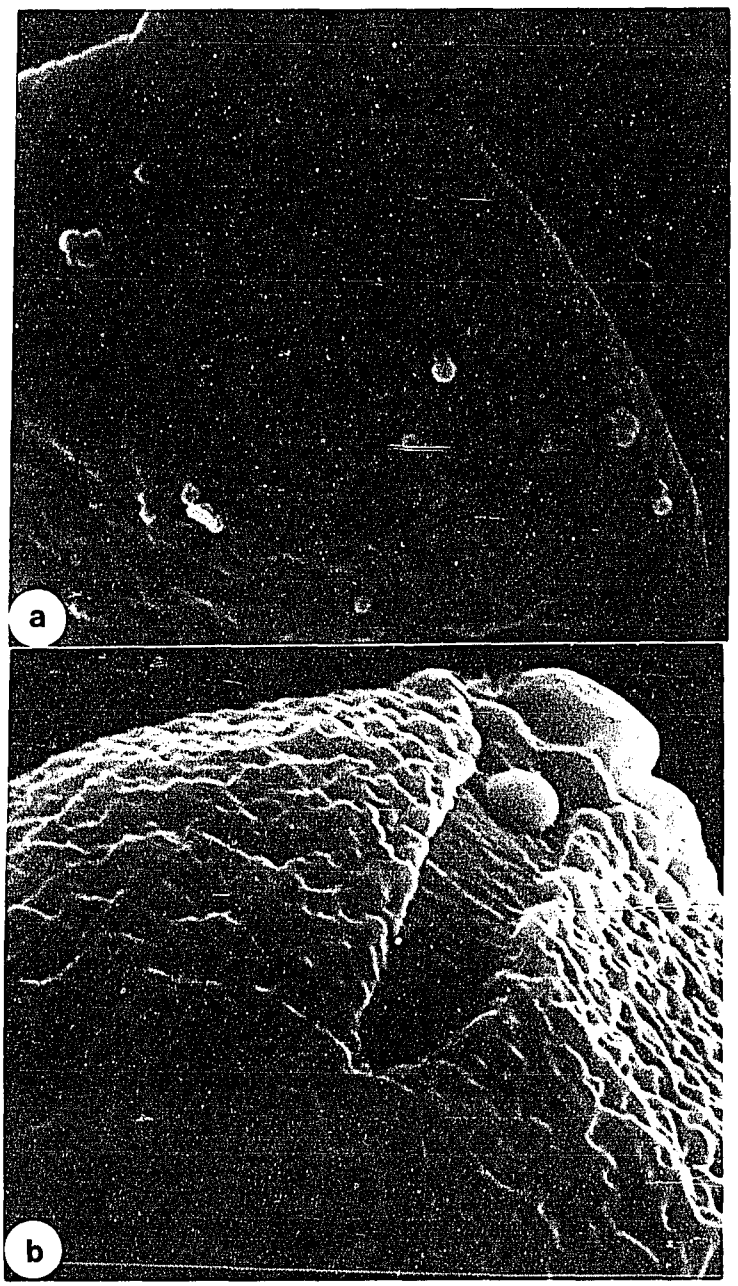


Fig. 27. Exine sculpture (V): a. S. proboscidea (6000x); b. S. microloba (6000x).

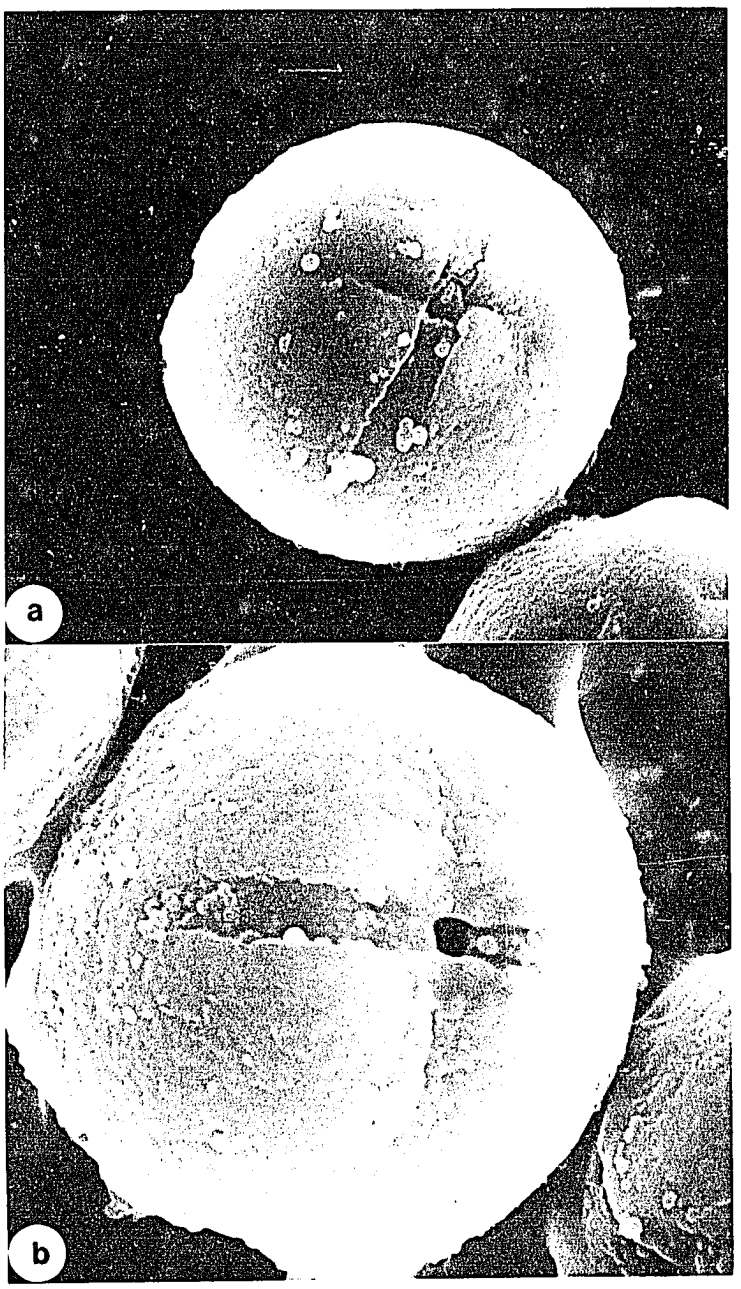


Fig. 28. Exine sculpture (VI): a. S. glandulosa subsp. glandulosa (2000x); b. S. glandulosa subsp. weddellii (2500x).

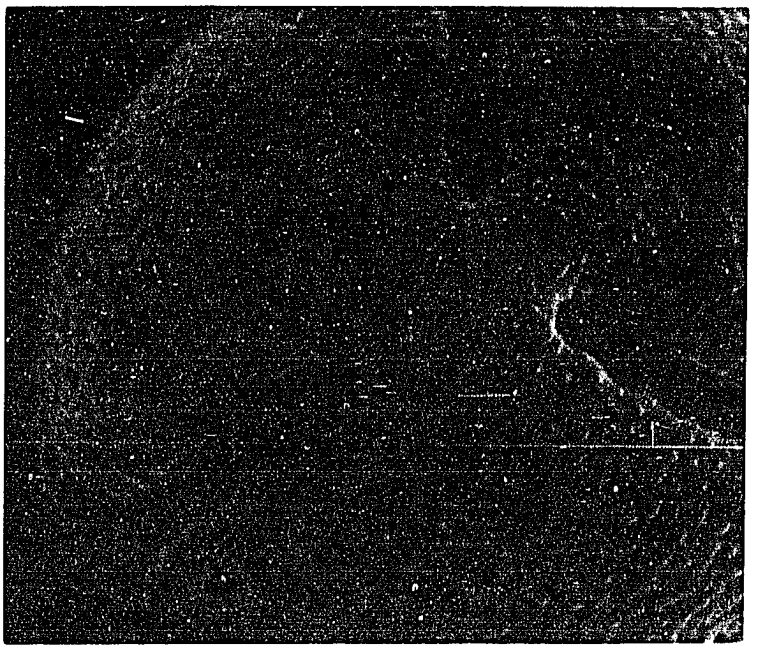


Fig. 29. Exine sculpture (VII) of S. scandens (6000x)

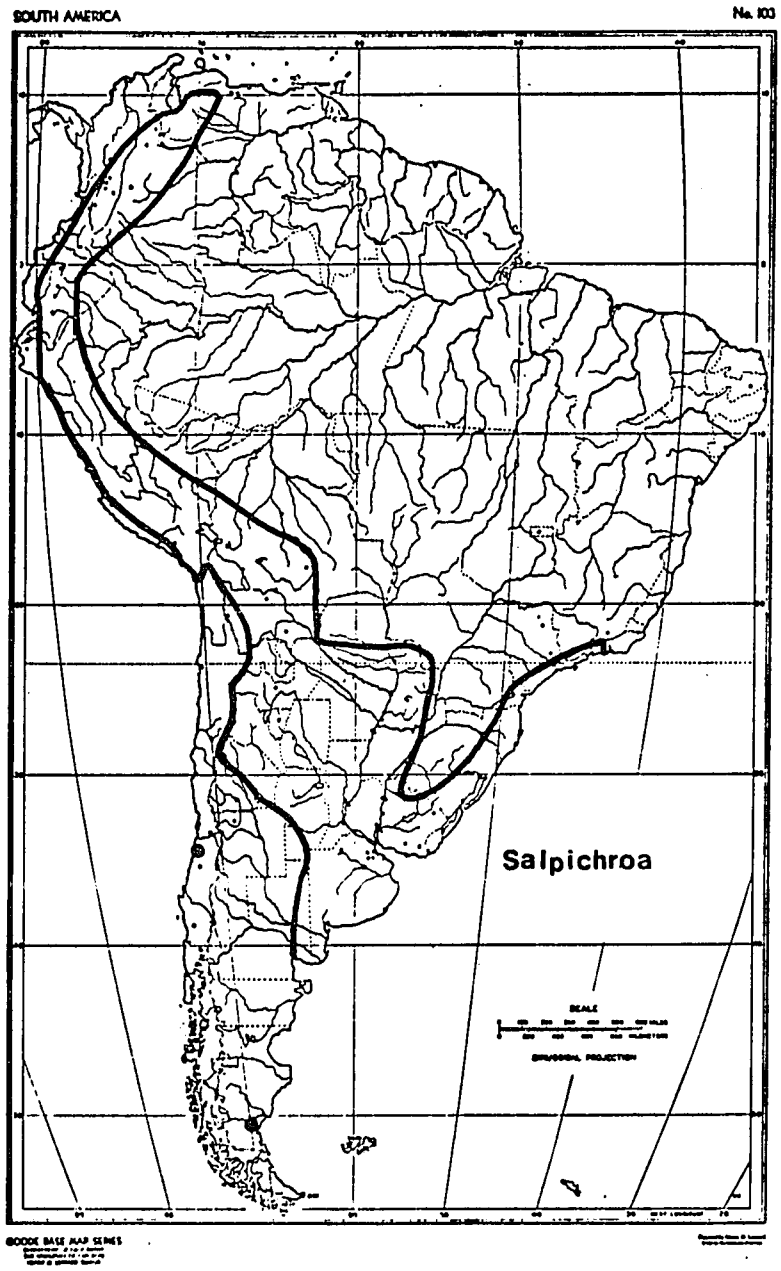


Fig. 30. Generic distribution of Salpichroa

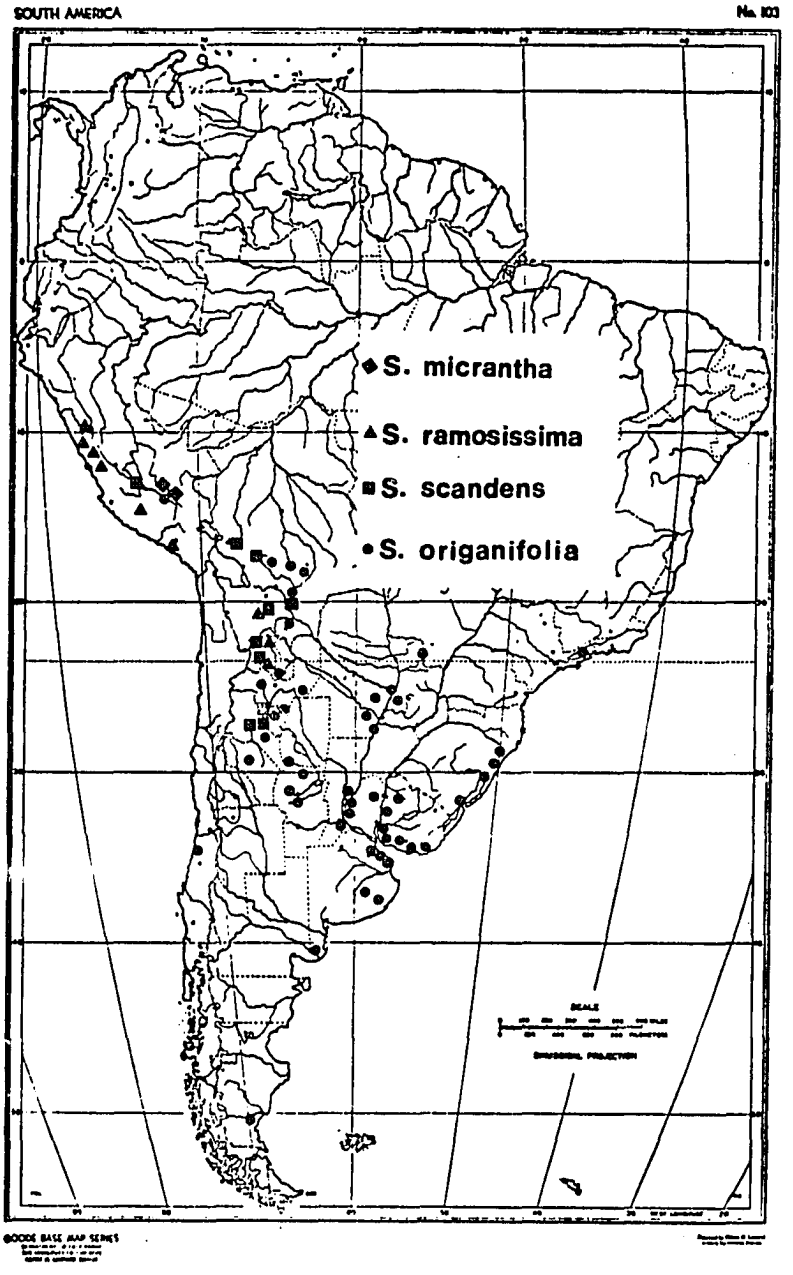


Fig. 31. Distribution of S. micrantha, S. origanifolia, S. ramosissima and S. scandens.

Fig. 32. Distribution of *S. dependens*, *S. gavi*, *S. hirsuta*, *S. tristis* var. *tristis*, *S. tristis* var. *lehmanni* and *S. weberbaueri*.

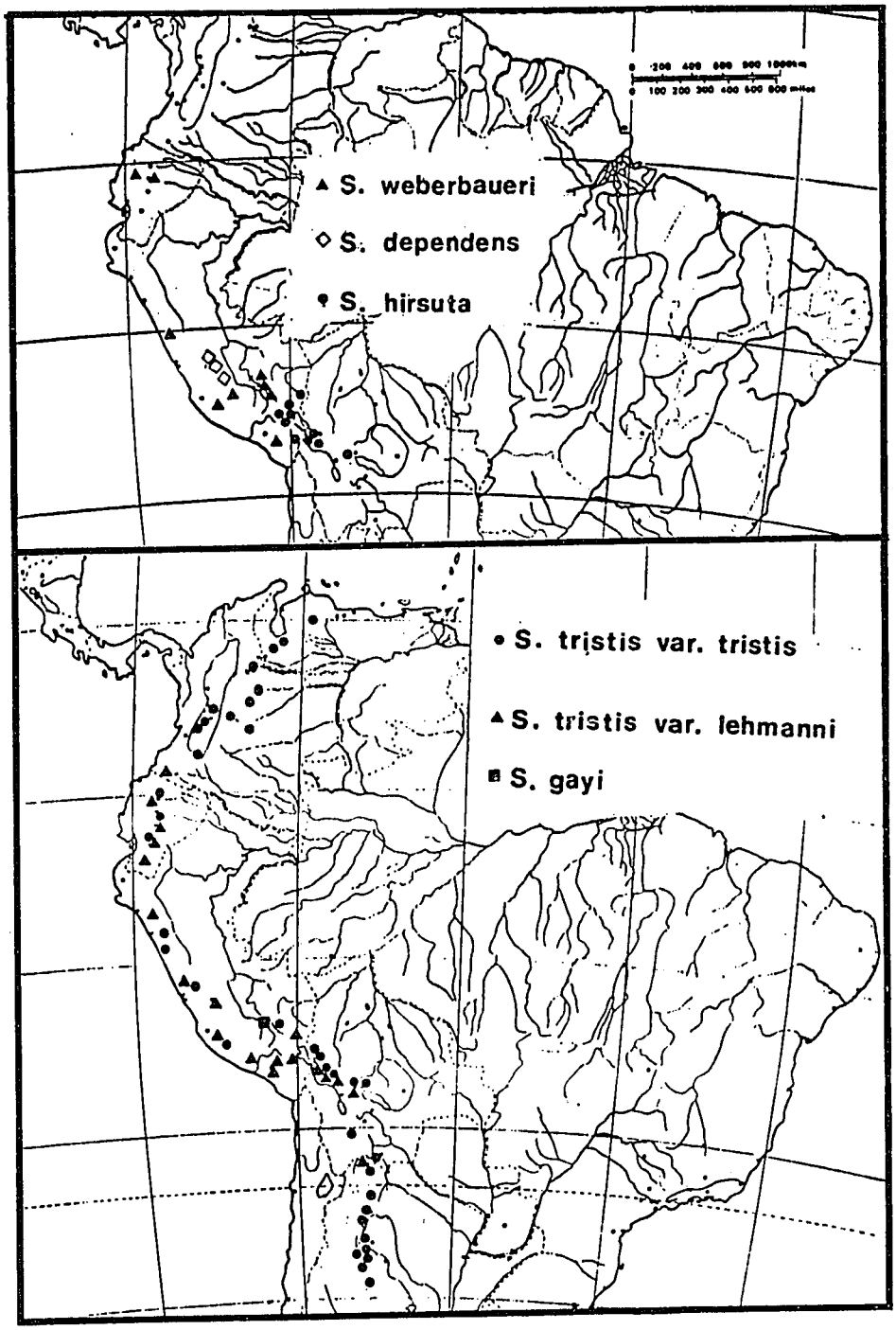
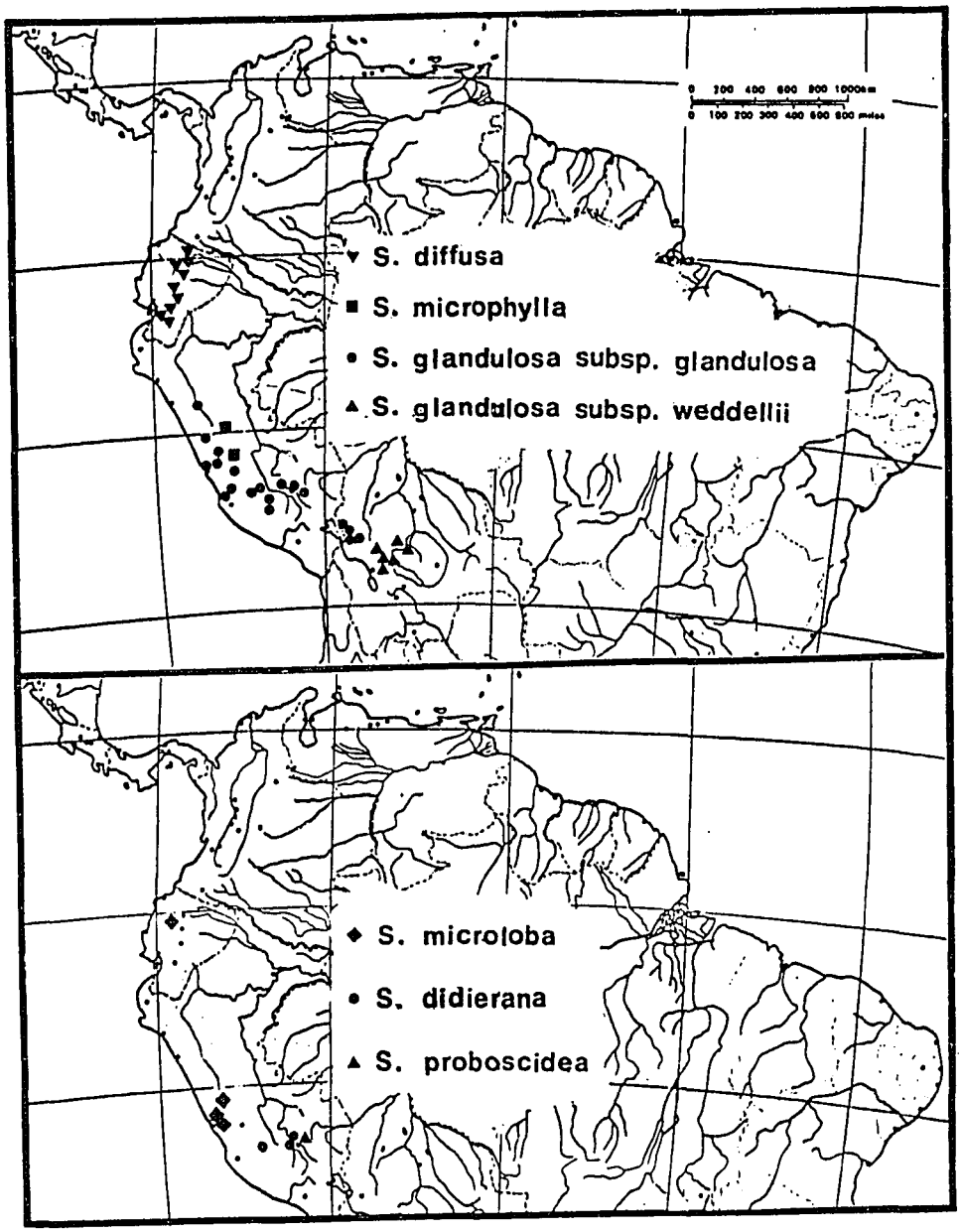


Fig. 33. Distribution of S. didierana, S. diffusa, S. glandulosa subsp. glandulosa, S. glandulosa subsp. weddellii, S. microloba, S. microphylla and S. proboscidea.



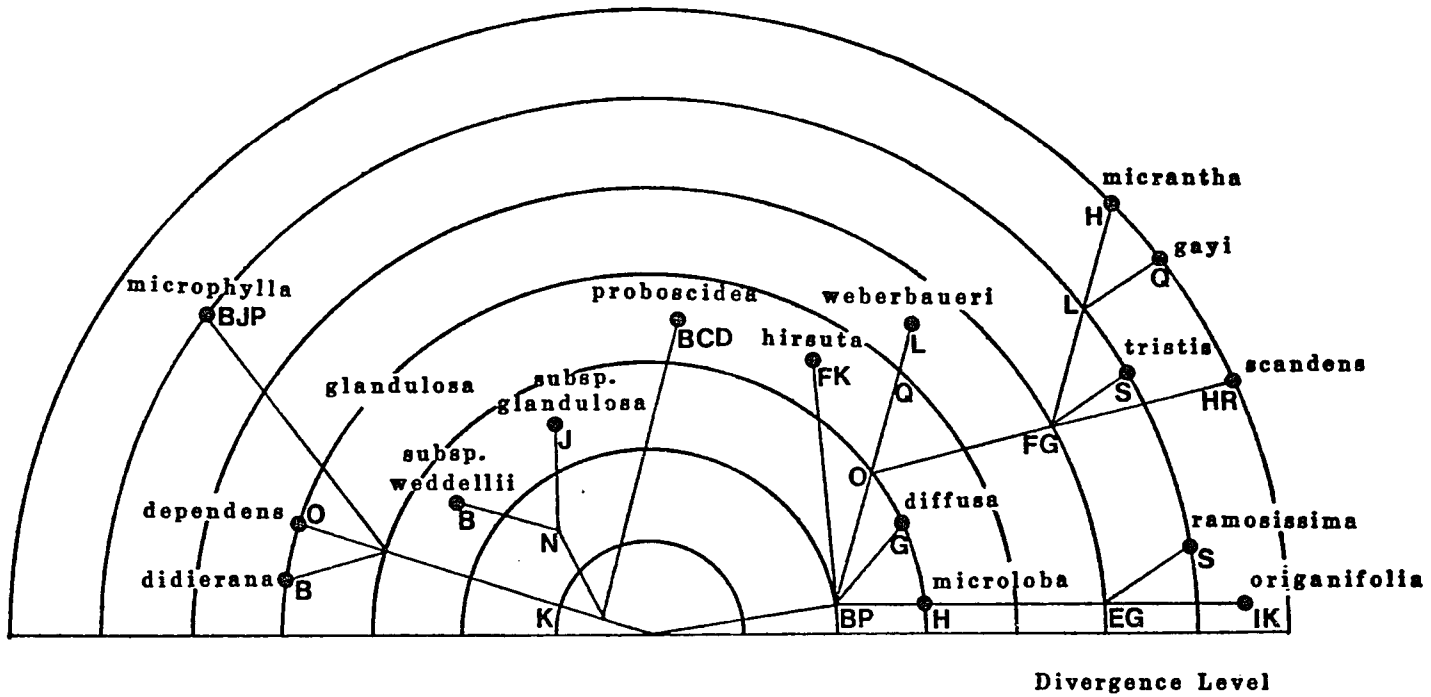
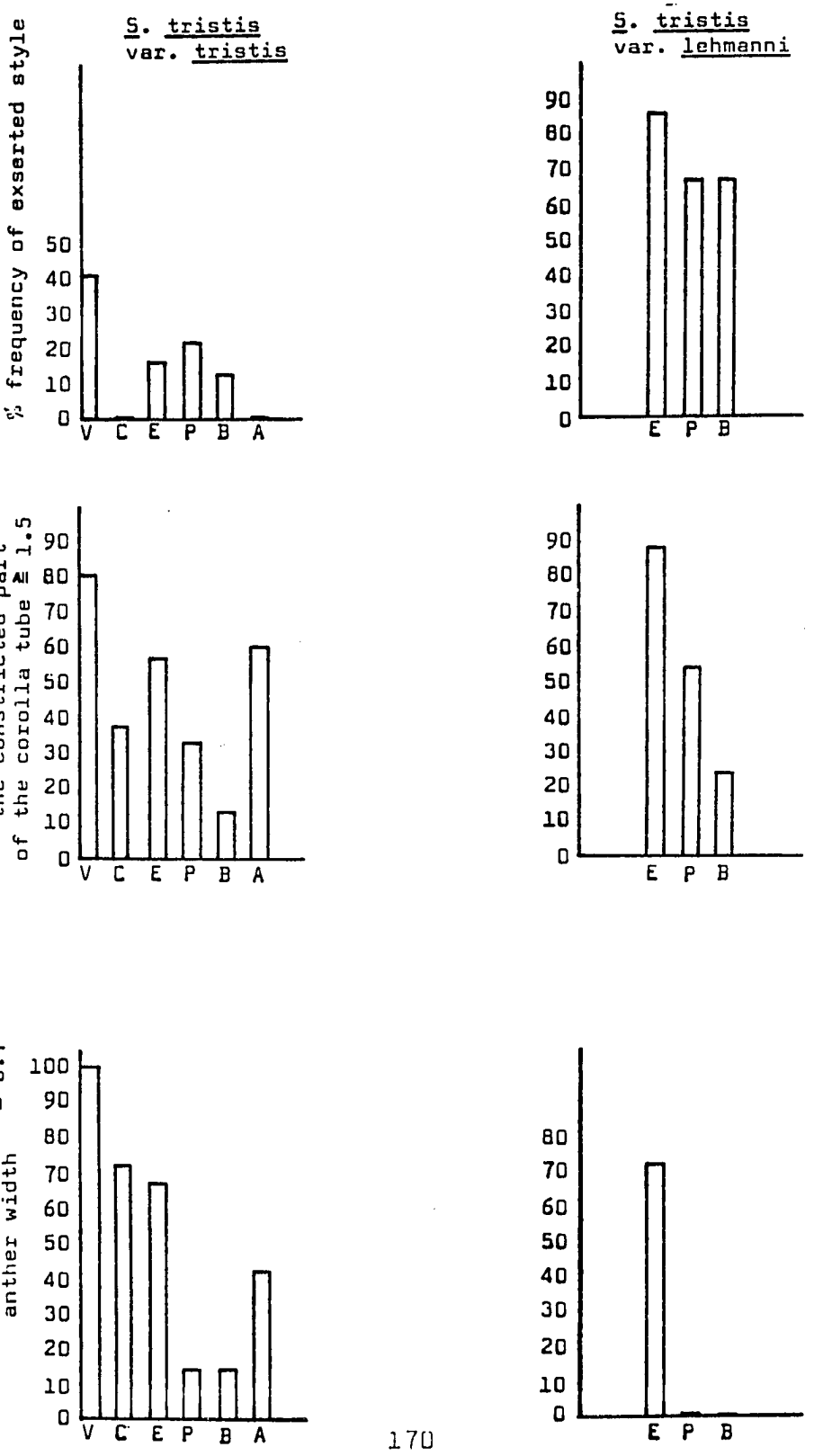
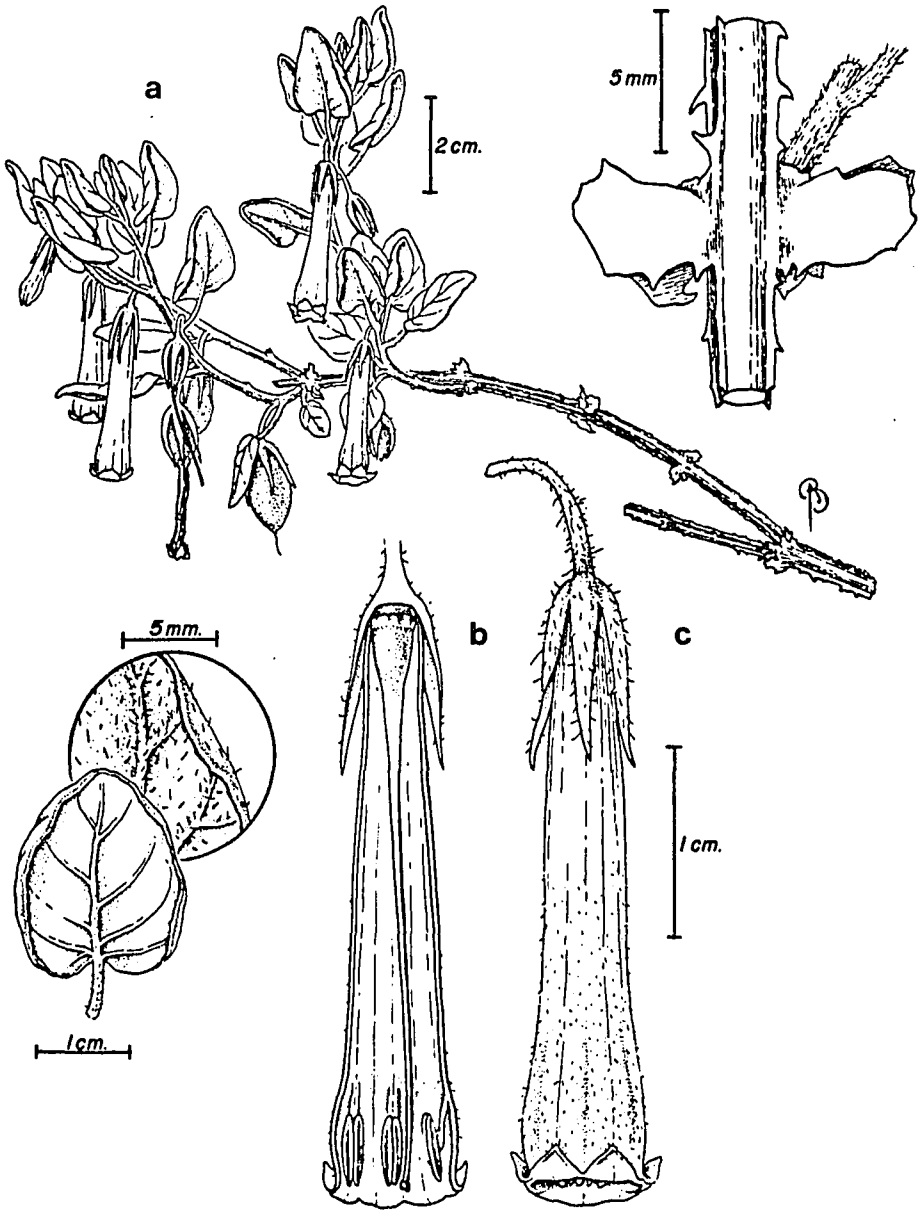


Fig. 34. Hypothetical cladogram for Salpichroa

Fig. 35. The geographical variation of 3 corolla characters in 2 varieties of S. tristis (V: Venezuela, C: Colombia, E: Ecuador, P: Peru, B: Bolivia, A: Argentina).





Salpichroa microloba sp. nov.

Fig. 36. S. microloba: a. Branch; b. Internal view of flower; c. External view of flower, note the small corolla lobes.

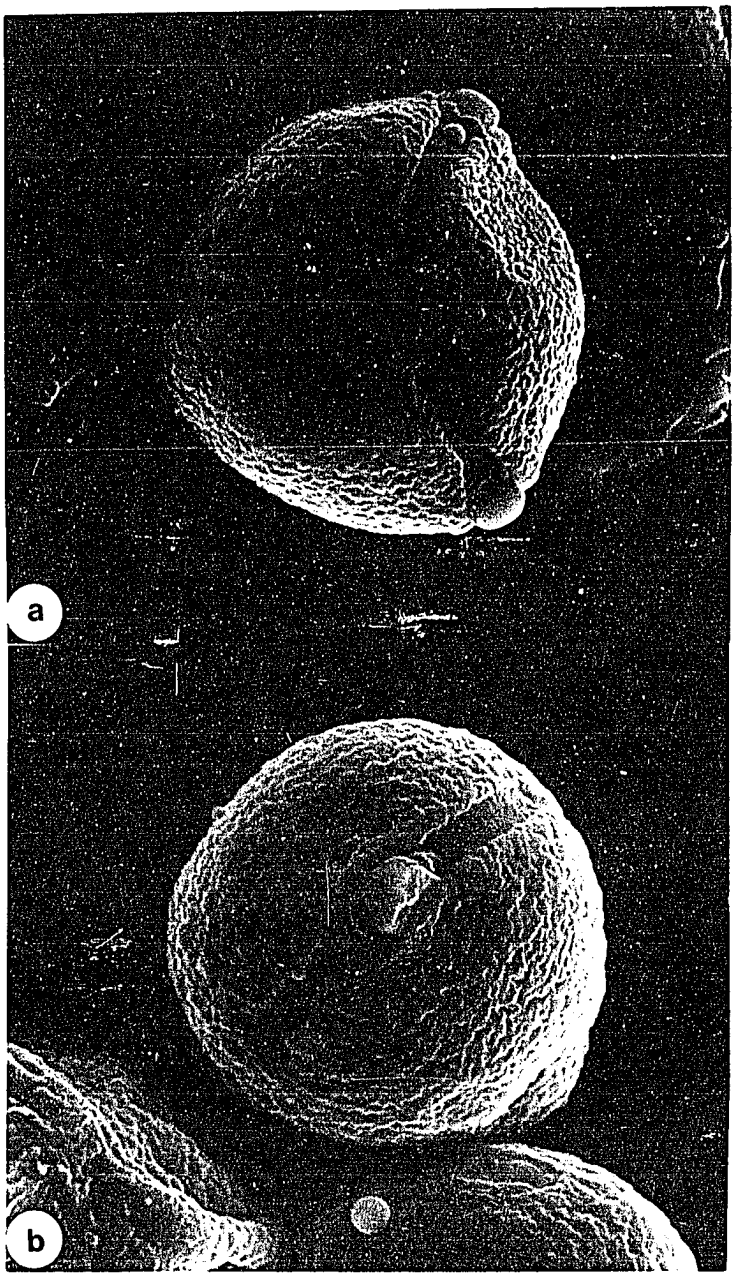


Fig. 37. Pollen of S. microloba: a. Polar view (2000x); b. Equatorial view (2000x).

Literature Cited

Al-Nowaihi, A. S. & S. F. Khalifa. 1974. A numerical classification of Solanaceae in Egypt. J. Indian Bot. Soc. 53: 224-248.

Baillon, H. 1888. Histoire des plantes p. 288 & 337. Librairie Hachette, Paris.

Benítez de Rojas, C. E. 1974. Géneros de las Solanaceae de Venezuela. Revista Fac. Agron. (Maracay) 7(3): 51.

Benoist, R. 1938a. Nouvelles espèces du genre Salpichroa (Solanacees). Bull. Soc. Bot. Fr. 85: 53-56.

_____ 1938b. Nouvelles espèces de Phanérogames sudamericaines. Bull. Soc. Bot. Fr. 85: 408-410.

Bentham, G. & J. D. Hooker. 1876. Genera plantarum 2(2): 885, 889. London.

Brisson, J. D. & R. L. Peterson. 1976. A critical review of the use of scanning electron microscopy in the study of the seed coat. Scanning Electron Microsc. 7: 477-495.

Burdet, H. M. 1975. Cartulae ad botanicorum graphicem VII. Candollea 30: 379-410.

Burkart, A. 1979. Flora ilustrada de Entre Ríos (Argentina) p. 397-398. Colección Científica del I.N.T.A., Buenos Aires.

Cabrera, A. L. 1953. Manual de la flora de los alrededores de Buenos Aires p. 414. Buenos Aires.

_____ 1965. Flora de la Provincia de Buenos Aires V: 220-221. Colección Científica del I.N.T.A., Buenos Aires.

Child, A. 1979. A review of branching patterns in the Solanaceae. In: Hawkes, J. G., R. N. Lester & A. D. Skelding, eds. The biology and taxonomy of the Solanaceae p. 345-356. Academic Press.

Colmeiro, Don M. 1858. La botánica y los botánicos de la península Hispano-Lusitana p. 179-181. Imprenta y Estereotipia de M. Rivadeneyra, Madrid.

Crisci, J. V. & T. F. Stuessy. 1980. Determining primitive character states for phylogenetic reconstruction. Syst. Bot. 5(2): 112-135.

Cruckshanks, A. 1831. Account of an excursion from Lima to Pasco. Bot. Misc. 2: 168-205.

Dammer, U. 1905. Solanaceae americanae. Bot. Jahrb. Syst. 37: 167-171.

_____ 1906. Solanaceae andinae. Bot. Jahrb. Syst. 37: 636-642.

Darlington, C. D. & A. P. Wylie. 1961. Chromosome atlas of flowering plants p. 304. George Allen & Unwin Ltd. London.

Desfontaines, R. 1829. Catalogus plantarum Horti Regii Parisiensis p. 396. Apud Editorem J. S. Chaude, Paris.

Drummond, B. A. in press. Coevolution of Ithomiine butterflies and Solanaceous plants.

Dunal, M. F. 1852. Solanaceae. In: de Candolle, A. P. Prodromus systematis naturalis regni vegetabilis 13(1): 471-476 & 531.

Erdtman, G. 1971. Pollen morphology and plant taxonomy I: 409-412. Hafner Publishing Company, New York.

Evans, W. C., A. Ghani & V. A. Woolley. 1972. Alkaloids of Salpichroa origanifolia. Phytochemistry 11: 469.

Gentry, J. L. Jr. in press. Pollen studies in the Solanaceae and Nolanaceae.

Grant, K. A. & V. Grant. 1968. Hummingbirds and their flowers p. 77-85. Columbia University Press, New York and London.

Gray, A. 1878. Synoptical flora of North America p. 231-232. Ivison, Blakeman, Taylor and Company, New York.

Grisebach, A. 1874. Plantae Lorentzianae p. 170. Göttingen.

Harborne, J. B. in press. Systematic significance of variations in defense chemistry in the Solanaceae.

Heiser, C. Jr. 1963. Numeración cromosómica de plantas Ecuatorianas. Ci. & Nat. (Quito, Ecuador) 6(1): 2-7.

Herter, W. 1937. Additamenta ad floram Urugayensem. In: Estudios botánicos en la región Uruguaya XV. p. 189. Montevedeo.

Herzog, T. 1916. Die von Dr. Th. Herzog auf seiner zweiten Reise durch Bolivien in den Jahren 1910 und 1911 gesammelten Pflanzen III. Meded. Rijks-Herb. 29: 1-94.

Heusser, C. J. 1971. Pollen and spores of Chile p. 58. The University of Arizona Press, Tucson, Arizona.

Hickey, L. J. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60(1): 17-33.

Hieronymus, J. 1882. Plantae diaphoricae florae Argentinae p. 194. Imprenta de Guillerma Kraft, Buenos Aires.

Hill, R. J. 1976. Taxonomic and phylogenetic significance of

seed coat microsculpturing in Mentzelia (Loasaceae) in Wyoming and adjacent western states. Brittonia: 28(1): 86-112.

Hooker, W. J. 1829 [1830]. Atropa rhomboidea. Bot. Misc. 1: 135-136.

_____ 1831. Atropa glandulosa. Bot. Misc. 2: 230.

_____ 1837. Atropa dependens. Hooker's Icon. Pl. 2: tab. 107. London.

Hunziker, A. T. 1979. South American Solanaceae: a synoptic survey. In: Hawkes, J. G., R. N. Lester & A. D. Skelding, eds. The biology and taxonomy of the Solanaceae p. 49-85. Academic Press.

Jaubert, M. le Comte. 1861. Note sur quelques plantes du haut Pérou. Bull Soc. Bot. Fr. 8: 114-117.

Lamarck, C. 1793. Tableau encyclopédique et méthodique des Trois règnes de la nature, Botanique 2: 28. Paris.

Lawrence, G. H. M. 1951. Taxonomy of vascular plants. The MacMillan Company, New York.

Lindley, J. 1847. The vegetable kingdom. 2nd. ed. Bradbury & Evans, London.

_____ 1853. _____ 3rd. ed. Bradbury & Evans, London.

Linnaeus, C. 1737. Hortus cliffortianus p. 62. Amsterdam.

_____ 1753. Species plantarum I: 182. Impensis Laurentii Salvii, Stockholm.

Macbride, J. F. 1962. Solanaceae. In: Flora of Peru. Field Mus. Nat. Hist. Bot. Ser. 13(5B)(1): 59-66, 83-86.

Metcalfe, C. R. & L. Chalk 1948. Anatomy of the Dicotyledons II: 965-978. Clarendon Press, Oxford.

Meyen, F. J. F. 1834. Reise um die Erde 1: 466. Berlin.

Miers, J. 1845. Contributions to the botany of South America. London J. Bot. 4: 319-329.

_____ 1848. Contributions to the botany of South America. London J. Bot. 7: 333-336.

_____ 1850. Illustrations of South American plants p. 1-10 & 132-135. H. Bailliere Publisher, London.

Milne-Edwards, A. 1864. De la famille des Solanacees. Martinet, Paris.

Paillieux, M. A. & M. D. Bois. 1884. Le potager d'un curieux. Bull. Soc. Nat. Acclim. France 4(1): 666-668.

Ruiz, H. 1940. Travels of Ruiz, Pavón and Dombey in Peru and Chile (1777-1788). Translated by B. D. Dahlgren. Field Mus. Nat. Hist., Bot. Ser. 21: 55-58.

Ruthsatz, B. 1974. Los arbustos de las estepas andinas del noroeste Argentino y su uso actual. Bol. Soc. Argent. Bot. 16(1-2): 27-45.

Savage, S. 1945. A catalogue of the Linnaean herbarium. Linnean Society of London.

Shinners, L. H. 1962. Salpichroa origanifolia instead of S. rhomboidea (Solanaceae). Leafl. W. Bot. 9: 257-259.

Simpson, B. B. 1975. Pleistocene changes in the flora of the high tropical Andes. Paleobiology 1: 273-294.

Small, J. K. 1903. Flora of the southeastern United States p. 991-992. New York.

Small, J. K. 1933. Manual of the southeastern flora. p. 1116-1117. New York.

Smith, L. B. 1962. Origins of the flora of southern Brazil. Contr. U. S. Natl. Herb. 35(3): 215-249.

Sodiro, A. S. J. 1905. Plantae ecuadorenses IV. Bot. Jahrb. Syst. 36: 377-388.

USDA technical bulletin No. 1471. Seed characteristics of 42 economically important species of Solanaceae in the United States p. 22.

Wagner, W. H. Jr. 1980. Origin and philosophy of the Groundplan-divergence method of cladistics. Syst. Bot. 5(2): 173-193.

Walker, J. W. & J. A. Doyle. 1975. The base of angiosperm phylogeny: palynology. Ann. Missouri Bot. Gard. 62(3): 664-723.

Walpers, G. G. 1847. Repertorium botanices systematicae VI. p. 612-613. Sumtibus F. Hofmeister, Lipsiae.

---------- 1852. Annales botanices systematicae p. 169-170. Sumtibus F. Hofmeister, Lipsiae.

Weddell, M. H. A. 1859. Chloris andina 2: 97-98. Libraire-Editeur Chez P. Bertrand, Paris.

---------- 1867. Notice sur M. G. Mandon. Bull. Soc. Bot. Fr. 14(1): 10-12.

West, E. 1952. Perizoma, a potential weed pest. Univ. Florida Agric. Exp. Sta. Circ. S-54.

Wettstein, R. V. 1891. Solanaceae. in: Engler, A. & K. Prantl. Die natürlichen pflanzenfamilien. 4(3b): 4-38.

Leipzig.

Wilkes, C. 1845. Narrative of the United States exploring expedition during the years 1838, 1839, 1840, 1841, 1842 I: 261-266. Lea & Blanchard, Philadelphia.

Numerical List of Taxa

1. S. didierana Jaubert
2. S. microphylla (Dunal) Keel
3a. S. glandulosa (Hooker) Miers subsp. glandulosa
3b. S. glandulosa (Hooker) Miers subsp. weddellii (Benoist) Keel
4. S. dependens (Mathews ex Hooker) Miers
5. S. proboscidea Benoist
6. S. hirsuta (Meyen) Miers
7. S. weberbaueri Dammer
8. S. origanifolia (Lamarck) Baillon
9. S. scandens Dammer
10. S. ramosissima Miers
11. S. micrantha Benoist
12. S. gayi Benoist
13. S. diffusa Miers
14a. S. tristis Miers var. tristis
14b. S. tristis Miers var. lehmanni (Dammer) Keel
15. S. microloba Keel

List of Exccicatae

Acosta-Solís, M., 7583 (14b)

Aguilar 319 (8)

Alvarez, R., s.n., 334, 582, 852 (8)

Amórtegui, B. G., 401 (14a)

Andersen, D., s.n. (8)

Anderson, J., 83 (8)

Andersson, J., s.n. (8)

André, E. F., K710 (14b); K1414 (8); 3177 (13); 4451 (14b)

Arbelaéz, E. P., 165, 1199 (14a)

Arbo, M. M., 50 (8)

Aristeguieta, L., 3283 (14a)

Aristeguieta, L. & E. Medina, 3584 (14a)

Asplund, E., 863 (8)

Auquier, P., 1528 (8)

Aurclius, N. G., s.n. (8)

Badillo, V. M., 824 (14a)

Balansa, B., 2124, 2124a (8)

Balegno, B., 799, 1012, 1071 (8)

Balls, E. K., 5911 (8); 6468 (3a)

Bang, M., 50 (14a); 50 (14b); 1048 (3a)

Barbey, W., s.n. (8)

Barclay, A. S. et al., 3375 (14a)

Barkley, F. A. & J. Araque M., 18S063, 18S167 (14a)

Barnum, C. C., s.n. (8)

Bartlett, H. H., 20027, 20170 (8)

Beal, J., s.n. (8)

Cabrera, A. L. & H. A. Fabris, 20846 (8)

Cabrera, A. L. & R. Kiesling, 20170 (14a)

Cabrera, A. L. et al., 21758 (9); 22245 (8)

Camp, W. H., E-1896 (14b)

Cárdenas, M., 41 (9); 303 (10); 374 (14a); 2068 (3b); 2294 (6); 4002 (8); 4096 (14a); 4130 (8); 6147 (3b)

Castañeda, R. R., 2486 (14a)

Castellanos 825 (8)

Castillón, L., s.n. (8); 3134 (14a)

Cazalet, P. C. D. & T. D. Pennington, 5497 (13)

Cerrate, E. & O. Tovar, 1909 (15)

Charpin, A., s.n. (8)

Chávez, R., AA, BB, CC (11)

Claren, F., 11404 (14a)

Clark, H. W., 39 (8)

Claude-Joseph, B., 1114 (14b)

Commerson s.n. (8)

Conrad, J. & W. Dietrich, 2552 (8)

Cook, O. F. & G. B. Gilbert, 92 (7)

Corrent, P., 45 (8)

Cory, V. L., 51554 (8)

Costa Sacco, Jose da 142, 464, 1372 (8)

Cruckshanks, A., s.n. (3a)

Cuatrecasas, J., 271, 1155, 1746, 20957 (14a)

Cuezzo, A. R., 699, 810 (8)

Curtiss, A. H., 6542, 6600 (8)

Czermak, J. & E. M. Reineck, 363 (8)

D'Arcy, W. G., 10508 (14a); 14086 (13)

Davidson, C., 3718 (3b)

Davis et al., 1420 (12); 1554, 1707(3a)

Descole 145 (8); 1531 (14a)

Deseglise, A., s.n. (8)

Desplantes, G., s.n. (8)

Destergren, T., s.n. (8)

Dieleman, P., 489 (8)

Dillon, M. & B. L. Turner, 1365 (14a)

Dolman, J., 364 (8)

Dombey s.n. (2); s.n., 332 (10)

Doppelbaur 231 (8)

D'Orbigny, A., 73, 269 (8); 1166 (9)

Dubugnon, N., 10 (8)

Dubuis, A. & L. Faurel, 3474 (8)

Duque-Jaramillo, J. M., 2773, 3391 (14a)

Dusén, P., 8409 (8)

Ellenberg, H., 102, 450 (14b); 589 (6)

Engelhardt, V., s.n. (8)

Estival, J. V., s.n. (8)

Evans, A. M. et al., 45513 (8)

Ex Herb. Corn. Osten 11515 (8)

Eyerdam, W. J. & A. A. Beetle, 23139, 23158 (8)

Eyerdam, W. J. et al., 23627 (8)

Felippone 3660, 3663 (8)

Fernández, A., 3260 (14a)

Fernández, A. et al., 1066 (14b); 7142 (8)

Ferreyra, R., 2630, 2652 (12); 5512 (14b); 6540 (3a); 7209, 7485 (10)

Fiebrig, K., 2144 (8); 2590 (9); 2625 (14a)

Fiori, A. et al., 634 (8)

Firmin, G., 16 (13)

Forsyth-Major, C. I., 4292-32 (8)

Fosberg, F. R., 22062 (14a); 23237 (13)

Freiberg, W., s.n. (8)

Fries, R. E., s.n., 620 (8); 951, 951a (10)

Fruchard, M., s.n. (8)

Fulvio, D., 75 (8)

Gadeceau, E., 9139 (8)

Gallinal et al., PE-4811 (8)

García, P., 877 (8)

García-B, H., 5145 (14a)

Garolera-Romero s.n. (8)

Gaudichaud, C., s.n. (8)

Gay, J., s.n. (8)

Gay, M., s.n. (8); 1061 (5); 1973 (11); 2308 (12)

Gehriger, W., 25 (14a)

Gibert 32, 961 (8)

Giler, M. A., 27 (14b)

Gillies s.n. (8)

Goble, R. L., s.n. (8)

Godfrey, R. K., 49770, 61528 (8)

Goncalves, B., 2017, 4126 (8)

Gonnot, M., s.n. (8)

Goodspeed, T. H., 23209 (8)

Gorter, A., 1340 (8)

Goudot, M. J., s.n. (14a)

Goulard s.n., 43 (8)

Graf, K., 268 (14b); 303 (3a)

Gremmen, J., s.n. (8)

Grisebach s.n. (8)

Grubb, P. J. et al., 67 (14a)

Günther, E., 5831 (3a)

Günther, E. & O. Buchtien, s.n. (8)

Gusterle, M., 5139 (8)

Gutierrez, G. & R. Jaramillo M., 274 (14a)

Haas, R. H., 297 (8)

Haas, J. H., 970 (8)

Hammarlund, C., 240 (6)

Hansen, A., s.n., 160, 161, 234, 708, 1043, 2086, 2320 (8)

Harling, G. & L. Andersson, 11648, 13265 (13)

Harling, G. et al., 6788 (13); 8402 (14a); 8605 (13);
8993 (15); 10317 (13)

Hartweg 1311 (13)

Hassler, E., 11445 (8)

Hastings, G. T., s.n. (8)

Haught, O., 5015, 5680, 5704, 5780 (14a)

Hauthal, R., 237 (14b); 644 (8)

Hawkes, J. G. et al., 3249 (8)

Hendrickx, F. L., 10076, 10091 (8)

Herbarium of the University of California 202564 (8)

Herren s.n. (8)

Herrera, F. L., s.n. (3a)

Herrera, J. R., 268 (8)

Herter, G., s.n., 280a, 280b, 280f, 2540 (8)

Herzog, T., 2435 (14a); 2507 (6)

Hicken, C. M., 42 (7); 965 (8)

Hieronymus, G., 25714 (8)

Hill, A. W., 352 (6); 353 (14b)

Hitchcock, A. S., 22392 (10)

Hjerting, J. P. et al., 97 (14a)

Horti Thenensis Herbarium 905 (8)

Hosseus, C. C., 88 (8)

Howell, J. T., 21332 (8)

Hrdlicka, A., s.n. (15)

Hubrich s.n. (8)

Huidobro, A. M. R., 1369, 1409, 1441, 1498, 1648, 1777, 3579, 3620, 3653 (8)

Humbert, M. H. et al., 26926 (14a)

Hunziker, A. T. & T. E. Di Fulvio, 19844 (14a)

Iltis, H. H. & D. Ugent, 453 (14b); 1158, 1218 (11); 1226, 1240 (7)

Iltis, H. H. et al., s.n. (7); 105, 141 (14a)

Isaäcson, A., s.n. (8)

Jallu, J., 1227 (8)

Jameson s.n. (8); 32 (13); 125 (14a); 754 (13)

Jaramillo, J., 100 (14a)

Job, M. M., 861 (8)

Mandon, G., 434, 435 (14a); 436 (14b); 437 (14a); 438 (3a)

Mann, A., 49 (8)

Mansel, M. G., s.n. (8)

Martinet, M., 1317 (2); 1605 (1); 1618 (2)

Mathews, M., s.n. (14a); 667 (3a); 829(4); 1053 (10)

Mayce, R. D., s.n. (8)

M'Courbon s.n. (8)

Mealme, G. O. A., 129, 1514 (8)

Meebold, A., 27676 (8)

Mennega 29 (8)

Meurillón, A., CNAD 641 (8)

Mexia, Y., 7779, 04198 (6)

Meyen s.n. (6)

Meyer, T., 3653(8); 4897 (9); 7243, 12350 (8); 16393 (14a); 33399 (9)

Michel, E. H., s.n. (8)

Miers, J., s.n., 724, 1331 (8)

Miranda, A. L., 1003, 1025 (14a)

Missouri Botanical Garden Herbarium 120659, 2537208, 2537209, 2537211 (8)

M'Lindley, D. C., 667 (3a)

Morel, I., 4768, 5534, 5670, 7405, 7938, 8848 (8)

Moreno, F. P. & Tonini, 274 (8)

Morong, T., 707 (8)

Mouetti, H., 1877 (14a)

Mutis, J. C., 1967 (14a)

Nellot s.n. (8)

Nieuwenkamp, M., 1076 (8)

O'Donell, C. A., 2452 (8); 4833 (14a)

O'Donell, C. A. & J. M. Rodríguez V., 263, 488 (8)

Ogilire, J., 47 (8)

Olea, D., 39 (8); 211 (14a)

Øllgaard, B. & H. Balslev, 8019 (13)

Olveira, G. B. T. de, s.n. (8)

Otto & H. Berof., s.n. (8)

Palmer, E. J., 27321 (8)

Hort. Gard. Paris s.n. (8)

Parker, K. F., 10, 0426 (8)

Parodi, L. R., 10665 (14a)

Pavón s.n. (2), (3a); 497 (14b)

Pearce, R., s.n. (8), (14b)

Pedersen, E. A., s.n. (8)

Pedersen, T. M., 1189 (8)

Pelgrims, C., s.n. (8)

Penland, C. W. & R. H. Summers, 592, 1081 (13)

Pennell, F. W., 3184 (14a); 13266 (14b)

Petersen, E., s.n. (14a)

Petersen, J. B., s.n. (8)

Phreiter 12382 (8)

Pickering, C. H. C., 158 (8)

Pierotti, S. A., s.n., 4135 (8)

Plowman, T., 2720 (8); 3197 (14a)

Plowman, T. & E. W. Davis, 4645 (3a); 4739 (12); 4746 (1); 4894 (7); 4897 (11); 4924 (5); 5138 (3a)

Prance, G. T., 26597 (13)

Prieto, F., P-173 (14b)

Pring, G. H., s.n. (8); 106, 106a (14a)

Quarín, C. et al., 2120 (8)

Qusset 87 (8)

Ragonese 2061 (8)

Raine, F., s.n. (8)

Rainha, B., 310, 1972 (8)

Rambo, B., s.n., 40732, 40847, 40978, 41271, 46672, 48910 (8)

Rapp, S., s.n., 5 (8)

Rauh-Hirsch P177 (10); P463 (7); P1013 (1); P1941 (3a)

Raven, P. H., 14737 (8)

Repton, J. E., 4881 (8)

Reündeis, W. Y., 1861 (8)

Richards, J., s.n. (8)

Risso, J. L., 171 (8)

Robertson, R., 119 (8)

Rodrigo, A. P., 456 (8)

Rodríguez, J. M., 339 (8); 376 (9); 892 (8); 1265 (14a)

Rojas, T., 11541 (8)

Romero, Y., s.n. (8)

Rose, J. N. & G. Rose, 23568 (14a)

Rose, J. N. et al., 22945 (14b)

Rothmaler, W., 14151 (8)

Ruijs, J. D., s.n. (8)

Ruiz, H. & Pavón, s.n. (3a)

Rusby, H. H., 830 (14b); 1935 (3a)

Sagástegui, A. et al., 6373 (14b)

Saint-Hilaire, A., s.n., 1792, 1873 (8)

Saudt s.n. (8)

Saunders, S. G. E., 726, 777, 817 (3a); 818 (10)

Sayago, M., 593 (8)

Scala, A. C., s.n. (8)

Schimpff, H. J. F., 835 (14a)

Schinini, A. & O. Ahumada, 12712 (8)

Schinini, A. & C. L. Cristóbal, 10796 (8)

Schinini, A. & R. M. Crovetto, 11611 (8)

Schinini, A. et al., 9439, 13041 (8)

Schlechter, R., s.n. (8)

Schneider, M., 186 (14a)

Schreiter 9465 (14a); 10513 (9); 11197 (14b); 11208 (8); 11511 (14a)

Schultz, D., s.n. (8)

Schwarz, G. J., 8151 (8)

Scolnik, R., 1707, 1773 (8)

Sellow s.n., 7188 (8)

Shear, W. E., s.n. (8)

Shepard, R. S., 76 (6); 77 (14b)

Shinner, L. H., 5 (8)

Skottsberg, C., s.n. (8)

Sleumer, H., 290, 1619, 1620 (14a); 3606 (9); 264-51 (8)

Sleumer, H. & F. Vervoorst, 2378 (9)

Sloet, C. J. M. & J. E. L. de Fouw, 72 (8)

Small, J. K. et al., 10834 (8)

Smith, H. M., 145 (8)

Sodiro, D., 114/93 (14a)

Soukup, J., 88 (6); 445 (14b); 750 (11); 3688 (3a); 4022 (9)

Spruce, R., 5057 (7); 5451 (13); 5847 (14a); 6064 (13)

Stafford, D., 21 (14a); 255 (14b); 524 (7); 767 (6); 890 (10)

Stearn, W. T., s.n. (8)

Steinbach, J., 3798, 8571 (8)

Stork, H. E., 10932 (3a)

Stork, H. E. & O. B. Horton, 10332 (4); 10804 (9)

Stuckert, T., 188, 542, 4701, 9056, 9765, 20146 (8)

Tate, G. H. H., 824 (3a)

Templeton, B. C., 7693 (8)

Terribile, M., 643 (8)

Thorne, R. F., 39311 (8)

Tideman, A. F., s.n. (8)

Tilforth, C. W., 235 (8)

Tololo, C. & R. Alvarez, 123 (13)

Tovar, O., 207 (14b); 3179 (3a)

Triana, J., s.n. (14a); 2275 (14b)

Troll, C., 2851 (14b)

Tweedie s.n. (8)

Ugent, D., 4758 (9)

Ugent, D & V. Ugent, 3994 (11)

Ule 1100 (8)

Universidad Central, Gabinete de Botánica 2220 (13)

United States National Herbarium 79230 (8)

Van Loon, J. C., s.n., 241 (8)

Vargas, C., 157 (7); 157 (11); 255 (8); 1274 (6); 3752 (3a); 9753 (7)

Veilex, J., 1029, 1030 (8)

Venturi, S., 29, 82, 82c, 82d (8); 2977, 4006, 9961 (14a)

Veth, J. A. C. & A. N. Koopmans, s.n. (8)

Vilcapoma, G., 128 (14b); 129 (10); 129, 130 (15)

Villafañe, M., 93 (8)

Villo, E., 43 (8)

Vindob, C. H., s.n. (8)

Voormolen, T., s.n. (8)

Wall, E. & B. Sparre, 33, 208, 575, 754, 1021 (8)

Walter, H. & E. Walter, 309 (8)

Watkins, C., s.n. (14b)

Weberbauer, A., 186 (10); 2679 (10); 2693 (7); 2936 (3a); 5785 (14a); 6596, 6603 (4); 6848 (14b); 7260 (7); 7515 (4)

Weddell, M. H. A., 3807 (9); 4116 (3b)

Welter, M., 5970 (8)

West, J., 3719 (3a); 3853 (12); 8127 (3a); 8248, 8484 (8)

White, E. W., 74 (8)

Whiteley s.n. (7), (11)

Wiggins, I. L., 10643 (13)

Wilbur, R. L., 9212 (8)

Wilkes, C., s.n. (15)

William, R. S., 1547 (3a)

Wilson, K. L., 1284 (8)

Woffenden, D., s.n. (8)

Zuccarinii s.n. (8)