SYSTEMATIC STUDIES OF CULTIVATED SPECIES OF *Codonanthe* (MARTIUS) HANSTEIN AND *Nematanthus* SCHRADER (GESNERIACEAE)

BY

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Codonanthe (Martius) Hanstein and *Nematanthus* Schrader (Gesneriaceae) are morphologically distinct genera of the evergreen and deciduous rain forests of Central and South America. Two subgenera and two sections had been recognized to accommodate the fourteen cultivated species of *Codonanthe*, whereas no subgeneric ranks were previously reported for the ten cultivated species of *Nematanthus*. Hybridizations between *Codonanthe* and *Nematanthus* have produced progeny that display a high degree of fertility, indicating that the species of *Codonanthe* and *Nematanthus* are closely related. The present study examined the species of *Codonanthe* and *Nematanthus* and attempted to resolve the relationship of species between genera and within each genus. Conventional taxonomic methods and systematic techniques of light and electron microscopy, microtomy, leaf clearings and karyology were utilized in the study of live plant material.

Flowers of *Codonanthe* species have obliquely funnelform-ventricose corollas that are primarily white and are presumably pollinated by

Euglossine bees, whereas species of *Nematanthus* have pouched corollas that are basically orange, red, pink or yellow and are presumably pollinated by hummingbirds. Possession of such differing corolla types and pollinators reproductively isolate these two genera, possibly indicating that *Codonanthe* and *Nematanthus* should remain as distinct taxa.

Species of subgenus *Codonanthe* section *Codonanthe* have orange berries, a diploid chromosome number of *n*=8, and a unilacunar nodal anatomy (except *C. carnosa* and *C. gracilis*), lack extrafloral nectaries, and are indigenous to southeastern Brazil. Species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella* have red, pink or purple berries or yellow-green fleshy capsules, a tetraploid chromosome number of *n*=16, and a trilacunar, split-lateral nodal anatomy, possess extrafloral nestaries, and are geographically widespread from southern Mexico through Central America to northern South America. *Nematanthus crassifolius*, *N. fissus*, *N. fritschii*, *N. hirtellus*, *N. maculatus* and *N. perianthomegus* have a shrubby growth habit, trilacunar, spilt-lateral nodal anatomy, and resupinate flowers, whereas *N. gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii* have a viny growth habit, unilacunar nodal anatomy, and nonresupinate flowers.

On the basis of these observations, sections *Nematanthus* and *Parvifolius* are established to accommodate the species of *Nematanthus*, and it is acknowledged that further studies are required before any conclusions are made on the relationships of the infrageneric taxa of *Codonanthe*. A synopsis of the infrageneric taxa and revised classification of the genera *Codonanthe* and *Nematanthus* is presented.

INTRODUCTION

Gesneriads have been in the horticultural trade for many years and are becoming very popular with the current indoor plant revolution. Potted plants of the Florist Gloxinia (*Sinningia speciosa*), African Violet (*Saintpaulia* spp.) and Cape Primrose (*Streptocarpus* spp.) are grown in the home, often in light gardens, and in the greenhouse. Nurserymen have recognized that epiphytic and terrestrial gesneriads are ideal candidates for hanging baskets. Species of *Aeschynanthus* (Lipstick Plant), *Codonanthe*, *Columnea*, *Episcia* (Flame Violet) and *Nematanthus* (Goldfish Plant) are widely cultivated in hanging baskets for their colorful flowers and foliage (Elbert & Elbert, 1976).

Plantsmen have hybridized many species of Gesneriaceae in an attempt to produce new cultivars. Interspecific crosses have generally yielded fertile progeny, whereas intergeneric combinations have always resulted in offspring of very low fertility to sterility (Wiehler, 1979b). An intergeneric hybrid between *Codonanthe* and *Nematanthus* was created in 1977 and designated X *Codonatanthus* (Saylor, 1978a). This was the first intergeneric combination that displayed a high degree of fertility, indicating that species of *Codonanthe* and *Nematanthus* may be more closely related than realized.

A doctoral program was initiated in 1979 to 1) examine species of *Codonanthe* and *Nematanthus* in cultivation, 2) determine the relationship of species between genera and within each genus, and 3) provide a synopsis of the infrageneric taxa of Codonanthe and Nematanthus. Conventional taxonomic observations were made of the cultivated species of the two genera to serve as the basis of this thesis.

Systematic methods were employed in an attempt to discover additional characters of taxonomic utility. Light and electron microscopy, microtomy, leaf clearing, chromosome techniques and hybridizations were applied to the study of live plant material. These tools of taxonomy were used to examine the morphology of the leaf epidermis and pollen, and anatomy of the stem and leaf. It is the additive nature of taxonomy that incorporates information from many differing sources to strengthen any final decision of a possible new classification.

CHAPTER I
TAXONOMIC REVIEW

Gesneriaceae Dumortier consists of three subfamilies--Gesnerioideae, Coronantheroideae Wiehler and Cyrtandroideae Endlicher (Wiehler, 1979b). Gesnerioideae includes 5 tribes, 54 genera and over 1300 species distributed throughout the Neotropics. Coronantheroideae includes 1 tribe, 9 genera and about 20 species in southern Chile, the South Pacific islands and Australia. Cyrtandroideae is composed of 4 tribes, 63 genera and over 1550 species mainly in the Paleotropics. Besides differing distributions, the subfamilies are distinguished by seedling morphology (e.g., anisocotyledonous seedlings in Cyrtandroideae and isocotyledonous seedlings in Gesnerioideae and Coronantheroideae).

Five tribes that form Gesnerioideae are Gesnerieae, Napeantheae Wiehler, Beslerieae Bartling & Wendland, Gloxinieae Fritsch and Episcieae Endlicher. Gesnerieae and Napeantheae are monogeneric, while Beslerieae is composed of seven genera. Gloxinieae and Episcieae are the larger tribes of this subfamily, and comprised 24 and 21 genera, respectively. Chromosome number serves as a distinguishing character in these tribes--i.e., Episcieae, $\underline{n} = 8, 9$; Gloxinieae, $\underline{n} = 10, 11, 12, 13$; Gesnerieae, $\underline{n} = 14$; Beslerieae, $\underline{n} = 16$; Napeantheae, unknown (Wiehler, 1979b).

Episcieae is the largest tribe of Gesnerioideae, with over 630 species in 21 genera. Wiehler (1979b) discusses three features of evolutionary significance intrinsic to Episcieae: a) an unusual trilacunar nodal anatomy with split lateral bundles, b) a predominance of epiphytic species, and c) ornithophily and euglossophily as the primary mode of pollination. Also, there are usually two enlarged, connate glands at the base of the ovary serving as a nectary in the hummingbird-pollinated and euglossine bee-pollinated flowers. The fruit is a berry or a fleshy capsule. Although the majority of genera in Episcieae have a chromosome number of *n* = 9, *Codonanthe* and *Nematanthus* are unique in possessing a chromosome number of *n* = 8.

A chronologically arranged taxonomic history of *Codonanthe* and *Nematanthus* is presented in Table I-1. A current classification system of these two genera according to Wiehler (1979b, 1982, & personal communication) is shown in Table I-2, with the known cultivated species tabulated.

Table I-1. Taxonomic history of the genera Codonanthe and Nematanthus.

DATE	TAXA	EVENT
1821	Nematanthus Schrader	The genus Nematanthus is first established in Gottingische gelehrte Anzeigen 1821 (2): 718.
1829	Hypocyrta Martius & Hypocyrta section Codonanthe Martius	The genus Hypocyrta is first established with the section Codonanthe, in Nova Genera et Species Plantarum 3: 49.
1854	Codonanthe (Martius) Hanstein	Hypocyrta section Codonanthe is elevated to the genus level with Codonanthe as the conserved name, in Linnaea 26: 209.
1855	Coccanthera C. Koch & Hanstein	A new genus established with its lectotype relegated to the synonymy of Codonanthe, in Index Seminum in Horto Regio Botanico Berolinensi 1855: Appendix 17.
1934	Codonanthopsis Mansfeld	The genus Codonanthopsis is first established, in Repertorium Specierum Novarum Regni Vegetabilis 36: 120.
1971	X Hypotanthus Saylor	New intergeneric taxon was created due to the cross of Hypocyrta and Nematanthus, in Gloxinian 21: 20-21, 31.
1973	Codonanthe section Codonanthopsis (Mansfeld) H. E. Moore	The genus Codonanthopsis is lowered to the sectional level of the genus Codonanthe, in Baileya 19: 4-23.
1973	Nematanthus Schrader	Moore combines many species of the genera Nematanthus and Hypocyrta into one genus, in Baileya 19: 35-41.
1978	X Codonatanthus Saylor	New intergeneric taxon was created due to the cross of Codonanthe and Nematanthus, in CrossWords 2: 11-12, Selbyana 5: 1-3.

Table I-1 - continued.

DATE	TAXA	EVENT
1979	Codonanthe (Martius) Hanstein & Codonanthopsis Mansfeld	Wiehler regards Codonanthopsis as a valid genus, in Wiehler, Ph. D. dissertation.
1979	Codonanthe subgenus Codonanthella Wiehler	New subgenus of Codonanthe established based upon species having fleshy capsules, in Wiehler, Ph. D. dissertation.
1982	Codonanthe subgenus Codonanthe section Spathuliformae L. B. Smith	New section of Codonanthe recognized based upon species having purple, red or pink berries, in Selbyana 6(in press) and personal communication with Wiehler.

Table I-2. Current classification system of the cultivated species in the *Nematanthus* according to Wiehler (1979b, 1982 and personal communication).

GENUS *Codonanthe* (Martius) Hanstein	Accession Number
SUBGENUS *Codonanthe*	
SECTION *Codonanthe*	
1. *C. carnosa* (Gardner) Hanstein	W-2199
2. *C. devosiana* Lemaire	W-2215
3. *C. digna* Wiehler	W-1139
4. *C. gracilis* (Martius) Hanstein	W-2203
5. *C. paula* Wiehler	W-2386
SECTION *Spathuliformae* L. B. Smith	
6. *C. calcarata* (F.A.W. Miquel) Hanstein	W-2116
7. *C. corniculata* Wiehler	G-932
8. *C. crassifolia* (Focke) Morton	W-2531
9. *C. uleana* Fritsch	W-1182
SUBGENUS *Codonanthella* Wiehler	
10. *C. caribaea* Urban	G-976
11. *C. chiricana* Wiehler	W-2267
12. *C. elegans* Wiehler	W-2588
13. *C. luteola* Wiehler	W-1630
14. *C. macradenia* Donnell-Smith	W-2552
GENUS *Nematanthus* Schrader	
1. *N. crassifolius* (Schott) Wiehler	G-134
2. *N. fissus* (Vellozo) L. Skog	G-661
3. *N. fritschii* Hoehne	G-611
4. *N. gregarius* D. Denham	G-597
5. *N. hirtellus* (Schott) Wiehler	G-1092
6. *N. maculatus* (Fritsch) Wiehler	W-2494
7. *N. nervosus* (Fritsch) H. E. Moore	G-734
8. *N. perianthomegus* (Vellozo) H. E. Moore	W-1718, W-2227
9. *N. strigillosus* (Martius) H. E. Moore	W-388
10. *N. wettsteinii* (Fritsch) H. E. Moore	G-655

CHAPTER II
MORPHOLOGICAL DESCRIPTION

Descriptions of the cultivated species of Codonanthe and Nematanthus species are based on the literature and personal observations of live plant material cultivated in a growth room at the Department of Ornamental Horticulture, University of Florida. The growth room provided uniform conditions of 22-25°C day temperature, 17-20° C night temperature, 4000-6000 Lux fluorescent lighting and a fourteen hour daylength. Descriptive terminology is based on Radford et al. (1974). Morphological characters of Codonanthe and Nematanthus are tabulated in Table II-1 for ease of comparison, with the species grouped into infrageneric categories based upon Wiehler (1979b, 1982 & personal communication).

Growth Habit

Species of Codonanthe and Nematanthus are phanerophytes (Raunkiaer, 1934). They are perennials that are one-to-many feet tall, have their vegetative buds fully exposed to surrounding air, and are epiphytes. As epiphytes, these species are attached to and depend upon another plant for physical support. Codonanthe and Nematanthus are among thirteen epiphytic genera in the tribe Episcieae (comprise only 21 genera) and 28 epiphytic genera of Gesneriaceae (Wiehler, 1979b).

Codonanthe (Figures II-1 to II-3) and *Nematanthus* (Figures II-4 to II-5) species have a vine-like and/or shrub-like growth habit. Vine-like species (e.g., *C. carnosa*, *C. gracilis*, *N. strigillosus*, *N. wettsteinii*) possess stems that initially grow in an upright direction with little branching. With continued growth and elongation, the stem acquires a reclining, clambering or decumbent habit due to the inability of the stem to support itself. Other species have a pendulous mode of growth (e.g., *C. elegans*, *C. luteola*, *C. macradenia*) or grow in an erect, shrub-like fashion (e.g., *C. uleana*, *N. crassifolius*, *N. maculatus*, *N. perianthomegus*). Table II-1 presents a list of the cultivated species of *Codonanthe* and *Nematanthus* and their growth habit types.

Root

Species of *Codonanthe* and *Nematanthus* have fine, thread-like fibrous roots that arise adventitiously from the stem. Some species possess pre-formed roots (e.g., *C. elegans*) or root initials (e.g., *N. hirtellus*) at the nodes. Adventitious root development corresponds well with the epiphytic habit of the plants. Epiphytes are better sustained on a host if they are anchored to the substrate at numerous locations, that is, attached by many roots. Also, a repent, spreading habit promotes the proliferation of the original plant in such a way that if a stem is severed, one or more individuals are formed. New plants have excellent chances of survival since they already possess well-developed roots.

In the ant-gardens of Codonanthe crassifolia, a mutualistic association is maintained with an arboreal, carton-building ant. Kleinfeldt (1978) proposes that the epiphyte's roots add structural support to the ant nests. Seeds of C. crassifolia are often carried by ants and placed in their nests (mode of seed dispersal). The seeds soon germinate in the nutrient-rich detritus and permeate their roots throughout the carton walls lending support to the framework of the ant-gardens.

Stem

Codonanthe and Nematanthus species have herbaceous stems that are suffrutescent. The stem epidermis is initially green with a smooth texture in many species, with exceptions occurring in N. fissus (tomentose indumentum) and N. strigillosus (strigose vestiture). The transition from the herbaceous condition results in a woody stem with greyish-tan to brown coloration. The texture may be smooth (e.g., C. gracilis) to rough with a fissured appearance (e.g., N. perianthomegus).

Extrafloral nectaries are present at the nodes of some Codonanthe species (e.g., C. crassifolia). These species are usually associated with ant-gardens and possess nectaries which attract ants--the agents of seed dispersal (Moore, 1973a; Kleinfeldt, 1978).

Table II-1 categorizes species of Codonanthe and Nematanthus into two groups based upon stem size: a) 2-4 mm or b) 5-9 mm stem diameter. This measurement is basically correlated to the growth habit of the taxon. Vine-like plants have stems 2-4 mm in diameter, whereas a 5-9 mm stem denotes a shrubby form. Most Codonanthe species have the small stem size. *Nematanthus gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii* form a distinct group of species with 2-4 mm stems and a viny habit, while the other six *Nematanthus* species exhibit a shrubby form with 5-9 mm stems.

Anatomical aspects of the stem are addressed in CHAPTER IV: COMPARATIVE ANATOMY OF THE STEM AND LEAF.

Leaf

Leaf characters are summarized in Table II-1 and descriptions follow Hickey's (1973) treatment with respect to architecture. Anatomical features of the leaf are given in CHAPTER IV: COMPARATIVE ANATOMY OF THE STEM AND LEAF.

Arrangement

Most species of *Codonanthe* and *Nematanthus* have isophyllous leaves in an opposite arrangement. Leaves are basically decussate but a few of the vine-like species have leaf blades oriented in a distichous-like manner, that is, appearing 2-ranked with the leaves facing one direction. For example, *N. fissus*, *N. maculatus* and *N. perianthomegus* have leaf blades in a 4-ranked arrangement, whereas *C. carnosa*, *C. digna* and *C. gracilis* have leaf blades in a 2-ranked placement.

Petiole

Most species of *Codonanthe* have rounded, green petioles (except *C. corniculata* with reddish petioles). *Nematanthus* species are more variable in possessing petioles that are slightly furrowed on the adaxial surface (e.g., *N. crassifolius*) and/or with a red coloration (e.g., *N. fissus* and *N. hirtellus*).

Petiole size may be classified into two length categories: a) 4-10 mm and b) 10-50 mm. *Codonanthe* species all possess 4-10 mm long petioles (Figures II-6 to II-8). *Nematanthus gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii* also have 4-10 mm petioles (Figure II-10), but the other six *Nematanthus* species exhibit petioles 10-50 mm long (Figure II-9).

Blade

Symmetry and Form. *Codonanthe* and *Nematanthus* are represented by species that have leaf blades with a symmetrical or asymmetrical lamina and/or base (Figures II-6 to II-10). Variations in leaf base balance include a) symmetrical lamina and base (e.g., *C. caribaea*), b) symmetrical lamina but an asymmetrical base (e.g., *N. maculatus*), c) asymmetrical lamina but a symmetrical base (e.g., *N. crassifolius*), and d) asymmetrical lamina and base (e.g., *C. uleana*).

Leaves in *Codonanthe* and *Nematanthus* are ovate (e.g., *N. nervosus*), elliptic (e.g., *N. fritschii*) and obovate (e.g., *N. maculatus*). Each leaf form is variously modified as narrow, normal or wide (Hickey, 1973). For example, *C. crassifolia*, *C. caribaea* and *C. macradenia* have elliptical leaves with a narrow, normal and wide form, respectively. Also, *Codonanthe* and *Nematanthus* have leaf length categories defined as a) 2-4 cm and b) 4-12 cm. Species of *Codonanthe* subgenus *Codonanthe* section *Codonanthe* have ovate to elliptic leaves and leaves 2-4 cm long (except *C. gracilis*), whereas species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella* have leaves with an elliptic to obovate form and 4-12 cm long (except C. chiricana). Nematanthus gregarius, N. nervosus, N. strigillosus and N. wettsteinii have leaves 2-4 cm long, whereas the other six Nematanthus species have 4-12 cm long leaves.

Apex and Base. Codonanthe and Nematanthus species have several leaf apex and base shapes. Leaf apex shapes include acute (e.g., N. strigillosus), acuminate (e.g., C. uleana), attenuate (e.g., N. nervosus) and obtuse (e.g., C. digna). Leaf base shapes include acute (e.g., N. gregarius), obtuse (e.g., N. hirtellus), rounded (e.g., C. paula) and cordate (e.g., C. gracilis).

Margin. Three types of leaf margins are evident in Codonanthe and Nematanthus. Most species have entire margins such as C. caribaea and N. wettsteinii. There are also species with slightly crenate margins (e.g., C. chiricana and N. perianthomegus) and fully crenate margins (e.g., C. calcarata and N. fissus).

Texture. Codonanthe and Nematanthus species exhibit generally three forms of leaf texture--smooth (e.g., N. gregarius), puberulous (e.g., N. hirtellus) and pubescent (e.g., N. fissus). Species of subgenus Codonanthe section Spathuliformae and subgenus Codonanthella display smooth leaf surfaces and species of subgenus Codonanthe section Codonanthe (except C. gracilis) possess puberulous to pubescent leaves.

Leaf epidermis characters are discussed in CHAPTER III: COMPARATIVE MORPHOLOGY OF THE LEAF EPIDERMIS, and include such morphological aspects of leaf surface features as glandular and nonglandular trichomes, stomata, extrafloral nectaries and surface ornamentations.

Coloration. Species of Codonanthe and Nematanthus have leaves that are generally green adaxially with a lighter green on the abaxial surface (e.g., _C. devosiana_ and _N. gregarius_). Various other markings or colorations are present and represented by _C. gracilis_ (red pigmentation at the leaf margins), _C. elegans_ and _N. fritschii_ (red coloration at or around the midvein and/or secondary veins), _N. wettsteinii_ (red lamina only, with no colored veins), and _C. carnosa_ and _C. paula_ (red coloration on total abaxial leaf surface).

Stipules

The leaves of _Codonanthe_ and _Nematanthus_ species are estipulate.

Inflorescence

The pair-flowered cyme is the basic inflorescence unit in Gesnerioideae and is typical for the Gesneriaceae (Wiehler, 1979b). _Codonanthe_ and _Nematanthus_ species possess a reduced cyme of one to several flowers (appearing one at a time) in the upper leaf axils. The inflorescence consists of short pedicels (except very long in _N. crassifolius_ and _N. fritschii_). Bracts are lacking (Moore, 1973a; Wiehler, 1977, 1979a; Skog, 1978).

Flower

Orientation and Pedicel

The orientation of the flower is an important taxonomic trait in delimiting _Nematanthus_ species (Moore, 1973b). Flowers of _N. gregarius_, _N. nervosus_, _N. strigillosus_ (Figures II-11E & II-11F) and _N. wettsteinii_ are consistently nonresupinate so that the pouch of the corolla is in a normal, ventral (abaxial) position. The other six species of *Nematanthus* (Figures II-11A to II-11D) display their flowers with the corolla pouch in a dorsal (adaxial), resupinate position. This resupinate flower orientation is the result of a 180° twisting of the pedicel from the ventral position.

Of the six *Nematanthus* species with resupinate flowers, *N. crassifolius* and *N. fritschii* have pedicels that are 25-200 mm long and flowers that are pendulous. *Nematanthus fissus*, *N. hirtellus*, *N. maculatus*, *N. perianthomegus*, *N. gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii* exhibit flowers that are erect in the leaf axil with pedicels 3-25 mm long.

Species of *Codonanthe* (Figures II-12A & II-12B) have pedicels 3-25 mm long and nonresupinate flowers that are erect in the leaf axil.

Calyx

The calyx of *Codonanthe* and *Nematanthus* species is deeply 5-parted with basally connate sepals and five unequal lobes. The dorsal lobe is often recurved about the corolla spur with the ventral and lateral lobes frequently connate towards the base presenting a bilabiate shape (Figure II-12C). *Codonanthe* species have calyx lobes that are linear to lanceolate, whereas species of *Nematanthus* possess linear to lanceolate and ovate to elliptic calyx lobes. The lobes are variously entire to shallow toothed, veined, glabrous to pubescent, and green to purple, red and orange. Some species of *Codonanthe* (e.g., *C. macradenia* and *C. crassifolia*) possess prominent red extrafloral nectaries (Figure II-14C) in the sinuses of the calyx lobe margins (Moore, 1973a, 1973b).

Corolla

Codonanthe species (Figures II-12A & II-12B) possess an obliquely funnelform-ventricose corolla with a base that is narrow and either rounded (e.g., *C. digna*) or prominently spurred (e.g., *C. chiricana*). The corolla tube gradually (e.g., *C. crassifolia*) or abruptly (e.g., *C. paula*) broadens towards the throat or is somewhat dorsiventrally compressed, arched and grooved (e.g., *C. macradenia*, Figures II-12E & II-12F). The three lower lobes are spreading and larger than the upper two lobes providing a bilabiate corolla configuration. The corolla is situated obliquely within the calyx and in a horizontal position. It is basically white or yellow (e.g., *C. luteola*), often with spots or lines on the outer areas or on the lower surface of the throat that are yellow, brown, pink, red, lilac or deep purple. The corolla is glabrous to pubescent (Moore, 1973a).

Nematanthus species (Figures II-11A, II-11C & II-11E) have a mildly to strongly ventricose corolla that is narrow above the base and often with a short spur. The corolla tube gradually expands to a broad, laterally compressed throat (e.g., *N. fritschii*), or quickly widens to form a pouch that abruptly narrows to form a constricted throat (e.g., *N. nervosus*), with five small rounded lobes. The latter corolla configuration has been named by Wiehler (1979b) as a *Hypocyrta*-type or hypocyrtoid corolla. The corolla tube is erect or slightly oblique within the calyx. The corolla is scarlet, red, pink, orange or yellow with maroon stripes, and glabrous to pubescent in texture (Moore, 1971, 1973a).

Androecium

The four stamens in Codonanthe and Nematanthus species (Figures II-12D & II-11B9 are didynamous, epipetalous and coherent, with the anthers in a rectangular configuration. Species of Codonanthe are unique in possessing anther locules separated spatially by a broad connective and dehiscing by a pore near the apex of the thecae. Species of Nematanthus have anthers that are more typical of genera of the Gesnerioideae. They display narrow, elliptical anther connectives and dehisce by a conventional longitudinal slit in the thecae (Wiehler, 1979b).

Gynoecium

Codonanthe and Nematanthus species (Figure II-14A) have a superior, unilocular ovary that is composed of two united carpels (paracarpum, cf., Ivanina, 1965). The parietal placenta is usually divided into two and intrudes into the locule from the basal wall of the fruit. In Codonanthe, the placenta forms two tuberculate projections. Ovules are numerous and anatropous. The style (Figure II-14A) is terete and slender, with a bilobed stigma (Figure II-13). The nectary (Figure II-14A) consists of two large, connate glands positioned adjacent (connivent) and dorsal to the ovary. Nectar collects within the corolla at the base of the superior ovary (Lawrence, 1951; Ivanina, 1965; Wiehler, 1979b).

Pollen

The morphology of Codonanthe and Nematanthus pollen is discussed in CHAPTER V: POLLEN MORPHOLOGY.

Fruit

Fruit type serves as a valuable taxonomic feature in the infrageneric classification of Codonanthe. Wiehler (1979b) delineates two subgenera for Codonanthe based upon the type of fruit: a) subgenus Codonanthe has berries (Figure II-14D) and b) subgenus Codonanthella has fleshy capsules (Figure II-14E). The berries are globose to subglobose with pulp consisting of funicular tissue. The fleshy capsules are laterally compressed and pointed to cone-shaped, bivalved and loculicidally dehiscent, and have carpel walls that are concave with reflexed tips. Dehisced capsules split open and display a cone-shaped mass of funicular tissue, seeds and placentae. Subgenus Codonanthe is further subdivided by Wiehler (1982 & personal communication) into sections based upon fruit color: a) section Codonanthe has orange berries and b) section Spathuliformae has pink, red or purple berries.

Nematanthus species possess fleshy capsules that are similar to the fruits of species of Codonanthe subgenus Codonanthella. Wiehler (1979b) designates this fruit type a "display fruit" and defines it as

> a fleshy bivalved capsule with loculicidal dehiscence whose valves separate at maturity from the placentae which form together with the mass of seeds and the enlarged, glistening funiculi an attractively colored cone-shaped structure or food body positioned upright on the receptacle. The two reflexed or convex carpel valves are usually strikingly colored on the inside (red, pink, yellow, or white) to further offset the food body. This display is surrounded by contrastingly colored calyx lobes which have grown in size since anthesis. This type of display fruit offers an outstanding visual target for the seed dispersal agents which are birds, fruit-eating bats, and possibly monkeys. (p. 69-70)

In summary, the fruit type, color and ability to dehisce appear to dictate the mode of fruit/seed dispersal. For Codonanthe subgenus Codonanthe species, orange berries of section Codonanthe and pink, red and purple berries of section Spathuliformae probably attract and are disseminated by birds. Fleshy capsules of subgenus Codonanthella species have the potential to attract birds and ants as the agent of fruit and seed distribution. The "display fruit" of Nematanthus species, as previously reported, are most likely dispersed by birds or fruit-eating bats.

Seed and Seedling

Seeds of Codonanthe and Nematanthus species (Figures II-15 to II-17) are comparatively large in Gesneriaceae, with such species as C. calcarata, C. crassifolia, C. macradenia and C. uleana having the largest gesneriad seeds (Wiehler, 1979b). Seeds range from 1-2 mm long, occasionally becoming 3.5-3.9 mm long, and are oblong-elliptic in outline (Ivanina, 1965). The seeds are brown, red, pink or yellow and longitudinally or obliquely striated (Moore, 1971, 1973a; Beaufort-Murphy, 1977). Wiehler has estimated that for gesneriaceous fruit, Codonanthe species probably contain the lowest number of seeds with between 15 to 125 seeds per berry (35 as an average).

Codonanthe (and probably Nematanthus) seeds are attached to the placenta via a glistening, hyaline funiculus that is 8-11 mm long and fleshy (Wiehler, 1979b). A translucent or opaque aril partially (e.g., N. gregarius) or entirely (e.g., C. crassifolia) surrounds the seeds (Moore, 1973a; Beaufort-Murphy, 1977).

Kleinfeldt (1978) and Madison (1979) have reported on the mutualistic association of a myrmecophyte (C. crassifolia and C. calcarata) and an ant species (Crematogaster longispina). It appears that ants are the agents of seed dispersal for C. crassifolia, carrying seeds to their carton nests. Wiehler (1979b) observed that the seeds are shaped like ant eggs, perhaps an example of mimicry to aid in seed dispersal. Ants eat the seed's fleshy aril, as well as the fruit pulp, and place the seeds in the wall of the nest. The seeds germinate and _C. crassifolia_ plants grow, and their roots provide the nest with structural support.

Pollination

Flowers of _Codonanthe_ and _Nematanthus_ species are protandrous (Moore, 1973a; personal observations), that is, anthers mature and shed their pollen before stigmas mature and become receptive. This outbreeding device essentially separates gametes of a flower in time and to some degree hinders self-fertilization (Allard, 1960). A species population will usually have many individuals flowering with flowers at various stages of anthesis.

Anthesis commences with extention and elongation of the filaments so that the anthers are positioned near the orifice of the corolla tube. In a nonresupinate flower, connate or connivent anthers are dorsally located above the corolla throat with the anther pores or slits shedding pollen downward and inward. Pollen will be deposited on top of the pollinating agents attracted to the flower. On the second or third day, the filaments will coil up and retract the anthers into the flower, removing the source of pollen. The elongating style will bring the stigma into the former position of the anthers (i.e., above the corolla throat). The stigma becomes receptive after retraction of the anthers, removing the opportunity for self-pollination. Pollen deposited on the dorsal surface of a pollinating agent will be picked up by the stigma, thus, completing the pollination cycle (Jones & Rich, 1972; Wiehler, 1979b).

In a resupinate flower, the sequence of pollination is similar to that of a nonresupinate flower except the flower is inverted by 180°. The anthers and stigma are in a ventral position facing upward, with pollen shedding and reception occurring on the lower surface of the pollinating agent. It appears that the pollination sequence is successful only among nonresupinate and resupinate flowering species, but not between the two flowering types.

In the pollination of a flower, a complex of characteristics is exhibited by the flower as a direct result of being adapted to the form and behavior of the pollinator. Pollination syndromes demonstrate the conformity between the flowers and the animals which pollinate them (van der Pijl & Dodson, 1969).

Wiehler (1979b) has estimated that 30% of the Neotropical gesneriads are pollinated by irridescent male and female Euglossine bees (gynandro-euglossophily), 60% pollinated by hummingbirds (ornithophily), and 10% by other biotic agents. Because there is such a high occurrence of bee- and bird-pollinated flowers among gesneriads, the syndromes of gynandro-euglossophily and ornithophily were examined. Flower characters are directly compared with the traits of the pollinator.

Codonanthe species have 5-merous flowers that are zygomorphic and held horizontally in the leaf axil. The three corolla lobes are often enlarged (a possible landing platform), white or yellow in color, sometimes flushed with yellow, and pink, lilac or deep purple on the lower surface of the throat (potential nectar guides). Nectar is contained within a relatively short corolla and/or short spur (nectar accessible to pollinators with short mouthparts) and anthesis is diurnal (feeding activity diurnal). These characters appear to fulfill the syndrome of gynandro-euglossophily flowers.

The white, funnel-form corolla of *Codonanthe* species is very similar to some corollas of *Achimenes*, *Alsobia*, *Drymonia*, *Nautilocalyx* and *Sinningia* species. Wiehler (1979b) states that these genera are pollinated by various kinds of female Euglossine bees. Species of *Codonanthe* were observed to be visited by Euglossine bees (Williams, personal communication).

Nematanthus species possess flowers that are tubular or pouched and held horizontally in or hanging from the leaf axil (pollinator must be able to hover in front of flower while feeding). Perianth lobes are curved back or absent (do not interfere with flight movements of the pollinator), and are scarlet, red, pink, orange or yellow with maroon stripes (visual sense of the pollinator must be strong). The flower wall is hard, the filaments are stiff and the corolla tube is broad (protection from pollinators' hard mouthparts). Nectar is abundant and stowed away (pollinator must possess long mouthparts to reach the hidden nectar), and the nectar guides and odor are absent (poor sense of smell). Anthesis is diurnal (feeding activity diurnal). These characters appear to fulfill the syndrome of ornithophilous flowers.

Of the four different types of hummingbird corollas present with Neotropical gesneriads, Wiehler (1979b) reports that the majority of *Nematanthus* species have a hypocyrtoid corolla (named after the former genus *Hypocyrta*). This corolla type consists of a tube with a ventrally inflated pouch, tightly constricted throat and narrow limb.

The red, orange and yellow calyx and corolla coloration is a primary attractant to hummingbirds, but *Nematanthus fritschii* and *N. maculatus* additionally display leaves with a red extrafloral attraction pattern. The leaves are red-splotched on the abaxial surface. Jones & Rich (1972) have observed hummingbirds being first attracted to the foliage of *Columnea florida*, which possess leaves with "two conspicuous red spots located on the upper surface near the apex of the large leaves." Some birds inspected various portions of the plant for several seconds before finding the flowers.

The function of the inflated pouch of *Nematanthus* corollas is unknown. It does not appear to operate as a receptacle for excess nectar since there are species which have flowers in a nonresupinate orientation (pouch ventrally located) as well as species with resupinate flowers (pouch dorsally located). In fact, *N. crassifolius* and *N. fritschii* have pendulous flowers that hang from the leaf axil; here, a pouch could not function as a nectar receptacle since the nectar would run out of the flower.

Wiehler (1979b) postulates that the inflated pouch could serve as a target enlargement. With the hummingbird's approach to the front of the flower, the pouch contributes to produce a larger target that would aid in a more effective pollination. The orientation of the flower would not disrupt this hypothesis since the position of the stamens and stigma, as discussed, would remain as a functional unit. Also, the constricted throat of the corolla may serve to exclude larger insects such as Euglossine bees.

Hummingbird-pollinated flowers frequently have some means of protecting the ovules. Grant (1950) surveyed the flowering plant families and examined the relationships between pollinators and any special means of ovule protection of the flowers they visited. He observed that *Nematanthus* (and *Hypocyrta*) species provided no special means of ovule protection. In studying *Columnea florida* (a hummingbird-pollinated species), Jones & Rich (1972) stated that "the 'V-shaped' nature of the connate anthers and the stigmatic surfaces (also present in *Nematanthus* species) serve to direct the bill away from the superior ovary and into contact with the nectar which collects in a slight depression in the lower portion of the corolla" (p. 115).

Chromosome Number

Codonanthe and *Nematanthus* are unique in the tribe Episcieae in possessing a basic chromosome number of $x = 8$, whereas all other genera have a basic chromosome number of $x = 9$. Table II-1 lists the known chromosome numbers of *Codonanthe* and *Nematanthus* species (Fussell, 1958; Lee, 1962, 1964, 1966; Ratter, 1963; Lee & Grear, 1963; Morley, 1975; Wiehler, 1971, 1975, 1977; Moore, 1973a; Skog, 1980, 1981; Yuen, personal observation, 1982).

Cultivated species of *Nematanthus* are diploid ($x = 8$, $n = 8$), whereas *Codonanthe* has diploid and tetraploid ($x = 8$, $n = 16$) representatives. Species of subgenus *Codonanthe* section *Codonanthe* are diploids, but species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella* are basically tetraploids; exceptions include *C. caribaea* (diploid) and *C. luteola* (diploid and tetraploid).

Distribution

Species of Codonanthe subgenus Codonanthe section Codonanthe are confined to the coastal areas of southeastern Brazil. In contrast, species of subgenus Codonanthe section Spathuliformae and subgenus Codonanthella inhabit regions from south Mexico, through Central America, to areas of northern South America--with the southernmost representatives in Bolivia, Peru and northwestern Brazil. Thus, the species of this genus have a disjunct distribution.

Nematanthus species are localized in small areas along the coast of southeastern Brazil as are species of Codonanthe subgenus Codonanthe section Codonanthe. Species of Nematanthus form a geographically continuous group with no apparent disjuncts.

A discussion of the implications of geographical distribution to the taxonomic status of Codonanthe and Nematanthus is presented in CHAPTER VI: CONCLUSION.

Table II-1. Morphological characteristics of the genera *Codonanthe* and *Nematanthus*.

TAXA	GROWTH HABIT*	STEM SIZE**	LEAF PETIOLE		
			Shape***	Coloration	Size****
GENUS *Codonanthe*					
SUBGENUS *Codonanthe*					
SECTION *Codonanthe*					
1. *C. carnosa*	viny	2-4	round	green	4-10
2. *C. devosiana*	viny	2-4	round	green	4-10
3. *C. digna*	viny	2-4	round	green	4-10
4. *C. gracilis*	viny	2-4	round	green	4-10
5. *C. paula*	viny	2-4	round	green	4-10
SECTION *Spathuliformae*					
6. *C. calcarata*	vin/shr	2-4	round	green	4-10
7. *C. corniculata*	viny	2-4	round	red	4-10
8. *C. crassifolia*	viny	2-4	round	green	4-10
9. *C. uleana*	vin/shr	2-9	round	green	4-10
SUBGENUS *Codonanthella*					
10. *C. caribaea*	vin/shr	2-4	round	green	4-10
11. *C. chiricana*	vin/shr	2-4	round	green	4-10
12. *C. elegans*	viny	2-4	round	green	4-10
13. *C. luteola*	viny	2-4	round	green	4-10
14. *C. macradenia*	viny	2-4	round	green	4-10
GENUS *Nematanthus*					
1. *N. crassifolius*	shrubby	5-9	rnd/fur	green	10-50
2. *N. fissus*	shrubby	5-9	rnd/fur	red	10-50
3. *N. fritschii*	shrubby	5-9	round	green	10-50
4. *N. hirtellus*	shrubby	5-9	round	red	10-50
5. *N. maculatus*	shrubby	5-9	round	green	10-50
6. *N. perianthomegus*	shrubby	5-9	round	red	10-50
7. *N. gregarius*	viny	2-4	rnd/fur	green	4-10
8. *N. nervosus*	viny	2-4	rnd/fur	green	4-10
9. *N. strigillosus*	viny	2-4	rnd/fur	green	4-10
10. *N. wettsteinii*	viny	2-4	round	green	4-10

---

* all species are epiphytes, vin/shr=viny/shrubby.

** diameter, in mm.

*** all species possess round petioles, some have a slight furrow on the adaxial surface of the petiole, rnd/fur=round/furrow.

**** length, in mm.

Table II-1 - continued.

TAXA	LEAF BLADE			
	Balance*	Form**	Apex***	Base****
1. *C. carnosa*	lam sym/base sym	wid ellip	obtuse	obt-rnd
2. *C. devosiana*	lam sym/base sym	wid ellip	acute	obt-rnd
3. *C. digna*	lam sym/base sym	wid ovate	obtuse	rounded
4. *C. gracilis*	lam sym/base asym	nar ovate	acute-acum	cordate
5. *C. paula*	lam sym/base sym	wid ovate	obtuse	rounded
6. *C. calcarata*	lam sym/base asym	nar obov	acute	cordate
7. *C. corniculata*	lam sym/base sym	wid ellip	acute	acute
8. *C. crassifolia*	lam sym/base sym	nar ellip	acute-atten	acute
9. *C. uleana*	lam & base asym	obovate	acuminate	acute
10. *C. caribaea*	lam sym/base sym	elliptic	attenuate	acute
11. *C. chiricana*	lam sym/base sym	wid obov	acute	acute
12. *C. elegans*	lam sym/base sym	obovate	acute	acute
13. *C. luteola*	lam sym/base sym	wid ellip	acute	acute
14. *C. macradenia*	lam sym/base asym	wid ellip	acute	acute
1. *N. crassifolius*	lam asym/base sym	elliptic	acum-atten	acute
2. *N. fissus*	lam sym/base sym	elliptic	acute	acute
3. *N. fritschii*	lam sym/base sym	elliptic	acum-atten	acute
4. *N. hirtellus*	lam sym/base sym	wid ellip	acute-obtuse	obtuse
5. *N. maculatus*	lam sym/base asym	nar obov	acum-atten	acute
6. *N. perianthomegus*	lam sym/base sym	elliptic	acute-acum	acute
7. *N. gregarius*	lam sym/base sym	wid ellip	acute	acute
8. *N. nervosus*	lam sym/base asym	nar ovate	attenuate	obt-rnd
9. *N. strigillosus*	lam sym/base sym	wid ellip	acute	acute
10. *N. wettsteinii*	lam sym/base sym	wid ellip	acute	acute

---

* lam=lamina, sym=symmetrical, asym=asymmetrical.

** wid=widely, nar=narrowly, ellip=elliptic, obov=obovate.

*** acum=acuminate, atten=attenuate.

**** obt=obtuse, rnd=rounded.

Table II-1 - continued.

	LEAF BLADE			
TAXA	Margin*	Size**	Texture	Coloration***
1. *C. carnosa*	slt cren	2-4	puberulous	red abax leaf surf
2. *C. devosiana*	entire	2-4	pubescent	green only
3. *C. digna*	entire	2-4	puberulous	red abax leaf surf
4. *C. gracilis*	slt cren	4-12	smooth	red leaf margins
5. *C. paula*	slt cren	2-4	puberulous	red abax leaf surf
6. *C. calcarata*	crenate	4-12	smooth	green only
7. *C. corniculata*	slt cren	4-12	smooth	red abax leaf surf
8. *C. crassifolia*	entire	4-12	smooth	red leaf margins
9. *C. uleana*	slt cren	4-12	smooth	green only
10. *C. caribaea*	entire	4-12	smooth	red leaf margins
11. *C. chiricana*	slt cren	2-4	smooth	green only
12. *C. elegans*	slt cren	4-12	smooth	red 1° & 2° veins
13. *C. luteola*	slt cren	4-12	smooth	green only
14. *C. macradenia*	slt cren	4-12	smooth	green only
1. *N. crassifolius*	entire	4-12	smooth	green only
2. *N. fissus*	crenate	4-12	pubescent	green only
3. *N. fritschii*	entire	4-12	smooth	red 1° & 2° veins
4. *N. hirtellus*	entire	4-12	puberulous	green only
5. *N. maculatus*	entire	4-12	smooth	red 1° & 2° veins
6. *N. perianthomegus*	slt cren	4-12	smooth	green only
7. *N. gregarius*	entire	2-4	smooth	green only
8. *N. nervosus*	entire	2-4	smooth	green only
9. *N. strigillosus*	entire	2-4	pubescent	red 1° & 2° veins
10. *N. wettsteinii*	entire	2-4	smooth	red lam/green veins

---

* slt cren=slightly crenate.

** length, in cm.

*** all species possess green adaxial leaf surface, coloration pertains to the abaxial leaf surface besides green, abax=abaxial, surf=surface, 1° & 2° veins=midrib & secondary veins, lam=lamina.

Table II-1 - continued.

	FLOWER		FLOWER: Calyx		
TAXA	Orientation*	Pedicel**	Shape***	Color****	Size**
1. *C. carnosa*	nonresup/erect	3-25	linear-lanc	green	2-10
2. *C. devosiana*	nonresup/erect	3-25	linear-lanc	green	2-10
3. *C. digna*	nonresup/erect	3-25	linear-lanc	green-pur	2-10
4. *C. gracilis*	nonresup/erect	3-25	linear-lanc	green-red	2-10
5. *C. paula*	nonresup/erect	3-25	linear-lanc	green	2-10
6. *C. calcarata*	nonresup/erect	3-25	linear-lanc	green	2-10
7. *C. corniculata*	nonresup/erect	3-25	linear-lanc	green-red	2-10
8. *C. crassifolia*	nonresup/erect	3-25	linear-lanc	green	2-10
9. *C. uleana*	nonresup/erect	3-25	linear-lanc	green	2-10
10. *C. caribaea*	nonresup/erect	3-25	linear-lanc	green-pur	2-10
11. *C. chiricana*	nonresup/erect	3-25	linear-lanc	green-red	2-10
12. *C. elegans*	nonresup/erect	3-25	linear-lanc	green	2-10
13. *C. luteola*	nonresup/erect	3-25	linear-lanc	green-red	2-10
14. *C. macradenia*	nonresup/erect	3-25	linear-lanc	green-red	2-10
1. *N. crassifolius*	resup/pendulant	25-200	linear-lanc	green	10-30
2. *N. fissus*	resup/erect	3-25	linear-lanc	green	10-30
3. *N. fritschii*	resup/pendulant	25-200	linear-lanc	green-pur	10-30
4. *N. hirtellus*	resup/erect	3-25	ovate-ellip	green	10-30
5. *N. maculatus*	resup/erect	3-25	ovate-ellip	green	10-30
6. *N. perianthomegus*	resup/erect	3-25	ovate-ellip	green	10-30
7. *N. gregarius*	nonresup/erect	3-25	ovate-ellip	green	10-30
8. *N. nervosus*	nonresup/erect	3-25	ovate-ellip	green	10-30
9. *N. strigillosus*	nonresup/erect	3-25	ovate-ellip	green	10-30
10. *N. wettsteinii*	nonresup/erect	3-25	linear-lanc	green	10-30

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* nonresup=nonresupinate, resup=resupinate.

** length, in mm.

*** all species possess a 5-parted calyx, shape pertains to calyx lobes, lanc=lanceolate, ellip=elliptic.

**** pur=purple.

Table II-1 - continued.

TAXA	FLOWER: Corolla		
	Shape*	Color	Size**
1. *C. carnosa*	funnelform	white + yellow, red, brown	2-4
2. *C. devosiana*	funnelform	white + brown	1-2
3. *C. digna*	funnelform	white + pink	1-2
4. *C. gracilis*	funnelform	white + yellow, red, purple	2-4
5. *C. paula*	funnelform	white + pink, red	1-2
6. *C. calcarata*	funnelform	white + pink, red, purple	2-4
7. *C. corniculata*	funnelform	white + yellow	2-4
8. *C. crassifolia*	funnelform	white + yellow, pink	1-4
9. *C. uleana*	funnelform	white + yellow, pink, red	2-4
10. *C. caribaea*	funnelform	white + yellow, purple	2-4
11. *C. chiricana*	funnelform	white + red	2-4
12. *C. elegans*	funnelform	white + yellow	2-4
13. *C. luteola*	funnelform	yellow	2-4
14. *C. macradenia*	funnelform	white + pink, red	2-4
1. *N. crassifolius*	pouched	red	4-6
2. *N. fissus*	pouched	red	2-4
3. *N. fritschii*	pouched	red	4-6
4. *N. hirtellus*	pouched	yellow	2-4
5. *N. maculatus*	pouched	pink + yellow	2-4
6. *N. perianthomegus*	pouched	yellow + purple	2-4
7. *N. gregarius*	pouched	orange + yellow	2-4
8. *N. nervosus*	pouched	red	2-4
9. *N. strigillosus*	pouched	orange	2-4
10. *N. wettsteinii*	pouched	orange + yellow	2-4

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* all species possess an obliquely ventricose corolla, pouched=*Hypocyrta*-type corolla of Wiehler, 1979b.

** length, in cm.

Table II-1 - continued.

TAXA	FRUIT TYPE*	POLLINATION AGENT**	CHROMOSOME NUMBER***	DISTRIBUTION****
1. *C. carnosa*	indeh/orange	bee	2*n*	se Brazil
2. *C. devosiana*	indeh/orange	bee	2*n*	se Brazil
3. *C. digna*	indeh/orange	bee		se Brazil
4. *C. gracilis*	indeh/orange	bee	2*n*	se Brazil
5. *C. paula*	indeh/orange	bee		se Brazil
6. *C. calcarata*	deh/red-pur	bee	4*n*	s Mex-CA-nw SA
7. *C. corniculata*	?deh/red-pur	bee	4*n*	s Mex-CA-nw SA
8. *C. crassifolia*	deh/red-pur	bee	4*n*	s Mex-CA-nw SA
9. *C. uleana*	deh/red-pur	bee	4*n*	s Mex-CA-nw SA
10. *C. caribaea*	deh/red-pur	bee	2*n*	s Mex-CA-nw SA
11. *C. chiricana*	deh/red-pur	bee		s Mex-CA-nw SA
12. *C. elegans*	deh/yel-grn	bee	4*n*	s Mex-CA-nw SA
13. *C. luteola*	deh/yel-grn	bee	2*n*,4*n*	s Mex-CA-nw SA
14. *C. macradenia*	deh/red-pur	bee	4*n*	s Mex-CA-nw SA
1. *N. crassifolius*	deh/yel-grn	bird	2*n*	se Brazil
2. *N. fissus*	deh/yel-grn	bird	2*n*	se Brazil
3. *N. fritschii*	deh/yel-grn	bird	2*n*	se Brazil
4. *N. hirtellus*	deh/yel-grn	bird	2*n*	se Brazil
5. *N. maculatus*	deh/yel-grn	bird		se Brazil
6. *N. perianthomegus*	deh/yel-grn	bird	2*n*	se Brazil
7. *N. gregarius*	deh/yel-grn	bird	2*n*	se Brazil
8. *N. nervosus*	deh/yel-grn	bird	2*n*	se Brazil
9. *N. strigillosus*	deh/yel-grn	bird	2*n*	se Brazil
10. *N. wettsteinii*	deh/yel-grn	bird	2*n*	se Brazil

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* indeh=indehiscent berry, deh=dehiscent, tardily dehiscent or occasionally splitting berry or fleshy capsule, red-pur=red, purple or pink, yel-grn=yellow-green.

** bee=euglossine bees, bird=hummingbirds.

*** base chromosome number is x=8, 2*n*=16 or diploids, 4*n*=32 or tetraploids.

**** se Brazil=southeastern Brazil, s Mex-CA-nw SA=southern Mexica through Central America to northwestern South America.

Figure II-1. Growth habit of species of *Codonanthe* subgenus *Codonanthe* section *Codonanthe*.

A. *C. carnosa*.

B. *C. devosiana*.

C. *C. digna*.

D. *C. gracilis*.

E. *C. paula*.

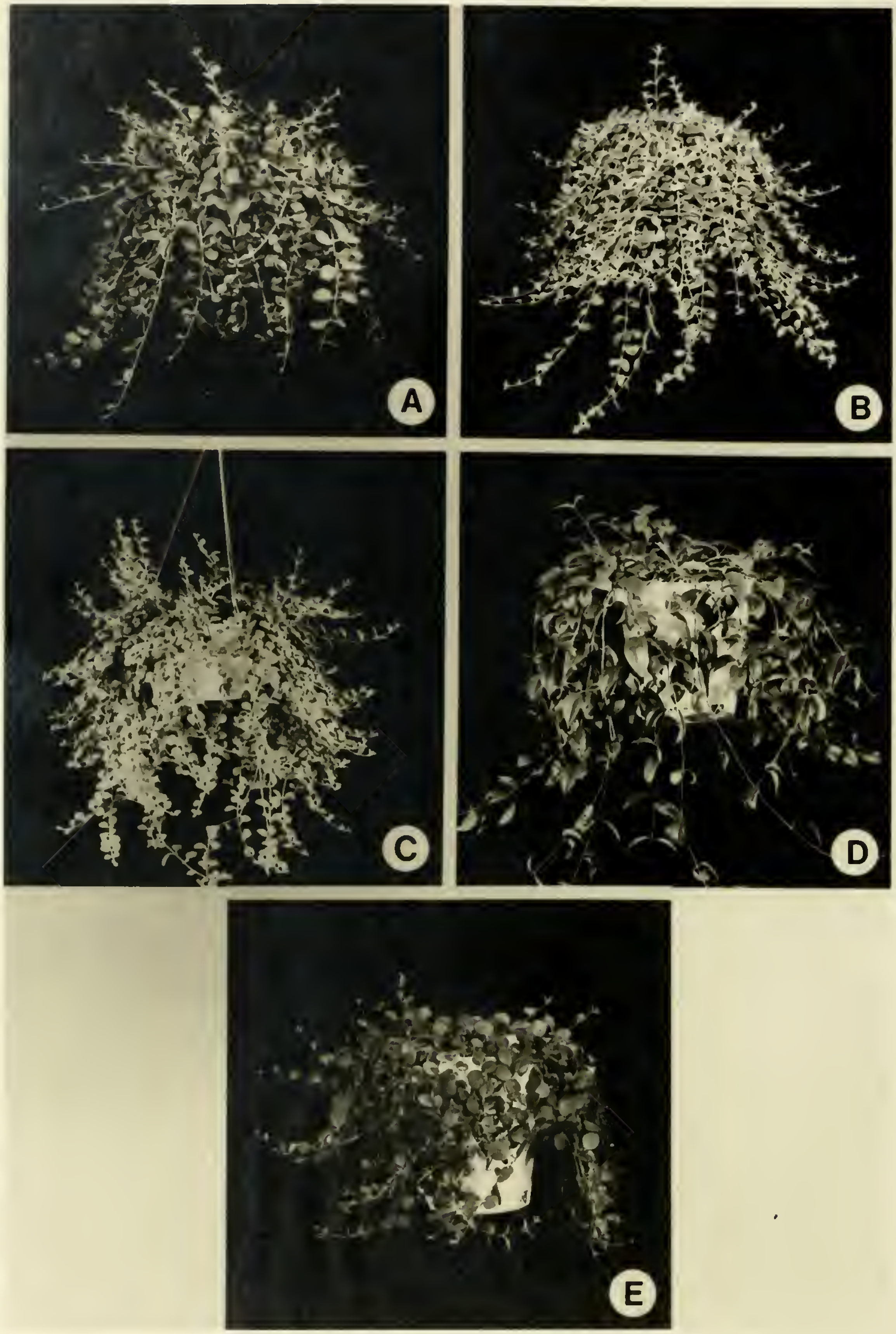
A
B
C
D
E

Figure II-2. Growth habit of species of _Codonanthe_ subgenus _Codonanthe_ section _Spathuliformae_.

A. _C. calcarata_.

B. _C. corniculata_.

C. _C. crassifolia_.

D. _C. uleana_.

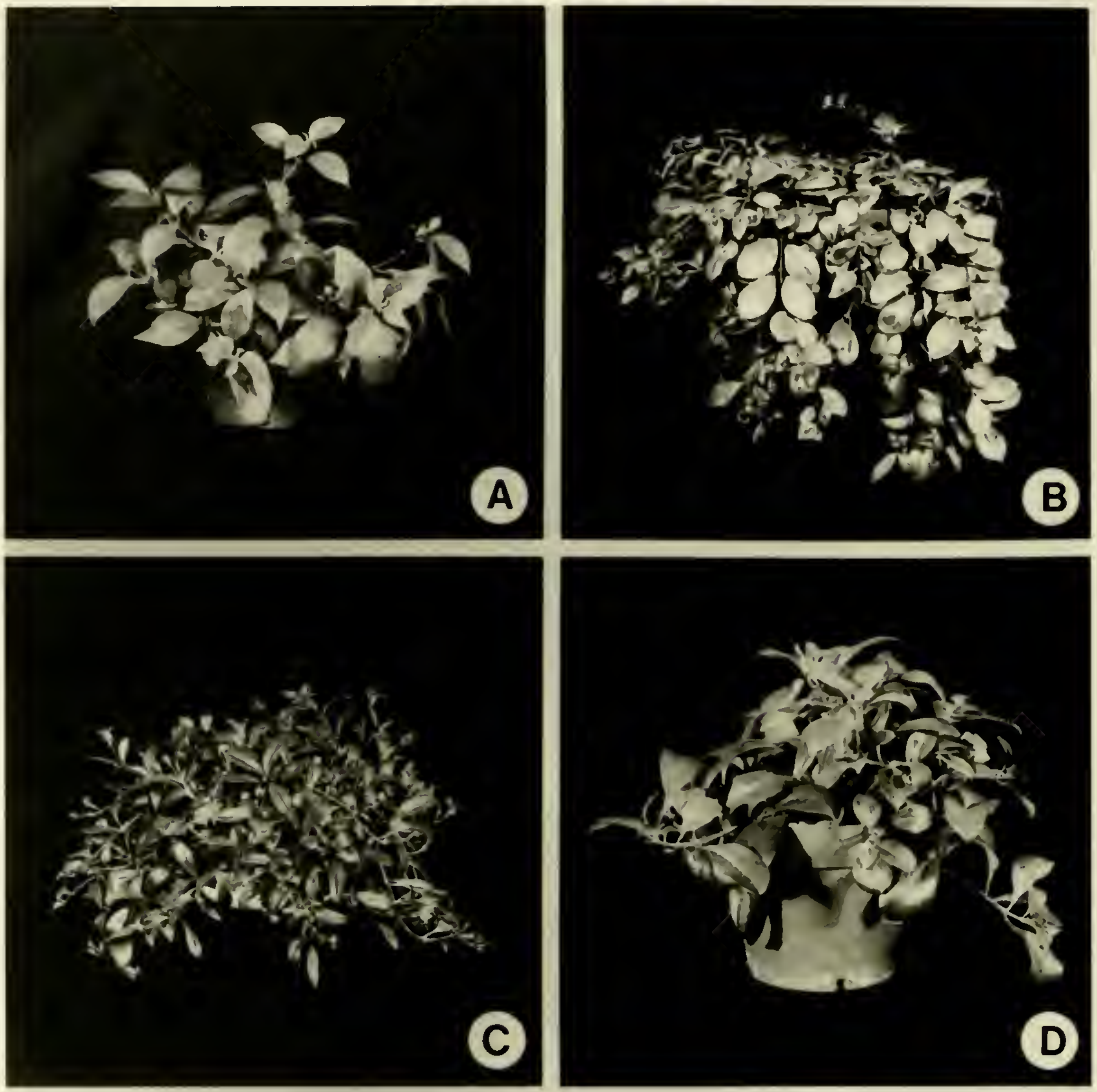
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Figure II-3. Growth habit of species of _Codonanthe_ subgenus _Codonanthella_.

A. _C. caribaea_.

B. _C. elegans_.

C. _C. luteola_.

D. _C. macradenia_.

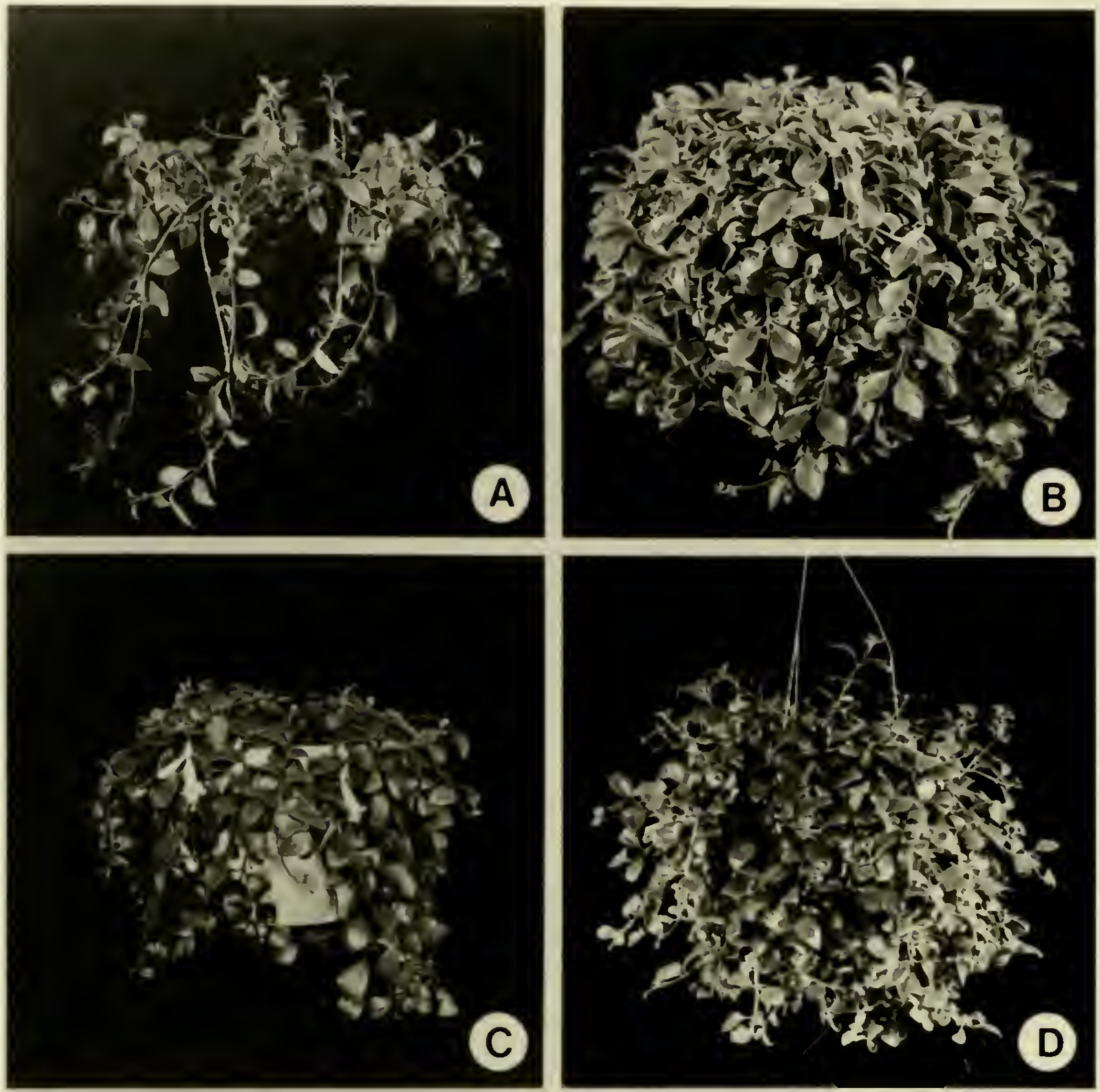
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Figure II-4. Growth habit of species of *Nematanthus*.

A. *N. crassifolius*.

B. *N. fissus*.

C. *N. fritschii*.

D. *N. hirtellus*.

E. *N. maculatus*.

F. *N. perianthomegus*.


A
B
C
D
E

Figure II-5. Growth habit of species of _Nematanthus_.

A. _N. gregarius_.

B. _N. nervosus_.

C. _N. strigillosus_.

D. _N. wettsteinii_.

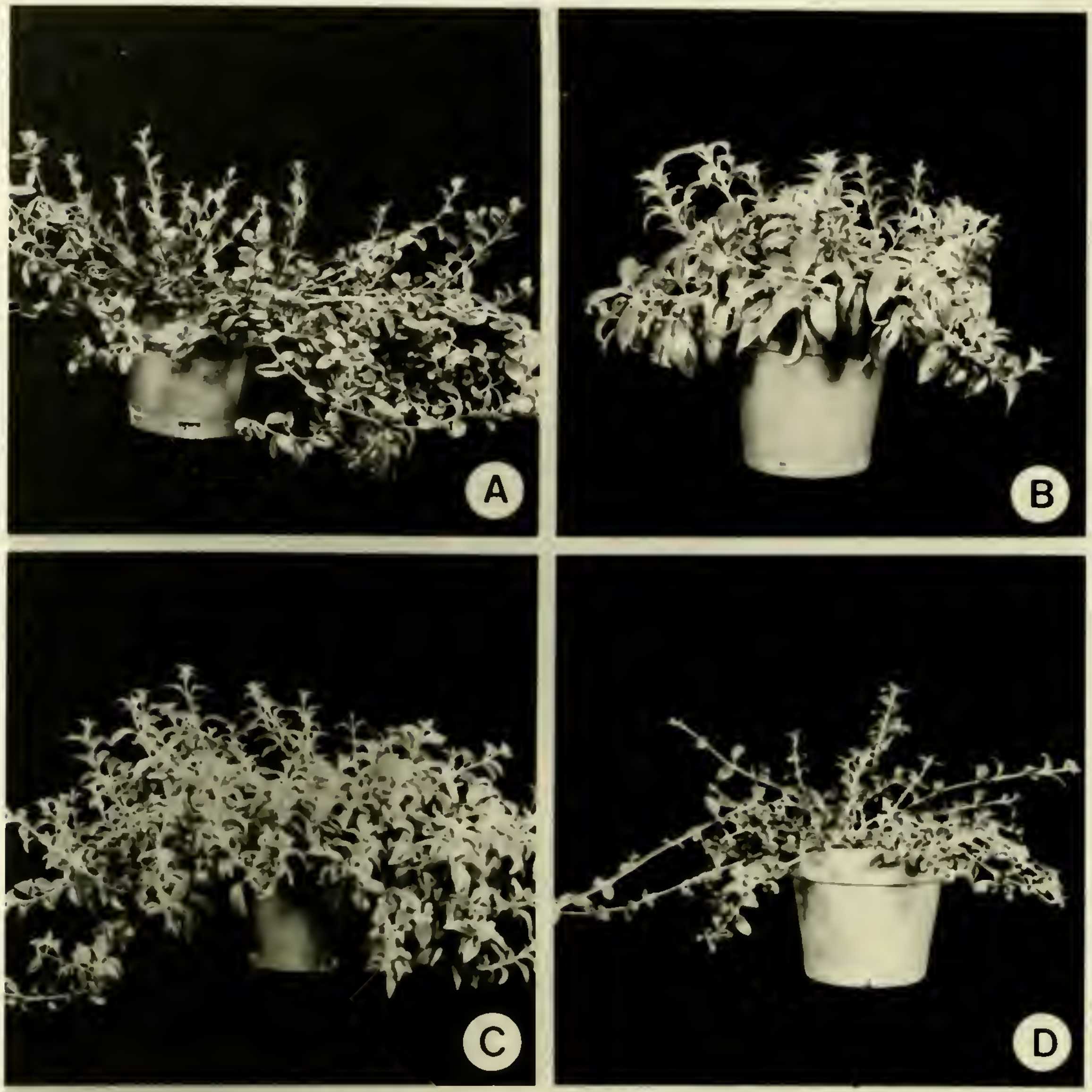
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Figure II-6. Leaf blade shape of species of *Codonanthe* subgenus *Codonanthe* section *Codonanthe*.

A. *C. carnosa*, X1.

B. *C. devosiana*, X1.

C. *C. digna*, X1.

D. *C. gracilis*, X1.

E. *C. paula*, X1.

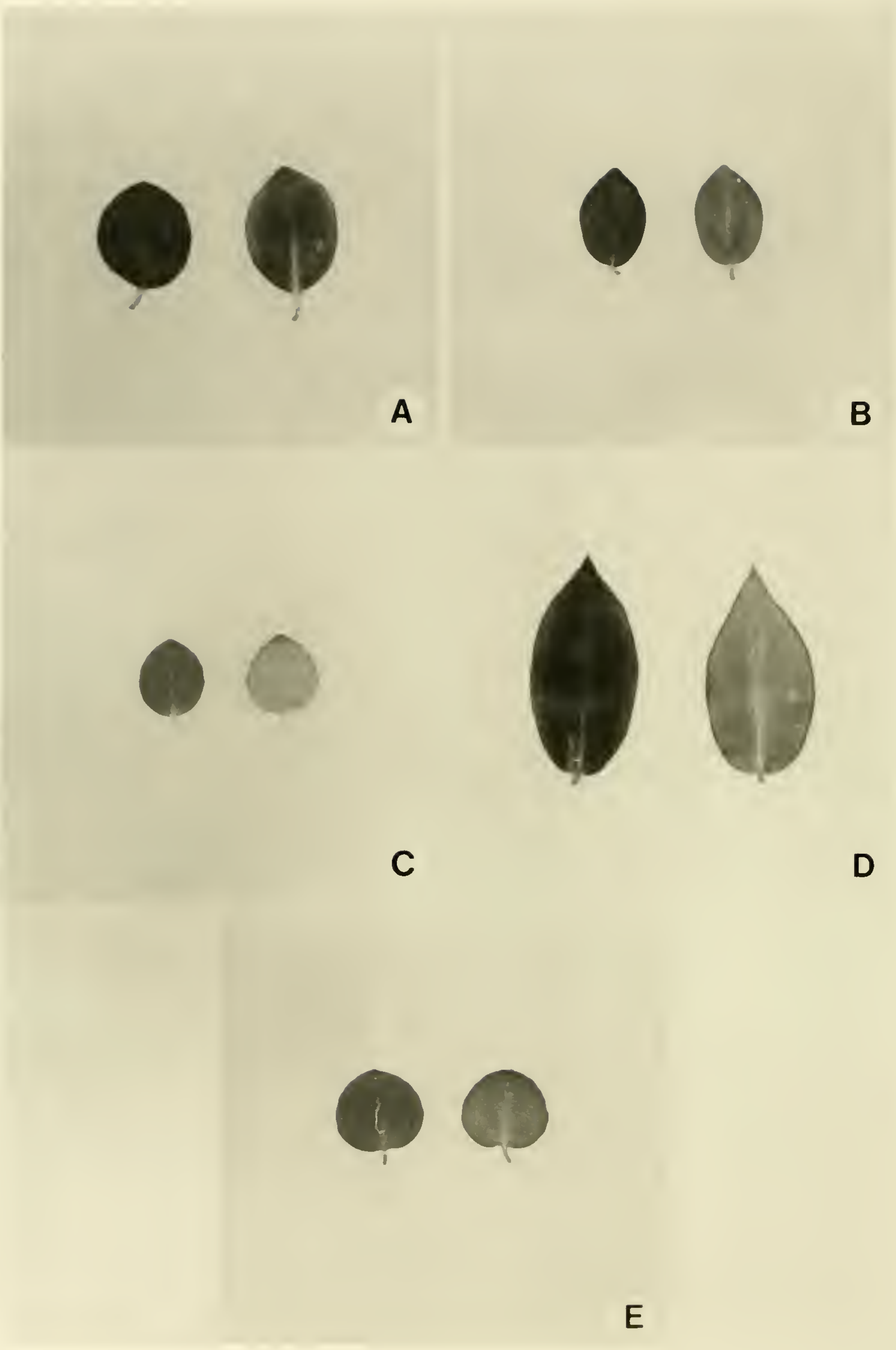
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Figure II-7. Leaf blade shape of species of *Codonanthe* subgenus *Codonanthe* section *Spathuliformae*.

A. *C. calcarata*, X1.

B. *C. corniculata*, X1.

C. *C. crassifolia*, X1.

D. *C. uleana*, X1.

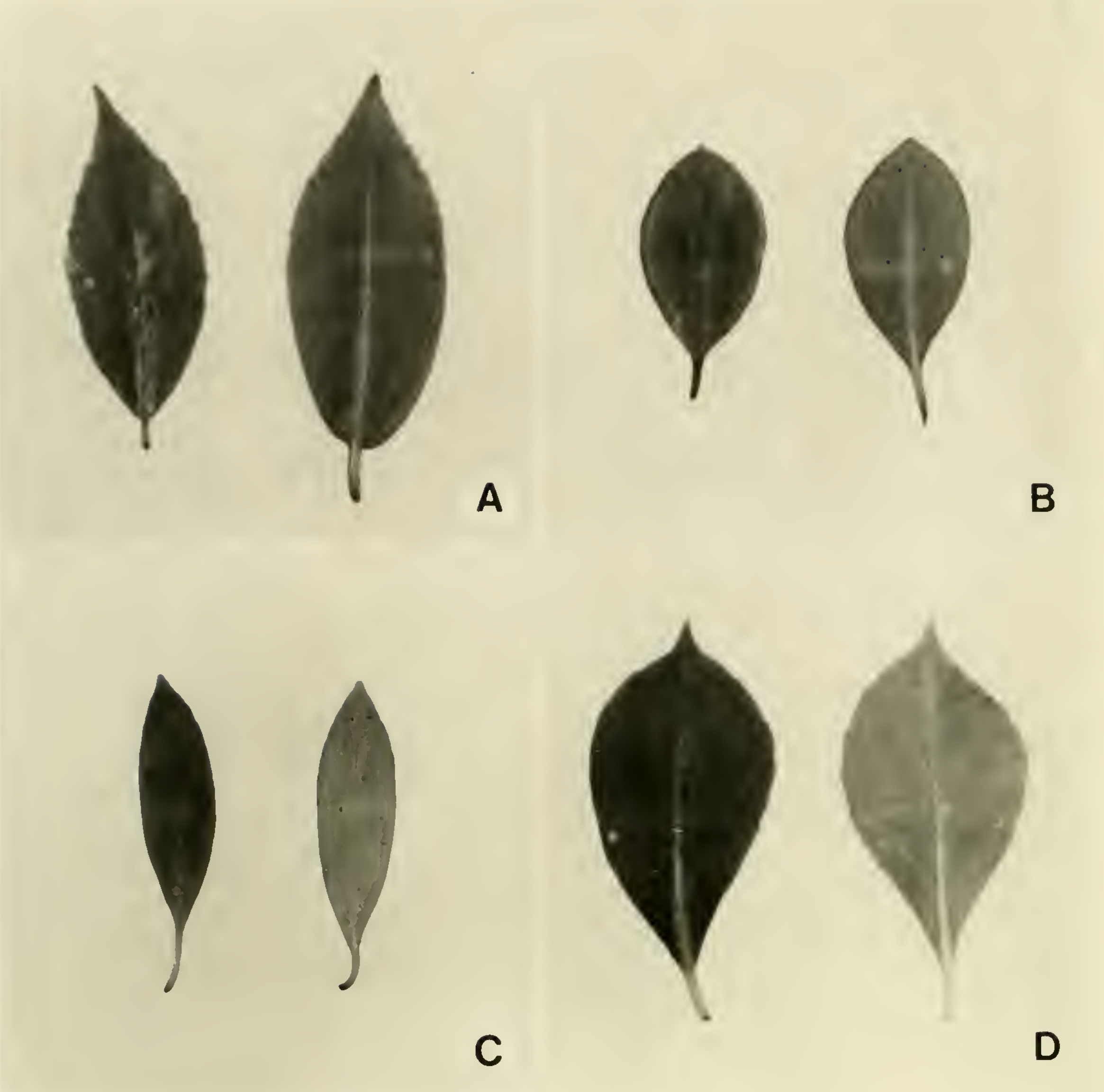
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Figure II-8. Leaf blade shape of species of *Codonanthe* subgenus *Codonanthe*.

A. *C. caribaea*, X1.

B. *C. elegans*, X1.

C. *C. luteola*, X1.

D. *C. macradenia*, X1.

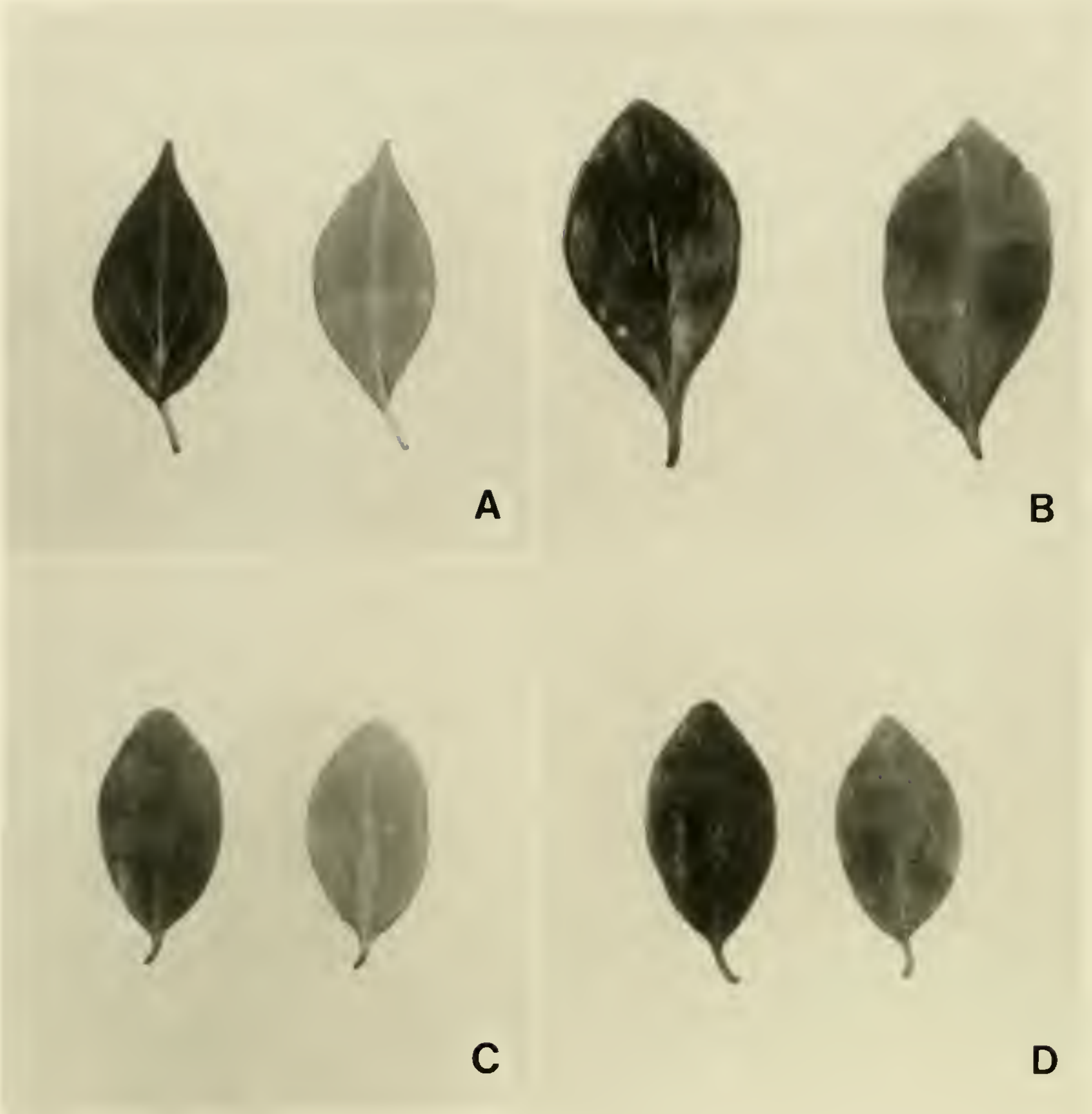
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Figure II-9. Leaf blade shape of species of *Nematanthus*.

A. *N. crassifolius*, X1.

B. *N. fissus*, X1.

C. *N. fritschii*, X1.

D. *N. hirtellus*, X1.

E. *N. maculatus*, X1.

F. *N. perianthomegus*, X1.

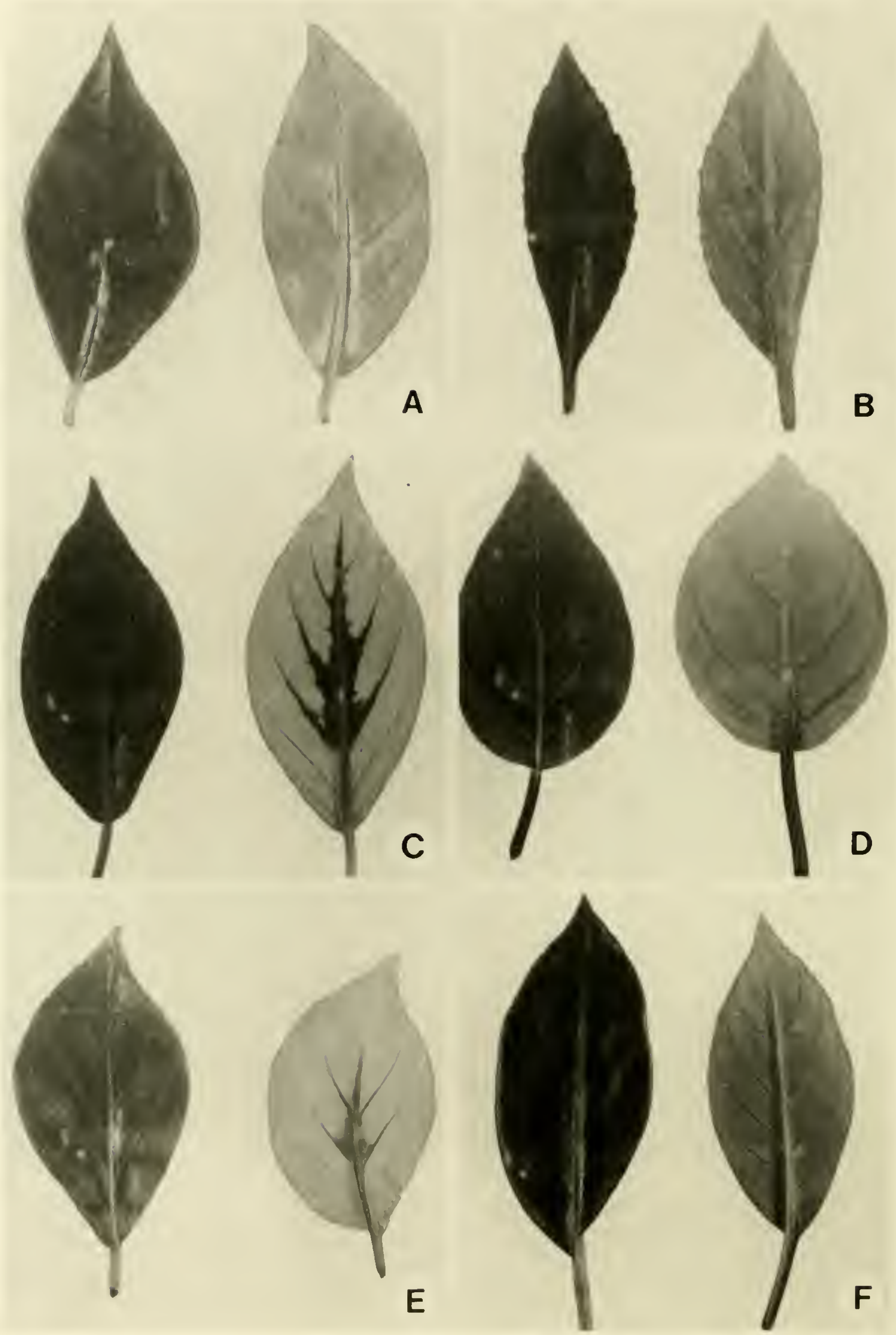
A
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Figure II-10. Leaf blade shape of species of *Nematanthus*.

A. *N. gregarius*, X1.

B. *N. nervosus*, X1.

C. *N. strigillosus*, X1.

D. *N. wettsteinii*, X1.

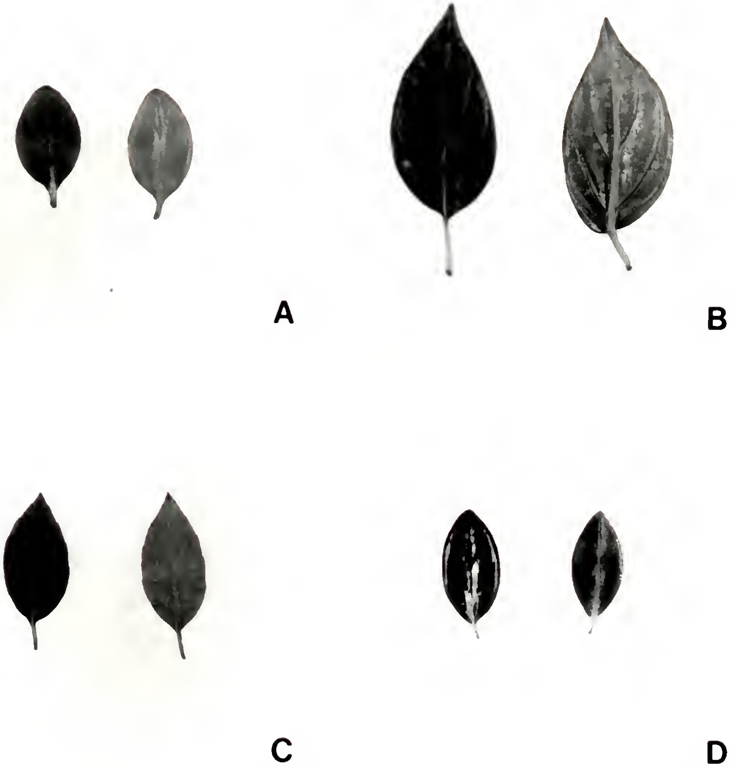
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Figure II-11. Floral morphology of species of Nematanthus.

A. N. perianthomegus, side view of resupinate flower with dorsally-located pouch, X1.5.

B. N. perianthomegus, face view of resupinate flower. Note anthers within corolla are facing upwards, X6.

C. N. maculatus, side view of resupinate flower with dorsally-located pouch, X1.5.

D. N. maculatus, face view of resupinate flower. Note anthers within corolla are facing upwards, X6.

E. N. strigillosus, side view of nonresupinate flower with ventrally-located pouch, X2.5.

F. N. strigillosus, face view of nonresupinate flower. Note the stigma of the elongating style moves into the former dorsal position of the retracting anthers, X11.

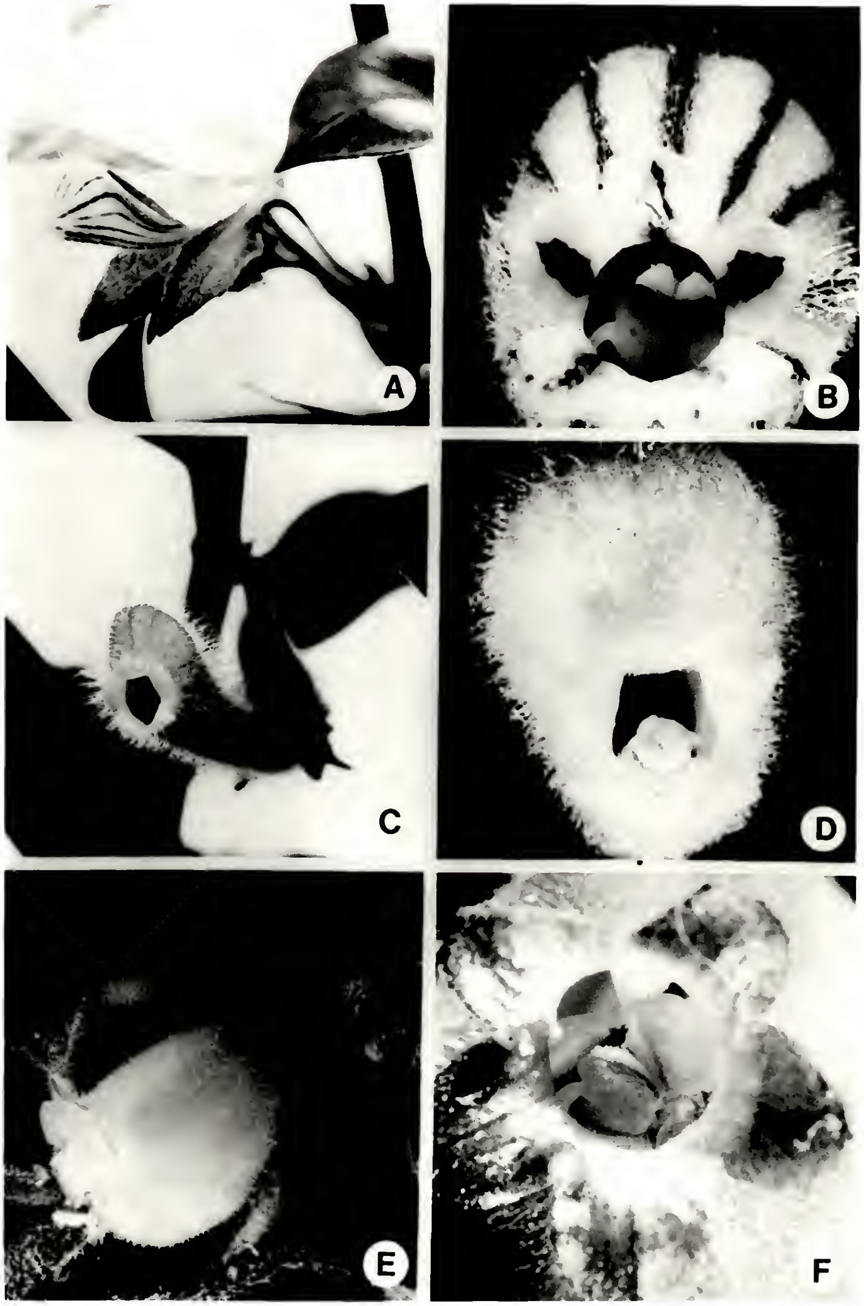
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Figure II-12. Floral morphology of species of Codonanthe.

A. *C. luteola*, side view of nonresupinate flower with obliquely funnelform-ventricose corolla, X1.5.

B. *C. crassifolia*, side view of nonresupinate flower with obliquely funnelform-ventricose corolla, X3.

C. *C. luteola*, side view of flower displaying obliquely-situated corolla within calyx and prominent spur, X7.

D. *C. digna*, face view of nonresupinate flower. Note anthers are dorsally-located within corolla, X8.5.

E. *C. macradenia*, ventral view of flower depicting a groove within the corolla, X5.5.

F. *C. macradenia*, face view of flower depicting a groove within the corolla, X18.

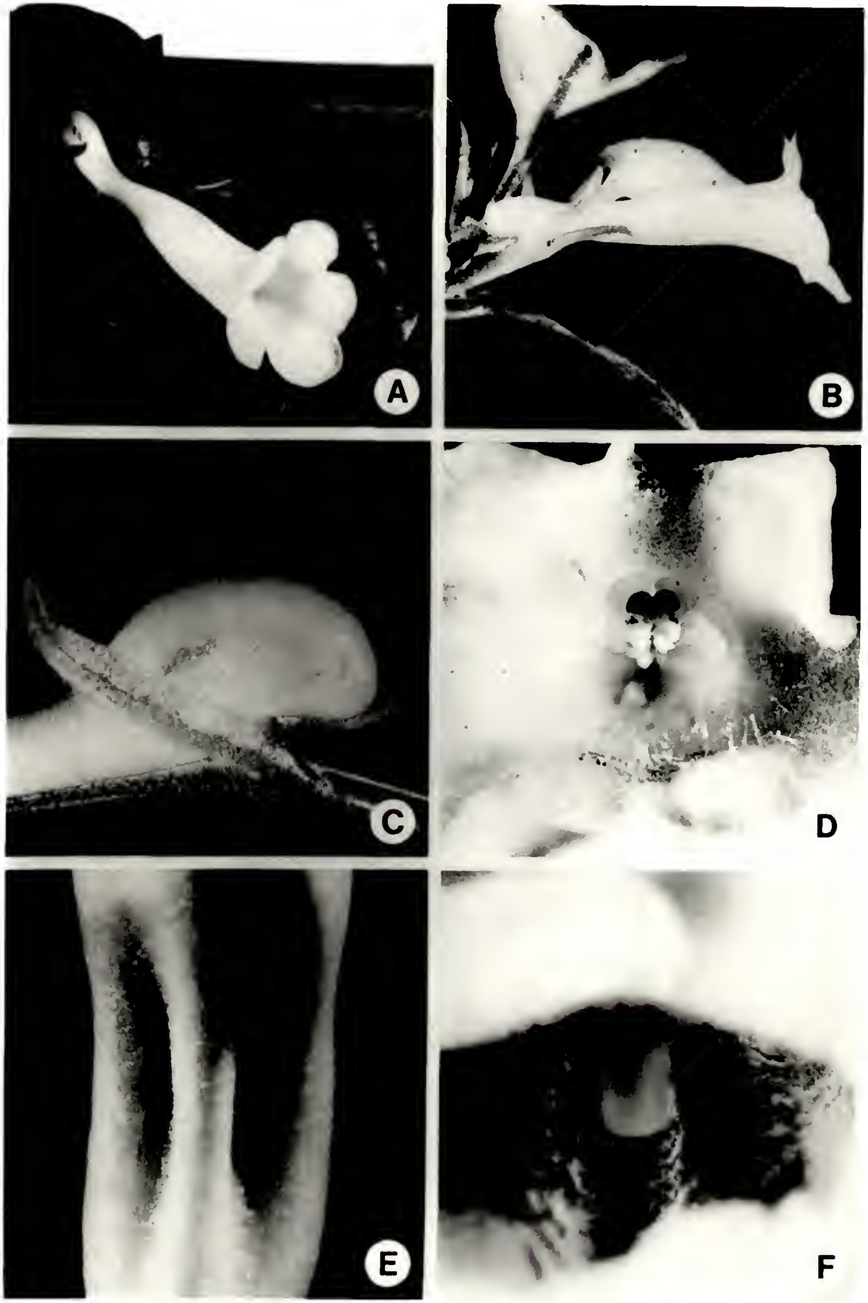
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Figure II-13. Stigma and stigmatic surface.

A. *C. devosiana*, apical portion of stigma, X120.

B. *N. fissus*, apical portion of stigma, X71.

C. *N. crassifolius*, papillae of stigmatic surface, X240.

D. *N. fissus*, papillae of stigmatic surface, X210.

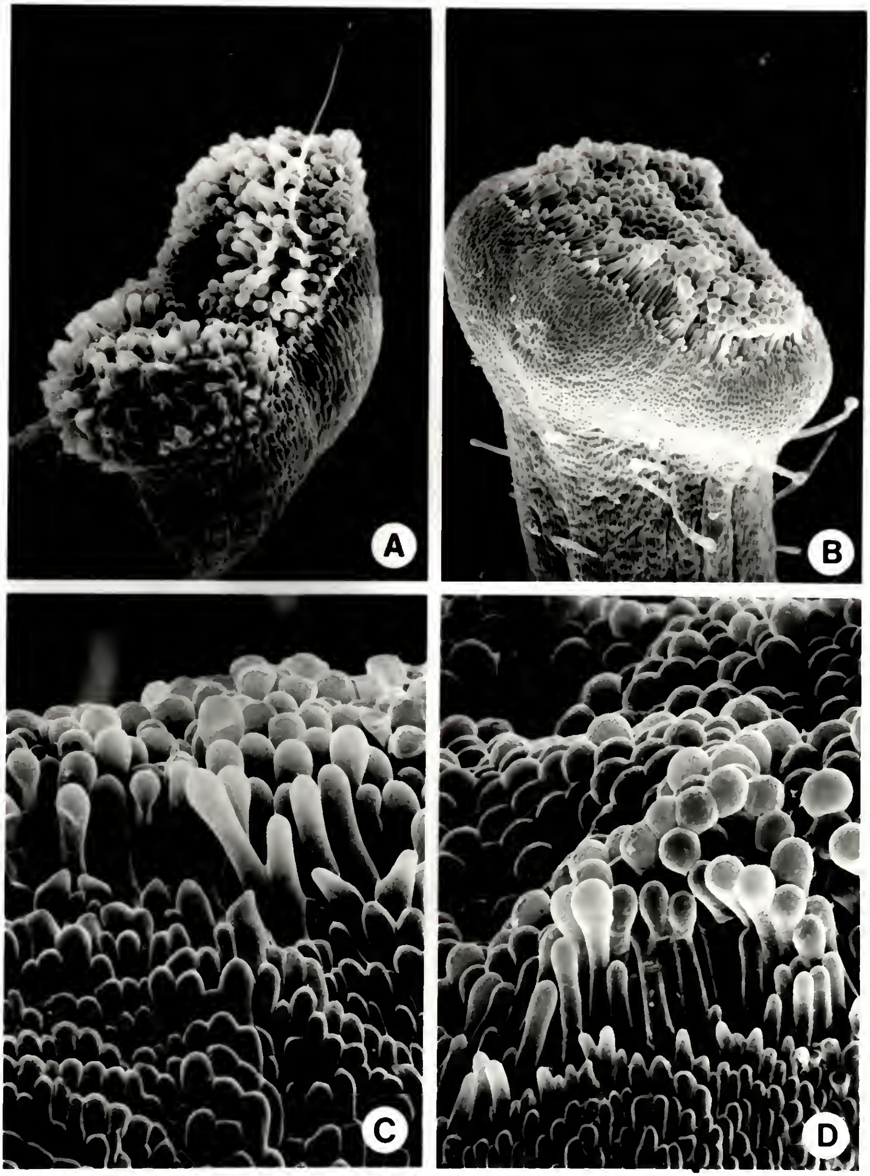
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Figure II-14. Floral morphology and fruit of species of *Codonanthe*.

A. *C. luteola*, side view of flower with corolla removed to reveal gynoecium with a nectary connivent and dorsal to the ovary, X3.

B. *C. corniculata*, dorsal view of flower with corolla and dorsal sepal removed to reveal nectary, X30.

C. *C. crassifolia*, side view of flower with prominent extrafloral nectary in the sinus of the calyx lobe margin, X30.

D. *C. crassifolia*, side view of subglobose berry, X1.5.

E. *C. luteola*, side view of pointed capsule, X1.5.

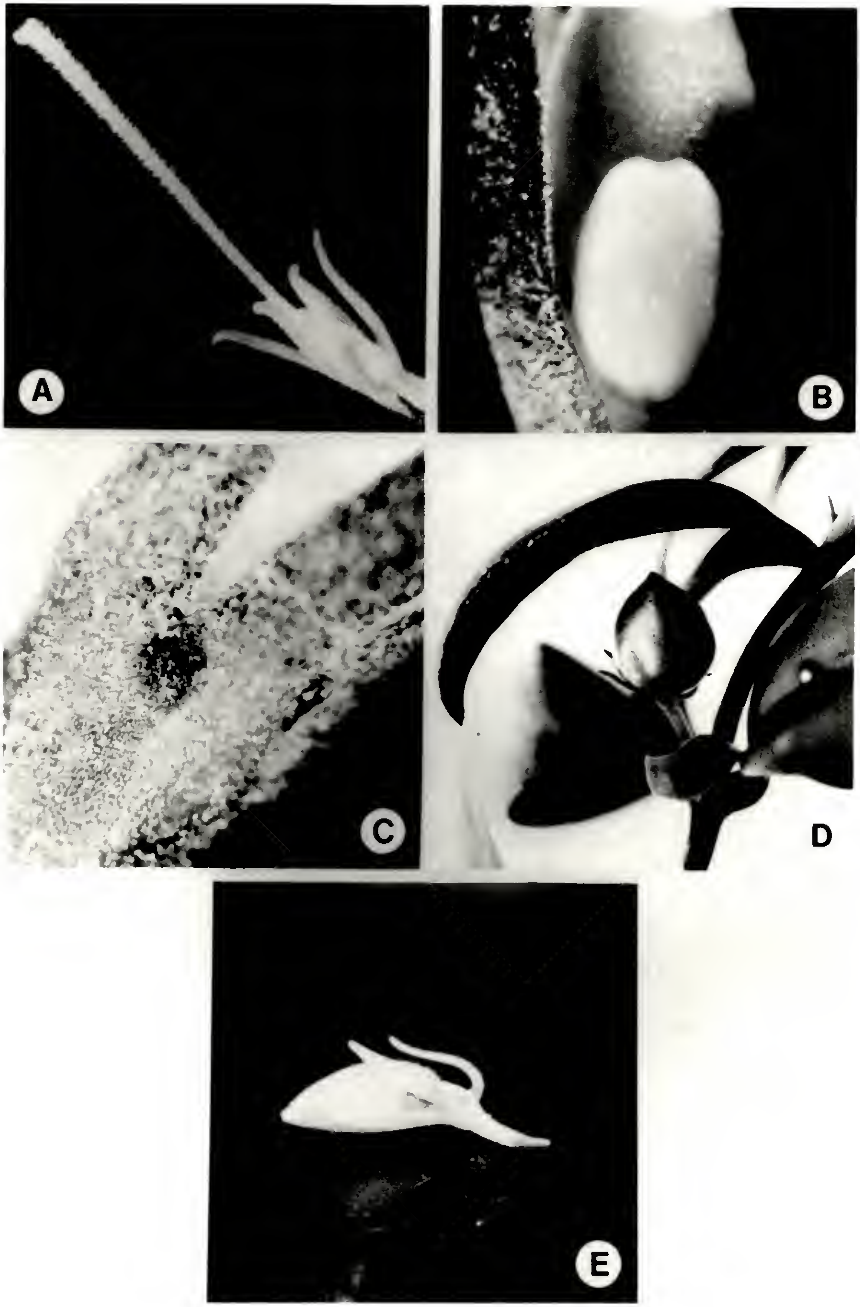
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Figure II-15. Seeds of species of _Codonanthe_ subgenus _Codonanthe_ section _Codonanthe_.

A. _C_. _devosiana_, X75.

B. _C_. _digna_, X75.

C. _C_. _paula_, X75.

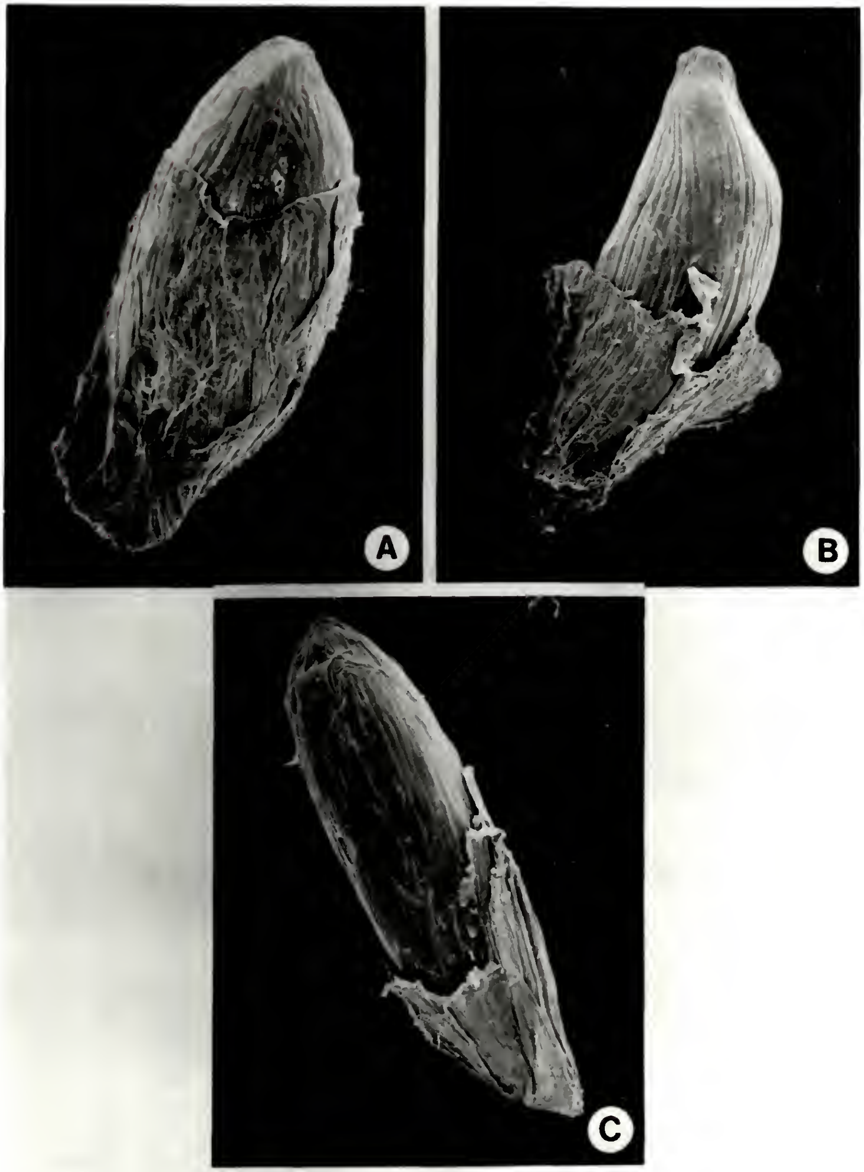
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Figure II-16. Seeds of species of *Codonanthe* subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella*.

A. *C. calcarata*, X30.

B. *C. crassifolia*, X50.

C. *C. caribaea*, X50.

D. *C. macradenia*, X50.

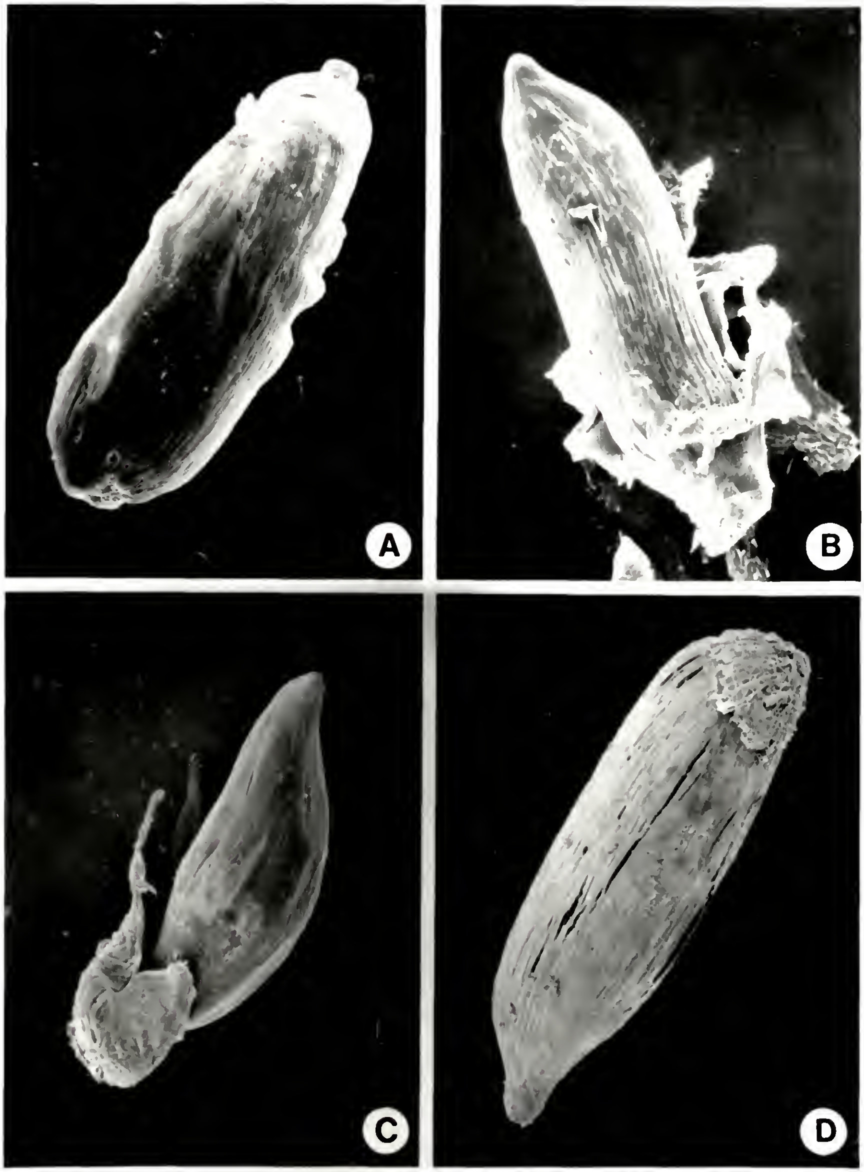
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Figure II-17. Seeds of species of _Nematanthus_.

A. _N_. _gregarius_, X75.

B. _N_. _nervosus_, X75.

C. _N_. _fissus_, X75.

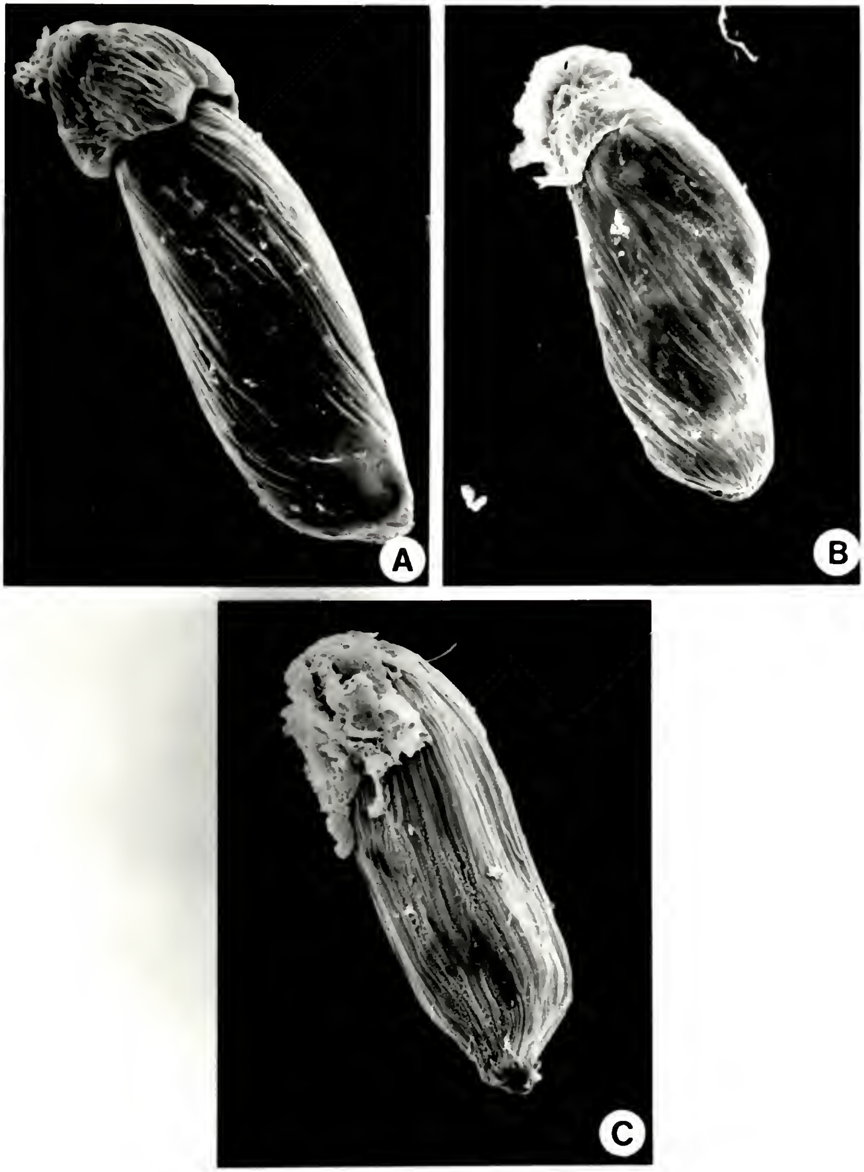
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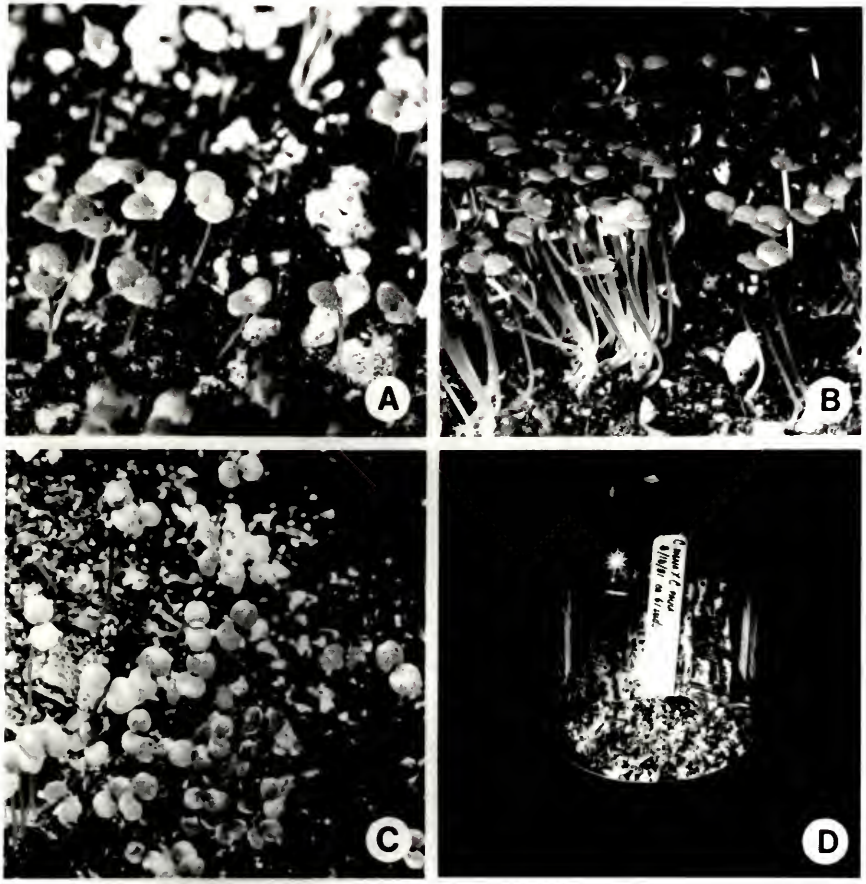
Figure II-18. Seedlings of primary hybrids of *Codonanthe* and *Nematanthus*.

A. Seedlings of *C. digna* X *C. devosiana*, X4.

B. Seedlings of *N. nervosus* X *N. strigillosus*, X2.

C. Seedlings of *N. strigillosus* X *C. carnosa*, X4.

D. Seed germinating container with *C. digna* X *C. paula* seedlings, X1/3.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CHAPTER III
COMPARATIVE MORPHOLOGY OF THE LEAF EPIDERMIS

Introduction

The taxonomic value of the morphology of leaf epidermal surfaces has been expounded by Stace (1965) and Sinclair & Sharma (1971). Conventional light microscopy (LM) methods of examining Gesneriaceae leaf surfaces have been used in the study of the genera *Columnea* and *Alloplectus* (Stearn, 1969), *Gesneria* (Skog, 1976), and in some gesneriads of Africa and Asia (Sahasrabudhe & Stace, 1974), Sri Lanka (Herat & Theobald, 1979) and the Neotropics (Wiehler, 1979b). Taxonomic investigations utilizing scanning electron microscopy (SEM) have been relatively limited. Some recent SEM studies include those of Atwood & Williams (1979) for Cypripedioideae (Orchidaceae), Thomson & Mohlenbrock (1979) for *Quercus* (Fagaceae), Hardin (1979, 1981) for some North American woody plants, Dehgan (1980) for *Jatropha* (Euphorbiaceae) and Rudall (1980) for *Hyptis* (Labiatae). However, the comparative morphology of Gesneriaceae leaf epidermis utilizing SEM has not been reported. This study of leaf surfaces was initiated to discover more characters of taxonomic utility in evaluating the subgeneric categories of *Codonanthe* and to establish natural groupings in *Nematanthus*.

Materials and Methods

All plant materials examined were from a live collection cultivated in a growth room at the Department of Ornamental

Horticulture, University of Florida. Uniform conditions were maintained via a 22-25° C day temperature, 17-20° C night temperture, 4000-6000 Lux fluorescent lighting and a 14 hour daylength. Voucher specimen are deposited at the University of Florida herbarium (FLAS).

In the SEM preparation (cf., Hayat, 1978), mature leaves were sampled using a no. 2 cork borer to punch out 5 mm leaf discs which were fixed overnight in 2% glutaraldehyde. Leaf samples were then dehydrated in a 20-100% ethanol series for 2 hours, critical point dried for 30 minutes, mounted on aluminum stubs with TV Tube Koat (GC Electronics), and coated with a gold-palladium mixture. A Hitachi S-450 Scanning Electron Microscope was used to view the specimens and photographs were recorded on Polaroid Type 55 Positive/Negative film.

In the LM preparation, immature and mature leaves were sampled for ontogenetic studies of the stomata and the examination of leaf surfaces, respectively. Free-hand paradermal sections were taken with a razor blade and mounted in water for observation. Guard cell length and width were measured with an eyepiece micrometer and presented as a mean value ± the standard error of the mean ($\bar{x} \pm S.E.\bar{x}$). A guard cell area index was calculated by multiplying the mean length by the mean width of the guard cells. A Wild M-20EB Light Microscope was used to examine the specimens.

Observations

Descriptive terminology of epidermal features is based on Dilcher (1974) and summarized in Table III-1. Definitions of terms used in the text are briefly reviewed below.

Trichomes. Glandular and nonglandular trichomes can be recognized on the adaxial and abaxial leaf surface. Nonglandular trichomes may be unicellular or multicellular-uniseriate. Glandular trichomes are multicellular and composed of a head and a body. The head consists of 2, 4 or more cells and the body is either short or long (cf., Esau, 1965). Short glandular trichomes have a unicellular body while long (stalked) glandular trichomes have a multicellular-uniseriate body. Basal cells of glandular trichomes may be randomly-arranged, radially-arranged or sunken. The sunken basal cell type gives the glandular head a sessile appearance, as though it were attached directly to the epidermis with no basal trichome cell (Sahasrabudhe & Stace, 1974; Wiehler, 1979b).

Stomata. Anisocytic and helicocytic stomata have been observed on the abaxial leaf surface. Anisocytic stomata have guard cells surrounded by three unequal subsidiary cells of which one is distinctly smaller than the other two. Helicocytic stomata have guard cells surrounded by four or more subsidiary cells arranged in a helix (Fryns-Claessens & Van Cotthem, 1973).

Extrafloral Nectaries. These are nectaries (distinct from glandular trichomes) that appear other than on the flower (Moore, 1973a). In the plants studied here they occur on the abaxial surface of the leaf. These extrafloral nectaries are composed of a central area where the epidermal cells form a pigmented swelling in the leaf surface and a surrounding area which is encircled with short glandular trichomes.

Epidermal Cells. Epidermal cell surfaces are rather smooth or contain surface ornamentations in the form of echinate papillae or striations (Dilcher, 1974).

GENUS *Codonanthe* (Martius) Hanstein

Several leaf epidermal features were consistent in all species of *Codonanthe*. Epidermal cells were isodiametric and randomly-arranged. Stomata occurred abaxially and were randomly distributed. Surface ornamentations were not evident on subsidiary or guard cells and all cells were topographically at the same level.

SUBGENUS *Codonanthe*

Nine known species of this subgenus were examined.

SECTION *Codonanthe*. Five species were studied (Figures III-1A to III-1F): *C. carnosa* (Gardner) Hanstein, *C. devosiana* Lem., *C. digna* Wiehler, *C. gracilis* (Martius) Hanstein, and *C. paula* Wiehler.

Multicellular-uniseriate nonglandular trichomes, occurring on both leaf surfaces (except abaxially only in *C. gracilis*), had basal epidermal cells radially-arranged (except randomly-arranged in *C. gracilis*). Multicellular glandular trichomes, present on both leaf surfaces, had a 4-celled head, a short (unicellular) body and randomly-arranged basal epidermal cells (except basal cell sunken in *C. gracilis*). Anisocytic stomata were observed on the abaxial leaf surface. Extrafloral nectaries were absent. No surface ornamentations were evident, except in *C. gracilis* which had epidermal cells with echinate papillae. Guard cells had a mean length of 23.2um, mean width of 19.7um and area index of 458um^2.

SECTION *Spathuliformae* L. B. Smith. Four species were examined (Figures III-2A, III-2C, III-3A to III-3D): *C. calcarata* (F. A. W. Miquel) Hanstein, *C. corniculata* Wiehler, *C. crassifolia* (Focke) Morton and *C. uleana* Fritsch.

Unicellular nonglandular trichomes, present on both leaf surfaces, had randomly-arranged basal epidermal cells. Multicellular glandular trichomes, also present on both leaf surfaces, had a 2-celled head, a short (unicellular) body and randomly-arranged basal epidermal cells. Anisocytic stomata and extrafloral nectaries were present on the abaxial leaf surface. No surface ornamentations were evident. Guard cells had a mean length of 30.3um, mean width of 26.2um and area index of 796um^2.

SUBGENUS *Codonanthella* Wiehler

Five species in this subgenus were examined (Figures III-2B, III-2D to III-2F): *C. caribaea* Urban, *C. chiricana* Wiehler, *C. elegans* nomen nudum (to be described by Wiehler, 1982), *C. luteola* Wiehler and *C. macradenia* Donnell-Smith.

Unicellular nonglandular trichomes, present on both leaf surfaces (except abaxially-occurring multicellular trichomes of *C. caribaea*), had randomly-arranged basal epidermal cells. Multicellular glandular trichomes, present on both leaf surfaces, had a 2-celled head (except 4-celled in *C. caribaea*) and a short (unicellular) body. Basal epidermal cells were randomly-arranged (except basal cell sunken in *C. caribaea*). Anisocytic stomata and extrafloral nectaries were present on the abaxial leaf surface in *C. chiricana*, *C. elegans*, *C. luteola* and *C. macradenia* but not in *C. caribaea*. No surface ornamentations were evident except in *C. caribaea* which had epidermal cells with echinate papillae. Guard cells had a mean length of 33.1um, mean width of 28.2um and area index of 936um^2.

GENUS *Nematanthus* Schrader

Several leaf epidermal features were consistent in all species of *Nematanthus*. Epidermal cells were isodiametric and randomly-arranged. Stomata were abaxially occurring and randomly oriented. No surface ornamentations were evident on subsidiary and guard cells, and all cells were topographically at the same level.

Ten species placed in this genus were examined (Figures III-4A to III-6F): *N. crassifolius* (Schott) Wiehler, *N. fissus* (Vellozo) L. Skog, *N. fritschii* Hoehne, *N. gregarius* D. Denham, *N. hirtellus* (Schott) Wiehler, *N. maculatus* (Fritsch) Wiehler, *N. nervosus* (Fritsch) H. E. Moore, *N. perianthomegus* (Vellozo) H. E. Moore, *N. strigillosus* (Martius) H. E. Moore and *N. wettsteinii* (Fritsch) H. E. Moore.

Multicellular-uniseriate nonglandular trichomes with radially-arranged basal epidermal cells occurred in all species. Multicellular glandular trichomes with a 4-celled head and only one trichome per basal epidermal cell, a short (unicellular) or long (multicellular) body, and anisocytic stomata were characteristic of *N. crassifolius*, *N. fissus*, *N. fritschii*, *N. hirtellus*, *N. maculatus* and *N. perianthomegus*. Multicellular glandular trichomes with a 4-or-more-celled head and/or more than one trichome per basal epidermal cell, a short (unicellular) body, and helicocytic and anisocytic stomata were characteristic of *N. gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii*. The occurrence of nonglandular trichomes varied among *Nematanthus* species while glandular trichomes

Table III-1. Leaf epidermal characters of *Codonanthe* and *Nematanthus*.

	NONGLANDULAR TRICHOMES		
	Occurrence	Number of Cells	Basal Epidermal Cell Arrangement
TAXON	AB=abaxial AD=adaxial	1=unicellular #=multicellular -uniseriate	
GENUS *Codonanthe*			
SUBGENUS *Codonanthe*			
SECTION *Codonanthe*			
C. carnosa	AB + AD	#	radial
C. devosiana	AB + AD	#	radial
C. digna	AB + AD	#	radial
C. gracilis	AB	#	random
C. paula	AB + AD	#	radial
SECTION *Spathuliformae*			
C. calcarata	AB + AD	1	random
C. corniculata	AB + AD	1	random
C. crassifolia	AB + AD	1	random
C. uleana	AB + AD	1	random
SUBGENUS *Codonanthella*			
C. caribaea	AB	#	random
C. chiricana	AB + AD	1	random
C. elegans	AB + AD	1	random
C. luteola	AB + AD	1	random
C. macradenia	AB + AD	1	random
GENUS *Nematanthus*			
N. crassifolius	AB	#	radial
N. fissus	AB + AD	#	radial
N. fritschii	AB	#	radial
N. hirtellus	AB + AD	#	radial
N. maculatus	AB	#	radial
N. perianthomegus	AB + AD	#	radial
N. gregarius	absent	---	---
N. nervosus	AB + AD	#	radial
N. strigillosus	AB + AD	#	radial
N. wettsteinii	AB	#	radial

Table III-1 - continued.

TAXON	GLANDULAR TRICHOMES[1]		
	Glandular Head	Body S=short unicellular L=long multicellular	Basal Epidermal Cell Arrangement[3]
GENUS *Codonanthe*			
SUBGENUS *Codonanthe*			
SECTION *Codonanthe*			
C. carnosa	4-celled	S	unmodified
C. devosiana	4-celled	S	unmodified
C. digna	4-celled	S	unmodified
C. gracilis	4-celled	S	modified
C. paula	4-celled	S	unmodified
SECTION *Spathuliformae*			
C. calcarata	2-celled	S	unmodified
C. corniculata	2-celled	S	unmodified
C. crassifolia	2-celled	S	unmodified
C. uleana	2-celled	S	unmodified
SUBGENUS *Codonanthella*			
C. caribaea	4-celled	S	modified
C. chiricana	2-celled	S	unmodified
C. elegans	2-celled	S	unmodified
C. luteola	2-celled	S	unmodified
C. macradenia	2-celled	S	unmodified
GENUS *Nematanthus*			
N. crassifolius	4-celled	S or L	modified
N. fissus	4-celled	S or L	modified
N. fritschii	4-celled	S or L	modified
N. hirtellus	4-celled	S or L	modified
N. maculatus	4-celled	S or L	modified
N. perianthomegus	4-celled	S or L	modified
N. gregarius	>4-celled[2]	S	modified
N. nervosus	>4-celled	S	modified
N. strigillosus	>4-celled	S	modified
N. wettsteinii	>4-celled	S	modified

---

[1] Occurs on both surfaces of the leaves in all species.

[2] More than 4 cells per head and/or more than 1 trichome per basal epidermal cell.

[3] Unmodified=randomly-arranged; modified=trichomes with a unicellular body have a sunken epidermal cell while trichomes with a multicellular stalked body have radially-arranged epidermal cells.

Table III-1 - continued.

TAXON	STOMATA TYPE AN=anisocytic HEL=helicocytic	EXTRAFLORAL NECTARY	EPIDERMAL CELL ORNAMENTATION
GENUS *Codonanthe*			
SUBGENUS *Codonanthe*			
SECTION *Codonanthe*			
C. carnosa	AN	absent	none
C. devosiana	AN	absent	none
C. digna	AN	absent	none
C. gracilis	AN	absent	echinate papillae
C. paula	AN	absent	none
SECTION *Spathuliformae*			
C. calcarata	AN	abaxial	none
C. corniculata	AN	abaxial	none
C. crassifolia	AN	abaxial	none
C. uleana	AN	abaxial	none
SUBGENUS *Codonanthella*			
C. caribaea	AN	absent	echinate papillae
C. chiricana	AN	abaxial	none
C. elegans	AN	abaxial	none
C. luteola	AN	abaxial	none
C. macradenia	AN	abaxial	none
GENUS *Nematanthus*			
N. crassifolius	AN	absent	none
N. fissus	AN	absent	striations
N. fritschii	AN	absent	none
N. hirtellus	AN	absent	none
N. maculatus	AN	absent	none
N. perianthomegus	AN	absent	none
N. gregarius	AN + HEL	absent	none
N. nervosus	AN + HEL	absent	none
N. strigillosus	AN + HEL	absent	none
N. wettsteinii	AN + HEL	absent	striations

were situated abaxially only. Glandular trichomes had modified basal epidermal cells, i.e., trichomes with a unicellular body had a sunken basal epidermal cell while trichomes with a multicellular body had radially-arranged basal epidermal cells. Extrafloral nectaries and surface ornamentations were absent, except for striations on epidermal cells in N. fissus and N. wettsteinii. Guard cells had a mean length of 29.5um, mean width of 22.5um and area index of 666um^2.

Discussion

Although features of the adaxial and abaxial surfaces of the leaves are consistent within sections of genus Codonanthe, differences are noted among sections in subgenus Codonanthe. Species of subgenus Codonanthe section Spathuliformae share more epidermal characters with species in subgenus Codonanthella than with those species in subgenus Codonanthe section Codonanthe. Multicellular-uniseriate nonglandular trichomes (Figures III-1A & III-1B) with radially-arranged basal epidermal cells (Figure III-1C), glandular trichomes with 4-celled heads (Figure III-1D), and the absence of extrafloral necteries are consistent characters in species of section Codonanthe. Species in section Spathuliformae and subgenus Codonanthella share certain epidermal characters which include unicellular glandular trichomes (Figures III-2A & III-2B) with randomly-arranged basal epidermal cells, multicellular glandular trichomes with 2-celled heads (Figures III-2C & III-2D), and the presence of extrafloral nectaries (except in C. caribaea; Figures III-3A & III-3D).

Codonanthe gracilis and C. caribaea (Figure III-2F) have been placed in different subgenera (Wiehler, 1982), but are identical in all leaf epidermal characters. For example, both species possess multicellular-uniseriate nonglandular trichomes, multicellular glandular trichomes with a 2-celled head and a short (unicellular) body, anisocytic stomata and epidermal cells with echinate papillae. *Codonanthe caribaea* also shares some epidermal characters with the section *Codonanthe*.

Kleinfeldt (1978) and Madison (1979) described the mutualistic association between *Codonanthe crassifolia*, *C. calcarata* and *C. uleana* and tropical arboreal ants. Ants are the agents of seed dispersal, carrying *Codonanthe* seeds to their carton nests. The seeds germinate and penetrate the carton with fibrous roots. The roots function as a framework, providing the ant nests with structural support. *Codonanthe* plants furnish food to the ants in the form of floral and extrafloral nectar, fruit pulp and seed arils. Kleinfeldt (1978) observed that the major food source for the ants is the nectar of *Codonanthe*. Extrafloral nectaries are located on the abaxial leaf surface and occur in species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella*, but are absent in species of subgenus *Codonanthe* section *Codonanthe*. The presence of foliar extrafloral nectaries in *Codonanthe* species appears to be associated with the occurrence of an ant-plant mutualism.

Species of *Nematanthus* exhibit similar leaf epidermal features, but differ with respect to the type of glandular trichomes and stomata. In *N. gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii*, glandular trichomes have a head of more than 4 cells (Figures III-6D to III-6F) and/or more than one trichome per basal epidermal cell (Figure III-4D). The capacity for secretion appears to be greater in these four species, when compared to the six species of Nematanthus, perhaps due to the greater number of cells in the head of the glandular trichomes. Although N. gregarius has only a 4-celled glandular head, two or more glandular trichomes occur in a single locale and this arrangement may increase the potential of secretion by compensating for the 4-celled condition with more secreting heads.

The anisocytic type of stomata (Figure III-5C) is present in all species of Nematanthus, whereas the anisocytic and helicocytic stomatal types (Figure III-5D) occur in N. gregarius, N. nervosus, N. strigillosus and N. wettsteinii. The occurrence of two stomatal types in one species is unusual, however, the anisocytic and helicocytic stomatal types are derived from the same developmental sequence (Payne, 1970 and personal observation), so their occurrence together might not be unexpected. The stomatal initial forms only three subsidiary cells in the anisocytic stomatal type but continues to divide forming four or more subsidiary cells in a helix in the helicocytic type of stomata. Since guard cells and subsidiary cells originate from the same stomatal initial, the developmental sequence is referred to as mesogenous (Fryns-Claessens & Van Cotthem, 1973) or eumesogenous (Stevens & Martin, 1978). Stomatal types in Nematanthus, therefore, are classified ontogenetically as aniso-mesogenous or aniso-eumesogenous, and helico-mesogenous or helico-eumesogenous.

Guard cell area indices are calculated to provide a value representative of guard cell size, allowing a comparison among taxa. Subgenus Codonanthe section Spathuliformae (area index 796um^2) have guard cells that are more similar in size with subgenus Codonanthella (area index 936um^2) than with subgenus Codonanthe section Codonanthe (area index 458um^2). Wiehler (1975) reported that species of subgenus *Codonanthe* section *Codonanthe* are diploids (*n*=8) while species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella* are tetraploids (*n*=16), except *C*. *caribaea* (diploid) and *C*. *luteola* (diploid and tetraploid). The larger size of the guard cells of the tetraploid species is apparently related to the gigas effect of polyploidy (Stebbins, 1971).

Species of *Nematanthus* are diploids (*n*=8; Skog, 1981) and have a guard cell area index of 666um^2. This area index is intermediate between area indices of diploid and tetraploid species of *Codonanthe*. *Nematanthus* species appear to be distinct from species of *Codonanthe* with respect to guard cell dimensions and ploidy level.

Nematanthus species share many epidermal characters with species in subgenus *Codonanthe* section *Codonanthe* (including multicellular-uniseriate nonglandular trichomes) and only a few characters with species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella*. Morphological similarities in the epidermal surfaces of the leaves in subgenus *Codonanthe* section *Codonanthe* and *Nematanthus* are either an ancestral feature shared by the two genera, or are the result of parallel evolution related to a similarity of ecogeographical conditions.

Figure III-1. Leaf epidermal features of species of _Codonanthe_ subgenus _Codonanthe_ section _Codonanthe_.

A. _C_. _paula_, multicellular nonglandular and glandular trichomes, X100.

B. _C_. _digna_, multicellular nonglandular and glandular trichomes, X250.

C. _C_. _carnosa_, radially-arranged basal epidermal cells of nonglandular trichomes, X1000.

D. _C_. _gracilis_, 4-celled head of glandular trichome, X1650.

E. _C_. _gracilis_, echinate papillae and stoma, X1000.

F. _C_. _devosiana_, anisocytic stoma, X1500.

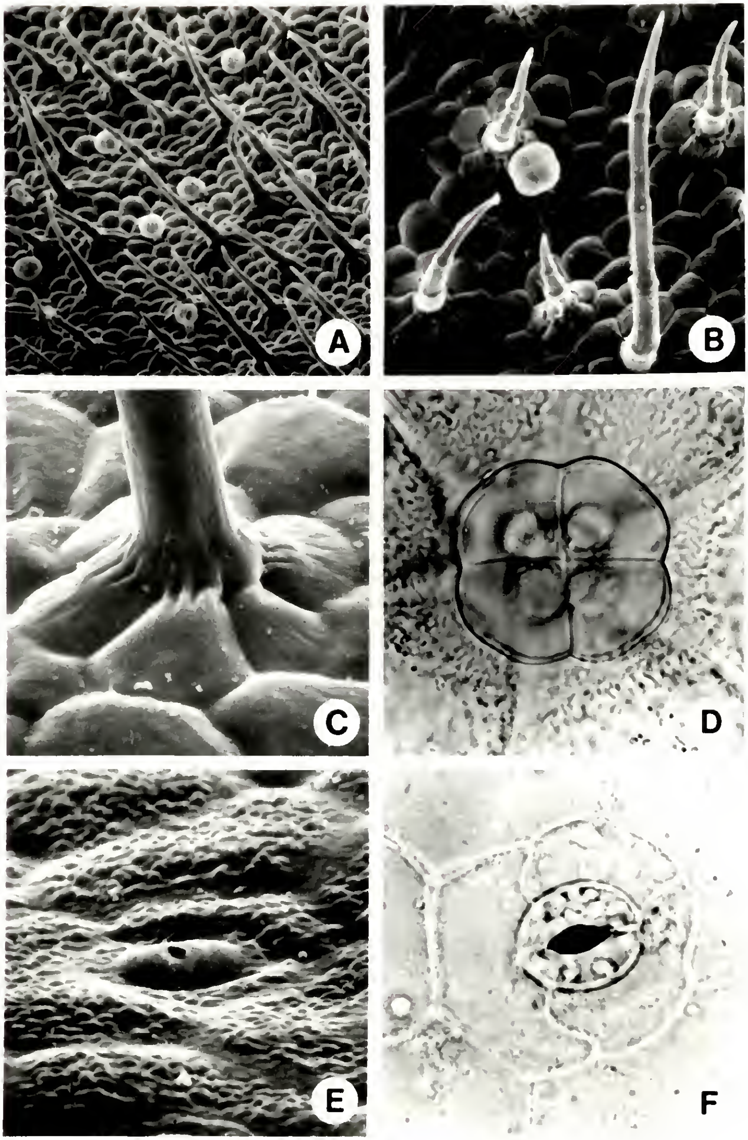
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Figure III-2. Leaf epidermal features of species of _Codonanthe_ subgenus _Codonanthe_ section _Spathuliformae_ and subgenus _Codonanthella_.

A. _C_. _crassifolia_, unicellular nonglandular trichome, X1000.

B. _C_. _elegans_, unicellular nonglandular trichome, X1200.

C. _C_. _calcarata_, 2-celled head of glandular trichome, X2000.

D. _C_. _luteola_, 2-celled head of glandular trichome, X1120.

E. _C_. _macradenia_, anisocytic stoma, X1260.

F. _C_. _caribaea_, multicellular nonglandular trichome and sunken epidermal cell of glandular trichome, X350.

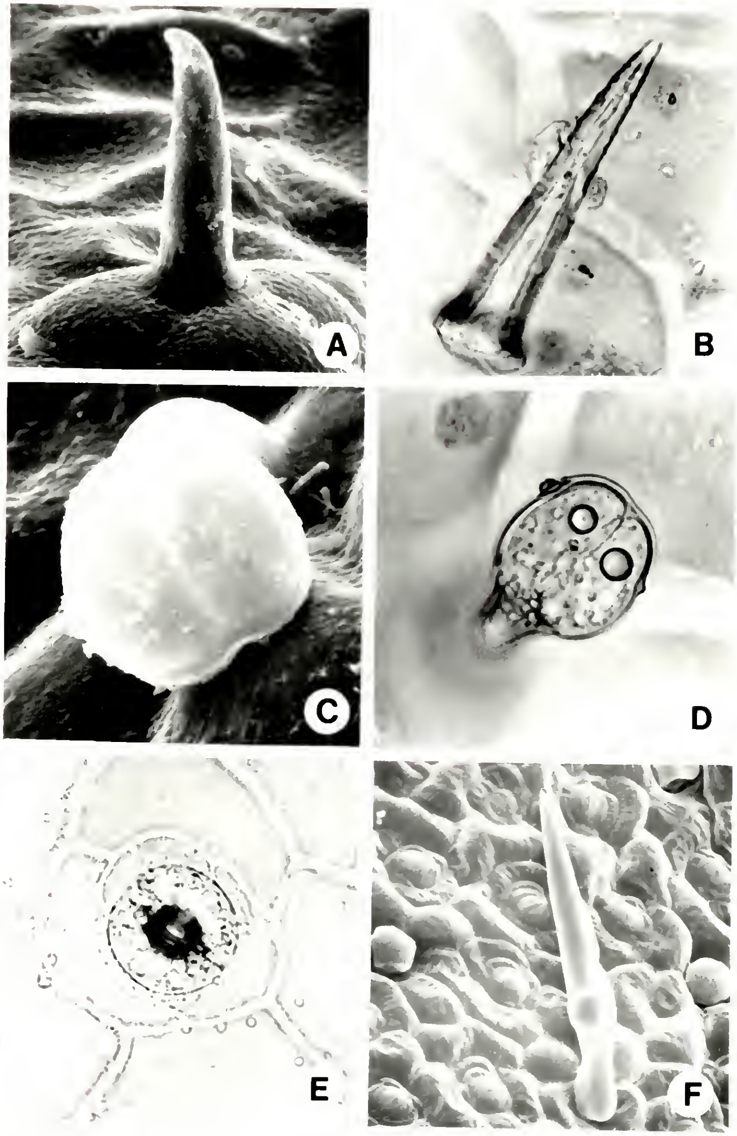
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Figure III-3. Leaf epidermal features of species of *Codonanthe* subgenus *Codonanthe* section *Spathuliformae*.

A. *C. crassifolia*, extrafloral nectary, X100.

B. *C. uleana*, extrafloral nectary, X150.

C. *C. uleana*, glandular trichomes that encircle extrafloral nectary, X1000.

D. *C. corniculata*, extrafloral nectary, X110.

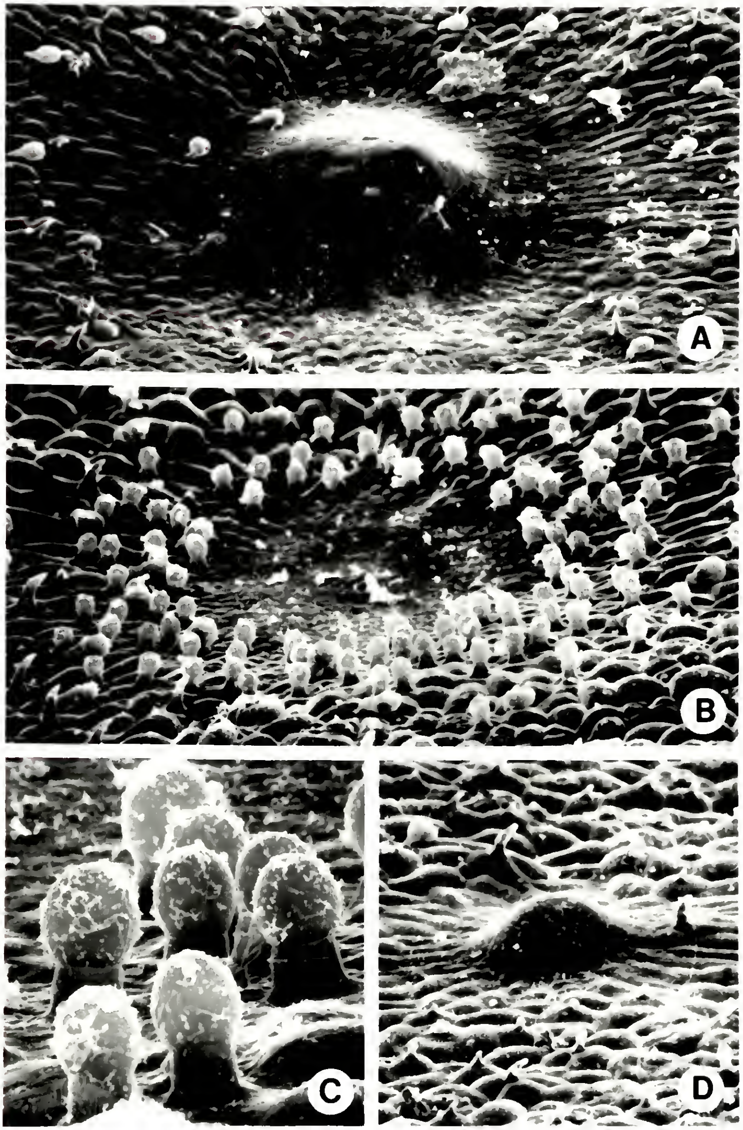
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Figure III-4. Leaf epidermal features of species of _Nematanthus_.

A. _N_. _fissus_, multicellular nonglandular trichome, X110.

B. _N_. _strigillosus_, multicellular nonglandular trichome, X500.

C. _N_. _perianthomegus_, glandular trichome with short (unicellular) and long (multicellular) body cells, X500.

D. _N_. _strigillosus_, 2 short glandular trichomes per single basal epidermal cell, X400.

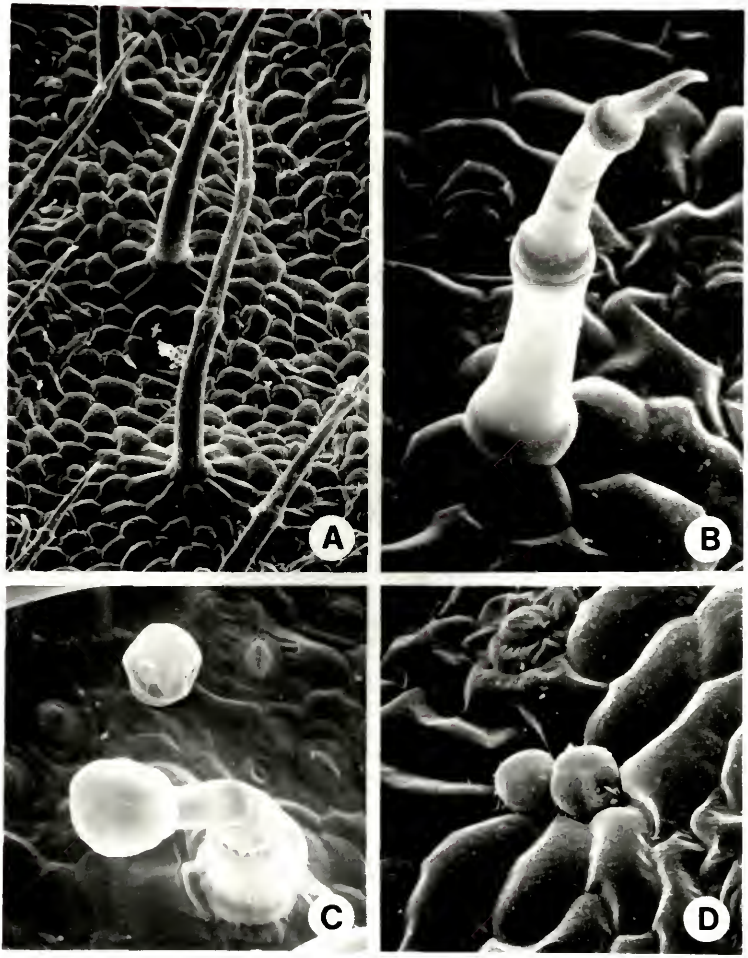
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Figure III-5. Leaf epidermal features of species of *Nematanthus*.

A. *N. hirtellus*, glandular trichome with bicellular body, X1500.

B. *N. wettsteinii*, glandular trichome, stomata and striated epidermis, X500.

C. *N. crassifolius*, anisocytic stoma, X1330.

D. *N. gregarius*, helicocytic stoma, X1230.

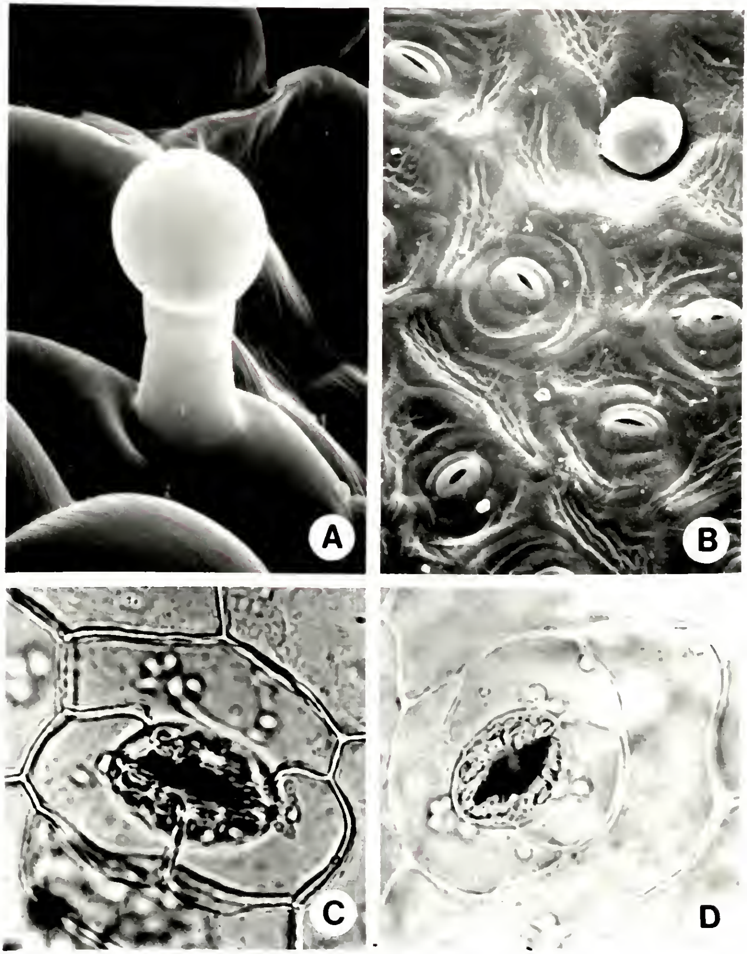
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Figure III-6. Leaf epidermal features of species of *Nematanthus*.

A. *N. fissus*, 4-celled head of glandular trichome, X500.

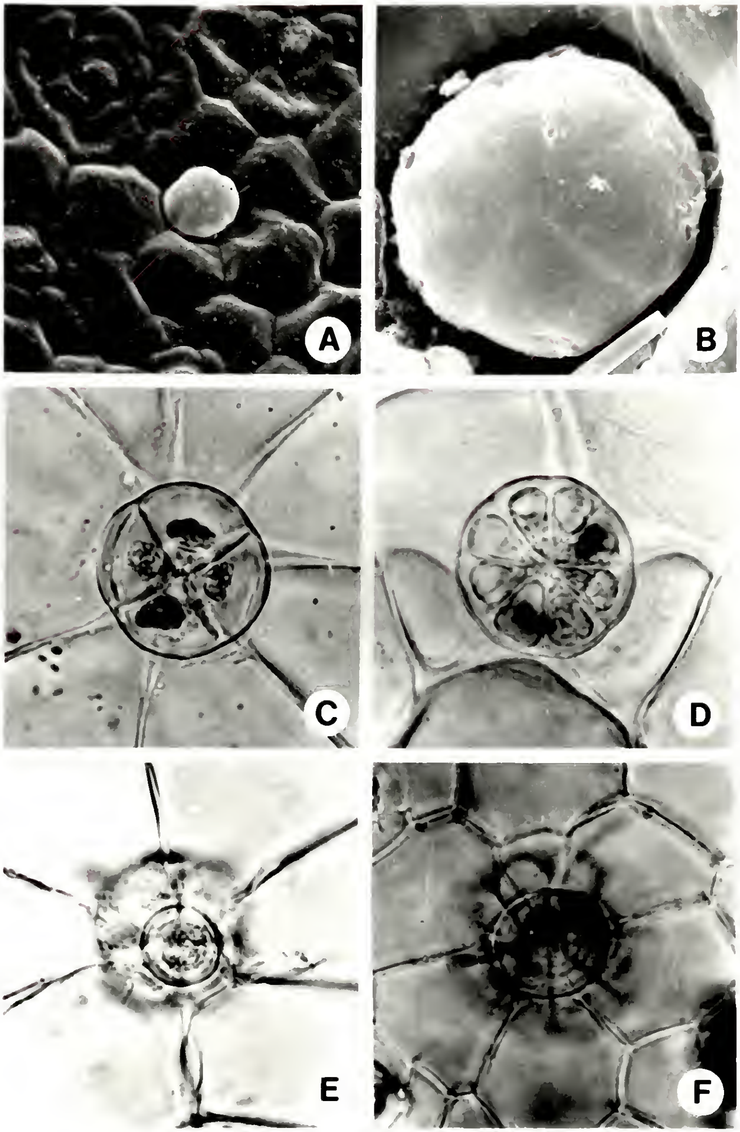
B. *N. nervosus*, 6-celled head of glandular trichome, X2000.

C. *N. hirtellus*, 4-celled head of glandular trichome, X500.

D. *N. wettsteinii*, 8-celled head of glandular trichome, X1400.

E. *N. maculatus*, unicellular basal epidermal cell of glandular trichome, X1450.

F. *N. wettsteinii*, unicellular basal epidermal cell of glandular trichome, X1300.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CHAPTER IV
COMPARATIVE ANATOMY OF THE STEM AND LEAF

Introduction

Anatomical studies of Codonanthe and Nematanthus are restricted to plants considered in Wiehler's (1970, 1979b, 1982) taxonomic treatment of the Neotropical Gesneriaceae, where node, petiole and leaf structure were described for some species. Related anatomical studies are presented by Skog (1976) for the genus Gesneria, Jong & Burtt (1975) for the genus Streptocarpus, Herat & Theobald (1979) for various gesneriad species of Sri Lanka, Rosser & Burtt (1969) for the tribe Trichosporeae, and Solereder (1908) and Metcalfe & Chalk (1950) for various species of Gesneriaceae. Nodal and wood anatomy were discussed by Howard (1970) for the genus Alloplectus, and Bierhorst (1964), Chalk (1937), Sinnott (1914) and Sinnott & Bailey (1914) for Gesneriaceae. Bokhari & Burtt (1970) and Burtt & Bokhari (1973) described foliar sclereids in gesneriads of the Old World. This preliminary study of stem and leaf anatomy of Codonanthe and Nematanthus species was initiated to disclose more taxonomically useful characters.

Materials and Methods

Live specimens of all known cultivated species of Codonanthe and Nematanthus were examined. Plant materials were cultivated in a growth room at the Department of Ornamental Horticulture, University of Florida. The growth room provided uniform conditions of 22-25°C day temperature, 17-20° C night temperature, 4000-6000 Lux fluorescent lighting and a fourteen hour daylength. Voucher specimens were deposited at the University of Florida herbarium (FLAS).

Mature portions of nodes and internodes, petioles and blades were collected. Freehand serial sections of fresh material were stained with and mounted in toluidine blue O (Sakai, 1973; Dehgan, 1982). Microtome serial sections of paraffin-embedded material were stained with toluidine blue O and safranin-fast green (Berlyn & Miksche, 1976) and mounted in Permount (Fisher Scientific Company). Specimens were examined with a Wild M-20EB Light Microscope.

The leaf clearing method of Shobe & Lersten (1967) was utilized for the study of leaf architecture. All steps were followed except chloral hydrate was omitted and only safranin O stain was used. Terminology employed for describing the leaf venation patterns is based upon Hickey's (1973) classification of the architecture of dicotyledonous leaves. Specimens were examined with a Wild M8 Zoom Stereomicroscope.

Observations

Stem Anatomy

The epidermis consisted of a single layer of tabular cells (rarely 2-3 cells thick). The cuticle was thin, and glandular and nonglandular trichomes were randomly situated around the stem. The cortex and pith were composed of chlorenchyma of basically isodiametric cells among which were many intercellular spaces or cells were irregularly-shaped with few intercellular spaces (i.e., cells tightly appressed to each other). Druses were often present in cortex cells, whereas prismatic cells were frequently observed in pith cells. Sclereids with thick secondary walls and numerous pits were seen in the cortex as single cells or small groups of cells (Figures IV-1A, IV-4A & IV-4B). Vessel elements of the xylem had a helical structure. A thin suberized layer or periderm completely encircled the stem and was located between the epidermis and cortex.

Node and Petiole Vasculature

Nodes were unilacunar or trilacunar in Codonanthe and Nematanthus. The unilacunar condition (Figures IV-1A & IV-1B) was marked by one leaf trace diverging from a single leaf gap (1:1) in the stele. Since Codonanthe and Nematanthus species possess opposite leaves, each node maintained two opposing leaf gaps with one leaf trace per leaf gap. The leaf trace continued to separate from the stem proper and entered the petiole as an arc-shaped, collateral vascular bundle (Figure IV-3A). The curvature of this vascular bundle was aligned with the abaxial surface of the petiole. At the abscission zone, two (e.g., N. wettsteinii) to five (e.g., C. digna) small vascular bundles branched adaxially from the large arc-shaped vascular bundle.

The trilacunar condition (Figures IV-1C to IV-1F & Figure IV-2) was marked by three leaf traces originating from three leaf gaps (3:3) in the stele. With the opposite leaf condition in species of Codonanthe and Nematanthus, each node displayed two median and two lateral leaf gaps with one leaf trace per gap. The median leaf trace diverged from the stem proper and entered the petiole as an arc-shaped, collateral vascular bundle. The curvature of this large vascular bundle was aligned with the abaxial surface of the petiole. The lateral leaf traces divided upon entering the stem cortex and each 'split-lateral' trace (cf., Howard, 1970) branched-off towards a leaf. Two pairs of split-lateral traces (i.e., each trace of a pair derived from a different lateral leaf gap) traveled laterally through the stem cortex and converged upon the median leaf trace. At the abscission zone region, 2-3 small vascular bundles often separated from the arc-shaped median leaf trace. Small vascular bundles originating from the split-lateral and median leaf traces were situated within the petiole cortex tissue adaxial to the large arc-shaped vascular bundle.

Species of subgenus *Codonanthe* section *Codonanthe* (except *C. gracilis* and *C. carnosa*), as well as *Nematanthus gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii*, displayed the unilacunar nodal anatomy. Species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella*, as well as *Nematanthus crassifolius*, *N. fissus*, *N. fritschii*, *N. hirtellus*, *N. maculatus* and *N. perianthomegus*, possessed the trilacunar, split-lateral nodal configuration.

The presence of prismatic crystals in the pith (Figure IV-4A) and sclereids in the cortex (Figure IV-4E) coincided with the formation of leaf gaps. Crystals and sclereids frequently occurred in areas adjacent to lacunae and leaf traces, respectively (Figure IV-1B).

Leaf Mesophyll

Species of *Codonanthe* and *Nematanthus* possessed simple, dorsiventral leaves (Figure IV-3B). Adaxial and abaxial epidermis consisted of a single layer of tabular-shaped cells with a thin cuticle. Stomata, glandular and nonglandular trichomes occurred on the epidermis and were discussed in CHAPTER III.

A hypodermis (cf., Esau, 1965) of enlarged parenchyma cells was located adjacent to the adaxial epidermis. The cells were isodiametric and tightly-appressed such that few intercellular spaces were present. Hypodermal cells were filled with water and chloroplasts were not evident. Depending upon the location on the blade and species of *Codonanthe* and *Nematanthus*, the hypodermis was 2-12 cells thick. For example, *C. elegans* and *N. hirtellus* had a 2-3 cell thick hypodermis, *C. luteola* and *N. fissus* had a 5-6 cell thick hypodermis, and *C. carnosa* and *C. paula* had a 10-12 cell thick hypodermis in the midvein area.

A uniseriate palisade mesophyll was adaxial to the hypodermis and consisted of elongated parenchyma cells oriented perpendicular to the blade surface. Numerous chloroplasts occurred along the anticlinal and abaxial periclinal walls. Spongy mesophyll was located abaxial to the palisade mesophyll and consisted of isodiametric to irregularly-shaped parenchyma cells. The cells contained few chloroplasts that were smaller than palisade mesophyll chloroplasts. Many large intercellular spaces were present. Depending upon the location on the blade and the species of *Codonanthe* and *Nematanthus*, the spongy mesophyll was 2-10 cells thick. For example, *N. strigillosus* had a 2-5 cell spongy mesophyll while *C. digna* had a 7-10 cell spongy mesophyll.

The midrib and secondary veins often protruded from the lamina and consisted of collateral vascular bundles encircled by small, tightly-appressed parenchyma cells. Collenchyma often occurred abaxial to the vascular bundles, adjacent to the lower epidermis (e.g., *C. gracilis*). The vascular bundles were rounded (e.g., *C. digna*) to arc-shaped (e.g., *N. crassifolius*). *Codonanthe caribaea* displayed a large arc-shaped bundle and a small dorsally-located bundle in the midrib (Figure IV-3C).

Leaf Vascular Skeleton

Species of Codonanthe and Nematanthus possessed leaves with pinnate venation (Figure IV-3D). The course of the single primary vein (i.e., midvein) was straight and its size diminished towards the leaf apex as secondary veins branched-off. Secondary veins diverged from the midvein in an opposite, subopposite and/or alternate arrangement and at moderate angles of 45° to 65°. The course of the secondary veins was a series of prominent arches extended towards the leaf margins, upturned and gradually diminished apically inside the margin to tertiary veins. This eucamptodromous venation type (cf., Hickey, 1973) had the secondary veins join superadjacent secondary veins via tertiary veins at acute angles.

Tertiary veins had a random reticulate pattern with variable angles of anastomoses. Tertiary veins often diverged from the petiolar vascular bundle while still within the petiole (Figure IV-3D) and traveled along the leaf margin upon entering the leaf blade (e.g., C. luteola). It was not possible to resolve higher order venation. Areoles were often imperfectly-developed, randomly-arranged and irregularly-shaped. Terminal veinlets were either absent or, if present, were simple and linear (cf., Hickey, 1973). One median, tertiary vein and 1-2 lateral, smaller veins fused together before supplying marginal teeth (Figure IV-3F).

Sclereids often occurred along the petiolar vascular bundle (Figure IV-4F) and midvein (e.g., N. fritschii and N. gregarius), sometimes also traveling along secondary veins (e.g., N. perianthomegus, Figure IV-4D). Styloids were grouped into small clusters parallel to the higher order veins of all *Nematanthus* species observed, as well as in *Codonanthe caribaea* (Figure IV-4C), *C. gracilis* and *C. paula*.

Discussion

Anatomical features of the stem, petiole, leaf mesophyll and leaf vascular skeleton were uniform among species of *Codonanthe* and *Nematanthus*. Only nodal anatomy proved to be taxonomically useful in distinguishing subgenera and sections of *Codonanthe* and *Nematanthus*.

In the genus *Codonanthe*, species of subgenus *Codonanthe* section *Codonanthe* (except *C. carnosa* and *C. gracilis*) possessed the unilacunar nodal configuration (Figures IV-1A & IV-1B), whereas species in subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella* displayed the trilacunar, split-lateral nodal anatomy (Figures IV-1C to IV-1F & Figure IV-2). Although all species of *Codonanthe* have 2-4 mm thick stems (cf., Table II-1), *C. devosiana*, *C. digna* and *C. paula* of subgenus *Codonanthe* section *Codonanthe* maintained the smallest stem size of ca. 2 mm thick and shorter leaf blade lengths of 20-40 mm.

In the genus *Nematanthus*, *N. gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii* had the unilacunar nodal anatomy, whereas *N. crassifolius*, *N. fissus*, *N. fritschii*, *N. hirtellus*, *N. maculatus* and *N. perianthomegus* possessed the trilacunar, split-lateral nodal configuration. The former four *Nematanthus* species consistently displayed 2-4 mm thick stems, 4-10 mm long petioles and 20-40 mm long leaf blades while the latter six species had 5-9 mm thick stems, 10-50 mm long petioles and 40-120 mm long leaf blades (cf., Table II-1).

The occurrence of the unilacunar nodal anatomy is apparently correlated with the smaller stem and leaf size in *Codonanthe* and

Nematanthus species. In reference to epiphytes that are very thin-stemmed, Wiehler (1979b: p. 115) states that "there is just not enough space left in the small node for either lateral lacunae in the stele or lateral traces in the cortex." The single leaf trace appears to be sufficient in fulfilling the vascular requirements of the small leaves. Thus, the structure and size of the stem may provide an explanation of the occurrence of the unilacunar nodal anatomy.

Howard (1970) reported nodal vascular pattern changes when wild plants of Alloplectus ambiguus were grown under cultivation. Originally-collected, split-lateral trace plants were observed to possess two separate trilacunar nodes when cultivated in a greenhouse. Species of Codonanthe and Nematanthus sampled in this study were only cultivated in a growth room and it is not known how these plants would react if they were placed under greenhouse or natural conditions.

The presence of water-filled hypodermal cells (Figure IV-3B) within the leaf blade of Codonanthe and Nematanthus species relates well with their epiphytic habit. Occurring adaxially to the palisade mesophyll, the hypodermis is derived from the protoderm (Esau, 1965), i.e., the primary meristem which develops into the epidermis, and evidently functions in the storage of water. Epiphytes usually do not have access to the readily-available water source of the forest floor and must possess some means of water storage and conservation. Yellowing, old leaves were observed as enlarged and swollen with water in such taxa as C. devosiana (Wiehler, 1979b) and C. luteola (Yuen, personal observation). In a sense, whole leaves were serving as water-storage organs.

Figure IV-1. Nodal anatomy of species of *Codonanthe*.

A. *C. digna*, transverse section of stem at internode, X350.

B. *C. digna*, transverse section of unilacunar node with leaf trace extending into cortex. Note prismatic crystals associated with pith in lacunae and cortex adjacent to leaf trace, X350.

C. *C. corniculata*, transverse section of trilacunar node with lateral leaf trace occurring in cortex, X350.

D. *C. corniculata*, transverse section of trilacunar node with lateral leaf trace dividing in half, X350.

E. *C. corniculata*, transverse section of trilacunar node with split-lateral leaf trace diverging towards leaf, X350.

F. *C. carnosa*, tangential section of node with lateral leaf trace splitting towards leaf base, X350.

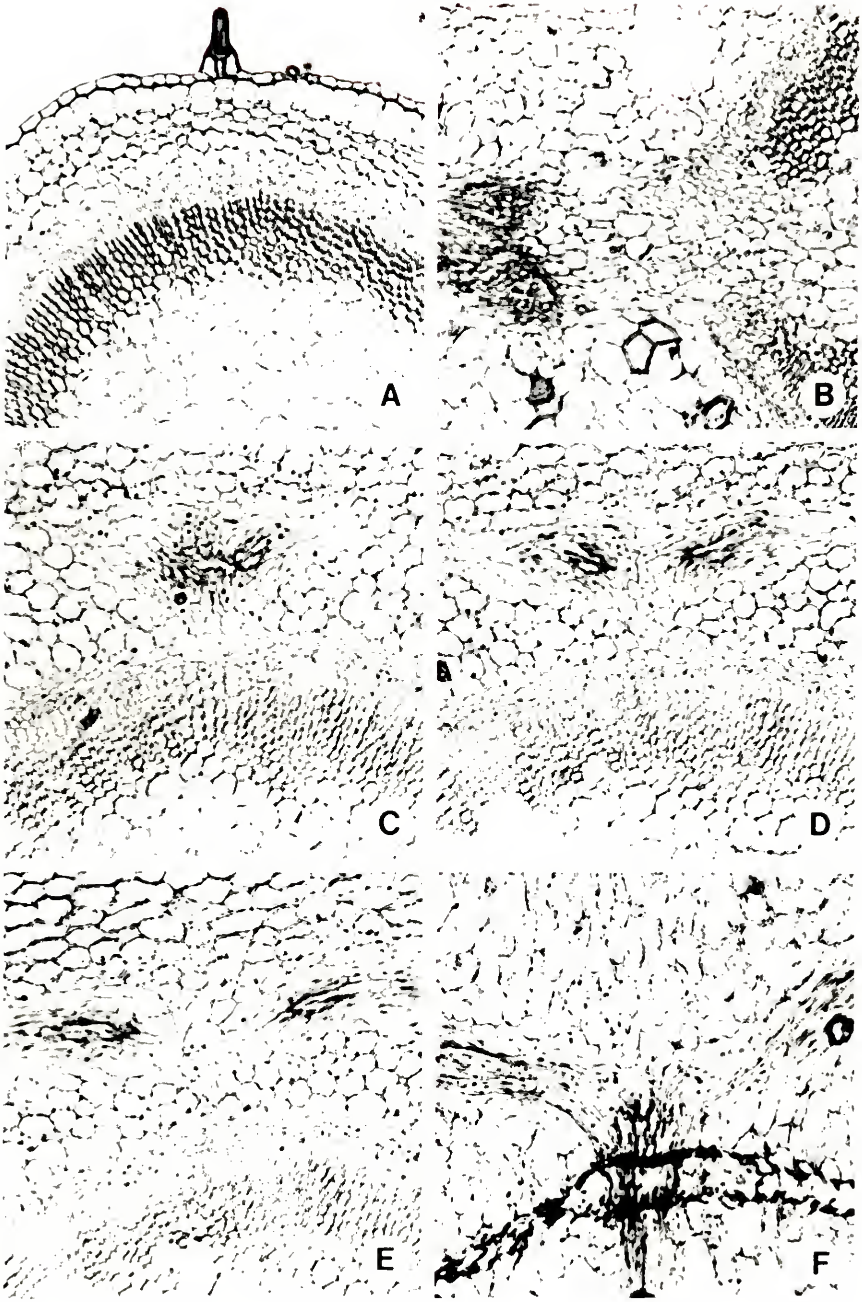
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Figure IV-2. Transverse sections of the node of *Codonanthe corniculata*, X80.

A. Internode prior to divergence of leaf traces.

B. Median and lateral leaf traces diverging from the vascular cylinder.

C. Lateral leaf trace beginning to split in half and median leaf trace continuing to separate from vascular cylinder.

D. Split-lateral leaf traces traveling through cortex towards the median leaf traces.

E. Split-lateral leaf traces converging upon median leaf trace.

F. Median leaf trace enters petiole with two split-lateral leaf traces approaching the leaf abscission zone.

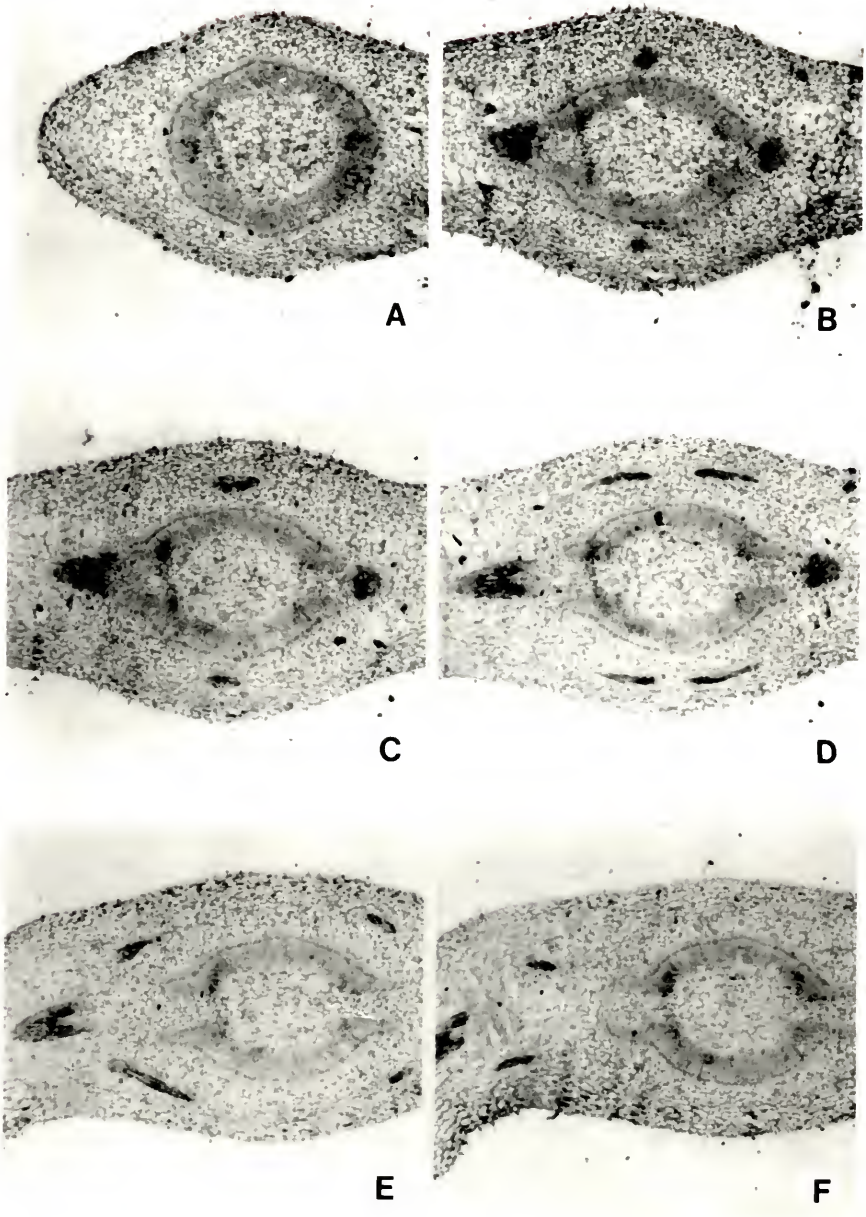
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Figure IV-3. Leaf anatomy of species of *Codonanthe* and *Nematanthus*.

A. *N. wettsteinii*, transverse section of petiole with arc-shaped vascular bundle, X350.

B. *C. digna*, transverse section of leaf at the margin. Note multiple layer of hypodermal cells, X350.

C. *C. caribaea*, transverse section of leaf midrib with an unusual double arc-shaped vascular bundle, X350.

D. *C. carnosa*, clearing of leaf with xylary elements of secondary veins diverging from midvein, X180.

E. *N. strigillosus*, clearing of leaf displaying leaf apex innervated by midvein and smaller lateral veins, X180.

F. *C. carnosa*, clearing of leaf with two lateral higher order veins joining a median tertiary vein at the leaf margin, X180.

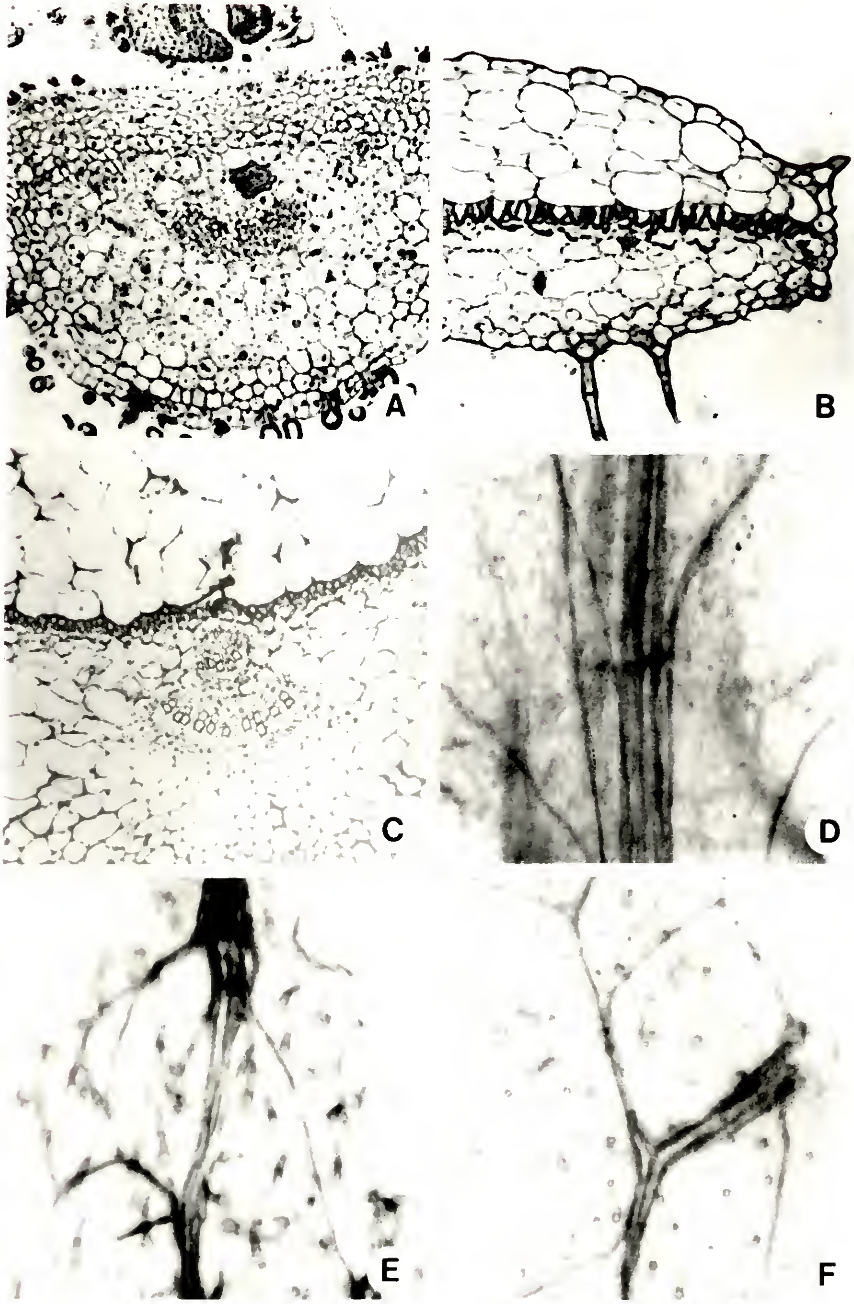
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Figure IV-4. Crystals and sclereids in species of _Codonanthe_ and _Nematanthus_.

A. _N. wettsteinii_, transverse section of stem with prismatic crystals in pith cells, X1400.

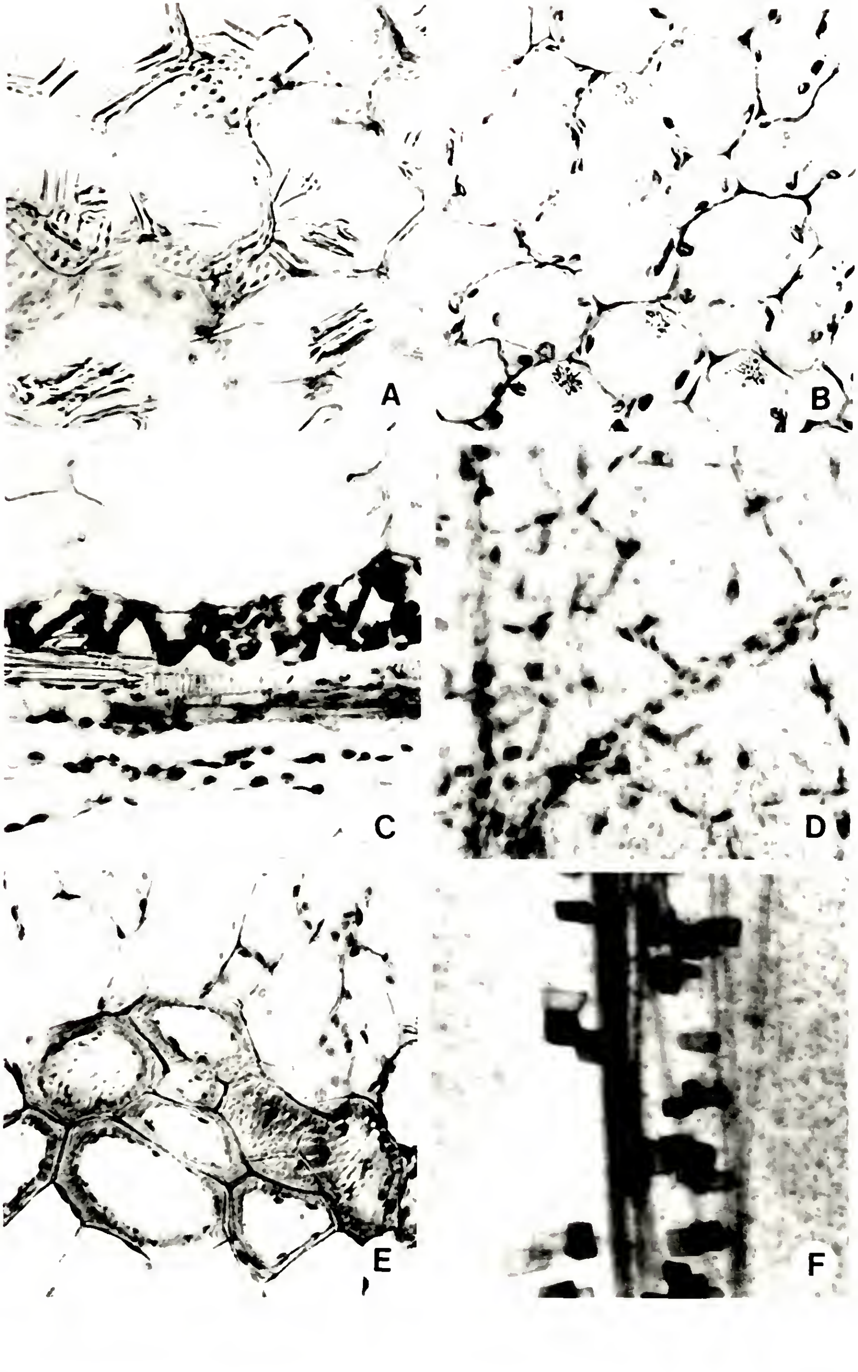
B. _C. corniculata_, transverse section of stem with druses in cortex cells, X1400.

C. _C. caribaea_, transverse section of leaf with styloid crystals associated with vascular bundles, X1400.

D. _N. perianthomegus_, clearing of leaf with styloid crystals associated with leaf venation, X180.

E. _C. digna_, transverse section of stem with sclereids clustered in cortex, X1400.

F. _C. elegans_, clearing of leaf with sclereids associated with petiole vasculature, X180.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CHAPTER V
POLLEN MORPHOLOGY

Introduction

The significance of pollen morphology as a taxonomic tool has been recognized since the comprehensive palynological work of Wodehouse (1935, 1936). Light microscopy (LM) methods were used by Erdtman (1952) and Woods (1964) to examine and characterize the pollen of Gesneriaceae, and to distinguish between the pollen of Cyrtandroideae and Gesnerioideae, respectively. Melhem & Mouro (1973) also used LM to describe the pollen morphology of Brazilian species of Gesneria, Hypocyrta and Nematanthus.

Scanning electron microscopy (SEM) methods were utilized by Skog (1976) to observe the pollen of 27 species from the tribe Gesnerieae. Williams (1978) studied the pollen structure of the Neotropical Gesneriaceae in an attempt to support or refute the new classification system of Wiehler (1979b). Preliminary results of pollen surface features of 30 Neotropical gesneriads of Gesnerioideae were reported.

This preliminary study of the pollen morphology of Codonanthe and Nematanthus species was undertaken to uncover more characters of taxonomic utility. Only pollen surface features are presented as determined through LM and SEM. Pollen structure as determined through LM and transmission electron microscopy (TEM) will be addressed at a later time.

Materials and Methods

Pollen of Codonanthe and Nematanthus species was collected from live specimens cultivated in a growth room at the Department of Ornamental Horticulture, University of Florida. The growth room provided uniform conditions of 22-25°C day temperature, 17-20°C night temperature, 4000-6000 Lux fluorescent lighting and a fourteen hour daylength. Voucher specimens were deposited at the University of Florida herbarium (FLAS).

In the SEM preparation (after Hayat, 1978), nondehisced and dehiscing anthers were sampled, fixed overnight in 2% glutaraldehyde, dehydrated in a 20-100% ethanol series for 2 hours and critical point dried for 30 minutes. The dried anthers were pierced with a needle and pollen was sprinkled onto double-sticky tape that was mounted on an aluminum stub. The pollen was coated with a gold-palladium mixture, viewed with a Hitachi S-450 Scanning Electron Microscope and photographed with Polaroid Type 55 Positive/Negative film.

In the LM preparation, dehiscing anthers were sampled and pollen was mounted directly in a drop of Alexander's stain (1969). This differential stain preparation permitted the observation of pollen stainability (i.e., viability) and pollen structure. A Wild M-20EB Light Microscope equiped with an eyepiece micrometer was used to examine and measure the pollen specimens. Pollen size is presented as a mean value ± the standard error of the mean ($\bar{x} \pm S.E.\bar{x}$).

Observations

The basic descriptive terminology of pollen characters is according to Walker & Doyle (1975) and Moore & Webb (1978). SEM photomicrographs of Nowicke & Skvarla (1977, 1980) were consulted as a reference in the designation of pollen exine sculpturing types. Definitions of terms used in the text are briefly reviewed below.

Pollen aperture. Any thin or missing part of the exine which is independent of the exine pattern is called an aperture. Elongate, furrow-like apertures are known as colpi. Pollen with colpi located equidistantly on the equator and aligned with the polar axis are referred to as zonocolpate pollen. The area bordered by two colpi is the mesocolpium while the polar area of the pollen is the apocolpium.

Pollen shape. Pollen shape is globose (globe-shaped), isopolar (with two poles) and radiosymmetric (Figure V-1C). The outline of the pollen grain as seen in polar view is referred to as the amb. A polygonal pollen (angular in appearance) with the apertures situated in the angles of the amb is known as angulaperturate (Figure V-1D).

Pollen size. Small-sized pollen are 10-24 um and medium-sized pollen are 25-49 um for the longest pollen axis length.

Pollen wall stratification. The pollen wall is composed of an inner intine strata and an outer exine strata which is further subdivided into endexine and ektexine layers. Extexine consists of a foot-layer, rod-like columellae arranged perpendicular to the pollen surface, and a roof-like tectum (Figure V-1A).

Exine structure. Three basic exine structure types are tectate, semitectate and intectate (Figure V-1B). Tectate pollen may be further subdivided into tectate-imperforate pollen (without any holes in the tectum) and tectate-perforate pollen (with holes in the tectum). Semitectate pollen possess larger spaces or lumina in the tectum providing a reticulated surface appearance. Intectate pollen have no tectum but display rod-like columellae.

Exine sculpturing. Exposed surface features of the pollen wall are referred to as exine sculpturing. Some exine sculpturing types are psilate (smooth), foveolate (pitted), fossulate (grooved), verrucate (warty), rugulate (elongate sculpturing elements irregularly distributed tangentially over the pollen surface), reticulate (sculpturing elements forming an open nerwork or reticulum over the pollen surface) and spinulose (spiny).

GENUS Codonanthe (Martius) Hanstein

Pollen grains were solitary as monads, globose, isopolar and radiosymmetric with three zonate colpi (i.e., 3-zonocolpate except C. chiricana with some 4- and 5-zonocolpate pollen; Figures V-6C & V-12A). Apertures were simple without a margo (Figure V-12E). Polar views displayed a circular to slightly triangular, angulaperturate amb with convex mesocolpia and retiulate apocolpia. Equatorial views yielded circular to slightly elliptic profiles.

SUBGENUS Codonanthe

Nine known species of this subgenus were examined.

SECTION Codonanthe. Five species were studied (Figures V-2 & V-3): C. carnosa (Gardner) Hanstein, C. devosiana Lemaire, C. digna Wiehler, C. gracilis (Martius) Hanstein and C. paula Wiehler.

Pollen size was small with an 18.1 ± .75 um polar axis (P) and an 18.5 ± .35 um equatorial diameter (E). The P/E index of 0.98 designates an oblate spheroidal pollen shape (Figure V-1C). Exine structure was tectate-perforate. Exine sculpturing was fossulate for

C. carnosa, foveolate for *C. devosiana* and *C. paula*, and finely reticulate for *C. digna* and *C. gracilis*.

SECTION *Spathuliformae* L. B. Smith. Four species were studied (Figures V-4 & V-5): *C. calcarata* (F. A. W. Miquel) Hanstein, *C. corniculata* Wiehler, *C. crassifolia* (Focke) Morton and *C. uleana* Fritsch.

Pollen size was medium with a 26.7 ± .93 um polar axis (P) and a 29.6 ± .94 um equatorial diameter (E). The P/E index of 0.90 designates an oblate spheroidal pollen shape (Figure V-1C). Exine structure was tectate-perforate. Exine sculpturing was spinulose-verrucate for *C. calcarata*, spinulose-reticulate for *C. corniculata*, spinulose-irregularly microreticulate for *C. crassifolia* and rugulate for *C. uleana*.

SUBGENUS *Codonanthella* Wiehler

Five known species of this subgenus were examined (Figures V-6 & V-7): *C. caribaea* Urban, *C. chiricana* Wiehler, *C. elegans* nomen nudum (to be described by Wiehler, 1982), *C. luteola* Wiehler and *C. macradenia* Donnell-Smith.

Pollen size was medium with a 29.7 ± .60 um polar axis (P) and a 32.6 ± .94 um equatorial diameter (E). The P/E index of 0.91 designates an oblate spheroidal pollen shape (Figure V-1C). Exine structure was tectate-perforate (Figure V-12C). Exine sculpturing was reticulate-secondarily foveolate for *C. caribaea*, slightly spinulose-microreticulate for *C. chiricana* and *C. luteola*, spinulose-irregularly microreticulate for *C. elegans* and spinulose-microreticulate for *C. macradenia*.

GENUS Nematanthus Schrader

Pollen grains were solitary as monads, globose, isopolar and radiosymmetric with three zonate colpi (i.e., 3-zonocolpate except N. hirtellus with some 4-zonocolpate pollen; Figure V-12B). Apertures were simple with a margo (Figure V-12F). Polar views displayed a triangular, angulaperturate amb with straight to convex mesocolpia and nonreticulate to reticulate apocolpia. Equatorial views yielded circular to strongly elliptic profiles.

Ten species placed in this genus were examined (Figures V-8 to V-11): N. crassifolius (Schott) Wiehler, N. fissus (Vellozo) L. Skog, N. fritschii Hoehne, N. gregarius D. Denham, N. hirtellus (Schott) Wiehler, N. maculatus (Fritsch) Wiehler, N. nervosus (Fritsch) H. E. Moore, N. perianthomegus (Vellozo) H. E. Moore, N. strigillosus (Martius) H. E. Moore and N. wettsteinii (Fritsch) H. E. Moore.

Pollen size was medium with a 25.3 ± .80 um polar axis (P) and a 25.5 ± .48 um equatorial diameter (E). The P/E index of 0.99 designates an oblate spheroidal pollen shape. Exine structure was tectate-perforate to semitectate (Figure V-12D). Exine sculpturing was reticulate with foveolate reticula in the mesocolpia of all Nematanthus species. Nematanthus crassifolius, N. fritschii and N. perianthomegus possessed narrow reticula and the other seven Nematanthus species exhibited relatively wider reticula. Nematanthus gregarius, N. nervosus, N. strigillosus, N. wettsteinii and N. hirtellus possessed reticulate apocolpia, N. fritschii had sparcely foveolate apocolpia and N. crassifolius, N. fissus, N. maculatus and N. perianthomegus exhibited psilate apocolpia.

Discussion

Species of Codonanthe and Nematanthus possess pollen that are solitary as monads, isopolar, radiosymmetric, globose-oblate spheroidal and 3-zonocolpate (except C. chiricana and N. hirtellus with some 4- and 5-zonocolpate pollen; Figure V-6C, V-12A and V-12B) with an angulaperturate amb, but differ in some key aspects. Codonanthe pollen have apertures without a margo (Figure V-12E), a basically circular polar configuration, a tectate-perforate exine structure (Figure V-12C) and various degrees of finely reticulate exine sculpturing, whereas Nematanthus pollen have apertures with a margo (Figure V-12F), a basically triangular polar configuration, a tectate-perforate and semitectate (Figure V-12D) exine structure and coarsely reticulate exine sculpturing.

Walker (1975) postulates that primitive angiosperm pollen was psilate with a tectate-imperforate exine structure. The evolutionary trend was the succesive dissolution of tectum areas in the tectate-imperforate exine to form tectate-perforate, semitectate and intectate exine configurations (Figure V-1B; Walker, 1974).

In the genus Codonanthe, exine sculpturing differences are noted among sections of subgenus Codonanthe. Species of subgenus Codonanthe section Codonanthe have foveolate, fossulate and finely reticulate exines, whereas species of subgenus Codonanthe section Spathuliformae and subgenus Codonanthella possess verrucate, rugulate to reticulate and microreticulate pollen surfaces.

The foveolate and fossulate exine patterns of C. carnosa, C. devosiana and C. paula are possible the preliminary stages of tectum dissolution of an ancestral psilate exine type, with the pollen surface simply appearing pitted and grooved. The finely reticulate exine sculpturing of *C. digna* and *C. gracilis* may be a more advanced stage of tectum dissolution, but the pattern is still a simple network of reticula. Further tectum dissolution appears to occur with the rugulate and reticulate-secondarily foveolate exine patterns of *C. uleana* and *C. caribaea* that lack spines, the slightly spinulose-microreticulate exine types of *C. chiricana* and *C. luteola* that have few small spines, and the various spinulose-verrucate and spinulose-microreticulate exine configurations of *C. calcarata*, *C. corniculata*, *C. crassifolia*, *C. elegans* and *C. macradenia* that possess distinct spines.

Species of subgenus *Codonanthe* section *Codonanthe* have small-sized pollen and are diploids (*n* = 8; Wiehler, 1975), while species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella* possess medium-sized pollen and are tetraploids (*n* = 16; Wiehler, 1975), except *C. caribaea* (n = 8) and *C. luteola* (n = 8, 16). This difference in pollen size is possibly correlated to the ploidy level of the species and the related to the gigas effect of polyploidy (Stebbins, 1971).

In the genus *Nematanthus*, species possess reticulate exine sculpturing with foveolate reticula in the mesocolpia. The narrow reticula of *N. crassifolius*, *N. fritschii* and *N. perianthomegus* are apparently correlated to the semitectate exine structure, whereas the wider reticula of the other seven *Nematanthus* species correspond to the tectate-perforate structure type. Since tectate-perforate and semitectate pollen are contiguous stages in the trend of pollen evolution (Walker, 1974), it is conceivable that two exine structural types occur in one genus.

Reticulate apocolpia are present in *N. gregarius*, *N. nervosus*, *N. strigillosus*, *N. wettsteinii* and *N. hirtellus*, whereas very sparcely foveolate to psilate apocolpia occur in *N. crassifolius*, *N. fissus*, *N. fritschii*, *N. maculatus* and *N. perianthomegus*.

Although species of *Nematanthus* have medium-sized pollen, they are diploids (*n* = 8; Skog, 1981) and apparently do not follow the gigas effect of polyploidy of *Codonanthe* species, that is, medium-sized pollen denoting tetraploidy. *Nematanthus* species are distinct from species of *Codonanthe* with respect to pollen size and ploidy level.

Figure V-1. Diagrams depicting the pollen terminology used in the text (according to Walker & Doyle, 1975).

A. Cross-section of pollen wall illustrating the strata of a tectate-imperforate pollen.

B. Evolutionary trends in exine structure types. Cross-sectional views of pollen wall to the left and surface views to the right. Arrows 1-3 indicate direction and sequence of exine structure evolution and arrows 4-5 depict possible reversibility of the evolutionary trend.

C. Isopolar-radiosymmetric, globose-spheroidal and globose-oblate pollen grains, respectively, that are zonocolpate.

D. Pollen grains with polygonal, angulaperturate ambs.

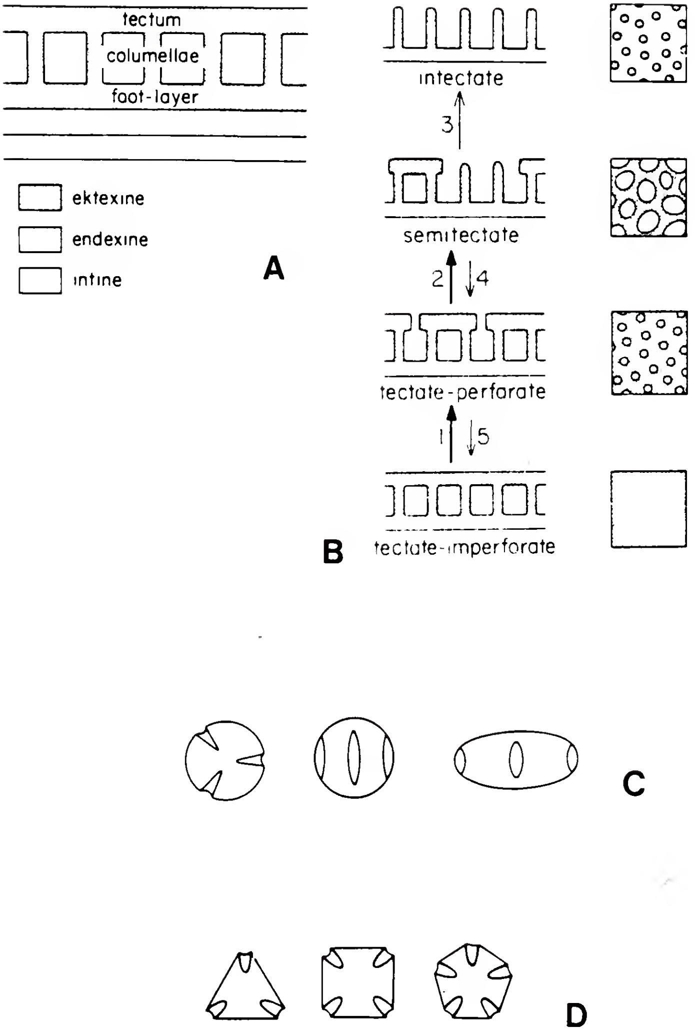
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Figure V-2. Pollen morphology of species of *Codonanthe* subgenus *Codonanthe* section *Codonanthe*.

- A. *C. carnosa*, pollen grain, X3000.
- B. *C. carnosa*, fossulate exine sculpturing, X10,000.
- C. *C. devosiana*, pollen grain, X3000.
- D. *C. devosiana*, foveolate exine sculpturing, X10,000.
- E. *C. digna*, pollen grain, X3000.
- F. *C. digna*, finely reticulate exine sculpturing, X10,000.

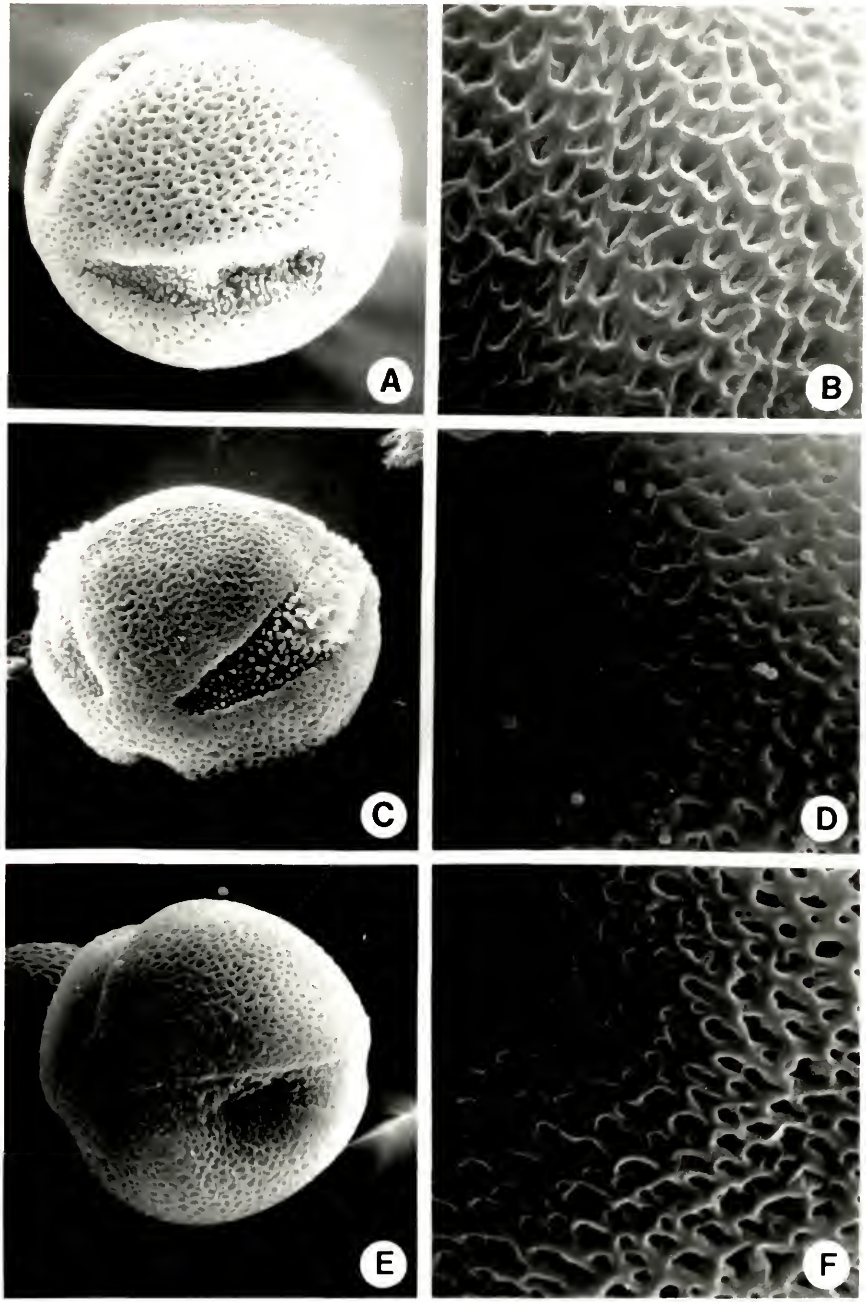
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Figure V-3. Pollen morphology of species of *Codonanthe* subgenus *Codonanthe* section *Codonanthe*.

A. *C. gracilis*, pollen grain, X3000.

B. *C. gracilis*, finely reticulate exine sculpturing, X10,000.

C. *C. paula*, pollen grain, X3000.

D. *C. paula*, foveolate exine sculpturing, X10,000.

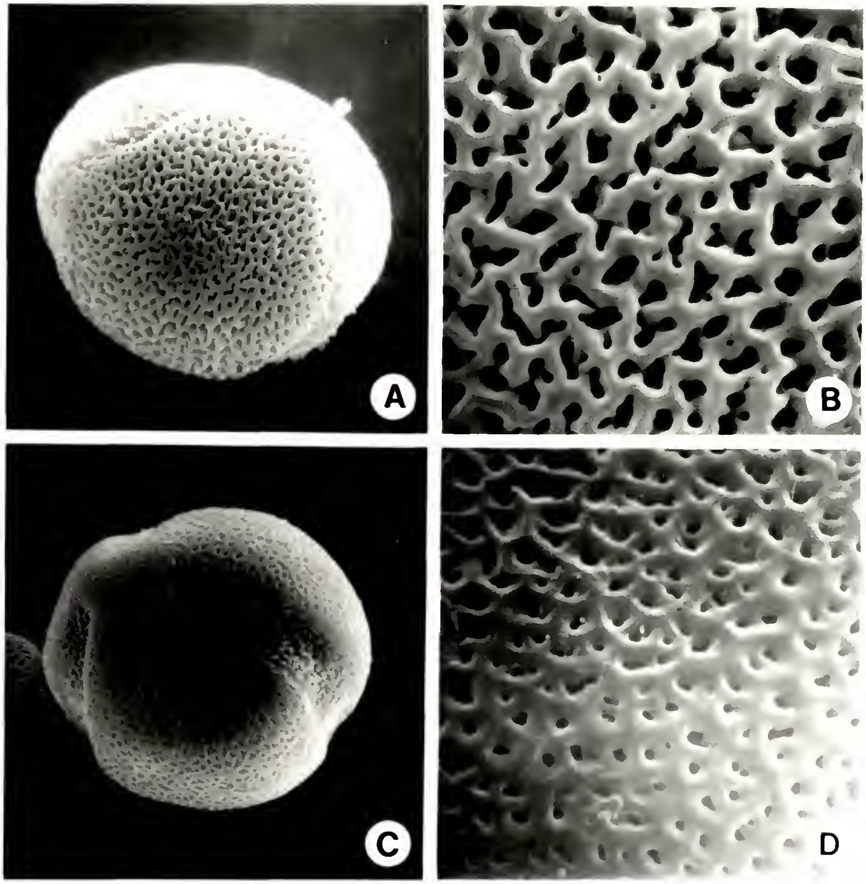
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Figure V-4. Pollen morphology of species of *Codonanthe* subgenus *Codonanthe* section *Spathuliformae*.

A. *C. calcarata*, pollen grain, X2000.

B. *C. calcarata*, spinulose-verrucate exine sculpturing, X10,000.

C. *C. corniculata*, pollen grain, X2000.

D. *C. corniculata*, spinulose-reticulate exine sculpturing, X10,000.

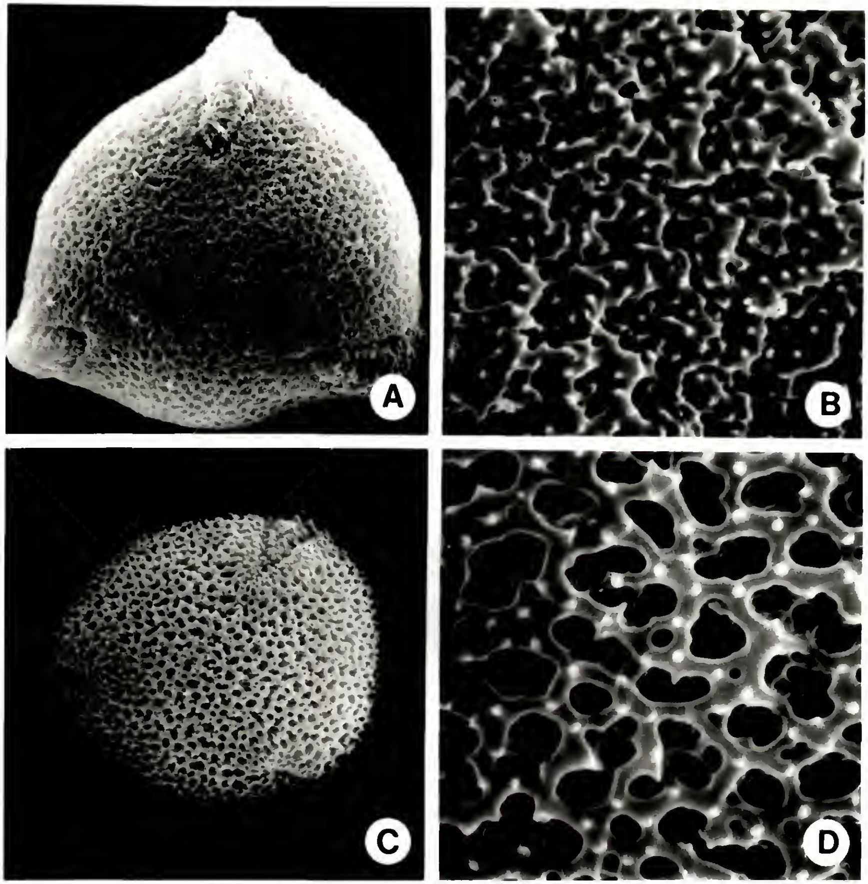
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Figure V-5. Pollen morphology of species of _Codonanthe_ subgenus _Codonanthe_ section _Spathuliformae_.

A. _C_. _crassifolia_, pollen grain, X2000.

B. _C_. _crassifolia_, spinulose-irregularly microreticulate exine sculpturing, X10,000.

C. _C_. _uleana_, pollen grain, X2000.

D. _C_. _uleana_, rugulate exine sculpturing, X10,000.

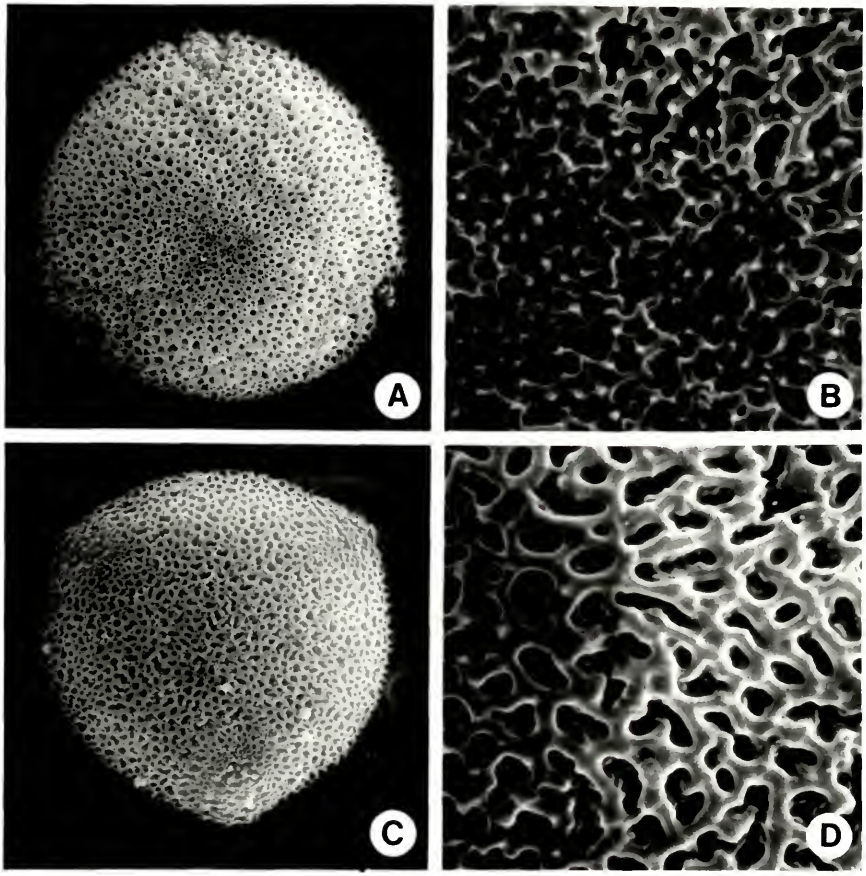
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Figure V-6. Pollen morphology of species of _Codonanthe_ subgenus _Codonanthella_.

A. _C. caribaea_, pollen grain, X2000.

B. _C. caribaea_, reticulate-secondarily foveolate exine sculpturing, X10,000.

C. _C. chiricana_, pollen grain, X1500.

D. _C. chiricana_, slightly spinulose-microreticulate exine sculpturing, X10,000.

E. _C. elegans_, pollen grain, X1500.

F. _C. elegans_, spinulose-irregularly microreticulate exine sculpturing, X10,000.

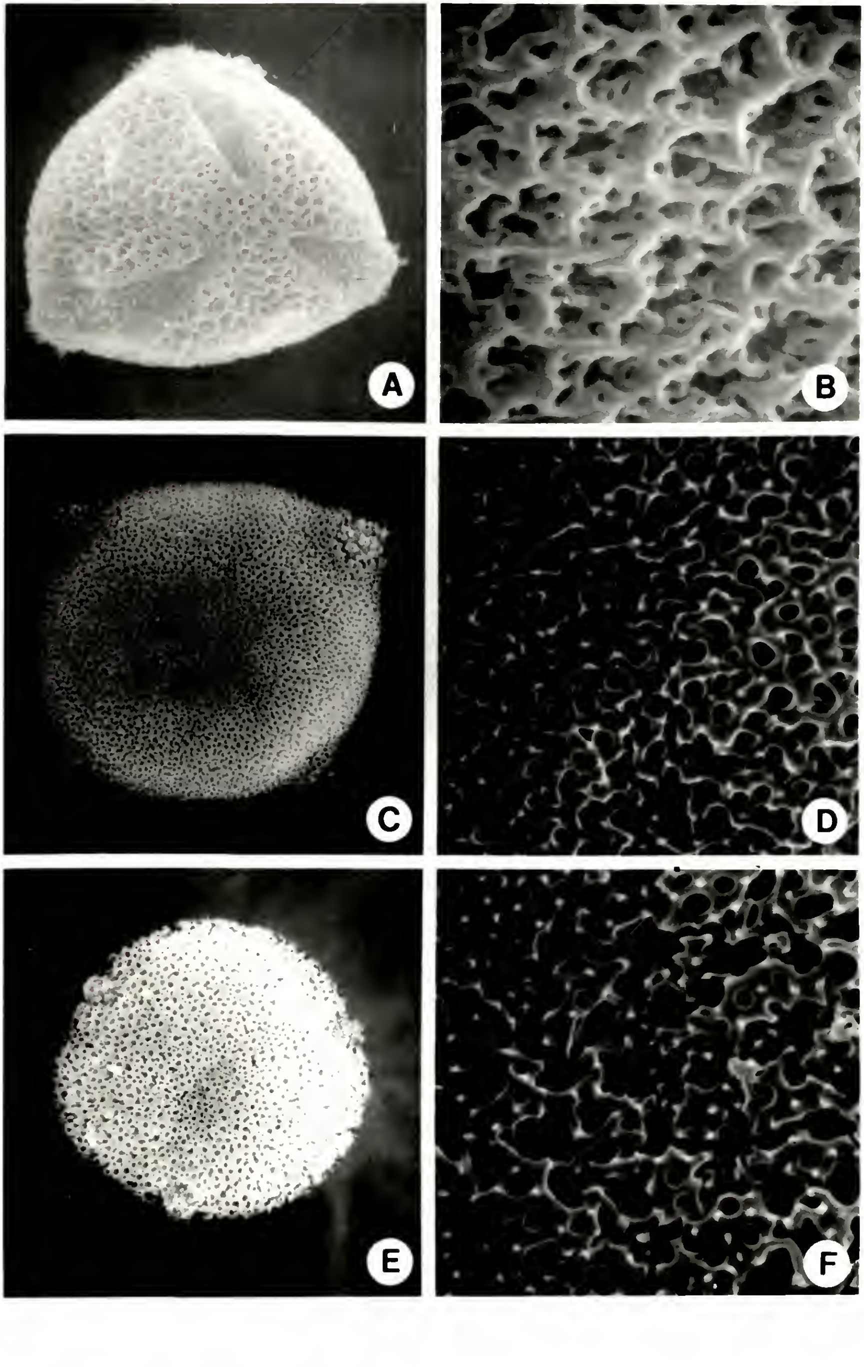
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Figure V-7. Pollen morphology of species of *Codonanthe* subgenus *Codonanthella*.

A. *C. luteola*, pollen grain, X1500.

B. *C. luteola*, slightly spinulose-microreticulate, X10,000.

C. *C. macradenia*, pollen grain, X2000.

D. *C. macradenia*, spinulose-microreticulate, X10,000.

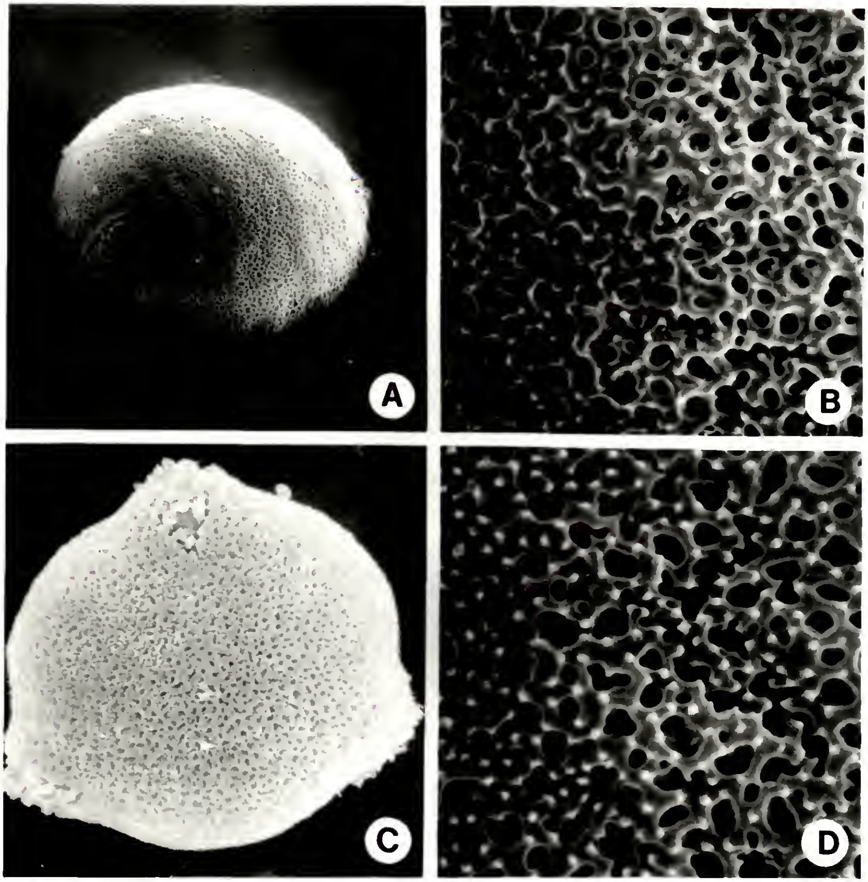
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Figure V-8. Pollen morphology of species of *Nematanthus* (section *Nematanthus*, cf. CONCLUSION and APPENDIX).

A. *N. crassifolius*, pollen grain, X2000.

B. *N. crassifolius*, reticulate exine sculpturing with narrow, foveolate reticula in the mesocolpia, X10,000.

C. *N. fissus*, pollen grain, X2500.

D. *N. fissus*, reticulate exine sculpturing with wide, foveolate reticula in the mesocolpia, X10,000.

E. *N. fritschii*, pollen grain, X2500.

F. *N. fritschii*, reticulate exine sculpturing with narrow, foveolate reticula in the mesocolpia, X10,000.

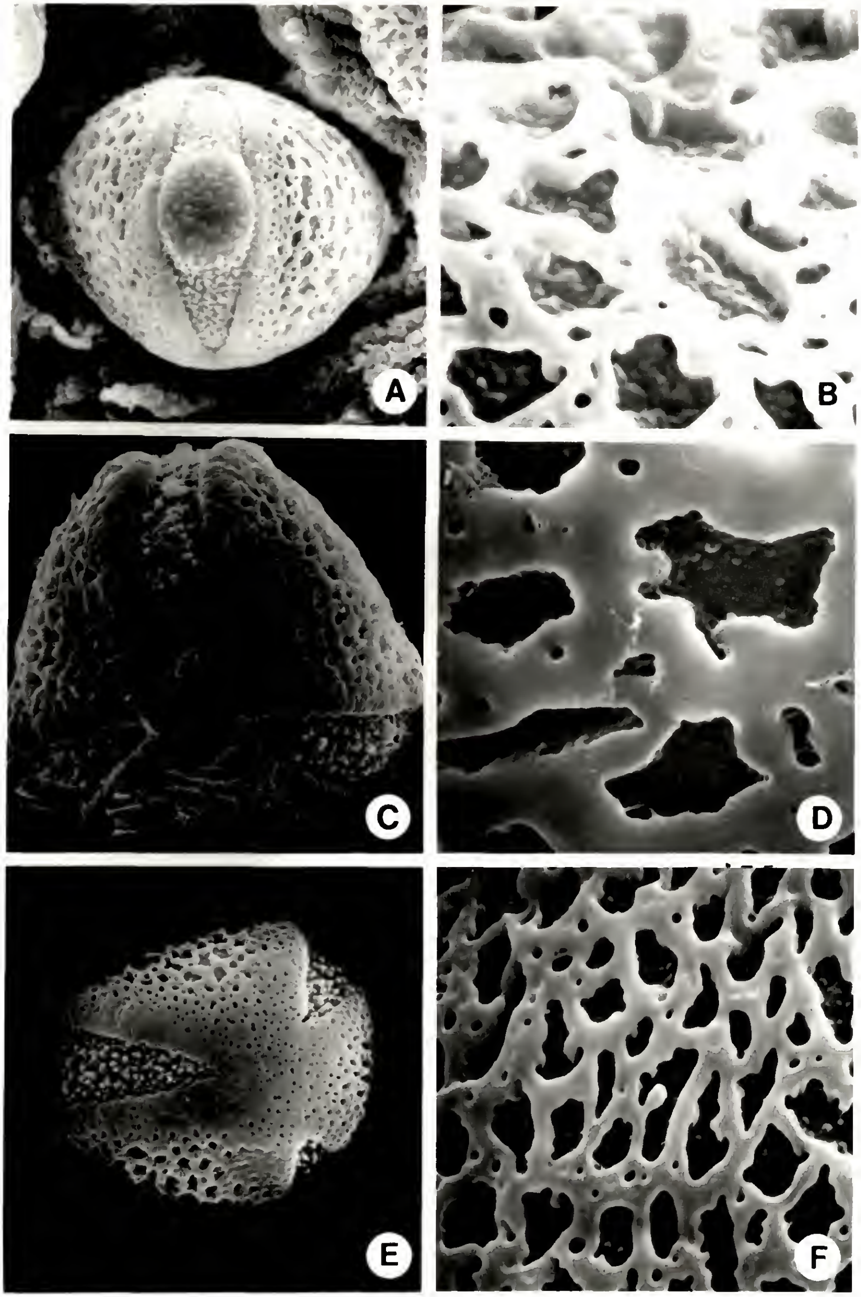
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Figure V-9. Pollen morphology of species of *Nematanthus* (section *Nematanthus*, cf. CONCLUSION and APPENDIX).

A. *N. hirtellus*, pollen grain, X2500.

B. *N. maculatus*, pollen grain, X2500.

C. *N. perianthomegus*, pollen grain, X2000.

D. *N. perianthomegus*, reticulate exine sculpturing with narrow, foveolate reticula in the mesocolpia, X10,000.

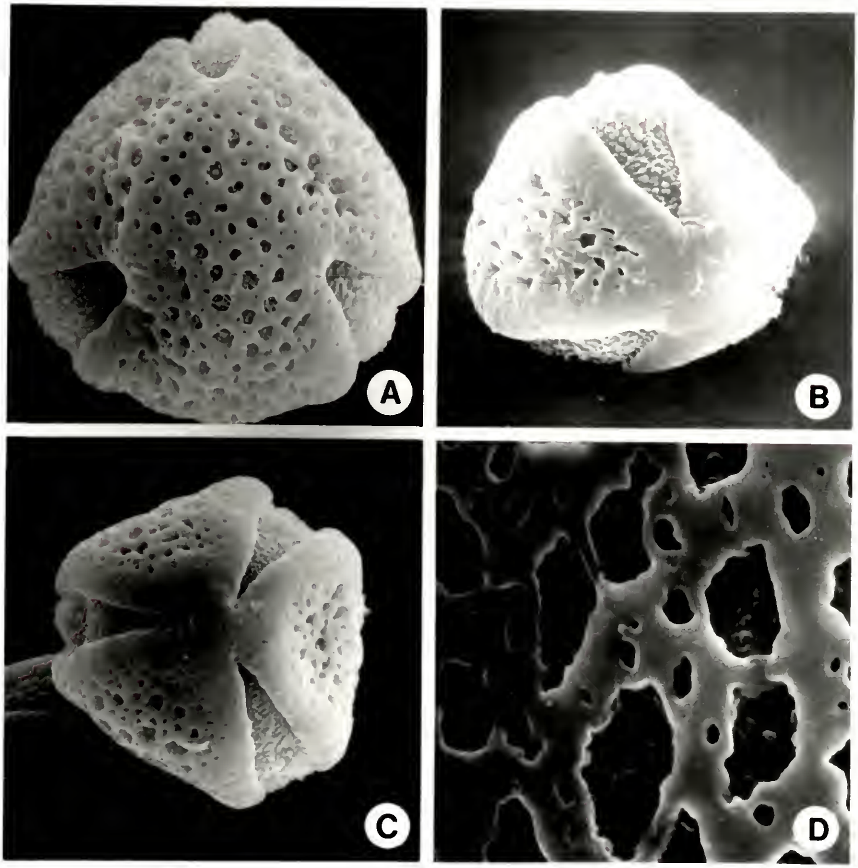
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Figure V-10. Pollen morphology of species of _Nematanthus_ (section _Parvifolius_, cf. CONCLUSION and APPENDIX).

A. _N. gregarius_, pollen grain, X2500.

B. _N. gregarius_, reticulate exine sculpturing with wide, foveolate reticula in the mesocolpia, X10,000.

C. _N. nervosus_, pollen grain, X2500.

D. _N. nervosus_, reticulate exine sculpturing with wide, foveolate reticula in the mesocolpia, X10,000.

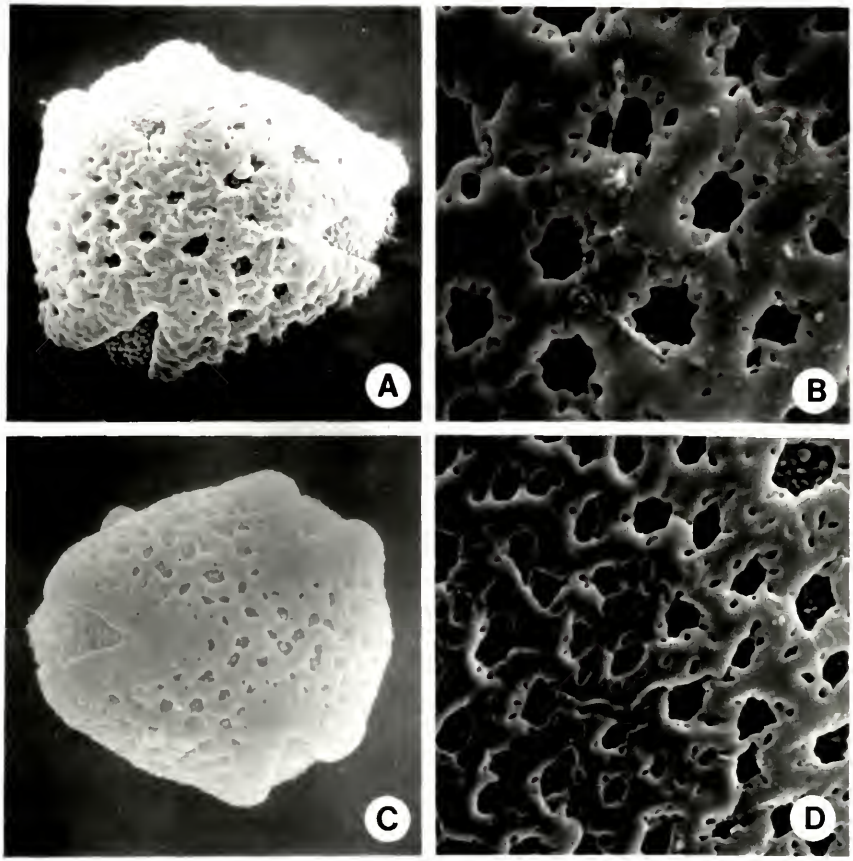
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Figure V-11. Pollen morphology of species of _Nematanthus_ (section _Parvifolius_, cf. CONCLUSION and APPENDIX).

A. _N. strigillosus_, pollen grain, X2500.

B. _N. strigillosus_, reticulate exine sculpturing with wide, foveolate reticula in the mesocolpia, X10,000.

C. _N. wettsteinii_, pollen grain, X3000.

D. _N. wettsteinii_, reticulate exine sculpturing with wide, foveolate reticula in the mesocolpia, X10,000.

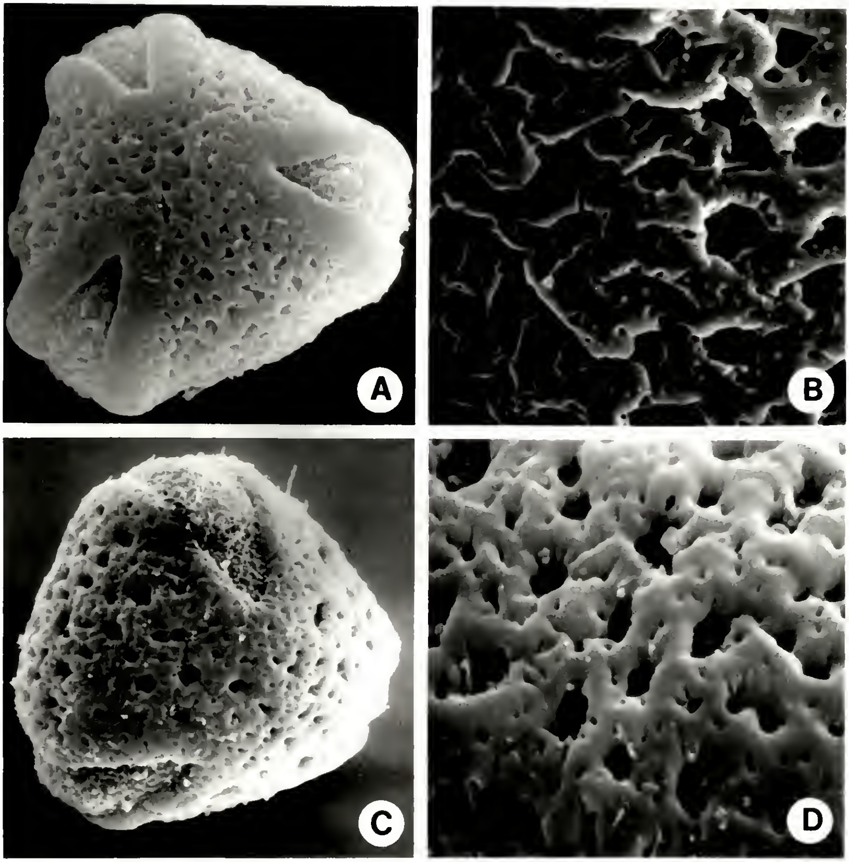
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Figure V-12. Varying features of pollen morphology and exine structure.

A. *C. chiricana*, 5-apertured pollen, X1500.

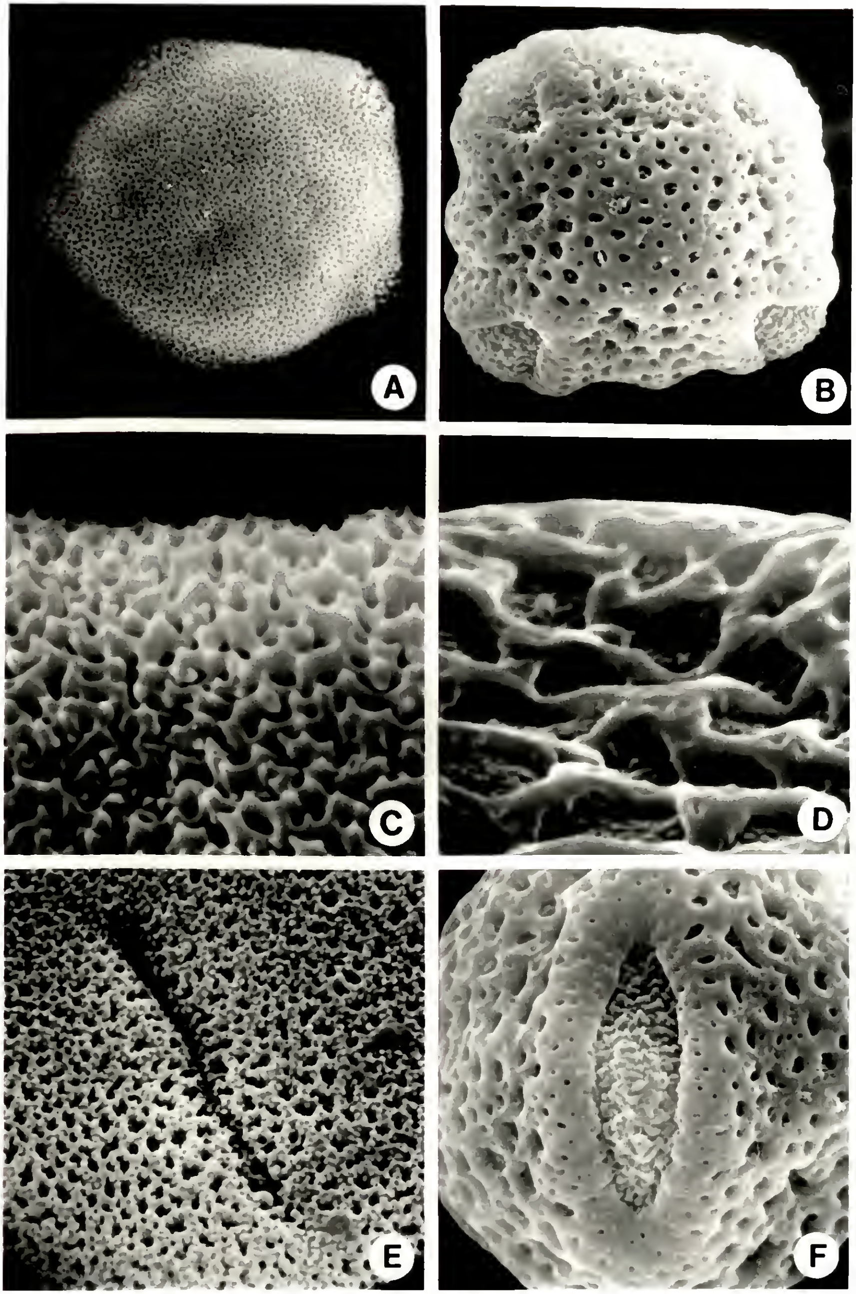
B. *N. hirtellus*, 4-apertured pollen, X2500.

C. *C. crassifolia*, profile of tectate-perforate pollen, X10,000.

D. *N. perianthomegus*, profile of semitectate pollen, X10,000.

E. *C. macradenia*, aperture without margo, X3400.

F. *N. hirtellus*, aperture with margo, X3500.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CHAPTER VI
CONCLUSION

Lawrence (1951) states that a genus is a taxonomic and biological category and should consist of morphologically similar species as well as be indicative of genetic relationships. Codonanthe and Nematanthus share many characters of taxonomic significance, including an identical basic chromosome number, similar fleshy fruit types and geographical distribution, an exclusively epiphytic growth habit, and numerous morphological and anatomical traits of the stem and leaf (Table VI-1). Since the first intergeneric cross was made in 1977 (Saylor, 1978a), several fertile X Codonatanthus hybrids have been produced (Saylor, 1978b, 1979, 1981; Yuen, personal hybridizations, 1982), demonstrating a kinship between Codonanthe and Nematanthus species. Should the genera Codonanthe and Nematanthus be united based upon these results?

Flower type and pollination ecology of Codonanthe and Nematanthus species are very distinct. Species of Codonanthe have an obliquely funnelform-ventricose corolla that is primarily white and is pollinated by Euglossine bees, whereas species of Nematanthus have a pouched corolla that is basically orange, red, pink or yellow and is presumably pollinated by hummingbirds. Possession of such differing corolla types and pollinators reproductively isolates these two genera though species of Codonanthe subgenus Codonanthe section Codonanthe occur sympatrically with Nematanthus species. Natural hybrids between species of *Codonanthe* and *Nematanthus* have not been reported. Also, *Codonanthe* pollen have apertures without a margo, a basically circular polar configuration, small- and medium-sized pollen (10-24 & 25-49 um, respectively), a tectate-perforate exine structure and various degrees of finely reticulate exine sculpturing, whereas *Nematanthus* pollen have apertures with a margo, a basically triangular polar shape, medium-sized pollen, a tectate-perforate and semitectate exine structure and coarsely reticulate exine sculpturing. It appears that though *Codonanthe* and *Nematanthus* are closely related genera, they should remain as distinct entities since they differ in these significant traits.

For *Codonanthe*, species of subgenus *Codonanthella* share many significant taxonomic traits with species of subgenus *Codonanthe* section *Spathuliformae* and relatively few features with species of subgenus *Codonanthe* section *Codonanthe* (Table VI-2). Species of subgenus *Codonanthe* section *Codonanthe* have orange berries, a diploid chromosome number of *n*=8 and small pollen grains (10-24 um), a unilacunar nodal anatomy (except *C. carnosa* and *C. gracilis*), multicellular nonglandular trichomes with radially-arranged basal epidermal cells, glandular trichomes with a 4-celled head, and a guard cell area index of 458 um^2, lack extrafloral nectaries, and are indigenous to southeastern Brazil. Species of subgenus *Codonanthe* section *Spathuliformae* and subgenus *Codonanthella* have red, pink, purple or yellow-green berries or fleshy capsules, a tetraploid chromosome number of *n*=16 (except *C. caribaea* is a diploid and *C. luteola* has diploid and tetraploid representatives) and medium pollen grains (25-49 um), a trilacunar, split-lateral nodal anatomy, unicellular nonglandular trichomes with randomly-arranged basal epidermal cells (except *C. caribaea*), glandular trichomes with a

2-celled head (except *C. caribaea*), and a guard cell index of 796 um^2 and 936 um^2, possess extrafloral nectaries, and are geographically widespread from southern Mexico through Central America to northern South America. Based upon these observations, it is acknowledged that further studies are required before any final conclusions are made on the relationships of the infrageneric taxa of *Codonanthe*.

There are two morphologically distinct groups of *Nematanthus* species (Table VI-3). *Nematanthus crassifolius*, *N. fissus*, *N. fritschii*, *N. hirtellus*, *N. maculatus* and *N. perianthomegus* have a shrubby growth habit with thick stems (5-9 mm diameter), long petioles (10-50 mm length), large blades (4-12 cm length), a trilacunar, split-lateral nodal anatomy, glandular trichomes with a 4-celled head and unicellular or multicellular body, anisocytic stomata, pollen with psilate apocolpia (except *N. hirtellus*), and resupinate flowers that are erect or hanging from the leaf axil. *N. gregarius*, *N. nervosus*, *N. strigillosus* and *N. wettsteinii* have a viny growth habit with thin stems (2-4 mm), short petioles (4-10 mm length), small blades (2-4 cm length), a unilacunar nodal anatomy, glandular trichomes with a more-than-4-celled head and unicellular body, anisocytic and helicocytic stomata, pollen with reticulate apocolpia, and nonresupinate flowers that are erect in the leaf axil. Based upon these observations, two new sections are established for *Nematanthus*-- section *Nematanthus* for the former group and section *Parvifolius* for the latter group.

Codonanthe and *Nematanthus* possess several contrasting features that are important in determining possible modes of speciation. Species of subgenus *Codonanthe* section *Codonanthe* are exclusively located in southeastern Brazil and separated from species of subgenus Codonanthe section Spathuliformae and subgenus Codonanthella by a savanna and scrub expanse (cf., Strahler, 1967; Walter, 1973). Codonanthe species, being epiphytes, are restricted to areas where their host trees occur, that is, regions of tropical evergreen and deciduous rain forests. The sizeable savanna and scrub expanse serves as a possible spatial or geographical isolating mechanism of these two disjunct groups (cf., Grant, 1971, 1977).

In addition, species of subgenus Codonanthe section Codonanthe are diploid (n=8), whereas species of subgenus Codonanthe section Spathuliformae and subgenus Codonanthella are tetraploids (n=16; except C. caribaea is diploid and C. luteola is diploid or tetraploid). This difference in ploidy, theoretically, would not obstruct the interbreeding of species in the two groups nor the subsequent production of interspecific hybrids. It is the isolating mechanism of hybrid sterility (cf., Grant, 1977) that would hinder the establishment of future generations of interspecific hybrids in that these hybrids would be triploid and sterile. Stebbins (1971) reports that polyploidy is indeed important in the diversification of tropical woody genera. Hence, varying ploidy levels and disjunct geographical distribution effectively isolate the species of these two groups and may lead to allopatric speciation.

Species of section Nematanthus may be reproductively isolated from species of section Parvifolius because the orientation of the flower effectively excludes pollen exchange between species of these two sections. Species of section Nematanthus possess flowers that are resupinate with anthers and stigma in the ventral position facing upward, and pollen shedding and reception occurring on the lower surface of the pollinating agent. In contrast, species of section *Parvifolius* possess flowers that are nonresupinate with the anthers and stigma in the dorsal position facing downward, and pollen shedding and reception occurring on the upper surface of the pollinating agent. Hummingbirds are presumably the pollinating agents and deposition of *Nematanthus* pollen is on the lower or upper surface of their beaks. If a hummingbird was to first visit a flower of a species in section *Nematanthus*, pollen would be deposited on the lower surface of its beak. Visiting another flower of a species in section *Nematanthus* would effect pollination because pollen reception is also from the lower surface of the hummingbird's beak, but visiting a flower of a species in section *Parvifolius* would not effect pollination because pollen reception is from the upper surface of the hummingbird's beak. Cross pollination between species of these two sections is unlikely due to the differing pollination mechanism, thus, possibly isolating these two taxa reproductively (cf., Grant, 1971, 1977).

Table VI-1. Key morphological and anatomical characters of the genera *Codonanthe* and *Nematanthus*.

CHARACTER	Codonanthe	Nematanthus
1) FLOWER		
a) Corolla Shape	funnelform	pouched
b) Corolla Color	white, yellow	red, yellow, pink, orange
c) Anther Connective	broad	narrow
d) Anther Dehiscence	pores	longitudinal slits
2) POLLINATION AGENT (presumed)	euglossine bees	hummingbirds
3) FRUIT	berry, fleshy capsule	fleshy capsule
4) CHROMOSOME NUMBER	diploid (n=8), tetraploid (n=16)	diploid (n=8)
5) GEOGRAPHICAL DISTRIBUTION	southern Mexico through Central America to northern South America; southeastern Brazil	southeastern Brazil
6) LEAF EPIDERMIS MORPHOLOGY		
a) Nonglandular Trichomes	unicellular, multicellular	multicellular
b) Glandular Trichomes	2- & 4-celled head; unicellular body	4- & >4-celled head; unicellular & multicellular body
c) Stomata Type	anisocytic	anisocytic, helicocytic
d) Extrafloral Nectaries	present & absent	absent
7) POLLEN MORPHOLOGY		
a) Margo around Aperture	absent	present
b) Polar View	circular (slightly triangular)	triangular
c) Equatorial View	circular to slightly elliptic	circular to strongly elliptic
d) Pollen Size	small (10-24 um) & medium (25-49 um)	medium (25-49 um)
e) Exine Structure	tectate-perforate	tectate-perforate & semitectate
f) Exine Sculpturing	psilate to finely reticulate	coarsely reticulate

Table VI-2. Key morphological and anatomical characters of *Codonanthe* at the subgenus and section level.

	SUBGENUS *Codonanthe*		
CHARACTER	SECTION *Codonanthe*	SECTION *Spathuliformae*	SUBGENUS *Codonanthella*
1) FRUIT			
a) Type	berry	berry	fleshy capsule
b) Color	orange	red, pink, purple	red, pink, purple; yellow-green
2) CHROMOSOME NUMBER	diploid (*n*=8)	tetraploid (*n*=16)	tetraploid (*n*=16); (except *C. caribaea*, *n*=8; *C. luteola*, *n*=8, 16)
3) GEOGRAPHICAL DISTRIBUTION	southeastern Brazil	Central America to South America (excluding southeastern Brazil)	southern Mexico through Central America to northern South America
4) LEAF EPIDERMIS MORPHOLOGY			
a) Nonglandular Trichome Cells	multicellular	unicellular	unicellular (except *C. caribaea*)
b) Nonglandular Trichome Basal Cell Arrangement	radial (except *C. gracilis*)	random	random
c) Glandular Trichome Head	4-celled	2-celled	2-celled (except *C. caribaea*)
d) Extrafloral Nectaries	absent	present	present (except *C. caribaea*)
e) Guard Cell Area Index	458 um^2	796 um^2	936 um^2
5) NODAL ANATOMY	unilacunar (except *C. carnosa* & *C. gracilis*)	trilacunar, split-lateral	trilacunar, split-lateral
6) POLLEN SIZE	small (10-24 um)	medium (25-49 um)	medium (25-49 um)

Table VI-3. Key morphological and anatomical characters of *Nematanthus* at the section level.

CHARACTER	SECTION Nematanthus	SECTION Parvifolius
1) GROWTH HABIT	shrubby	viny
2) STEM SIZE (diameter)	5-9 mm	2-4 mm
3) LEAF SIZE (length)		
a) Petiole	10-50 mm	4-10 mm
b) Blade	4-12 cm	2-4 cm
4) FLOWER ORIENTATION	resupinate	nonresupinate
5) LEAF EPIDERMIS MORPHOLOGY		
a) Glandular Trichome Head	4-celled	>4-celled
b) Glandular Trichome Body	unicellular, multicellular	unicellular
c) Stomata Type	anisocytic	anisocytic, helicocytic
6) NODAL ANATOMY	trilacunar, split-lateral	unilacunar
7) POLLEN APOCOLPIA	psilate (except *N. hirtellus*)	reticulate

APPENDIX
SYNOPSIS OF INFRAGENERIC TAXA OF CODONANTHE AND NEMATANTHUS

Description of the Genera, Subgenera and Sections

GENUS *Codonanthe* (Martius) Hanstein, Linnaea 26: 209. April 1854 ('1853'), nom. cons.
Hypocyrta section *Codonanthe* Martius, Nova Genera et Species Plantarum 3: 49. 1829.
Type: *Hypocyrta gracilis* Martius. (=*Codonanthe gracilis* (Martius) Hanstein).
Coccanthera C. Koch & Hanstein, Index Seminum in Horto Regio Botanico Berolinensi 1855: Appendix 17. 1855.
Type: *C. Hookerana* C. Koch & Hanstein. (=*Codonanthe gracilis* (Martius) Hanstein).
Codonanthopsis Mansfeld, Repertorium Specierum Novarum Regni Vegetabilis 36: 120. 1934.
Type: *C. Ulei* Mansfeld. (=*Codonanthe Ulei* (Mansfeld) H. E. Moore).

Type species: *Codonanthe gracilis* (Martius) Hanstein.

Vine-like or shrub-like epiphytes sparsely branched. *Roots* adventitious and fibrous; often mutualistically associated with ants with the roots providing structural support to the ant nests. *Stems* woody, erect, repent or pendulous, 2-9 mm in diameter, with extrafloral nectaries frequently produced near compressed nodes. *Leaves* opposite, decussate or 2-ranked, equal or subequal in a pair; petioles 4-19 mm in length; blades entire, sinuate or serrulate towards the apex, ovate, oval, obovate or elliptic in shape, with some species 2-4 cm and some 4-12 cm in length, reddish, mammillate extrafloral nectaries on the abaxial surface present or absent, mostly pubescent, usually fleshy and thick with a prominent dorsal hypodermis; estipulate. *Inflorescences* are cymes reduced to one or a few flowers borne in upper leaf axils; peduncles very short if present; bracts absent; pedicels 3-25 mm in length. *Flowers* having a calyx deeply 5-parted with subequal to very unequal lobes, linear to lanceolate, or bilabiate, 2-10 mm in length, with the dorsal calyx lobe recurved about the spur, red extrafloral nectaries often in sinuses of the calyx lobe margins; corolla white and yellow, sometimes flushed with yellow, brown, pink, red, lilac or deep purple spots or lines on the lower surface of the throat or outer areas, obliquely funnelform-ventricose, 1-4 cm in length, base rounded to prominently spurred, then gradually or abruptly broader towards the throat, or somewhat dorsi-ventrally compressed and arched/grooved, limb of 5 rounded, spreading lobes, bilabiate with the upper lobes shorter than the three lower lobes; stamens 4, filaments epipetalous and didynamous, distinct or connate at the base, recoiled or lowered towards the ventral surface of the corolla after pollen is shed, anthers connivent in pairs by tips or margins in a square at anthesis, sometimes separating after anthesis, laterally oblong with connectives narrow or often broad, anther sacs more or less separated, dehiscing by round or ellipsoid pores; ovary superior, unilocular, with 2 parietal placentas ovuliferous on the inner side, ovules numerous and anatropous, style terete and slender, elongating after pollen is shed, stigma stomatomorphic to bilobed; nectary or disc of 2 large, connate glands positioned adjacent and dorsal to the ovary. Fruit a fleshy capsule, dehiscent or tardily dehiscent by 2 valves, or a berry with distinct sutures, globose, ovoid or compressed, red pink, orange, purple or yellow-green, placentas fleshy; seeds often with thickened fleshy funicles that are entirely or partially surrounded by a translucent or opaque aril, fusiform or ellipsoid, longitudinally or obliquely striated, red, pink or yellow. Chromosome number as $x = 8$ with $n = 8$ & 16. Distribution from southern Mexico through Central America to northern South America, and southeastern Brazil (Moore, 1973a; Skog, 1978; Wiehler, 1979b).

SUBGENUS *Codonanthe*

Fruit a globose berry.

SECTION *Codonanthe*

SECTION *Codonanthe*, H. E. Moore, Baileya 19: 9. 1973.

Fruit an orange berry.

Type species: *Codonanthe gracilis* (Martius) Hanstein.

Additional species: *C. carnosa* (Gardner) Hanstein, *C. devosiana* Lemaire, *C. digna* Wiehler, *C. paula* Wiehler.

SECTION *Spathuliformae* L. B. Smith, Bulletin of the Torrey Botanical Club 60: 657. 1933.

Fruit a red, pink or purple berry.

Type species: *Codonanthe calcarata* (F. A. W. Miquel) Hanstein.

Additional species: *C. corniculata* Wiehler, *C. crassifolia* (Focke) Morton, *C. uleana* Fritsch.

SUBGENUS *Codonanthella* Wiehler, Selbyana 6 (in press). 1982.

Fruit a yellow-green, pointed, fleshy capsule.

Type species: *Codonanthe luteola* Wiehler.

Additional species: *C. caribaea* Urban, *C. chiricana* Wiehler, *C. macradenia* Donnell-Smith.

GENUS Nematanthus Schrader, Gottingische gelehrte Anzeigen 1821(2): 718. 1821.

Hypocyrta Martius, Nova Genera et Species Plantarum 3: 48. 1829.

Type species: Nematanthus crassifolius (Schott) Wiehler.

Shrub-like or vine-like epiphytes sparsely branched. Roots fibrous, often adventitious at compressed nodes. Stems woody, erect or repent, with some species 2-4 mm or 5-9 mm in diameter. Leaves opposite, decussate or 2-ranked, equal or subequal in a pair; petioles either 4-10 mm or 10-50 mm in length, slightly furrowed adaxially, green to red and maroon; blades entire, serrulate or slightly crenate towards the apex, ovate, oval, obovate or elliptic in shape, with some species 2-4 cm and some 4-12 cm in length, sometimes red or maroon-splotched on the abaxial surface, mostly pubescent, usually fleshy and often coriaceous with a notable dorsal hypodermis; estipulate. Inflorescences are reduced cymes of one or a few flowers in upper leaf axils; peduncles very short if present; bracts absent; pedicels either 3-25 mm or 25-200 mm in length, usually exceeding subtending leaves; orientation of flowers nonresupinate, resupinate or pendulous. Flowers having a calyx deeply 5-parted with subequal to very unequal lobes, ovate to elliptic, sometimes toothed, 10-30 mm in length, with dorsal calyx lobe recurved about the spur; corolla scarlet, red, pink, orange or yellow with maroon stripes, erect or oblique in the calyx, mildly to strongly ventricose, 2-6 cm in length, often with a short spur, narrow above the base, gradually expanding to a broad, laterally compressed throat or quickly widening to form a pouch and abruptly narrowing to form a constricted throat (hypocyrtoid), limb of 5 rounded, small lobes; stamens 4, filaments epipetalous and didynamous, distinct or connate at the base, recoiled towards the corolla base after pollen is shed, anthers coherent in a rectangle, laterally oblong in shape, with elliptical connectives, dehiscing by slits; ovary superior, unilocular, with 2 parietal placentas ovuliferous on the inner side, ovules numerous and anatropous, style terete and slender, elongating after pollen is shed, stigma stomatomorphic; nectary or disc of 2 large, connate glands positioned adjacent and dorsal to ovary. Fruit a fleshy capsule, dehiscent or tardily dehiscent by 2 valves, sometimes laterally compressed and ovoid, placentas fleshy; seeds often with thickened fleshy funicles that are entirely or partially surrounded by a translucent or opaque aril, fusiform or ellipsoid, longitudinally or obliquely striated, often shiny brown. Chromosome number as $x = 8$ with $n = 8$. Distribution localized in southeastern Brazil (after Moore, 1971, 1973b).

SECTION Nematanthus

Shrub-like epiphytes. Stems erect, 5-9 mm in diameter, with nodes trilacunar. Leaves with petioles green to red and maroon, 10-50 mm in length; blades entire, serrulate or slightly crenate towards the apex, 4-12 cm in length, sometimes red or maroon-splotched on the abaxial surface, glandular trichomes with a 4-celled head and unicellular or multicellular-uniseriate body cells, stomata anisocytic. Flowers resupinate or pendulous with pedicels either 3-25 or 25-200 mm in length; corolla scarlet, red, pink, orange or yellow with maroon stripes, mildly to strongly ventricose or pouched.

Type species: Nematanthus crassifolius (Schott) Wiehler.

Additional species: N. fissus (Vellozo) L. Skog, N. fritschii Hoehne, N. hirtellus (Schott) Wiehler, N. maculatus (Fritsch) Wiehler, N. perianthomegus (Vellozo) H. E. Moore.

SECTION Parvifolius Yuen, sect. nov.

Vine-like epiphytes. Stems repent, 2-4 mm in diameter, with nodes unilacunar. Leaves with petioles green, 4-10 mm in length; blades entire, narrowly ovate to widely elliptic, 2-4 cm in length, sometimes red on the abaxial surface, glandular trichomes with more-than-4-celled heads and only unicellular body cells, stomata anisocytic and helicocytic. Flowers nonresupinate with pedicels 3-25 mm in length; corolla red, orange or yellow, pouched.

Type species: Nematanthus wettsteinii (Fritsch) H. E. Moore.

Additional species: N. gregarius D. Denham, N. nervosus (Fritsch) H. E. Moore, N. strigillosus (Martius) H. E. Moore.

Diagnostic Key to the Genera, Subgenera and Sections

A. Corolla obliquely funnelform or mildly ventricose, white, pink, lilac or deep purple; flowers nonresupinate; fruit a berry or fleshy capsule; extrafloral nectaries present or absent; hairs unicellular or multicellular-uniseriate on leaves; chromosome number *n* = 8 & 16; distribution from southern Mexico through Central America to northwestern South America, and southeastern Brazil...GENUS *Codonanthe*

B. Fruit a globose berry.....................SUBGENUS *Codonanthe*

C. Fruit an orange berry..............SECTION *Codonanthe*

C. Fruit a red, pink or purple berry..SECTION *Spathuliformae*

B. Fruit a yellow-green, pointed, fleshy capsule...SUBGENUS *Codonanthella*

A. Corolla mildly to strongly ventricose or pouched (hypocyrtoid), scarlet, red, pink, orange or yellow with maroon stripes; flowers nonresupinate, resupinate or pendulous; fruit a fleshy capsule; extrafloral nectaries absent; hairs multicellular-uniseriate on leaves; chromosome number *n* = 8; distribution in southeastern Brazil only.......................................GENUS *Nematanthus*

D. Growth form shrub-like epiphyte; nodal anatomy trilacunar; flowers resupinate or pendulous; leaves having glandular trichomes with 4-celled heads and unicellular and multicellular-uniseriate body cells, stomata anisocytic...SECTION *Nematanthus*

D. Growth form vine-like epiphyte; nodal anatomy unilacunar; flowers nonresupinate; leaves having glandular trichomes with more-than-4-celled heads and unicellular body cells; stomata anisocytic and helicocytic..SECTION *Parvifolius*

Checklist of Known Species in Cultivation

GENUS *Codonanthe* (Martius) Hanstein

C. calcarata (F. A. W. Miquel) Hanstein, Linnaea 34: 416. 1865.
Nematanthus calcaratus F. A. W. Miquel, Linnaea 22: 472. 1849.
Type: Surinam, Berlyn, *Focke 941* (U).
Codonanthe bipartita L. B. Smith, Bulletin of the Torrey Botanical Club 60: 657. 1933.
Type: Guyana, Kartabo Region. *I. W. Bailey 181* (GH; fragment NY).

C. caribaea Urban, Symbolae Antillanae 2: 365. 1901.
Type: Guadeloupe, Riviere Noire, *Duss 3776* (Isotype, NY, US).
C. Eggersii Urban, Symbolae Antillanae 2: 366. 1901.
Type: Tobago, Morne d'Or, *Eggers 5848* (B?, destroyed?).
C. triplinervia Britton, Bulletin of the Torrey Botanical Club 48: 399: 1922.
Type: Trinidad, Ortoire River, *Britton, Freeman & Nowell 2543* (Isotypes, GH, US).
C. triplinervia var. *latifolia* Morton in R. O. Williams *et al.*, Flora of Trinidad and Tobago 2(5): 308. 1954.
Type: Trinidad, Mt. Tocuche, *Simmonds 241* (Herb. Trinidad 14061; fragment US).
C, triplinervia var. *purpurea* Morton in R. O. Williams *et al.*, Flora of Trinidad and Tobago 2(5): 308. 1954.
Type: Trinidad, Arima-Blanchisseuse Rd., *Simmonds 147* (Herb. Trinidad 13796; fragment US).

C. carnosa (Gardner) Hanstein in Martius, Flora Brasiliensis 8(1): 418. 1864.
Hypocyrta carnosa Gardner in W. J. Hooker, London Journal of Botany 1: 178. 1842.
Type: Brazil, Corcovado, *Gardner 73* (K).
Orobanche carnosa Vellozo, Florae Fluminensis 1: 225. 1829; Atlas 6: *plate 61*. 1831.
Type: Brazil, Florae Fluminensis description and plate.
Codonanthe carnosa (Vellozo) Hoehne, Sellowia 9: 52. 1958; *nom. illeg.*
Codonanthe Hookeri Lemaire, L'Illustration Horticole 2: sub *plate 56*. 1855.
Type: *Hort. Backhouse* (K) (Curtis's Botanical Magazine 76: plate 4531. 1850.)
Coccanthera Hookerana C. Koch & Hanstein, Index Seminum in Horto Regio Botanico Berolinensi 1855: Appendix 17. 1855, *nom. illeg.*
Codonanthe florida Pampanini, Nuovo Giornale Botanico Italiano series 2, 14: 597. 1907.
Type: Brazil, Bahia, cultivated in Florence Botanical Garden.

C. chiricana Wiehler, Selbyana 2(1): 95. 1977.
Type: Panama, Chiriqui, *Dressler s.n.* (Holotype, SEL; Isotype, K, MO, PMA, US).

C. corniculata Wiehler, Selbyana 2(1): 95. 1977.
Type: Panama, Loreto, *Dressler s.n.* (Holotype, SEL; Isotype, F, K, MO, NY, US).

C. crassifolia (Focke) Morton, Field Museum of Natural History, Botanical Series 18: 1159. 1938.
Hypocyrta crassifolia Focke, Tijdschrift voor de wissen natuurkundige Wetenschappen 5: 199. 1852.
Type: Surinam, *Focke*, colored pencil drawing (L; photograph US).
Codonanthe confusa Sandwith, Kew Bulletin 1931: 492. 1931.
Type: French Guiana, *Sagot 426* (K; Isotype W).
Episcia Hookeri Hanstein, Linnaea 34: 350. 1865.
Type: Trinidad, *Purdie*, Hooker's Icones Plantarum 9: 873. 1852.

C. devosiana Lemaire, L'Illustration Horticole 2: sub *plate 56*. 1855.
Type: Brazil.
C. picta Lemaire, L'Illustration Horticole 4: sub *plate 144*. 1857.

C. digna Wiehler, Selbyana 5(2): 214. 1979.
Type: Cultivated plants of unknown origin, *Wiehler 7330* (Holotype, SEL; Isotype, F, HB, K, MO, NY, R, RB, SP, US).

C. elegans Wiehler, Selbyana 6(in press). 1982.

C. gracilis (Martius) Hanstein, Linnaea 26: 209. 1854.
Hypocyrta gracilis Martius, Nova Genera et Species Plantarum 50. Jan.-Jun. 1829.
Lectotype: Brazil, Rio de Janeiro, *Martius* (M, photograph US).
Orobanche crenata Vellozo, Florae Fluminensis 1: 254. Sept.-Nov. 1829; Atlas 6: *plate 60*. 1831.
Type: Florae Fluminensis, Atlas 6: *plate 60*.
O. ventricosa Vellozo, Florae Fluminensis 1: 259. Sept.-Nov. 1829; Atlas 6: *plate 74*. 1831.
Type: Florae Fluminensis, Atlas 6: *plate 74*.
Codonanthe ventricosa (Vellozo) Hoehne, Sellowia 9: 53. 1958.

C. luteola Wiehler, Selbyana 1(2): 159. 1975.
Type: Panama, Cerro Jefe, *Wiehler & Dressler 71184* (Holotype, US; Isptype, PAN, SEL, MO, NY, GH, F, UC, K, P, B).

C. macradenia Donnell-Smith, Botanical Gazette 25: 154. 1898.
Lectotype: Costa Rica, Boruca, *Tonduz 6769* (US).

C. paula Wiehler, Selbyana 5(2): 215. 1979.
Type: Brazil, Sao Paulo, *Wiehler 79360* (Holotype, SEL; Isotype, F, HB, K, MO, NY, R, RB, SP, US).

C. uleana Fritsch, Botanische Jahrbucher fur Systematik 37: 492. 1906.
Type: Brazil, Rio Jurua, *Ule 5617* (B, destroyed).
Columnea calcarata Donnell-Smith, Botanical Gazette 33: 254. 1902.
Type: Guatemala, Cubilquitz, *Tuerckheim 7645* (US; Isotype GH).
Codonanthe decurrens I. M. Johnston, Sargentia 8: 275. 1949.

GENUS *Nematanthus* Schrader

N. crassifolius (Schott) Wiehler, Selbyana 5(3-4): 382. 1981.
Besleria crassifolia Schott, Oesterreichische medicinische Jahrbucher 6(2): 93. 1820; reprinted in K. von Schreibers, Nachrichten von den kaiserlichen oesterreichischen Naturforschern in Brasilien, Anhang 7, p. 93. 1820.
Nematanthus corticola Schrader, Gottingische gelehrte Anzeigen 1: 718. 1821.
N. chloronema Martius, Nova Genera et Species Plantarum 3: 47. tab. 220. 1829.
N. jonema Martius, Nova Genera et Species Plantarum 3: 48. 1829.
Orobanche brasiliensis Vellozo, Florae Fluminensis 1: 240. 1829.
O. fluminensis Vellozo, Florae Fluminensis 1: 240. 1829, pro parte (sp, mixta).
Nematanthus fluminensis (Vellozo) Fritsch, Botanische Jahrbucher fur Systematik 37: 488. 1906.
N. longipes DC, Prodromus 7: 544. 1839.
N. guillemii Brongn., L'Horticulteur Universal 3: 327. 1842.
Columnea splendens Paxton, Paxton's Mag. Bot. 10: 5. 1843.
Nematanthus calycinus Presl, Botanische Bemerkungen 145. 1844.
N. heterophyllus Presl, Botanische Bemerkungen, non Poeppig. 1840.
N. pereskiaefolius Presl, Botanische Bemerkungen 143. 1844.
N. radicans Presl, Botanische Bemerkungen 143. 1844.
N. serrulatus Presl, Botanische Bemerkungen 144. 1844.

N. fissus (Vellozo) L. Skog, Baileya 19(4): 150. 1975.
Orobanche fissa Vellozo, Florae Fluminensis 257. Sept.-Nov. 1829; Atlas 6: *plate 69*. 1831.
Hypocyrta Selloana Klotzsch & Hanstein in Hanstein in Martius, Flora Brasiliensis 8: 409. 1864.
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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