Revision of the genus *Nastanthus* (Calyceraceae)

Revisión del género *Nastanthus* (Calyceraceae)

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**ABSTRACT**

The nomenclatural revision of 51 names previously published, combined or synonymized under the genus *Nastanthus* (Calyceraceae) is presented. Six species are recognized with correct names and new synonyms established. The nomenclature of *Nastanthus ventosus*, *Nastanthus scapigerus* and *Nastanthus compactus* is updated, giving a total of 45 synonyms. Lectotypes for *Boopis caespitosa*, *Boopis scapigera*, *Boopis spathulata*, *Nastanthus laciniatus*, *Boopis araucana*, *Calycera ventosa*, *Nastanthus pinnatifidus* and *Boopis breviflora* are here designated. A map with the geographic distributions, complete species descriptions, corrected illustrations, and a new key to accepted species of *Nastanthus*, are included.

**KEYWORDS:** Calyceraceae, *Nastanthus*, taxonomy.

**INTRODUCTION**

The family Calyceraceae includes 54 small herbs or subwoody plants species, annuals or perennials, endemic to southern South America (southern Brazil, Bolivia, Paraguay, Uruguay, Chile and Argentina; Chiapella 1999a, 1999b, Zanotti & Pozner 2008). Most species grow in arid Andean or Patagonian habitats; a few species inhabit eastern, more humid environments, and only one grows in Malvinas (Falkland) Islands (Chiapella 1999a, 1999b; Zanotti & Pozner 2008). Six genera have been distinguished within Calyceraceae: *Acicarpha* Juss. (5 species from Argentina, Bolivia, Brasil, Perú and Uruguay); *Boopis* Juss. (13 species from Argentina and Chile); *Calycera* Cav. (14 species from Argentina, Bolivia and Chile); *Gamocarpha* DC. (6 species from Argentina and Chile); *Moschopsis* Phil. (7 species from Argentina and Chile) and *Nastanthus* Phil. (9 species from Argentina and Chile). About 90% of the species grow along the Andes of Argentina and Chile (Zanotti & Pozner 2008). The most complete information on systematics and taxonomy of Calyceraceae was published by Pontiroli (1963), Chiapella (1999a, 1999b), Galvão Magenta & Pirani (2002), Hellwig (2007), Zanotti & Pozner (2008), and literature therein.

Calyceraceae morphology deserves an exhaustive reevaluation. Some contributions have been published during the last 20 years, and these new data confirm a major problem with this family: the lack of sharp boundaries among genera. Reitz (1988) was one of the first authors to suggest the synonymy among *Boopis*, *Gamocarpha* and *Nastanthus* due to poor morphological differences. The palynological results published by Hansen (1992) showed at least two main pollen morphologies in the family, which were not uniform within genera. According to Carlquist & DeVore (1998) the diversity of wood anatomy in
Calyceraceae (14 species from 5 genera sampled) suggests adaptations to particular ecological conditions, with little phylogenetic information. Characters of fruit morphology are used to delimit Calyceraceae genera. However, Zanotti & Pozner (in prep.) did not find enough morphological or anatomical evidence to distinguish Boopis from Nastanthus, in agreement with Hellwig (2007), who suggested the synonymy among Nastanthus, Boopis and Moschopsis. Finally, a preliminary molecular phylogeny of the family (Pozner et al. in prep.), suggests that Calycera, Nastanthus and Boopis are not monophyletic.

Because of that poor generic delimitation, some species (particularly those of Nastanthus) are difficult to identify, even with the most comprehensive keys (Pontirolli 1963; Chiapella 1999a), and consequently the identification of herbarium collections is not reliable. In addition, the most recent nomenclatural synopsis of Calyceraceae for southern South America (Zanotti & Pozner 2008) revealed names that need revision, particularly those combined or synonymyzed under Nastanthus. For these reasons, and toward a complete and comprehensive taxonomic revision of Calyceraceae, we present here the nomenclatural revision of 51 names published, combined or synonymyzed under Nastanthus. We recognized six species, established correct names, new synonyms, lectotypes, updated distribution, and included morphological observations. We do not attempt to present any hypothesis about evolutionary relationships or monophyletic groups, rather just to delimitate species and clear up the nomenclature, which is useful whether Nastanthus later remains as a segregate genus or is merged with another genus, or if a species accepted here is transferred to another genus.

MATERIALS AND METHODS

Collections of Calyceraceae housed at BAB, CORD, CTES, LIL, MERL, SGO, SI were studied (Holmgren et al. 1990). Type material from BAB, CORD, E, GH, K, LP, P, RNG, SGO, S, SI, W, or their digital images, and original descriptions were also consulted. Drawings of the new species were based on rehydrated herbarium material. Illustrations of Nastanthus patagonicus, N. falklandicus and N. scapigerus were taken from Chiapella (1999a) and reproduced with the editor’s authorization.

TAXONOMIC TREATMENT


Perennial, rosulate herbs with napiform, contractile root, and a central, usually unbranched stem (only N. falklandicus D.M. Moore might have a rizomatous habit). Leaves more or less fleshy, oblong-oblancoelate to spatulate, glabrous, base attenuate, apex obtuse, blade entire, lobate to pinnatifid, margin entire to dentate. Flowers in head-like pedunculate inflorescences. Peduncles scapiform, fleshy, terete or compressed, smooth or sulcate, solid at anthesis and probably fistulose at fruit maturity, simple or branched, sometimes densely aggregated or coalescent even into a compound terminal inflorescence. Involute with a patelliform basal tube (absent or very reduced in N. falklandicus), with 5-12 uniseriate lobes, oblong, obtuse, sinuate to trilobate. Receptacle large, fleshy, accrescent during fruit ripening. Palea linear-espataulate, or absent. Flowers numerous. Calyx with suborbicular sepalis, with open, valvate or imbricate aestivation, accrescent with the fruit. Corolla funnel-shaped or cyllindrical, usually with a differentiated cup-shaped limb, lobes triangular to oblong, uncinate, with valvate aestivation. Staminal tube inserted in the corolla tube, with 5 oblong nectarial glands, and distally ending in 5 very short filaments. Anthers connate, base sagittate. Style exserted, terete, distally thicker. Stigma globose papilllose. Ovary cylindric, 5-sulcate. Achene prismatic, ridged, corky, crowned by the sepalis that surround a terminal apiculum more or less evident. Seed oblong.

According to Miers (1860-1869), Nastanthus forms fertile, short-tubulose flowers and sterile long-tubulose flowers in the same inflorescence. We did not find that flower dimorphism, but a continuous variation in the corolla tube length among flowers in the same inflorescence, being all of them apparently fertile. However, field observations (L. Zavala-Gallo) revealed two types of long-tubulose flowers morphologically alike: one type secondarily exposes pollen on the stigma, while the other type does not, suggesting male sterility. Therefore, Nastanthus does have flower dimorphism, but its relationship with sex expression needs a more detailed anatomical analysis.

Nastanthus includes species endemic to Chile and Argentina (Chiapella 1999b, Zanotti & Pozner 2008), which grow along the Andes from the 25° S towards the south, and all over Patagonia, including Tierra del Fuego and Malvinas ( Falkland Islands). This area corresponds to the phytogeographic Andea-Patagonean Dominion (Andoaide, “del Desierto”, Chilean and Patagonean Provinces) and the Subantarctic Dominion (Subantarctic and Insular Provinces) (Cabrera & Willink 1980) (Fig. 1). Although some species of Nastanthus may grow in woody habitats, most of them prefer arid, steppe-like habitats, frequently related to high altitudes, and probably also to streams or ponds due to the presumable hydrocoric dispersal of their fruits (Hellwig 2007).
FIGURE 1. Geographical distribution of *Nastanthus* species.

FIGURA 1. Distribución geográfica de las especies de *Nastanthus*. 
The genus Nastanthus: Zavala-Gallo, L. et al.

Key to the species of Nastanthus

1. Plants not rosulate, leaves densely arranged along the stem, oblong to oblanceolate or subspatulate. Inflorescence terminal, compound, made of pedunculate basal heads, progressively shorter, sessile and coalescent towards the apex. Involucre tube reduced, lobes 3. .....................................................................................................................................................................................3. N. falklandicus

1’. Plants rosulate, leaves spatulate. Inflorescences terminal and lateral, simple, made of scapiform peduncles, distinct, aggregated or partially coalescent, but never forming a compound inflorescence; the terminal inflorescences equal or larger than the lateral ones. Involucre tube developed, lobes 5-12.


3. Corolla cylindrical with a longitudinal, hyaline, thick membrane, accrescent and persistent on the fruit. ........................................................................................................2. N. compactus

3’. Corolla funnel-shaped, without a longitudinal membrane, not persistent on the fruit.

4. Corolla about 5.5-7.5 mm long. Nectarial staminal glands of distal position. Achene with uneven ridges. Leaves deeply lobed, almost pinnatisect. ........................................................................................................1. N. caespitosus

4’. Corolla about 4-5 mm long. Nectarial staminal glands of median position. Achene with even ridges. Leaves shortly lobed, pinnatifid. .........................................................................................................................6. N. ventosus

2’. Corolla deeply lobed, lobes narrowly triangular to oblong. Stems and inflorescences usually not aggregated or caespitose. Receptacle with linear, spatulate or rectangular paleae.

5. Achenes with narrow laminar ridges, transversely wrinkled. Sepals reduced, non-distinct in the fruit. Central peduncle thick, 1-3 cm diam., bearing a large inflorescence, 1-6 cm diam., surrounded by slender peduncles bearing smaller inflorescences. Corolla tube 2.5-3 mm long, limb 1.6-1.8 mm long. ..................................................................................4. N. patagonicus

5’. Achenes with expanded laminar ridges, smooth. Sepals distinct in the fruit. Peduncles many, 0.3-1 cm diam., regularly distributed in the plant, all similar in length and thickness, bearing inflorescences of similar size, 0.6-3.5 cm diam. Corolla tube 4-4.5 mm long, limb 2.5 mm long. .....................................................................................................................5. N. scapigerus


Perennial, rosulate herbs about 3.5 cm tall and 10 cm in diam., with a central, short stem. Leaves thick, spatulate, 4-5.5 cm long, base attenuate into a petiole of 2.5-4 x 0.3-1 cm; blade almost pinnatisect, 0.5-1.5 x 0.3-0.5 cm, uneven lobules linear, obtuse. Peduncles many, cylindrical, frequently forked, crowded, with a distinctive basal foliaceous bract, 0.8-1.5 x 0.25-0.4 cm. Involucre with 5 free lobes, rectangular-elliptic, apex obtuse, barely mucronate, 0.6 x 0.2-0.3 cm. Receptacle convex, 0.4-0.8 cm in diam., slightly accrescent during fruit ripening. Palea fleshy, rectangular-lanceolate, apex obtuse, 3 x 0.8 mm, about 10 per inflorescence. Flowers 25-30 per inflorescence. Calyx with open or imbricated aestivation, sepals widely triangular, obtuse, 0.8 x 0.4 mm. Corolla infundibuliform, tube 3.5-5 mm long x 0.15 mm wide at base to 0.5 mm distally, limb 2.5 mm long x 1-2.5 mm wide, lobes triangular, 0.3-0.6 x 0.25-0.5 mm, with valvate aestivation. Staminal tube 3-5 mm, inserted on the upper third of the corolla tube, with 5 oblong nectarial glands, 0.5 x 0.1-0.2 mm, of distal position, and free apical filaments 0.6 mm long. Anthers 1.4 mm long. Style exserted, 6 mm (staminate phase) to 10.5-12 mm long (pistillate phase). Ovary cylindrical, 1.25-1.6 x 1-1.2 mm. Achenes prismatic, depressed, 2.5-3 x 2.5-3 mm, asymmetric because of the uneven development of the ridges, ridges 5, longitudinal, thick, inflated, frequently 1 or 2 very reduced, rarely with wrinkles on the median portion, crowned by an obvious apiculum, 0.4-0.8 mm long, sepals mostly very reduced on the fruit, or enlarged and scarios, mucronate. Seed 1.7 x 0.6 mm.

Distribution. Endemic to Antofagasta and Atacama, in northern Chile (Fig. 1).
ETYMOLOGY. The specific epithet refers to the aggregated disposition of inflorescences, occurring in densely caespitose masses.

This species is denoted by the nectarial glands being located just below the free filaments, at the distal end of the staminal tube, by few flowers per inflorescence, and by depressed fruits. Flowers have a green corolla tube and a white limb.

The specimen SGO-043609 is chosen as lectotype since it is the only one whose label is clearly correlated. On SGO-057221 the type material was assembled along with other specimens, so that we can not distinguish which label corresponds to each specimen.

SPECIMENS EXAMINED


Perennial rosulate, glabrous herbs about 3 cm tall and 10 cm diam., with a central short stem. Leaves thick, spatulate, 3.5-4.5 cm long, base attenuate into a petiole of 2-3 x 0.3 cm; blade entire or pinnatifid, 1-1.5 x 0.7-1 cm, with triangular lobes. Peduncles crowded, cylindrical, fleshy, 2-3 x 0.5 cm, usually with a sessile, larger, central inflorescence up to 3 cm in diam. Involucre with 7 widely triangular lobes,
The genus *Nastanthus*: Zavala-Gallo, L. et al.

**Distribution.** Andes of Chile and Argentina, between 32°-36°S, since 3000 m (Fig. 1).

**Etymology.** The specific epithet refers to the inflorescences that grow in a confluent mass, strongly aggregated.

This is the only species of *Nastanthus* with an accrescent corolla persistent on the fruit (in the remaining species the corolla may persist, but it is non-accrescent and withered) and without inflorescence paleas. The corolla is tubulose and white, but during fruit ripening the tube turns green towards the apex, and the limb turns reddish, while most of the corolla tube remains white, and swells by the development of a spongy tissue, similar to that of the fruit ridges.

**Figure 3.** *Nastanthus compactus*. A. Habit. B. Leaf. C. Flower at the staminate phase. D. Flower at the pistillate phase. E. Fruit with persistent, accrescent corolla. F. Fruit (corolla removed). Drawn from J. Solervicens s.n. (SGO-130759).


0.3 mm long x 0.4 mm wide each. Receptacle convex, 0.5-3 cm in diam., accrescent during fruit ripening. Palea absent. Flowers white, 100-115 per inflorescence, up to some hundred in the central inflorescence. Calyx with open aestivation, sepals suborbicular, obtuse, 0.5 x 0.3 mm. Corolla cylindrical, tube 3 x 1 mm, limb slightly campanulate, 2-2.5 mm long x 1.4 mm wide, lobes triangular, uncinate, 0.7-1 x 0.5-0.8 mm, aestivation valvate. Staminal tube 3-4 mm long, inserted in the upper third of the corolla tube, with 5 oblong nectarial glands 0.5 x 0.2 mm of median position, apical free filaments of 0.3-0.5 mm. Anthers 1.1 mm long. Style exserted, 4.5 mm (staminate phase) to 7 mm (pistillate phase). Ovary cylindrical 1.8-2.2 x 0.6-0.8 mm. Achenes white, prismatic, 2.2-2.6 x 1-1.7 mm, with 5 narrow, longitudinal, flat ridges crowned by the sepals, 0.5-0.7 x 0.35-0.8 mm, surrounding a central cupuliform apiculum, 0.2-0.4 mm long; corolla accrescent on the fruit, green-reddish, tube 5.5-5 x 2-2.5 mm, limb 1.3 x 1.2-1.4 mm. Seed 1.6-1.8 x 0.6 mm.
The analysis of original material reveals that *Boopis diazi* is based on an specimen that should have been assigned to *N. compactus*. This specimen possesses all distinct attributes of the species (spatulate-pinnatifid blades, short peduncles, flowers with reddish calyx teeth, long and cylindrical corolla tube, and an accrescent corolla persistent on the fruit).

*Gamocarpha pumila* is a nomenclatural synonym of *Boopis compacta* because the type material of the former housed at K is an isotype of the latter. This conclusion is based on the finding that both types are fragments of a single plant. Moreover, labels on both sheets specify the same collector and date (Ph. Germain, 1856-1857), but differ in location. The holotype in SGO indicates “Cordillera de Linares” and the type in K “Cordiliéres de Maule (sede orient)”; nevertheless, from 1826 to 1873, Linares was part of the administrative subdivision of Maule province.

**Specimens examined**


3. *Nastanthus falklandicus* D.M. Moore, Bot. Not. 120:18, 1967. TYPE: Falkland Islands (Islas Malvinas). “West Falkland (Gran Malvina): Port Stephens, Ten Shilling Bay Peninsula, west coast ca. 3 miles SE Stephens Peak, in gravel and sand between loose rock slabs near cliff top, also on bare cliff ledges”, 90 m. 28-I-1964, Moore 707 (holotype K-000634091, photo SI!; isotypes: BAB!, GH-00283130, photo SI!, RNG, photo SI!, S09-36193, photo SI!). Fig. 4.

**Figure 4. Nastanthus falklandicus.** A. Habit. B. Flower at the pistillate phase. C. Dissected corolla showing the staminal tube (flower at pistillate phase). D. Leaf. (Taken from Chiapella 1999a).

The genus *Nastanthus*: Zavala-Gallo, L. et al.

Perennial, glabrous herb; stem about 2-7 cm tall and 0.5-1.8 cm in diam., fleshy, solid, wider towards the apex, ending into a compound inflorescence, narrowing to the base into a more or less horizontal structure (rhizome?). Leaves densely imbricate, 1.2-4 cm long x 0.2-0.4 cm wide, narrowly oblong to oblanceolate or subspatulate, base attenuate into a petiole; blade entire, fleshier than the petiole, with a median longitudinal groove, apex acute to rounded. Inflorescence terminal, compound, made of basal pedunculate heads that becomes sessile and coalescent towards the apex of the stem; basal peduncles usually simple, 2 cm long, one-headed, with a basal foliar bract, which becomes closer to the involucre in the upper heads. Involucre with 3 narrowly triangular bracts, 0.2-0.3 x 0.3-0.4 cm, basally connate. Receptacle 0.4-0.8 cm in diam. Palea 6-10 per head, narrowly elliptic to oblanceolate, 0.05 x 0.15-0.3 cm. Flowers white. Sepals obtuse to rounded, 0.5 x 0.5 mm. Corolla cylindric, 3 mm long, tube 2 mm long, lobes acute triangular, cucullate, 0.8 mm long. Staminal tube inserted in the basal half of the corolla tube, with 5 nectarial glands, and free, distal, short filaments. Anthers 0.6 mm long. Style exerted, about 1 mm long. Immature achenes prismatic, 2.5 mm long, with 5 longitudinal ridges crowned by the sepals. Mature achenes unknown.

**Distribution.** It is endemic to the Malvinas (Falkland) Islands, apparently restricted to the southwestern coast of the Gran Malvina/West Falkland Island (Moore 1967; Fig. 1).

**Etymology.** The specific epithet refers to the geographic site where this species is circumscribed (Malvinas (Falkland) Islands).

Species only known by the type collection and one paratype collected in 1839, Robinson s.n. (K) (Moore 1967). As we could not study the type material, the description was based on the original publication of Moore (1967). According to this author, *N. falklandicus* is protogynous, a very improbable feature considering the mechanism of secondary pollen presentation typical of Calyceraceae (Erbar & Leins 1995).

This species is distinguishable by its habit, with narrowly oblong to oblanceolate or subspatulate leaves densely arranged along the stem, and compound inflorescences. Flowers are white and smell strongly of nectar.


Perennial rosulate herbs about 2-25 cm tall and 6-20 cm in diam., with a short stem. Leaves thick, spatulate, 2-7 cm long, base attenuate into a petiole of 1.3-4 x 0.15-0.5 cm; blade 0.8-3 x 0.8-3 cm, lobed, margin dentate, lobes obtuse to triangular, mucronate. Peduncles cylindrical, 2-20 x 0.1-0.5 cm, with a central, larger peduncle of 15 x 3 cm in old specimens. Involucre with 5-7 lobes, 0.5-1 x 0.35-0.8 cm, variable in shape: triangular mucronate at apex; triangular, minutely dentate, with apex and teeth mucronate; or spatulate lobate with apex and lobules mucronate. Receptacle convex, 1-6 cm in diam., accrescent during fruit ripening. Palea thick, spatulate to rectangular, apex obtuse mucronate, 0.35 x 0.1 cm in receptacles with flowers to 1 x 0.7 cm in receptacles with fruits. Flowers whitish-green, 20-500 per inflorescence, up to 1,000 in the central, larger head. Calyx with open or imbricate aestivation; sepals small, suborbicular, emarginate, translucent, 0.3-0.4 x 0.5-0.7 mm. Corolla infundibuliform, tube 2.5-3 mm long x 0.8-1.2 mm wide, limb 1.6-1.8 x 0.9 mm, lobes triangular, uncinate, 1.4-1.8 x 0.8-0.9 mm, with valvate aestivation. Staminal tube 3 mm, inserted on the upper third of the corolla tube, with 5 oblong, indistinct, nectarial glands, 0.6 x 0.2 mm, of median position, and apical free filaments 0.2-0.4 mm. Anthers 1 mm long. Style exerted, 5 mm (staminate phase) to 6 mm long (pistillate phase). Ovary cylindrical, 1.4-2 x 0.8-1 mm. Achenes prismatic, wrinkled, 2.4-2.7 x 1-1.6 mm, with 5 longitudinal, thin, narrow, laminar ridges, crowned by an apiculum 0.25-0.35 mm long, with reduced or accrescent lanceolate sepals (1 x 1 mm). Seed 2 x 0.7 mm.

**Distribution.** Endemic to southern Argentina, from north Neuquén to Santa Cruz (Fig. 1), occurring both in the steppe and the Andean forests.

**Etymology.** The specific epithet refers to the geographic region where this species exclusively grows.

This species is distinguishable by the largest inflorescences within the genus, with a central head of 1-6 cm diam., which may sustain ca. 1,000 flowers; paleas are also large. Flowers are greenish-white with long corolla limbs.

According to Chiapella (1999a), young individuals of *N. patagonicus* can be misidentified as *N. sacergerus* due to the overall similarity of the leaves, flower colour, inflorescences and habit. The absence of a central, larger peduncle and inflorescences of similar size in young individuals of *N. patagonicus* increase the similarity between both species. However, both entities can be still discerned by the morphology of fruit ridges and sepals, and flower size.

**Specimens examined**

Gayana Bot. 67(2), 2010

166

Figure 5. Nastanthus patagonicus. A-B. Habit. C. Flower (ovary removed). D-E. Fruit variation. (Taken from Chiapella, 1999a: A, C and D, sub. N. patagonicus; B and E, sub. N. scapigerus).

Figure 5. Nastanthus patagonicus. A-B. Hábito. C. Flor (ovario removido). D-E Variación del fruto. (Tomado de Chiapella, 1999a: A, C y D, sub. N. patagonicus; B y E, sub. N. scapigerus).


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**Figure 6.** *Nastanthus scapigerus*. A. Habit. B. Fruit. C. Corolla partially showing the staminal tube (ovary removed). (Taken from Chiapella 1999a, sub. *N. spathulatus*).

**Figura 6.** *Nastanthus scapigerus*. A. Hábito. B. Fruto. C. Corola que muestra parcialmente el tubo estaminal (ovario removido). (Tomado de Chiapella 1999a, sub. *N. spathulatus*).

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167
Boopis dubia Phil., Anales Univ. Chile 85: 815, 1894.
TYPE: Chile. “Cordillera de Peuco in provincia O’Higgins (Cádiz)”, without collector (holotype SGO-057218, photo SI!).

Boopis miersii Phil., Anales Univ. Chile 85: 817, 1894.
TYPE: Chile. “Andes de Linares en las provincias de Curicó, Colchagua, Santiago” . XI-1885. Germain s.n. (holotype SGO-057238!).


Perennial, rosulate, glabrous herbs, about 3-10 cm tall and 10-25 cm in diam., with a central short stem. Leaves spatulate, thick, 5-10 cm long, apex obtuse, base attenuate into a petiole of 2-8 x 0.2-0.3 cm; blade 1-4 x 0.5-2.5 cm, entire with margin entire to dentate, or irregularly pinnatifid, and lobes obtuse to triangular, minutely mucronate. Peduncles many, densely crowded, terete, fleshy, sometimes branched, 2-12 x 0.3-1 cm, occasionally a central larger peduncle, 6 x 1 cm. Involucre with 5-7 widely triangular, mucronate lobes, 0.55 x 0.5 cm (sometimes spatulate, 0.75 x 0.35 cm), margin entire or with few teeth. Receptacle convex, 0.6-3.5 cm in diam., accrescent during fruit ripening. Palea sparse, green, fleshy, linear spatulate, apically mucronate, 0.5 mm long. Flowers green, usually 45-80 per head up to 150 in the larger central inflorescences. Calyx with aestivation imbricated; sepals suborbicular, apex usually emarginate, margin minutely toothed, 1-1.4 x 1-1.4 mm. Corolla infundibuliform, tube 4-4.5 mm long x 0.2-0.4 mm in diam. at base to 0.8 mm distally, limb 2.5 mm long. x 0.5-1 mm in diam., completely cleat, lobes triangular, uncinate, 2.2 x 0.8 mm, with valvate aestivation. Staminal tube 4-5 mm, inserted in the upper third of the corolla tube; with 5 oblong nectarial glands, 0.8 x 0.2 mm, of median position, and apical free filaments 0.5 mm long. Anthers 1.4 mm long. Style exserted, 6 mm (staminal phase) to 10 mm long (pistillate phase). Ovary cylindrical 2.2-3 x 1.4-2.2 mm. Achenes prismatic 3-5.5 x 2.5-4 mm, with 5 longitudinal, smooth, well developed, expanded ridges crowned by the sepalas (1-2.15 x 1.2-2.8 mm), apiculum 0.8 mm long. Seed 2-3.5 x 0.75 mm.

Distribution. Andes of Chile and Argentina, mostly between 32°-40°S and isolated records occurring in Chubut and Santa Cruz provinces (Argentina) and Tierra del Fuego island (Inútil Bay, Chile; Fig. 1).

Etymology. The specific epithet appears to refer to the scapiform inflorescence peduncle.

There are three specimens of the original material from Claudio Gay collection with labels of Herb. Mus. Paris; one of them is housed at P and the other two are conserved at K. The P specimen is selected as lectotype since vegetative and reproductive structures are well preserved and it better matches Rémy’s description. One of the specimens at K also matches the original description but it consists in a single and fragmentary plant. The other sheet at K includes poorly preserved fragments of a plant that do not match with Rémy protologue of Boopis scapiger. This material was originally identified as ‘Boopis scapigera Remy”, it shows the pencil inscription “non” on the name, and, at the margin of the sheet, an incomplete inscription where “Nastan...” can be read. These inscriptions appear in all specimens revised by Miers for his Contributions to Botany (1860-1869). This specimen from K is part of the material used by Miers to typify Nastanthus pinnatifidus (= Nastanthus ventosus); its references agree with the protologue and it has been relocated on the same sheet with the syntype Cuming 325.

The name Nastanthus spathulatus is one of the better known among Chilean and Argentinean botanists and it is based on Boopis spathulata. Nevertheless, all characters of the B. spathulata types found at SI and W clearly match the type material of Boopis scapiger; the only difference is that B. spathulata holotype is a specimen bearing flowers and broad blades, whereas the B. scapigera lectotype (P) bears fruits. Miers (1860-1869) noted the similarity between both species but he drew no conclusion because he had not seen the Philippi holotype. However, these similarities are evident in the illustration of N. scapigerus in Miers (1860-1869). The specimen at SI is chosen as lectotype since is the best conserved and has the Philippi’s label.

Miers (1860-1869) established the new species Nastanthus laciniatus based on three specimens from different collectors. Later, Reiche (1900) treated this taxon as a variety of N. agglomeratus. The analyses of their syntypes revealed that they correspond to N. scapigerus, because of their corolla limb completely cleat. Considering the three syntypes available in K, Cuming 326, from “Cordillera de Chile”, is the best preserved, retaining the plant form with many inflorescences and achenes, and perfectly matches Miers’ description. The remainder syntypes, Gillies s.n. from “Los Palomares” and Bridges s.n. from “Ojos de Agua”, conserve more vegetative structures (leaves and roots), but fewer reproductive ones, that are required to identify the species and were especially used by Miers.

Some of the synonymies here listed were cited in synonymy before: Boopis dubia and Boopis reichei under Nastanthus spathulatus; and Boopis miersii under Nastanthus scapigerus (Reiche 1900, Zanotti & Pozner 2008). All of them represent morphological forms related with distinct environmental pressures that exist in the Andean-Patagonian distribution of the species, including longitudinal, latitudinal and altitudinal ranges.
Boopis araucana, only known from type material, is a specimen with longer, more branched and leafy peduncles than the typical condition in N. scapigerus, but an exhaustive study on inflorescences form, flowers and leaves, show that both taxa are conspecific. The specimen SGO-057225 is chosen as lectotype since it possesses more reproductive material than SGO-043594.

Due to the existence of many forms within N. scapigerus and the lack of characters to distinguish between both taxa we consider Boopis bellidifolia as a synonym of N. scapigerus.

Nastanthus chubutensis was created based on two specimens from the Andean limit of Chubut province of Argentina. Its characters match the Boopis scapigera description of Remy and also its general aspect resembles the lectotype of B. scapigera since all possess fruits. Probably, these similarities were noted before by Hicken (1919), who considered Nastanthus chubutensis as a variety of N. bellidifolius.

The comparison between N. scapigerus and related taxa, treated here as synonyms, shows that vegetative morphological characters are scarcely variable, and the reproductive ones (floral characters) remain constant (Table I).

The illustration published by Chiapella (1999a: 514, Fig. 397) of N. scapigerus corresponds to N. patagonicus.

Specimens Examined


The illustration published by Chiapella (1999a: 514, Fig. 397) of N. scapigerus corresponds to N. patagonicus.


**Figure 7.** *Nastanthus ventosus*. A. Habit. B-C. Leaf variation. D. Flower at pistillate phase. E. Young fruit, corolla withered. F-G. Fruit variation. A, B, D, E, drawn from F. Roig s.n. (MERL-18719); C, G, from A. Ruiz Leal 23417 (MERL); F, from A. Ruiz Leal 6611 (MERL).

The genus *Nastanthus*: Zavala-Gallo, L. et al.

Perennial, rosulate herb about 2.5-10 cm tall and 5-20 cm in diam., with a central short stem. Leaves partially fleshy, spatulate, 3-12 cm long, apex obtuse, base attenuate into a petiole of 2-3 x 1 cm; blade pinnatifid, 1-6 x 1-3 cm, lobes obtuse to lanceolate. Peduncles many, crowded, shorter than the leaves, compressed, fleshy, bearing one terminal head each. Involucre with 8-12 wide triangular lobules of 0.2-1 x 0.3-0.5 cm. Receptacle convex, 0.5-3 cm in diam., accrescent during fruit ripening. Palea absent, or 1-2 minute, filiform, at most 0.5 mm long in receptacles with fruits. Flowers 20-150 per inflorescence. Calyx with open or valvate aestivation, sepals 5, triangular, obtuse, emarginate, 0.3-0.4 x 0.4-0.5 mm. Corolla infundibuliform, tube 2.35 x 0.9 mm, limb 2 x 1.5 mm; lobes triangular, uncinate, 1 x 0.7-1 mm, aestivation valvate. Stamina tube 2.5 mm long, inserted at the upper third of the corolla tube, with 5 oblong nectarial glands 0.5 x 0.2 mm, of median position; with apical free filaments of 0.3 mm. Anthers 1.3 mm long. Style exserted, 5 mm (staminate phase) to 7 mm (pistillate phase). Ovary cylindrical, 2-2.5 x 1.2 mm. Achenes prismatic, 5-ridged, 2-8.5 x 2-4 mm, conical apiculum absent to 0.5 mm long, and crowned by the persistent sepals, 1-2.5 x 0.5-1.5 mm, continuous to the longitudinal ridges. Seed 1.25-4 x 0.2-0.8 mm.

**Distribution.** Andes of Chile and Argentina, between 27º-37ºS, also occurring near the Pacific coast in Chile and in Cerro Nevada, Mendoza province, Argentina (Fig. 1).

**Etymology.** The specific epithet, *ventosus*, is a Latin term which has many meanings, all of them related to the wind and its attributes. In this case, it may refer to the kind of environment in which the species occurs (*ventosus* = windy), or the wide morphological variability which characterizes this species (*ventosus* = fickle, changeable). It may also denote the intensely aggregated arrangement of inflorescences (*ventosus* = puffed up).

Plants usually produce many scapiform peduncles aggregated into a hemispherical, caespitose mass (Pontiroli 1963), resembling the general shape of a cauliflower (Reiche 1900). Condensed or lax forms may be observed under different environmental conditions along its Andean distribution. The nectarial glands are more evident during the staminate phase. Flowers are green in the corolla tube and white at the limb.

Miers (1860-1869) considered *Calycera ventosa* Meyen under *Nastanthus* and established the combination *Nastanthus ventosus* (Meyen) Miers. Nevertheless, *Calycera ventosa* was usually considered as a synonym of *Boopis scapigera* J.Remy since Weddell (1857), and later as *Nastanthus scapigerus* (J.Remy) Miers by Reiche (1900, 1901), Hicken (1919), Chiapella (1999a) and Zanotti & Pozner (2008). The study of the type material of both *Calycera ventosa* and *Boopis scapigerus* provides the separation of the former species by its smaller sepals, pinnatifid leaves, and many condensed inflorescences (see also Remy, 1847[1848]).

In addition, the analyses of numerous herbarium specimens corresponding to *Nastanthus agglomeratus* and the type material of *Calycera ventosa* revealed that they share mostly the same characters on reproductive structures, and that *Calycera ventosa* can be placed within the morphological variation considered for *N. agglomeratus*, differing only by its longer and less condensed peduncles. Therefore, we consider both taxa as conspecific, and the earliest correct name is *Nastanthus ventosus* (Meyen) Miers.

The holotype of *Calycera ventosa* Meyen, presumably housed at B, and the complete Meyen collection, were destroyed. All herbaria where Meyen specimens could be conserved (BR, CAS, CGE, K, L and P; Stafleu & Cowan,
1988) were consulted but no isotype of Calycera ventosa was found. Meyen (1834) did not cite paratypes either. Therefore, Weddell’s illustration is chosen as lectotype since evidence suggests it was based on Meyen’s original material: “The drawings (probably based in part on sketches by Weddell) are by Alfred Riocreux…” (Staffeuf & Cowan, 1988, vol. 7, p. 140), and Reiche (1900: 1031) stated: “La figura de Weddell se estableció sobre una muestra original”.

The specimen Gillies s.n. from BM is considered as the holotype of N. agglomeratus, since it has Miers’ original labels. It is worth mentioning that isotypes of N. agglomeratus (Gillies s.n.), N. laciniatus (Cuming 326) and N. pinnatifidus (Cuming 325) are mounted on the same herbarium sheet at E, but labels have been mismatched to specimens. This becomes evident when comparing isotypes from E, types from K and BM, illustrations and protologues (Miers, 1860-1869). We concluded that the specimen of N. laciniatus is associated with Cuming 325 (E-00259116) label (see synonymy of N. scapigerus below), the specimen of N. pinnatifidus with Gillies s.n. (E-00259115) label (see synonymy of N. ventosus above) and the specimen of N. agglomeratus with Cuming 326 (E-00259114) label (see synonymy of N. ventosus above). Furthermore, mistakes have been repeated in another two sheets from E, where a specimen of N. pinnatifidus is labeled as Cuming 326 (E-00259117), and a specimen of N. laciniatus is labeled as Cuming 325 (E-00259118).

Nastanthus agglomeratus var. pinnatifidus is not considered here as a good variety because the foliar morphology of N. ventosus includes characters used to define the variety. The specimen Cuming 325 is chosen as lectotype since it better describes the plant morphology and it is better conserved than the syntype Gay s.n. from “Cordillera de Coquimbo”; the later is fragmented and poorly preserved.

The remaining varieties of N. agglomeratus (N. agglomeratus var. gayanus, N. agglomeratus var. gilliesii and N. agglomeratus var. breviflorus) were previously considered as synonyms of N. agglomeratus by Zanotti & Pozner (2008). About Boopis breviflorus, the specimen SGO-043591 is chosen as lectotype since it has better conserved material and greater number of flowers and fruits than SGO-057222.

The holotype of Boopis oocaulis is probably housed at NY (Zanoni 1982, O’Leary 2006). The isotype possesses short blades, consisting of five small lobules, few-flowered inflorescences of 20-30 flowers, flowers with a short corolla tube with abbreviated whitish lobules, closely matching N. ventosus. Differences with N. ventosus (more flowers per inflorescence and leaves with more than 5 lobules) may be caused by environmental conditions such as soil development and water availability. Besides, B. oocaulis is known only from the type material, and other authors (Pontiroli 1963) have pointed out the doubtful validity of this taxon.

The type specimen of Boopis sanjuanina can be placed confidently within the morphological variation of Nastanthus ventosus; even Hieronymus (1881) remarked about his uncertainty when creating the species. Moreover, Pontiroli (1963) confused N. agglomeratus with N. caespitosus and erroneously cited Boopis sanjuanina in synonymy to the later species.

The comparison between N. ventosus and related taxa, here treated as synonyms, shows that vegetative morphological characters vary, whereas the reproductive ones (floral characters) remain constant (Table II).

**Specimens examined**

The genus *Nastanthus*: Zavala-Gallo, L. et al.


Doubtful names


We have only seen a digital image of the holotype, and the specimen is so depauperate, poorly preserved and folded that its morphology can hardly be evaluated. Although some features resemble *N. venosus*, the decision about its synonymy is postponed until an examination of the type material can be made.
## Table II. Morphological variation of *N. ventosus* and related taxa

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Blade margin</th>
<th>Peduncles</th>
<th>Phenological stage of the type</th>
<th>Agglomeration of inflorescences</th>
<th>Corolla tube : limb</th>
<th>Corolla limb</th>
<th>Free filaments</th>
<th>Nectarial glands</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. ventosus</em></td>
<td>Pinnatifid</td>
<td>Erect</td>
<td>Flowers and fruits</td>
<td>Lax</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
<tr>
<td><em>B. gayana</em></td>
<td>Pinnatifid</td>
<td>Prostrate</td>
<td>Fruits</td>
<td>Compact</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
<tr>
<td><em>N. agglomeratus</em></td>
<td>Pinnatifid</td>
<td>Prostrate</td>
<td>Flowers and fruits</td>
<td>Compact</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
<tr>
<td><em>N. pinnatifidus</em></td>
<td>Pinnatifid</td>
<td>Prostrate</td>
<td>Flowers</td>
<td>Compact</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
<tr>
<td><em>N. gilliesii</em></td>
<td>Pinnatifid</td>
<td>Erect</td>
<td>Fruits</td>
<td>Lax</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
<tr>
<td><em>B. sanjuanina</em></td>
<td>Pinnatifid</td>
<td>Prostrate</td>
<td>Flowers and fruits</td>
<td>Compact</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
<tr>
<td><em>B. breviflora</em></td>
<td>Pinnatifid</td>
<td>Erect</td>
<td>Flowers and fruits</td>
<td>Compact</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
<tr>
<td><em>B. oocaulis</em></td>
<td>Pentalobed</td>
<td>?</td>
<td>Flowers + 1 achene</td>
<td>Compact</td>
<td>1 : 1</td>
<td>Split</td>
<td>Subnull</td>
<td>Evident</td>
</tr>
</tbody>
</table>
CONCLUSIONS

Based on our results, *Nastanthus* includes six species: *N. caesiptosus*, *N. compactus*, *N. falklandicus*, *N. patagonicus*, *N. saccigerus*, and *N. ventosus*. Five species and three variety names, up to date in use, are newly placed into synonymy (*N. agglomeratus*, *N. sphenolatus*, *N. chubutensis*, *N. araucanus*, *N. diazi*, *N. agglomeratus* var. *pinnatifidus*, *N. agglomeratus* var. *laciniatus*, and *N. sphenolatus* var. *bellidifolius*).

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