

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

BY

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

Table I-1 - continued.

<u>DATE</u>	<u>TAXA</u>	<u>EVENT</u>
1979	<u>Codonanthe</u> (Martius) Hanstein & <u>Codonanthopsis</u> Mansfeld	Wiehler regards <u>Codonanthopsis</u> as a valid genus, in Wiehler, Ph. D. dissertation.
1979	<u>Codonanthe</u> subgenus <u>Codonanthe</u> Wiehler	New subgenus of <u>Codonanthe</u> established based upon species having fleshy capsules, in Wiehler, Ph. D. dissertation.
1982	<u>Codonanthe</u> subgenus <u>Codonanthe</u> section <u>Spathuliformae</u> L. B. Smith	New section of <u>Codonanthe</u> 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 <u>Codonanthe</u> (Martius) Hanstein	Accession Number
SUBGENUS <u>Codonanthe</u>	
SECTION <u>Codonanthe</u>	
1. <u>C. carnosa</u> (Gardner) Hanstein	W-2199
2. <u>C. devosiana</u> Lemaire	W-2215
3. <u>C. digna</u> Wiehler	W-1139
4. <u>C. gracilis</u> (Martius) Hanstein	W-2203
5. <u>C. paula</u> Wiehler	W-2386
SECTION <u>Spathuliformae</u> L. B. Smith	
6. <u>C. calcarata</u> (F.A.W. Miquel) Hanstein	W-2116
7. <u>C. corniculata</u> Wiehler	G-932
8. <u>C. crassifolia</u> (Pocke) Morton	W-2531
9. <u>C. uleana</u> Fritsch	W-1182
SUBGENUS <u>Codonanthe</u> <u>lla</u> Wiehler	
10. <u>C. caribaea</u> Urban	G-976
11. <u>C. chiricana</u> Wiehler	W-2267
12. <u>C. elegans</u> Wiehler	W-2588
13. <u>C. luteola</u> Wiehler	W-1630
14. <u>C. macradenia</u> Donnell-Smith	W-2552
GENUS <u>Nematanthus</u> Schrader	
1. <u>N. crassifolius</u> (Schott) Wiehler	G-134
2. <u>N. fissus</u> (Vellozo) L. Skog	G-661
3. <u>N. fritschii</u> Hoehne	G-611
4. <u>N. gregarius</u> D. Denham	G-597
5. <u>N. hirtellus</u> (Schott) Wiehler	G-1092
6. <u>N. maculatus</u> (Fritsch) Wiehler	W-2494
7. <u>N. nervosus</u> (Fritsch) H. E. Moore	G-734
8. <u>N. perianthomegus</u> (Vellozo) H. E. Moore	W-1718, W-2227
9. <u>N. strigillosus</u> (Martius) H. E. Moore	W-388
10. <u>N. wettsteinii</u> (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 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 funnellform-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 Hypocyrtta-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. Dehiscent 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 Codonanthe 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 extension 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 iridescent 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 Hypocyrtia). 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 Columnnea 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 Hypocyrtia) 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 Codonanthe section Codonanthe 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 Codonanthe 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 <u>Codonanthe</u>						
SUBGENUS <u>Codonanthe</u>						
SECTION <u>Codonanthe</u>						
1. <u>C. carnosa</u>	viny	2-4	round	green	4-10	
2. <u>C. devosiana</u>	viny	2-4	round	green	4-10	
3. <u>C. digna</u>	viny	2-4	round	green	4-10	
4. <u>C. gracilis</u>	viny	2-4	round	green	4-10	
5. <u>C. paula</u>	viny	2-4	round	green	4-10	
SECTION <u>Spathuliformae</u>						
6. <u>C. calcarata</u>	vin/shr	2-4	round	green	4-10	
7. <u>C. corniculata</u>	viny	2-4	round	red	4-10	
8. <u>C. crassifolia</u>	viny	2-4	round	green	4-10	
9. <u>C. uleana</u>	vin/shr	2-9	round	green	4-10	
SUBGENUS <u>Codonanthe</u>						
10. <u>C. caribaea</u>	vin/shr	2-4	round	green	4-10	
11. <u>C. chiricana</u>	vin/shr	2-4	round	green	4-10	
12. <u>C. elegans</u>	viny	2-4	round	green	4-10	
13. <u>C. luteola</u>	viny	2-4	round	green	4-10	
14. <u>C. macradenia</u>	viny	2-4	round	green	4-10	
GENUS <u>Nematanthus</u>						
1. <u>N. crassifolius</u>	shrubby	5-9	rnd/fur	green	10-50	
2. <u>N. fissus</u>	shrubby	5-9	rnd/fur	red	10-50	
3. <u>N. fritschii</u>	shrubby	5-9	round	green	10-50	
4. <u>N. hirtellus</u>	shrubby	5-9	round	red	10-50	
5. <u>N. maculatus</u>	shrubby	5-9	round	green	10-50	
6. <u>N. perianthomegus</u>	shrubby	5-9	round	red	10-50	
7. <u>N. gregarius</u>	viny	2-4	rnd/fur	green	4-10	
8. <u>N. nervosus</u>	viny	2-4	rnd/fur	green	4-10	
9. <u>N. strigillosus</u>	viny	2-4	rnd/fur	green	4-10	
10. <u>N. wettsteinii</u>	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. <u>C. carnos</u>	lam sym/base	sym	wid ellip	obtuse	obt-rnd	
2. <u>C. devosiana</u>	lam sym/base	sym	wid ellip	acute	obt-rnd	
3. <u>C. digna</u>	lam sym/base	sym	wid ovate	obtuse	rounded	
4. <u>C. gracilis</u>	lam sym/base	asym	nar ovate	acute-acum	cordate	
5. <u>C. paula</u>	lam sym/base	sym	wid ovate	obtuse	rounded	
6. <u>C. calcarata</u>	lam sym/base	asym	nar obov	acute	cordate	
7. <u>C. corniculata</u>	lam sym/base	sym	wid ellip	acute	acute	
8. <u>C. crassifolia</u>	lam sym/base	sym	nar ellip	acute-atten	acute	
9. <u>C. uleana</u>	lam & base	asym	obovate	acuminate	acute	
10. <u>C. caribaea</u>	lam sym/base	sym	elliptic	attenuate	acute	
11. <u>C. chiricana</u>	lam sym/base	sym	wid obov	acute	acute	
12. <u>C. elegans</u>	lam sym/base	sym	obovate	acute	acute	
13. <u>C. luteola</u>	lam sym/base	sym	wid ellip	acute	acute	
14. <u>C. macradenia</u>	lam sym/base	asym	wid ellip	acute	acute	
1. <u>N. crassifolius</u>	lam asym/base	sym	elliptic	acum-atten	acute	
2. <u>N. fissus</u>	lam sym/base	sym	elliptic	acute	acute	
3. <u>N. fritschii</u>	lam sym/base	sym	elliptic	acum-atten	acute	
4. <u>N. hirtellus</u>	lam sym/base	sym	wid ellip	acute-obtuse	obtuse	
5. <u>N. maculatus</u>	lam sym/base	asym	nar obov	acum-atten	acute	
6. <u>N. perianthomegus</u>	lam sym/base	sym	elliptic	acute-acum	acute	
7. <u>N. gregarius</u>	lam sym/base	sym	wid ellip	acute	acute	
8. <u>N. nervosus</u>	lam sym/base	asym	nar ovate	attenuate	obt-rnd	
9. <u>N. strigillosus</u>	lam sym/base	sym	wid ellip	acute	acute	
10. <u>N. wettsteinii</u>	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.

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

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

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

\* 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. <u>C. carnosa</u>	indeh/orange	bee	$2\bar{n}$	se Brazil
2. <u>C. devosiana</u>	indeh/orange	bee	$2\bar{n}$	se Brazil
3. <u>C. digna</u>	indeh/orange	bee		se Brazil
4. <u>C. gracilis</u>	indeh/orange	bee	$2\bar{n}$	se Brazil
5. <u>C. paula</u>	indeh/orange	bee		se Brazil
6. <u>C. calcarata</u>	deh/red-pur	bee	$4\bar{n}$	s Mex-CA-nw SA
7. <u>C. corniculata</u>	?deh/red-pur	bee	$4\bar{n}$	s Mex-CA-nw SA
8. <u>C. crassifolia</u>	deh/red-pur	bee	$4\bar{n}$	s Mex-CA-nw SA
9. <u>C. uleana</u>	deh/red-pur	bee	$4\bar{n}$	s Mex-CA-nw SA
10. <u>C. caribaea</u>	deh/red-pur	bee	$2\bar{n}$	s Mex-CA-nw SA
11. <u>C. chiricana</u>	deh/red-pur	bee		s Mex-CA-nw SA
12. <u>C. elegans</u>	deh/yel-grn	bee	$4\bar{n}$	s Mex-CA-nw SA
13. <u>C. luteola</u>	deh/yel-grn	bee	$2\bar{n}, 4\bar{n}$	s Mex-CA-nw SA
14. <u>C. macradenia</u>	deh/red-pur	bee	$4\bar{n}$	s Mex-CA-nw SA
1. <u>N. crassifolius</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
2. <u>N. fissus</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
3. <u>N. fritschii</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
4. <u>N. hirtellus</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
5. <u>N. maculatus</u>	deh/yel-grn	bird		se Brazil
6. <u>N. perianthomegus</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
7. <u>N. gregarius</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
8. <u>N. nervosus</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
9. <u>N. strigillosus</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil
10. <u>N. wettsteinii</u>	deh/yel-grn	bird	$2\bar{n}$	se Brazil

\* 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  $x=8$ ,  $2\bar{n}=16$  or diploids,  $4\bar{n}=32$  or tetraploids.

\*\*\*\* se Brazil=southeastern Brazil, s Mex-CA-nw SA=southern Mexico 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.

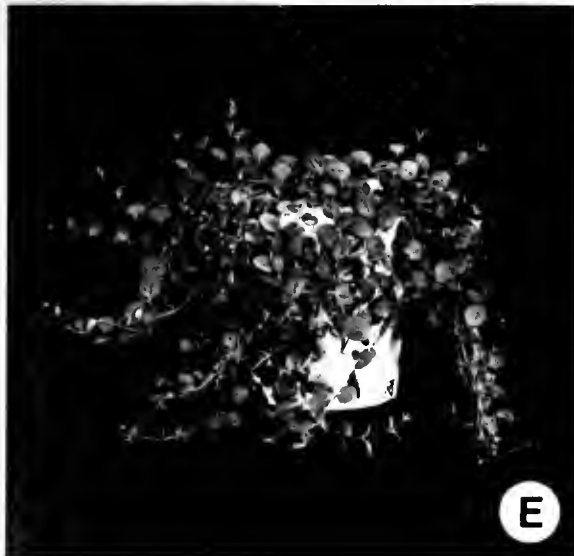
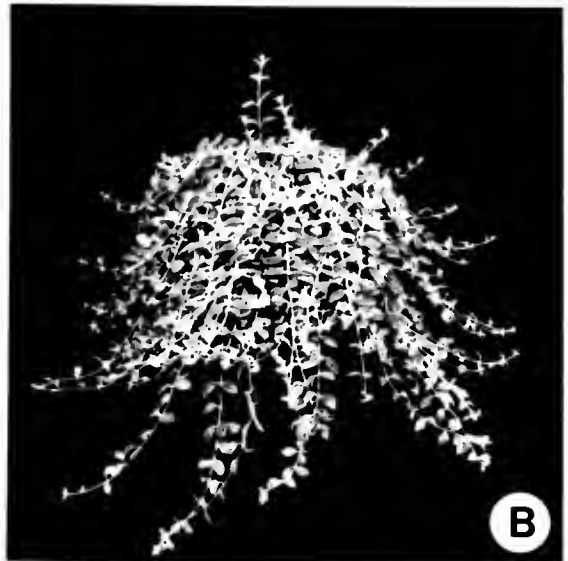
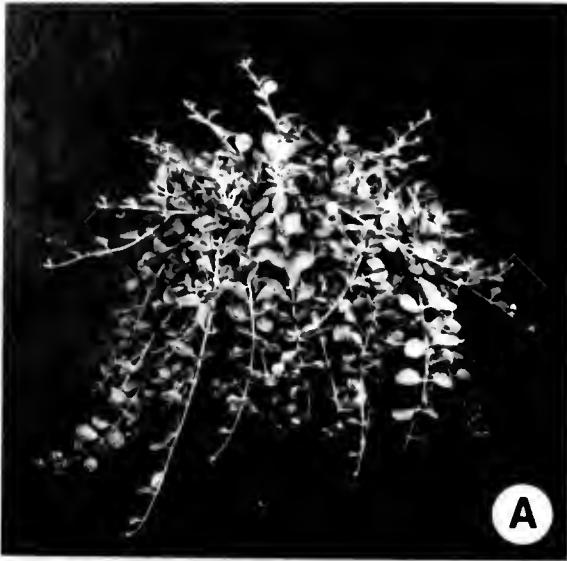


Figure II-2. Growth habit of species of Codonanthe subgenus  
Codonanthe section Spathuliformae.

- A. C. calcarata.
- B. C. corniculata.
- C. C. crassifolia.
- D. C. uleana.





Figure II-3. Growth habit of species of Codonanthe subgenus Codonanthe.

- A. C. caribaea.
- B. C. elegans.
- C. C. luteola.
- D. C. macradenia.

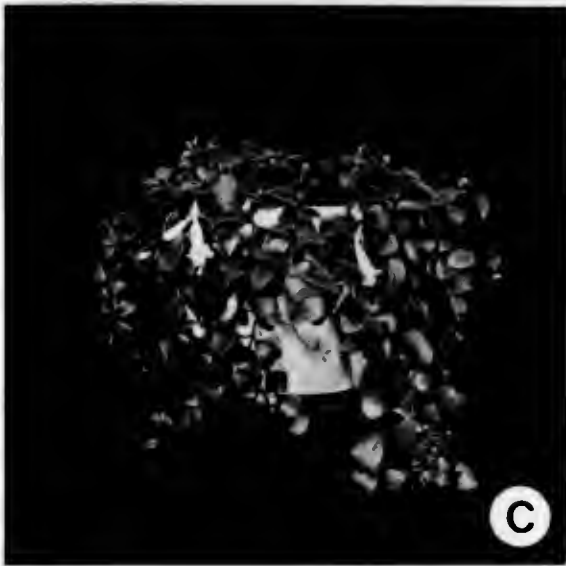


Figure II-4. Growth habit of species of Nematanthus.

- A. N. crassifolius.
- B. N. fissus.
- C. N. fritschii.
- D. N. hirtellus.
- E. N. maculatus.
- F. N. perianthomegus.



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

- A. N. gregarius.
- B. N. nervosus.
- C. N. strigillosus.
- D. N. wettsteinii.

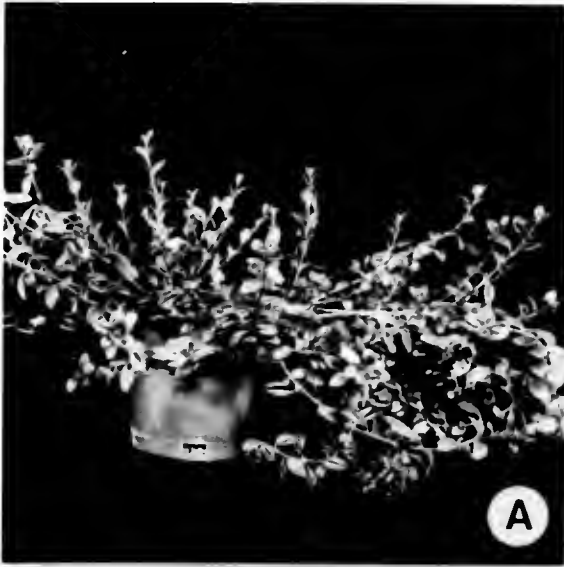
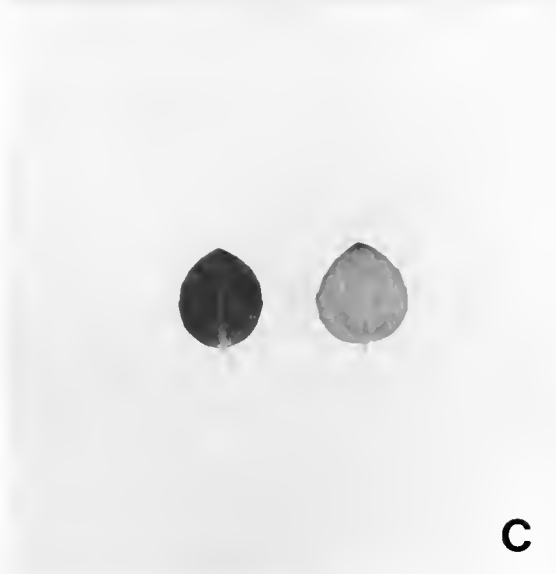
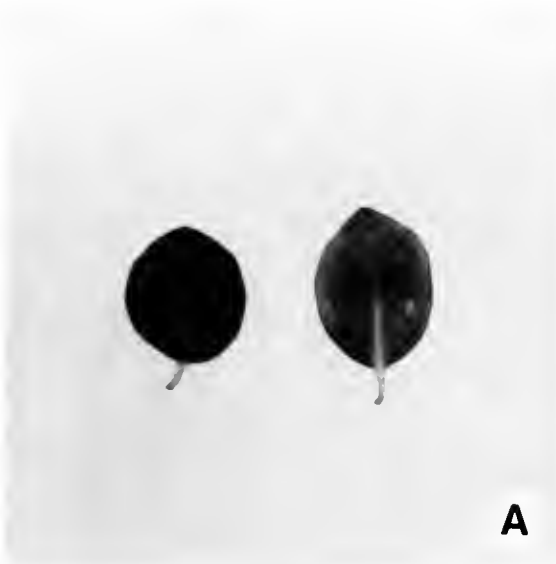


Figure II-6. Leaf blade shape of species of Codonanthe subgenus  
Codonanthe section Codonanthe.

- A. C. carnosa, X1.
- B. C. devosiana, X1.
- C. C. digna, X1.
- D. C. gracilis, X1.
- E. C. paula, X1.





**A**

**B**

**C**

**D**

**E**

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.



A



B



C



D

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.



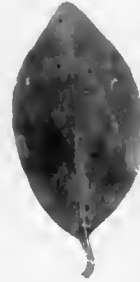
**A**



**B**



**C**



**D**

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**



**B**



**C**



**D**



**E**



**F**

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.





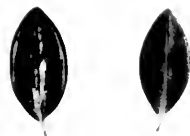
A



B



C



D

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.

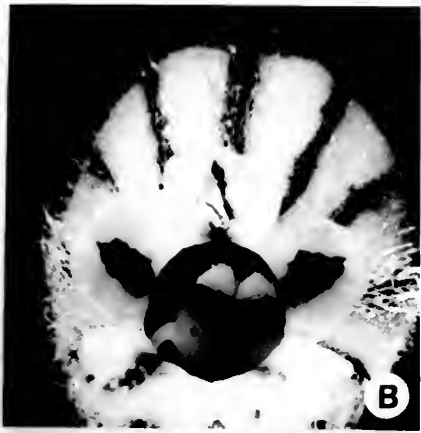


Figure II-12. Floral morphology of species of Codonanthe.

- 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.

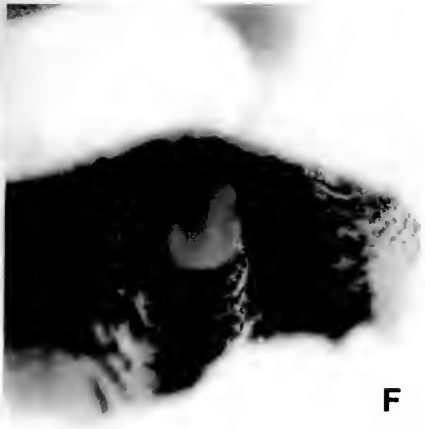
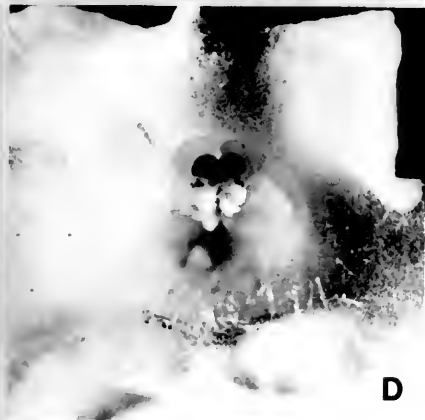


Figure II-13. Stigma and stigmatic surface.

- 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.

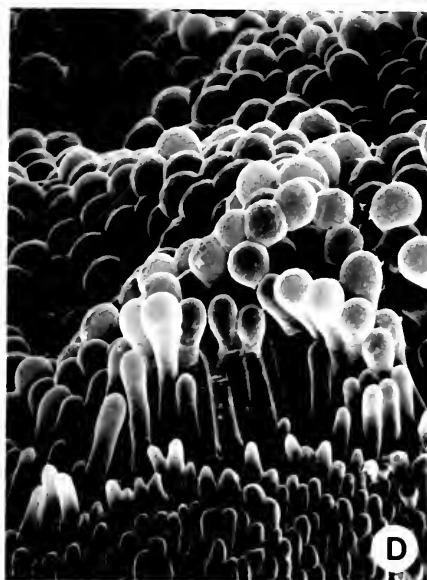
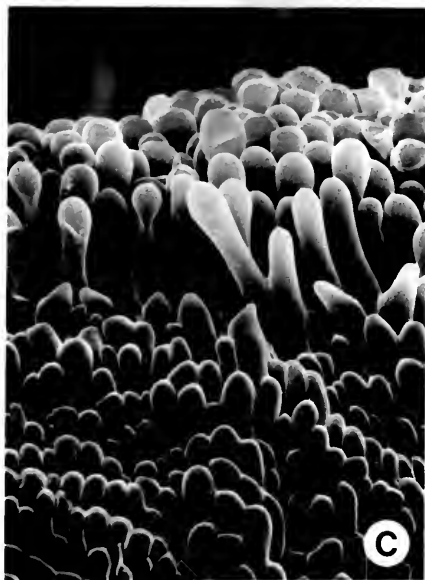
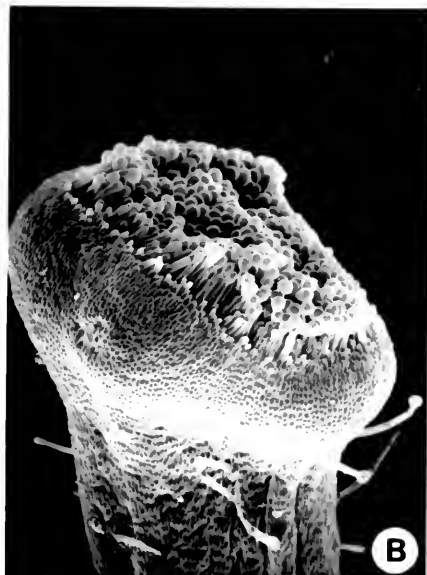


Figure II-14. Floral morphology and fruit of species of Codonanthe.

- 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.





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

A. C. devosiana, X75.

B. C. digna, X75.

C. C. paula, X75.



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

- A. C. calcarata, X30.
- B. C. crassifolia, X50.
- C. C. caribaea, X50.
- D. C. macradenia, X50.



Figure II-17. Seeds of species of Nematanthus.

A. N. gregarius, X75.

B. N. nervosus, X75.

C. N. fissus, X75.



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.





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 Columnnea 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 temperature, 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 Coat (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  $\pm$  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). Aniscytic 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 23.2 $\mu$ m, mean width of 19.7 $\mu$ m and area index of 458 $\mu$ m<sup>2</sup>.

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 30.3 $\mu$ m, mean width of 26.2 $\mu$ m and area index of 796 $\mu$ m<sup>2</sup>.

SUBGENUS Codonanthe 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 33.1 $\mu$ m, mean width of 28.2 $\mu$ m and area index of 936 $\mu$ m<sup>2</sup>.

#### 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.

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



Table III-1 - continued.

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

<sup>1</sup> Occurs on both surfaces of the leaves in all species.

<sup>2</sup> More than 4 cells per head and/or more than 1 trichome per basal epidermal cell.

<sup>3</sup> 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	EXTRAFLOREAL NECTARY	EPIDERMAL CELL ORNAMENTATION
	AN=anisocytic HEL=helicyotic		
GENUS <u>Codonanthe</u>			
SUBGENUS <u>Codonanthe</u>			
SECTION <u>Codonanthe</u>			
<u>C. carnosa</u>	AN	absent	none
<u>C. devosiana</u>	AN	absent	none
<u>C. digna</u>	AN	absent	none
<u>C. gracilis</u>	AN	absent	echinate papillae
<u>C. paula</u>	AN	absent	none
SECTION <u>Spathuliformae</u>			
<u>C. calcarata</u>	AN	abaxial	none
<u>C. corniculata</u>	AN	abaxial	none
<u>C. crassifolia</u>	AN	abaxial	none
<u>C. uleana</u>	AN	abaxial	none
SUBGENUS <u>Codonanthe</u> lla			
<u>C. caribaea</u>	AN	absent	echinate papillae
<u>C. chiricana</u>	AN	abaxial	none
<u>C. elegans</u>	AN	abaxial	none
<u>C. luteola</u>	AN	abaxial	none
<u>C. macradenia</u>	AN	abaxial	none
GENUS <u>Nematanthus</u>			
<u>N. crassifolius</u>	AN	absent	none
<u>N. fissus</u>	AN	absent	striations
<u>N. fritschii</u>	AN	absent	none
<u>N. hirtellus</u>	AN	absent	none
<u>N. maculatus</u>	AN	absent	none
<u>N. perianthomegus</u>	AN	absent	none
<u>N. gregarius</u>	AN + HEL	absent	none
<u>N. nervosus</u>	AN + HEL	absent	none
<u>N. strigillosus</u>	AN + HEL	absent	none
<u>N. wettsteinii</u>	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 29.5 $\mu$ m, mean width of 22.5 $\mu$ m and area index of 666 $\mu$ m<sup>2</sup>.

### 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 Codonanthe 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 nectaries are consistent characters in species of section Codonanthe. Species in section Spathuliformae and subgenus Codonanthe 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 Codonanthe section Codonanthe, 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  $796\mu\text{m}^2$ ) have guard cells that are more similar in size with subgenus Codonanthe section Codonanthe (area index  $936\mu\text{m}^2$ ) than with subgenus Codonanthe section Codonanthe

(area index  $458\mu\text{m}^2$ ). 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  $666\mu\text{m}^2$ . 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.

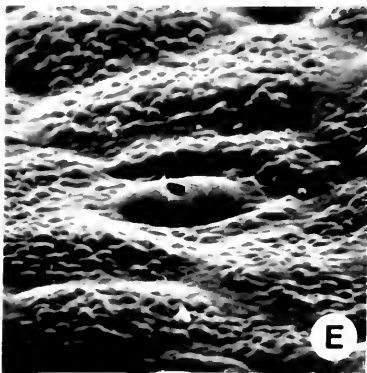
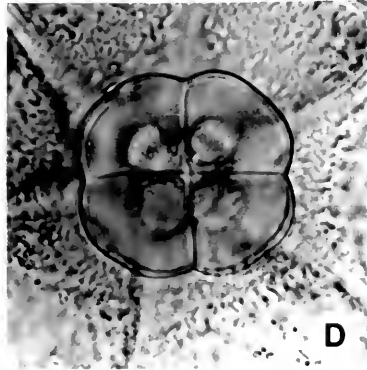
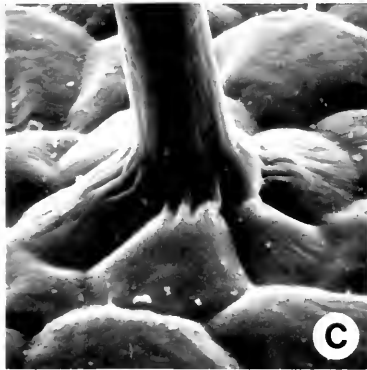
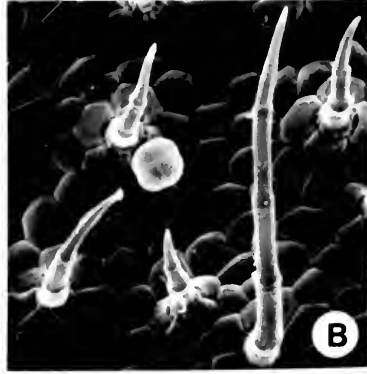
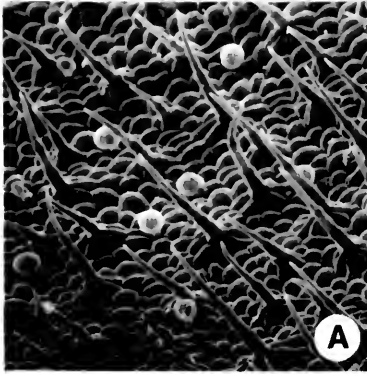




Figure III-2. Leaf epidermal features of species of Codonanthe subgenus Codonanthe section Spathuliformae and subgenus Codonanthella.

- 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.

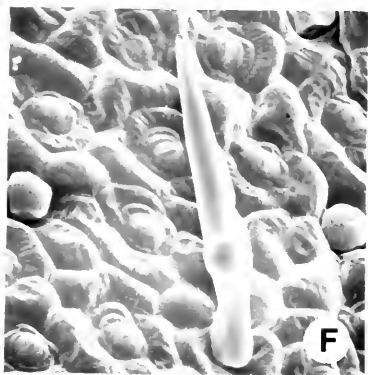
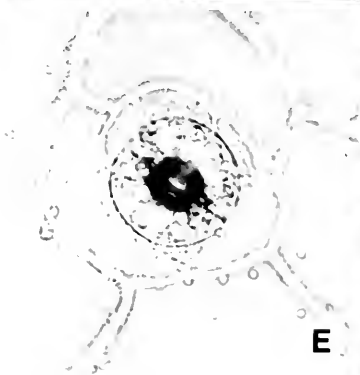
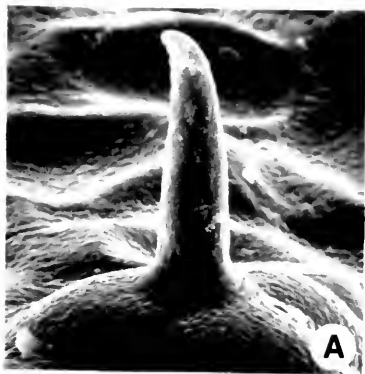


Figure III-3. Leaf epidermal features of species of Codonanthe subgenus Codonanthe section Spathuliformae.

- 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.

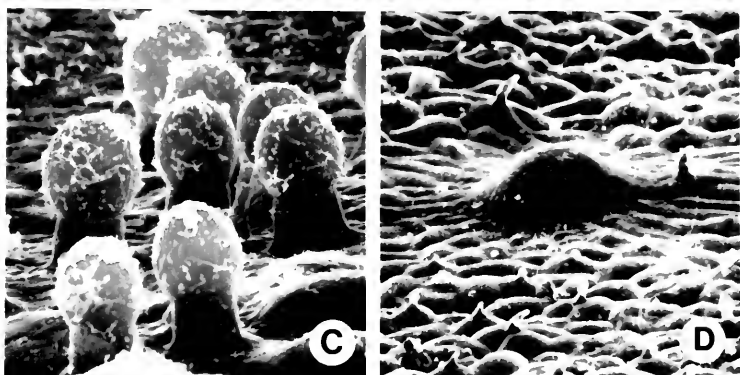
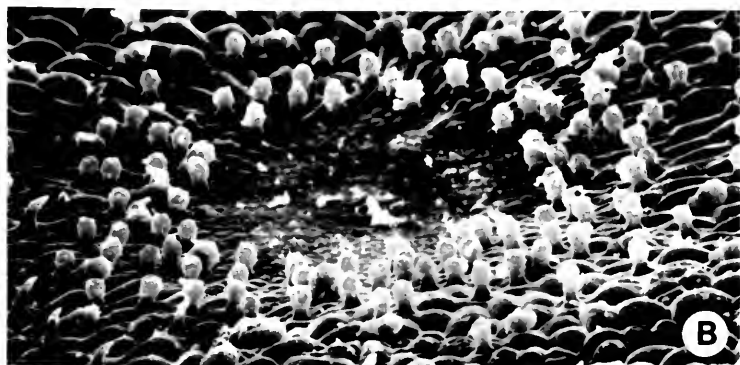


Figure III-4. Leaf epidermal features of species of Nematanthus.

- 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.

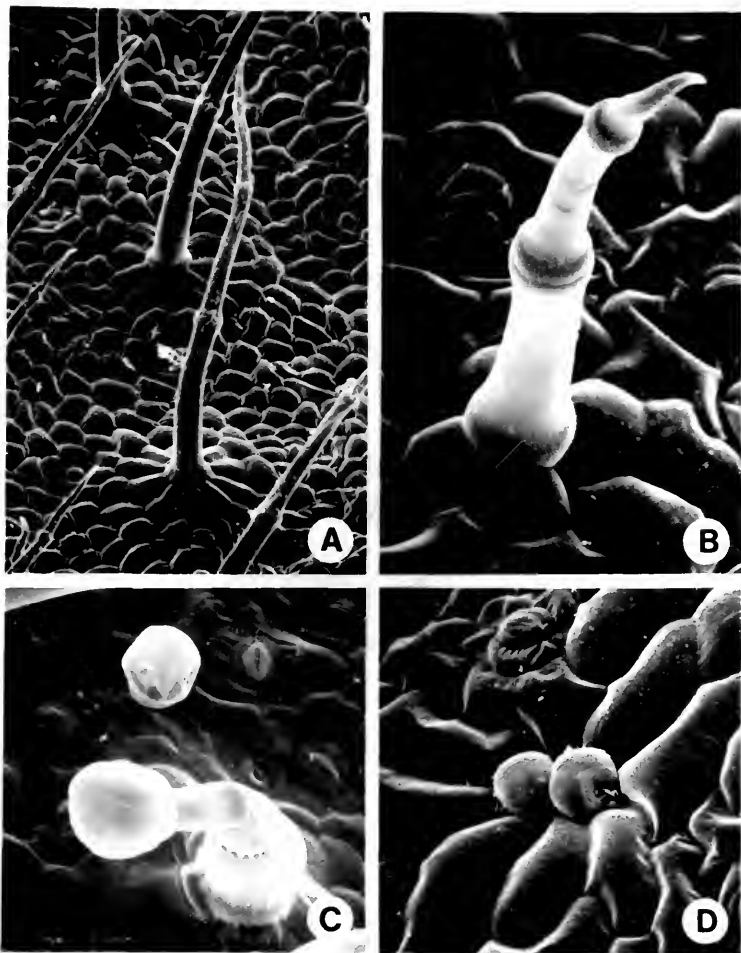


Figure III-5. Leaf epidermal features of species of Nematanthus.

- 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.

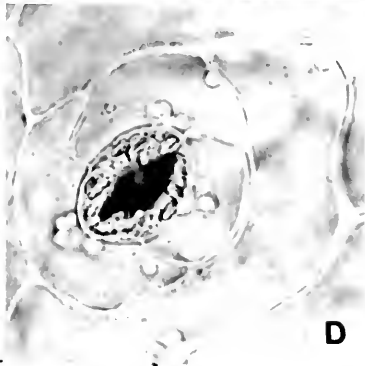
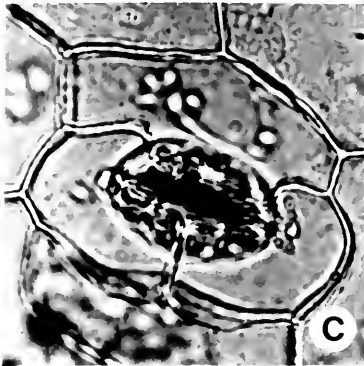
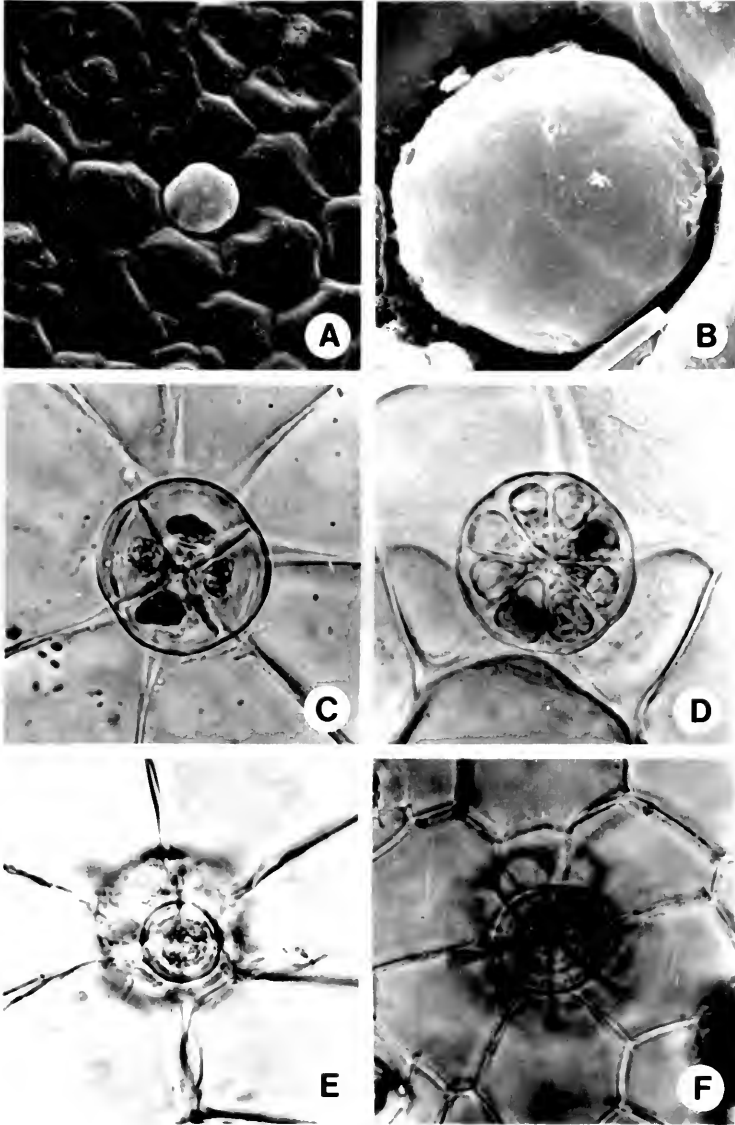




Figure III-6. Leaf epidermal features of species of Nematanthus.

- 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.



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  $45^{\circ}$  to  $65^{\circ}$ . 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 Codonanthe section Codonanthe 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.

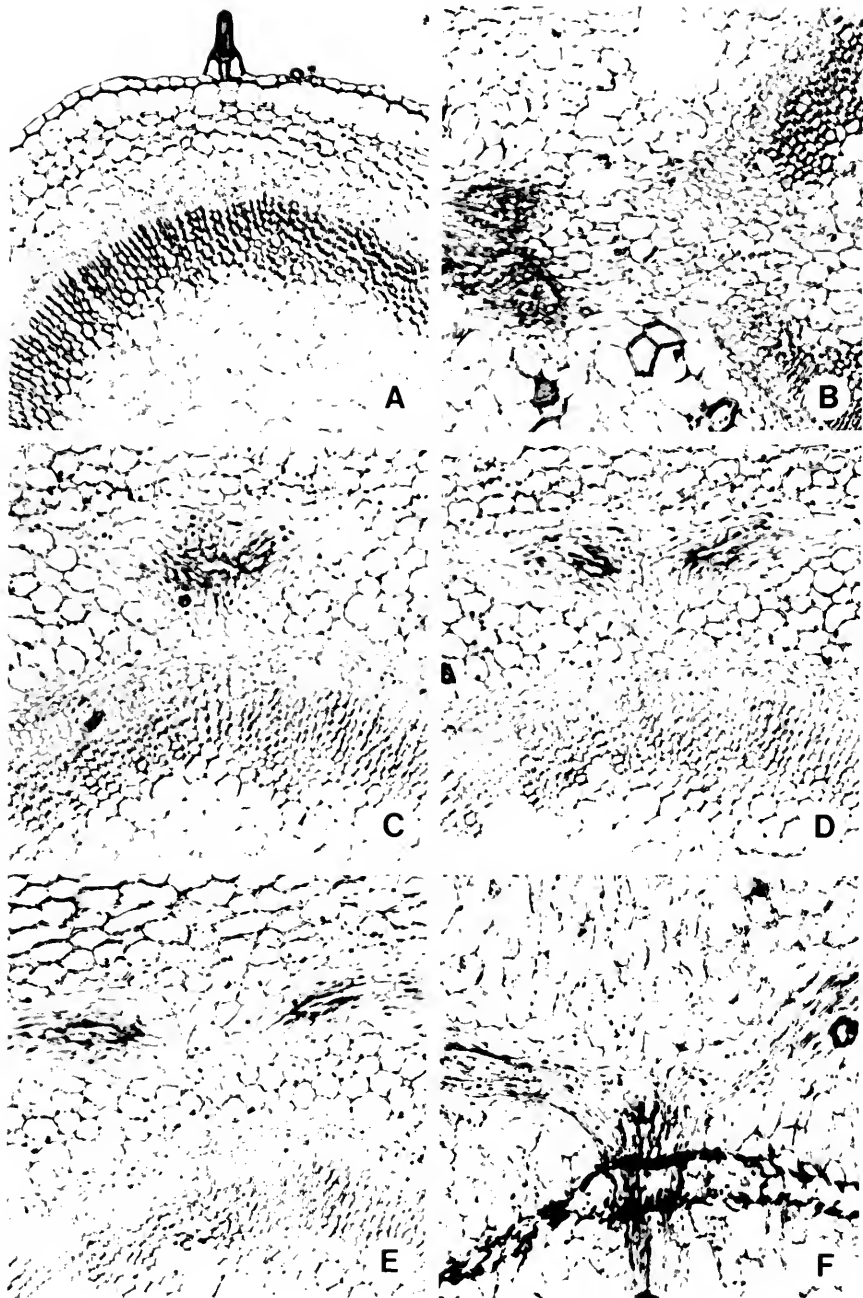


Figure IV-2. Transverse sections of the node of Codonanthe corniculata, X80.

- 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.

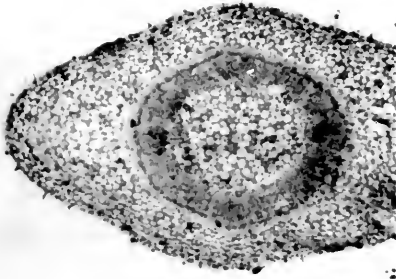
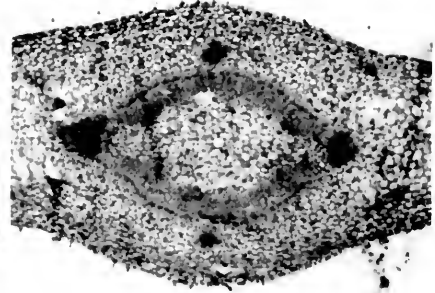
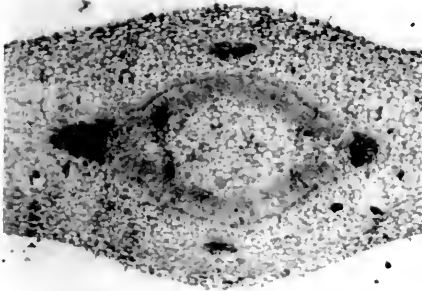
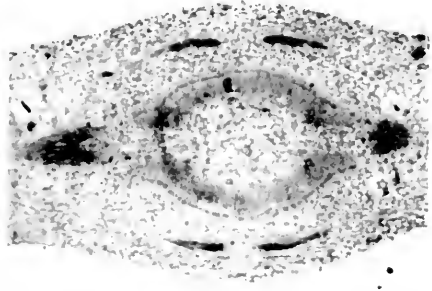
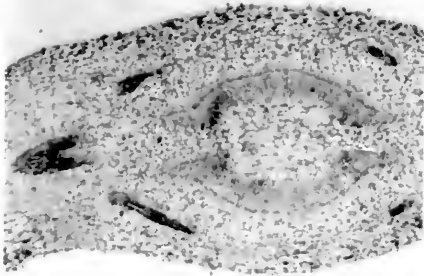
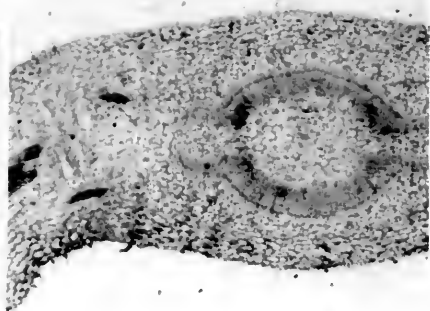
**A****B****C****D****E****F**

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.

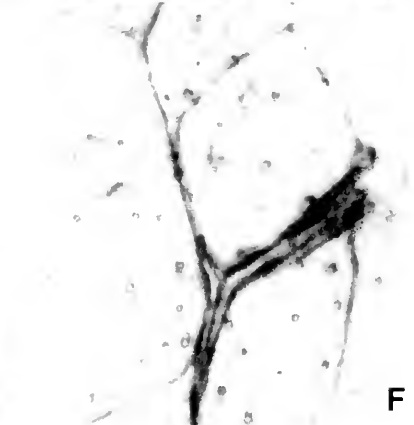
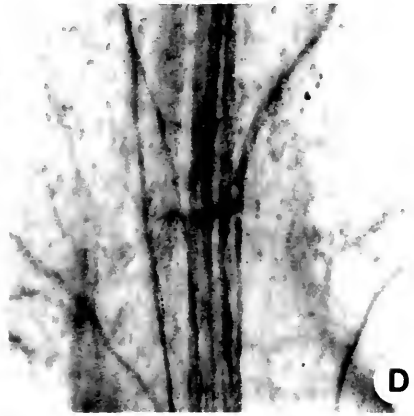
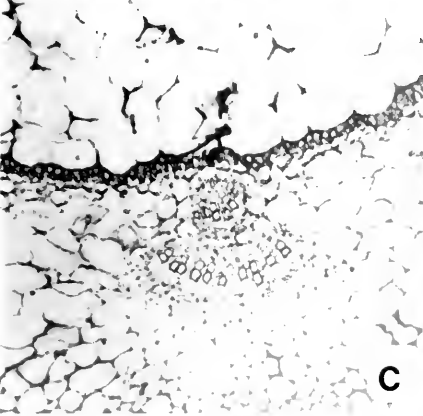
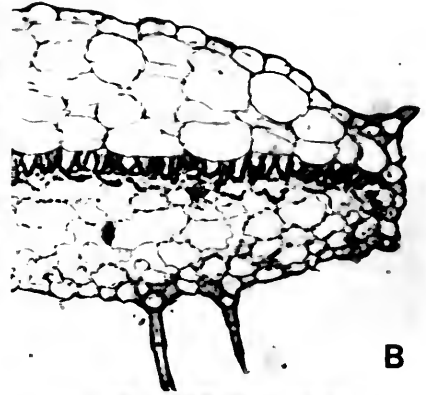
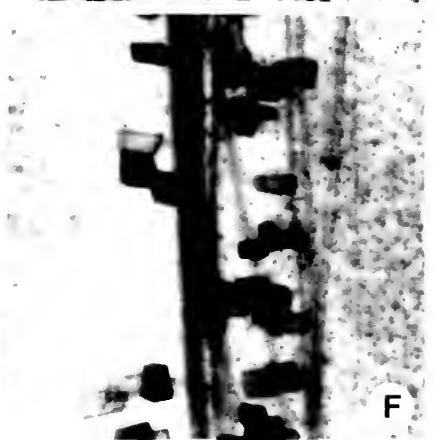
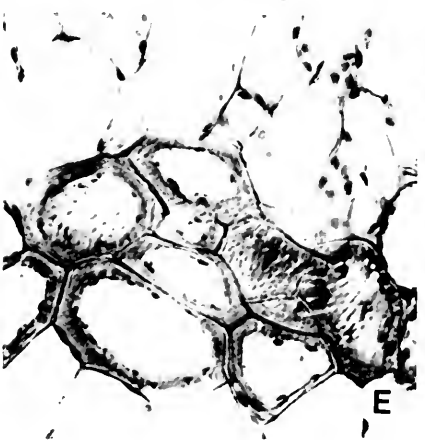
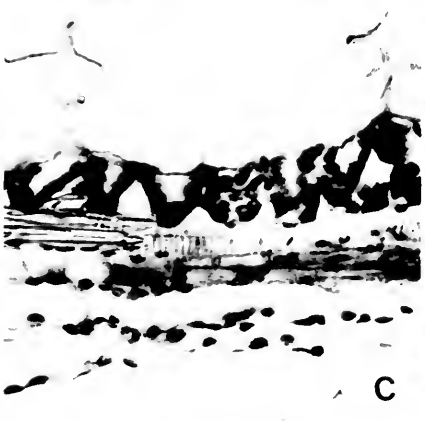
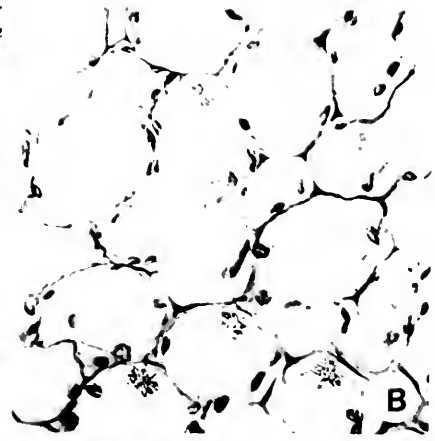
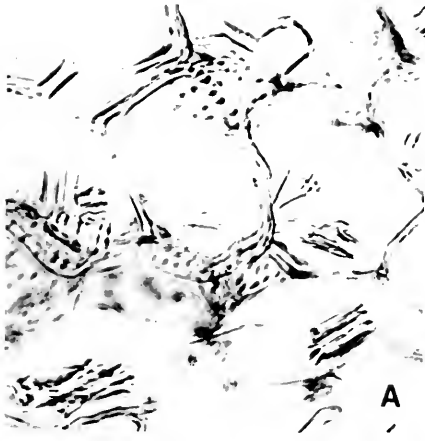




Figure IV-4. Crystals and sclereids in species of Codonanthe and Nematanthus.

- 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.



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, Hypocyrtia 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 dehiscent 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, dehiscent 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 equipped with an eyepiece micrometer was used to examine and measure the pollen specimens. Pollen size is presented as a mean value  $\pm$  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  $\mu\text{m}$  and medium-sized pollen are 25-49  $\mu\text{m}$  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 extexine 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 network 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 reticulate 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  $18.1 \pm .75$   $\mu$ m polar axis (P) and an  $18.5 \pm .35$   $\mu$ m 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  $26.7 \pm .93$   $\mu$ m polar axis (P) and a  $29.6 \pm .94$   $\mu$ m 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  $29.7 \pm .60$   $\mu$ m polar axis (P) and a  $32.6 \pm .94$   $\mu$ m 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  $25.3 \pm .80$   $\mu$ m polar axis (P) and a  $25.5 \pm .48$   $\mu$ m 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 sparsely 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 successive 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 Codonanthe section Codonanthe 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 Codonanthe section Codonanthe 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 sparsely 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-oblolate pollen grains, respectively, that are zonocolpate.
- D. Pollen grains with polygonal, angulaperturate amb.

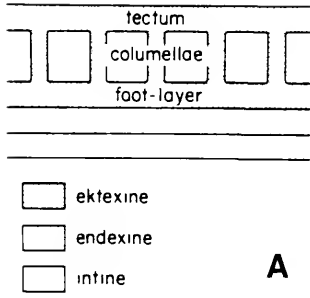
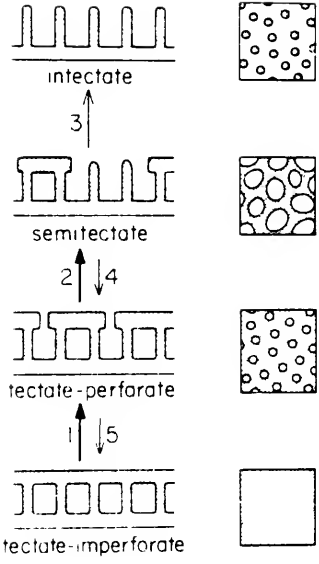
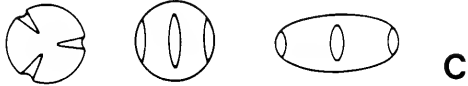
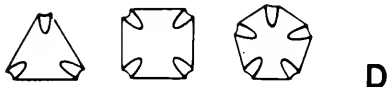
**A****B****C****D**

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.

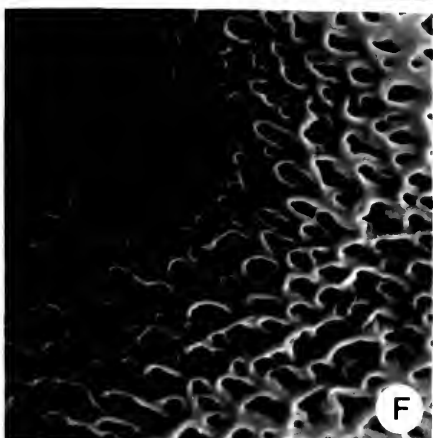
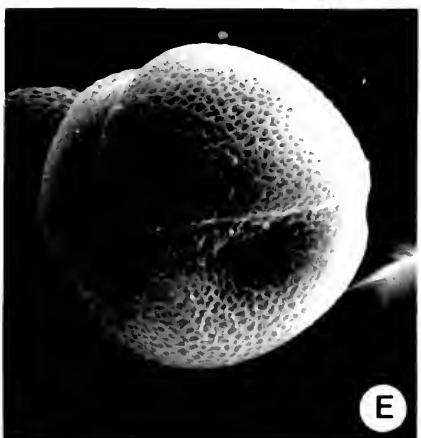
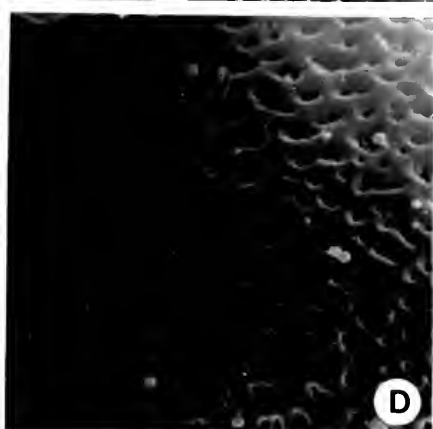
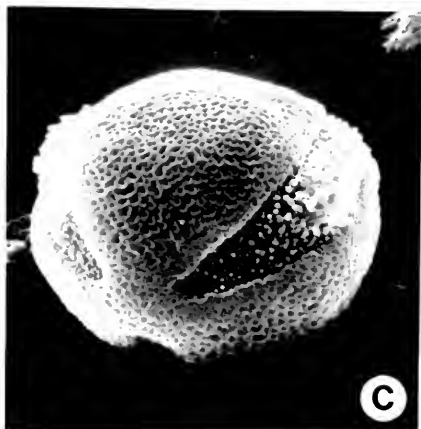
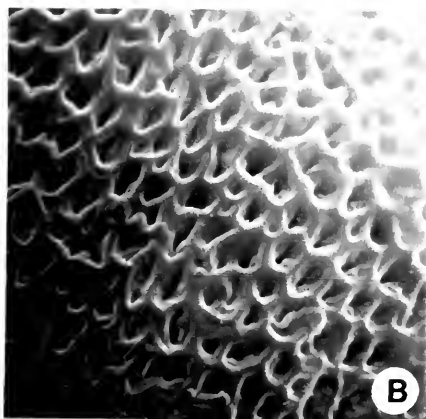
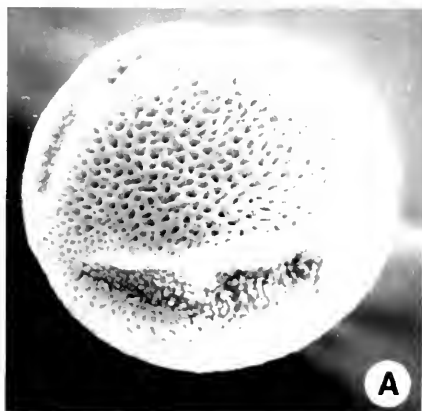


Figure V-3. Pollen morphology of species of Codonanthe subgenus  
Codonanthe section Codonanthe.

- 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.



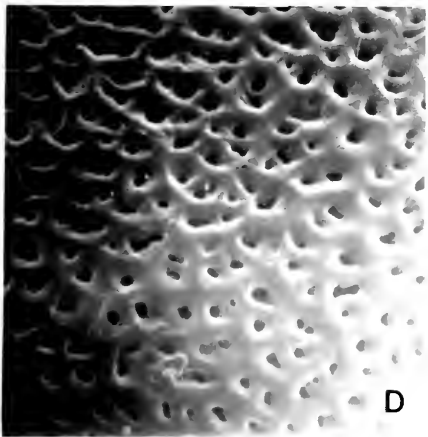
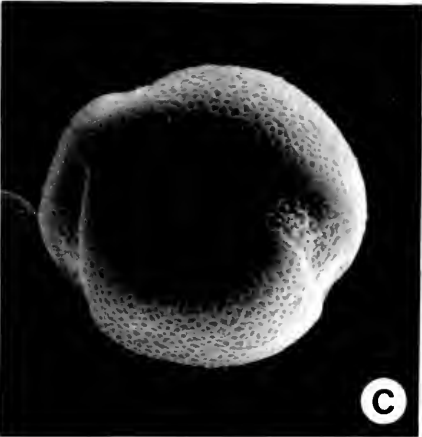
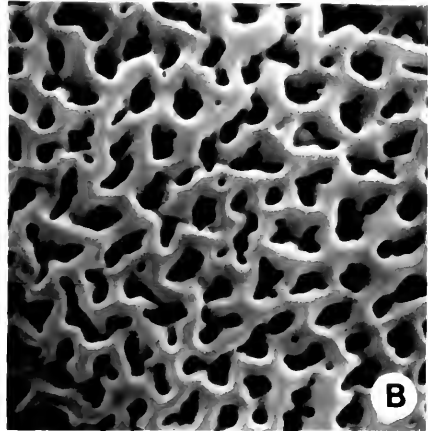
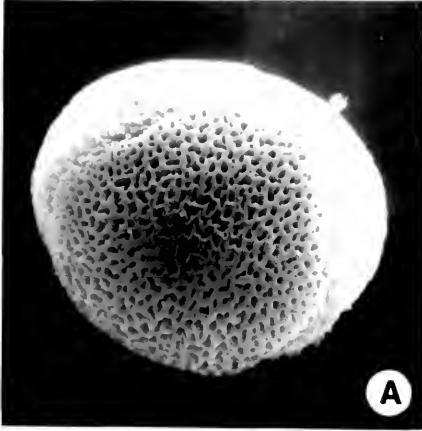


Figure V-4. Pollen morphology of species of Codonanthe subgenus  
Codonanthe section Spathuliformae.

- 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.

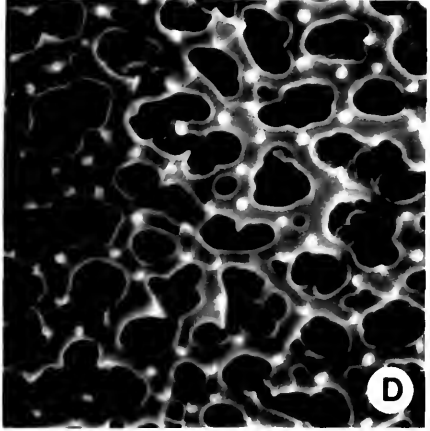
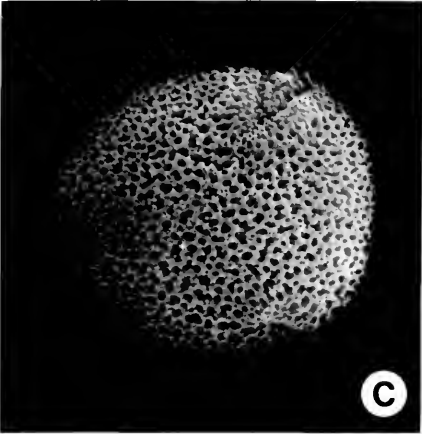
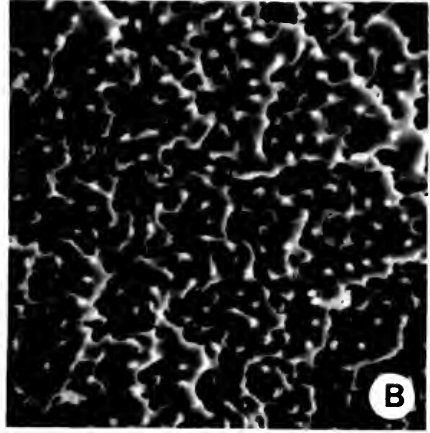
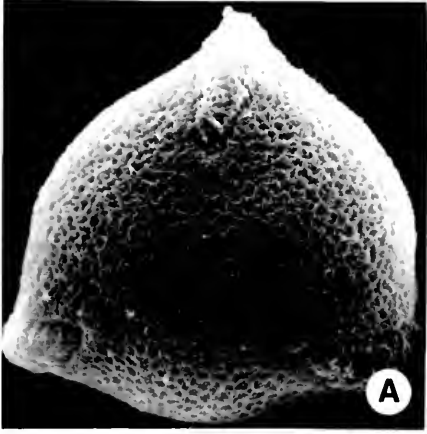


Figure V-5. Pollen morphology of species of Codonanthe subgenus  
Codonanthe section Spathuliformae.

- 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.

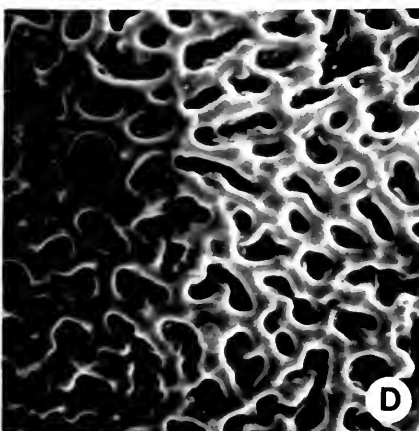
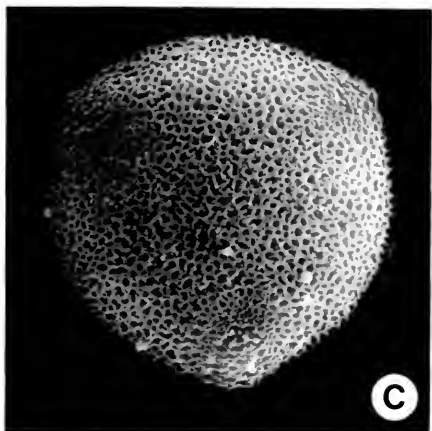
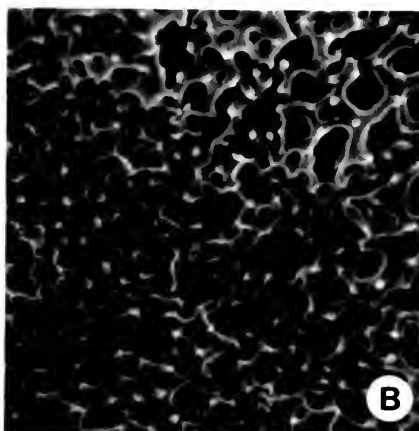
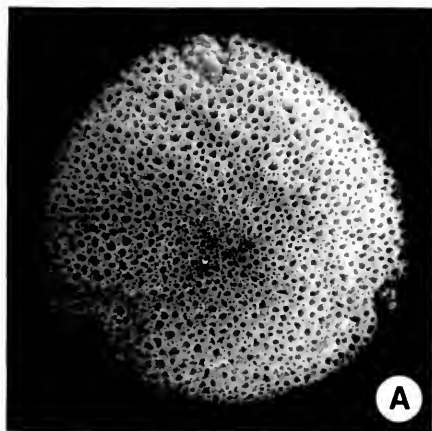


Figure V-6. Pollen morphology of species of Codonanthe subgenus Codonanthe.

- 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.

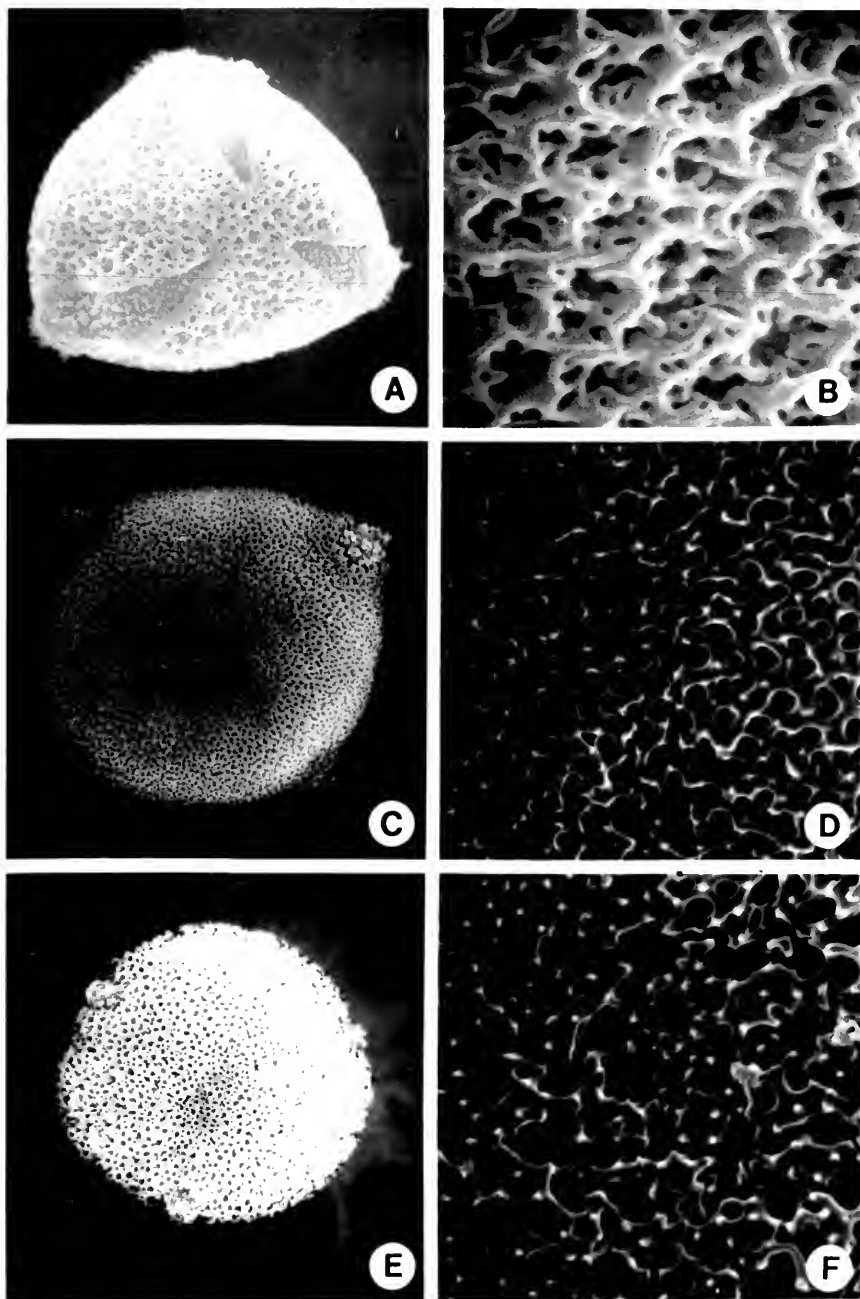


Figure V-7. Pollen morphology of species of Codonanthe subgenus Codonanthe.

- 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.



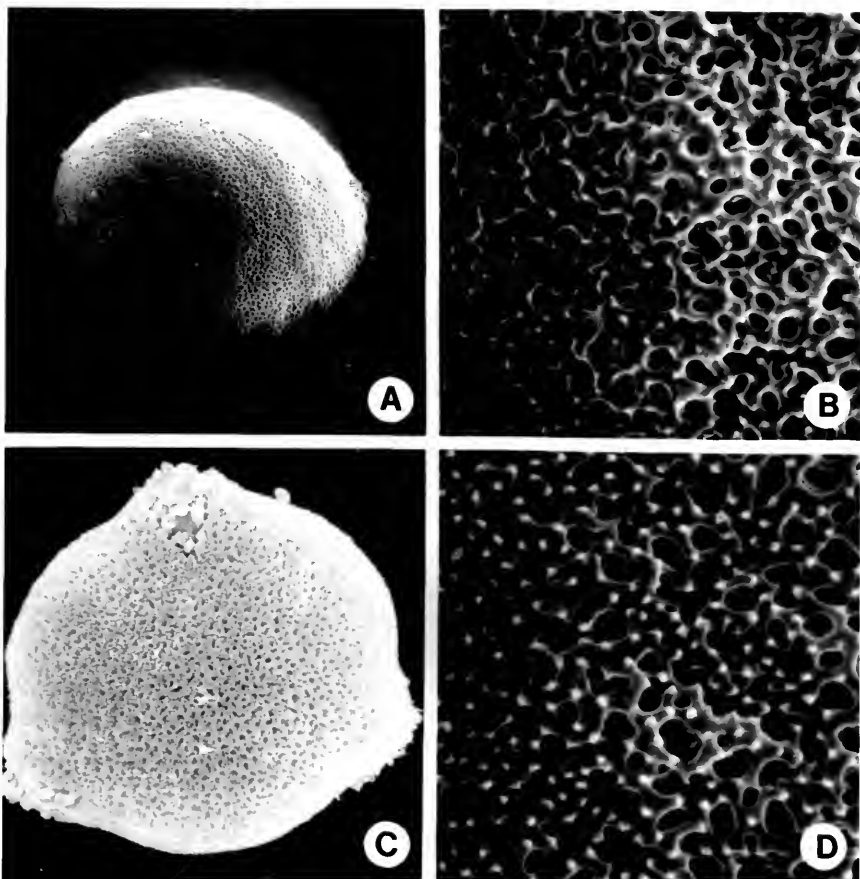


Figure V-8. Pollen morphology of species of Nematanthus (section Nematanthus, cf. CONCLUSION and APPENDIX).

- 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.

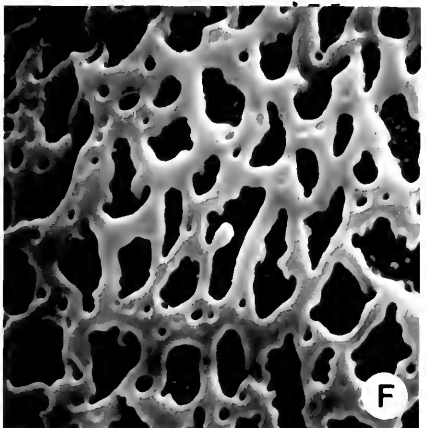
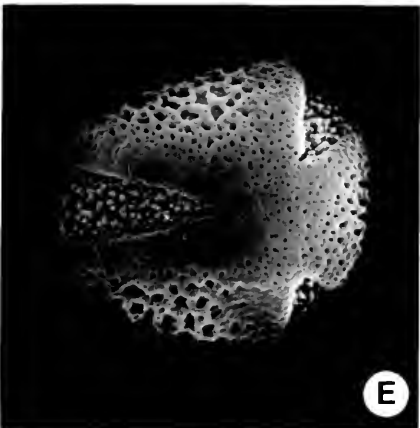
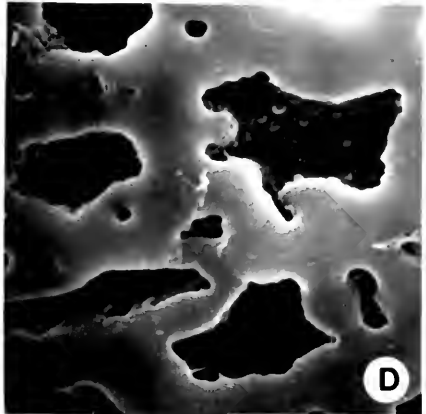
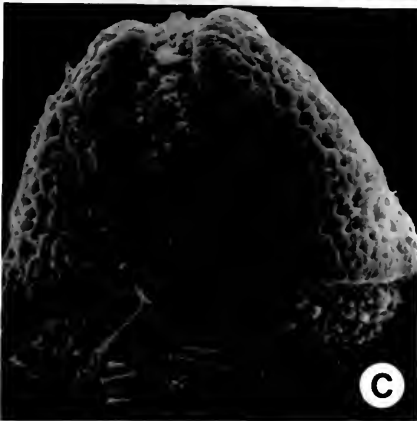
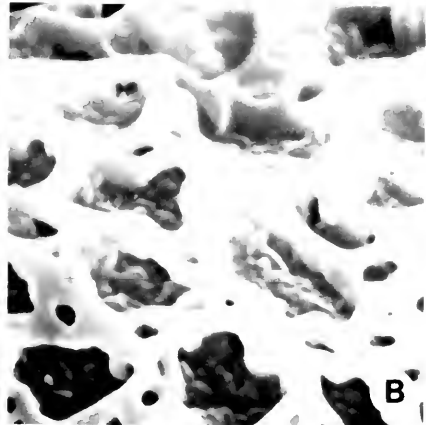
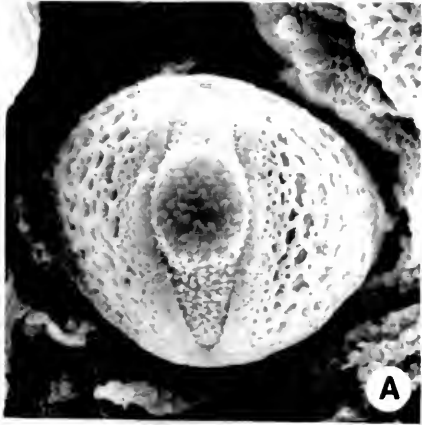


Figure V-9. Pollen morphology of species of Nematanthus (section Nematanthus, cf. CONCLUSION and APPENDIX).

- 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.

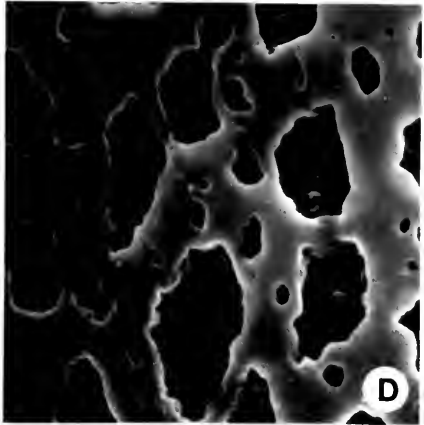
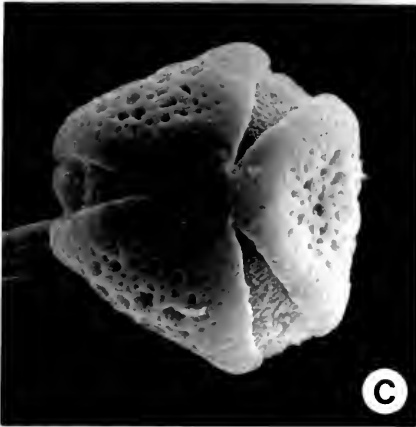
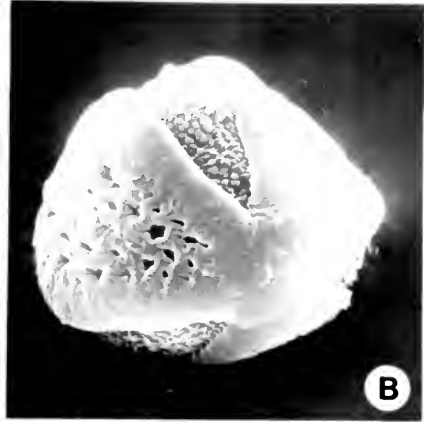
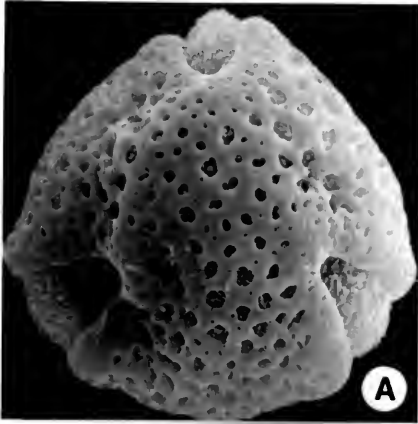


Figure V-10. Pollen morphology of species of Nematanthus (section Parvifolius, cf. CONCLUSION and APPENDIX).

- 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.

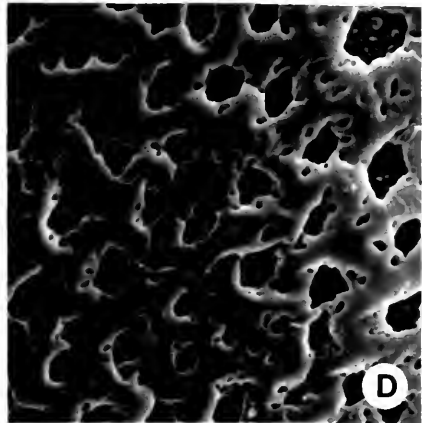
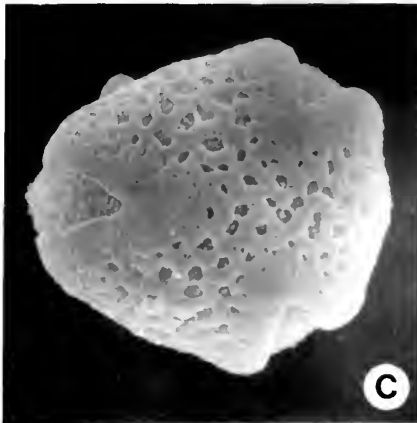
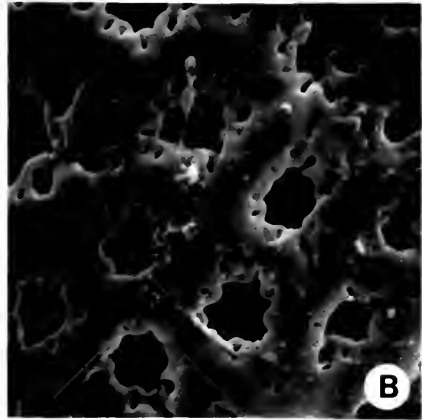
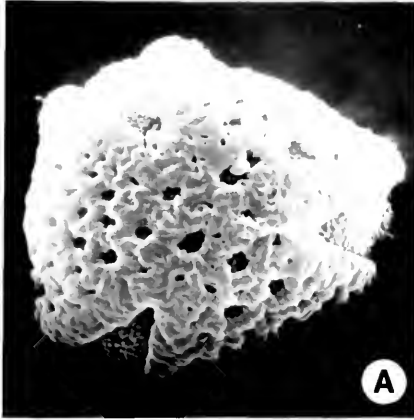


Figure V-11. Pollen morphology of species of Nematanthus (section Parvifolius, cf. CONCLUSION and APPENDIX).

- 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.



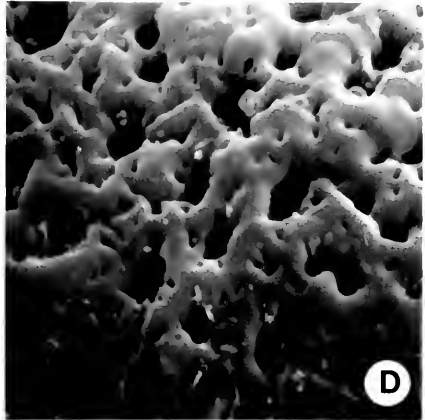
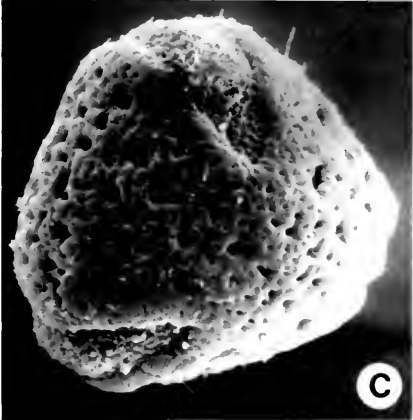
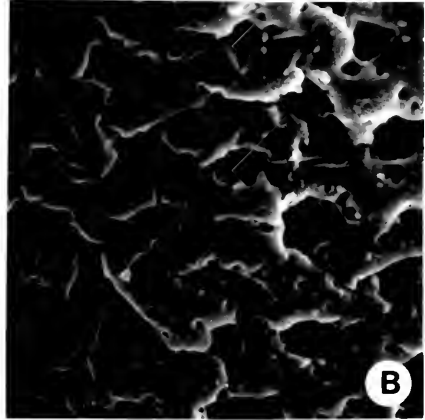
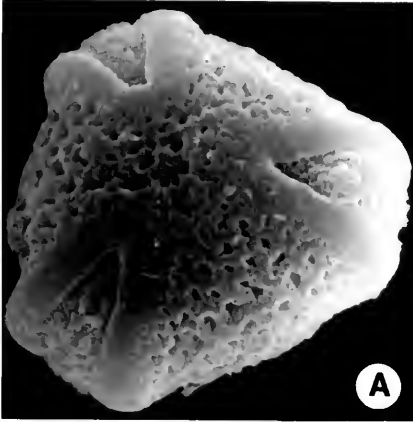
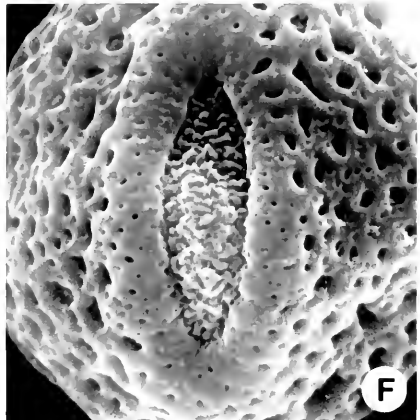
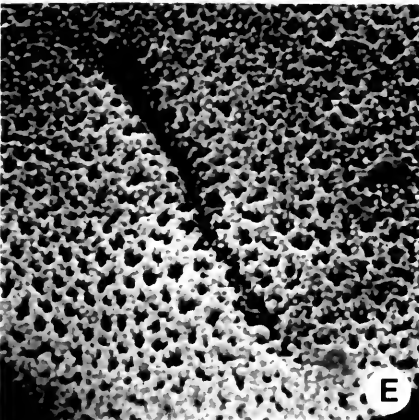
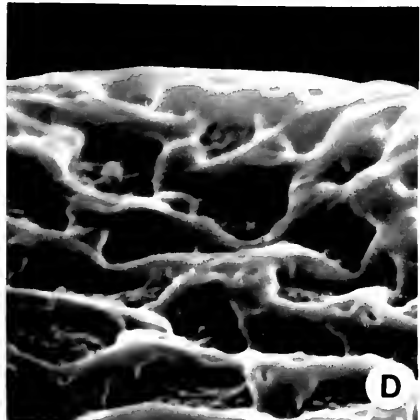
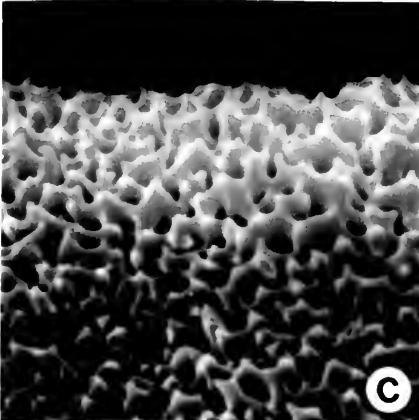
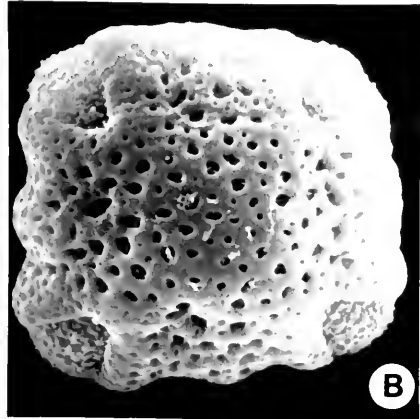
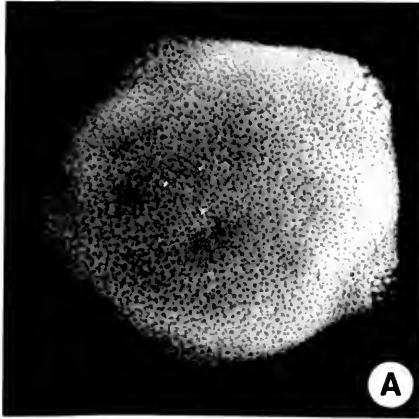


Figure V-12. Varying features of pollen morphology and exine structure.

- 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.



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 funnellform-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  $\mu\text{m}$ , 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 Codonanthe 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  $\mu\text{m}$ ), 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  $458 \mu\text{m}^2$ , lack extrafloral nectaries, and are indigenous to southeastern Brazil. Species of subgenus Codonanthe section Spathuliformae and subgenus Codonanthe section Codonanthe 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  $\mu\text{m}$ ), 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  $796 \mu\text{m}^2$  and  $936 \mu\text{m}^2$ , 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 ( $\underline{n}=8$ ), tetraploid ( $\underline{n}=16$ )	diploid ( $\underline{n}=8$ )
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 $\mu\text{m}$ ) & medium (25-49 $\mu\text{m}$ )	medium (25-49 $\mu\text{m}$ )
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.

CHARACTER	SUBGENUS <u>Codonanthe</u>		
	SECTION <u>Codonanthe</u>	SECTION <u>Spathuliformae</u>	SUBGENUS <u>Codonanthe</u>
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 <u>C. caribaea</u> , $n=8$ ; <u>C. luteola</u> , $n=8, 16$ )
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	multicellular	unicellular	unicellular (except <u>C. caribaea</u> )
Cells			
b) Nonglandular			
Trichome	radial (except	random	random
Basal Cell	<u>C. gracilis</u> )		
Arrangement			
c) Glandular	4-celled	2-celled	2-celled (except <u>C. caribaea</u> )
Trichome			
Head			
d) Extrafloral	absent	present	present (except <u>C. caribaea</u> )
Nectaries			
e) Guard Cell	458 $\mu\text{m}^2$	796 $\mu\text{m}^2$	936 $\mu\text{m}^2$
Area Index			
5) NODAL ANATOMY	unilacunar (except <u>C. carnosa</u> & <u>C. gracilis</u> )	trilacunar, split-lateral	trilacunar, split-lateral
6) POLLEN SIZE	small (10-24 $\mu\text{m}$ )	medium (25-49 $\mu\text{m}$ )	medium (25-49 $\mu\text{m}$ )

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

CHARACTER	SECTION <u>Nematanthus</u>	SECTION <u>Parvifolius</u>
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, helicoctytic
6) NODAL ANATOMY	trilacunar, split-lateral	unilacunar
7) POLLEN APOCOLPIA	psilate (except <u>N. hirtellus</u> )	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.

Hypocyrtia section Codonanthe Martius, Nova Genera et Species Plantarum 3: 49. 1829.

Type: Hypocyrtia 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 funnellform-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, dehiscent 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.

Hypocyrtia 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-splotted 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, dehiscent 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 aniscocytic 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 Codonanthe
- 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 CultivationGENUS 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.  
Hypocyrtia 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.  
Hypocyrtia 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; Isotype, 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).  
Columnnea 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.  
Columnnea 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.  
Hypocyrtia Selloana Klotzsch & Hanstein in Hanstein in Martius, *Flora Brasiliensis* 8: 409. 1864.  
H. fissa (Vellozo) Handro & L. B. Smith, *Phytologia* 20: 390. 1970.  
Nematanthus Selloana (Klotzsch & Hanstein) H. E. Moore, *Baileya* 19: 38. 1973.
- N. fritschii Hoehne, *Sellowia* 9: 76. 1958; O. Handro, *Arquivos de Botanica de Estado de Sao Paulo*, series 2, 3(5): 228, plate 57B. 1962.  
Hypocyrtia Kuhlmannii O. Handro, *Arquivos Botanica de Estado de Sao Paulo*, series 2, 3(6): 339, plate 79B. 1964.  
Hypocyrtia Mattosiana O. Handro, *Arquivos Botanica de Estado de Sao Paulo*, series 2, 3(6): 338, plate 79A. 1964.  
Nematanthus Mattosiana (O. Handro) H. E. Moore, *Baileya* 18: 143. 1972.  
N. fluminensis Hort. not N. fluminensis (Vellozo) Fritsch.

- N. gregarius D. Denham, *Baileya* 19: 126. 1974.  
Hypocyrtia radicans Klotzsch & Hanstein in Martius, *Florae Brasiliensis* 8(1): 409. t. 67, f. 2. 1 Dec. 1864.  
Columna radicans (Klotzsch & Hanstein) O. Kuntze, *Revisio Generum Plantarum* 2: 472. 5 Nov. 1891.  
Nematanthus radicans (Klotzsch & Hanstein) H. E. Moore, *Baileya* 19(1): 38. 20 Nov. 1973, illegitimate name, not Nematanthus radicans K. Presl, *Abhandlung der Bohmischen Gesellschaft der Wissenschaften* V, 3: 573. 1845 and in *Botanische Bemerkungen* 143 (typographic error '145') "1844" (1846?).
- N. hirtellus (Schott) Wiehler, *Baileya* 18(4): 134. 1971.  
Besleria hirtella Schott, *Medicinische Jahrbucher* 6(2): 94. (=p. 66). 1820.  
Alloplectus sparsiflorus Martius, *Nova Genera et Species Plantarum* 3: 55, t. 55, fig. 1. 1829.  
A. parviflorus (in error for sparsiflorus) Hanstein, *Linnaea* 34: 377. 1865.  
Crantzia parviflora Fritsch in Engler & Prantl, *Naturlichen Pflanzenfamilien* 4(3b): 168. 1894.  
Hypocyrtia discolor Lindley, *Botanical Register* 31, Misc. 19. 1845.  
Alloplectus dichrous Hooker, *Botanical Magazine* 72: t. 4216. 1846, not A. dichrous De Candolle, *Prodromus* 7: 546. 1839.  
Crantzia hirtella (Schott) Fritsch, *Beiblatt zu den Botanischen Jahrbucher* 65: 8. 1900.  
Alloplectus hirtellus (Schott) Preston ex Hoehne, *Sellowia* 9: 45. 1958; cf. Preston in Chittendon, *RHS Dictionary of Gardening* 1: 79. 1951.
- N. maculatus (Fritsch) Wiehler, *Selbyana* 5(1): 63. 1978.  
Hypocyrtia maculata Fritsch, *Beiblatt zu den Botanischen Jahrbucher Systematik* 65: 10. 1900.
- N. nervosus (Fritsch) H. E. Moore, *Baileya* 19(1): 38. 1973.  
Hypocyrtia nervosa Fritsch, *Denkschriften der Kaiserlichen Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse*, Wien 79: 288. 1908.
- N. perianthomegus (Vellozo) H. E. Moore, *Baileya* 19(1): 38. 1973.  
Orobanche perianthomega Vellozo, *Florae Fluminensis* 257. 1829.
- N. strigillosus (Martius) H. E. Moore, *Baileya* 19(1): 38. 1973.  
Hypocyrtia strigillosa Martius, *Nova Genera et Species Plantarum* 3: 52. 1829.
- N. wettsteinii (Fritsch) H. E. Moore, *Baileya* 19(1): 38. 1973.  
Hypocyrtia Wettsteinii Fritsch, *Denkschriften der Kaiserlichen Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse*, Wien 79: 287. 1908.

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## BIOGRAPHICAL SKETCH

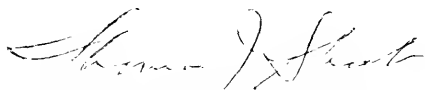
Clayton Kazuo Kwock Hung Yuen was born in Honolulu, Hawaii, on August 30, 1953. He graduated from Saint Louis High School, Honolulu, Hawaii, in May 1971.

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In September 1977, he began work towards a Master of Science degree majoring in Horticulture. He worked as a graduate assistant and research technician during this time and graduated in August 1979.

In September 1979, he entered the graduate program at the University of Florida, majoring in Horticultural Science and minoring in Botany, and pursued the degree of Doctor of Philosophy. He worked as a greenhouse manager (Department of Botany) and graduate assistant (Department of Ornamental Horticulture) during this time.

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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Thomas J. Sheehan, Chairman  
Professor of Horticultural Science

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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Bijan Dehgan  
Assistant Professor of Horticultural  
Science

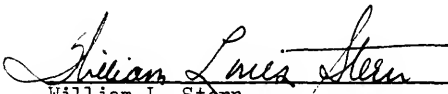
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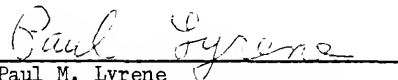
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Hans Wiehler  
Director of the Gesneriad Research  
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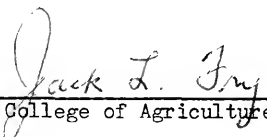
  
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William L. Stern  
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 1982

  
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