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SILVIA ARROYO-LEUENBERGER[1] & BEAT ERNST LEUENBERGER[1*]

Revision of *Zephyranthes andina (Amaryllidaceae)* including five new synonyms

Abstract

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The taxonomic history of *Zephyranthes andina* (≡ *Haylockia andina*) and five related taxa is analysed. The study of herbarium material and photographs, and observation of live plants in the field and in cultivation allowed an evaluation of the variation of flower characters, such as style length, used by other authors for taxonomic delimitation of *Z. andina* and five additional species, three published in *Zephyranthes* and two in *Haylockia*. A lectotype for the name *Haylockia andina* is designated. Five names are reduced to synonymy. The generic position of the single taxon is discussed. The first chromosome counts ($2n = 20$), a distribution map, phenological data, an evaluation of its conservation status and ample photographic illustration of flowering plants in nature and in cultivation are provided.

Additional key words: *Haylockia andina,* taxonomy, chromosomes, lectotype, Andes, Peru, Bolivia, Argentina

1. Introduction

Zephyranthes andina was originally described by Fries (1905) as *Haylockia andina*. It was, at that time, the second species of *Haylockia,* a genus established by Herbert (1830) shortly after *Zephyranthes* Herb. (Herbert 1821) and its segregate *Habranthus* Herb. (Herbert 1824). The species from the Andes of Jujuy has been variously treated as *Z. andina* (e.g., by Traub 1951) or as *H. andina* (e.g., by Arroyo-Leuenberger 1997). Due to its remote habitat in the Andean Altiplano and even more due to its ephemeral flowering, the species has remained little known and is still poorly represented in herbarium collections.

In 1998 the authors had the opportunity to observe a small population of *Zephyranthes andina* in flower in Jujuy, Argentina. Subsequent study of photographs and herbarium material of the same collection and the repeated observation of flowers in cultivation triggered a study of the variation of flower characters.

Aims of the present study were (1) to investigate the variation in flower and other characters among and between different populations of *Zephyranthes andina* by making use of observations in the field and in cultivation, of herbarium material and photographs; (2) to evaluate the similar species described from the Andean Altiplano and their delimitation from *Z. andina* and to test the hypothesis that they all represent a single species; (3) to gain insight in characters used for the disputed delimitation of the genera *Zephyranthes, Haylockia* and *Habranthus*.

2. Material and methods

For herbarium material the following herbaria were consulted: B, BM, BOLV, CORD, F, G, GH, HBG, HSB, JUA, K, LIL, LP, MCNS, MO, P, S, SI, STR, US, USM and Z (abbreviations following Holmgren & al. 1990). Three accessions originating from seed or bulb collections made in Argentina in 1998 within Proyecto PROFLORA permitted a comparison of live plants over several years in the Botanic Garden Berlin-Dahlem and preparation of voucher specimens deposited in the garden herbarium at B. Flowers were documented in nature and in cultivation by colour photographs, from 2005 onwards by digital photographs, facilitating the accumulation of valuable additional data for interpretation of characters, developmental changes and variation.

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Ample photographic documentation of habitat and individual plants by M. Giorgetta near Uyuni, Bolivia, contributed valuable additional data on the variation of flower characters.

Chromosome counts using standard techniques were obtained from somatic mitosis in root tips from three bulbs each, of two collections from Argentina, Jujuy *(Leuenberger & al. 4579a)* and Salta *(Leuenberger & al. 4626a)*. Voucher specimens at B are marked (*) under Specimens studied. Chromosomes were classified after Levan & al. (1964).

3. Results

3.1. Taxonomic history and original characterization of *Zephyranthes andina* and related species

Haylockia was described by Herbert (1830) as monotypic genus from southeastern South America based on *H. pusilla*. He considered it to be closely related to *Zephyranthes* Herb. (Herbert 1821), a genus of c. 50 species ranging from the southeastern United States through Mexico, Central America and the Caribbean to southern South America. Criteria for the distinction of *Haylockia* from *Zephyranthes* were the lack of a scape (at least at flowering stage), lack of pedicel and presence of a well developed floral tube. Both genera are also close to *Habranthus* Herb., a genus of similar range, distinguished by Herbert (1824) for its "filaments of four lengths, fasciculate, declined".

The first reports of plants later included in *Haylockia* date back even a few years before the establishment of the genus: Hoffmannsegg (1824) described and illustrated *Sternbergia americana* from "Maldonado prope Buenos ayres. Dom. Bescke" (in Uruguay). The illustration shows the flower with well developed tube and rather long stigma lobes nearly at the level of the anthers. The description and illustration of the genus *Haylockia,* based on *H. pusilla* (now a synonym of *H. americana*) agree well, but the stigma lobes are situated in the throat of the tube below the anthers, as also expressed in the description of the species: "stylo in tubo delitente" (Herbert 1830).

Herbert (1837) characterised the genus again with "stigma deeply trifid, ... concealed in the tube." He cited *Sternbergia americana* Hoffmanns., as well as its "var. 2 *Rubella*", as synonym of *Haylockia pusilla*. Dietrich (1840) did not accept the genus and treated its only species under *Zephyranthes,* but later, Kunth (1850), Baker (1888) and Bentham (1883) accepted *Haylockia* without comments. So did Hooker (1900), who illustrated a cultivated specimen sent by Canteras from Montevideo and mentioned the stigma lobes to be "shortly exserted from the throat of the perianth". Herter (1930) accepted *H. pusilla,* with two varieties (var. *aurea* and var. *cremea*). Herter (1956) finally made the necessary new combination *H. americana* (Hoffmanns.) Herter. This lowland species is distributed from S Brazil and Uruguay to NE Argentina (Misiones to Buenos Aires).

The Andean species revised in the present paper became known only in the 20th century. Fries (1905) described the first highland species as *Haylockia andina* from Jujuy, Argentina. He referred the new plant to this genus because it shared with it general flower characters (lack of aerial scape, short to lacking pedicel, conspicuous flower tube). Apart from its disjunct highland habitat, *H. andina* differs in the short stigma lobes (1-2 mm versus 4-8 mm long) from *H. americana.*

Between 1907 and 1999 five additional species similar to *Haylockia andina* were described, all from high elevations (2800-4000 m) in the Andes of Bolivia and Peru, two in *Haylockia* and three in *Zephyranthes*.

(1) *Haylockia pseudocrocus* was published by Solms-Laubach (1907) based on a specimen collected by Steinmann in Bolivia in 1903. In the list of material studied, the date is given as "15.11.1902", but this must be an error because other specimens cited from the same place were dated 1903, when Steinmann collected in Bolivia (Solms-Laubach 1907: 122). Solms-Laubach mentioned neither collection dates nor where the material was deposited. The description is not very detailed and lacks an illustration. It seems nevertheless significant that Solms-Laubach found the species to be similar to *H. andina,* from which he distinguished it by only minor characters such as the size of the bulb (1 cm diam., versus 2-3 cm diam. in *H. andina*), the colour of the tepal apices and the length of the stigma lobes. Traub (1951) made the combination *Zephyranthes pseudocrocus.*

(2) *Zephyranthes parvula:* Killip (1926) described this species based on a plant collected by Herrera in Peru near Cuzco at 3500 m. He differentiates it by the much smaller plant size and "stigmas capitate" from Peruvian taxa with trifid stigma, *Z. albicans* (Herb.) Baker and *Z. boliviensis* Baker, as treated by Baker (1888). The species is cited also for Peru by Herrera (1930), Macbride (1936) and Brako (1993). Hume (1938), who did not mention *Haylockia andina* but recognised *H. pusilla,* placed *Z. parvula* in *Haylockia* and added two more species. The first one, *H. pseudocolchicum* (Kraenzl.) H. H. Hume from Bolivia, was synonymised by Ravenna (1971) with *Stenomesson humile* Herb. and is now referred to *Clinanthus humilis* (Herb.) Meerow (Meerow & al. 2000: 723). The second one, *H. briquetii* (J. F. Macbr.) H. H. Hume from Peru, was excluded by Ravenna (1982) after the study of the protologue of its basionym *Z. briquetii* (Macbride 1931) and of the photograph of the holotype at F (*Weberbauer 7322,* B, destroyed). The "stigma 3-lobato folioso" led to its correct placement in the *Iridaceae* with the new combination *Mastigostyla briquetii* (J. F. MacBr.) Ravenna (1982).

(3) *Haylockia cochabambensis:* In a study of the genus *Haylockia* in Bolivia, Cárdenas (1973) only mentioned, without discussion of their characters, the two species of Fries and Solms-Laubach, and *H. pseudo-*

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Table 1. Comparison of flower characters in six Andean species described as *Haylockia* and *Zephyranthes* according to the protologues and type specimens (measurements in mm)

Characters	***Haylockia andina***	***Haylockia andina***	***Zephyranthes parvula***	***Zephyranthes parvula***
Data source:	Fries (1905)	*Fries 661* (lectotype)	Killip (1926)	*Herrera 822* (type coll.)
Length of perianth segment	c. 20-25	20-25	15-20	c. 20
Length of perianth tube	c. 20-25	25-35	15-20	c. 20
Filament length	8 + 10	8 + 10	6-8	c. 7
Style length	longer than filaments	c. 20	20-25	c. 25
Stigma position relative to the flower tube	exserted	exserted	exserted	exserted
Stigma position relative to the anthers	same level or slightly surpassing	same level or slightly surpassing	?	same level or slightly below

Characters	***Haylockia pseudocrocus***	***Haylockia cochabambensis***	***Zephyranthes challensis***	***Zephyranthes fragrans***
Data source:	Solms-Laubach (1907)	Cárdenas (1973)	Ravenna (1974)	Ravenna (1999)
Length of perianth segment	15	40	37-45	26.5-27.3
Length of perianth tube	10	35	16-30	24
Filament length	two different length	7 + 11	6.8 + 8.8	4.6 + 6
Style length	?	15	26-34	c. 24
Stigma position relative to the flower tube	unknown	exserted	near throat	near throat
Stigma position relative to the anthers	slightly below	below	?	?

colchicum (Kraenzl.) H. H. Hume. Cárdenas (1973) simultaneously described two new species. One is *H. chihuanhuayu* from Potosí, later also synonymised with *Stenomesson humile* and *Clinanthus humilis* respectively (Ravenna 1981; Meerow 2000). The other species is *H. cochabambensis* from Cochabamba, also based on a single collection. In the description and illustration of *H. cochabambensis* there are no evident differences to distinguish it from *H. andina* with the exception of, at first sight, the position of the stigma, which is described as "much lower than stamens".

(4) *Zephyranthes challensis:* Unaware of the publication of Cárdenas (1973), Ravenna (1974) described *Z. challensis* from Cochabamba, considering it to be close to *Z. andina*. According to the protologue, including two photographs, this species can have a scape of 0-11 mm, the style is longer than the flower tube and the stigma more or less at the level of the anthers (Ravenna 1974: 39, fig. 11). Ravenna (1978) made the new combination *Z. cochabambensis* and placed *Z. challensis* in its synonymy. Later, Ravenna (1999) reinstated *Z. challensis* as different from *Z. cochabambensis* with the allusion that Cárdenas had mentioned the flower tube to be 3.5 cm and the style 15 mm long, which would mean that the stigma is enclosed in the flower tube. However, a comparison with the drawing of Cárdenas (1973: 43, fig. 13B) shows that the style is illustrated as protruding from the tube. The contradictory data found within the protologue suggest that the character may be of little value.

(5) In the same year, Ravenna (1999) distinguished a third species, *Zephyranthes fragrans* from Cochabamba, explicitly related to *Z. andina*. He noted a shorter flower tube and longer style, slight differences in colour of the tepals, and a "sweet scent, a condition not found in any other species of the genus".

The discussion about the generic position of *Haylockia* has continued from the beginning until today, based essentially on two species (*H. americana* and *H. andina*). Holmberg (1905), Hauman & Vanderveken (1917), Pax & Hoffmann (1930), Hume (1938), Foster (1958), Traub (1963), Cárdenas (1973), Hunziker & Arroyo (1984) and Arroyo-Leuenberger (1997) accepted *Haylockia,* while Traub (1951), Ravenna (1971, 1974, 2003), Meerow & Snijman (1998) and Arroyo-Leuenberger & Dutilh (2008) united it with *Zephyranthes*. Ravenna (1971) placed *Haylockia* as subgenus in *Zephyranthes,* with *Z. americana* as type and *Z. andina*. Ravenna (2003) included Z. *challensis, Z. cochabambensis* and *Z. fragrans* as accepted species in the subgenus. He did not mention *Z. parvula* as related species.

Selected flower characters used by the authors of new species to distinguish taxa are presented in a tabular comparison (Table 1). Data were retrieved from descriptions and illustrations in the protologues and (only in two cases available) from type specimens. It should be noted that all except *Haylockia andina* were described as new on the basis of a single collection.

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3.2. Chromosomes

According to our results the chromosome number of *Zephyranthes andina* is $2n = 20$, with the chromosome set 2m + 8sm, i.e., 2 metacentric pairs, 8 submetacentric pairs (Fig. 1). This is the first chromosome number report for this taxon. The material from Argentina includes plants of two different clones with varying style length.

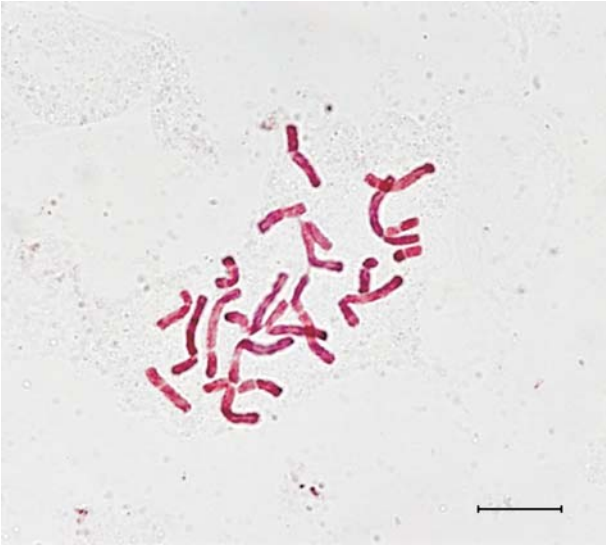


Fig. 1. Root tip metaphase of *Zephyranthes andina,* showing $2n = 20$ chromosomes. – From *Leuenberger & al. 4626a*, scale bar = 10 µm, photograph by M. Lüchow.

3.3. Flower development in cultivation

The flower bud normally appears in the leafless stage of the plant. It is first enclosed by and emerging between the erect, connivent bracts (Fig. 2A). The bracts are dark green, with stiff and subulate tips. The ovary remains below soil surface. The buds just before anthesis are white outside, purplish striate or more pink at the base, and usually with green tip. In the flower at anthesis, the tube is purplish to white and the perigone segments white to pink outside, at the base with purplish striation. The inside is white with faint to conspicuous purplish striation at least at the base (Fig. 2B-E).

It takes about ten days from the first appearance of the flower bud to anthesis. However, this may vary depending on the temperature and watering. The flowers open in the morning and remain open 2-3 days, rarely up to 5 days (in cool weather). During anthesis the flower grows and expands. The scape remains subterranean or may elongate, finally protruding up to 0.5 cm from the soil surface (Fig. 2E). In a flower observed over three consecutive cool days, the not yet widely expanded tepals closed half-way the first night but remained completely expanded the second and third night.

Without pollination and after self pollination there is no fruit development. No flowers were available for cross pollination and thus no fruit development could be observed in cultivation. The flowers wither (Fig. 2F), the ovary often remains green for some days but then shrivels and dries out.

While most *Amaryllidaceae* are self-incompatible (Meerow & Snijman 1998), studies of *Zephyranthes* by Raina & Khoshoo (1972) have indicated that species with styles longer than the stamens are self-incompatible, species with styles of more or less equal length as the stamens are mostly self-incompatible, and taxa with styles shorter than the stamens are mostly self-compatible. However, Broyles & Wayatt (1991) report an exception with the long-styled *Z. atamasca* (as *"Z. atamasco"*) being self-compatible. Our plants of *Z. andina* observed in cultivation from three localities within Argentina were all self-incompatible regardless of style length.

3.4. Variation of inflorescence and flower characters

In herbarium material, very few quantitative observations can be made because well-pressed specimens are rare. Observations of cultivated plants allowed the comparison of some characters during early and late stages of anthesis and comparison of the same flower in fresh and dried stage. This also facilitated the interpretation of slight differences in herbarium material. Special attention was paid to the androecium and stigma position.

Some notes on our own collections are summarised below and presented in Table 2. In the only population observed and documented by the authors in nature in Jujuy *(Leuenberger & al. 4546)* stigma position varied from anther level to slightly surpassing level anther, without correlation with the development stage of the flower. The flower at early stage of anthesis has a longer style than the older flower (Fig. 3B-C).

In the two populations documented by photographs of M. Giorgetta at two localities near Uyuni, Bolivia, the flowers vary from erect to slightly declined but the latter may in part be an effect of the difficulty of flower buds breaking through the hard soil surface. Normally, no scape is visible (Fig. 4A, E), but in very few flowers a short scape of few mm length is present, in one case in a flower emerging between stones (Fig. 4G, H). A very short peduncle may be present at fruiting stage (Fig. 4D). The style is always longer than the tube and the stigma always above the anthers, but style length varies or the style is accrescent during anthesis (Fig. 4A, H). In some flowers the style is erect and central (Fig. 4A, B, G), in others it is notably curved and lateral (Fig. 4F, H). The filaments are straight in the majority of the flowers, but curved in some (Fig. 4H). No evident reason or variation pattern could be established based on the c. 25 flower photographs with visible androecium and style. Flowers with curved filaments and style seem more frequent in declined flowers and approach the illustration of *Habranthus nullipes* by Ravenna (1981: 68, fig. 22A & B). They occur within the same population flowering on the same day.

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Fig. 2. Flower development of *Zephyranthes andina* and variation in cultivation – A: young flower bud; B: flower bud; C: flower with short tube, ovary subterranean; D: medium-sized tube, ovary just below soil level; E: flower with long tube and ovary protruding on short scape; F: withering flower with exposing the dry bracts, ovary subterranean. – A, B, C, F from *Leuenberger & al. 4546;* D from *Leuenberger & al. 4626a,* E from *Leuenberger & al. 4579a;* photographs by B. Leuenberger.

Table 2. Stigma position in different collections and populations of *Zephyranthes andina.*

Source		Stigma position relative to the flower tube	Stigma position relative to the anthers
In situ	*Leuenberger & al. 4546,* Jujuy, Yavi	exserted	same level or surpassing
	Photos M. Giorgetta: Uyuni, Cerro Escara	exserted	surpassing
	Photos M. Giorgetta: Uyuni, Cerro Khajas	exserted	surpassing
Cultivated	*Leuenberger & al. 4626a* (bulb)	exserted	slightly surpassing
	Leuenberger & al. 4579a (bulb)	enclosed	below
	Leuenberger & al. 4579a (seed grown)	enclosed	below
	Leuenberger & al. 4546 (bulb)	exserted	same level or surpassing

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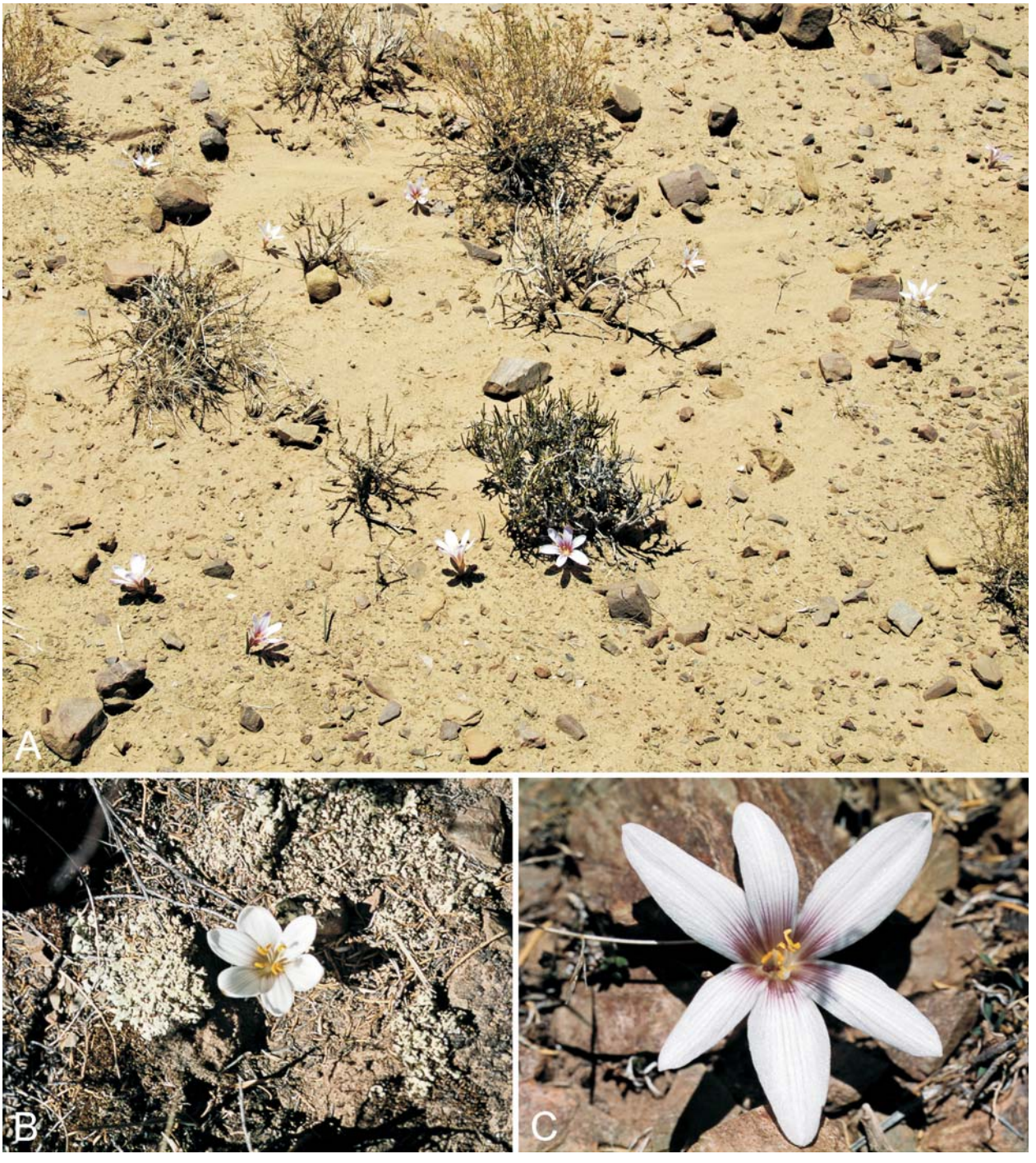


Fig. 3. A: Habitat of *Zephyranthes andina*, Cerro Escara, Uyuni, Bolivia; B-C: flowers of *Z. andina* in habitat in Jujuy, Argentina; flower at early stage of anthesis, with long style (B), flower at late stage of anthesis, with accrescent, more expanded tepals, with medium style, on the same day in the same population (C), from locality of *Leuenberger & al. 4546.* – Photographs: A by M. Giorgetta, B-C by B. Leuenberger.

In cultivated material from Jujuy, Yavi *(Leuenberger & al. 4546),* flowers were always erect and without scape above soil level (Fig. 2C, F). The aspect of the flowers was exactly as those observed in the field, but none developed a longer style.

In material from the department of Tumbaya *(Leuenberger & al. 4579a)* a very short scape of up to 1 cm developed in four of five flowers observed over the years (Fig. 2E). The style was always straight and stigma position was constantly below the upper anthers (Fig. 5B). This locality is not far from the type locality, but in the protologue and lectotype specimen of *Haylockia andina* the style is a little longer than the stamens.

In the specimens from the neighbouring province of Salta *(Leuenberger & al. 4626a),* about 150 km S of the

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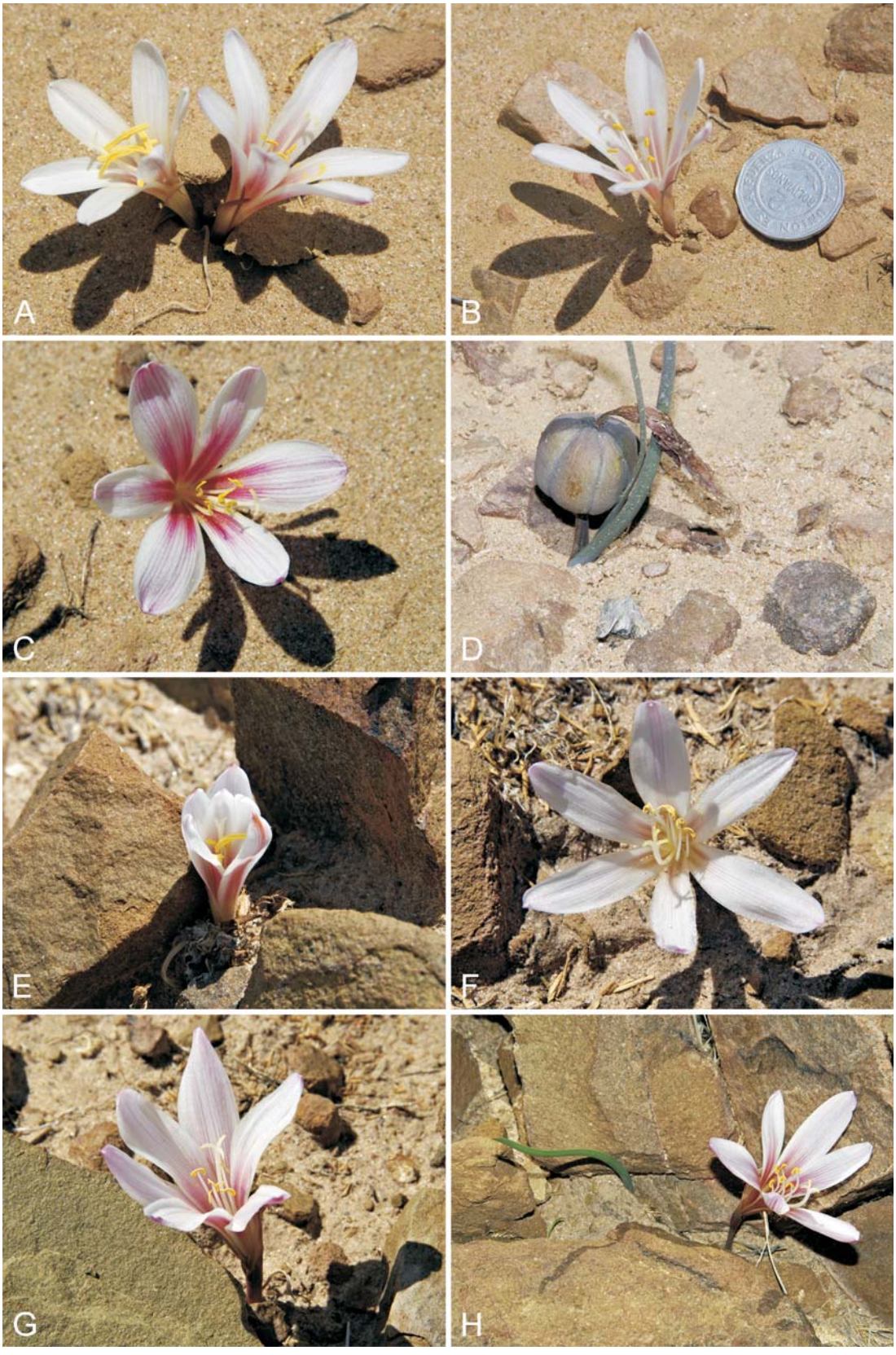


Fig. 4. Flowers and fruit of *Zephyranthes andina* in habitat, Cerro Escara and Cerro Khajas, Uyuni, Bolivia – A: two flowers at different stages of anthesis, left with undehisced anthers, right at later stage of anthesis; B: fully open flower with straight filaments and style (coin as scale = 29 mm in diam.); C: flower with slightly curved filaments and marked striation of tepals; D: immature fruit with flower remnants, and two leaves; E: young flower; F: flower at full anthesis, straight filaments and curved style; G: flower with short scape, straight filaments and style; H: flower with peduncle, curved filaments and style. – Photographs by M. Giorgetta.

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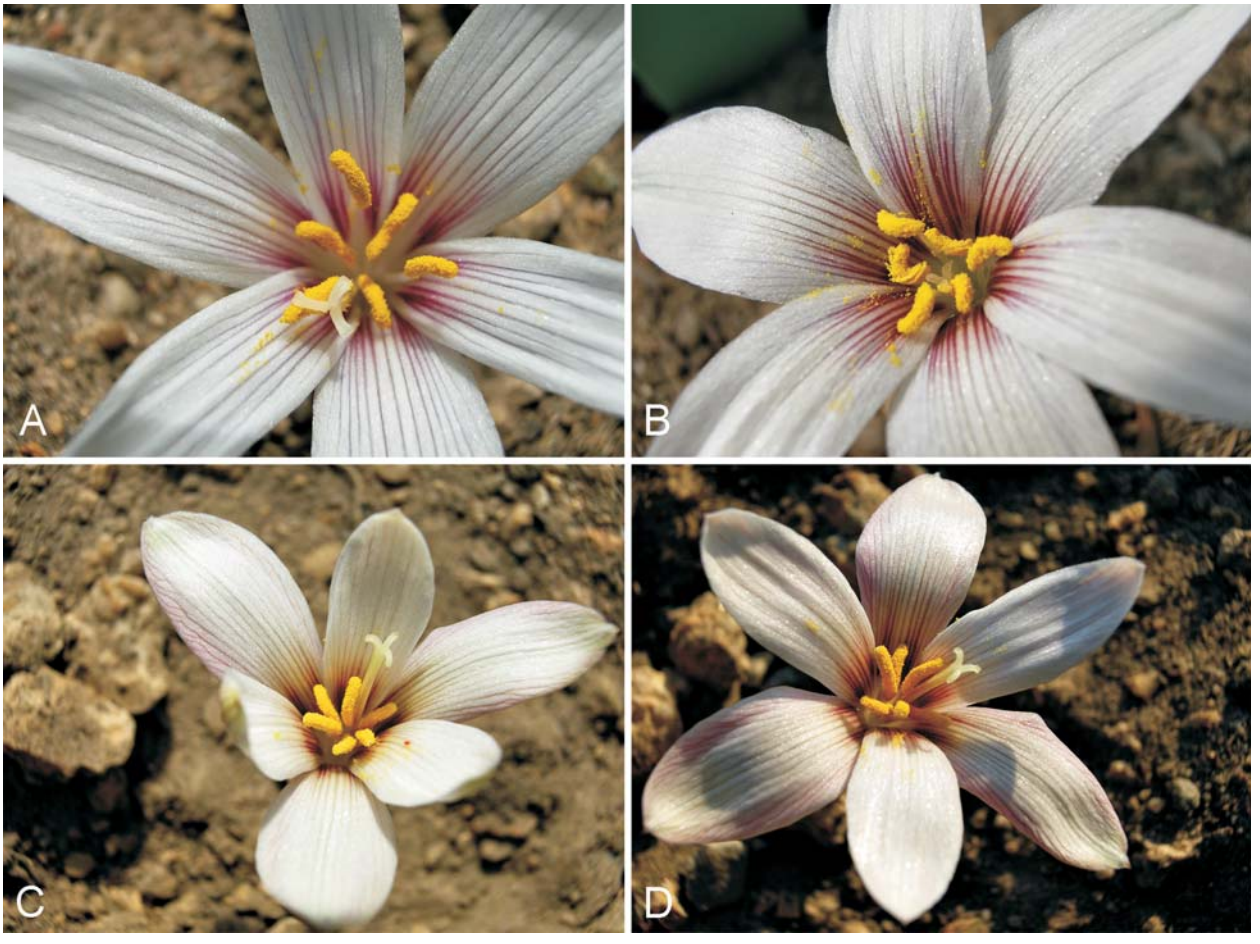


Fig. 5. Flowers of *Zephyranthes andina* in cultivation – A: style of medium length (*Leuenberger et al. 4546*); B: style short (*Leuenberger & al. 4579a*); C: flower on the first day of anthesis, style long (*Leuenberger & al. 4626a*); D: flower on the second day of anthesis, style long (*Leuenberger & al. 4626a*). – Photographs by B. Leuenberger.

type locality, no scape was observed, the ovary remained partly subterranean (Fig. 2D). The style was lateral and more or less straight, more exserted, with the stigma above the level of the anthers (Fig. 5C, D).

Although only in few herbarium specimens the relative position of the stigma and anthers could be observed, long styles were found in geographically distant localities from Dpto. Cachi (Salta) to Santa Victoria (Jujuy). Short styles were found in two specimens from Jujuy (Parque Nacional Calilegua, Valle Grande). All are within a radius of 200 km from the type locality.

From these observations it can be concluded that some populations may be constant in their characters but some variation exists. The filaments always exceed the perigone tube and reach more or less one half of the length of the tepal segments. The position of the anthers is more or less constant. The style can be of the same length as the tube, erect and in central position, or slightly longer, exceeding the tube, and then slightly curved to a lateral position. In cultivated specimens, the relative position of the stigma was constant within one accession over several years.

Our observations suggest that material from different localities shows different degrees of variation and that the slight differences represent populations rather than distinguishable taxa.

In *Haylockia americana* similar variation exists. In the illustrations and descriptions, variably short styles are indicated by Herbert (1830), Hoffmannsegg (1824) and Hooker (1900), but in one flower of nine in a collection of *St Hilaire 2574* (P) from Rio Grande do Sul, the style is slightly longer than the stamens. Floral variation with different style lengths was also reported in species of *Narcissus* from the Mediterranean area (Arroyo & al. 2002; Graham & Barrett 2004).

In other species of *Zephyranthes* and *Habranthus* studied here with ample material in cultivation (e.g., *Z. filifolia* Herb. ex Kraenzl., *Z. mesochloa* Herb. ex Lindl., *Z. carinata* Herb., *H. tubispathus* (L'Hér.) Traub, *H. pedunculosus* Herb.), no marked variation of style length was observed. In most species the style and stigma are slightly protruding beyond the level of the anthers, except in *Z. carinata* where the style is always markedly longer.

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Variation of the length of the stigma lobes can also be observed. In styles with short stigma lobes particularly at an early stage of anthesis prior to full expansion the stigma lobes sometimes become agglutinated especially in dried material. The report of capitate stigma for *Zephyranthes parvula* by Killip (1926) can be explained by this phenomenon, especially as compared with species with long stigma lobes, e.g., 6-10 mm in *Z. boliviensis,* one of the species mentioned by Killip. A study of the details of the holotype and isotype material of *Z. parvula* shows this to fall within the variation of *Z. andina*.

The variation of characters found in all material studied and identified by the authors as *Zephyranthes andina* is summarised in Table 3.

Table 3. Variation of morphological characters in *Zephyranthes andina.*

Character	Variation
Scape length above soil surface	0-5(-10) mm
Spathe (length, posture)	20-30 mm, erect
Flower (length)	(25-)30-65(-70) mm
Flower colour (before anthesis / at senescence)	white, or white with pink, or pink / dark pink
Perigone tube (length)	(10-)15-35 mm
Tepal (length, shape)	(15-)20-45 mm, oblanceolate
Paracorona	lacking
Stamina (length)	biseriate, short ones 4-8 mm, long ones 6-16 mm long
Anthers (length before / after dehiscence)	5-8 mm / 2-4 mm
Style (position, length)	lateral (to central in the perigone tube), 15-35 mm, equal as to longer than perigone tube
Stigma lobes (length)	(0.5-)1-1.5(-2) mm
Stigma (position)	at the level of the upper anthers, or surpassing them, or slightly below them

3.5. Phenology in the field and in cultivation

Study sites. — Argentina, Jujuy, Dpto. Yavi: 24 km W of La Quiaca, 3700 m, 27.11.1998, same site as collection *Leuenberger & al. 4546,* with c. 10 flowers observed in one population, most plants without leaves, some with 1-2 young leaves (Fig. 3B, C).

Bolivia, Potosí, Prov. Quijarro, Cerro Escara, 21.12. 2007 (obs. M. Giorgetta, photos, Fig. 3A, 4A-C): numerous plants in flower, leafless or few with 1-3 leaves. Plants on same site observed on 29.2.2008 with fruit and 1-3 leaves (Fig. 4D). – Cerro Khajas, 22.12.2007 (obs. M. Giorgetta, photos, Fig. 4E-H): numerous plants in flower, leafless or few with 1 leaf. The same plants observed on 1.3. 2008 with fruit and 1-2 leaves.

The photographs and observations of M. Giorgetta indicate ample flowering at the end of December 2007 (Fig. 3-4). The rare presence of immature fruits at the same time indicates an earlier flowering event c. four weeks before following precocious summer rain at the end of November 2007. Regular fruiting but no more flowers were found in a second visit at the end of February and beginning of March. These fruits, observed in about 2 % of individuals, correspond to the mass flowering with thousands of flowers observed two months earlier. At that time no pollinating insects were observed, which may be the reason for the low percentage of fruiting specimens. Flower remnants were still present in individuals without fruit development. Seeds were found around dehisced capsules and widely dispersed and distributed by wind, apparently ignored by birds, insects and other animals. In a further visit in December 2008, no flowers could be observed at all, presumably due to prolonged drought (M. Giorgetta, pers. comm.).

In Peru, mass flowering was documented on 26 December 2003 near Laguna de Parinacochas (Roque, pers. comm.) consistent with the local name “navidad, navidad waytacha, navidad wayta” of the plant (Roque & Ramírez 2008).

No observations on pollinators are known so far. Unspecific pollination by bees can be suspected from the general similarity of flower structure with other Andean *Amaryllidaceae* and from such observations in *Rhodophiala* (Arroyo-Leuenberger & Leuenberger 1992).

Phenology of plants in cultivation. — In cultivation in the northern hemisphere, plants from Argentina flowered in Berlin between late March and mid June, under frost free, temperate glasshouse conditions, maintaining a flowering time in spring, seasonally corresponding to those in nature on the southern hemisphere. Plants grown from seed took 4 to 6 years to flower. These observations are based on only few bulbs and may depend on cultivation technique. Each accession appears to maintain more or less constant flowering time. The dates vary only between one week and one month. Of each accession there are two to three bulbs, and flowering was recorded between 2004 and 2007. Some bulbs produced up to three flowers per season, but not necessarily every year.

Leaves are formed in spring (April, May) and remain until November if the plants are watered sufficiently. The first leaves appear few days after flowering, but under low spring temperatures leaf development is slow. In one case, a second flower was produced by the same bulb, simultaneously with the leaves (not documented by photographs). More vigorous leaf formation was observed in the summer months. The leaves wither (under dry conditions) or rot away (under humid conditions) in fall. From November to March the bulbs remain dormant. Neither leaves nor flowers are formed.

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4. Taxonomy of *Zephyranthes andina*

The analysis leads to the conclusion that the Andean collections referred hitherto to six different species are best interpreted as belonging to one single species, *Zephyranthes andina.* Another possible synonym is *Habranthus nullipes,* described by Ravenna (1978) based on a single collection with inaccessible type and without exact locality from Uyuni, Bolivia.

Zephyranthes andina (R. E. Fr.) Traub in Pl. Life (Stanford) 7: 42. 1951 ≡ *Haylockia andina* R. E. Fr. in Nova Acta Reginae Soc. Sci. Upsal., ser. 4, 1(1): 160. 1905. – Lectotype (designated here): Argentina, Jujuy, Moreno, en monte saxoso, c. 3800 m, 15.10.1901, *Fries 661* (S!). – Note: Fries cites under *"Fr 661a"* a fruiting specimen from a different locality, Nevado de Chañi, c. 4500 m, 28.11.1901, hence a syntype. This material, however, could not be located at S.

= *Zephyranthes pseudocrocus* (Solms-Laubach) Traub in Pl. Life (Stanford) 7: 42. 1951 ≡ *Haylockia pseudocrocus* Solms-Laubach in Bot. Zeit. 65: 135-136. 1907, **syn. nov.** – Type: Bolivia, "Cordillera südöstlich von Sucre (Chuquisaca); c. 4000 m, 15.11.1902" [actually 1903], *Steinmann s.n.* (not located). – Note: According to Funk & Mori (1989: 16), *Steinmann* material was at B, also at STR, where Solms-Laubach (1907: 119) studied *Steinmann* collections.

= *Zephyranthes parvula* Killip in J. Wash. Acad. Sci. 16: 566. 1926 ≡ *Haylockia parvula* (Killip) H. H. Hume in Proc. Florida Acad. Sci. 2: 91. 1938, **syn. nov.** – Holotype: Peru, Cuzco, near Cuzco, 3500 m, Oct 1925, *F.L. Herrera 822* (US!; isotype: GH!).

= *Haylockia cochabambensis* Cárdenas in Pl. Life (Stanford) 29: 43-45. 1973 ≡ *Zephyranthes cochabambensis* (Cárdenas) Ravenna in Pl. Life (Stanford) 34: 83. 1978, **syn. nov.** – Holotype: Bolivia, Depto. Cochabamba, Prov. El Cercado, Cerro de San Pablo east of Cochabamba, 2800 m, [s.d.], *Cárdenas 6337* ("in herbarium Cardenasianum", BOLV, not located). – Note: The type material was neither found at BOLV, nor at LIL, where relevant parts of the Cárdenas collection were deposited (Vargas Calderón 1973, see also Eggli & Leuenberger 2005).

= *Zephyranthes challensis* Ravenna in Pl. Life (Stanford) 30: 39, f. 11. 1974, **syn. nov.** – Holotype: "Culta in Santiago Chiliae ex bulbis in decliviis pr. Challa civit. Cochabamba Boliviae collectis", 3500 m, Sep 1972, *Ravenna 2022* (herb. Ravenna, not seen; isotype: herb. Traub in MO, not located).

= *Zephyranthes fragrans* Ravenna in Onira 3(16): 52. 1999, **syn. nov.** – Holotype: "Culta in Santiago Chiliae ex bulbis in decliviis pr. Huertas, inter Apillapa et Ansaldo civit. Cochabamba Boliviae lectis", 3500 m, Sep 1977, *Ravenna 2070* (herb. Ravenna, not seen).

?= *Habranthus nullipes* Ravenna in Pl. Life (Stanford) 34: 86. 1978. – Note: The drawing of the flower, published later in a complementary note by Ravenna (1981), looks much like the photographs of some *Zephyranthes andina* by M. Giorgetta (Fig. 4H), with filaments and style slightly curved upwards near the tip. No features in the protologue of *Habranthus nullipes* and the later illustration convincingly point to a specific or generic difference. The geographical origin from within the area and habitat of *Z. andina* also suggests that it may be the same, pending further evidence.

Ic. – Fig. 1-8; Fries 1905: t. 9, fig. 1,2 (as *Haylockia andina*); Cárdenas 1973: 43, fig. 13, B (as *Haylockia cochabambensis*); Ravenna 1974: 39, fig. 11 (as *Zephyranthes challensis*); Roque & Ramírez 2007: 1, f. 4 (as *Zephyranthes* cf. *challensis*); Roque & Ramírez 2008: 66, fig. 3, b.

Vernacular names. — Peru: navidad wayta, navidad waytacha, navidad, navidad huayta, navidad huaytacha (Spanish-Quechua for "Christmas day" and "flower" or "little flower", Roque & Ramírez 2008; Roque, pers. comm.); pulla-pulla (James West in sched.). No vernacular names are indicated on herbarium labels for Bolivia and Argentina.

Description. — Bulbs tunicate, (1-)2-3.5 × 1.5-3 cm, subglobose, hypogaeous, solitary, with a neck 2-10 cm long. *Leaves* hysteranthous, (1-)2-3(-4), linear, ascending, distichous, up 20 cm long and up to 3 mm broad, glaucous green, adaxial surface flat to channelled, with 7-11 vascular bundles, margin smooth. *Scape* none (subterranean at least until anthesis) or rarely to 1 cm long. *Bracts* 2, fused and tubular below, upwards free, green to greenish purple, inner bracteole rarely present. *Flowers* solitary, sessile, erect or slightly declinate, funnelform, actinomorphic to slightly zygomorphic; perigone tube up to 3.5 cm long, greenish to purplish pink or white; perigone segments in two series, (15-)20-45 × c. 10 mm, oblanceolate, spreading, outside white to pink, purplish striate, tepal apices pink to purplish, green in bud, inside white with pink to dark pink flush and striate towards the base; the outer series normally wider with glandular tip and median purplish striation. *Filaments* inserted in the upper third of the tube, subequal or of two different lengths, (4-)8-14(-16) mm, white, erect or slightly curved, filiform; paracorona absent. *Anthers* dorsifixed, c. 7 mm before dehiscing, pale yellow, c. 2 mm at full anthesis. *Pollen* yellow. *Style* filiform, white, erect in most flowers but apically slightly curved and lateral; stigma trifid, at the level of the upper anthers, or slightly below or above, enclosed in, or protruding from the flower-tube; stigma lobes (0.5-)1-1.5(-2) mm long. *Ovary* subcylindric, 4-7 × 3-4 mm, green to purplish, with numerous ovules. *Scape* in fruiting stage 0-1 cm. *Fruit* a loculicidal capsule, subcylindric, c. 2 × 2 cm, with up to c. 12 seeds per locule. *Seeds* flattened, D-shaped, c. 6.5 mm (based on a

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single collection); testa smooth, black. *Chromosome number:* 2*n* = 20.

Habitat and distribution — S Peru, W and central to SW Bolivia, NNW Argentina, from (2500-)3000 to 3800(-4500) m altitude. No reports from Chile exist so far but the range may extend into NNE Chile. The known localities fall into the vegetation zones described as Puna formation (Ibisch & al. 2003) in Bolivia, and "Provincia Puneña" and "Provincia de la Prepuna" in Argentina (Cabrera 1957, 1994). The habitat is in open, low shrub or less commonly grass formations on sandy, gravelly and rocky soil, often weathered schists and quartzites. For one habitat near Uyuni, M. Giorgetta (pers. comm.) noted "schists partly covered by shifting sand, bulbs often in rock fissures (Fig. 3A, 4E-H). In the other he noted "compact sand deposits with flowers breaking through the hard surface." (Fig. 4A).

On herbarium labels, habitat characteristics indicate some variation of habitat, e.g., in Peru as "herbaceous vegetation with scattered shrubs", "on dry grassy slopes", "east slope, grass and low shrub", "near cultivated fields, edge of moorland, volcanic rock, dry stony, among grass, low spiny shrubs, solitary"; in Bolivia as "between sandstone outcrops usually in loose sandy soil with spaced vegetation", "short, heavily grazed pasture, ... one colony on a steep grassy slope", "dry hillside above town"; in Argentina as "on rocky-gravelly to schistose-rocky ground with sparse to dense cover with low (40 cm) shrublets", "steep rocky to sandy slopes with N exposition, Prepuna with a partly quite dense shrub cover and grass", "gentle hills on the roadside with lax Puna vegetation".

Associated plants recorded, or visible on photographs, are scattered shrubs of *Parastrephia quadrangularis* (Meyen) Cabrera in Peru; *Ephedra* sp., *Baccharis* sp., *Tetraglochin alatum* (Hook. & Arn.) Kuntze, *Maihueniopsis nigrispina* (K. Schum.) R. Kiesling, *Portulaca* sp. in Bolivia (Fig. 3A); low shrublets, some underneath with soil partly covered with lichens (Fig. 3B) and mosses, scattered *Cactaceae* such as *Rebutia steinmannii* (Solms) Britton & Rose, *Echinopsis ferox* (Britton & Rose) Backeb., *Parodia maassii* (Heese) A. Berger, *Austrocylindropuntia shaferi* (Britton & Rose) Backeb., *Cumulopuntia boliviana* (Salm-Dyck) F. Ritter, *Tunilla soehrensii* (Britton & Rose) D. R. Hunt & Iliff, *Neowerdermannia vorwerkii* Fric and *Oreocereus celsianus* (Salm-Dyck) Riccob., several *Portulacaceae* (*Grahamia kurtzii* (R.E. Fr.) Carolin, *Portulaca perennis* R. E. Fr., *P. rotundifolia* R. E. Fr., *Talinum punae* (R. E. Fr.) Carolin) in northern Jujuy; *Stipa* sp., *Alchemilla* sp. at another locality, *Echinopsis formosa* (Pfeiff.) Salm-Dyck, *Oreocereus trollii* (Kupper) Backeb., *Tunilla soehrensii* (Britton & Rose) D. R. Hunt & Iliff and *Cumulopuntia boliviana* (Salm-Dyck) F. Ritter and *Rebutia pygmaea* (R. E. Fr.) Britton & Rose in southern Jujuy.

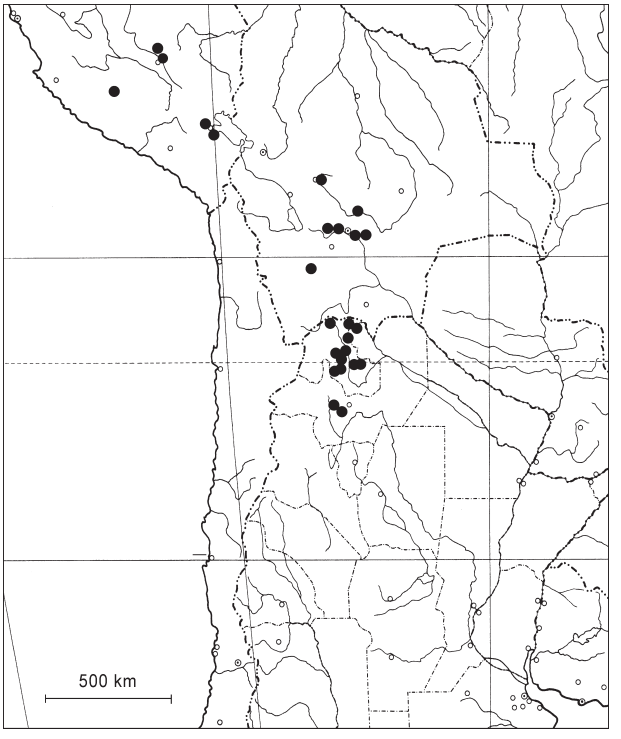


Fig. 6. Distribution of *Zephyranthes andina.*

Additional specimens studied. — ARGENTINA: JUJUY: DPTO. HUMAHUACA: Entre Arroyo el Condor y Chaupi Rodeo, 3800 m, 16.10.1949, *Vervoorst 504* (LIL 439332); Mina Aguilar, 4200 m, 10.1959, *R. Guerrero s.n.* (LIL 504943). – DPTO. LEDESMA: Camino a Alto de Calilegua, 2500 m, 13.10.1974, *Cabrera & al. 25662* (LP); Parque Nac. Calilegua, camino a Cerro Hermoso, 21.10.1985, *Iudica-Ramadori 113* (SI). – DPTO. TILCARA: Al oeste de Huacalera, 3850 m, 30.10.1967, *Werner 896* (LP). – DPTO. VALLE GRANDE: Valle Grande, subida a Cerro Amarillo, c. 3000 m, 2.1.1978, *Kiesling & al. 1609 bis* (SI); Alto de Calilegua, 23°30'S, 64°59'W, 2600 m, 17.2.1995, *Deginani & al. 953* (SI). – DPTO. TUMBAYA: 34 km on Ruta 52 measured from junction with Ruta 9, 23°41.45'S, 65°38.10'W, 3900 m, 30.11.1998, *Leuenberger & al. *4579a,* cult. hort. Berol., 25.3.2002, *Cubr 39445* (B); camino de Purmamarca a Susques, Abra de Lipán, 24°09.24'S, 65° 28.52'W, 12.11.2005, *Zuloaga & al. 8689* (SI). – DPTO. YAVI: 24 km W of La Quiaca on Ruta Provincial 5 towards Santa Catalina, 22°6.51'S, 65°46.69'W, 3700 m, 27.11.1998, *Leuenberger & al. 4546* (B, JUJ, Z), cult. hort. Berol., 7.6.2004, *Cubr 41848* (B). — SALTA: DPTO. CACHI: ruta 33 Chicoana-Cachi, 7 km E of pass Piedra del Molino towards Cachi, at the turnoff to Amblayo, 25°14.02'S, 65°52.69'W, 3240 m, 3.12.1998, *Leuenberger & al. *4626a,* cult. hort. Berol., 24.4.2005, *Cubr 42794* (B); Piedra del Molino, en cerro cercano, c. 3500 m, 7.11.1983, *Kiesling & al. 4336* (SI). – DPTO. IRUYA: San Isidro, Pantipampa, 3200-3400 m, 12.12. 1994, *Quiroga 1389* (MCNS); entre Abra Cumbre de

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Organo y Sunchollada, 22°44'S, 64°59'W, 2500-3500 m, 16.10. 1999, *Tolaba & al. 2210* (MCNS). – Dpto. Santa Victoria: Pie del Cerro Campanario, 22°15'S, 65°04'W, 3700-3750 m, 11.11.1991, *Charpin & Novara 23166* (G, MCNS).

Bolivia: Chuquisaca: Prov. Zudañez, Cordillera de los Sombreros, c. 2 km W from Icla to Tarvita, 19°3'S, 64°38.40'W, 3724 m, 1.12.2005, *J. R. I. Wood 22157A* (HSB); prov. Oropeza, entre km 11 y Ravelo, 3300 m, 19.11.1993, *Kiesling & Metzing 8433* (SI); prov. Oropeza, between Punilla and Chaunaca, 3600 m, 6.11. 1993, *J. R. I. Wood 7616* (K); prov. Yamparaez, Tarabuco, 9500 ft, 26.8.1973, *Mullins 93* (K). — Cochabamba: 4100 m, *Weddell s.n.* (P). — Potosi: Prov. Charcas, *Uzeda-Ocampo s.n.* (HBG).

Peru: S.loc. 1839-40, *Gay 380* (P). — Apurimac: Cotabambas, Chalhuahuacho (Pumamarca), 3900- 4350 m, 2.11.2007, *Cano & al. 18147* (USM). — Ayacucho: Prov. Parinacochas, Distrito Puyusca, Ejansale, Pampa de la Laguna de Parinacochas, 3100 m, 26.12.2003, *Roque & Ramírez 4082* (USM). — Cuzco: Pass between Cuzco and Paruro, 3800 m, 1.9.1976, *Palner 112* (K); Cuzco, 11000 ft, 10.11.1933, *Stanfford 207A* (K); 20 km north of Cuzco, 3600-3900 m, 6.8. 1936, *James West 7168* (MO). — Puno: Near town of Puno, hill behind Puno, 12.300 ft, 21.10.1975, *Holt 158* (K), cult. R. B. G. Kew, acc. 401-75-04547, 19.11.1975 (K); Salcedo, 6.1937, *Soukup s.n.* (USM); Prov. Melgar, Granja Model de Chuquibambilla, 3914 m, 20.11.1935, *Mexia 4188* (MO).

Phenology. — Phenological data from the field are available mostly from herbarium collections, and from few field observations documented by photographs (see 3.5., above). No continuous observations over a longer period exist. *Zephyranthes andina* flowers in spring in the southern hemisphere (early in the summer rainfall season). Flowering dates are recorded from October to December, very exceptionally earlier. One seed bearing plant was observed in December among flowering individuals.

Conservation status. — Concise data for the assessment of the conservation status of *Zephyranthes andina* following the criteria proposed by IUCN (2001) are still sparse because of relatively few documented collections and observations in nature. Its habitats on the Altiplano and in remote areas do not seem under particular pressure from advancing civilization. They are mostly in areas of minimal land use by agriculture but grazed by lamas and sheep in populated areas, or by vicuñas in nature. Predation of leaves by caterpillars and of seeds by rodents seems possible but no observations are recorded. Local threats in more populated areas seem possible but no information exists. No data on selective collecting for whatever reason are known. Vast areas are inaccessible by road. The species has not been exploited by horticulture. It is unlikely to become so because of the ephemeral and rather unpredictable flowering.

The lack of data is in part a consequence of the phenology of the species. The plant is conspicuous only in flowering stage. The flowering events last only very few days, in total only few days per year. The leaves are neither long-lived, from few weeks to few months. The leaves alone are unsuitable for species identification, true population size thus remains little known. The few observations and photographiv documents available demonstrate that, at a determinate locality, the frequency varies from a scattered occurrence to mass populations (thousands of flowering bulbs, observed by M. Giorgetta, pers. comm. 2008) and by a photograph of Roque (pers. comm. 2008). The photograph of part of a population within sight of a human settlement on pastured land permits to count more than 1000-1200 flowers within an estimated area of 100-150 square metres.

The species in the circumscription adopted here has a wide though probably discontinuous range. For the time being it can be classified as "NT = near threatened" in the natural habitat, possibly qualifying for "LC = least concern" pending further data.

5. Discussion of generic placement

The distinction of *Haylockia* from *Zephyranthes* and *Habranthus* has been based on the lack of an aerial scape and sessile flowers. Based on the analysis of variation of scape length and flower characters in *Zephyranthes,* there is little justification to maintain *Haylockia* as distinct from *Zephyranthes* (Table 4). Reduced scapes and sessile flowers occur also in some species of *Zephyranthes* from southern North America and Mexico, e.g., in *Z. simpsonii* Chapm. and *Z. verecunda* Herb. At first sight, the Andean *Habranthus nullipes,* described with a scape of only 2 cm by Ravenna (1978), could be another argument, but much doubt remains on this name. In this context it is noteworthy that, in some herbarium specimens of *Haylockia americana* (= *Z. americana*), scapes of up to 0.5-1 cm were found. Lack of scape or an extremely short scape must be considered to be a weak character for genus distinction in this group.

In typical *Zephyranthes,* the scape carries only one actinomorphic, pedicellate or rarely sessile flower, with more or less erect filaments of subequal or of two different lengths. In *Habranthus,* flowers are usually single (or rarely 2-4), actinomorphic to slightly zygomorphic, normally pedicellate. Most *Habranthus* species have declinate fasciculate filaments of four different lengths. Meerow & Snijman (1998) and Meerow & al. (1999) suggest that the change between actinomorphy and zygomorphy is relatively facile and probably under simple genetic control.

In the genus *Zephyranthes* several basic chromosome numbers have been reported, of which $x = 6$, 7 and 10 are the most common (Greizerstein & Naranjo 1987).

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Table 4. Selected characters of *Zephyranthes andina,* the genera *Zephyranthes* and *Habranthus,* and the type of *Haylockia.*

Characters	*Zephyranthes andina*	*Zephyranthes*	*Habranthus*	*Haylockia americana*
Scape at flowering time [cm]	mostly 0-0.5(-1)	mostly 5-50	mostly 5-50*	mostly 0-0.2(-1)
Flower number per inflorescence	1	1(-2)	mostly 1, few species with 2(-3) (*H. pedunculosus* 1-4)	1
Flower insertion	sessile	pedicellate or rarely sessile	pedicellate*	sessile
Perianth symmetry	actinomorphic to slightly zygomorphic	actinomorphic	actinomorphic or zygomorphic	actinomorphic
Orientation	erect or suberect	erect or suberect	suberect or declinate	erect or suberect
Perianth tube [cm]	1.5-3	mostly 0.2-1.5(-3)	mostly 0.1-0.5	1.6-3
Tepal morphology	equal to subequal	equal to subequal	subequal to different shape	equal to subequal
Filaments	erect or declinate, subequal or of two different lengths	erect, subequal or of two different lengths	declinate, fasciculate 4 different lengths	erect, subequal
Stigma position relative to the anthers	among the upper anthers, surpassing them or rarely below	surpassing or rarely below	mostly surpassing	below the anthers, rarely among the upper anthers

* excepting *Habranthus nullipes,* a doubtful species from Uyuni, Bolivia (see 4., above)

The same numbers of $x = 6$ and 7, as well as 11 and 13 are recorded in many *Habranthus* species (Naranjo 1969). Chromosome polymorphisms, as well as numerical alterations, such as aneuploidy, disploidy and polyploidy and occurrence of supernumerary chromosomes were already reported by Felix & al. (2008) based on other authors as well as their detailed study of *Z. sylvatica* Baker in NE Brazil. The mitotic chromosome count of $2n = 20$ for *Z. andina* is thus not unusual in the genus. According to Naranjo (1974), *Z. minima* Herb. has $2n = 20$ and 21. Greizerstein & Naranjo (1987, under the synonym *Z. stellaris* Ravenna) found $2n = 20$ in *Z. seubertii* (Seub.) H. H. Hume, and Daviña (2001) confirmed this, adding the polyploid counts of 30, 40, and 50. *Z. tucumanensis* Hunz. has $2n = 20$ (Arroyo-Leuenberger, unpubl.). The three species show similar karyotypes, but minor differences are observed.

The other species that was placed in *Haylockia, H. americana,* is reported with $2n = 18$ chromosomes by Flory (1977, under *H. pusilla*). This chromosome number was also reported for species of *Habranthus* by Hunziker & Di Fulvio (1973), Naranjo (1969), Daviña (2001) among others.

Chromosome counts do not prove helpful for distinction of the genera discussed here.

Molecular data are still scarce. Contrary to morphological characters, Meerow & al. (2000) found *Haylockia americana* (incl. *H. pusilla*) to be closer to *Habranthus* (not to *Zephyranthes*). Meerow & al. (2000) showed *Zephyranthes* to be a polyphyletic group with *Habranthus* as paraphyletic genus. Based on these data, *Habranthus* is included in *Zephyranthes* in more recent local studies, e.g., by Dutilh (2005) on *Amaryllidaceae* of São Paulo, Brasil, also by Fernandez-Alonso & Groenendijk (2004) in a study on species of *Amaryllidaceae* of Colombia. This inclusion had earlier been supported but not formally proposed by Arroyo & Cutler (1984) based on anatomical data.

Taxonomically relevant characters are not present unequivocally in all species of *Habranthus* and *Zephyranthes* (Table 4) and this has led to changes in the circumscription of the genera. For lack of sufficient data and personal observation in the field and cultivation, no assessment is made here of *Haylockia americana* and its generic status.

Since the justification of a separate genus *Haylockia* remains doubtful pending further data on its type *(H. americana)* and since *Zephyranthes andina* is in all other characters very similar to other *Zephyranthes* with longer scapes (e.g., *Z. tucumanensis*), we prefer to leave *Z. andina* in the genus *Zephyranthes,* contrary to the earlier listing under *Haylockia* by Arroyo-Leuenberger (1997).

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