Flower anatomy and morphology of *Exodeconus maritimus* (Solanaceae, Solaneae) and *Nicandra physalodes* (Solanaceae, Nicandreae): importance for their systematic relationships

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ABSTRACT

A comparative analysis of anatomical and morphological features of the flower was conducted on *Exodeconus maritimus* (Benth.) D'Arcy (Solanaceae, Solaneae) and *Nicandra physalodes* (L.) Gaertn. (Solanaceae, Nicandreae). The histology of the dehiscence zone, fertility and degree of pubescence of the anthers differ markedly between the two. The shape of the stigma, the cytology of its receptive surface, epidermical characters of the style, carpel number, degree of nectary development, and the shape, number and distribution of stomata on the secretory tissue further distinguish *E. maritimus* from *N. physalodes*. These characters support a suprageneric position for *Exodeconus* independent of *Nicandra*.

KEY WORDS
Solanaceae,
Exodeconus,
Nicandra,
flower morphology,
flower anatomy,
systematics,
taxonomy.

RÉSUMÉ

Anatomie et morphologie florales dans Exodeconus maritimus (Solanaceae, Solaneae) et Nicandra physalodes (Solanaceae, Nicandreae): importance pour leurs relations systématiques.

Une analyse comparative de l'anatomie et la morphologie florales dans *Exodeconus maritimus* (Benth.) D'Arcy (Solanaceae, Solaneae) et *Nicandra physalodes* (L.) Gaertn. (Solanaceae, Nicandreae) a été réalisée. L'histologie de la zone de déhiscence, le degré de fertilité et la pilosité des anthères diffèrent beaucoup entre ces deux espèces. La forme du stigmate, la cytologie de la surface réceptive, les caractères épidermiques du style, le nombre de carpelles de l'ovaire, le degré de développement du nectaire, la forme, le nombre et la distribution des stomates sur le tissu sécréteur distinguent de plus *E. maritimus* de *N. physalodes*. Ces caractères contribuent à confirmer la position suprагénérique de *Exodeconus*, indépendant de *Nicandra*.

MOTS CLÉS
Solanaceae,
Exodeconus,
Nicandra,
anatomie florale,
morphologie florale,
systématique,
taxonomie.

INTRODUCTION

The genus *Exodeconus* Raf. comprises 6 species (AXELIUS 1994), distributed in Peru, Ecuador and the north of Chile, with *E. miersii* occurring in the Galapagos Islands (HUNZIKER 1979). These annual herbaceous plants are often viscid, prostrate, and adapted to dry environments with stony soil. The genus has been traditionally placed in subfamily Solanoideae. This position is supported by phytochemical analysis that demonstrates that *Exodeconus* shares the presence of withanolids with the 13 others members of the subfamily (BARBOZA & HUNZIKER 1994; GIL et al. 1998).

Other aspects of *Exodeconus* have been recently analyzed: pollen morphology (HEUSSER 1971), karyology (DIERS 1961), vegetative anatomy (RODRIGUEZ 1995), and fruit characters (BARBOZA et al. 1997). AXELIUS (1994) investigated vegetative and reproductive morphology, without reference to anatomy.

Nicandra Adanson is a monotypic genus. Although *Nicandra physalodes* (L.) Gaertn. is native to Peru (HOGSTAD 1923; HORTON 1979; HUNZIKER 1979), it is widely dispersed in many tropical regions of the world. This plant easily adapts to different habitats with varying soil types, and is an invasive species of pea, oat, and maize crops (HORTON 1979).

Several works have examined aspects of *Nicandra,* from flower vasculature (MURRAY 1945), geographical distribution and morphology (HORTON 1979; HUNZIKER 1979), fruit histogenesis (KANIEWSKI 1965), and pollen morphology (PUNT & MONNA-BRANDS 1977), to leaf, stem anatomy, and chemistry (HOGSTAD 1923). Nevertheless, investigations on the anatomy of reproductive organs have not been carried out.

The taxonomy of Solanaceae based on morphological characters places *Nicandra* in a monotypic tribe (Nicandreae Miers) and *Exodeconus* in tribe Solaneae (HUNZIKER 1979, 1993; HUNZIKER et al. 1996). However, a molecular analysis using cp-DNA conducted by OLMSTEAD & PALMER (1992) suggests that *Exodeconus* and *Nicandra* are closely related. This was pointed out again by OLMSTEAD & SWEERE (1994) and OLMSTEAD (1995), who propose the transfer of *Exodeconus* to tribe Nicandreae, placing it next to *Nicandra*. Nevertheless, a more recent cladistic analysis based on flower morphological and anatomical data of several genera of Solanaceae supports the notion that *Nicandra* and *Exodeconus* are weakly related (RODRIGUEZ, in press).

The purpose of this study is: 1) to investigate the flower anatomy and morphology of *E. maritimus* and *N. physalodes*, 2) to evaluate their taxonomic value, 3) to compare flower anatomy and morphology of *E. maritimus* and *N. physalodes*, and 4) to analyze the supposed relationship between the two genera, taking into account all available information.

MATERIALS AND METHODS

Flowers were fixed in FAA, and then transferred to 70% ethanol. For light microscopy, only flowers at the beginning of anthesis were used. Material was dehydrated through an ethyl alcohol/xylol series and embedded in paraffin (JOHANSEN 1940). Sections, both cross and longitudinal, were cut at 10-12 µm, mounted serially, and stained with safranin-astrablue (MAÁCZ & VÁGÁS 1961). Photographs were taken with a Zeiss Axiophot and WILD M 420 stereoscopic dissecting scope using Kodak film, ISO 100.

The gynoecium was diaphanized with 5% HCL, and colored with Lugol to observe stomata in the nectaries. Drawings were made using camera lucida.

For scanning electron microscopy, specimens were washed in FDA (GERSTERBERG & LEINS 1978). Flowers were critical-point dried using CO_2 and coated with 250 Å of gold. Observations were carried out using a Zeiss 940 A scanning electron microscope and microphotographs were taking using AgfaPan APX 100.

MATERIAL STUDIED. — *Exodeconus maritimus* (Benth.) D'Arcy: *Bernardello & Leiva 870,* Peru, Dpto. La Libertad, City of Trujillo, approach ruins of Chanchán (CORD). — *Nicandra physalodes* (L.) Gaertn.: *A.A. Cocucci s.n.*, 7 July 1986, Germany, cultivated, Mainz Botanical Garden.

RESULTS

General characters

Flowers are hypogynous, pentamerous, actinomorphic, and perfect. The calyx is gamosepalous, actinomorphic and accrescent. The 5-lobed corolla is gamopetalous with a more or less cylindrical basal tube. There are five stamens opposite the sepals, which are adnate to the corolla tube. The filaments are filiform, subulate, always pubescent at their bases and in their upper half, straight or geniculate and included (Figs. 1C, 5C). Anthers are basifixed, dithecal and tetrasporangiate with longitudinal dehiscence. When dehiscence occurs, both pollen sacs are connected after septa breakage. Placentoids (parenchymatous longitudinal bulges of the septa intruding in each pollen sac) are always present. The wall layers comprise an epidermis, fibrous endothecium, two parietal layers, and a single-layered glandular tapetum with binucleate cells (Figs. 1D,F,G, 5D). The ovary is bicarpellate and tetralocular due to false septa (Figs. 2D,F, 5E,F). The anacampilotropous ovules are generally numerous (> 10) and borne on more or less fleshy axile placentae (Figs. 2F, 5E). A circular nectariferous tissue develops at the ovary base (Figs. 2A,D, 5A-D,F). The ovarian nectaries are not supplied by special vascular tissue (Fig. 4A,H).

Exodeconus maritimus

Calyx

The sepals are triangular, overlapping up to half of their length, 5.5-6.5 mm long and 1.5-1.8 mm wide. Trichomes vary considerably: eglandular, simple, pluricellular, and glandular with spherical unicellular or elipsoidal head (Fig. 1A,B), and are located over the external face of the sepals. Anatomically, the calyx is formed by two epidermises, with a thick cuticle, and five to six layers of parenchymatous tissue (Fig. 2D). These cells are isodiametric in cross sections leaving reduced spaces among them (Fig. 2D). Chloroplasts and starch are usually observed in the parenchyma cells.

Corolla

The shape is tubular-infundibuliform; it is white, with a violet throat, 17-18 mm long and 4.5-6.5 mm wide. The anatomical structure is very similar to the calyx, with slight differences: the petals' epidermis is covered by a thin cuticle, and the parenchyma cells possess a large lumen. — Fig. 2D,F.

Androecium

The filaments are pubescent at the base with simple eglandular trichomes (Fig. 1A,C), and are composed of an epidermis, parenchymatic tissue, and a single vascular strand. The length of filaments is distinctive; three filaments are shorter than the other two (Fig. 1C). The anthers are small (3.2-3.5 mm), glabrous, and formed of a simple epidermis and an endothecium constituted of two cell strata with fibrous thickenings (Fig. 1D,F). Dehiscence occurs at the stomium (Fig. 1D,E), which is formed by a layer of seven to ten cells with crystalline sand. After dehiscence, the walls disorganize, and their contents are leaked into the lysigenous cavity they form (Fig. 1D,E,G). Andro-sterility is observed in *E. maritimus*, where the flowers display two or three sterile anthers (Fig. 1G). The pollen sacs possess normal endothecium, collapsed tapetum and empty pollen grains (Fig. 1G).

Gynoecium

The stigma is depressed and enlarged toward its flanks, giving it a fan-like shape (Fig. 3A). The receptive surface is covered by unicellular papillae enlarged at the base and rounded towards the apex (Fig. 3B,C). The style bears eglandular, simple, pluricellular trichomes and stomata shared on the epidermis (Fig. 3B,D). The ovary is ring-shaped in cross section (Fig. 2D,F), bicarpellar, with 4 locules at the base due to the false septa (Fig. 2D). This characteristic disappears at the apex of the ovary (Fig. 2F). Crystalline sand is frequently found in the parenchymatic tissue of the ovary. The nectary, located at the base of the ovary (Fig. 2A), has the shape of a ring with two swellings at opposite sides and at the level of the septa (Fig. 2A,C-E). The secretory tissue is constituted by 5-6 layers of isodiametric cells with large nuclei and vacuolated cytoplasm (Fig. 2D). Also, there are 12-15 layers of cells (Fig. 2D,E) and 20 ± 3 stomata concentrated at the upper part of the nectary swellings (Fig. 2B). The secre-
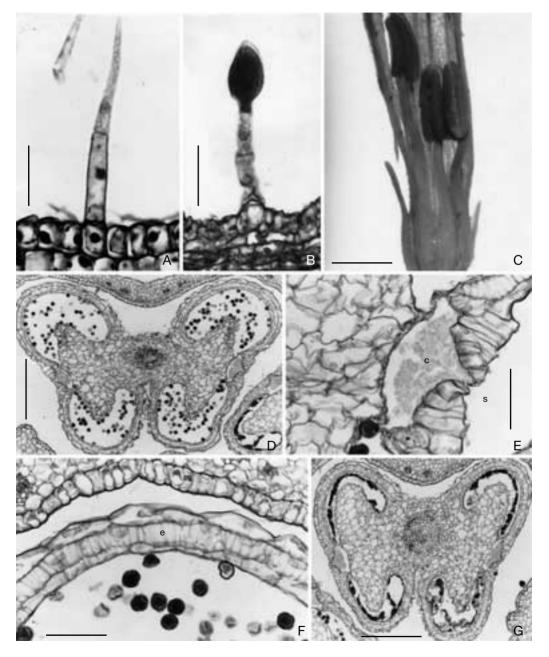
Fig. 1. — ***Exodeconus maritimus***, androecium and flower trichomes: **A**, eglandular trichome; **B**, glandular trichome; **C**, stamens; **D-F**, cross section of anther, details of the stomium and endothecium; **G**, cross section of anther with sterile pollen sacs. Scale bars: A, B = 2 µm; C = 3 mm; D, G = 800 µm; E, F = 10 µm. Abbreviations: e = endothecium; c = crystals; s = stomium.
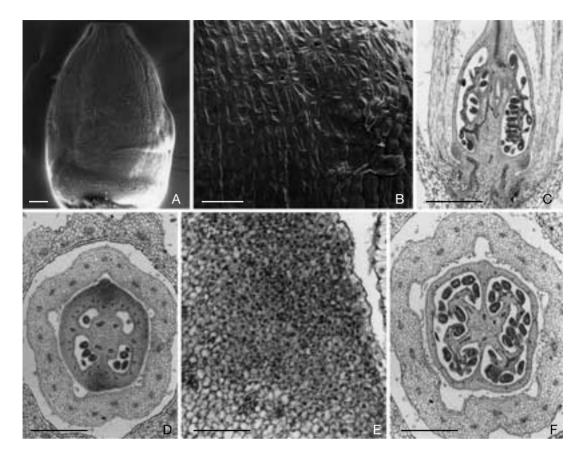
Fig. 2. — ***Exodeconus maritimus***, ovary: **A**, **B**, ovary, nectary, and their stomata (SEM); **C**, longitudinal section of ovary; **D-F**, cross section at different levels of the ovary. Scale bars: A = 200 µm; B = 50 µm; C, D, F = 800 µm; E = 100 µm. Abbreviation: n = nectary.

tory tissue is supplied by two dorsal and several lateral vascular bundles that ascend to the external wall of the ovary (Fig. 4A,H).

Vascularization

The peduncle shows a siphonostele, which divides into 10 vascular bundles forming a circle (Fig. 4A-C). Five traces split to constitute the main sepal bundles, which give rise to lateral ramifications (Fig. 4A,D-F). The five remaining vascular bundles are reorganized, acquiring a star shape (Fig. 4A,E,F). Five main corolla bundles are immediately formed taking an external position (each one produces two or three lateral ramifications). The five staminal bundles acquire an internal position (Fig. 4A,G). After these divisions, the remaining vascular tissue is reordered in a circle, entering the gynoecium (Fig. 4A,G,H). The ovary has 2 or 4 ventral vascular bundles in the central region (Fig. 4A,H); when 4, they then decrease to only 2 by fusion at the level of the apical portion of the ovary (Fig. 4A,I,J). The dorsal vascular bundles enter the style, reaching the base of the stigma without ramifications (Fig. 4A,K,L).

Nicandra physalodes

Calyx

The sepals are sagittate, overlapping only at their base, 20-22 mm long and 14-15 mm wide. Their epidermis is covered by various trichomes: eglandular, simple, pluricellular with a length-
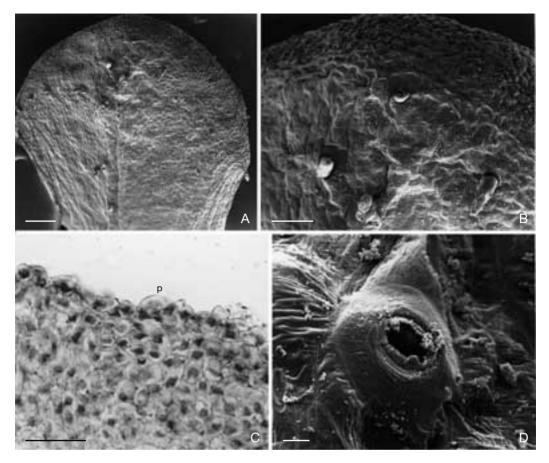
Fig. 3. — ***Exodeconus maritimus***, stigma: **A**, **B**, stigma and stigmatic papillae (SEM); **C**, longitudinal section of stigmatic surface; **D**, stoma. Scale bars: A = 100 µm; B = 50 µm; C = 10 µm; D = 5 µm. Abbreviation: p = unicellular papilla.

ened cuticle at its apex (Fig. 5A), and glandular with a head formed by 4-5 cells (Fig. 5B).

Corolla

The color is blue at the border with a white throat. The corolla is 30-32 mm long and 20-21 mm wide. On the external epidermis, trichomes similar to those of the calyx are observed. The anatomical features of the calyx and corolla are very similar to those described for *E. maritimus*.

Androecium

The androecium is formed by five equal length stamens (Fig. 5C). The filaments are geniculate and pubescent at the base (Fig. 5C), where eglandular, simple hairs are especially abundant, form-

ing compact pads (Fig. 5C). The anthers are 5-6 mm long and bear eglandular, simple trichomes throughout their surface. In this case, the endothecium is composed for two or three strata of cells with fibrous thickenings and the stomium is formed by two or three layers of small isodiametric cells with light colored contents (Fig. 5D,E). When such cells disorganize, the stomium zone does not have crystalline sand (Fig. 5E). On the other hand, the pollen sacs are all fertile with a completely normal endothecium, tapetum and pollen grains (Fig. 5D,E).

Gynoecium

The stigma is capitate, formed by five prominent stigmatic areas (Fig. 6A,C). The receptive
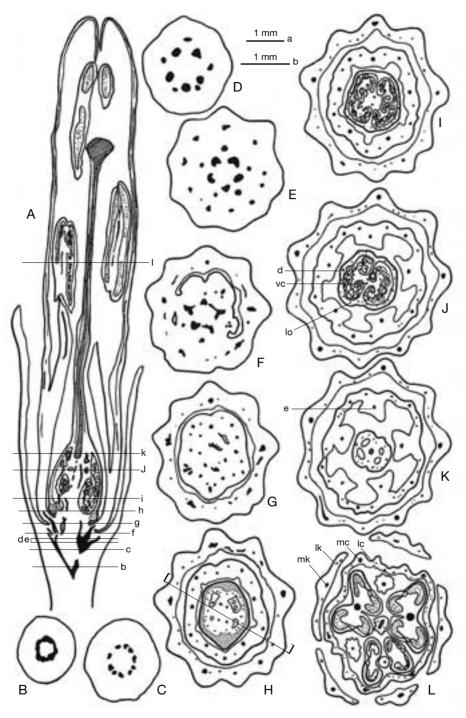
Fig. 4. — ***Exodeconus maritimus***, flower vascularization: **A**, longitudinal section of mature bud, along plane indicated in H; **B-L**, cross sections from peduncle to apex, as indicated in A. Symbols: Blackened areas, vascular tissue; gray areas, nectary; diagonal lines, transmitting tissue. Abbreviation: d, dorsal vascular bundles; e, staminal bundle; lc, lateral petal bundle; lk, lateral sepal bundle; lo, lateral ovarian bundle; mc, median petal bundle; mk, median sepal bundle; vc, ventral vascular bundle. Scale bars: for Fig. A is **a**; for Figs. B-L is **b**.
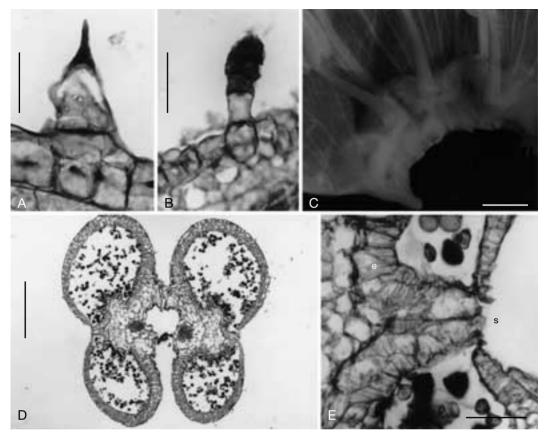
Fig. 5. — **Nicandra physalodes**, androecium and flower trichomes: **A**, eglandular trichome; **B**, glandular trichome; **C**, stamens; **D**, **E** cross section of anther and detail of the stomium. Scale bars: A, B = 2 µm; C = 4 mm; D = 800 µm; E = 10 µm. Abbreviations: e = endothecium; s = stomium.

surface has pluricellular papillae (Fig. 6C,D), which are intertwined and contribute to the formation of stigmatic channels (Fig. 6B-D). The style is glabrous and lacks stomata. The ovary is composed by five carpels (Fig. 7E) and contains seven locules due to the presence of false septa at the base of the ovary (Fig. 7F). The parenchymatic cells of the ovary show mixed-shaped crystals: druse crystals, crystalline sand and amorphous glasses. The nectary at the base of the ovary is a ring with five soft swellings (Fig. 7A-D,F). The secretory tissue possesses 18-22 layers of cells (Fig. 7C,D,F) and 40 ± 5 stomata distributed only around the base of the nectary (Fig. 7B). Five dorsal and many lateral vascular bundles that ascend to the external wall of the ovary irrigate the nectary.

Vascularization

The vascular pattern of *Nicandra* flowers is equivalent to that described for *Exodeconus maritimus*. However, some differences can be observed. *Nicandra* has a siphonostele that is not divided into discrete vascular bundles. The vascular bundles of sepals, petals and stamens branch off without leaving lacunae. The calyx is irrigated by 15 vascular bundles (five are main bundles and the others lateral ramifications). The corolla has 15 vascular bundles (five are main bundles and the others lateral ramifications). The carpellary vascular system arises from the divided stele. The ovary is irrigated by 10 ventral bundles and 5 dorsal bundles, irrigating the style and the 5 stigmatic areas respectively. These observations agree with MURRAY'S (1945) data.
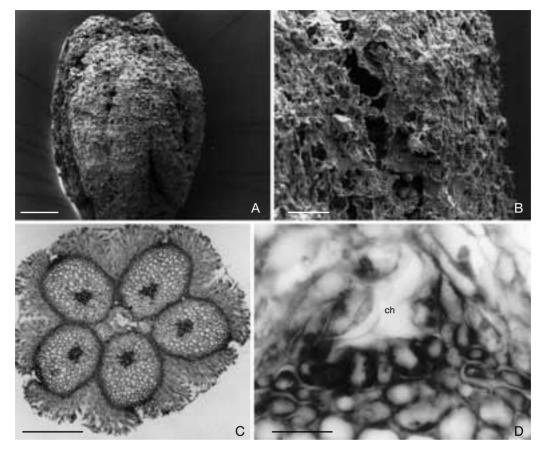
Fig. 6. — ***Nicandra physalodes***, stigma: **A**, **B**, stigma and detail of stigmatic area (SEM); **C**, cross section of stigma; **D**, stigmatic channel. Scale bars: A = 200 µm; B = 50 µm; C = 250 µm; D = 10 µm. Abbreviation: ch = stigmatic channel.

DISCUSSION

Differences in flower anatomy and morphology between *E. maritimus* and *N. physalodes*

Data published on flower morphology (HORTON 1979; HUNZIKER 1979) and flower vascularization (MURRAY 1945) indicate that *E. maritimus* and *N. physalodes* are indeed different. Even though the morphological and anatomical features of their sterile whorls are similar to those described for the family by other authors (D'ARCY 1973; ARMSTRONG 1986), it is important to point out that *E. maritimus* and *N. physalodes* show many differences, fundamentally, in their fertile organs.

The androecium of *N. physalodes* is homoantherous and comprised of physically large anthers that are equal in length to their filaments. This property is coincident with the stamens of the more widespread "Solanum-type" flowers (ENDRESS 1996). *Exodeconus maritimus*, on the other hand, has a heterantherous androecium, combining sterile and fertile anthers.

The staminal filaments of both genera bear eglandular trichomes. However, in *N. physalodes* the trichomes are especially abundant, forming compact pads, which probably serve as means to increase the anther area and consequently its visibility, as has been observed by BARTH (1991) and BERNHARDT (1996) for other species.
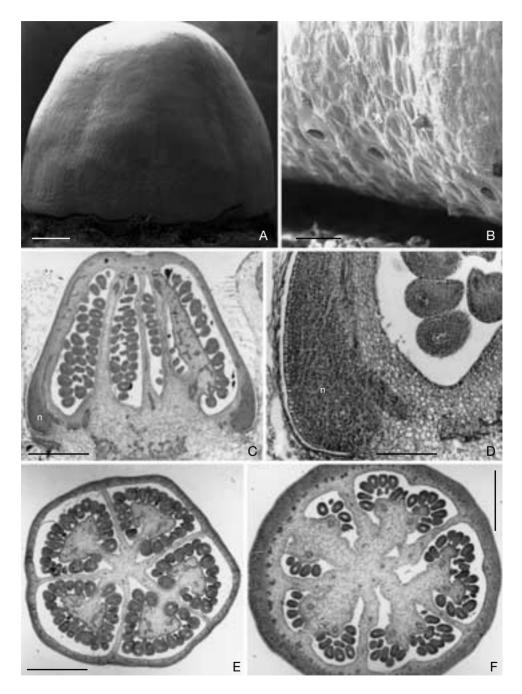
Fig. 7. — **Nicandra physalodes**, ovary: **A**, **B**, ovary, nectary, and their stomata (SEM); **C**, **D**, longitudinal sections of ovary and nectary, respectively; **E**, **F**, cross sections at different levels of the ovary. Scale bars: A = 500; B = 20 µm; C, E, F = 800 µm; D = 100 µm. Abbreviation: n = nectary.

BONNER & DICKINSON (1989) affirm that the trichomes of the anthers in *Lycopersicon esculentum* Mill. function as a cohesion mechanism. *Nicandra physalodes* also has pubescent anthers, though the arrangement of the trichomes is different and the linking function is absent. Perhaps the trichomes help in attracting insects as FADEN (1992) suggests. *Exodeconus maritimus*, on the other hand, lacks anther trichomes, but has stamens with other specializations.

Crystals are found appearing in the early stages of flower development in most Solanaceous anthers. Oxalate crystals are disposed in a band of cells just inside the epidermis at the stomium level. When pollen is mature the anthers break down, releasing their crystals (D'ARCY et al. 1996). The observations in *E. maritimus* and *N. physalodes* agree with previous analyses carried out by D'ARCY et al. (1996). The present work also supports their hypothesis that the stomium structure of *Exodeconus* propitiates the formation of crystals, while it does not do so in *Nicandra*. This feature is regarded as a principal reason for placing *Nicandra* taxonomically distant from other members family (D'ARCY et al. 1996).

Anther sterility has been observed in several Solanaceae: *Capsicum* L., *Datura* L., *Lycium* L., *Lycopersicon* Mill., *Solanum* L., *Nicotiana* L., and *Petunia* Juss., occurring spontaneously or after interspecific crossing (IZHAR 1984). The present analysis shows that *E. maritimus* bears sterile pollen sacs in its anthers. This characteristic has not been previously reported for the genus.

The stigma of both *Exodeconus* and *Nicandra* is wet-papillate (HESLOP-HARRISON & SHIVANNA 1977; HESLOP-HARRISON 1981), a type found in many Solanaceae. However, differences in the stigma shape, and stigmatic papillae type and distribution, contribute to the separation of *E. maritimus* from *N. physalodes*.

The style anatomy is coincident to that of typical Solanaceae. It is solid with a central portion occupied by transmission tissue. Furthermore, *E. maritimus* shows stomata in the style, a feature not previously observed in Solanaceae. The ovary of members of the family is commonly 2-carpellate, just as found in *E. maritimus*. Nevertheless, a pluricarpellate ovary has been reported in *Vassobia breviflora* (Sendt.) A.T.

Hunz. (MOSCONE 1986), *Lycopersicon esculentum* (HAYWARD 1953), and *Nicandra physalodes* (HUNZIKER 1979). SYMON (1987) describes a plurilocular ovary in *Solanum*, a character also observed in *E. maritimus* and *N. physalodes*. HUNZIKER (1979) proposes that the plurilocular ovary in *N. physalodes* arises by increment of the carpel number. However, the results reported here show that this structure is formed by false ovarian septa.

Critical examination of floral nectaries has long provided an extra measure of confidence for the resolution of systematic problems (FAHN 1979). According to his topographic nectary classification, the nectaries found in *E. maritimus* and *N. physalodes* would be type 4 (disc-shape nectary at base of the ovary). The exomorphological and anatomical features are coincident with those found by other authors for various species of Solanaceae (MOSCONE 1986; COCUCCI 1992). The development, stomata location, and nectary shape make it possible to distinguish differences that clearly separate *E. maritimus* from *N. physalodes*.

The taxonomic value of flower vascularization has been shown in many comparative studies (e.g., CUTLER 1987; DICKISON 1994; SUGIYAMA 1997). Flower vascularization in *E. maritimus* and *N. physalodes* is coincident with the observations of MURRAY (1945) for several Solanaceae. Nevertheless, small differences exist in the irrigation of the peduncle and flower whorls, the number of dorsal and ventral vascular bundles of the ovary, and the number of vascular bundles of the style. These differences further help to discriminate between the two genera.

Systematic location and putative relationship between *E. maritimus* and *N. physalodes*

There are two hypotheses regarding the taxonomic position and relationships of these genera within Solanaceae. 1) *Exodeconus* and *Nicandra* belong to different tribes. This interpretation is based upon micromorphological characters (HUNZIKER 1979, 1993; HUNZIKER et al. 1996) and was recently reinforced by carpological studies (BARBOZA et al. 1997). 2) *Exodeconus* and

Nicandra should be placed in the same tribe. This concept is supported by molecular data (OLMSTEAD & PALMER 1992; OLMSTEAD & SWEERE 1994), and OLMSTEAD (1995) recently proposed the transfer of *Exodeconus* from Solaneae to the monotypic tribe Nicandreae.

The results of the present work support the traditional hypothesis (HUNZIKER 1979, 1993; HUNZIKER et al. 1996; BARBOZA et al. 1997), and are consistent with anatomical, chromosomal, palynological, and phytochemical data (HEUSSER 1971; PUNT & MONNA-BRANDS 1977; AXELIUS 1994; RODRIGUEZ 1995; BARBOZA et al. 1997). They do not confirm the ideas of OLMSTEAD & SWEERE (1994) and OLMSTEAD (1995). Characteristics of flower morphology and anatomy, and in particular those related with the fertile whorls, clearly show that *E. maritimus* and *N. physalodes* are completely different, and that the only features they share are those found generally among Solanaceae.

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