

The genus *Tubocapsicum* (Solanaceae)

William G. D'Arcy¹, Richard C. Keating¹, Zhi-Yun Zhang², and Ching-I Peng^{3,*}

¹Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, USA

(William G. D'Arcy passed away on December 16, 1999)

²Institute of Botany, Chinese Academy of Sciences, Xiangshan, Nanxincun 20, Beijing 100093, China

³Institute of Botany, Academia Sinica, Taipei 115, Taiwan

(Received November 23, 1999; Accepted June 22, 2000)

Abstract. *Tubocapsicum* (Solanaceae: Solanoideae), a genus of two Asian species, was formerly included in *Capsicum*. *Tubocapsicum anomalum* is a herb with small yellow flowers and red berries that is found in Japan, southern China, Taiwan, and the Philippines; *T. obtusum* is found in Japan. A general taxonomic description is complemented by new detailed descriptions and illustrations of growth morphology, vegetative histology and stomata, floral structure, vasculature, fruit structure, seeds, and pollen. On the basis of this analysis as well as cpDNA investigations by of Olmstead et al. (1999), the genus *Tubocapsicum* appears to be most closely related to subfamily Solanoideae genera *Aureliana* and *Withania*.

Keywords: Anatomy; Anther; Branching; *Capsicum*; Floral vasculature; Fruit; Growth pattern; Nectar; Pollen; Revision; Seeds; Solanaceae; Stomata; Taxonomy; *Tubocapsicum*.

Introduction

The genus *Tubocapsicum* Makino is confined to eastern Asia (Figures 1, 2). It embraces one widespread species, *T. anomalum* (Franch & Sav.) Makino and a poorly known second species, *T. obtusum* (Makino) Kitamura, of Japan. The genus is not well known since there has been little published information, and there are few specimens in western herbaria. In order to redress this obscurity, we undertook a study of living plants of the genus cultivated from seeds from Taiwan, as well as herbarium material from throughout its range. Here we report our observations and provide a treatment of the genus *Tubocapsicum* with descriptions, drawings, photos, and an analysis of its possible relationships within the Solanaceae. Nearly all of the observations on the structure and biology of the genus to follow are of *T. anomalum* as *T. obtusum* is only known thus far from a few herbarium specimens.

Plants of *Tubocapsicum anomalum* (Figures 3, 4, 5, 6) are erect or sprawling herbs with entire leaves, few-flowered inflorescences, small campanulate flowers, and red juicy berries with discoid seeds. In most features, they resemble members of *Acnistus* Schott, *Aureliana* Sendt., *Capsicum* L., *Vassobia* Rusby, *Witheringia* L'Her. and other genera of the American tribe Capsiceae. However, as discussed below, seed comparisons and cpDNA studies (Olmstead et al., 1999) argue for separating *Tubocapsicum* and *Aureliana* from tribe Capsiceae, along

with *Withania* Pauq. which has been placed in tribe Physaleae.

In this paper we present a summary of our observations of living plants and herbarium material of *Tubocapsicum anomalum*. We include a report on germination and growth patterns, vegetative histology and vasculature, floral structure and vasculature, fruit structure, pollen, seeds, quality of the nectar, notes on its cultivation, and a general discussion of how it differs from other genera. We conclude with a systematic revision based on literature and herbarium collections including nomenclature of the genus, its two species, and a map of its distribution.

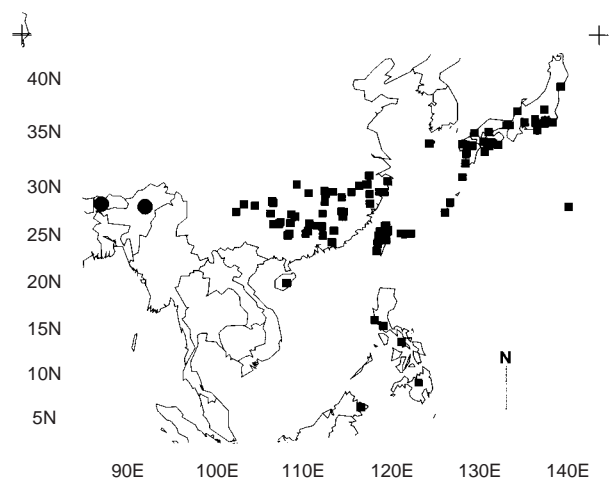


Figure 1. Distribution of *Tubocapsicum anomalum*. Solid squares indicate specimens seen by the authors. Large circles indicate reports from the literature.

*Corresponding author. E-mail: bopeng@gate.sinica.edu.tw

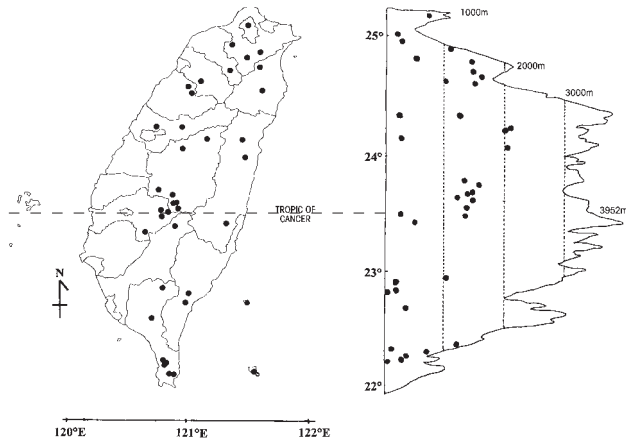


Figure 2. Distribution and altitudinal maps of *Tubocapsicum anomalum* (dots) in Taiwan.



Figure 3. Mature plant of *Tubocapsicum anomalum* (Franch. & Sav.) Makino reclining to the horizontal.

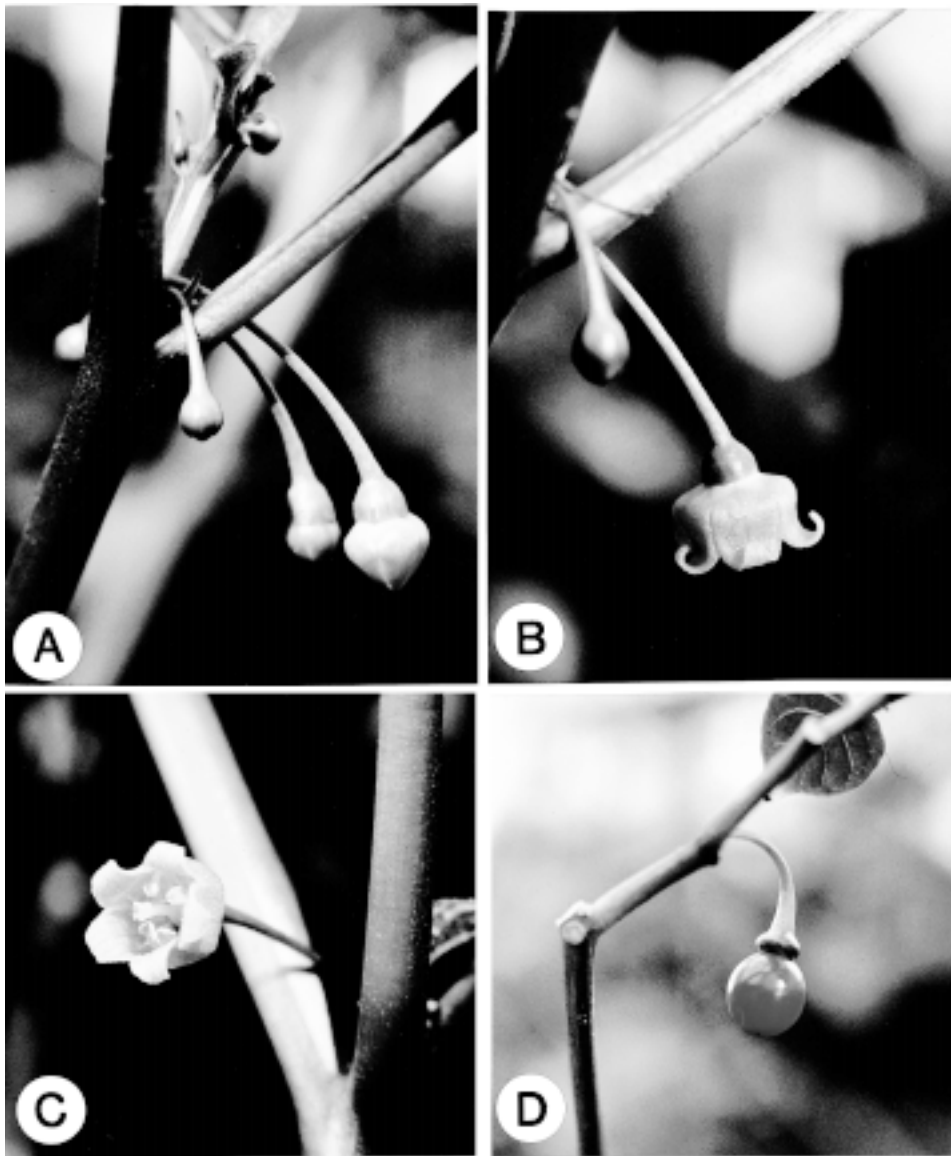


Figure 4. *Tubocapsicum anomalum* (Franch. & Sav.) Makino. A, Inflorescence with flower buds; B, Inflorescence with flower in lateral view; C, Flower in frontal view; D, Fruit.



Figure 5. Interior of *Tubocapsicum anomalum* flower showing anthers in erect position.

Materials and Methods

Plants of *Tubocapsicum anomalum* grown from seed from Taiwan (*Chen 231*, HAST, MO) in greenhouses and outdoors at the Missouri Botanical Garden, St. Louis, Missouri, USA, for several years were studied morphologically and anatomically and compared with plants of its putative relatives, also grown there. All cultivated specimens are vouchered and deposited at MO.

Comparative Living Material Studied: *Capsicum annum* L. var. *annuum*. Various commercial seeds and fruits available in markets in St. Louis, not vouchered; *Capsicum annum* var. *aviculare* (Dierb.) D'Arcy & Eshb., Mexico, Sonora, La Argentina, seed from W. H. Eshbaugh, *D'Arcy 17723* (MO); *Capsicum lanceolatum* (Greenm.) C.V. Morton & Standl., Mexico, Capes, Tay-

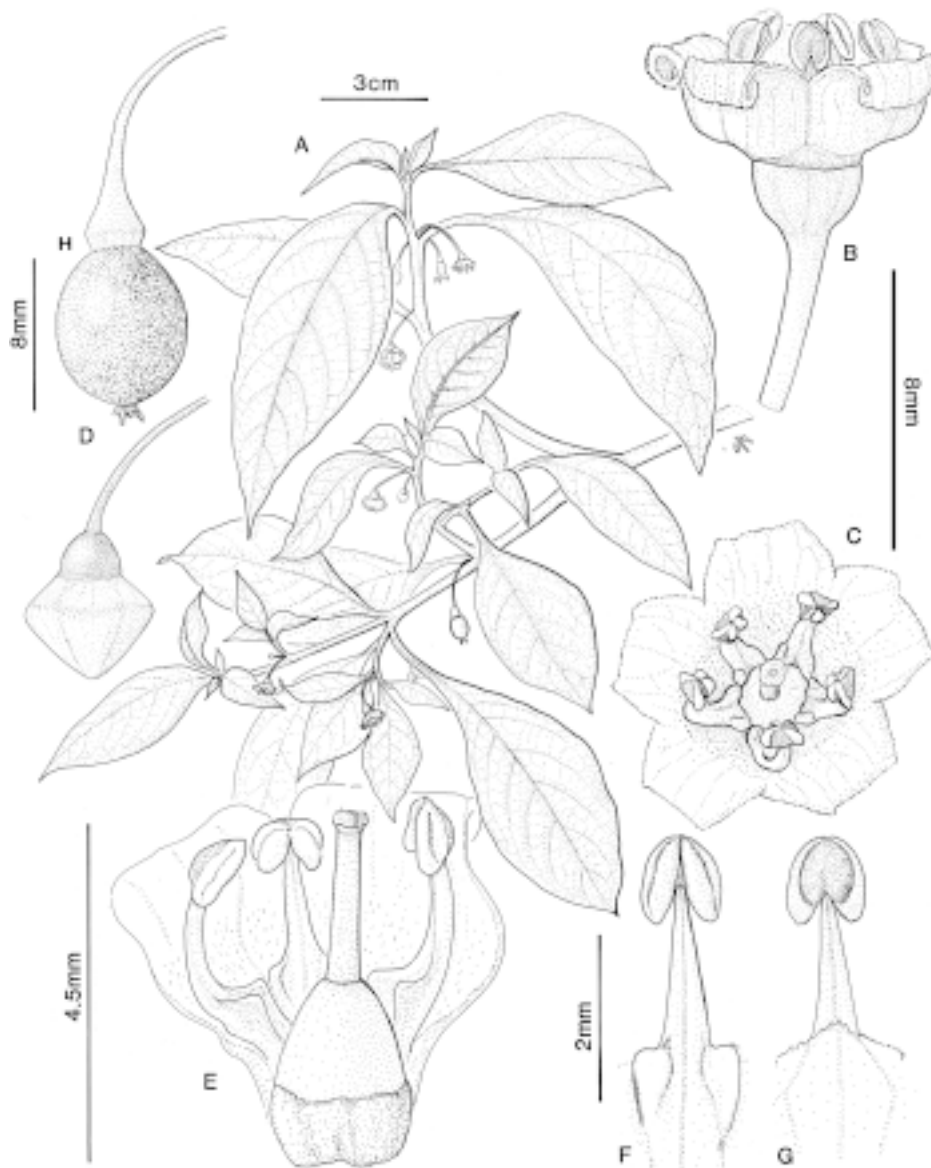


Figure 6. *Tubocapsicum anomalum*. A, Habit; B, Flower; C, Flower from the front; D, Flower bud; E, Opened flower showing pistil and part of androecium; F, Stamen, ventral (adaxial) view; G, Stamen, dorsal (abaxial) view; H, Fruit.

lor & Bree love 41082 (MO); *Tubocapsicum anomalum*, seeds from Taiwan, Nantou Hsien: Fenghuangshan, 1280 m, 24 Oct 1987, Chen 231 (HAST), vouchered as *D'Arcy 19501* (MO); *Vassobia breviflora* (Sendt.) Hunz., Argentina, Prov. Córdoba, *D'Arcy & Hunziker 13949* (MO); *Withania riebeckii* Balf. f., Socotra, seed from Conservatoire et Jardin Botanique de Nancy, *D'Arcy 17750* (MO); *Withania somnifera* (L.) Dunal, source unknown, *D'Arcy 17745* (MO).

A comprehensive sample of herbarium specimens of *Tubocapsicum* and putative relatives were also studied as cited below. Except specimens used to judge the validity of *T. obtusum*, all material studied was of *T. anomalum* var. *anomalum*.

Seeds of *Tubocapsicum*, *Vassobia*, and *Withania* were prepared for study by a 30-second extraction from fresh berries using a juice blender, followed by air drying. Seeds of *Aureliana* were prepared in the same way from intact, unflattened berries taken from herbarium sheets and rehydrated. Hand sections of seeds and leaves were stained in 15% ethanolic iodine-potassium iodide (2.0% potassium iodide and 0.2% iodine) and mounted in 40% calcium chloride, which is a stain-differentiating mountant with a high refractive index (Herr, 1992; Keating, 1996).

Nectar sugar ratios were obtained by C.E. Freeman (pers. comm.) using the protocol outlined in Freeman et al. (1984).

Observations

Germination

Tubocapsicum anomalum is phanerocotylar, the seedling often emerging completely from the testa. The coty-

ledons are ovate, with slight differentiation of the distal region into an area suggestive of an apicule. The cells of the upper epidermis are quadrate, uniform, and oriented perpendicular to the midvein. Cells of the lower epidermis are rounded and less regularly oriented, with those near the midvein arranged parallel to it. Cotyledon venation is irregular, looped, brochidodromous. Secondary veins are irregularly and widely spaced. There are sparse uniseriate trichomes on both surfaces. The petiole is slender, slightly flattened, about 3/4 as long as the blade. The stem and petioles of the cotyledon are beset with minute, transparent unicellular subconical trichomes.

The ephylls are alternate, petiolate, estipulate, linear or oblong, the lateral veins ca. 2 on each side of the midvein, ascending, the upper (adaxial) surface, petiole and stalk with tiny, linear, transparent unicellular hairs that sometimes bear apical glands. These details conform to those reported by Duke (1969) for the Solanaceae, and they also correspond with our observations of seedlings of *Capsicum lanceolatum*, *Vassobia breviflora*, *Withania somnifera*, and *W. riebeckii*, except that in these the ephylls are much broader.

Adult Growth Architecture

After germination, *T. anomalum* plants develop through branching or structural phases (Figure 7) as follows. Following development of the ephylls, the plant develops a straight, relatively stout, erect trunk with a large pith. In this orthotropic or monopodial phase, leaves are inserted in a spiral 2/5 phyllotaxy, and axillary buds or shoots are usually not evident. After several leaf nodes, at a height of about 30-50 cm, an inflorescence is produced, subtended on each side by a plagiotropic (sympodial) branch, and these branches are subtended by a single leaf. Each

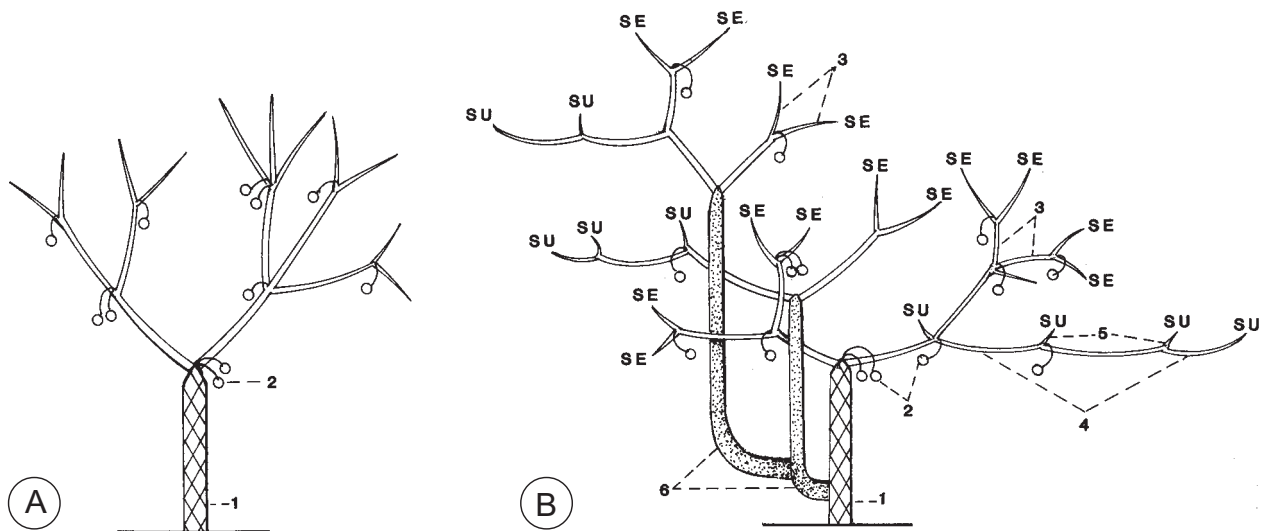


Figure 7. Adult growth patterns of *Tubocapsicum anomalum*. (A) Early maturity: Growth begins with an orthotropic phase which results in a relatively stout, erect trunk with a large pith (1). After appearance of the first inflorescence (2), more or less equal pairs or triads of plagiotropic branches continue the plant's growth, each terminating in an inflorescence and another tier of plagiotropic branches. The plant is usually erect. (B) Advanced maturity: Distal branches become, thin, weak, and senescent (3). When a branch declines to the horizontal, the branches it produces are unequal, the lower branch of the pair becomes dominant (4) and the upper one is reduced in size or subordinate to it (5). Reiteration shoots (6) that resemble the initial orthotropic trunk appear from near the base of the plant. SE = senescent branches, SU = subordinate branches.

branch in turn grows on to produce an inflorescence subtended by a tier of branches. Under favorable growing conditions, each subsequent node usually displays this 2-tiered or dichasial arrangement or rarely a 3-tiered arrangement, though sometimes only a single subtending branch appears. The two or three plagiotropic branches appear to be parallel in development, neither showing dominance. These branches in turn end in inflorescences and tiers of branching, and they tend to have only occasional leaves except at the branch nodes. The branching pattern here is dichasial and the sympodial unit is unifoliate (Knapp, 1989: 66).

After a succession of 2-5 branch nodes, the branches are often thinner, and senescence may appear in the distal 1-2 nodes of one of the branches of a node. At about this time, reiteration or rejuvenation shoots appear, usually at the base of the plant. These shoots resemble the initial, stout, orthotropic trunk except that they have much larger leaves than the older shoots, and they subtend axillary shoot initials near the base of the parent trunk. These shoot initials are evident as fascicles of 2-6 small leaves that do not develop further. The first dichotomy of the reiteration shoot occurs after 6-13 leaf-nodes and is terminated by an inflorescence as in the initial orthotropic trunk.

Branching architecture of the plant tends to be plastic, and a number of modifications to the above pattern are found. Commonly, after the initial period of growth just described, the stems of *Tubocapsicum anomalum* are weak and spindly, and originally erect branches may decline in part or entirely to the horizontal or arch downwards. When a branch is no longer close to erect, the branch of the pair that is lowermost (closest to the ground) tends to grow faster and it soon assumes dominance in the pair. The more erect, subordinate, branch of the pair may cease elongation and remain as a short-shoot or fascicle of leaves, while the dominant, more horizontal member arches upward, its base horizontal and its apex assuming a more vertical orientation. The dominant lower branch often does not attain a fully erect position, and its subsequent nodes are also somewhat horizontal with their branch pairs, in turn, also showing inequality and dominance by the lower member. Thus, a lengthy but spindly trunk may be formed with leafy fascicles at each node representing the shorter members of tier pairs.

Another common growth form modification occurs when branches decline greatly from the vertical, the emergence of one or more reiteration shoots from the axils of leaves on the primary or parent stem. If the plagiotropic parent branch arches downward, these reiteration shoots tend to form on the highest part of the arch. Because plants are usually unable to maintain erect growth after the first few tiers of plagiotropic branches are produced, plants that are past their initial flowering period of 2-5 dichotomies tend to have a mixture of senescing plagiotropic shoots and reiteration shoots that may have reinitiated plagiotropic branching. At this point there may be no main trunk, although a number of minor trunks are

present as a result of the dominance of members of tier pairs. The plant now consists of a number of distinct sympodial modules, and the architecture is reminiscent of the Prevost and Nozeran models (Halle et al., 1978) in which new modules appear below the first branch tier of the previous module. In this case, however, the new module may appear at various places, depending on the vertical orientation of the plant and perhaps other factors, although under good growing conditions when the plants can maintain an upright orientation, the new modules appear well below the previous tier, at the base of the plant at ground level.

Older plants of *T. anomalum* may thus display two distinct kinds of branching, one consisting of 2-part tiers around an inflorescence, and one resulting from the emergence and development of a reiteration shoot into a successional trunk module. These two branching patterns usually look quite different, the first with evidence of the inflorescence in the fork of the tier and no leaves subtending the branches, and the second with no inflorescence in the fork and usually evidence of leaves subtending each branch. As the series of reiteration shoots matures into senescing upper branches and declining lower branches, inflorescences are sometimes aborted, and new leaves become smaller. Older leaves fall from the plant but senescing branches are not dehiscent, and the aged plant finally becomes a tangle of intervening branches, an herbaceous thicket.

The Robinson (1996) formula for this architecture approximates [O]t[O]t, but architectural patterns in *Tubocapsicum* are actually somewhat intermediate between several of the growth models of Halle et al. (1978), notably Chamberlain's, Leewenberg's, Prevost's and Nozeran's. Early growth stages resemble those described by Bohs (1989) for *Cyphomandra* Mart. ex Sendtn., but reiterative branching is usually from near the base of the plant in *Tubocapsicum* rather than immediately below branch tiers as in *Cyphomandra*. In neither *Capsicum* nor *Vassobia* was an initial, orthotropic phase observed, and plants of those genera developed directly from the eophylls to plagiotropic branching. Subsequent growth in these two genera was continuous rather than reiterative as in *Tubocapsicum*. Mature growth architecture of *Tubocapsicum* is thus distinctive in the dominance assumed by lowest branches in a tier and the usually accompanying reduction or senescence of the subordinate branches.

Vegetative Histology

Leaves. The leaf is thin and dorsiventral with a weakly differentiated boundary between palisade and spongy mesophyll. The midrib has a prominent, rounded adaxial ridge and a larger protruding abaxial ridge. The cuticle is striate. Epidermal cells are flat and thin on both surfaces. Stomata are more common abaxially. The stomata (Figures 8E, F, G) are either anisocytic or anomocytic. Guard cell pairs are subcircular and the outer and inner stomatal ledges, or flanges, are nearly smooth.

Adjacent epidermal cells are usually three, sometimes four. Paradermally, adaxial epidermal anticlinal walls are undulate to sinuous; abaxial epidermal anticlinal walls are more strongly sinuous and very irregular. The palisade is one-layered, with wide cells (1.5:1 l/w ratio) comprising ca. 25% of the mesophyll thickness. Spongy mesophyll is 3-5 layered. Spongy air space in representative cross-section is ca. 50%. The cells are irregular with short or long lobes. Substomatal air cavities are large and extend up to the pali-

sade layer. Midrib vasculature is a broad arc with more or less continuous xylem and strands of adaxial and abaxial phloem. Small vascular bundles may be bicollateral. Smaller vascular bundles have weakly differentiated sheath cells which contain plastids and often appear similar to neighboring mesophyll cells. Occasional druses are present at the spongy/palisade border. Crystal sand is present, especially in midrib ground tissue.

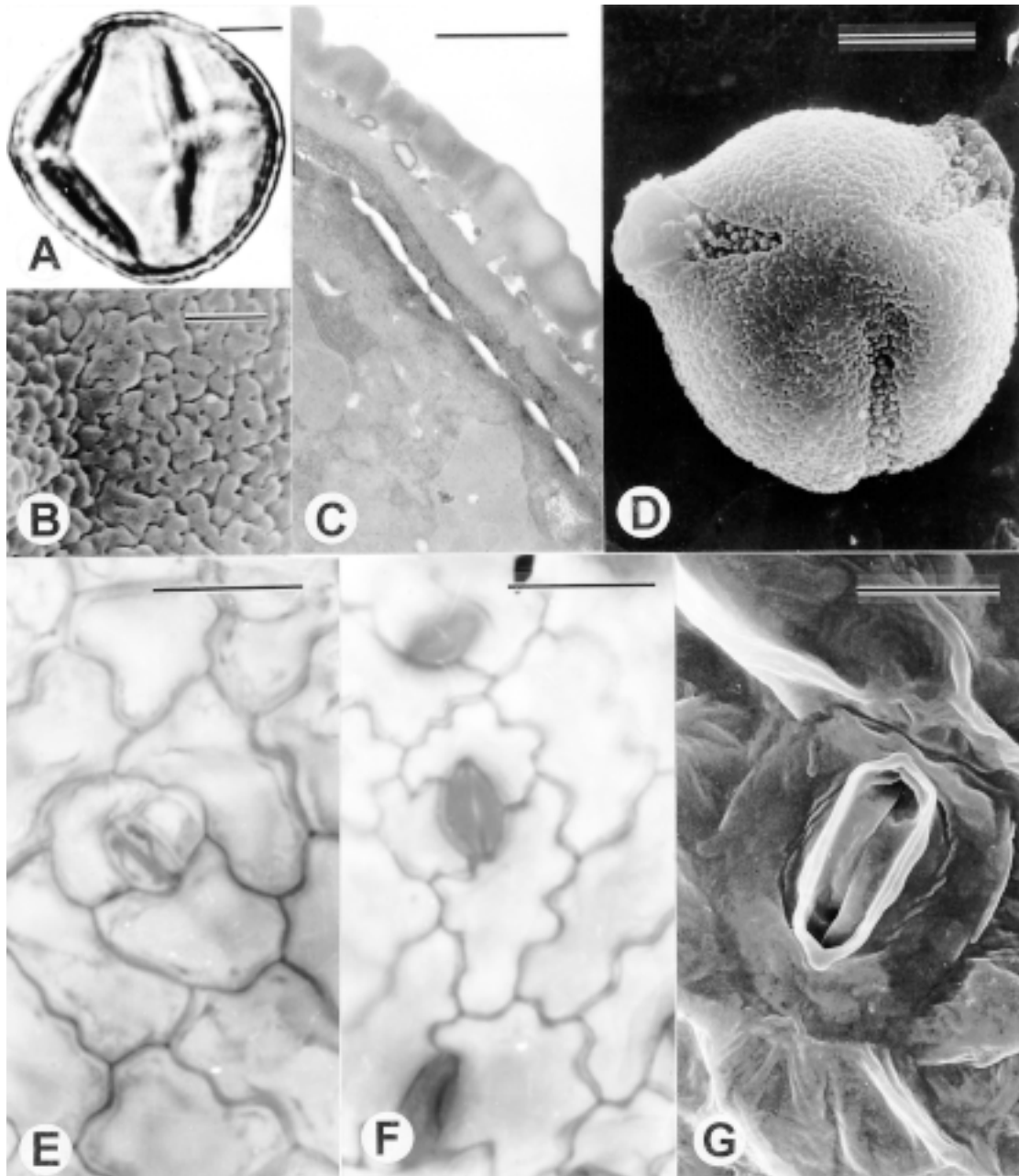


Figure 8. *Tubocapsicum anomalum* (Franch. & Sav.) Makino, pollen and leaf structure. A-C, Pollen structure; E-G, leaf epidermal features. A, Pollen grain, LM view. Scale bar = 7 μ m; B, Pollen surface SEM view. Scale bar = 2 μ m; C, Pollen grain exine section, TEM view. Scale bar = 2 μ m; D, Pollen grain polar view, SEM view. Scale bar = 10 μ m; E, Leaf adaxial epidermis and stomate (LM). Scale bar = 50 μ m; F, Leaf abaxial epidermis and stomate (LM). Scale bar = 50 μ m; G, Leaf abaxial surface SEM view showing stomate. Scale bar = 10 μ m.

Lamina development. This description is based on appearance of tissues in transsections. The expected mosaic growth patterns cannot be demonstrated with this material. The young primordium begins the expansion of a lamina several hundred micrometers above the point of attachment (base) of the leaf peg. The lamina is six layers deep at inception and the eventual thickness of all developing laminae observed is seven layers. The outer two layers at the margin of laminal growth appear autonomous and provide for the epidermal and layers immediately beneath. The third layer below the margin produces the two central layers. A few millimeters proximal to the margin, the fourth layer down from the adaxial surface produces two layers by division of the cell line. This was noted in all but the youngest primordia that have a lamina.

Stem and node. The stem has a thin epidermal layer with small, stalked glandular trichomes. Trichomes have uniseriate bases and rounded capitate heads of about 4 cells. Beneath the epidermis is an irregular layer of angular collenchyma, 3-10 layers deep. The remainder of the cortex and pith comprise medium-sized parenchyma cells with no idioblastic cells. Dispersed crystal sand is common in the ground tissue, and large druse-sized clusters of crystal sand are found there occasionally. In the young stem, several millimeters below the apex, the xylem in the circular-appearing siphonostele is only differentiated in the leaf traces. Phloem occurs in separate strands, both internal and external to the xylem.

The stele appears continuous and is lobed in the vicinity of leaves. The stele bulges into a leaf buttress and has three well-matured areas of xylem: a median and two lateral traces arranged as a three-trace, unilacunar (3:1) node. An examination of the nodal cross sections from proximal to distal shows the following pattern. A bulge of siphonostele in the leaf buttress produces a median and two large lateral traces that become separated from a single stelar gap. At higher levels, the gap is closed by newly differentiating procambium that extends in the direction of the leaf base to form a crescent. The crescent surrounds the axillary bud. At a higher level where the leaf base is entirely separate from the stem, the axillary bud is still included within the adaxial ridge of the leaf base. It becomes free several hundred micrometers above the point of separation of the leaf.

Just below the level of leaf base separation, the lateral bundles of the petiole fork at their proximal (ventral) ends to form two small round veins that assume a marginal position. When the lamina begins to protrude from the edges of the primordium, these new veins become the marginal veins of the decurrent lamina.

At the shoot apex, young leaf primordia are semicircular in outline and show an early onset of abaxial deformation and the protrusion of a pair of laminal primordia. After cessation of expansion of the abaxial side of the primordium, the adaxial side undergoes periclinal divisions that form the adaxial ridge.

Floral Structure

Morphology. Flowers of *Tubocapsicum* are similar to those in *Capsicum*, *Aureliana*, *Withania*, and *Vassobia*, and as in the last three, the filaments are inserted into stamens or stirrups (Huber, 1980) which are fused to the corolla tube. The stamens (filament base) is appressed to the ovary, and in *Tubocapsicum*, *Aureliana*, *Vassobia*, and *Withania*, a groove between each stamens allows nectar to flow upwards from the nectary at the ovary base. Flowers of *Tubocapsicum* are distinctive in the adnation of the filaments to the corolla tube above the stamens to as high as the corolla sinuses. Anthers are basifixed and versatile. When the corolla opens all anthers are bent inwards nearly 90° forming a spoke-like shield over the corolla entrance. Soon, they become erect again (Figures 5, 6C, E, F, G). The ovary is superior, smooth, glabrous, and greenish white. Nectaries are the Type I of Bernardello (1986) in which the form is hardly visible from outside, although they do have an ill-marked yellowish color that is distinct from the rest of the ovary. The base of the style is sunken into the top of the ovary.

Gynoecium. The ovary is two-locular with no basal cross septum to create a false four-locular appearance. Dorsal carpel bundles continue to the top of the style. The style, hollow in the lowermost portion, is comprised of solid ground tissue through most of its length. Near the tip, the style divides into 2 very short lobes that are covered with short, thin-walled, multicellular, uniseriate trichomes. The septum/placenta is inserted at the base of the ovary and is free from it except at the apex. At the base it consists of a blade-like septum that bears no ovules. Slightly above the base, the blade-like septum expands on its two lateral faces into a pair of hemispherical or hemiellipsoidal ovule-bearing placentas. The internal wall of the ovary and the septum are bounded by a differentiated epidermal layer, but this is not evident on the placenta. At the apex, the placental region ends leaving as a continuation the blade-like septum, which at this point divides into two branches just before uniting with the apex of the ovary wall at the position where the style is inserted.

Androecium. An Oxalate Package (OP, D'Arcy et al., 1996) is present in the anthers of *Tubocapsicum*. At the distal ends of the anther septa, just interior to the epidermis, a series of 6-8 cells differentiate by the time of mitosis. The walls of these cells then disintegrate, leaving a cavity partially filled with calcium oxalate. The epidermal cells bounding these cells remain small, and at anthesis they are much smaller than the epidermis covering the rest of the anther. Anther dehiscence takes place by rupture of these differentiated small epidermal cells.

Pollen. The pollen of *Tubocapsicum anomalum* was described by Huang (1972) and Zhang & Lu (1995) as being nearly spheroidal with a mean size of 27.2 × 28.5 μm (Figures 8A, D); 3-colporate; colpi wide, the middle parts nearly as thick as the ends; colpus membrane tuberculate; os alongate, short and narrow 8.0 × 0.8 μm in size; exine 2.0 μm thick; exine fine rugulate (Figures 8B, C, D); columellae uneven in size, foot layer nearly as thick as

the endexine (Figure 8C). Huang reported *Tubocapsicum* pollen to be among the smallest of the 21 taxa of Solanoideae he described, but in the work by Zhang & Lu (1995) it was nearly the same as the *Physalis* and *Capsicum* taxa they described. Neither study noted characters that would separate the pollen of *Tubocapsicum* from the similar genera *Capsicum*, *Lycopersicon* Mill., *Physalis* L., or *Solanum* L.

Gynoecial Vasculature. Above the divergence of the perianth and androecial traces within the receptacle, the remaining vasculature does not converge into a continuous cylinder but continues as two ventral traces that diverge at higher levels. First, below the locules, the traces move inward, and at the base of the locules they are at the sides of the emerging placental septum. The septum is at first nearly plane but it soon develops thickenings on each side in the medial region which enlarge and become the ovule bearing placentas. At the level of the base of these thickenings, the two vascular traces branch in the plane of the septum, the smaller outer branch moving to the periphery of the ovary where it assumes the position of the dorsal trace, soon branching again in the ovary wall. The stronger branches of the ventral traces move slightly inwards where they are within and near the edge of the placental thickened region.

Near the top of the ovary, still within the placentas, these major ventral traces branch again, this time tangentially to the septum. The branches arch across the top of the placenta and downwards into the placenta where they branch and anastomose further, now in a downward orientation. Above these upper placental branches, the major traces continue to the top of the ovary. Near the top of the ovary, the septum and placentas are separated into two parts which fuse with the ovary wall. The two vascular traces continue into the style, which is sunken in the top of the ovary and is hollow basally.

In lateral view, the two major gynoecial traces branch weakly near the base of the ovary which provides a weak vasculature for the ovary wall. Near the top of the placenta, the traces branch again and the branches arch downward enervating the marginal regions of the placentas. Continuation of vasculature in the style is quite weak.

The floral vasculature of *Tubocapsicum* may be considered against descriptions of other Solanaceae by Bernardello (1986), Murray (1945), Huber (1980), and Moscone (1986). In comparing Murray's survey of the floral vasculature of the Solanaceae, the vasculature of *Tubocapsicum* resembles that of *Capsicum frutescens* L. in which the vasculature continues as two traces above the divergence of the perianth traces, rather than converging into a cylinder as in other taxa she observed. It also resembles her *Physalis* description, in that the two adaxial bundles move to the center and then issue branches in the septum or above to supply the numerous ovules on the massive placentas.

The gynoecium of *Tubocapsicum* is quite like that of *Vassobia* sect. *Vassobia*. Comparisons of *Vassobia* (mostly

on *V. breviflora*), are based on publications of Hunziker (1984), Moscone (1986), and our own preparation of flowers of *V. breviflora*. In *V. breviflora*, the vasculature converges into a ring above the corolla/androecium divergences, and from this, two traces extend into the ovary, which with branching, extend into the style to the stigma. However, the septum proliferates near the base into a false septum which partitions the basal half of the ovary into four locules. Also, the lowermost ovules are immersed in tissue of the ovary wall, and according to Hunziker (1984), at maturity there is a mixture of ovary parenchyma and ovule tissues. This last feature was indicated by Hunziker as significant for separating *Vassobia* from *Capsicum* at the generic level. In *Vassobia*, the style is solid throughout rather than basally hollow as in *Tubocapsicum*.

Gynoecial vasculature in *Tubocapsicum* displays several differences from that seen in tribe Lycieae as outlined by Bernardello (1986). In *Lycium* L., Bernardello reported extension of the two dorsal traces through the style, but the style was solid, not hollow as appears to be the case in *Tubocapsicum* judging from serial sections. In *Lycium* too, the style is not recorded as being immersed in the ovary apex. In most species of *Lycium* and in *Grabowskia* Schtdl. the septum and placenta are supplied by four ventral traces, 2 for each carpel. In *Tubocapsicum* and some species of *Lycium*, there is only the single ventral trace for each carpel which branches at the base of the ovary to yield traces in the dorsal and ventral positions. Also, the separation of the septum into two elements occurs only at the very apex of *Tubocapsicum*, whereas in *Lycium* it sometimes involves the top half of the ovary. The species of *Lycium* with a single ventral trace per carpel, *L. ameghinoi* Speg. and *L. californicum* A.Gray have single ovules and are regarded as advanced in the genus (Bernardello, 1986).

Embryogeny. Ovules of *Tubocapsicum* are anatropous, unitegmic, and tenuinucellate. The integument is four cells thick before it has surrounded the single-walled nucellus at the archesporial cell stage. At this time, the vascular tissue has not differentiated into the funiculus. Finally, a vascular bundle does differentiate within the funiculus. While the integument is still growing, there is no nucellar beak. By late stages, no micropyle or nucellar beak is distinguishable. The nucellus has produced a thick tissue by periclinal divisions adjacent to the funiculus. At this stage, the integument is about seven layers thick. There is no observable micropyle at the point where the nucellus and integument merge at the surface.

In contrast, *Vassobia* has campylotropous ovules. There is neither a nucellar beak nor periclinal buildup of tissue in the micropylar area. The micropylar canal is clearly distinguishable back to the tenuinucellate embryo sac.

Fruit. While sclerocytes or stone cells are common in the Solanaceae, none of any kind were found in any of the hundreds of fruits of *Tubocapsicum anomalum* examined. In *Vassobia*, Hunziker (1984) noted "Bayas donde la placenta crece centrifugamente y se confunde con

el pericarp; en este ultimo concreciones esclerosas,” but we found no such mixing of pericarp and placentas in the serial sections of *Vassobia breviflora* that we examined. No giant cells were seen, a feature recorded by Fridvalsky & Nagy (1966) for *Capsicum* and perhaps confined to that genus.

The juicy, ripe berry is bitter to the taste. The fruit persists as a shiny berry for more than a month and then darkens, wrinkles and shrivels on the yellowing, tardily

thickened calyx. Fruits placed in FAA and FPA preservatives retained their bright red color for more than a year. Both fresh, juicy fruits and dried, aged fruits are buoyant in fresh water.

Seeds. In *Tubocapsicum* (Figure 9E), *Aureliana*, and *Withania*, seeds are pale straw colored and do not darken, even after years of storage under refrigeration or at ambient temperatures. They are suborbiculate, laterally compressed (lenticular) (Figure 9A), and have a cavernulous

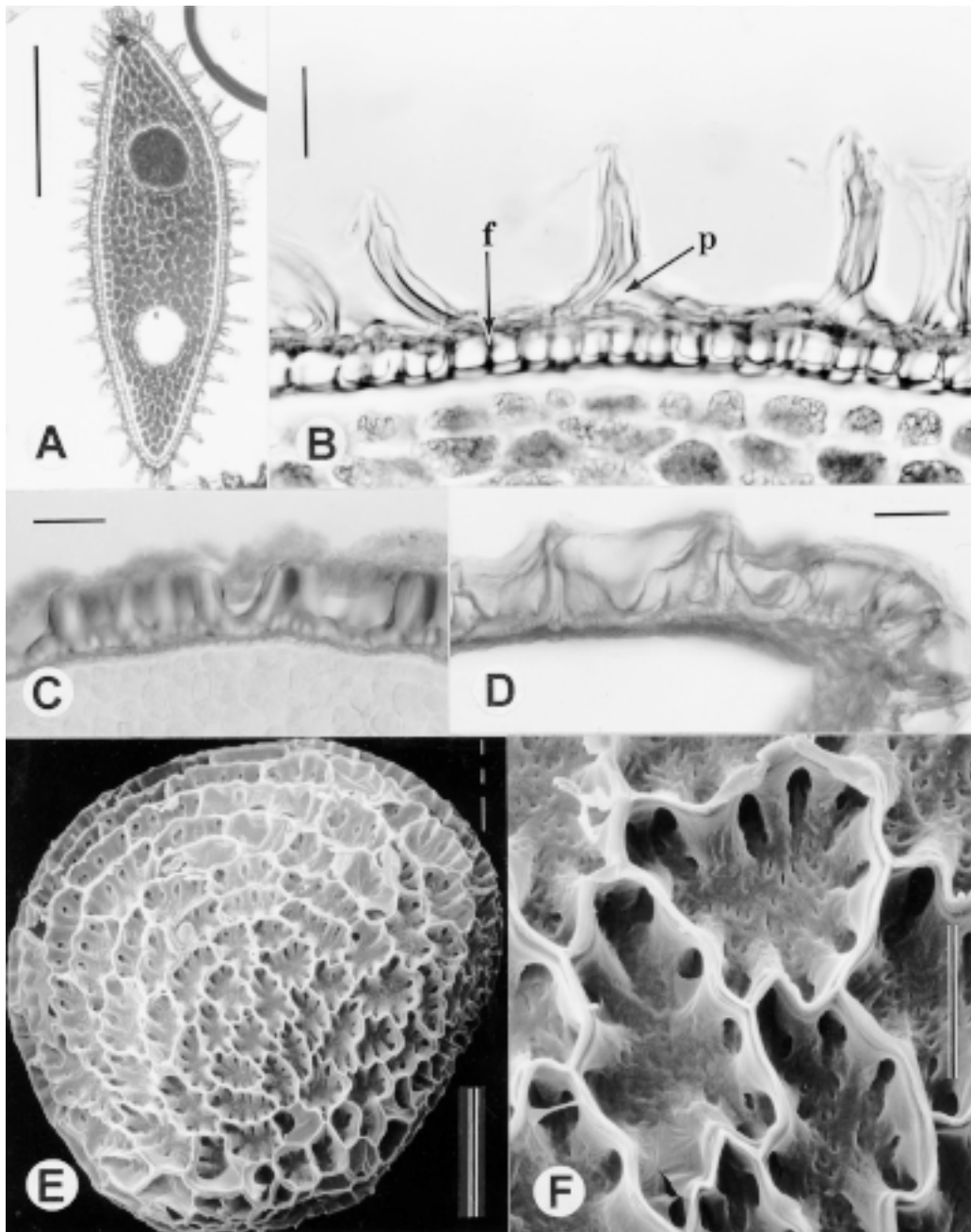


Figure 9. *Tubocapsicum anomalum* (Franch. & Sav.) Makino (A, B, E, F), *Withania somnifera* (L.) Dunal (C), and *Aureliana fasciculata* (Vell.) Sendt. (D). A, Seed cross section through testa and endosperm (LM). Curved embryo position is seen twice. Scale bar = 500 μ m; B, Testa cross section (LM) showing blind pockets (p) and fiber layer (f). Scale bar = 50 μ m; C, Testa LM cross section showing lack of pockets. Scale bar = 100 μ m; D, Testa cross section showing lack of pockets. Scale bar = 100 μ m; E, Entire seed, SEM view. Scale bar = 200 μ m; F, Testa surface (SEM), close up of E. Scale bar = 50 μ m.

reticulate surface architecture (Figure 9F) noticeable at 10X magnification. The hilum is inconspicuous, linear, and located between the radicle and cotyledon lobes. It is uniform in color, ca. 0.8 mm long, and is not recessed nor does it form a notch.

The testa is formed of three physically distinguishable layers, the inner two of which can be readily characterized from dried seeds. The outermost layer is formed of collapsed distal portions of large surface cells. Such cells, at least some members of Solanaceae, are filled with hydrophilic colloidal material. Cell walls of this layer are very thin and cellulosic, and are illustrated by Soueges (1907) and Edmonds (1983). These thin-walled portions collapse as seeds dry. The second layer, which is the first to be encountered when examining dried or cleaned seeds, is composed of the basal walls of the large surface cells. This layer forms durable, prominent, lignified reticulate ridges that extend to form a periclinal layer or floor in each islet. They are symmetrically thickened around a compound middle lamella, which is the point of attachment of the collapsed layer. The innermost, or third layer, is a fibrous, variably thickened or opaque tissue, lignified in these specimens. Within these testal layers a curved embryo is seen twice in seed transection (Figure 9A) and having appressed cotyledon tips. The surrounding endosperm ground tissue is packed with storage granules that test negatively for the presence of starch.

The diagnostic testa features of *Tubocapsicum* and two putatively related genera can be summarized as follows:

Tubocapsicum anomalum: seeds are ca. 1.5 mm long, 0.5 mm thick. Cleaned surfaces show a reticulate pattern of lignified ridges, undulate at the surface, and deeply sinuous near the base. Ridge height is ca. 90 μm , the reticulum islets ca. 150 μm in diameter. Basal sinuosities appear perforated in surface view, but testa transsections show "perforations" to be deep, blind pockets at the base of sinuosities (Figure 9B, F). Beneath the outer reticulate layer is a single transverse layer of tracheids, cells square in outline, forming the inner seed coat (Figure 9B).

Withania somnifera (L.) Dunal: seeds are 1.8-2.0 mm long, and ca. 1 mm thick. The surface pattern is reticulate, openings having a polygonal pattern of straight anticlinal walls. Ridge height is ca. 70 μm , and reticulum islets ca. 90-130 μm in diameter. Ridges are rounded at the surface and heavily thickened. The inner seed coat layer is thin and homogeneous (Figure 9C). *Tubocapsicum* seed, compared to that of *Withania*, is slightly smaller, has sinuous rather than polygonal reticulations, and the reticulation walls are much thinner.

Aureliana: (*A. velutina* Sendt. and *A. fasciculata* (Vell.) Sendt): seeds are 2.0-2.6 mm long and 0.6-0.7 mm thick. The outer testa is variably reticulate with ridges formed of straight heavily thickened walls in *A. velutina* and narrow walls showing sinuosities and blind pockets in *A. fasciculata*. Ridge height in *A. fasciculata* is ca. 110 μm , with islets being ca. 220 μm diameter. Ridge height is 50-60 μm in *A. velutina* and islets to 142 μm diameter.

The inner testa wall is not lignified and possesses no visible cellular structure (Figure 9D). *Tubocapsicum* seed, compared to that of *Aureliana*, is smaller, and has blind pockets and sinuosities similar to those of *A. fasciculata*, as well as comparable ridge height and islet size. Seed of *Aureliana velutina* is quite different, with smaller, polygonal islets and lower reticulate walls.

Axelius (1992) illustrated testa patterns in many species of *Physalis* and *Chamaesaracha* (A. Gray) Benth. The seeds of *P. heterophylla* Nees, *P. angulata* L., and *C. crenata* Norhona that she illustrated are morphologically similar, and the testa patterns are very close to those described above for *Tubocapsicum*. In fact, several species have the "very characteristic holes through the bottom thickening" (Axelius, 1992), which we interpret as blind pockets, based on our sectioned samples.

In the key of Gunn & Gaffney (1974), the seeds of *Tubocapsicum* follow the same sequence of couplets as *Solanum torvum* Sw. They differ from the species of *Cap-sicum* presented in the key by their much smaller size, and by the hilar area not being drawn out into a prominent point or knob. They differ from these authors' other species of Solaneae (except *Lycium*) in the embryo being seen only twice in cross section, not three times (imbricate or coiled). In relation to *Vassobia breviflora*, the seeds of *Tubocapsicum* are slightly smaller; have higher, narrower reticulation walls; and much larger, more open reticulation islets. The first wall layer, seen in section, is also much larger in *Tubocapsicum*. Blind pockets are absent in *Vassobia*.

Seeds of the genera of Solanoideae compared in this study share several common architectural features, including overall shape, position of the embryo, layering of the testa wall, and the surface reticulations of the second wall layer. Some characters, however, such as the presence of blind pockets, can be used for generic diagnosis. The comparisons provided above record some observable characters for use in assessing generic relationships, but they are insufficient by themselves to place *Tubocapsicum* in an evolutionary context with putative relatives. *Aureliana* and *Withania* may well prove to be close allies of *Tubocapsicum*, but the many similarities between *Tubocapsicum* and other members of the subfamily as seen by us and recorded by Axelius (1992) argue for caution in espousing this conclusion.

Cytology

Tubocapsicum anomalum is reported (Walker, 1976) to have a meiotic chromosome number of $n = 24$. The diploid number $2n = 12$ is usually recorded for other members of subfamily Solanoideae.

Cultivation Notes

Seeds displayed no dormancy, showing a high rate of germination after immediate planting from ripe fruits or after cleaning and dry storage for many months. Seeds germinated in about 24 days.

In the seasonal climate of St. Louis, Missouri (38° N latitude), plants began to flower after about four months, and bloomed continuously for several months. Several specimens planted out-of-doors in June in beds with tomatoes and *Physalis alkekengi* L. soon withered and perished, displaying symptoms of heat/light stress, although the other species accompanying them flourished. At cooler times of the year, plants cultivated in near-full sun and partial shade showed no differences in appearance or performance, but significant differences were seen when plants were held under 55% shade. These plants appeared very healthy with darker green, somewhat smaller, more broadly ovate leaves, and more compact growth, but inflorescences remained arrested at a juvenile stage, and few flowers appeared.

Fruit set was high under insect-free conditions, the time from anthesis to mature fruit being about six weeks. Fruits did not abscise and fall but persisted on the plants several months. After about four weeks they begin to shrivel somewhat but remain bright colored, and usually are ultimately shed with the pedicel. Sometimes, however, pedicel and shriveled fruit persist for many months.

From these observations, we presume that, in nature, occurrence of the species is limited by high temperatures and by excessive shade. The distribution map suggests that the species grows only in areas of mild winters. Our greenhouse experience suggests that *Tubocapsicum anomalum* also requires an abundant and continuous supply of water. When plants went unwatered for 2-3 days, they usually fell over, but they would return to an erect posture 1-3 hours after watering.

Nectar and Pollination. No pollinator observations are known. The size and shape of the flowers suggest small insects, possibly bees or flies, as vectors based on the dictum that “flowers borne singly are generally larger, but not enormously larger, than the insects that pollinate them.” (Proctor et al., 1996: 41). No scent was detected from the flowers, even after they had been placed in new glass vials for several hours to accumulate any scents present.

Nectar is sometimes copious, and sugar hygrometer measurements usually indicated sugar concentrations exceeding 55%. Such high concentrations are suggestive of bee pollination (Proctor et al., 1996: 41). The specific nectar components and their relative abundance were found to be: fructose 9.3-10.6%, glucose 7.4-8.8% and sucrose 80.6-83.3% (C.E. Freeman, pers. comm.). High sucrose to hexose ratios [sucrose/(fructose+glucose)] such as the 4:1 found in *Tubocapsicum anomalum* are notably attractive to the mainly nocturnal moths, and to diurnal butterflies and long-tongued bees (Proctor et al., 1996: 41). Flowers of *Tubocapsicum anomalum* remain open day and night, which is unusual in Solanaceae.

Discussion, Relationships

Tubocapsicum is clearly a member of the Solanaceae subfamily Solanoideae, sharing such characters as discoid

seeds, curved embryo, baccate fruit, floral actinomorphy, chromosome number $x = 12$, and others noted by D'Arcy (1975, 1991) and Hunziker (1979). These characters exclude it from the other subfamily, Cestroideae. However, the relationship of *Tubocapsicum* within the Solanoideae is not clear from morphological evidence. Tribal arrangement in the Solanoideae is still poorly defined, but the works by Hunziker (1979), D'Arcy (1975, 1991), and Benítez & D'Arcy (1997) recognize eight tribes (Capsiceae, Datureae, Hyoscyameae, Jaboroseae, Juanulloaeae, Lycieae, Nicandreae, Physaleae) in addition to the tribe Solanaeae which remains quite heterogenous.

Fusion of calyx lobes and accrescence of the calyx in fruit are a common characteristic of the Solanoideae, but the degree of fusion varies greatly and has been used in assigning taxonomic relationships. In tribe Capsiceae, including *Aureliana*, *Lycianthes* (Dunal) Hassl., *Vassobia*, and *Witheringia*, flowering calyx lobes are fused for much of their length (complete prefloration), and floral egress is by stretching (D'Arcy, 1986; Benítez and D'Arcy, 1997). However, in *Tubocapsicum anomalum* (Figure 3D), the mature calyces remain small at the base of the fruit in most specimens.

In tribe Physaleae, which embraces *Physalis*, *Withania* and other genera, the calyx is lobed, and floral egress requires little or no stretching. In fruit, the calyx is accrescent, enveloping the fruit. Corollas in both the capsicoid and physaloid genera generally have a short tube that is basally appressed to the ovary, a more or less campanulate limb, and short lobes, although in some, the lobing is more than halfway down the limb. The calyx of *Tubocapsicum anomalum* is of the capsicoid form: the lobes are fused around the bud leaving only a minute apical opening for floral egress, and the body of the calyx is not accrescent after anthesis. Thus, the calyx and other features of the plants are highly suggestive of a relationship with *Capsicum* and other similar genera.

However, in *Tubocapsicum*, where corolla and adnate filaments are appressed to the ovary, there are grooves between the filaments that permit nectar release. Such grooves are also found in *Aureliana*, *Withania* and perhaps other genera, but not in the species of *Capsicum* that we examined. In *Tubocapsicum* and *Aureliana*, the staped (or stirrup), where the filaments are inserted, is continued into small teeth. This condition was not found in the other capsicoid species or *Withania* species we examined.

Tubocapsicum differs conspicuously from other members of the Solanoideae in the adnation of its filaments to the corolla limb. Diagnostic for *Tubocapsicum* is the continuation of adnation of the filament above the level (or what corresponds to the level) of filament insertion in other groups, so that the filament is adnate to the corolla limb, from the base of the tube to the base of the sinuses in the limb. Such adnation of the filament up into the corolla limb was not seen in other putatively related plants. The recurved corolla lobes of *Tubocapsicum* are also distinctive. *Tubocapsicum* differs conspicuously from *Capsicum* in lacking giant cells of the ovary as reported by Fridvalsky & Nagy (1966).

In their analysis of chloroplast DNA, Olmstead et al. (1999) found *Tubocapsicum*, *Withania*, and *Aureliana* associated on a clade well separated from others in their inferred phylogeny of the family. Relationships among the three genera are not particularly close (weakly supported, Olmstead, pers. comm.), and their geography is disparate. *Withania* ranges from the Canary Islands to the Himalayas, *Aureliana* is restricted to Argentina, Bolivia, and Brazil, and *Tubocapsicum* is restricted to eastern Asia. This study of *Tubocapsicum* is not concordant with the DNA-based conclusions, but examination of a larger sample of species from similar genera in the Solanoideae may further illuminate the phylogeny.

Taxonomic Treatment

The first species of *Tubocapsicum* was described in 1879 by the French botanists Franchet and Savatier, as *Capsicum anomalum*. Over the years, it was described again several times under different names, as noted below. When von Wettstein (1898) treated the Solanaceae for Engler & Prantl's treatment of the world's plants, he separated *C. anomalum* from other species of *Capsicum* as "Sect. II. *Tubocapsicum*" with only the comment, "flower broadly campanulate." Then in 1908, the Japanese botanist Makino, elevated Wettstein's name to the rank of genus, and he transferred the single the species, *Capsicum anomalum*, into *Tubocapsicum*.

Georg Bitter (1913, 1917) placed two names, *Solanum anodontum* and *Solanum philippinense*, into synonymy under *Capsicum anomalum*, and outlined the geographic range of the genus. Bitter did not concur with Makino's ranking of *Tubocapsicum* as a distinct genus and followed Wettstein in ranking it as a section of *Capsicum*. Since Makino's establishment of the genus and Bitter's comment on it, there has been scant reference to *Tubocapsicum*. Hunziker (1958), who had not seen material at the time, considered it to be a section of *Capsicum*. Numerous non-descriptive references to the plant are found in Asiatic floras, and short descriptions have appeared in a few floras: Makino (1963) and Ohwi & Kitagawa (1983) for Japan, Liu & Ou (1978) and D'Arcy & Peng (1998) for Taiwan, and Kuang & Lu (1978) for mainland China.

Additional limited information on *Tubocapsicum* has been published by: Zhang & Lu (1995); Franchet & Savatier (1875); Makino (1926: 7; 453); Liu & Ou (1978: 548); Kitamura (1937: 18); Walker (1976: 919); Huang (1972: 227) (pollen); Makino (1963: 545) (in Japanese); and Ohwi & Kitagawa (1983: 1317) (in Japanese). The only illustrations of the plants that we know of are: Savatier (1874); Liu & Ou (1978: 549); Wu & Raven (1998) and D'Arcy & Peng (1998). The text and illustration from Zhang et al. (1994) can be seen on the World Wide Web at <http://herbaria.harvard.edu/china/solan/tubocaps.htm>. Pollen was treated by Zhang & Lu (1995) and leaves and seeds by Zhang & Wen (1996), and these authors also illustrated pollen, leaf surfaces and seeds.

All except Liu & Ou (1978) are in the language of the country treated, and in these works, *Tubocapsicum* has usually been recognized as a genus. Walker's English-language Flora of Okinawa (1976), an exception, recognized the species under *Capsicum*.

TUBOCAPSICUM (Wettst.) Makino, Bot. Mag. Tokyo 22: 18.1908.

Capsicum sect. *Tubocapsicum* Wettst. in Engl. & Prantl, Nat. Pflanzenfam. IV(3b): 21. 1891.—TYPE: *T. anomalum* (Franch & Sav.) Makino.

Description

Herbs, glabrate, the trichomes simple. **Leaves** alternate, simple, subentire, ovate, secondary veins arcuate, brochidodromous. **Inflorescences** few-flowered fascicles in the upper leaf axils, sometimes subtended by a small, early-deciduous, leaflike bract; peduncle wanting; pedicels only slightly expanded upwards, glabrous. **Flowers** 5-merous; prefloration almost complete (the budding perianth fused almost to the top, enclosing the inner parts), in bud the calyx showing 5 minute terminal lobules and a minute hole or port; calyx cupular, apically truncate, with only the slightest evidence of five terminal points, hardly accrescent; corolla oriented with the mouth facing downward, glabrous outside, actinomorphic, the tube short, included in the calyx, the limb broadly campanulate, glabrous, lobed 1/4 its distance, the lobes deltoid or obtuse, recurved, with no plicate area evident after opening; stamens inserted at the base of the corolla limb; the filaments basally broad, thinner upwards, narrowed into a slender neck just below the anther, each with 2 teeth or umbos just above the point of insertion, adnate to the corolla tube a short distance above the insertion, free from one another with narrow grooves between them, the filaments at first bent outwards at the top of the corolla tube and adnate to base of limb before arching upwards to the corolla mouth; anthers half-exserted from the corolla, deltoid-oblong, ca. 1 mm long, dehiscing laterally but the pollen sacs (thecae) opening inwards (ventrally, adaxially), the ventral sacks folding flat against one another; ovary included in the filament expansions, the lower half differentiated into a copious-flowing yellow nectary to which the filament expansions are applied, the style straight, terete. **Fruit** a subglobose or ellipsoidal berry (Figure 4D); seeds pale yellow, discoid, favose. (Figure 9A, B, E, F).

Tubocapsicum includes the widespread species *T. anomalum*, and populations from near the sea on the southeastern end of Shikoku Island, Japan. The Japanese specimens were recognized by Makino as *T. anomalum* var. *obtusum* and as the species, *T. obtusum*, by Kitamura.

Key to the Species of *Tubocapsicum*

- 1a. Leaf apices acute or acuminate; fruiting calyx apically contracted, the thin, distal sleeve region not accrescent, inconspicuous, mostly free from the berry; seeds mostly 1.4-1.7 mm across 1. *T. anomalum*

- 1b. Leaf apices obtuse and short acuminate; fruiting calyx not contracted apically, the thin apical sleeve area slightly accrescent and applied to the base of the berry; seeds mostly 1.5-2 mm across 2. *T. obtusum*

1. *Tubocapsicum anomalum* (Franch. & Sav.) Makino, Bot. Mag. Tokyo 22: 19. 1908. *Capsicum anomalum* Franch. & Sav., Enum. Plant. Jap. 2: 452. 1879. SYNTYPES: Japan, Tanaka (P), Hakone and Nikko, Savatier 2166 (P). A suite of five specimens, seen and cited below, was annotated as collected by Savatier, 2 from Hakone, 3 from Nikko, but the number 2166 does not appear on any of them. A specimen labeled Tanaka, Savatier 2166 (K ex L), might be taken as the holotype, but it is labelled as "*Capsicum cordiforme* Mill. var. *truncata* Miq.," and we strongly doubt that it was actually seen or collected by Savatier. LECTOTYPE, designated here: in tractu Nikko, Savatier s.n. (P). The specimen chosen as the lectotype has a packet or small envelope mounted on it, upon which there is a sketch of a stamen inserted on the corolla and "Capsicum! (anomal.)." We believe that this specimen is of the same gathering as that cited by Franchet and Savatier in the protologue, and that the writing on the packet may be the work of Georg Bitter. The specimen bears a stamp saying "Donné par M. Franchet, juillet 1882," and it was annotated by Bitter.

Solanum anodontum Lévl. & Vaniot, Le Mond Pl. 10: 37. 1908.—TYPE: Korea, Cheju Do (Quelpaert), Urb. Faurie 776 (E).

Solanum philippinense Merr., Philip. J. Sci. 7: 351. 1912.—TYPE: Philippines, Luzon, Williams 1275 (K).

Capsicum boninense Koidz., Fl. Symb. Orientali-Asiaticae. 3: 1. 1930. *Tubocapsicum benignancy* (Koidzumi) H. Hara, Enum. Sperm. Japan. 245. 1948.—TYPE: Bonin Is., Wright 200 (K, P, US).

?*Capsicum minimum* auct. non Roxb: Henry, Trans. Asiat. Soc. Japan 24 Suppl. 65. 1901. Henry's report is based on Henry 356 (MO).

Solanum biflorum auct. non Loureiro: Savatier in Iinuma, Somoku-Dzusetsu, ed. 2, 3: 47. 1874.

Capsicum cordiforme ?Mill. var. *truncata* Miq. in sched.—TYPE: Japan (K, P). Bitter (1917) referred to a specimen in (BREM), probably a duplicate of ones we cite below, annotated as *Capsicum cordiforme* Mill. var. *truncata* Miq. We have not been able to verify the valid publication of this varietal name.

Description

Erect **herbs** to 1.5 m tall; first stems stout, soon terete, later stems weak, green, terete, glabrate, drying ridged, the few trichomes short, simple. Branching mostly in dichotomous tiers. **Leaves** alternate, simple, subentire, ovate, 7-40 cm long, apically acuminate, basally obtuse or acuminate and narrowed into the petiole, sometimes somewhat oblique, the margins sometimes somewhat wavy, membranous, glabrate, with sparse minute simple tri-

chomes scattered on the lamina and vein, the midvein beneath continuous with the petiole, lateral veins arcuate, mostly 5-6 on each side, brochidromous. **Inflorescences** few (to 6)-flowered fascicles in the upper leaf axils, sometimes subtended by a small, early-deciduous, leaflike bract; peduncle wanting; pedicels ca. 5 mm long, only slightly expanded upwards, glabrous. **Flowers** 5-merous; prefloration almost complete, in bud the calyx showing 5 minute terminal lobules and a minute hole or port; calyx 2.5-3 mm long, glabrous, cupular, apically truncate, with only the slightest evidence of five terminal points, not splitting, not accrescent; corolla oriented with the mouth facing downward, opening uniformly yellow, later becoming brownish, almost waxy or shiny, glabrous outside, actinomorphic, subglobose or turbinate in bud, the tube short, not exerted from the calyx, the limb broadly campanulate, glabrous, 3-6 mm long, the mouth ca. 6 mm across, lobed 1/4 way down, the lobes deltoid or obtuse, recurved, minutely puberulent adaxially, the margins granular with minute trichomes on the edges, and no plicate area evident after opening; stamens inserted at the base of the corolla limb, glabrous, the filaments 2.5 mm long, basally broad, thinner upwards, each with 2 teeth or umbos just above the point of insertion, adnate to the corolla tube a short distance above the insertion, free from one another with narrow grooves between them, the filaments at first bent outwards at the top of the corolla tube and adnate to the base of the limb before arching upwards to the corolla mouth, narrowed into a slender neck just below the anther; anthers half exerted from the corolla, deltoid-oblong, pale yellow, 1 mm long, not apiculate, dehiscent laterally but the pollen sacs (thecae) opening inwards (ventrally, adaxially), the ventral sacks folding flat against one another, the dorsal sacks held apart by the broad shiny anther dorsum; ovary glabrous, included in the filament expansions, the lower half differentiated into a copious-flowing yellow nectary to which the filament expansions are applied, the style white, straight, terete, uniform in diameter, 2.5 mm long, inserted in a short depression in the ovary apex, the stigma minute, green, capitate, situated at about the level of the anthers. **Fruit** a subglobose or ellipsoidal shiny scarlet juicy berry, long persistent on the plant, 9 × 7 mm, the pericarp thin, translucent, the endocarp scarlet, soft and juicy, partly immersing the abhilar edges of the seeds; calyx not accrescent; fruiting pedicels somewhat elongating but not thickening until extreme age; seeds, pale yellow, discoid, favose, 1.7 × 1.4 × 0.6 mm (Figure 9).

Distribution and Phenology

Tubocapsicum anomalum ranges (Figure 1) from the Japanese island of Honshu, south through the Bonin and Ryukyu Islands, Taiwan, the Philippine Islands and as far south as eastern Borneo. From this northeast-southwest axis (from 38°N to the equator), it ranges westward to the Korean island of Cheju Do, and into China between the Huang He (Yellow River) and Hongshui River.

The species occurs from sea level to 2,100 m elevation (Mt. Mukwashan Forest, Shoufeng District, Taiwan). North

of 27°N latitude, all collections seen were below 900 m. Merrill (1923) recorded its occurrence in the Philippines in "mossy forest, 1,800 to 2,200 m, and along streams in shaded ravines at low and medium altitudes."

In Asia, most flowering specimens have been collected from August to November, but some were made as early as March. Most fruiting specimens were made between September and November, but at least some have been made in nearly every month.

Herbarium material of *Tubocapsicum anomalum* is commonly misidentified as *Capsicum annuum*, *Lycianthes* spp., or *Solanum* spp. *Capsicum annuum* can be distinguished by elongate and mostly bluish anthers; in *Lycianthes* and *Solanum*, the anthers have terminal pores. Specimens of *Tubocapsicum* with fruits but lacking flowers in particular to have been confused with these genera. *Capsicum annuum* can be distinguished by its seed that are mostly more than 3 mm across in contrast to the 2 mm or less of *Tubocapsicum anomalum* seeds, and the fruiting calyx that is usually much larger. Pedicels of most *Capsicum* specimens from Asia are straight and stiff, while those of *Tubocapsicum* are curved and flexuous. The fruiting calyx of *Tubocapsicum* lacks the evident nervation of *Lycianthes* calyces, and the evident lobes of the *Solanum* species that occur in Asia.

Common Names: Chinese "Long zhu (Dragon Ball)" (Zhang et al., 1994). Japanese "Hadaka-h_dzuki (Naked Balloon)" (Savater, 1874; Anon.a, 1887: 158; Anon.b, 1895: 126; Yokohama Nursery, 1908; Kawakami, 1910); Tachihiyodori (Standing brown-eared bulbul.), Yama-h_dsuki (Mountain or Wild Balloon) (Anon.b, 1895: 126).

Specimens Examined. **BORNEO.** N. Borneo, Lahad Datu Dist., Kennedy Bay, *D. Brand SAN 20102* (LL). SW Borneo, Kuntim Lian?, Batu Leabi, *Winkler 2734* (LL). **CHINA.** FUJIAN: Jianning Xian, *Li 10551* (PE); [Fukien] Siong-gu-liang, Hok-Chang, *Tang Siu Ging 16367* (A, MO); Wuyi Shan, 1,100 m, *Wuyi Shan Team 80-0634* (MO). GUANGDONG: Lechang Xian, *Chen 42079* (PE); Liannan Co., *Li 414* (MO); Renhua Xian, 900 m, *Liang Deng 7916* (PE); Shixing Co., Zhangdongshui, 400 m, *Xing & Ye 942* (MO); Xinfeng Xian, 700 m, *Liang Deng 7916* (PE); Yangshan Xian, 420 m, Guangdong & Guangxi Exped. 0383 (PE); Zijin Xian, 450 m, *Wei 120883* (PE). GUANGXI: Damiaoshan Co. *Luo Tong Xiang 15680* (MO), Sangfang Qu, Pingshi Xiang, Luo Tong Xian, *Chen 15680, 15735* (both MO); Antai Qu, Xiaoshang Xian, 600 m, *Chen 17319* (MO); Dayao Mt., *Lu 4492* (PE); Without other locality, Longshen Exped. 50396 (PE); Witsap District, Tou Ngok Shan near Tung Chung village, *Tsang 23227* (P); Yongshui Xian, *Chen 15680* (PE); Damiaoshan Co., Sanfang Qu, Pingshi Xiang, *Chen 16590* (MO); Xingan Xian, 800 m, *Yu 9000242* (PE); (Other counties ("Xians")): Jinxiu, Rongschui Xian, fide Zhang Zi-yun). GUIZHOU: Fanjing Mountain, Sino-British Plant Exped. 38 (K), Fanjingshan Mt., Guiyang Teacher College *F0038* (PE); Bijie Xian, 1,430 m, *Yu 857* (PE); Jiangkuo Xian 800 m, *Bartholemew et al. 146* (PE); 950 m, *Bartholemew et al.*

537 (PE); Jianning Xian, *Li 10551* (PE); Leigong Mt., Qiannan Exped. 3800 (PE); Songtao Xian, 600 m, *Bartholemew et al. 2342* (PE); Yongjing Xian, Qiannan Exped. 3379 (PE); (Other counties: Zunyi, fide Zhang Zi-yun). HAINAN: without other locality, *Wang 35210* (E); HUNAN: Chili Xian, 600 m, Hunan Exped. 636, 647 (both PE); Mang Shan, Pinkeng, 200 m, *Huang Maoxian 112942* (MO); Xiangyi Xian 700 m, *Liu 10294* (PE); Xinning, Ziyunshan, 1,150 m, *Liu 15116* (PE); 1,100 m, *Zhen-yu et al. 1791* (MO). JIANGXI: Anfu Xian, 570 m, *Yue 3098* (PE); Dagenshan, Fenyi City, *Yao 9262* (K, MO), 9264 (MO); Dexing Xian, without collector 5233 (PE); Guangchang Xian, *Hu 5249* (PE); Jiangan Xian, 300 m, *Shu-kun Lai 784* (PE); 400 m, *Lai 1518* (PE); Jinggang Mt. 1,000 m, *Jie Xiong 2763* (PE); Jiulian Shan, 510 m, *Xie 93167* (MO); Lichuan Co., (Flora of Chien-Xi), near Lan-Uk village, Nungan District, *Lau 4701* (US); Wuning Co., Wuning Yan, 300 m, *Tan 941123* (MO); Xunwu Xian, *Yue 2240* (PE); (Other counties: Jing'an, fide Zhang Zi-yun). YUNNAN: Zhenxiong Co., fide Wu (1984: 1565). XIZANG (Tibet): Between Sikkim and Bhutan, Chumby-Valley, *Searight 261* (VRSL, not located, B, destroyed, cited by Bitter, 1917). ZHEJIANG: Changuha Xian, *He 26350, 29803* (both PE), without collector 30428, 30623 (both PE); Chunan Co., Jinzhijian, Maanli, *Chiu 2138* (MO); Jian Co., Longwang Shan, Mafengan, *Chiu 3305* (MO); Jin Xian, without collector 9221 (PE); Kaihua Xian, without collector 29924 (PE); Souchang Co., Xihuasha Zhou, *Chiu 671* (MO), without collector 29568 (PE); Tianmu Mt., 550 m, Zhejiang Exped. 29022 (PE), without collector 25353, 31270 (both PE); Taishun Co., Wuyanlin, *Chang 8661* (MO); Xianju, Shisandu, Zhongkeng, Zhejiang Bot. Resource Team 29966 (MO); Zenhai Co., Ruiyan Shi, *Chiu 133* (MO), without collector 2043 (PE); (Other counties: Jiande, Lin'an, Yinxian, fide Zhang Zi-yun). TAIWAN. Sakahen, *Gressit 460* (K, LL); Mt. Taiheizan, *Suzuki 275* (MO); *Namba et al. C 557* (TI). CHIAYI HSIEN: Shihcho, 400 m, *Yen 6073* (HAST); Tapu Hsiang, Tingpinglin, 600-700 m, *Yen 6604* (HAST); Chuchi Hsiang, Shihcho, *Yen 6873* (HAST, MO). HSINCHU HSIEN: Wufeng District, en route from Tuchang to Kuanwu ca. 16.5 km S of Tuchang, 1,520 m, *Peng 9364* (HAST). HUALIEN HSIEN: Shoufeng District, Mt. Mukwashan Forest, Halun Station. 2,000-2,100 m, *Peng 7270* (HAST, MO). Hsiulin Hsiang, from Kuailin to Chilai, 1,425-2,160 m, *Ho et al. 679* (HAST). Shuiyuan to Luanschan NW of Hualien, 1,600-1,900 m, *Tamura et al. 21517* (E). Ta-Yu-Ling, *Chuang & Kao 4373* (LL). ILAN HSIEN: From Chi-lan Forest Station to Yuen-yang Lake Natural Reserve, 500-1,500 m, *Boufford et al. 19413* (MO). Fu Shan Botanical Garden, 700-720 m, *Peng 3878* (HAST). Fu Shan, 650 m, *Bufford et al. 25099* (MO). Between Kungliao and Hutzupe (a stone tablet), en route from Kungliao to Tali, 40 m, *Peng 13566* (HAST). Nanhutaschan, Nanshan-Kiretei, 1,600 m, *Yamazaki et al. 737* (MAK-142083, TI). MIAOLI HSIEN: Nanchuang Hsiang, along bank of Fengmeihsi, 1,500-1,700 m, *Liu 339* (HAST, MO). NANTOU HSIEN: Hsinyi Hsiang, Petyushan, cut from Shalihshien Forest Road through a

valley up to a mountain ridge 1,300-1,700 m, *Chang 86* (HAST). Between Chi-tow & Sunkinksea, 1,100-1,600 m, 1983, *Peng 5396* (HAST, MO). Hsinyi District: Shenmu, *Peng 10975* (HAST). Luku Hsiang, Hsitou. *Peng 6983* (HAST), *Lin 623* (HAST). Chitou to Fenghuangshan, *Chen 231, 779* (both HAST). En route from Tungpu Hot Spring to Rainbow Waterfall. 1,200-1,400 m, *Peng 8228* (HAST, MO). Feng-shan, Chi-tou, 1,400 m, *Yamazaki 160* (TI). PINGTUNG HSIEN: Bankinsing, *Henry 356* (MO). Tahanshan, *Amenotaxus formosana* Preserved Area, 1,300-1,500 m, *Chaw 806* (HAST). Chunjih Hsiang, along Tahan Forest Trail from Shitiliao to Tahanshan, 500-1,300 m, *Yen et al. 572* (HAST); Wutai Hsiang, en route from Wutai to Payutzu (Little Ghost Lake), entrance of Ching-Chieh-Shan, *Lin 306* (HAST). TAICHUNG HSIEN: *Sasaki 6* (TI). Hoping Hsiang, Wushihkeng, from The Low Altitude Experimental Station, Taiwan Endemic Species Research Institute to Wushihkenghsi, 1,000-1,250 m, *Shen 218* (HAST). TAIPEI HSIEN: Wulai Hsiang, Fushan Village, Kuaishan, 1,350-1,590 m, *Liao 1005* (HAST); Wulai, 150-200 m, *Peng 10008* (HAST, MO). Pinglin Hsiang, Taiyuku, from Chinkualiaohsi (stream) to Preserve of *Keteleeria davidiana*, 210-350 m, *Liu 4* (HAST, MO); Mt. Chihsingshan, en route to Mr. Yu You-jeu Graveyard, 800 m, *Peng 9879* (HAST, MO); Yangmingshan National Park, Tatunshan mountain from the parking lot of Tarun Nature Park to Erhtzuping, 825-840 m, *Shen 273* (HAST). TAITUNG HSIEN: Orchid Island (Lanyu) trail up to Tein Tsiu, 325 m, *Lammers 8543* (MO); Green Island (Lutao). Forested drainage ditch leading to the sea by Hot Spring, *Peng 7616* (HAST); Along Yeh-yin stream from Yung-hsing-nung-chuang to Ao-pen-ling, 100-250 m, *Leu 1378* (HAST, MO). TAOYUAN HSIEN: Lalashan Nature Preserve, NE of Shang Paling, along trail, entrance to Lalashan Mt. peak, 1,550-1,700 m, *Peng 14619* (HAST). **INDIA.** ASSAM: *Masters* (B, ex CAL, destroyed, not seen, cited by Bitter 1917). **JAPAN.** Without locality or collector. "*Capsicum cordiforme* Mill var. *truncata* Miq." ex herb. Lugduno-Batavo (K, LL, P); [-Labelled in pencil as *Tanaka Savatier 2166*.] Without other locality, *Bissett* yr 1877 (K); *Dickins* 10/81 (K); *Mohnike s.n.* (LL); *Oldham* 1861 (LL); *Tanaka* 263 (P). BONIN ISLANDS: *Wright 200* (K, P, US). RYUKYU ISLANDS: Ins. Iriomote, Komi-Komidake, 50 m, *Yamazaki* 17 Jun 1971 (TI); Ins. Amami-oshima, *Hatusima* 19988 (LL); *Hatusima & Sako* 23893 (LL); Ins. Eshaki Shima, *Fosberg* 37371 (LL, US); Ins. Ishigaki, Mt. Banna, *Iwatsuki et al.* 893 (LL, MO); Ins. Okinawa, without other locality, (MAK-97977). Ryukyu University Experimental forest, Yona, Kunigami-son, *Tamaki* 12 Oct 1957 (MAK-141633). *Amano* 6858 (US). *Moromizato*, 31 Oct 1957 (US). Tanyoeake, *Walker* 83183 (LL, US). Common but scattered at seaside, *Tawada* 2226 (US). *Elliot* 1081 (US); Ins. Yagashima, 170 m, *Kanei et al.* 10084 (TI); Ins. Yonakuni, *Furuse* 2501, 4179, 4196, 4524, 4525, 4643 (all K). KYUSHU. Bungo, *Takenouchi* 2776 (US); Segiri, 100 m, *Yamazaki* 7001 (TI); Yakushima, Nagata, Kuniwari-dake, 400 m, *Yamazaki* 6923 (F, TI); -note rounded leaves. Yakuchō along river Nakamagawa, *Chizu Chuma*, 4 Mar 1968 (TI); Pref. Oita, Mt. Kujusan (MAK-97972). Kujusan,

Jusan-magarari, Yobikogawa, *Togashi 7356* (TI); Kagoshima: Shiroyama, Kagoshima City (MAK-97954); Goino, Hirakawa, *Murata 16044* (TI); Kumamoto: Fukabayama, Aso-machi, Aso-gun (MAK-75361). Aso, Takamoricho, Takamori-toge, 800 m, *Yamazaki* 7 Oct 1988. (TI); Mii Sagamigawa, Oct 1886 *Bissett* 3822 (E). HONSHU. Without other locality, ?Yokacku, *Bissett* 928, 2224 (both E); Nikko, 1873, *Savatier* (P-2); Hiroshima, Miyajima in Aki, *Togasi* 31 Oct 1955, *TNS 1259* (E, K, TI, US); Mt. Amagi, *Suzuki* 18 Jul 1980 (US). Prof. Mt. Rokkosan, Kobe City (MAK-97966). Yamakita, Yamakita-cho, Ashigarakami-gun, (MAK-75359); Imaizumi, Kamakura City, *Kobayashi 3176* (3 Nov. 1983) (MAK-212869); Enoshima, Fujisawa City (MAK-75357); Hakone, Hakone-machi, Ashigarashimogun. *Makino*, Oct 1924 (MAK-97965); Hakone, *Savatier* (P-3); Mt. Takatoriyama, toward the east, Zushi City, *Momiyama s.n.* (MAK-234896); Mt. Takatoriyama, Yakushido, Yusaka, Zushi City, *Momiyama s.n.* (MAK-234756); Yokohama, *Maximowicz*. Iter secundum (LL, P); *Amano* 8 (MO). Kifune, N of Kyoto, *Murata 18647* (E, LL, P, US); *Satomi 9414* (MAK-236457); *Takahashi 431*, (MO); Tokyo, Sep 1910 without collector (E); without collector, (E); Azusawa, Itabashi-ku, (MAK-97955); Inokashira, Mitaka City, *Makino, s.n.* (CAL, MAK-75354); *Makino 75355* (LL); Prov. Musashi: Tabata, Aug 1910 without collector (E, US); Prov. Musashi: Tabata, Aug. 1910 without collector (E); Tokyo, Tahata-Mura, Tabata, Aug 1910 without collector (US); Musashi (Oji), 21 Aug 1908, s. coll. (VRSL); Yokohama Nursery, July 1808 (E); Pref. Yamaguchi, Mt. Tokusagamine, Abu-gun, (MAK-130188). Pref. Nara: *Takahashi 774*, (MO); Pref. Shizuoka, Amagi Pass, Mt. Amagi, 800 m, *H. Kaman* 18 Sep 1961 (TI). SHIKOKU: Ehime: Izushidera, *Satomi 9088* (MAK-236454); Mt. Iwayayama, Mikawa-mura, Kamiukena-gun, (MAK-97970); Kochi: Mt. Dogamori, Nakamura City (MAK-97963); Iyoki: Otoyo-mura, Nagaoka-gun (MAK-97967); Shimonanaka, Agawa-mura, Agawa-gun, 300 m, *Murata 18864* (TI); Muroto-city, Moroto-misaki, near seaside, *Takahashi 1223* (TI); Ziyadani, Kitagawa-mura, Aki-gun, 400 m, *Murata et al.* 63 (TI). **KOREA.** Cheju Do (Quelpaert Island) Hongno? 33°24'N, 126°24'E, *Chung Ing-Cho* 3756 (F); *Faurie* 776 (E); *Nakai 6463* (TI); *Nakai* 6 Jun 1913 (TI); *Taquet 1145* (E); 3078 (E, K), (both B-cited by Bitter 1917, destroyed) (*Taquet 1144* (K) is a species of *Solanum*). **MALAYSIA.** locality illegible, *Winkler 2734* (K); Sabah, Ulu Segama, *Argent et al.* 108201 (K). **PHILIPPINES.** *Loher 6643* (B, ex K, B-cited by Bitter 1917, destroyed); Bandschan, *Loher 4377* (K); Mindoro, *Escritor*, Jul 1913 (Bur. Sci. 21306) (K); Laguna, Mt. Meguiling, *Elmer 17592* (LL); Ins. Luzon, *Elmer 6561* (K-2, US, B-cited by Bitter 1917, destroyed); *Elmer 16996* (K); *Serviñas s.n.* (Bur. Sci. 16862) (MO); Benguet, *Merrill 8003* (K, LL, US, B-cited by Bitter 1917, destroyed); Mariveles Island, Manila Harbor, *Day 185* (MO); Luzon, Mt. Magras, *Edaño 6279* (LL); Benquet Prov., Mt. Tonglon, *Ramos 5406* (LL); Sorsogon, *Ramos* Jul-Aug 1925 (Bur. Sci. 23438) (K); Ins. Mindanao, *Merrill 8164* (K, LL, US, B-cited by Bitter 1917, destroyed).

2. **Tubocapsicum obtusum** (Makino) Kitamura, Acta Phytotax. Geobot. 6: 18. 1937. *Tubocapsicum anomalum* var. *obtusum* Makino, J. Jap. Bot. 3(2): 7. 1926.—TYPE: Japan, Prov. Tosa, Muroto-zaki (*Torama Yoshinaga*), 3 Jan 1921 (MAK-97979).

Description

Glabrous **herbs**, stems drying grooved, fine lenticellate. **Leaves** succulent, broadly ovate, mostly 3-8 cm long, apically obtuse and short acuminate, basally truncate or cordate, sometimes acuminate and narrowed into the petiole, lateral veins arcuate, mostly 3 on each side. **Inflorescences** few-flowered fascicles in the axils of leaf pairs, mostly with 1-2 small (-1 cm), apically rounded leaves in addition to the paired normal leaves; pedicels 1-2 cm long. **Flowers** with calyx 4 mm long, cupular, apically truncate, the apical sleeve region 2 mm long; corolla deeply lobed, the lobes narrow, acute, ca 5 mm long; anthers oblong, 1.5 mm long, not apiculate, the thecal region light colored, the narrow connective dark. **Fruit** a subglobose or ellipsoidal red or orange berry, 8-10 mm across, the pericarp thin, translucent; calyx slightly accrescent; pedicels somewhat elongating and thickening; seeds, pale yellow, discoid, favose, 1.7-2.0 mm across.

The species differs from *Tubocapsicum anomalum* in its smaller, thicker and more blunt-tipped leaves, in its larger fruiting calyces, and perhaps in having slightly larger seeds. In some collections, the fruiting pedicel expands somewhat apically, thus resembling some specimens of feral *Capsicum annuum*, but the seeds are much smaller than in that species. Although several specimens were available for study, only one (MAK-44282) bore a flower that could be dissected. The anthers are different from those of *T. anomalum*, and it is probable that this taxon is member of a different genus. The stamens and corolla shown by Liu & Ou (1978) in their illustration of *Tubocapsicum anomalum* are more like those of *T. obtusum* than those of *T. anomalum*, in that the corolla lobes are not recurved and the anthers lack the broad dorsum characteristic of *T. anomalum*.

Because some (or most) collections were taken near the sea, it is possible that their succulent appearance shows the salt-succulence commonly found in seaside vegetation (Boyce, 1954).

The specimen we refer to as the type specimen has no collector indication, but Makino recorded the collector as *Torama Yoshinaga*, and noted that this taxon grows "at the littoral place." Kitamura, who transferred Makino's varietal name to the rank of species, indicated his doubt that the taxon belongs to *Tubocapsicum*. Until additional material becomes available, it seems best to accept Kitamura's disposition of these plants.

Distribution. *Tubocapsicum obtusum* is reported from Japan.

Specimens Examined. JAPAN. RYUKYU ISLANDS: Ins. Iriomote, Komi-Komidake, 50 m, *Yamazaki* 17 June 1971 (TI); Ins. Eshaki Shima, *Fosberg* 37371 (US); Ins.

Ishigaki, Mt. Banna, *Iwatsuki et al.* 893 (MO); Ins. Okinawa, Yona, Kunigami-son, *Tamaki* 13 Jan 1970 (MAK-128613) [depauperate]. Common but scattered at seaside, *Tawada* 2226 (US); Ins. Tokunoshima, Hetono, Amagi-cho, *Sugawara* 2067 (MAK-206083). HONSHU: Island of Miakao, *Koidzumi* 11 Jun 1923 (US); Honshu. Pref. Chiba: Matsudo, Matsudo City (MAK-75352). KYUSHU: Pref. Kagoshima: Hashima, Kushikiko City, *Hatusima & Sako* 27989 (MAK-51647). SHIKOKU: Kochi: Shimokanoe, Tosashimizu City, (MAK-97962); [intermediate] Muroto-saki, Muroto City, [*Torama Yoshinaga*] 3 Jan 1921 (MAK-97979, type collection).

Acknowledgements. Thanks are offered to curators of institutions who arranged for our loans of herbarium specimens (A, CAL, E, K, MAK, P, TI, US, VRSL) as well as curators and staff of our own institutions, HAST, MO and PE. We thank also the Conservatoire et Jardin Botanique, Nancy, France, for providing seed of *Withania riebeckii*, Hardy Eshbaugh for seed of *Capsicum annuum* var. *aviculare* and Peter H. Raven for assistance with literature. Particular thanks are extended to C. E. Freeman, University of Texas, El Paso, who provided sugar analyses of nectars, and to Suzanne Eder, Southern Illinois University-Edwardsville for microtechnique. The authors are grateful for detailed reviews of the manuscript by Thomas G. Lammers and Charlotte Taylor.

Literature Cited

- Anon, A. 1887. A Catalogue of Plants in the Botanic Garden of the Imperial University. Imperial University, Tokyo.
- Anon, B. 1895. Useful Plants of Japan Described and Illustrated. Agricultural Society of Japan, Tokyo.
- Axelius, B. 1992. Testa patterns in some species of *Physalis* L. and some other genera in the tribe *Solaneae* (Solanaceae). *Int. J. Plant Sci.* **153**: 488-502.
- Barboza, G.E. and A.T. Hunziker. 1992. Estudios sobre Solanaceae XXXIII. El género *Lycianthes* en La Argentina. *Darwiniana* **31**: 17-34.
- Bell, A.D. and T.D. Dines. 1995. Branching patterns in the Solanaceae. In P.C. Hoch and A.G. Stephenson (eds.), *Experimental and Molecular Approaches to Plant Biosystematics*. Monog. Syst. Bot. Missouri Bot. Gard. Vol. 53, pp. 157-172.
- Bernardello, L.M. 1986. Estudios en *Lycium* (Solanaceae). V. El gineceo de Lycieae. *Kurtziana* **18**: 23-45.
- Benítez, C. and W.G. D'Arcy. 1997. The genus *Lycianthes* (Solanaceae) in Venezuela. *Ann. Missouri Bot. Gard.* **84**: 167-200.
- Bitter, G. 1913. Solana nova vel minus cognita. VII: XVIII. Species e genere excludenda. *Fedde Rep.* **11**: 491.
- Bitter, G. 1917. Solana nova vel minus cognita. XVI: XLV. Species e genere *Solanum* removenda. *Fedde Rep.* **15**: 96-98.
- Bohs, L. 1989. *Solanum allophyllum* (Miers) Standl. and the generic delimitation of *Cyphomandra* and *Solanum* (Solanaceae). *Ann. Missouri Bot. Gard.* **76**: 1129-1140.
- Boyce, S.G. 1954. The salt spray community. *Ecol. Monogr.* **24**: 29-67.
- D'Arcy, W.G. 1975. The Solanaceae: an overview. *Solanaceae Newsl.* **2**: 8-15.

- D'Arcy, W.G. 1986. The calyx in *Lycianthes* and some other genera. *Ann. Missouri Bot. Gard.* **73**: 117-127.
- D'Arcy, W.G. 1991. The Solanaceae since Birmingham, 1976 with a review of its biogeography. In J.G. Hawkes, R. Lester, M. Nee, and N. Estrada (eds.), *Solanaceae 3: Taxonomy-Chemistry-Evolution*. Royal Botanical Gardens, Richmond, United Kingdom, pp. 75-137.
- D'Arcy, W.G., R.C. Keating, and S.L. Buchmann. 1996. The calcium oxalate package or so-called resorption tissue in some angiosperm anthers. In W.G. D'Arcy and R.C. Keating (eds.), *The Anther: Form, Function and Phylogeny*. Cambridge Univ. Press, United Kingdom, pp. 189-191.
- D'Arcy, W.G. and C.-I. Peng. 1998. *Solanaceae*. In T.C. Huang, D. E. Boufford, C.F. Hseih, P.P. Lowry II, H. Ohashi, and C.-I. Peng (eds.), *Flora of Taiwan*, 2nd ed., Vol. 4. Editorial Committee of the Flora of Taiwan, Second Edition, Taipei, pp. 549-582.
- Duke, J.A. 1969. On tropical seedlings I. Seeds, seedlings, systems, and systematics. *Ann. Missouri Bot. Garden* **56**: 125-161.
- Edmonds, J.M. 1983. Seed coat structure and development in *Solanum* L. section *Solanum* (Solanaceae). *Bot. J. Linn. Soc.* **87**: 229-246.
- Franchet, A. and L. Savatier. 1879. *Enumeratio Plantarum in Japonia Sponte Crescentium*. Paris.
- Freeman, C., W.H. Reid, J.E. Becvar, and R. Scogin. 1984. Similarity and apparent convergence in the nectar-sugar composition of some hummingbird-pollinated flowers. *Bot. Gaz.* **145**: 132-135.
- Fridvalsky, L. and J. Nagy. 1966. The differentiation, microscopic and submicroscopic structure of giant cell wall in the pericarp of *Capsicum annum* L. *Acta Agron. Acad. Sci. Hungar.* **15**: 69-78.
- Gunn, C.R. and F.B. Gaffney. 1974. Seed Characteristics of 42 Economically Important Species of Solanaceae in the United States. U. S. D. A. Agric. Res. Serv. Techn. Bull. 1471.
- Hallé, F., R.A.A. Oldeman, and P.B. Tomlinson. 1978. *Tropical Trees and Forests: an Architectural Analysis*. Springer-Verlag, Berlin.
- Henry, A. 1896. A list of plants from Formosa. *Trans. Asiatic Soc. Japan* 24 (suppl.): 65-67.
- Herr, J.M. 1992. Applications of a new clearing technique for the investigation of vascular plant morphology. *J. Elisha Mitchell Sci. Soc.* **88**: 137-143.
- Huang, T.C. 1972. *Pollen Flora of Taiwan*. Natl. Taiwan Univ. Bot. Dept. Press, Taipei. Solanaceae, pp. 224-227.
- Huber, K.A. 1980. *Morphologische und entwicklungs-geschichtliche Untersuchungen an Blütenständen von Solanaceen und von *Nolana paradoxa* Lindl. (Nolanaceae)*. Dissert. Bot. 55.
- Hunziker, A.G. 1984. Estudios sobre Solanaceae. XIX. Sinopsis de *Vassobia*. *Kurtziana* **17**: 91-118.
- Hunziker, A.G. 1958. Synopsis of the genus *Capsicum*. VIII Congr. Intl. Bot. sect. **3-6**: 73-74.
- Hunziker, A.G. 1979. [Estudios sobre Solanaceae. X] South American Solanaceae: a synoptic survey. In J.G. Hawkes, R.N. Lester, and A.D. Skelding (eds.), *The Biology and Taxonomy of the Solanaceae*. Academic Press, London, pp. 49-85.
- Kawakami, T. 1910. A List of Plants of Formosa. Taihoku.
- Keating, R.C. 1996. Anther investigations: a review of methods. In W.G. D'Arcy and R.C. Keating (eds.), *The Anther, Form, Function, and Phylogeny*. Cambridge Univ. Press, United Kingdom, pp. 255-171.
- Kerr, A. 1954. Solanaceae. In W.G. Craig and A.F.G. Kerr. (eds.), *Florae Siamensis Enumeratio*, Vol 3, pp. 35-52.
- Kitamura, Siro. 1937. Expositiones plantarum novarum Orientali-Asiaticarum 2. *Acta Phytotax. Geobot.* **6**: 18-23.
- Knapp, S. 1989. A revision of the *Solanum nitidum* group (section *Holophylla* pro parte): Solanaceae. *Bull. Brit. Mus. (Nat. Hist.) Bot.* **19**: 63-102.
- Koidzumi, G. 1930. *Florae Symbolae Orientali-Asiaticae*. Kyoto, Japan.
- Kuang, K. and A. Lu (eds.). 1978. Solanaceae. *Fl. Reipub. Popul. Sin.* **67**(1): 1-175.
- Léveillé, H. and E. Vaniot. 1908. Solanacées nouvelles. *Monde Plantes* **53**: 37.
- Liu, Y.C. and C.H. Ou. 1978. *Tubocapsicum*. In H. L. Li, T.S. Liu, T.C. Huang, T. Koyama and C.E. DeVol (eds.), *Flora of Taiwan*, Vol 4. Epoch Publ. Co., Ltd., Taipei, pp. 548-550.
- Makino, T. 1908. Observations on the flora of Japan. *Bot. Mag. (Tokyo)* **22**: 18-20.
- Makino, T. 1926. A contribution to the knowledge of the flora of Japan. *J. Jap. Bot.* **3**(2): 2-7.
- Makino, T. 1963. Solanaceae. In Makino's *New Illustrated Flora of Japan*, pp. 542-551.
- Merrill, E.D. 1923. *An Enumeration of Philippine Flowering Plants*, Vol. 3. Manila, pp. 424.
- Merrill, E.D. 1912. New or noteworthy Philippine plants, IX. *Philipp. J. Sci.* **7**: 259-357.
- Moscone, E.A. 1986. Sobre el gineceo de *Vassobia* (Solanaceae). *Bol. Soc. Argentina Bot.* **24**(3-4): 319-331.
- Murray, M. A. 1945. Carpellary and placental structure in the Solanaceae. *Bot. Gaz.* **107**: 243-260.
- Ohwi, J. and M. Kitagawa. 1983. *New Flora of Japan*. Shibundo Co., Tokyo.
- Olmstead, R. G., J. A. Sweere, R. E. Spangler, L. Bohs, and J. D. Palmer. 1999. Phylogeny and provisional classification of the Solanaceae based on chloroplast DNA. In M. Nee, D. E. Symon, J. P. Jessop and J. G. Hawkes (eds.), *Solanaceae IV: Advances in Biology and Utilization*. Royal Botanic Gardens, Kew, Surrey, pp. 111-137.
- Proctor, M., P. Yeo, and A. Lack. 1996. *The Natural History of Pollination*. Timber Press, Portland.
- Robinson, D.F. 1996. A symbolic framework for the description of tree architecture models. *Bot. J. Linn. Soc.* **121**: 243-262.
- Sasaki, S. 1930. A Catalogue of the Government Herbarium Dept. of Forestry, Taihoku, Formosa.
- Savatier, P.A.L. 1874 Hadaka-H dzuki, in Iinuma's *Somoku-Dzusesu*, ed. 2, **3**: 47.
- Souéges, M.R. 1907. Développement et structure du tégument séminal chez les Solanacées. *Ann. Sci. Nat. Bot. Sér.* **9**, **6**: 1-124.
- Von Wettstein, R. 1898. Solanaceae. In A. Engler & K. Prantl (eds.), *Die Natürlichen Pflanzenfamilien*. Leipzig, Vol. 4 (3b), pp. 1-38.

- Walker, E. H. 1976. Solanaceae. In Flora of Okinawa and the Southern Ryukyu Islands. Smithsonian Inst. Press, Washington, pp. 911-924.
- Wu, C.Y. 1984. (ed.). Index Florae Yunnanensis. Yunnan, China.
- Wu, C.Y. and P.H. Raven (eds.). 1998. Flora of China Illustrations, Vol. 17, Verbenaceae through Solanaceae. Science Press (Beijing) & Missouri Bot. Gard. (St. Louis), p. 380.
- Zhang, Z.Y., A.M. Lu, and W.G. D'Arcy. 1994. Solanaceae. In Z.Y. Wu and P.H. Raven (eds.), Flora of China. vol. 17, Verbenaceae through Solanaceae. Science Press (Beijing) & Missouri Bot. Gard. (St. Louis), pp. 300-332.
- Zhang, Z.Y. and A.M. Lu. 1995. Pollen morphology of *Physalis* (Solanaceae) in China and its systematic significance. *Cathaya* 7: 63-74.
- Zhang, Z.Y. and J. Wen. 1996. Characters of leaf epidermis and seed coats in *Physalis* (Solanaceae) from China and its Systematic Significance. *Acta. Bot. Yunnanica* 18: 419-423.

龍珠屬（茄科）植物之系統學研究

William G. D'Arcy¹ Richard C. Keating¹ 張志耘² 彭鏡毅³

¹美國密蘇里植物園

(William G. D'Arcy 先生於 1999 年 12 月 16 日過逝)

²中國科學院植物研究所

³中央研究院植物研究所

過去分類學家對龍珠屬 [*Tubocapsicum*, Solanoideae (茄亞科)] 植物是否應該歸併於辣椒屬 (*Capsicum*) 或自成一屬一直有許多的爭議。本研究針對龍珠 (*Tubocapsicum anomalum*) 的營養器官、花朵構造、雌器、果實、種子、花粉、表皮氣孔等進行形態學、解剖學及胚胎學等研究，觀察植物生長之分枝結構，並檢閱典藏於世界主要標本館的標本進行分類研究。本研究結果支持龍珠屬為特產於東亞的茄科植物，包括龍珠及另一分佈於日本，但分類地位仍待進一步研究的 *Tubocapsicum obtusum*。本文並詳細的描述龍珠的形態，提供線繪圖，並討論龍珠屬與茄亞科相關屬的關係。

關鍵詞：解剖學；辣椒屬；形態學；分類訂正；茄科；植物分類學；龍珠屬；龍珠；*Tubocapsicum obtusum*。