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HAAGEOCEREUS: TAXONOMY FOR THE CONSERVATION OF THE GENUS IN PERU

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N. CALDERÓN: "*HAAGEOCEREUS*: TAXONOMY FOR THE CONSERVATION OF THE GENUS IN PERU"

ABSTRACT

The genus *Haageocereus* (Cactaceae) is mostly endemic of Peru, occupying arid areas draining westwards of Andes. In Peru, *Haageocereus* is found between 50 to 2800 m, from 79°54'W, 5°7'S (dept. Piura) to 70°52'W, 18°0'S (dept. Tacna).

The understanding of this genus has been limited by several nomenclature problems such as multiple descriptions for relatively few species, and most of the types are very poor or absent, and cases of misapplication of names also exist. In terms of conservation, speed of habitat loss is worrying for most of the environments where *Haageocereus* occurs, especially because there are very few populations included in national protected areas.

Extensive fieldwork, morphological studies, literature revision and study of types led to the delimitation of 9 species and 6 heterotypic subspecies recognized in this work. Descriptions and keys are accompanied by line drawings, photos and distribution maps. SEM photos were also produced for almost every taxon. Exsiccata prepared during this study constitute approximately the 79.2% of existing *Haageocereus* herbarium samples from wild origin.

Conservation assessments based on the Red List IUCN categories (2001) determined 3 taxa as *Critically Endangered*, 8 taxa as *Endangered* and 5 taxa as *Vulnerable* in Peru. Five different types of habitat for *Haageocereus* have been identified, described and correlated to different kinds of threats in order to present a list of *proposed protected areas and recommendations* for the conservation of these taxa.

CONTENTS

Page

LIST OF FIGURES, PLATES, MAPS AND TABLES

Page

Figures

Plates

Maps

Tables

INTRODUCTION

The family Cactaceae, represented mostly by succulent plants with areoles and spines, is placed by Cronquist (1981) as the single family of the Order Cactales in the Sub-class Caryophyllidae.

Genetic studies (Wallace 1995, Wallace et al. 1996, 2002a) as well as seed anatomical, pollen and gross morphological data have led to the definition of four sub-families: Cactoideae, Opuntioideae, Pereskioideae and Maihuenioideae. Although recent molecular studies (Edwards et al. 2005) have cast doubts upon the relative importance of these, presenting a new hypothesis of phylogenetic relationships at the base of the Cactaceae, supporting a basal split in Cactaceae -thus, possible paraphyly- between a clade of eight *Pereskia* species, centered around the Caribbean basin, and all other cacti. However, additional genes are still going to be tested before reclassifying the Cactaceae.

This is a Neotropical family with approximately 1500 species (Hunt 1999), distributed in a broad variety of environments, from tropical rainforest to extremely arid deserts. After Mexico and the south-western USA, the second most important geographical centre of diversity for Cactaceae is within the Andean chain, with Peru and Bolivia being especially rich, where the taxonomic complexities of the family are considerable and inadequately understood (Taylor & Zappi 2004).

In Peru, the cactus family is found along the Pacific coast, mostly on western slopes of the Andean mountains, and also inter-Andean valleys, with an altitude range between sea level and 5100 m. With over 250 species and 34 genera (Hunt 1999), the Cactaceae form an important part of the arid and semi-arid zone landscape. Important communities of cacti have already been underlined in the north (depts. Amazonas and Cajamarca) and in the south (depts. Arequipa and Cuzco) (Pennington 2004).

Monographic treatments of Peruvian Cactaceae were published by Britton & Rose (1919–23), Rauh (1958), Backeberg (1958–62) and Ritter (1981). The most recent species checklists including Peruvian cacti are provided by Hunt (1999), and Hunt et al. (2006 in press).

Taxonomically, the majority of Peruvian cactus species belong to the subfamily Cactoideae, tribe Trichocereeae, which together with the tribes Browningieae and Cereeae forms the "BCT" Clade, with a shared deletion in the *rpl*16 Intron (Wallace & Gibson 2002). Considering traditional circumscriptions, Trichocereeae is apparently more closely related to Cereeae than Browningieae, but unlike the Cereeae with naked flowers, Trichocereae presents flowers covered by hairs, spines and/or wool borne on the hypanthial areoles (Taylor & Zappi 2004).

According to the phylogenetic system of Buxbaum (1962), *Haageocereus* Backeb. (1934) belongs to tribe Trichocereeae. Allied genera of *Haageocereus* are postulated as *Espostoa*, *Weberbauerocereus* and *Cleistocactus*; they all have columnar stems and similar spination characters but flowers are distinctively different, especially in shape and size, relating to differing pollination syndromes. In nature, *Haageocereus* hybridizes with *Espostoa*, forming the intergeneric hybrid ×*Haagespostoa*, which displays a range of characters inherited from both parent genera.

Haageocereus is distributed over much of Peru, with its northern limit in Piura (Peru) extending to the south along the Peruvian territory reaching northernmost Chile. In Peru, the genus can be found in most arid areas draining westwards, between 50 to 2800 m altitude, including the Pacific coastal desert, the northern dry forest and western Andean valleys. These habitats have a very low annual rainfall, especially in the coast and southern Andes (18–100 mm). In the central Andes and in the northern dry forest the precipitation is higher (100–500 mm).

The species of *Haageocereus* are generally characterized by their shrubby habit, branching typically from the base, bearing crepuscular nocturnal flowers, which may remain open until the next morning, a pericarpel covered by trichomes, and ovoid to globose fruits, which are generally indehiscent. The phenology is highly variable amongst species, flowering being ephemeral, unpredictable and not easy to observe.

Haageocereus species have had a very intricate history, both in taxonomy and nomenclature. *Haageocereus* synonyms include a number of species names published under *Binghamia* (Britton & Rose 1920) and *Peruvocereus* (Akers 1947a).

For conservation purposes it is a prerequisite to establish a stable taxonomy and nomenclature, something which *Haageocereus* species have lacked during recent decades.

The family Cactaceae as a whole is listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) and some species threatened by trade are included in Appendix I.

In Peru, there are serious threats to members of the family Cactaceae and especially to *Haageocereus*, due to the location of many populations in the proximity of major cities. Disturbance of the habitats of cactus populations is caused by human expansion, environmental pollution and agricultural development (Ostolaza 1995a). In relation to human disturbance, population studies of *Haageocereus* have been undertaken (Calderón 2002) showing that the closer these cacti are to human settlements, the poorer is their health, particularly in terms of longevity and reproductive effectiveness.

Establishing the status of these species under the Red List categories of the International Union for the Conservation of the Nature and Natural Resources (IUCN 2001) will enable new Conservation proposals and action plans for the natural habitats to be developed for these taxa as has been achieved for other kind of habitats involving many non-cacti plant species in Peru.

Aims and objectives

The aim of this project is to produce a monograph which enable a better understanding of the taxonomy of *Haageocereus* to facilitate the conservation of its species and natural habitats. For this purpose the following specific objectives have to be achieved:

- To publish a comprehensive morphological study of *Haageocereus*,
- To report on the current situation of the natural habitats of *Haageocereus*,
- To establish a complete herbarium record of *Haageocereus* species, and
- To provide essential information for an improved understanding of the conservation of Peruvian cacti.

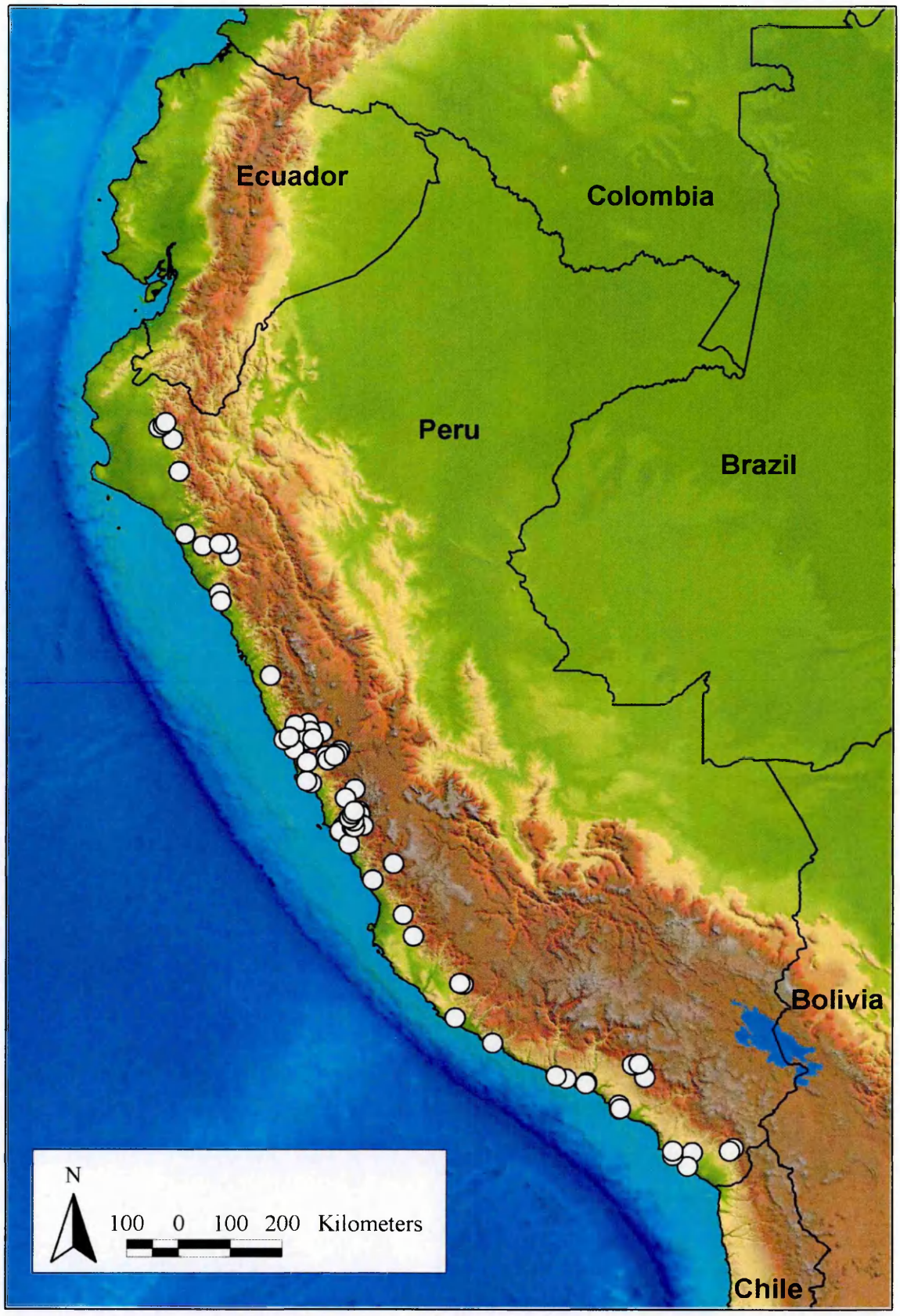
MATERIALS AND METHODS

Study Area

The area of study is mainly located in diverse deserts, valleys and dry forests along the length of the Peruvian territory (**Map 1**), between 50 m and 2800 m altitude, from *Haageocereus versicolor* in the north (79°54'W, 5°7'S) to *Haageocereus decumbens* (70°52'W, 18°0'S) in the south. The location records for each species vary according to the availability of data, including not only bibliographic sources but also information obtained during fieldwork and personal communications by reliable cactus enthusiasts.

Data collection

Bibliographic studies were initiated with scientific articles and books provided in the first place by the Peruvian Cactus & Succulent Society. Most bibliographic records, especially the oldest ones, were located at the Main Library of the Royal Botanic Gardens, Kew (London). Bearing in mind the great number of *Haageocereus* names, individual files were prepared listing all publications for every species name.



Map 1. Study Area. Localities of *Haageocereus* visited in Peru= ○.

Fieldwork studies included not only the recording of morphological characters of the species but also data regarding the distribution range and environmental quality of the habitats involved. The Botanic Garden "Octavio Velarde Núñez" of La Molina University, together with the Peruvian Cactus & Succulent Society initiated the "Cactus of Lima Project" in 2001, making possible most of the field trips for this study during 2001–2005 (**Table 1**).

Study of herbarium material was also initiated with the collections from the Herbarium of the Botanic Garden of La Molina University (Herb. B. G. La Molina). Herbarium specimens were also prepared following the methodology proposed by Zappi (1994), these specimens are currently held at Herb. B. G. La Molina, and most of them will be incorporated into the La Molina University Herbarium (MOL) when this study is completed. Visits to the European herbaria of Utrecht (U) and the Succulent Collection of Zürich (ZSS) were undertaken. These herbaria include 21 holotypes, 6 isotypes and several non-type exsiccata of *Haageocereus*. Loans requested from ZSS and Berlin (B) collections were also provided for study at the Kew Herbarium. Additional seed samples of *Haageocereus* were also kindly provided by Graham Charles from his large private collection of known wild provenance.
It is estimated that this study has prepared 79.2 % of the current *Haageocereus* exsiccata from wild provenance, but the genus still remains poorly represented in most of the Herbaria.

Study Methodology

For morphological studies, fresh and dried cactus specimens were carefully measured to enable the comparison of characters and elaboration of descriptions. A stereoscopic Leica MZ6 microscope was used to observe small structures like stamens and trichomes. Records of rib number, stem diameter and distance between areoles were taken from fresh samples, since these structures shrink when dried, while flowers and fruit characters were recorded, where possible, from samples kept in spirit. It is important to record the colour, texture and

odour of reproductive structures before these are preserved. Areoles, spines and hairs can be measured reliably from fresh or dry material.

For making line drawings, the stereoscope Leica MZ6 and a professional vernier were especially useful to determine diameters of hairs, spines, and floral indumentation. The plates illustrate the typical growth habit, detail of spines and areoles, as well as complete flowers and fruit longitudinal sections. Diagnostic taxonomic characters are given special attention in the figures.

The study of *Haageocereus* seeds was carried out with the aid of the Scanning Electron Microscope (HITACHI S-2400 SEM) at the Palynology Unit of the Jodrell Laboratory (located in the Kew Herbarium). The treatment of seeds prior to scanning started with ultrasonic cleaning using distilled water with a few drops of industrial detergent (dil. to 1%). Seeds were dried and mounted on stubs with double-sided sticky tape. After a period of 1–2 days in a desiccation capsule, mounted seeds were coated with platinum using the EMITECH K550X coater for 2×4 minutes prior to scanning. In the SEM, seeds were scanned and photopraphed at ×60 and ×600 to determine the variability of seed morphology. Side views were selected in order to show as many characters as possible, and details of testa surface were observed by close-ups of the peripheral region of the seed, as proposed by Barthlott and Hunt (2000).

The Geographic Information System (GIS) Unit of the Kew Herbarium provided base maps, to which locality data collected in this study have been added, in order to illustrate *Haageocereus* distribution in Peru, as well as in relation to current National Protected Areas. ArcView computer software was modified at Kew's GIS Unit to assess the IUCN (2001) Red List criteria, mainly for the application of criterion B of geographic range, based on the "extent of occurrence" and "area of occupancy", and thus automatically generating the IUCN rating and categories of threat for each species (Willis et al 2003). The use of criterion A (IUCN 2001), based on the reduction of population, is alternatively applied when there is

evidence that population decline constitutes the worst threat for the species and this has been observed in the past, present and is likely to occur in the future.

Table 1. Fieldtrips related to the Master's thesis: "*Haageocereus*: Taxonomy for the conservation of the genus in Peru"

Date(s)	Place (Area visited)	Fieldtrip purpose	Institutions involved & Collaborators
Jan.–Mar., July, Sep. 2001; Jan.–Mar., May, Jun.– July, Oct. 2002; Jan.– Mar. 2003	Central LIMA; Lurín valley (Manchay, Cardal, Picapiedra, Tinajas), Rímac valley (Santa Clara, Jicamarca), Chillón valley (California hills) & Santa Eulalia (Barba Blanca) valley. Northern LIMA; Rio Seco-Huaral, Chancay, Huaura valley (Sayán, Churín, Cochamarca, Andajes, Oyón). Southern LIMA; Caracoles hills-km 57 Pan Highway, Omas-km 97 Pan Highway.	Taxonomic study of *Haageocereus* in Lima (Bachelors Thesis) & Cacti population study at Manchay.	La Molina Univ. Botanic Garden & Peruvian Cactus & Succulent Society.
Aug. 2003	Northern LIMA; Huaura valley (Acotama, Ambar, Churín, Caujul, Naván, Chiuchín, Jucul, Matobamba, Cochamarca, Andajes, Oyón).	Expedition of the V International Course of Cactus & Succulents. Photographing, noting distribution records.	La Molina Univ. Botanic Garden & Peruvian Cactus & Succulent Society.
Nov. 2003	Central & Northern PERU: Lima, Ancash, Lambayeque, La Libertad, Piura, Cajamarca	Photographing, noting distribution records.	G. Charles, C. Pugh, C. Ostolaza & N. Calderón.
Feb. 2004	Northern LIMA; Chancay, Huaura valley (Cochamarca, Paccho, Andajes).	Master's thesis research.	La Molina Univ. Botanic Garden and Peruvian Cactus & Succulent Society.
Mar. 2004	Southern PERU: AREQUIPA; Yura valley, Tiabaya valley, Camaná, Mollendo. TACNA; Morro Sama	As above.	La Molina Univ. Botanic Garden.
Mar.– May. 2005	Central PERU: LIMA; Chancay Km 118 Panamericana norte highway and Huaura valley, Paccho canyon. Southern PERU: AREQUIPA; Huanca, Yura valley. TACNA; Tacahuay, Tarata. Northern PERU: PIURA; Morropón.	As above.	La Molina Univ. Botanic Garden.
July 2005	Central PERU: LIMA; Lurín valley, Tinajas canyon.	Collecting material for above.	La Molina Univ. Botanic Garden and Ricardo Palma Univ.
Aug. 2005	Northern LIMA; Pativilca and Fortaleza valleys.	Expedition of the VII Course of Cacti & Succulents: Photographing, noting distribution records and collecting material for above.	La Molina Univ. Botanic Garden and Peruvian Cactus & Succulent Society.
Aug.– Oct. 2005	Central LIMA; Lurín valley (Queb. Verde, Picapiedra, Antioquía), Rímac valley (California hills) and Santa Eulalia (Barba Blanca) valley.	Photographing, noting distribution records and collecting material.	La Molina Univ. Botanic Garden and Peruvian Cactus & Succulent Society.

THE GENUS *HAAGEOCEREUS* (WERDERM. & BACKEB.) BACKEB.

History of the genus

Because of its particularly difficult preservation, type material of names of cactus species is in many cases poor or lacking and this makes the taxonomic treatment of the species difficult. The earliest publications possibly referring to *Haageocereus* according Ritter (1981) refer to the name *Cereus limensis* Salm-Dyck (1845), which lacks a preserved type, any illustration and a meaningful description, and *Cactus multangularis* Willdenow (1809), which is even more uncertain and according to Leuenberger (2004) should be avoided.

The first descriptions certainly referring to *Haageocereus* were published by Vaupel (1913) who described two species as *Cereus decumbens* and *Cereus acranthus* based on the collections of A. Weberbauer held at the Berlin-Dahlem Herbarium.

The genus *Binghamia* Britton & Rose (1920) was created to include Vaupel's species *Cephalocereus melanostele* and *Cereus acranthus*. Nevertheless, to judge by the description and photos, Britton & Rose had misrecognised a new species (currently *Haageocereus pseudomelanostele*) with *C. melanostele* (now *Espostoa melanostele*) and also did not notice that the genus *Binghamia* had been previously assigned to an algae (Agardh 1894).

Werdermann & Backeberg (1931) described as *Cereus pseudomelanostele* the species Britton & Rose had misrecognised under *Cephalocereus melanostele*. Backeberg (1934a) created the genus *Haageocereus* to include *Cereus pseudomelanostele,* as well as *C. acranthus* Vaupel and *C. decumbens* Vaupel (Backeberg 1934b, 1937), and in later publications (Backeberg 1957, 1960) the genus *Haageocereus* was expanded with narrowly described taxa to include a total of 49 species names.

Akers (1947a), an American cactus grower, created the genus *Peruvocereus* to include a group of species he found in the central valleys of Peru and which he believed to be different from *Haageocereus pseudomelanostele* (the actual type of *Haageocereus*). Between 1947 and 1948, Akers published 10 species of *Peruvocereus* with detailed descriptions and photographs, but did not preserve their types. Some of these species names are currently synonyms of Backeberg's *H. pseudomelanostele*, or have been recognized as hybrids (See **Appendix 2**: List of names of *Haageocereus* (and *Peruvocereus*) possibly referring to ×*Haagespostoa*).

Rauh (1958) published "Beitrag zur Kenntnis der peruanischen Kakteen-vegetation"; a remarkable work that recognizes the 49 *Haageocereus* taxa that Backeberg diagnosed briefly in 1957 as new species based on Rauh collection numbers. The importance of Rauh's monograph reflects the collections he made in Peru in 1954 and 1956, including photographs and information about the environment and vegetation associated with these cacti. Rauh's type-material was kept at Heidelberg Botanic Garden and Herbarium (HEID), but unfortunately most of it has subsequently been lost, the few exsiccata still available having been transferred to the Zurich Succulent-Collection Herbarium (ZSS).

Backeberg (1960) published a key to *Haageocereus* species and varieties, which he arranged under 6 informal groups he called "kingdoms": "acranthi", "versicolores", "asetosi", "setosi", "decumbentes" and "repentes". Backeberg's classifications, as well as species concepts, were based on rather inconsistent vegetative characters. His key illustrates the difficulty to define clear morphological differences between the totality of taxa he described. Nevertheless, the volumes of "Die Cactaceae" (Backeberg 1958–1962) remain a much-consulted monographic treatment for Peruvian cacti.

Friedrich Ritter (1981) accepted 19 species of *Haageocereus*, describing 7 new species which included *H. tenuis* and *H. lanugispinus*. Unfortunately, he did not attempt to prepare keys to identify the species.

In the latest CITES Checklist (Hunt 1999), *Haageocereus* is credited with 13 accepted species plus 8 provisionally accepted species and 3 accepted heterotypic subspecies. In the present study, this number has been further reduced to reflect the narrow species concept several of these names were based on.

In relation to their conservation, several important *Haageocereus* populations have suffered a dramatic reduction in numbers of individuals and/or have disappeared in the past decades (Ostolaza 1995a). For instance, *H. pseudomelanostele* (Werderm & Backeb.) Backeb., can no longer be found in its type locality at Cajamarquilla in the Rímac valley (Vaupel 1913) because of housing developments. In the same way, several populations of *Haageocereus* surrounding Lima declined in the last five years, especially in the Lurín and Rímac valleys. In other parts of the country, these species remain vulnerable and are currently under similar threats.

Morphology

The present morphologic survey was based on the study of *Haageocereus* sp. for the present monograph.

Currently, infrageneric relationships among members of Trichocereeae and even the clade BCT are unclear. For this reason, is difficult to establish a basal or sister taxon for *Haageocereus* (especially among its proposed allied genera *Espostoa, Weberbauerocereus* and *Cleistocactus*) in order to elucidate possible derived morphological characters in this genus.

However, gene sequence studies developed by Wallace (1997) found evidence supporting a monophyletic genus *Harrisia* (Tribe Trichocereeae), and also that the sister group of

Harrisia was the Bolivian endemic *Samaipaticereus* (*S. corroanus*). From this, *Samaipaticereus* could be hypothesized as potential "ancestral morphotype" for *Haageocereus*, and in this sense, the characters present in *Samaipaticereus* will be hypothesized as plesiomorphic and the derived characters present in *Haageocereus* will be hypothesized as apomorphic.

There are several shared characters (potential plesiomorphies) between *Haageocereus* and *Samaipaticereus* best represented by their flowers, which are very alike, but also there are other interesting and contrasting features in the rest of their morphology.

Samaipaticereus corroanus are tree-like plants with erect branches and low number of ribs (4–6); triangular areoles; spines 5, 2.0–3.0 mm long, central spine 5.0–10.0 mm long; Flowers 4.5–5.0 cm long, narrowly funnelform, tube slightly curved and covered by hairs and few brown bristles emerging from the axils of bract-scales; outer perianth-segments whitish-green, inner perianth-segments white; stamens numerous; stigma lobes 7–10; nectar-chamber 1.0 cm long; fruit dehiscent, funicular pulp salmon-red; seeds broadly oval, 1.3 × 1.0 mm, black, glossy, cuticle weakly striate, hilum large and basal. According to this brief description, and in comparison to the characters presented in *Haageocereus*, it is possible to hypothesize the possible plesiomorphies and apomorphies of the latter genus (**Table 2**).

Table 2. Hypothesized plesiomorphic and apomorphic characters of *Haageocereus*, based on outgroup comparison with *Samaipaticereus* (Trichocereeae).

Plesiomorphies	Apomorphies
Erect branches	Prostrate and semi-prostrate branches
Radial spine number 7–20	Radial spine number (21–)56
Central spine present	Central spine absent
Flowering areoles not clearly differentiated	Flowering areoles well-differentiated
Seed microrelief weakly striated	Seed microrelief strongly striated
Flower tube straight to slightly curved	Flower tube well curved

As already evidenced in pollination syndromes, shifts to a plesiomorphic state are considered to represent a reversion, or a secondary derived syndrome (Wallace 2002). In the same manner, trends in the fruit morphology of *Haageocereus*, represented by the dehiscent fruits present in *H. pseudomelanostele* subsp. *turbidus,* and the pinkish funicular pulp of *H. tenuis*, could also be hypothesized as a reversion for the genus, as they are highly adapted characters that appear only sporadically within *Haageocereus.*

Habit and growth patterns

Haageocereus presents terete stems, branching mainly from the base in a prostrate, semi-prostrate and erect manner (**Fig. 1**). The plants are shrubby, the erect taxa up to 1.4–1.7 m, exceptionally reaching 2.4 m. Lacking a lignified vascular cylinder, the tallest stems usually fall to the ground in old age, and sometimes new branches may sprout from the fallen branches.

In some cases, erect-growing taxa may develop initially decumbent new branches, which eventually turn upwards and develop into erect stems. *Haageocereus* plants usually present 4–20 branches per individual, but sometimes develop into very profusely-branched individuals, with up to 95 branches in *H. acranthus* subsp. *acranthus*.

H. decumbens, *H. tenuis* and *H. lanugispinus* all have prostrate branches with ascending apices 5.0–10.0 cm above the ground. Semi-prostrate to erect species are represented by *H. repens*, *H. platinospinus* and *H. chilensis* growing at first decumbent and later erect at ≥20.0 cm above the ground. In the case of *H. platinospinus*, which is a short bushy plant, the stems may be totally erect, somewhat curved, or semi-prostrate.

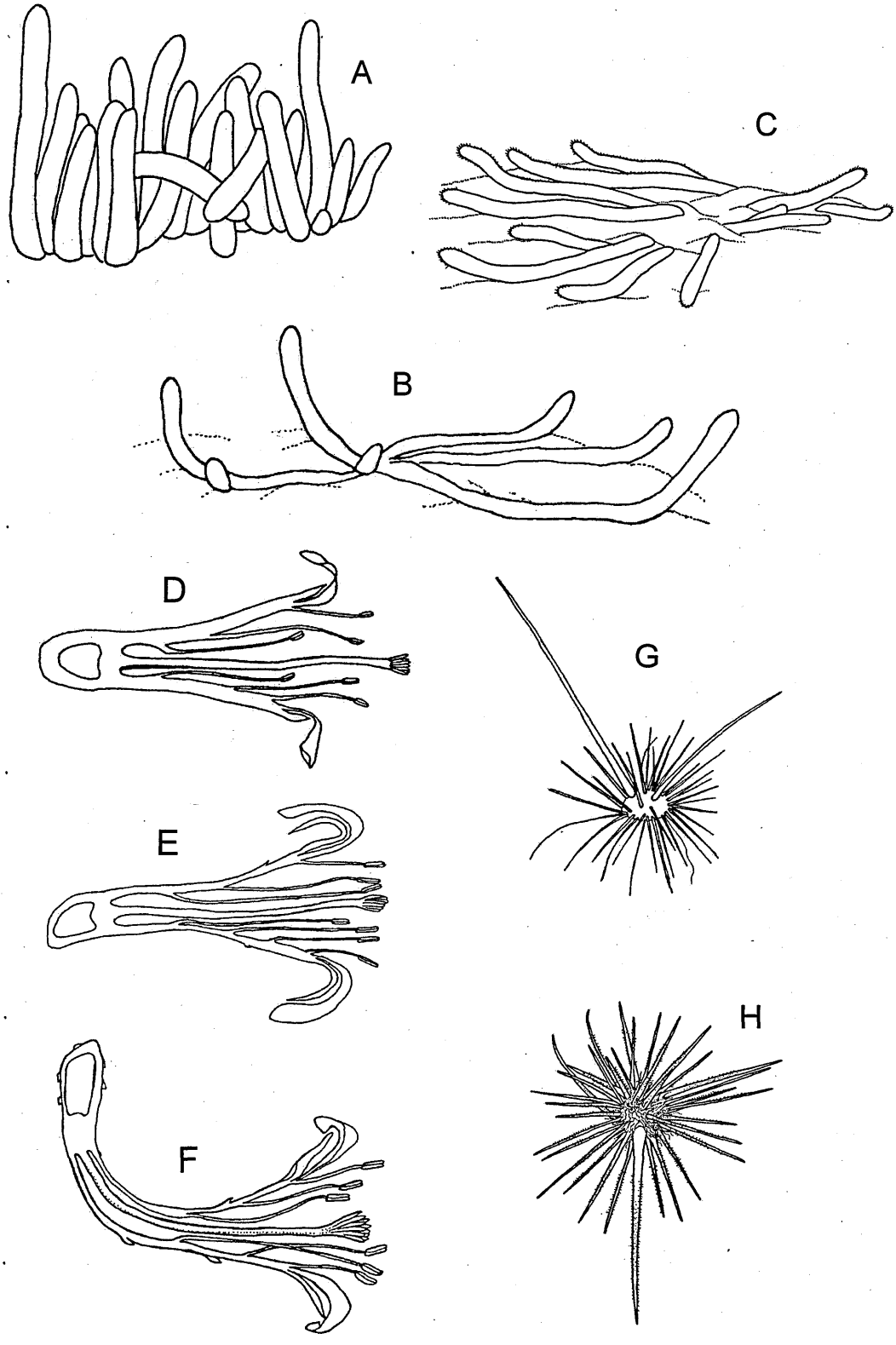


Fig. 1. Characters for species recognition. Types of growth habit: A, erect (*H. acranthus* subsp. *acranthus*, *N. Calderón* 211); B, semi-decumbent (*H. repens*, *N. Calderón* 358); C, decumbent (*H. tenuis*, *N. Calderón* 419). Types of flower tube curvature: D, straight (*H. platinospinus, N. Calderón* 444); E, slightly curved (*H. platinospinus, N. Calderón* 450); F, markedly curved (*H. tenuis, N. Calderón* 364). Areoles and spination: G, Areole with central spine, radial spines and bristle-spines (*H. pseudomelanostele* subsp. *pseudomelanostele, N. Calderón* 474); H, Areole with central and radial spines covered by trichomes (*H. tenuis, N. Calderón* 364).

H. pseudomelanostele, H. acranthus and *H. versicolor* present upright branches. The first two species form part of the so-called "vegetation of columnar cacti formation" of the Andean valleys, and the latter species is part of the "seasonal dry forest" in northern Peru.
Branch diameter varies from 1.2–1.4 cm (*H. lanugispinus* and *H. tenuis*) up to 7.5–8.0 cm (*H. pseudomelanostele* subsp. *acanthocladus* and *H. acranthus* subsp. *zonatus*).

Haageocereus species prove to have an extraordinary resistance to dry conditions, as is reflected by their thick, swollen stems characteristic of very arid environments.
Rib number varies from 10 ribs (*H. acranthus* subsp. *backebergii*) to 24 ribs (*H. pseudomelanostele* subsp. *pseudomelanostele* and *H. pseudomelanostele* subsp. *acanthocladus*). Rib number is, in most cases, inversely proportional to the rib width, and it is an important key character.

In the species with lower numbers of ribs, the observable stem colour is that of the epidermis when not obscured by the spines, being generally green for all the species, but brownish-green for the southern populations of *H. platinospinus* and greyish green for *H. chilensis*. The epidermis has a waxy cuticle, which can be easily observed in the species with few ribs and spines, like *H. platinospinus* and *H. acranthus*.

Areoles and Spination

Areole shape is typically oval at maturity, but circular when first developing at the stem apex. The areoles vary in size from 1.5–1.6 mm diam. (*H. lanugispinus* and *H. tenuis*) up to 10.0–11.0 mm diam. (*H. acranthus*). Areoles are spaced along the stem ribs between 1.4–16.5 mm apart. They change in colour depending on age, being generally yellow at first, turning brownish when older, but old areoles may darken because of pollution, especially in cacti growing close to cities and busy roads.

Areoles are conspicuous in *Haageocereus* in species with lower numbers of ribs, like *H. platinospinus*, *H. acranthus, H. chilensis* and *H. decumbens*. These species have compact cushions of brownish yellow trichomes, sometimes subtended and marked by transverse rib-folds, this last feature being considered as a plesiomorphic character because is related with the formation of "podaria" under areoles (Zappi 1994). For other *Haageocereus* species, like *H. tenuis* or *H. lanugispinus*, areoles are not easy to observe, presenting irregular white tufts of trichomes. Areoles may also be densely covered by numerous spines, as in *H. repens*, *H. pseudomelanostele* and *H. versicolor*, and therefore, their shape and hairiness may be difficult to observe.

Spines are comprised typically of numerous radials with 1–3 longer spines, called central spines, which are absent (a hypothesized apomorphy) in *H. lanugispinus*. Central spines vary in number from 1–2(–3), and in size from 0.3–15.0 cm long and 0.3–1.9 mm diameter at the base, *H. chilensis, H. platinospinus* and *H. pseudomelanostele* subsp. *turbidus* being the taxa with longest spines within the genus. Radial spines vary in number from 7–56, and in size from 2.0–15.4(–40.0) mm long and 0.2–0.7 mm diameter at the base. There is variation in spine size within individuals of similar age, as in *Haageocereus platinospinus,* which can have central spines in some individuals four-times the size of others.

As is the case with areoles, spines are yellow at the beginning, or sometimes reddish in *H. versicolor*, becoming brownish or greyish with age. The presence of white and yellow bristle-spines can be observed especially in the subspecies of *H. pseudomelanostele* and also in *H. repens*.

The spines bear white trichomes only in *H. lanugispinus* and *H. tenuis*, this character being rather rare within subfamily Cactoideae, and here hypothesized as an autoapomorphy, probably of high adaptative value, to enhance the deposition of water droplets from the annual sea-fog in their coastal habitats.

Flower-bearing areoles

In *Haageocereus*, flower-bearing areoles are recognisable by having few short white trichomes developed as the flower bud forms, and for most of the species these trichomes do not persist for long. More conspicuous flowering areoles can be seen in *H. versicolor* subsp. *versicolor*, *H. versicolor* subsp. *pseudoversicolor* and *H. acranthus* subsp. *zonatus*, which present a ring-like "pseudocephalium" (a hypothesized apomorphy), formed by the white tufts of trichomes that remain on the areoles after flowers and fruits have completed their development. As this character is present only in mature individuals, care has to be taken when identifying young plants of these species; on the other hand, old individuals show several of the characteristic ring-like pseudocephalia along their erect branches.

Flowers and Fruits

Haageocereus species present few ephemeral flowers developing terminally on the stem. They are crepuscular-nocturnal, but may remain open until the next morning. Flowers have a funnelform shape, generally between 6.0–8.5 cm long, but they can be smaller, such as in *H. pseudomelanostele* subsp. *pseudomelanostele* and *H. lanugispinus* (4.0–5.0 cm) or larger in some individuals of *H. tenuis*, *H. acranthus* subsp. *acranthus*, *H. acranthus* subsp. *zonatus* and *H. pseudomelanostele* subsp. *acanthocladus* (9.7–11.5 cm), with a perianth-limb regularly symmetric which presents numerous perianth-segments or tepals which vary in colour, being green to reddish outside, and white to pinkish and reddish inside. The elongate receptacle-tube may be somewhat flattened or curved, externally bearing hair-spines and trichomes that emerge from the bract-scale axils. Flower curvature varies from slightly curved (*H. versicolor, H. pseudomelanostele, H. acranthus, H. decumbens*) to strongly-curved (*H. repens* and *H. tenuis*), a hypothesized apomorphy (**Fig. 1**). The pericarpel encloses the ovary locule and bears few bract-scales and trichomes externally; the nectar-chamber is tubular, somewhat swollen, producing sweet translucent nectar; and the flower

exhales a "sweet-pungent" smell. Stamens are numerous (200–400), inserted in a single series; the stigma-lobes may be exerted or included.

Fruits are spherical to ovoid, between 2.0–6.5 cm long and 1.3–5.6 cm diameter, bright red when mature and easily seen from a long distance. The flower remnants are persistent on top of the fruit. The pericarp is thin and mostly indehiscent, but in the case of *Haageocereus pseudomelanostele* subsp. *turbidus*, fruits can split open when ripe. The funicular pulp is white and solid for most of the species, being translucent pink and mucilaginous in *H. tenuis*.

Seed-morphology

This study surveyed seeds of almost all *Haageocereus* taxa and has identified key characters from the micro-morphology of the testa. The terminology employed here is based on Barthlott & Hunt (2000), where 26 seed-characters are proposed to describe the seed diversity in the subfamily Cactoideae. These authors used general features of the morphology, testa appearance, individual testa-cells, anticlinal cell boundaries, periclinal wall sculpture, hilum-micropylar region, and other appendages of seeds.

Haageocereus seeds are mainly medium-sized (1.2–1.87 mm), which is the average size for subfamily Cactoideae, but can also be small (1.09–1.14 mm); typically mussel-shaped (*Cereus*-type), being broadly oval (**Plate 1.1**) to oval (**Plate 4.6**), calculated on the basis of seed length/breadth ratio (1.10–1.99). In general, the testa has a glossy appearance, but in *Haageocereus tenuis* it is semi-matt.

Cuticular striations, as a result of cuticle folding, are very strong in *Haageocereus repens* (**Plate 5.3**), *Haageocereus tenuis* (**Plate 5.6**) and *Haageocereus versicolor* (**Plate 6.1**), this character being hypothesized as an apomorphy for these species. The blackish testa presents a multi-cellular sculpture with interstitial craters, and low-domed convexities which are typical for all *Haageocereus* (**Plates 1–6**).

The presence of par-convexities (**Plate 1.5**) was observed only in *Haageocereus acranthus* subsp. *zonatus* towards the peripheral border of the seed. It should be noted that par-convex structures are mostly associated with Notocacteae subtribe Notocactinae and the Trichocereeae subtribe Gymnocalyciinae.

The hilum-micropylar region (HMR) is oblique and large for all *Haageocereus,* but does not present any diversity of form allowing differentiation amongst species.

Reproductive biology

Pollination

The family Cactaceae is entirely zoophilous (Barthlott & Hunt 1993), and more than one pollinator can probably be found in species of *Haageocereus* judging from flower morphology, where traits are found associated with bat, hummingbird and moth floral syndromes, although bats and hummingbirds have not been directly observed visiting *Haageocereus* flowers.

According to the pollination syndromes proposed by Faegri & Van der Pijl (1979), some assumptions can be made about the possible pollinators of *Haageocereus*. The typical funnel-form white flowers of *H. acranthus* subsp. *backebergii*, mostly nocturnal with a sweet-pungent smell, are a good example for possible chiropterophily. On the other hand, pinkish to reddish flowers that open in the afternoon until next morning, with slight scent and also producing abundant nectar, can be recognized as hummingbird flowers that might also secondarily attract bats. Such flowers are seen in *H. pseudomelanostele* subsp. *carminiflorus* and *H. acranthus* subsp. *acranthus.*

Studies of the allied genus *Weberbauerocereus* in southern Peru (Sahley 1996), confirm the presence of bats and hummingbirds interacting with the species *W. weberbaueri*. Because bat and hummingbird floral syndromes share several characteristics, evolutionary transitions between these syndromes within a plant lineage may occur relatively frequently (Helverson 1993).

Attracted by the abundant pollen of *Haageocereus* flowers, small colleoptera and diptera have been found within the perianth, among stamens, but not inside the nectar-chamber, which is closed by the filaments and thus inaccessible for these visitors that need special long tongues to obtain the nectar. Moth pollination could also be considered, due to the nocturnal and relatively long tubular receptacle of *Haageocereus* flowers, and also to their sweet smell. In relation to this, there is one photograph from Rauh (Backeberg 1960) showing a moth visiting a *Haageocereus* flower.

Another remarkable feature of *Haageocereus* flowers is the marked curvature of the flower tube in some species, namely *H. tenuis* and *H. repens*. These plants have prostrate and semi-prostrate habit and it is probable that the angle of presentation of the flower may be related to the right pollinator. Such flowers have a relatively large nectar chamber, suggesting bat pollination, a strategy that possibly facilitates the access to nectar by the pollinator, which reaches the nectar chamber with its body oriented horizontally.

In relation to flower symmetry, *Haageocereus* flowers typically have a radially symmetrical perianth, discounting that the tubular receptacle may be slightly to markedly curved, and in a few flowers of *H. pseudomelanostele* subsp. *carminiflorus,* a tendency towards a zygomorphic perianth has been observed.

The flowers of *Espostoa melanostele*, when open, exhibit a radial perianth resembling *Haageocereus*. *E. melanostele* also presents noctural flowers, but developing from a lateral

cephalium in contrast to *Haageocereus*. In this case nocturnal pollinators would have a role transferring pollen between these taxa and producing intergeneric hybrids. For instance, *H. pseudomelanostele* subsp. *carminiflorus* and *H. pseudomelanostele* subsp. *acanthocladus* have produced inter-generic hybrids with *Espostoa melanostele*. These hybrids are recognized under the genus ×*Haagespostoa* (See **Appendix 2**: List of names of *Haageocereus* (and *Peruvocereus*) possibly referring to ×*Haagespostoa*), and such plants seem to be stronger than their parents. In the valleys of Santa Eulalia and Pativilca, populations of hybrids are very well represented, it sometimes being difficult to find the parent *Haageocereus* species.

There is no evidence of intrageneric hybridization in the few cases of sympatry amongst *Haageocereus* species.

Dispersal

Fruits are mostly indehiscent, with one exception in *H. pseudomelanostele* subsp. *turbidus*, which opens by a lateral slit. The thin pericarp is reddish, a character that makes the fruits easy to see at a distance. The funicular pulp is characteristically solid and white, but in *H. tenuis*, the pulp is translucent, somewhat liquid and pink. *Haageocereus* fruits are moderately to very sweet and are also a source of liquid, which makes them very attractive to birds.

When fruits are damaged and then, the funicular pulp is exposed, the sweet pulp may attract ants, which may play a role as dispersal together with birds (ornitho-myrmecochorus strategy), as it occurs in other genera, like *Cereus* (Barthlott & Hunt 1993).

Haageocereus seeds present a striate cuticle, and testa cells with low-domed convexities towards the peripheral border of the seeds and, in one case, par-convexities. All these

characters could be associated with seed transportation by ants, as has been suggested for *Pilosocereus aureispinus* (Zappi 1994).

In a few cases, seed dispersal by wind may affect those seeds that remain attached to the dry fruit's pericarp.

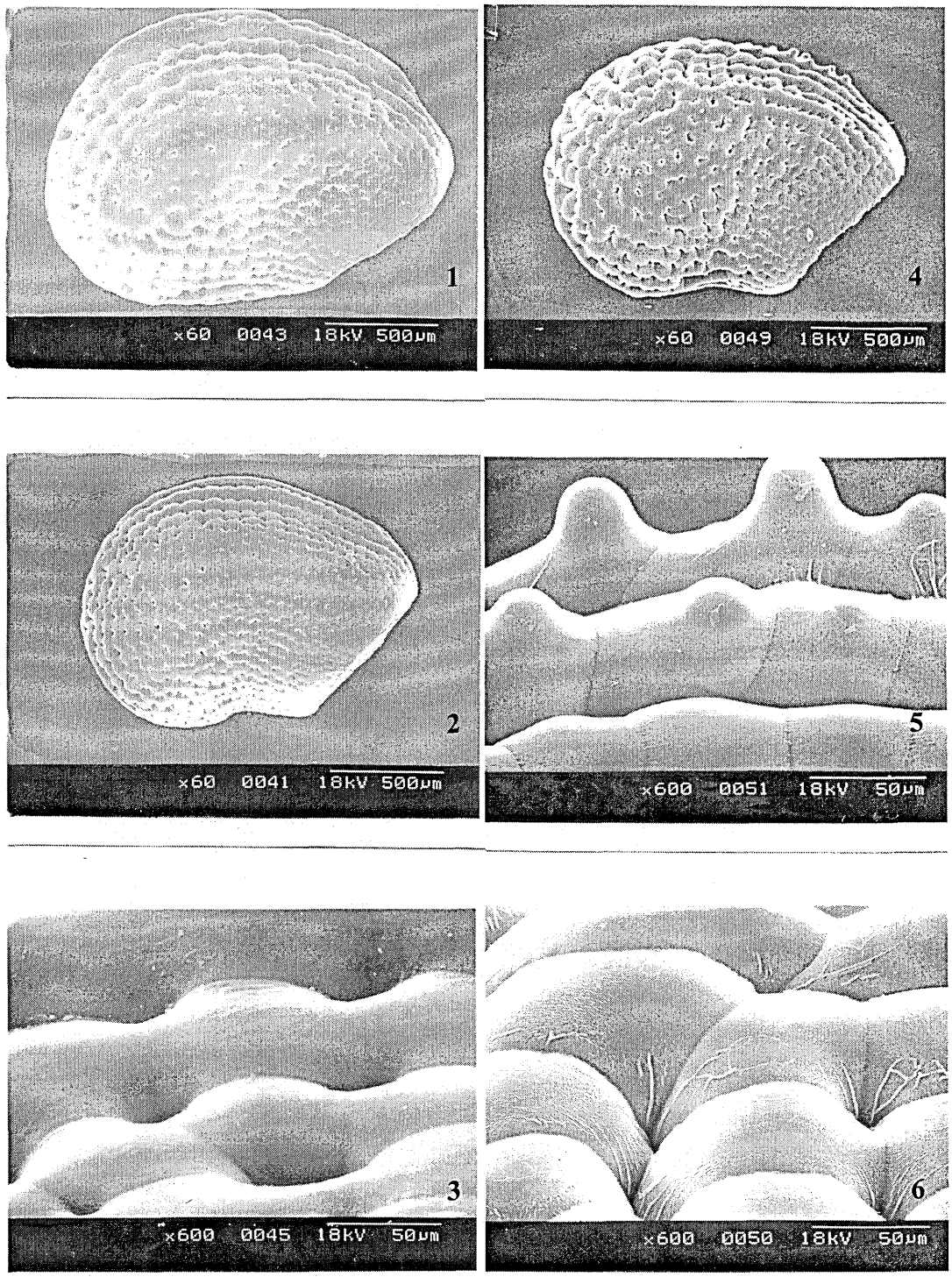


Plate 1. SEMs of seeds. **1.1** *Haageocereus acranthus* subsp. *acranthus. N. Calderón* 211, side view. **1.2** *Haageocereus acranthus* subsp. *backebergii. N. Calderón* 111, side view. **1.3** *Haageocereus acranthus* subsp. *acranthus. N. Calderón* 211, detail of testa surface, microrelief without striations. **1.4** *Haageocereus acranthus* subsp. *zonatus, N. Calderón* 379, side view. **1.5** *Ibid.*, detail of peripheral region with par-convexities. **1.6** *Ibid.*, detail of testa surface, microrelief weakly-striated.

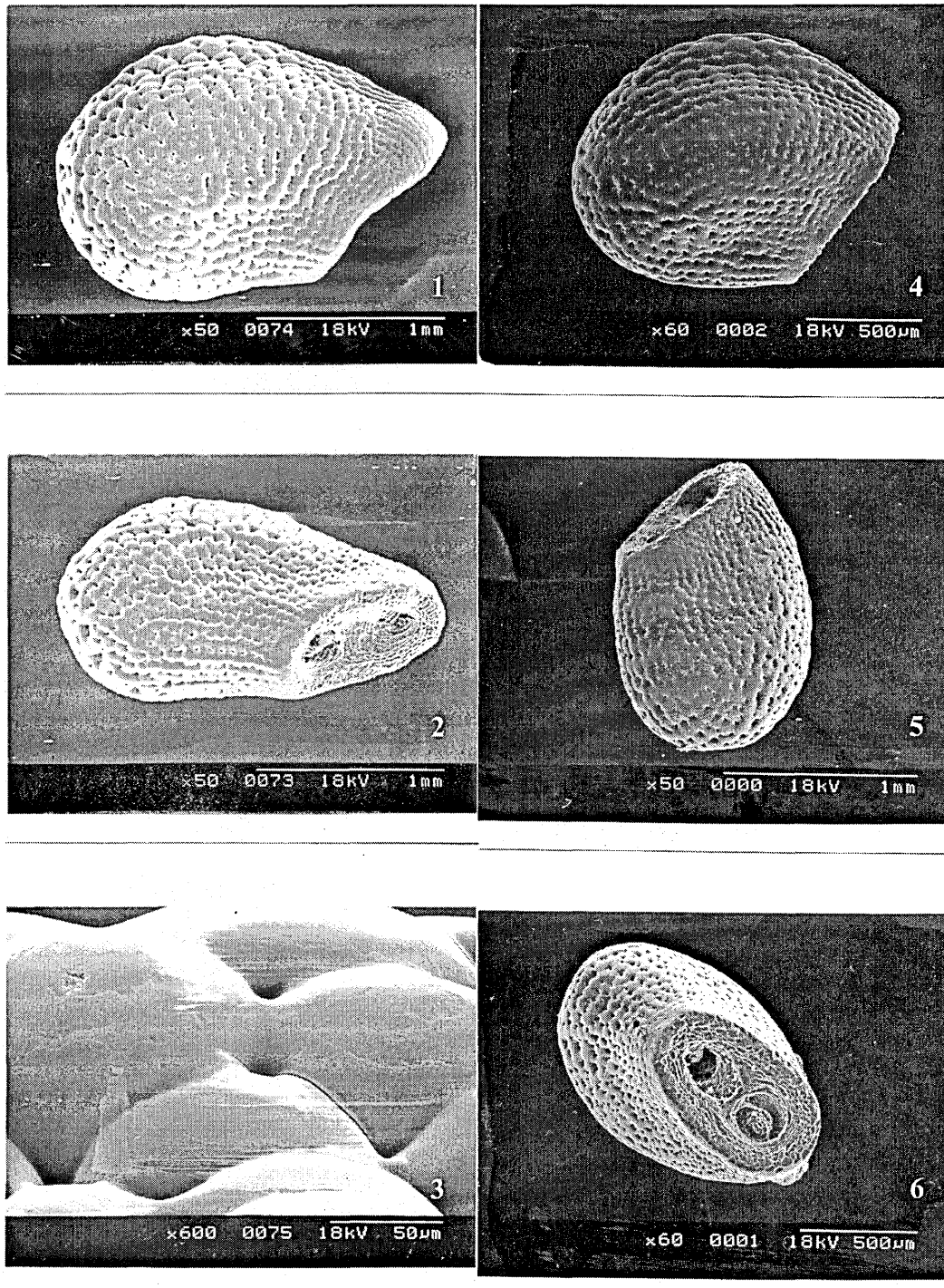


Plate 2. SEMs of seeds. **2.1** *Haageocereus chilensis. F. Ritter* 601, side view. **2.2** *Ibid.*, detail of hilum-micropylar region (HMR). **2.3** *Ibid.*, detail of testa surface, microrelief without striations. **2.4** *Haageocereus decumbens. N. Calderón* 414, side view. **2.5** *Ibid.* **2.6** *Ibid.*, detail of hilum-micropylar region (HMR).

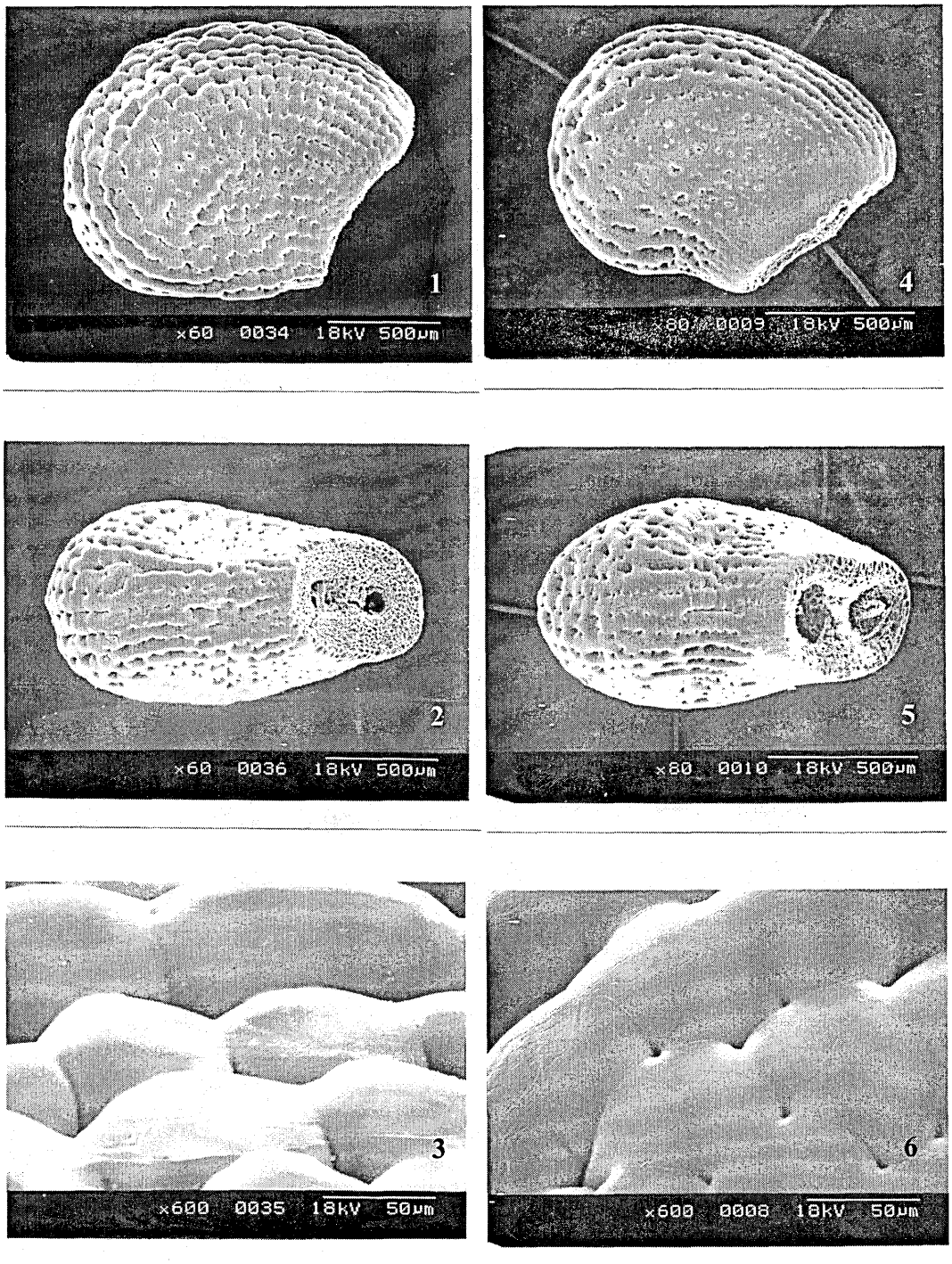


Plate 3. SEMs of seeds. **3.1** *Haageocereus platinospinus. N. Calderón* 404, side view. **3.2** *Ibid.*, detail of hilum-micropylar region (HMR). **3.3** *Ibid.*, detail of testa surface, microrelief without striations. **3.4** *Haageocereus pseudomelanostele* subsp. *pseudomelanostele. N. Calderón* 361, side view. **3.5** *Ibid.*, detail of hilum-micropylar region (HMR). **3.6** *Ibid.*, detail of testa surface, microrelief without striations.

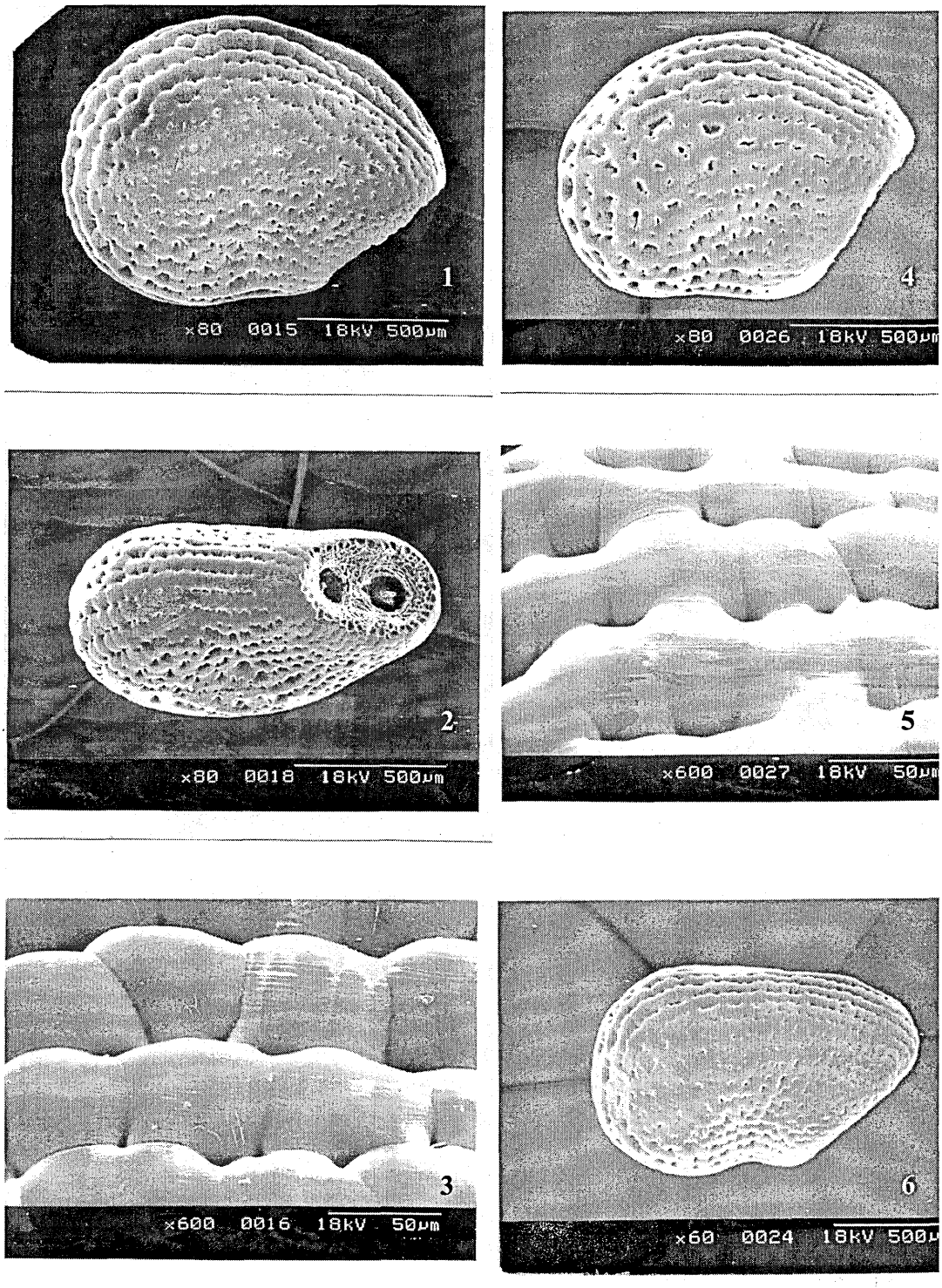


Plate 4. SEMs of seeds. **4.1** *Haageocereus pseudomelanostele* subsp. *carminiflorus. N. Calderón* 298a, side view. **4.2** *Ibid.*, detail of hilum-micropylar region (HMR). **4.3** *Ibid.*, detail of testa surface, microrelief without striations. **4.4** *Haageocereus pseudomelanostele* subsp. *acanthocladus. N. Calderón* 372, side view. **4.5** *Ibid.*, detail of testa surface. **4.6** *Haageocereus pseudomelanostele* subsp. *turbidus. N. Calderón* 276, side view.

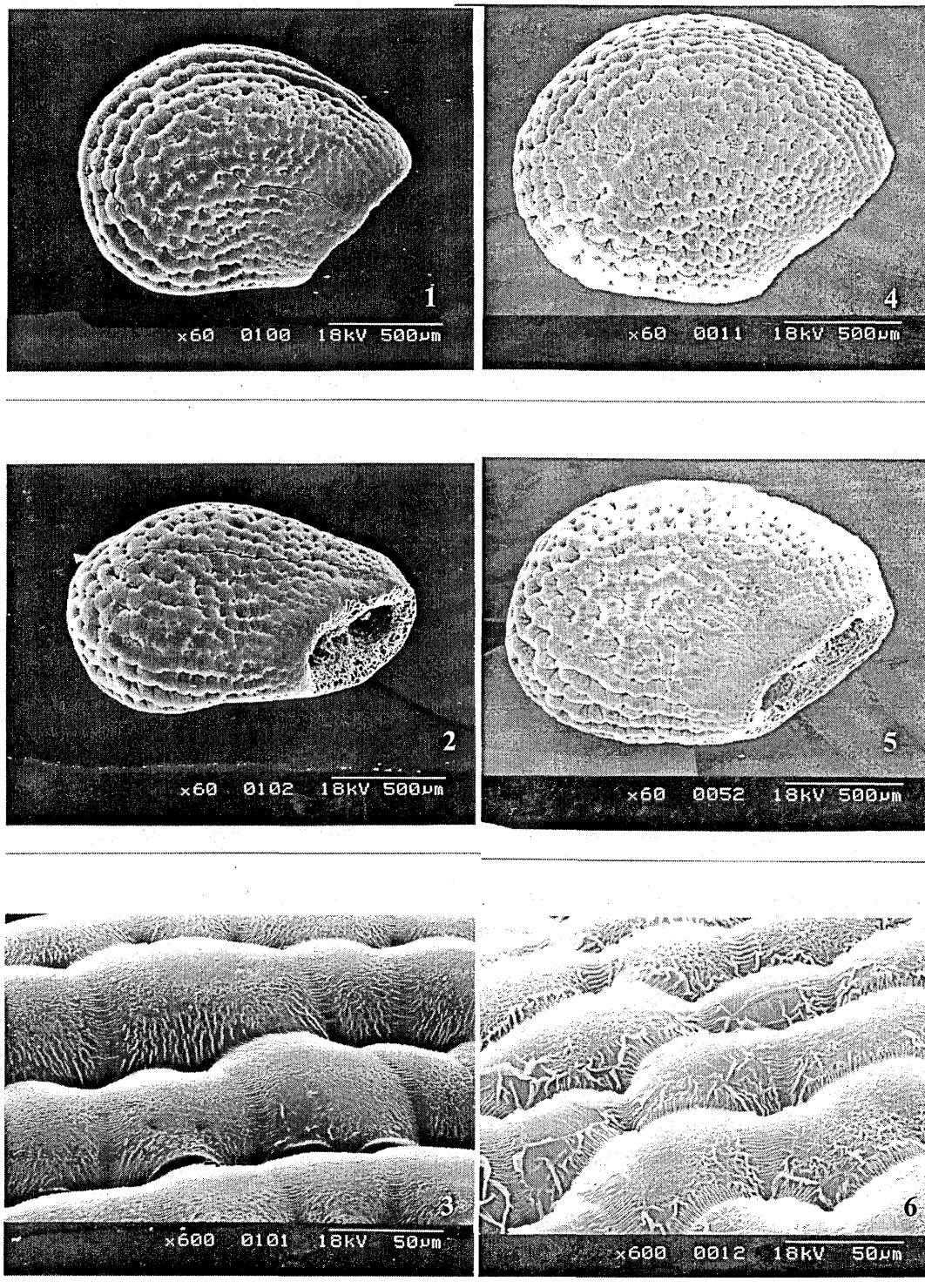


Plate 5. SEMs of seeds. **5.1** *Haageocereus repens. G. Charles* 254.01, side view. **5.2** *Ibid.*, detail of hilum-micropylar region (HMR). **5.3** *Ibid.*, detail of testa surface, microrelief with strong cuticular striations. **5.4** *Haageocereus tenuis. N. Calderón* 371, side view. **5.5** *Ibid.*, detail of hilum-micropylar region (HMR). **5.6** *Ibid.*, detail of testa surface, microrelief with strong cuticular striations.

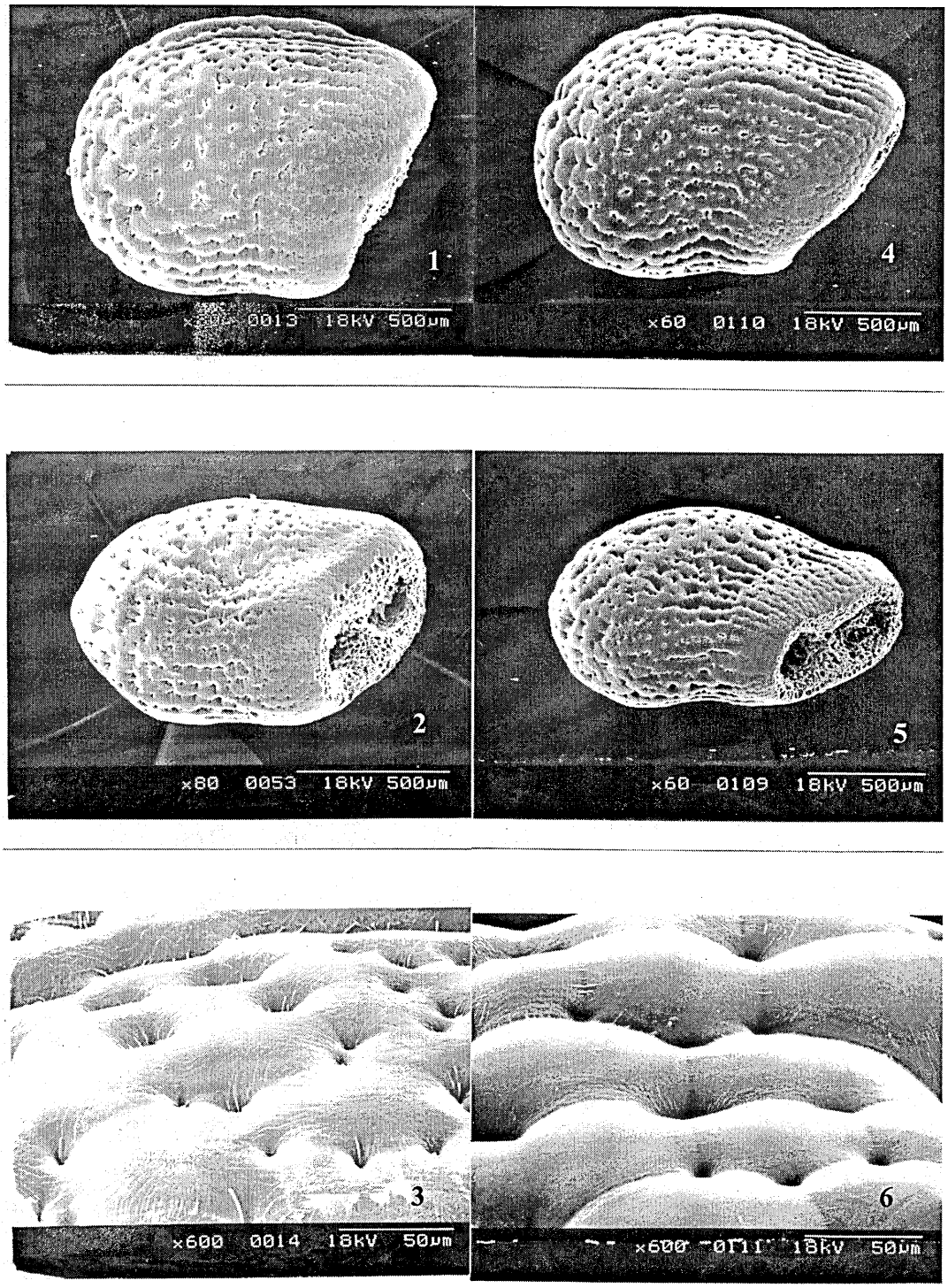


Plate 6. SEMs of seeds. **6.1** *Haageocereus versicolor* subsp. *versicolor. N. Calderón* 355, side view. **6.2** *Ibid.*, detail of hilum-micropylar region (HMR). **6.3** *Ibid.*, detail of testa surface, microrelief weakly striated. **6.4** *Haageocereus versicolor* subsp. *pseudoversicolor. G. Charles* 256.02, side view. **6.5** *Ibid.*, detail of hilum-micropylar region (HMR). **6.6** *Ibid.*, detail of testa surface, microrelief without striations.

Taxonomic treatment

The present treatment includes all taxa of *Haageocereus* (9 species and 9 subspecies) including their nomenclature and synonyms, details on typification, morphological descriptions, habitat, distribution, conservation status and further comments. Dichotomous keys for species and subspecies are also presented. Descriptions and keys include measurements connected by a multiplications sign (×) referring to the length (or height) followed by the width (or diameter), and, in the case of seeds, followed by the thickness.

Nomenclatural innovations that are presented in this work such as new names, types, synonyms, etc., are not effectively published in the thesis itself and are to be regarded as provisional and invalid under the International Code of Botanical Nomenclature (St Louis Code) Art 7.10 & 34.1 (ICBN 2000).

***Haageocereus* Backeb.,** Blätt. Kakt.-forsch. 1934(6): unpaged (1934a); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 368 (1958); Backeb., Die Cact. 2: 1159 (1960); Krainz, Die Kakteen 16(4): CVa, unpaged (1973). Type species: *Haageocereus pseudomelanostele* (Werderm. & Backeb.) Backeb. (1934a).

Binghamia Britton & Rose, Cact. 2: 167 (1920), pro parte, non *Binghamia* J. Agardh, Analecta Algologica 2: 63 (1894); ibid. 5: 158 (1899).

Peruvocereus Akers, Cact. Succ. J. (US) 19: 67 (1947).

Etymology of *Haageocereus* Backeb. (1934): From *Haage*, the surname of a famous German family of cactus nurserymen, and *Cereus*, meaning torch or candle-like in appearance.

Shrubby, branches terete, prostrate to erect, branching mainly at base; vascular cylinder weakly woody; tissues mostly mucilaginous; epidermis green, smooth or with a translucent waxy cover; ribs 10–24, straight. Areoles with felt, spination variable. Spines mostly

straight, opaque, rarely bearing trichomes. Flowering areoles, slightly to strongly differentiated by persistent white trichomes, sometimes seen as a ring-like pseudocephalium. Flowers crepuscular-nocturnal, appearing close to the apex of the stem, 4.0–11.5 × 2.5–8.0 cm, perianth-limb regularly symmetric; tube straight to markedly curved, green or reddish green, striated, covered by bract-scales and hair-spines emerging from their axils; outer perianth-segments thick, greenish to red; inner perianth-segments delicate, white, pinkish or red; nectar-chamber tubular, slightly swollen, protected by the innermost stamens; stamens 200–400, anthers 1.6–6.0 × 0.4–2.0 mm, ± verrucose; style 34.7–78.0 × 0.8–2.5 mm, stigma-lobes 9–13, 2.3–8.0 mm, exserted or included in relation to the anthers; ovary locule 3.6–12.0 × 3.5–11.0 mm, circular to elliptic in longitudinal section. Fruit 2.0–6.5 × 1.3–5.6 cm, spherical to ovoid, indehiscent or rarely dehiscent by a lateral slit, floral remnants persistent, blackening, erect or pendent, pericarp pinkish or red, covered by few small bract-scales with axillary trichomes; funicular pulp solid to mucilaginous, mostly white or translucent pink. Seeds broadly oval to oval, small to medium-size, 1.09–1.87 × 0.79–1.36 × 0.62–1.04 mm, glossy to semi-matt, blackish; border expanded around hilum; cells gradually smaller towards hilum and enlarged at the periphery, isodiametric, anticlinal boundaries channelled, straight; cell junctions cratered forming 'interstices'; relief convex, convexities low-domed and par-convex; microrelief non-striated to strongly-striated; hilum large, 0.34–0.86 mm, oblique, impressed, micropyle conjunct, but separated by sclerified band, hilum-micropylar region (HMR) oval.

Distribution: Along the western side of Peru and northern Chile, including coastal arid areas from 50 m alt. to western Andean valleys at 3000 m alt. (Pacific drainage). Northernmost limit in Morropón, Peru (79°54'W, 5°7'S) for the species *Haageocereus versicolor*; and the southernmost limit in Camiña, Chile (69°25'W, 19°18'S) for the species *Haageocereus chilensis*.

Key for the identification of *Haageocereus* species

1. Branches prostrate, with ascending apices 5.0–10.0 cm above the ground (coastal deserts, 50–620 m) **2**

   Branches upright, if semi-prostrate with part of branches erect ≥20.0 cm above the ground (coastal deserts, seasonally dry forest and west Andean valleys, 50–3000 m) **4**

2. Spines bearing trichomes, sometimes only visible with help of hand lens **3**

   Spines without trichomes ..... 3. ***H. decumbens***

3. Trichomes on the spines visible with lens; central spine 1–2; flower (6.5–)8.0–11.5cm long ..... 8. ***H. tenuis***

   Trichomes on the spines easily visible by the naked eye; central spine 0; flower 5.0 cm long. ..... 4. ***H. lanugispinus***

4. Radial spines 7–20 (southern Peru and northern Chile, 1000–3000 m) **5**

   Radial spines (21–)25–56 (central and northern Peru, 50–2800 m) **6**

5. Radial spines 7–10(–11), (10.0–)15.0–40.0 mm (southern Peru and northern Chile, 2000–3000 m) ..... 2. ***H. chilensis***

   Radial spines (12–)14–20, 4.6–10.0 mm (southern Peru, 1000–2600 m) ..... 5. ***H. platinospinus***

6. Ribs 10–15; epidermis easily observed between spines ..... 1. ***H. acranthus***

   Ribs 16–24; epidermis difficult to observe, obscured by spines **7**

7. Flowering areoles well differentiated, with tufts of white wool, generally disposed in ring-like pseudocephalia around the stem, persistent ..... 9. ***H. versicolor***

   Flowering areoles not clearly differentiated **8**

8. Branches erect; flower-tube slightly curved; seeds with microrelief non-striated to weakly-striated (SEM) ..... 6. ***H. pseudomelanostele***

   Branches semi-prostrate; flower-tube markedly curved; seeds with microrelief strongly-striated (SEM) ..... 7. ***H. repens***

1. *Haageocereus acranthus* (Vaupel) Backeb., Backeb. & F. M. Knuth, Kaktus-ABC: 207 (1935, publ. 1936); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 374 (1958); Backeb., Die Cact. 2: 1176 (1960). *Binghamia acrantha* (Vaupel) Britton & Rose, Cact. 2: 168 (1920). *Cereus acranthus* Vaupel in Engler Bot. Jahrb. Syst. 50(111): 14 (1913). Type: Peru, Lima, Rímac valley, Santa Clara, Lima–La Oroya road, Loma formation, 400–600 m, 26 October 1902, *Weberbauer* 1679 (B photo!).

H. olowinskianus Backeb., Blätt. Kakt.-forsch. 1937(5): unpaged (1937). *H. acranthus* subsp. *olowinskianus* (Backeb.) Ostolaza, Cact. Succ. J. (US) 67: 9 (1995a); Cact. Consensus Initiatives 6: 8 (1998a). Type locality: Peru, Lima (believed not to have been preserved). Lectotype (designated here): Backeb., Blätt. Kakt.-forsch. 1937(5): unpaged, photo (1937). **Synon. nov.**

H. olowinskianus var. *repandus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ. 1957). Type: Peru, Lima, desert areas, Pachacámac, 100 m, 1956, *Rauh* K177 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1188, fig. 1141 (1960). **Synon. nov.**

H. olowinskianus var. *repandus* subvar. *erythranthus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ. 1957). Type: believed not to have been preserved. Neotype (designated here): Backeb., Die Cact. 2: 1213, fig. 1171, bottom right (1960). **Synon. nov.**

H. olowinskianus var. *subintertextus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ. 1957). Type: Peru, Lima, Pachacámac, 1956, *Rauh* K177b (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1189, fig. 1143 (1960). **Synon. nov.**

H. lachayensis Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957). Type: Peru, Lima, Chancay, Lomas de Lachay, 1954, *Rauh* K5 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1177, fig. 1130 (1960).

H. limensis (Salm-Dyck) sensu Ritter, Kakt. Südam. 4: 1396 (1981), non *Cereus limensis* Salm-Dyck, A. Gartenz 13(45): 353 (1845b). Type: believed not to have been preserved.

H. clavispinus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21(1956, publ. 1957). *H. acranthus* ssp. *olowinskianus* forma *clavispinus* (Rauh & Backeb.) Ostolaza, Cact. Succ. J. (US) 67: 10 (1995). Type: Peru, east of Lima, Lomas de Atocongo, 200 m, 1956, *Rauh* K44 (ZSS iso T23411!).

H. vulpes Ritter, Kakt. Südam. 4: 1423 (1981). Type: Peru, Lima, Chancay, *Ritter* FR1059 (U holo!, ZZS seeds!). **Synon. nov.**

?H. olowinskianus var. *rubriflorior* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ. 1957). *H. olowinskianus* var. *subintertextus* subvar. *rubriflorior* Rauh & Backeb. in Rauh Beitr. Kenntn. Peruan. Kakt. veg.: 387 (1958), nom inval. (Art. 33.2, ICBN 2000), based on *H. olowinskianus* var. *rubriflorior*. *H. acranthus* var. *olowinskianus* forma *rubriflorior* (Rauh & Backeb.) Ostolaza, Brit. Cact. Succ. J. 14(4): 167 (1996). Type: Peru, Lima, Pachacámac, 1956, *Rauh* K177a (HEID, believed not to have been preserved).

Habit erect, branching at base, up to 1.55 m tall; branches 4.0–8.5 cm diam., epidermis green; ribs 10–15, 11.6–18.6 × 6.2–13.0 mm. Areoles 6.0–11.2 × 5.0–8.3 mm, 4.8–16.5 mm apart, oval to circular, felt yellow and grey. Spines, opaque, at first yellow and brown, later grey; central spines 1–2(–3), 7.4–55.0 × 0.8–1.9 mm at base; radial spines (21–)25–50, 3.0–15.4 × 0.2–0.7 mm at base. Flowering areoles not differentiated to markedly woolly. Flowers 7.0–10.0 × 3.5–7.5 cm; pericarpel 9.0–16.5 × 12.0–19.4 mm; tube 4.0–6.5 × 0.9–2.0 cm at base, widening towards apex to 2.25–3.0 cm diam., slightly curved, green, bearing hair-spines emerging from the bract-scale axils; outer perianth-segments 10–14, 18.0–29.0 × 4.0–8.6 mm, greenish; inner perianth-segments 10–24, 21.7–27.0 × 5.7–9.0 mm, white, pinkish or reddish; nectar-chamber 10.0–28.0 × 4.2–10.0 mm, tubular; anthers 2.8–6.0 × 0.6–1.3 mm; style 55.0–78.0 × 1.0–2.5 mm; stigma-lobes 10, 3.8–5.0 mm; ovary locule 4.0–12.0 × 4.6–11.0 mm, cylindric to elliptic in longitudinal section. Fruit 2.0–5.3 × 2.6–5.5 cm,

spherical to ovoid. Seeds broadly oval, medium-size, 1.36–1.62 × 1.06–1.28 × 0.73–0.93 mm, glossy; relief (SEM) convex and sometimes par-convex towards border; microrelief ± striated; hilum large, 0.59–075 mm, oblique, forming an angle of 26°–44° with long axis of seed.

Habitat and Distribution: Desert areas and rocky hillsides of valleys of Lima (100–2800 m) and arid valleys in Ica (863 m), (**Map 2**).

Conservation status: Vulnerable. VU[A4c]. An inferred population size reduction of ≥30% over ten years, including both past and future time period, where the causes of its reduction have not ceased and it is observed a decline in the area of occupancy, extent of occurrence and the quality of habitats (particularly those close the vicinity of Lima).

Comments:

The type of this species is one of the two important Weberbauer collections of *Haageocereus* held at the Berlin Herbarium. The specimen of *Cereus acranthus* Vaupel, collected by Weberbauer in 1902, was believed to be destroyed during the Second World War together with other important Cactaceae collections; fortunately these specimens were kept in the general spirit collection, surviving the war but remaining unnoticed until Leuenberger (1978) rediscovered them.

Britton & Rose included this species within *Binghamia*; however, the use of this generic name was left as it already belonged to an algae genus. Backeberg (1936) combined this species as *Haageocereus acranthus* (Vaupel) Backeb., but included in his concept other taxonomic entities that will be treated in this study as *H. acranthus* subsp. *backebergii.*

Ritter (1981) believed this species was in fact the long lost *Cereus limensis* Salm-Dyck (1845b), and published the combination *Haageocereus limensis* (Salm-Dyck) Ritter. However, the scant description and non-existent type of *C. limensis* Salm-Dyck prevents attribution of the name to the present species and it is considered a doubtful name (See **Appendix 2**: List of doubtful names attributed to the genus *Haageocereus*).

Haageocereus acranthus is characterized by conspicuous areoles (10.0–11.0 mm diam.) subtended by transverse rib-folds related with the formation of podaria, erect growth pattern, and some flowers (*H. acranthus* subsp. *backebergii* and *H. acranthus* subsp. *zonatus*) present the flower-tube covered by bract-scales subtended by decurrent podaria (**Plates 8.3, 8.4**).

In terms of both height and diameter of stems, this species is highly conspicuous within the genus, and its populations are restricted to the central coast and central-western valleys in Peru, being most diversified in Lima. *Haageocereus acranthus* is subdivided into three subspecies: *H. acranthus* subsp. *acranthus*, *H. acranthus* subsp. *zonatus* and *H. acranthus* subsp. *backebergii*.

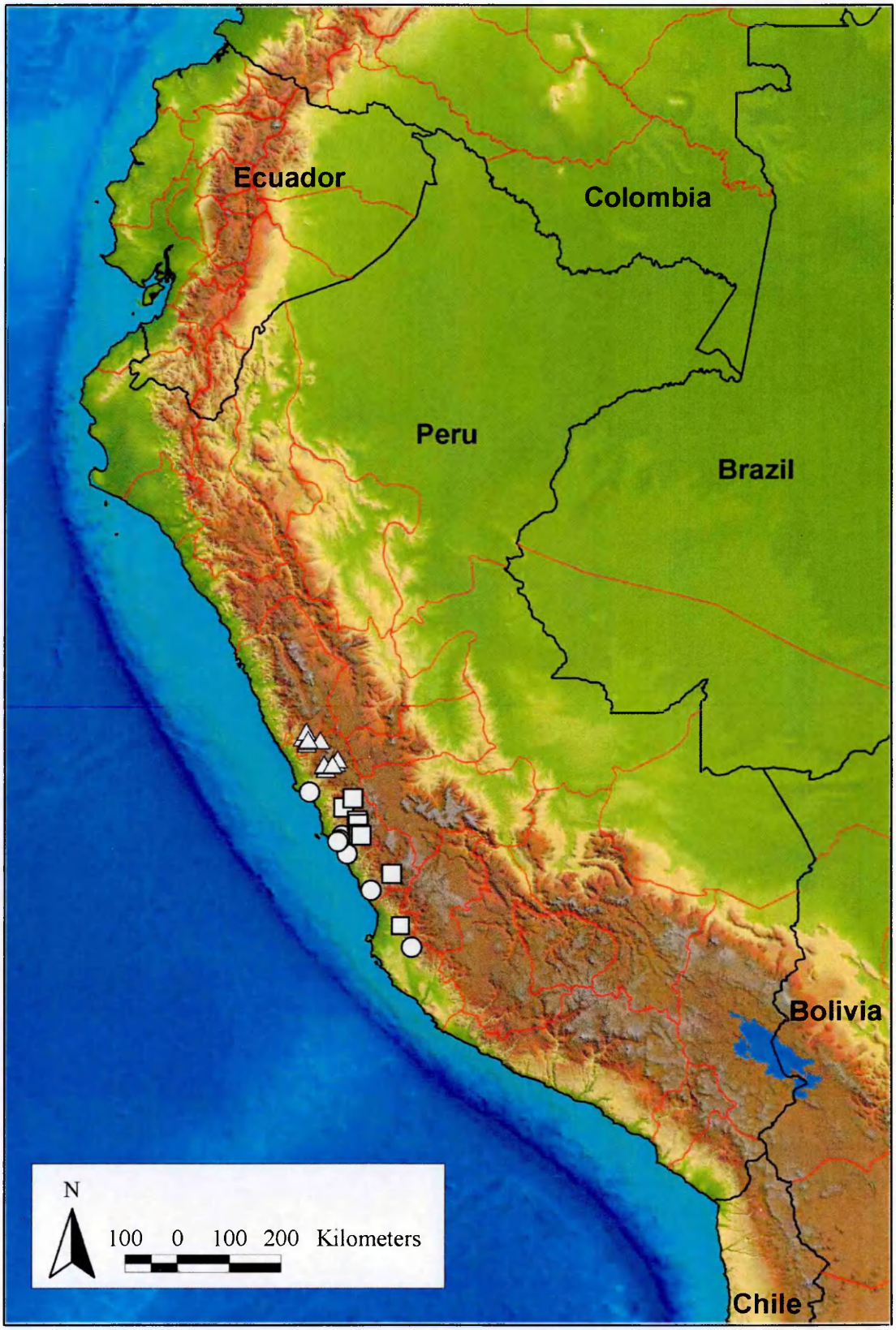
Key to subspecies of *Haageocereus acranthus*

1. Flowering areoles well differentiated, woolly, white, generally disposed in ring-like pseudocephalia; flower-tube covered by abundant white trichomes; seed relief with few (2–8) par-convex structures, testa-cell walls (SEM) with microrelief regularly and finely striated (northern Lima: Huaura and Pativilca valleys, 1520–2600 m) ..... **1c. *H. acranthus* subsp. *zonatus***

   Flowering areoles not clearly differentiated; flower-tube not covered by abundant white trichomes; seed relief without par-convex structures, testa-cell walls (SEM) without microrelief (central and southern Lima: Rímac, Lurín, Chillón and Santa Eulalia valleys, 100–2800 m; Ica: Ica valley, 863 m) **2**

2. Radial spines 30–50, covering rib edges; flower-tube covered by flat bract-scales (Lima: Lurín and Cañete valleys and deserts, 100–230 m; Ica: Ica valley, 863 m)..... **1a. *H. acranthus* subsp. *acranthus***

   Radial spines (21–)25–37, not covering rib edges; flower-tube covered by bract-scales subtended by decurrent podaria (Lima: Chillón, Rímac, Lurín and Cañete valleys, 1260–2800 m) ..... **1b. *H. acranthus* subsp. *backebergii***



Map 2. *Haageocereus acranthus* subsp. *acranthus* = ○; *Haageocereus acranthus* subsp. *backebergii*= □; *Haageocereus acranthus* subsp. *zonatus*=△.

1a. *Haageocereus acranthus* subsp. *acranthus*

Habit up to 1.4 m tall; branches 4.0–7.0 cm diam.; ribs 12–14, 11.6–18.6 × 6.2–13.0 mm. Areoles 6.0–10.0 × 5.0 mm diam., 4.8–7.8 mm apart. Central spines 1–2, 15.0–50.0 × 1.0–1.5 mm at base; radial spines 30–50, 5.0–14.0 × 0.2–0.5 mm at base. Flowering areoles not differentiated. Flowers 7.5–9.7 × 4.2–5.5 cm; pericarpel 12.0–16.5 × 12.0–17.4 mm; tube 4.4–6.5 × 0.9 cm at base, widening towards apex to 2.25 cm diam., bearing short brownish hair-spines emerging from the bract-scale axils; outer perianth-segments 12, 18.0–26.0 × 4.0–7.0 mm, greenish; inner perianth-segments 22, 22.0–27.0 × 5.7–9.0 mm, white, pinkish or reddish; nectar-chamber 10.0–28.0 × 6.0–10.0 mm, tubular; anthers 2.8–5.4 × 0.6–0.9 mm; style 59.0–78.0 × 1.1–1.3 mm; stigma-lobes 10, 4.9 mm; ovary locule 4.6–12.0 × 4.6–11.0 mm, cylindric to elliptic in longitudinal section. Fruit 2.0–5.3 × 2.6–4.2 cm. Seeds 1.62 × 1.28 mm, 0.93 mm thick, glossy; relief (SEM) convex; microrelief without cuticular striations; hilum large, 0.63 mm, oblique, forming an angle of 64° with long axis of seed **(Fig. 2, Plates 1.1, 1.3, 7.1–7.3)**.

Examined material: PERU. LIMA: Rímac valley, Santa Clara, Lima–La Oroya road, Loma formation, 400–600 m, 26 Oct. 1902, *Weberbauer* 1679 (B type, photo); East of Lima, Lomas de Atocongo, 200 m, 1956, *Rauh* K44 (ZSS T23411); Cerros Caracoles, Km 55 Panamericana Sur, 100 m, 1 Dec. 1980, *C. Ostolaza* 20 (USM); Lurín valley, Manchay, Km 7 Lima–Cieneguilla road, 76°51'57''W, 12°8'26''S, 200 m, Jan. 2001, *N. Calderón* 67 (Herb. B. G. La Molina); Cardal, 230 m, 20 Feb. 2002, *N. Calderón* 211, 213 (Herb. B. G. La Molina); ICA: Ica valley, 75°35'56''W, 14°0'59''S, 863 m, 2005, *O. Whaley*, photo.

Habitat and Distribution: Desert areas and rocky hillsides of valleys on the coast of Lima (100–600 m) and arid valleys in Ica (863 m), **(Map 2)**.

Phenology: *Flowers:* January; *Fruits:* February.

Conservation status: Endangered. EN[B1ab(ii,iii,iv)]. The extent of occurrence is estimated to be 2435.76 km^2, and is severely fragmented; continuing decline was observed in the area of occupancy, the quality of habitats and the number of subpopulations.

This subspecies grows in the proximity of Lima city, facing the constant and increasing threat of habitat loss, which already caused the disappearance of populations at Cajamarquilla, which were illustrated by Weberbauer (1945), and Santa Clara in the Rímac valley. Less than 50 individuals are protected at the Reserva Nacional de Lachay (Lima). The negative impact of human expansion is visible in the seriously deteriorated health of the cacti observed at Picapiedra and Cardal in the Lurín valley, which show spines and epidermis accumulating dust and, in some cases, plastic residue, a saddening situation accentuated by the dry weather in Lima, where rains are infrequent.

Comments:

Haageocereus olowinskianus Backeb. was considered by Ostolaza (1998a) as a subspecies of *H. acranthus*, and combined it as *H. acranthus* subsp. *olowinskianus*. By comparing the type-material of *H. acranthus* with the available illustration (lectotype) of *H. olowinskianus,* it became clear that this name is conspecific with *H. acranthus* subsp. *acranthus*.

A number of varieties and subvarieties were created by Rauh & Backeberg (1957) who attempted to describe the slight differences within the natural variation of *H. olowinskianus*, such as *H. olowinskianus* var. *repandus* (stems prostrate at base), *H. olowinskianus* var. *repandus* subvar. *erythranthus* (flower reddish); *H. olowinskianus* var. *rubriflorior* (flower reddish) and *H. olowinskianus* var. *subintertextus* (overlapping spines). These taxa were based on slight differences and even variable characters, as underlined by studies of the plants in their habitat, and are not enough to grant them taxonomic status.

Rauh & Backeberg (1957) also described *H. lachayensis* (from "Lomas de Lachay") which type was not preserved but a neotype is proposed here, and *H. clavispinus* Rauh & Backeb. (club-shaped spines). It was not possible to find significant differences between these taxa and *H. acranthus* subsp. *acranthus*.

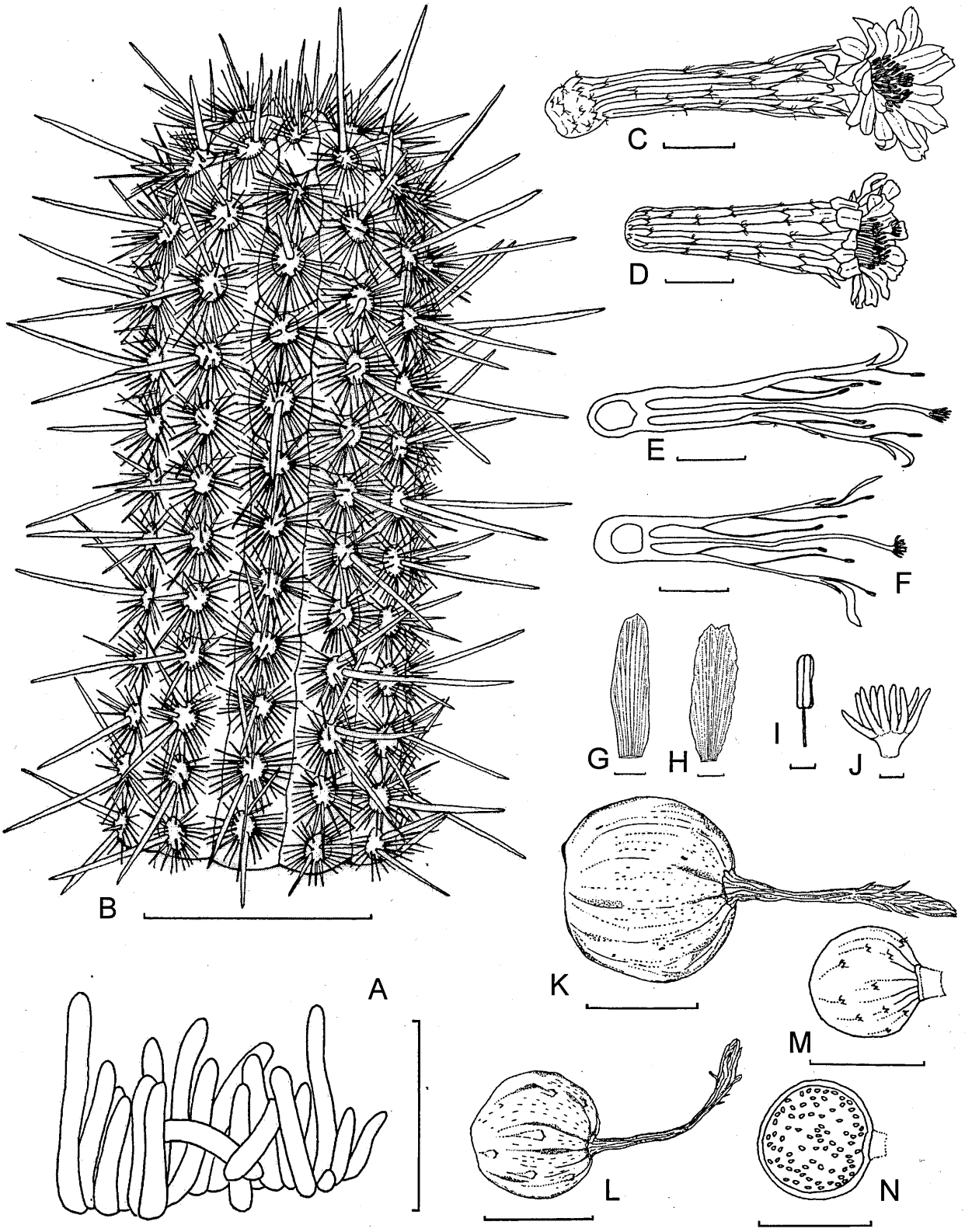


Fig. 2. *Haageocereus acranthus* subsp. *acranthus* (A, *N. Calderón* 211; B, *N. Calderón* 513; C, E, G, H, *N. Calderón* 224; D, F, I, J, M-N, *N. Calderón* 216; K-L, *N. Calderón* 213); A, habit (scale=50cm); B, stem (scale=6cm); C-F, flower, side view and longitudinal section (scale=2cm); G, outer perianth segment (scale=5mm); H, inner perianth segment(scale=5mm); I, anther (scale=1.5mm); J, stigma lobes (scale=1.5mm); K-N, fruits, side view, and longitudinal section (scale=3cm).

Plate 7. **7.1** *Haageocereus acranthus* subsp. *acranthus*. *N. Calderón* s.n., Cardal in the Lurín valley, 2001. **7.2** *Ibid.*, Picapiedra in the Lurín valley, 2001, in fruit. **7.3** *Ibid., N. Calderón* 213, Chillón valley, in bud and flower.

At the type locality of *H. clavispinus*, specimens with thicker central spines (≥1 mm thick) were observed, but this is not a unique character for this species and proved to be variable among the plants. It is proposed to follow Hunt (1999), who treated *H. clavispinus* Rauh & Backeb. and *H. lachayensis* Rauh & Backeb. as synonyms of *Haageocereus acranthus* (Vaupel) Backeb. subsp. *acranthus*.

H. vulpes Ritter (1981) is a taxon that refers to the same morphological characters of *H. acranthus* subsp. *acranthus* but for a different locality, in Chancay (close to *H. lachayensis* Rauh & Backeb.). The study of the type specimen as well as the SEM's of seeds of *H. vulpes* confirms that this name is better considered as a synonym of *H. acranthus* subsp. *acranthus*.

H. acranthus subsp. *acranthus* is characterized by erect columnar stems, relatively low rib number (12–14), thick greyish central spines (1.0–1.5 mm diam. at base), seed cuticle without striations (SEM), and undifferentiated flower-bearing areoles. The inner perianth-segments of the flower vary in colour from typically white to sometimes pinkish or reddish.

H. acranthus subsp. *acranthus* is sympatric with *H. pseudomelanostele* (Werderm. & Backeb.) Backeb., and can also be found growing with *Cleistocactus acanthurus* (Vaupel) Hunt, *Mila caespitosa* Britton & Rose (Cactaceae), *Tillandsia latifolia* Meyen (Bromeliaceae) and *Trixis cacalioides* D. Don (Asteraceae).

1b. *Haageocereus acranthus* subsp. *backebergii* N. Calderón subsp. nov. [ined.]. Holotype: East and above Chosica, in the Rímac valley, 1953, *Ritter* FR 145 (U 0008476!).

H. limensis var. *andicola* Ritter, Kakt. Südam. 4: 1397, diagn. lat. (1981). Type: as above.

H. acranthus var. *crassispinus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957); Die Cact. 2: 1177 (1960). Type: Peru, Ica. Cañete valley and Pisco valley,

1000 m, 1954, *Rauh* K31 (HEID, believed not to have been preserved). Neotype: Backeb., Die Cact. 2: 1182, fig. 1134 (1960). **Synon. nov.**

Habit up to 1.55 m tall, branching at base; branches straight, 5.1–7.6 cm diam.; ribs 10–13(–14), 11.6–18.6 × 6.2–13.0 mm. Areoles 8.0–11.2 × 5.0–8.1 mm, 7.0–16.5 mm apart. Central spines 1–2(–3), 7.4–28.7 × 1.0–1.9 mm at base; radial spines (21–)25–34, 3.0–6.8(–11.3) × 0.3–0.7 mm at base. Flowering areoles not differentiated. Flowers 7.0–8.4 × 3.5–6.0 cm; pericarpel 9.0–14.0 × 13.0–16.5 mm; tube 4.0–4.8 × 1.3–1.65 cm at base, widening towards apex to 2.4–2.5 cm diam., bearing short brownish hair-spines emerging from the bract-scale axils, being the bract-scales subtended by decurrent podaria; outer perianth-segments 10–12, 22.3–29.0 × 6.2–8.6 mm, green; inner perianth-segments 10–13, 21.7–26.0 × 7.2–8.3 mm, white; nectar-chamber 14.0–16.0 × 4.2–10.0 mm, tubular; anthers 2.9–4.0 × 0.8–1.0 mm; style 55.0–62.0 × 1.4–2.2 mm; stigma-lobes 10, 3.8–5.0 mm; ovary locule 4.0–8.0 × 7.0–9.5 mm, elliptic in longitudinal section. Fruit 2.3 × 2.9 cm. Seeds 1.36 × 1.06 mm, 0.73 mm thick, glossy; relief (SEM) convex; microrelief without cuticular striations; hilum large, 0.59 mm, oblique, forming an angle of 42° with long axis of seed (**Fig. 3, Plates 1.2, 8.1–8.4**).

Examined material: PERU. LIMA: Rímac valley, east and above Chosica, 1953, *Ritter* FR 145 (U holo 0008476); Km 70 Lima–La Oroya road, 2200 m, 14 April 1980, *C. Ostolaza* 47 (USM); Km 54 Lima–La Oroya road, 16 Feb. 2001, *N. Calderón* 89, 92 (Herb. B. G. La Molina); Km 55 Lima–La Oroya road, 76°31'34.8''W, 11°54'11.5''S, 1460 m, 19 Aug. 2005, *N. Calderón* 496, 497, 498, 499, 500 (Herb. B. G. La Molina); Santa Eulalia valley, Huinco, 1956, *Ritter* FR 145c (U holo 0008479); loc. cit. 1300 m, 6 March 2002, *N. Calderón* 240 (Herb. B. G. La Molina); loc. cit., Barba Blanca, 76°37'37.4''W, 11°50'51.8''S, 1400 m, 19 Aug. 2005, *N. Calderón* 510 (Herb. B. G. La Molina); Chillón valley, surroundings of Canta, 2700–2800 m, 3 July 1958, *R. Ferreyra* 12947 (USM); loc. cit., Umarcata hill, Km 69 Lima–Canta road, 76°46'54''W, 11°37'23.4''S, 1260 m, 8 March 2001, *N. Calderón* 110, 111a (Herb. B. G. La Molina); Lurín valley, Tinajas canyon, 76°37'40.7''W, 12°07'03.5''S, 1755 m, 24 July 2005, *N. Calderón* s.n., (Herb. B. G. La

Molina, photo), loc. cit., Antioquía–Langas road, 76°28'10.3''W, 12°06'14.2''S, 1804 m, 22 Oct. 2005, *N. Calderón* s.n. (Herb. B. G. La Molina, photo); Cañete valley, Cantera Baja, 75°56'42.6''W, 12°45'24.9''S, 1380 m, *C. Véliz*, photo.

Habitat and Distribution: Found in the Rímac, Chillón, Santa Eulalia, Lurín and Cañete valleys, all in Lima department (1260–2800 m), and Pisco valley in Ica department (1000 m), (**Map 2**).

Phenology: *Flowers:* February and August; *Fruits:* March and September.

Conservation status: Endangered. EN[B1ab(ii,iii,iv)]. The extent of occurrence is estimated to be 2379 km^2. It is known to exist at no more than five locations and continuing decline was observed in the area of occupancy, the quality of habitats and the number of subpopulations, especially in the Rímac and Santa Eulalia valleys.

Comments:

Backeberg (1936) misapplied the name *Haageocereus acranthus* to this taxon in the narrow sense. However, it is clearly different from the type of Vaupel's species, necessitating the creation of a new name for Backeberg's taxon at the rank of subspecies.

As noted in the discussion for *H. acranthus*, Ritter believed *Cereus limensis* Salm-Dyck was an earlier name for *H. acranthus* (Vaupel) Backeb. Ritter (1981) also recognized that the taxon misdetermined by Backeberg (1936) needed a new name and created *H. limensis* var. *andicola* Ritter to describe this taxon.

The present subspecific name is based on Ritter's *H. limensis* var. *andicola*, taking the opportunity to use a more appropriate epithet than Ritter's relatively meaningless choice of 'andicola'.

Rauh & Backeberg created *H. acranthus* var. *crassispinus* (1957) for a cactus with somewhat thicker and longer (to 3.0 cm) central spines than *H. acranthus*, found in the valleys of Cañete (Lima) and Pisco (Ica), and, as the type was not preserved, a neotype is being created in the present study from a later picture published by Backeberg (1960). The central spine

length of *H. acranthus* var. *crassispinus* is within the range of *H. acranthus* subsp. *backebergii* and therefore, there is not reason to consider this name as a different taxon. Studies in the type locality (Cañete valley) of *H. acranthus* var. *crassispinus* also confirm that this name is best recognised as synonym of *H. acranthus* subsp. *backebergii.*

H. acranthus subsp. *backebergii* is characterized by its few and short radial spines (21–)25–34, 3.0–6.8(–11.3) mm long, not covering the edges of the ribs. The flower-tube is covered by bract-scales subtended by podaria, bearing short brownish hair-spines in their axils.

In the Rímac valley, this taxon lives with other cacti, such as *Opuntia pascoensis* Britton & Rose, *Echinopsis peruviana* (Britton & Rose) Friedrich & Rowley and *Cleistocactus acanthurus* (Vaupel) Hunt, and with other plants such as *Trixis cacalioides* D. Don (Asteraceae), *Youngia* sp. (Asteraceae), *Acacia macracantha* Humb. & Bonpl. ex Willd. (Leguminosae), *Gaultheria* sp. (Ericaceae).

In the Chillón valley, it is sympatric with *H. pseudomelanostele* subsp. *acanthocladus* and shares its habitat with *Neoraimondia arequipensis* subsp. *roseiflora* (Werderm. & Backeb.) Ostolaza, *Melocactus peruvianus* Vaupel, *Mila nealeana* Backeb., *Cleistocactus acanthurus* (Vaupel) Hunt, *Austrocylindropuntia pachypus* (K. Schum.) Backeb. and *Espostoa melanostele* (Vaupel) Borg.; other succulent plants are *Cnidoscolus basiacanthus* (Pax & K. Hoffm.) J. F. Macbr. and *Jatropha macrantha* Müll. Arq. (both Euphorbiaceae).

In the Santa Eulalia valley, it is sympatric with *H. pseudomelanostele* subsp. *carminiflorus*, and other cacti such as *Espostoa melanostele*, *Cleistocactus acanthurus*, *Austrocylindropuntia pachypus* and ×*Haagespostoa.*

In the Tinajas canyon, of the Lurín valley, at 1755 m, it is also sympatric with *H. pseudomelanostele* subsp. *carminiflorus*, and also grows with other cacti such as *Espostoa melanostele* and *Cleistocactus acanthurus.*

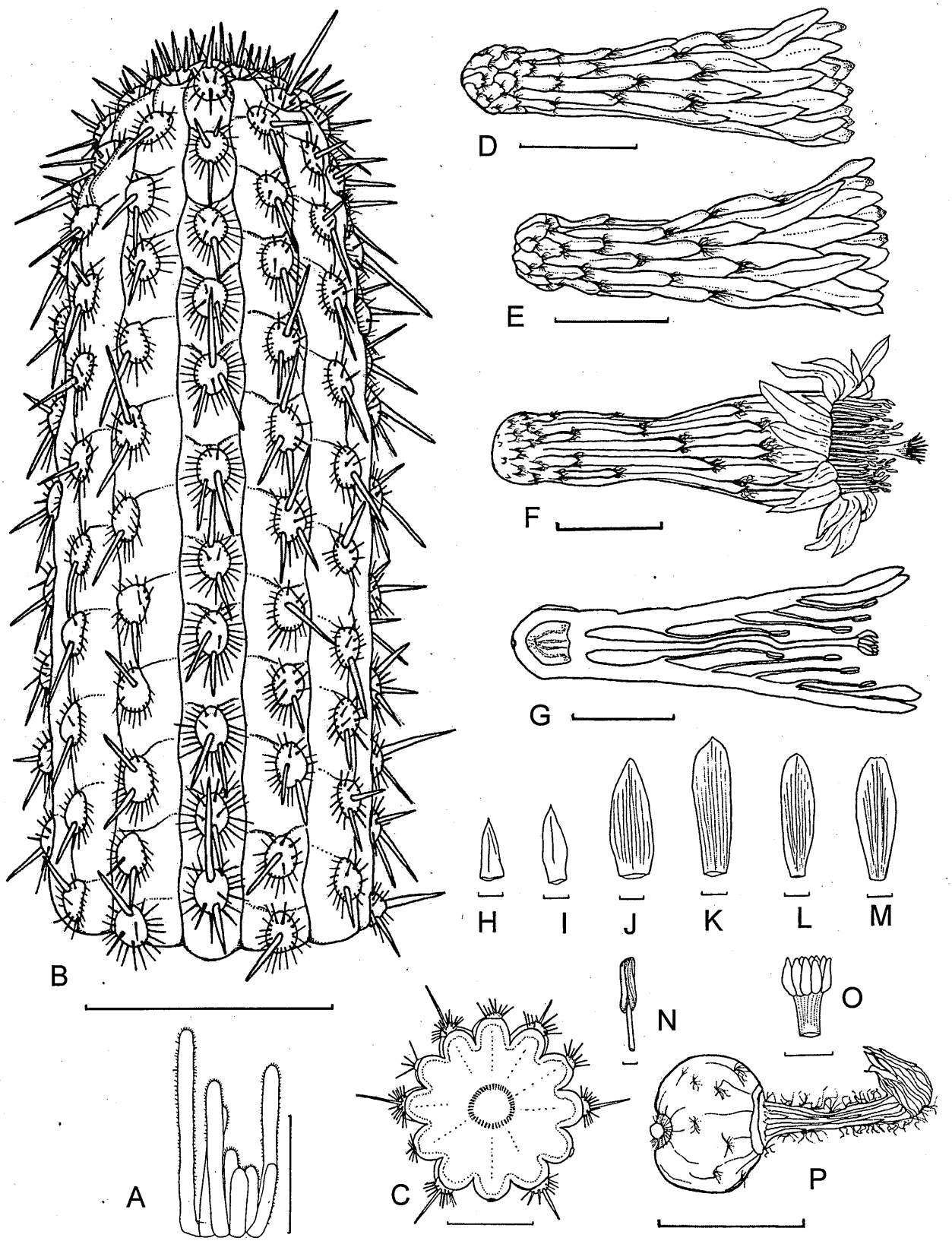


Fig. 3. *Haageocereus acranthus* subsp. *backebergii* (A, *N. Calderón* 516; B-E, G-O, *N. Calderón* 496; F, P, *N. Calderón* 240); A, habit (scale=50cm); B, stem (scale=5cm); C, transverse section of stem (scale=3cm); D-G, flower, side view and longitudinal section (scale=2cm); H-I, bract-scales (scale=5mm); J-K, outer perianth segments (scale=5mm); L-M, inner perianth segments (scale=5mm); N, anther (scale=1mm); O, stigma lobes (scale=5mm); P, fruit (scale=3cm).

Plate 8. **8.1** *Haageocereus acranthus* subsp. *backebergii*. *N. Calderón* 499, Rímac valley. **8.2** *Ibid.*, *N. Calderón* s.n., cult. La Molina Univ. Botanic Garden, 2005, in fruit. **8.3** *Ibid.*, *N. Calderón* s.n., Chillón valley, in bud. **8.4** *Ibid.*, *N. Calderón* 496, in bud.

1c. *Haageocereus acranthus* subsp. *zonatus* (Rauh & Backeb.) Ostolaza in Ostolaza et al. Brit. Cact. Succ. J. 21(2): 94 (2003). *H. zonatus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957); Die Cact. 2: 1180 (1959). *H. limensis* var. *zonatus* (Rauh & Backeb.) Ritter, Kakt. Südam. 4: 1400 (1981). Type: Peru, Lima, Huaura valley, Churín, 2400 m, 1956, *Rauh* K96 (ZSS holo!).

H. acranthus var. *fortalezensis* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957). Type: Peru, Lima, Fortaleza valley, 1400–1800m, 1956, *Rauh* K51a (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1184, fig. 1136 (1960). **Synon. nov.**

H. achaetus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 25 (1956, publ. 1957); Backeb., Die Cact. 2: 1176 (1959). Type: Peru, Lima, Churín valley, 1200 m, 1956, *Rauh* K92 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1210, fig. 1167 (1960). **Synon. nov.**

H. deflexispinus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957); Backeb., Die Cact. 2: 1179 (1959). *H. acranthus* subsp. *deflexispinus* (Rauh & Backeb.) Ostolaza in Ostolaza et al. Brit. Cact. Succ. J. 21(2): 94 (2003). *H. limensis* var. *deflexispinus* (Rauh & Backeb.) Ritter, Kakt. Südam. 4: 1399 (1981). Type: Peru, Lima, Churín valley, 1200 m, rocky desert area, 1956, *Rauh* K103 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1185, fig. 1137 (1960). **Synon. nov.**

Habit up to 1.4 m tall, branching at base; branches straight, 5.0–8.5 cm diam.; ribs 12–15, 12.0–18.0 mm. Areoles 6.8–10.0 × 5.3–8.3. mm, 5.0–9.0 mm apart. Central spines 1–2, 12.0–55.0 × 0.8–1.6 mm at base; radial spines (21–)25–37, 5.2–15.4 × 0.2–0.7 mm at base. Flowering areoles of mature branches woolly, white, generally disposed in ring-like pseudocephalia around the stems, persistent. Flowers 8.0–10.0 × 5.6–7.5 cm; pericarpel

13.0–15.0 × 13.0–19.4 mm; tube 5.0–5.4 × 1.3–2.0 cm at base, widening towards apex to 3.0 cm diam., bearing abundant long white trichomes and brownish yellow hair-spines emerging from the bract-scale axils, being the bract-scales subtended by decurrent podaria; outer perianth-segments 12–14, 20.0–27.5 × 4.3–4.4 mm, greenish; inner perianth-segments 22–24, 25.0–26.0 × 6.5–8.0 mm, white; nectar-chamber 17.0–18.0 × 7.0–8.5 mm, tubular; anthers 3.8–6.0 × 0.9–1.3 mm; style 69.0–75.0 × 1.0–2.5 mm; stigma 6.0 mm; ovary locule 7.0–9.2 × 8.0–10.0 mm, cylindric to elliptic in longitudinal section. Fruit 4.0–4.8 × 4.2–5.5 cm, pericarp bearing few to abundant white trichomes. Seeds 1.45 × 1.11–1.19 mm, 0.78–0.79 mm thick, glossy; relief (SEM) with par-convex structures; microrelief with cuticle weakly to fielded-striated; hilum large, 0.63–0.75 mm, oblique, forming an angle of 44° with long axis of seed (**Fig. 4, Plates 1.4–1.6, 9.1–9.4**).

Examined material: PERU. LIMA: Peru, Lima, Huaura valley, Churín, 2400 m, 1956, *Rauh* K96 (ZSS holo!); Churín–Andajes road, 2500 m, 10 June 2002, *N. Calderón* 280, 281 (Herb. B. G. La Molina); loc. cit., road towards Cochamarca, 77°07'11.58''W, 10°53'35.82''S, 2500 m, 22 Nov. 2003, *N. Calderón* 362 (Herb. B. G. La Molina); loc. cit., 77°05'26.6''W, 10°58'15.3''S, 1520 m, 17 Feb. 2004, *N. Calderón* 379 (Herb. B. G. La Molina); loc. cit., road towards Paccho, 76°58'40.1''W, 10°53'38.8''S, 1670 m, 18 Feb. 2004, *N. Calderón* 385 (Herb. B. G. La Molina); loc. cit., 76°58'42.1''W, 10°53'40.3''S, 1752 m, 5 March 2005, *N. Calderón* 425, 426, 429, 430, 437 (Herb. B. G. La Molina).

Habitat and Distribution: North of Lima, rocky hillsides of Huaura and Pativilca valleys, 1520–2600 m.

Phenology: *Flowers:* December, January and February; *Fruits:* January, February and March.

Conservation status: Endangered. EN[B1ab(ii,iii)]. The extent of occurrence is estimated to be 1880.21 km^2, and it is known to exist at no more than five locations, where continuing decline in the area of occupancy and the quality of habitats has been observed.

Comments:

This taxon was first described by Rauh & Backeberg (1957) and its type is held at ZSS.

Rauh & Backebeberg created *H. acranthus* var. *fortalezensis* (1957) to describe a cactus with "decumbent" branches, 14–15 ribs and persistent flower-bearing areoles in the Fortaleza valley, and as the type was not preserved, a neotype is being designated in this study from a picture published later by Backeberg (1960). According to this brief description, the one difference between *H. acranthus* var. *fortalezensis* and *H. acranthus* subsp. *zonatus* is the "decumbent" habit growth of *H. acranthus* var. *fortalezensis,* which appears illustrated in a later publication of Backeberg -also taken as the neotype- showing not exactly a decumbent plant but an erect cactus with several semi-prostrate, damaged (or dead) branches growing in a steep hillside. Recent studies in the type locality only found the erect growing *H. acranthus* susbp. *zonatus*, suggesting that *H. acranthus* var. *fortalezensis* is in fact a synonym of *H. acranthus* susbp. *zonatus.*

In contrast to the description of *H. acranthus* subsp. *zonatus*, the names *H. deflexispinus* Rauh & Backeb. (1957) and *H. achaetus* Rauh & Backeb. (1957) were described as lacking distinctive flowering areoles, and for the latter name, as having extremely thick stems (to 15 cm diam.). Nevertheless, the lack of flowering areoles constitutes merely a juvenile stage of *H. acranthus* subsp. *zonatus*, as observed in the field at Huaura and Pativilca valleys. In relation to the stem diameter, this character can be variable, although in fieldtrips undertaken in the past five years no *Haageocereus* has been observed to reach more than 8.5 cm diam., and it is presumed that there was an error in recording the quoted original stem measurement of *H. achaetus*. As the types of *H. deflexispinus* and *H. achaetus* were not preserved. neotypes are being designated in this study from illustrations published later by Backeberg (1960). Finally, *H. deflexispinus* and *H. achaetus* are better recognised as synonyms of *H. acranthus* subsp. *zonatus.*

H. acranthus subsp. *zonatus* is characterized by differentiated, woolly, flowering areoles, disposed in ring-like pseudocephalia, a hypothesized apomorphy, and by flowers and fruits

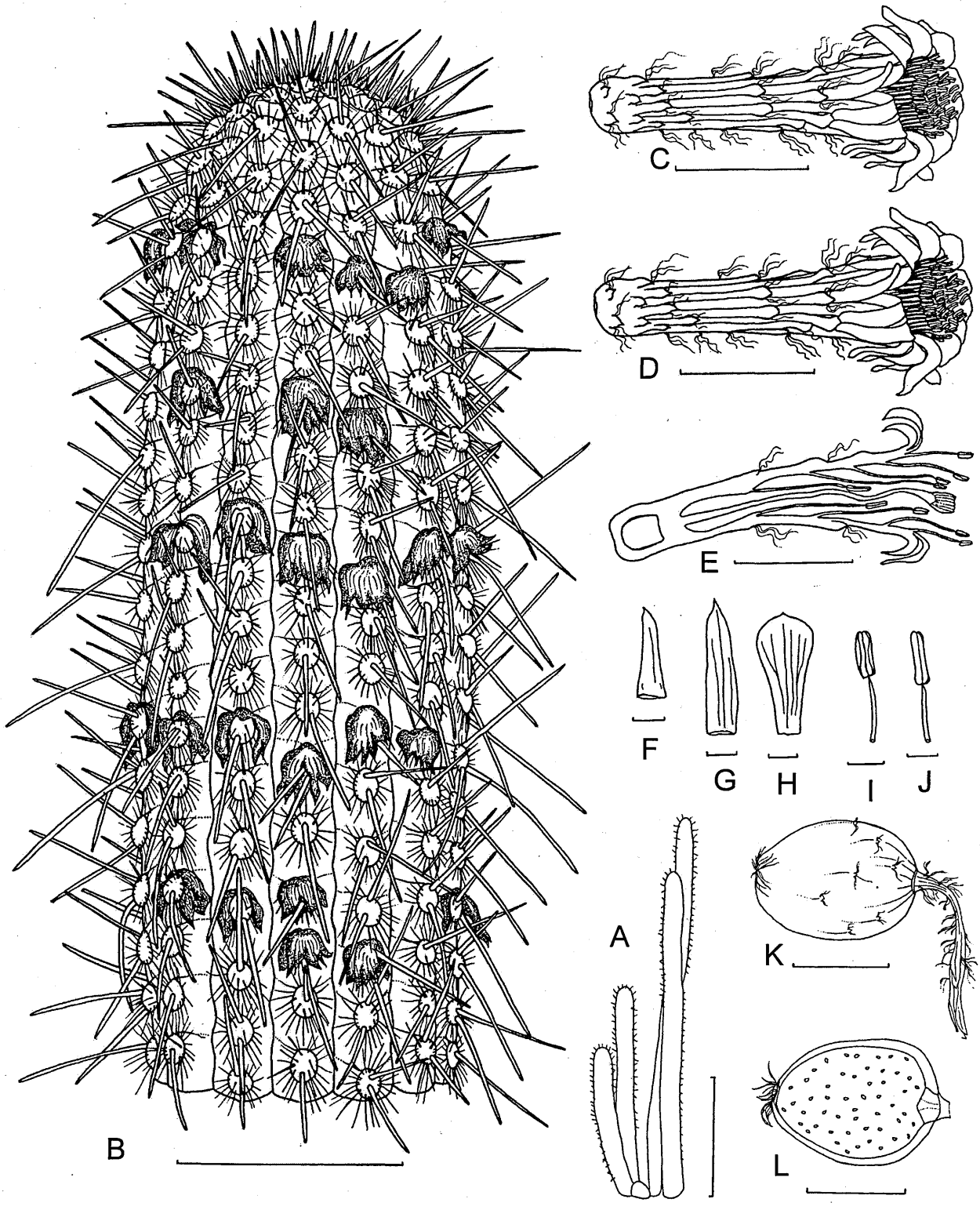


Fig. 4. *Haageocereus acranthus* subsp. *zonatus* (A-B, *N. Calderón* 437; C-J, *N. Calderón* 280; K-L, *N. Calderón 384*); A, habit (scale=50cm); B, stem (scale=5cm); C-E, flower, side view and longitudinal section(scale=3cm); F, bract-scale (scale=5mm); G, outer perianth segment (scale=5mm); H, inner perianth segment (scale=5mm); I-J, anthers (scale=3mm); K-L, fruits, side view and longitudinal section (scale=2cm).

Plate 9. **9.1** *Haageocereus acranthus* subsp. *zonatus*. *N. Calderón* s.n., Pativilca valley, 2005. **9.2** *Ibid. N. Calderón* 362, in flower. **9.3** *Ibid., N. Calderón* s.n., Huaura valley, 2005, in fruit. **9.4** *Ibid., N. Calderón* s.n., Pativilca valley, 2005.

bearing few to abundant white trichomes and/or hair-spines. The seed's testa-cells present par-convexities towards the seed border, this character being unique within the genus.

Growing on rocky hillsides of Huaura and Pativilca valleys, this taxon is sympatric with *H. pseudomelanostele* subsp. *acanthocladus*, and other cacti, such as *Espostoa melanostele* (Vaupel) Borg., *Melocactus peruvianus* Vaupel, *Mila nealeana* Backeb., *Neoraimondia arequipensis* (Meyen) Backeb. and the hybrid ×*Haagespostoa*. In these habitats there are woody shrubs, such as *Trixis* sp. (Asteraceae) and *Cnidoscolus basiacanthus* (Pax & K. Hoffm.) J. F. Macbr. (Euphorbiacae).

2. *Haageocereus chilensis* (Ritter) D. Hunt, Cact. Systematics Initiatives 20: 19 (2005). Type: Chile, dept. Arica, below Chapiquiña, 1957, *Ritter* s.n. (U holo!).

Haageocereus chilensis Ritter, Winter [seed] Katalog 5: 9 (1958), nom. nud. *H. fascicularis* sensu Ritter, Kakt. Südam. 3: 1125 (1980), non *Cactus fascicularis* Meyen, A. Gartenztg 1: 211 (1833).

Habit semi-decumbent to erect, up to 0.5 m tall, branching at base; branches upright, 4.0–7.0 cm diam., epidermis green to greyish; ribs 12–18, 5.0–8.0 mm tall. Areoles 4.0–8.0 mm diam., 10.0 mm apart, felt brownish at first, later grey. Spines opaque, brown and grey; central spines 1–2, 40.0–150.0 mm, ascending and descending; radial spines 7–10(–11), (10.0–)15.0–40.0 mm. Flowers 7.0–8.5 cm; tube 2.5 × 1.0 cm at base, widening towards apex, green, bearing by few hair-spines emerging from the bract-scale axils; outer perianth-segments reddish-green; inner perianth-segments 25.0 × 6.0–8.0 mm, white; nectar-chamber 20.0 × 10.0 mm, tubular; style 55.0; stigma-lobes 10, 6.0 mm; ovary locule 10.0 × 4.0 mm. Fruit ovoid. Seeds oval, medium-size, 1.87 × 1.13 mm, 1.03 mm thick, glossy; relief (SEM) convex; microrelief without cuticular striations; hilum large, 0.86 mm, oblique, forming an angle of 39° with long axis of seed (**Plates 2.1–2.3**).

Examined material: CHILE. ARICA: Below Chapiquiña, 2000–3000, 1957, *Ritter* s.n. (U holo); TARAPACÁ: Camiña, Sept. 1960, *Ritter* FR601 (ZSS SR13517, only seeds); IQUIQUE: 63 km from the Panamericana towards Mamiña, Quebrada Guataguata, small valley on the left side of the road, 69°15'49.8''W, 20°4'39''S, 2400 m, 2 Feb. 1997, *Eggli & Leuenberger* 2732 (ZSS 18040); loc. cit., Quebrada Mamiña, 69°12'33.6''W, 20°4'19.2''S, 2800 m, 24 Feb. 1997, *Eggli & Leuenberger* 2747 (ZSS 18046); loc. cit., hill north-east of the village of Mamiña, 69°25'24''W, 19°18'28.8''S, 2450 m, 24 Feb. 1997, *Eggli & Leuenberger* 2788 (ZSS).

Habitat and Distribution: Found in rocky hillsides of Andean valleys in northern Chile, 2000–3000 m, and also reported for southern Peru in Tacna (but not confirmed), (**Map 3**).

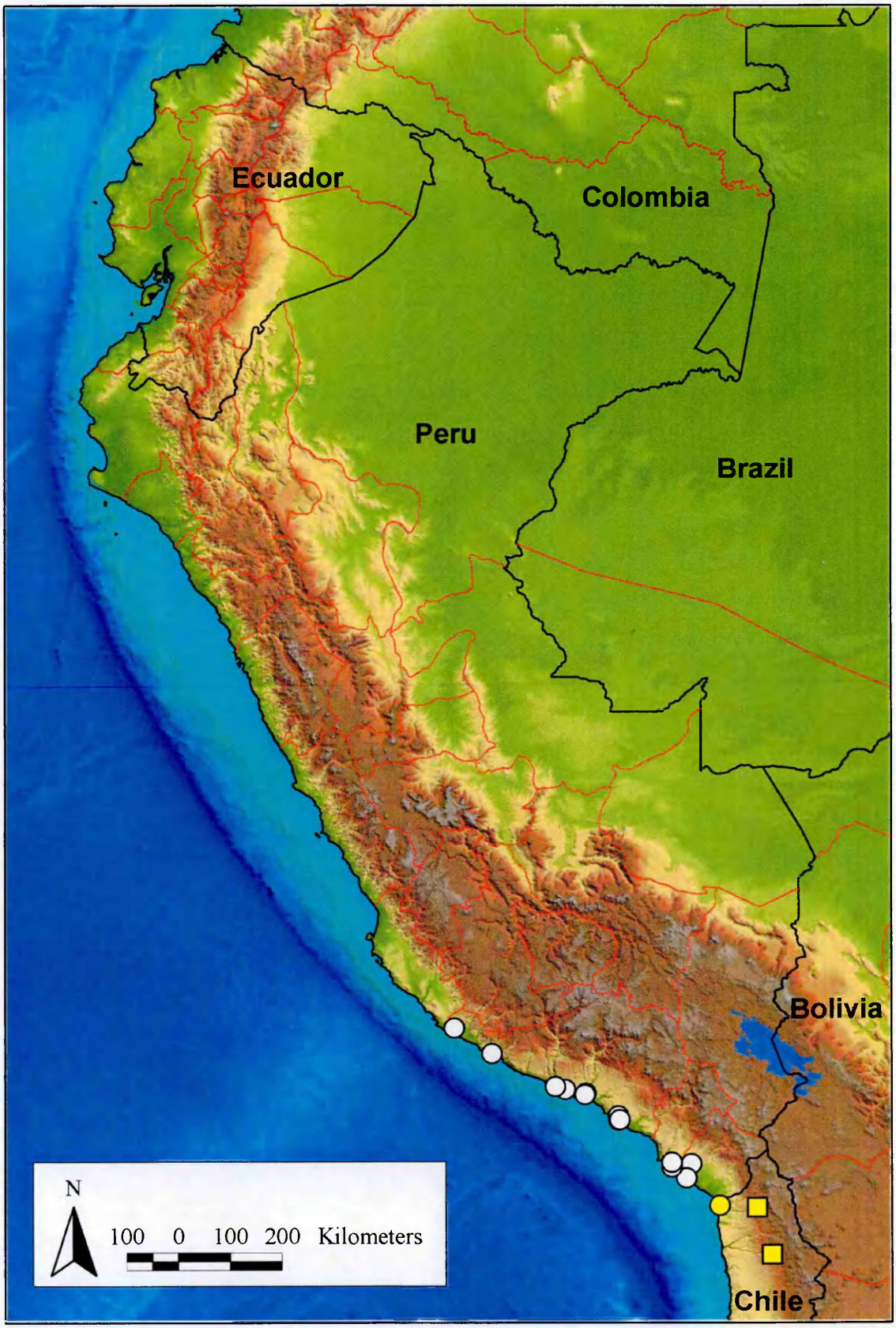
Phenology: *Flowers:* February; *Fruits:* February and March.

Conservation status: Ritter (1980) recorded this taxon for the southernmost part of Peru, in Tacna, but it has not been observed by the present author in Peru. Populations reported by Hoffmann & Walter (2004) for the region of Tarapacá in the Andean Cordillera are believed to be threatened.

Comments:

The name *Haageocereus chilensis* first appeared in H. Winter's seed catalogue (1958) as '100a FR 601 Ritter sp. nov.' without a description. Later, Ritter (1981) listed *H. chilensis* as a *nomen nudum* under *H. fascicularis* (Meyen) Ritter, based on his collections FR 601 (U!) and FR 125. Because *Haageocereus fascicularis* is based on the old *Cereus fascicularis* Meyen (1833), a name without extant material, illustration or a meaningful description, that also had been taken as the type species of *Weberbauerocereus,* it is preferable not to use this name (Hunt 2005). The only specimen originally labelled *Haageocereus chilensis* is Ritter FR s.n. (Utrecht Herbarium). D. Hunt (2005) cited this specimen as the holotype when validating Ritter's catalogue.

Haageocereus chilensis Ritter ex D. Hunt is characterized by a low radial spine number of 7–10(–11), long radial spines, to 4.0 cm and very long central spines, to 15.0 cm. The areoles are very conspicuous and the plant reaches to 0.5 m tall.



Map 3. *Haageocereus chilensis*=□; *Haageocereus decumbens*= ○. (Chilean localities in yellow).

According to Hoffmann & Walter (2004), in Chile this species lives together with *Browningia candelaris* Britton & Rose, *Cumulopuntia* sp. and *Tunilla* sp., at 1700–3000 m; and with *Oreocereus leucotrichus* at 2500 m.

3. *Haageocereus decumbens* (Vaupel) Backeb., Blätt. Kakt.-forsch. 1934(6): unpaged, (1934); Backeb. & F. M. Knuth, Kaktus-ABC: 207 (1935, publ. 1936); Krainz, Die Kakteen 1(11): CVa, unpaged (1965); Backeb., Die Cact. 2: 1237 (1960); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 391 (1958). *Binghamia decumbens* (Vaupel) Werderm., Kakteenkunde: 24 (1937c). *Cereus decumbens* Vaupel, Engler, Bot. Jahrb. Syst. 50, Beibl. 111: 18 (1913). Type: Peru, Arequipa, Mollendo, sandy coast, 50–100 m, 7 Oct. 1902, *Weberbauer* 1550 (B, photo!).

H. decumbens var. *spinosior* Backeb., Cact. Succ. J. (US) 23(2): 47, 1951; [First mentioned: Backeb. & F. M. Knuth, Kaktus-ABC: 208 (1935, publ. 1936), nom. inval. (Art. 36.1, ICBN 2000)]; *H. decumbens* fa. *spinosior* (Backeb.) Krainz, Die Kakt. CVa, 1965. Type locality: Peru, Arequipa, Mollendo (believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1239, fig. 1203 (1960). **Synon. nov.**

H. ambiguus var. *reductus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 25 (1956, publ. 1957). Type: Peru, Arequipa, Atico, Km 725 Panamericana, 1956, *Rauh* K133 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1247, fig. 1212 (1960). **Synon. nov.**

H. mamillatus var. *brevior* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 26 (1956, publ. 1957). Type: Peru, Arequipa, Ocoña–Camaná, desert, 800 m, gypsic, 1956, *Rauh* K137 (ZSS holo!). **Synon. nov.**

H. australis f. *nanus* Ritter, Kakt. Südam. 3: 1127 (1980). Type: Peru, Moquegua, Ilo, June 1954, *Ritter* FR 126c (ZSS iso!). **Synon. nov.**

H. decumbens var. *brevispinus* Ritter, Kakt. Südam. 4: 1392 (1981). Type: Peru, Arequipa, northern Ocoña, coast, *Ritter* FR1024 (U holo!). **Synon. nov.**

H. chalaensis Ritter, Kakt. Südam. 4: 1389 (1981). Type: Peru, Arequipa, Chala, coast, 1953, *Ritter* FR187 (U holo!); 9 September 1954, *Ritter* FR187 (ZSS iso!). **Synon. nov.**

H. subtilispinus Ritter, Kakt. Südam. 4: 1419 (1981). Type: Peru, Arequipa, Atico, 1954, *Ritter* FR582 (U holo!). **Synon. nov.**

?*H. australis* Backeb., Jahrb. Deutsch Kakt-Ges. 1: 104 (1936); Blätt. Kakt.-forsch. 1937(5): unpaged (1937). Type locality: South of Peru (believed not to have been preserved).

?*H. ambiguus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 25 (1956, publ. 1957). Type: Peru, Arequipa, Atico, Km 725 Panamericana highway, 1956, *Rauh* K132 (HEID, believed not to have been preserved).

?*H. litoralis* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 26 (1956, publ. 1957). Type: Peru, Arequipa, hills near Atico, 1956, *Rauh* K157 (HEID, believed not to have been preserved).

?*H. mamillatus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 25 (1956 publ. 1957). Type: Peru, Arequipa, Camaná, 400 m (Km 165 Arequipa–Camaná road), 1956, *Rauh* K139 (HEID, believed not to have been preserved).

?*H. ocona-camanensis* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 26 (1956, publ. 1957). Type: Peru, Arequipa, sandy desert Ocoña–Camaná, 200 m, 1956, *Rauh* K155 (HEID, believed not to have been preserved).

Habit decumbent, branching at base; branches prostrate, 2.0–5.0 cm diam., 0.25–0.6(–1.0) m. long. with ascending apices 5.0–10.0 cm above the ground, epidermis green; ribs 14–20, 5.6–8.0 × 2.3–3.9 mm. Areoles 2.5–6.0 × 1.5–3.5 mm diam., 1.4–8.8 mm apart, oval to circular, felt brownish grey and white. Spines opaque, light brown and grey; central spines 1–2, 7.0–28.0 × 1.0–1.5 mm at base, ascending and descending; radial spines 19–33, 3.0–7.0 × 0.2–0.5 mm at base. Flowers 6.0–6.5 cm; pericarpel 7.9–8.6 × 10.0–11.4 mm; tube 3.2–3.6 × 0.9–1.0 cm at base, widening towards apex to 1.6 cm diam., bearing few hair-spines emerging from the bract-scale axils; outer perianth-segments 15.0 × 4.0 mm; inner perianth-segments 10.0 × 5.0 mm, white; nectar-chamber 18.6–20.0 × 6.4–7.1 mm, tubular, straight;

anthers 3.2 × 1.1 mm; stigma-lobes 12; ovary locule elliptic, 3.6–4.0 × 5.7–6.8 mm. Fruits 4.0 × 3.8 cm. Seeds broadly oval, medium-size, 1.41 × 1.15 × 0.86 mm, lustre glossy; relief (SEM) convex; microrelief without cuticular striations; hilum large, 0.78 mm, oblique, forming an angle of 55° with long axis of seed (**Fig. 5, Plates 2.4–2.6, 10.1–10.3**).

Examined material: CHILE. TARAPACA: Arica, Jun. 1954, *Ritter* FR126b, (ZSS T4529); loc. cit., Ritter, Kakt. Südamer. 3: 1228, fig. 1089 (1980). PERU. AREQUIPA: Mollendo, sandy soils, 50–100 m, 7 Oct. 1902, *Weberbauer* 1550 (B, type); loc. cit., 70°52'44.8''W, 17°00'9.6''S, 150 m, 15 March 2004, *N. Calderón* 418 (Herb. B. G. La Molina); loc. cit., 1955, *Ritter* FR 126, (ZSS T4528); Ocoña–Camaná, 800 m, gypsic, 1956, *Rauh* K137 (ZSS); Northern Ocoña, coast, *Ritter* FR1024 (U); Atico, 1954, *Ritter* FR582 (U); Chala, coast, 1953, *Ritter* FR187 (U holo!); loc. cit., 9 September 1954, *Ritter* FR187 (ZSS); Camaná, Km 955 Panamericana Sur, 72°37'36.7''W, 16°34'10.4''S, 620 m, 16 March 2004, *N. Calderón* 415, 416, 417 (Herb. B. G. La Molina); MOQUEGUA: Ilo, June 1954, *Ritter* FR126c (ZSS); TACNA: Morro Sama, rocky hills facing the Pacific ocean, 72°1'28.8''W, 18°00'6.12''S, 128 m, 14 March 2004, *N. Calderón* 412, 413, 414 (Herb. B. G. La Molina); Km 113 Costanera highway, towards Tacahuay hills, sandy area, 71°7'45.2''W, 17°48'50.5''S, 84 m, 5 April 2005, *N. Calderón* 453, 454, 455 (Herb. B. G. La Molina).

Habitat and Distribution: Found in sandy and rocky areas of the Pacific coastal desert in southern Peru (Arequipa and Tacna) 50–620 m, and northern Chile (Arica), (**Map 3**).

Phenology: *Flowers:* October; *Fruits:* November.

Conservation status: In Peru, Vulnerable: VU[B1ab(ii,iii,iv)]. The extent of occurrence is estimated to be 14842.7 km^2. It is known to exist at no more than ten locations and continuing decline in the area of occupancy, the quality of habitats and the number of subpopulations has been observed.

According to Hoffmann and Walter (2004), this species is believed to be threatened in Chile. Populations of this species were observed growing on sandy and rocky areas close to the sea in Arequipa, Moquegua and Tacna along the southern coast of Peru. In the case of Morro Sama, in Tacna, housing development is increasing rapidly, resulting in habitat loss for this

species. The other populations, in Arequipa and Moquegua, are under indirect impact from human activities where they are close to highways and towns.

Comments:

The species was first published as *Cereus decumbens* by Vaupel (1913). The type of this name, together with that of *Cereus acranthus*, represent the two important Weberbauer collections of *Haageocereus* held currently at the Berlin Herbarium, which were previously believed to have been destroyed during the Second World War until Leuenberger (1978) rediscovered them.

Haageocereus decumbens includes a number of synonyms published by Backeberg (1936) and Rauh & Backeberg (1957) to describe prostrate forms growing in diverse localities along the southern coast of Peru. *H. decumbens* var. *spinosior, H. ambiguus* var. *reductus* and *H. mamillatus* var. *brevior* were described with characters found in *H. decumbens*, such as prostrate stems 0.2–0.9 m long × 4.0–5.0 cm diameter, ribs 15–18, and spines that, according to type and illustrations available lack trichomes on their surface, for these reasons, these names are better placed as synonyms of *H. decumbens*. As type-material of *H. decumbens* var. *spinosior* and *H. ambiguus* var. *reductus* was not preserved, neotypes are being designated here from illustrations published later by Backeberg (1960).

Ritter created *H. australis* f. *nanus* (1980) and *H. decumbens* var. *brevispinus* (1981) to refer to slight morphological differences he observed on these cacti. *H. australis* f. *nanus* has smaller branches (10 cm long) and *H. decumbens* var. *brevipinus* has shorter spines (central spines 1–2, 10.0–20.0 mm; radial spines 3.0–5.0 mm). Study of the type-material and field observations have led to the conclusion that both names are better treated as synonyms of *H. decumbens*.

Ritter (1981) also described two new species for populations from the south coast of Peru: *H. subtilispinus*, with stems 3.5–5.0 cm diameter, ribs 15–16, flowers 7.0 cm long., inner perianth-segments white, fruit reddish, 3.0–5.0 cm; and *H. chalaensis*, with stems 4.0–5.0 cm diam., stem 0.5–1.0 m long, ribs 12–19, central spine 2.0–(10.0) cm long., flower white,

fruit carmine, 2.5–4.0 cm. However, these characters are insufficient to distinguish these plants from *H. decumbens* and they are better treated as synonyms.

Other taxa possibly referring to *H. decumbens* published by Rauh & Backeberg (1957) are *H. ambiguus*, *H. litoralis*, *H. mamillatus*, and *H. ocona-camanensis*. For these taxa, original preserved material is lacking, and meaningful illustrations do not exist to enable firm decisions as to whether they are synonyms of *H. decumbens*. However, their prostrate growth habit, slender stems 2.0–4.0 cm diameter (except in *H. litoralis* to 8.0 cm) and proximity to the type locality suggest, these taxa are very likely to belong to *H. decumbens*.

Haageocereus australis Backeb. (1936), a poorly understood taxon, is possibly a synonym of *H. decumbens*, matching this species in its decumbent habit, stems 25.0 cm long, 6 cm diam., 14 ribs and with 28 radial spines. From field observations carried out in southern Peru, in the region where this taxon originated, it seems plausible that *H. australis* may well refer to *H. decumbens*.

H. decumbens (Vaupel) Backeb. is recognizable by its characteristic decumbent habit (hence its epithet), a possible apomorphy for the species. In contrast to the spines with trichomes and seeds with strong cuticular striations found in *H. tenuis*, *H. decumbens* lacks any of these characters.

In Peru, *H. decumbens* grows with other cacti like *Neoraimondia arequipensis* (Meyen) Backeb., but so far it has not been found sympatric with other *Haageocereus*.
In Chile, this species grows with *Eulychnia iquiquensis* Britton & Rose and *Eriosyce iquiquensis* (Ritter) Ferryman (Hoffmann & Walter 2004).

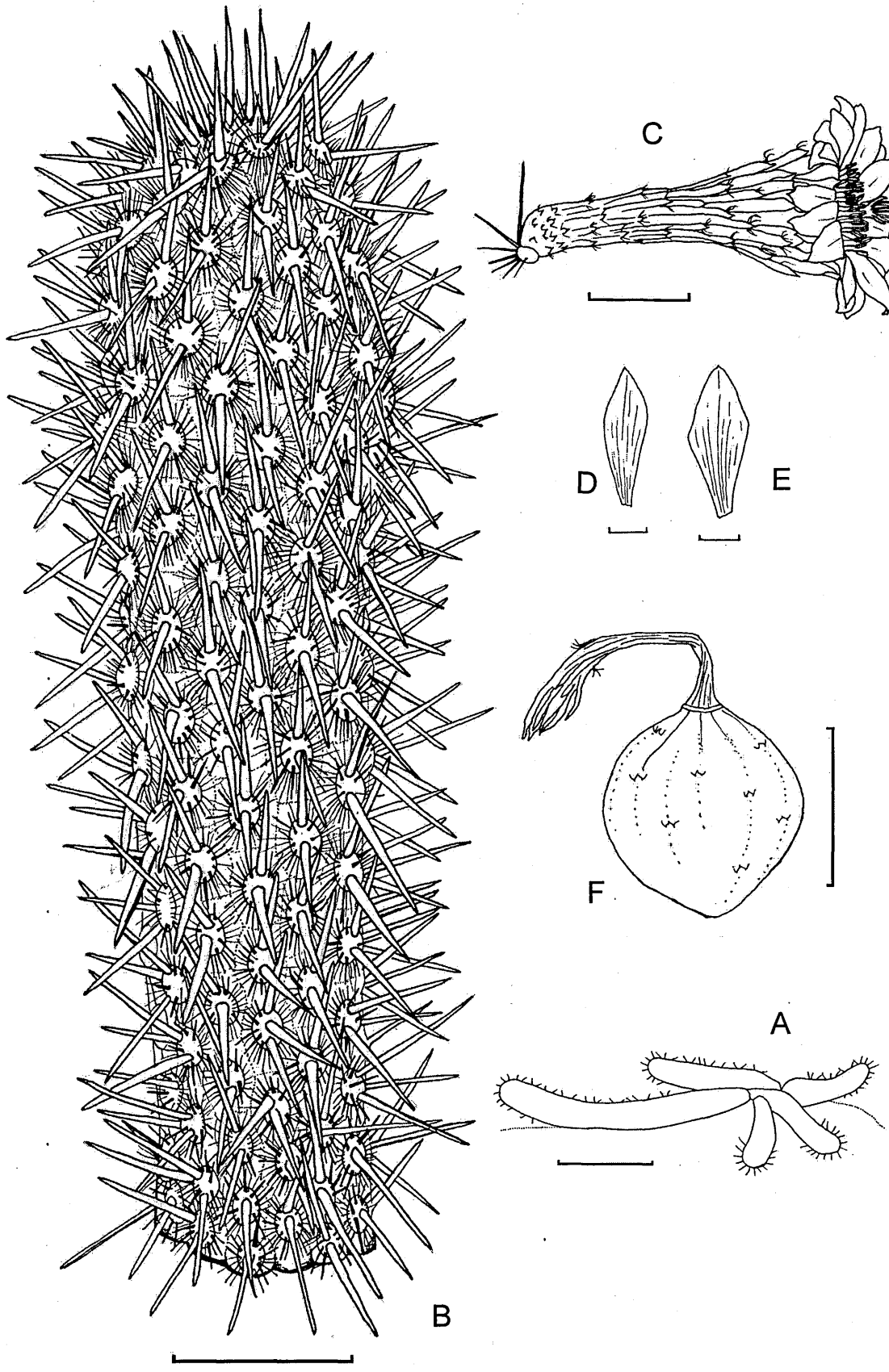


Fig. 5. *Haageocereus decumbens* (A, *N. Calderón* 451; B, *N. Calderón* 454; C-E, *Ritter* FR582; F, *Ritter* FR187); A, habit (scale=10cm); B, stem (scale=2cm); C, flower, (scale=2cm); D, outer perianth segment (scale=5mm); E, inner perianth segment (scale=5mm); F, fruit (scale=3cm.)

Plate 10. **10.1** *Haageocereus decumbens*. *N. Calderón* 451, Tacahuay at Tacna. **10.2** *Ibid*., *N. Calderón* 454. **10.3** *Ibid., N. Calderón* 451.

4. *Haageocereus lanugispinus* Ritter, Kakt. Südamer. 4: 1395 (1981). Type: Peru, between Lima and Ancash, North of Pativilca, 1957, *Ritter* FR 583, (U holo!).

Habit decumbent, 0.1–0.2 m, branching at base; branches 1.2–2.0 cm diam., epidermis green; ribs 12–15, 1.5–2.0 mm high. Areoles 1.5 × 0.8–1.0 mm, 2.0 mm apart, oval, brownish and white. Spines opaque, densely covered by white plumose trichomes; central spines 0; radial spines 25–35, 3.0–5.0 × 0.25 mm diam. at base. Flowers 5.0 cm, tube bearing white trichomes emerging from the bract-scale axils; inner perianth-segments white; nectar-chamber 12.0 × 2.0 mm, tubular; stigma-lobes included.

Examined material: PERU. LIMA: North of Pativilca, 1957, *Ritter* 583 (U holo).

Habitat and Distribution: North of Pativilca, between Lima and Ancash (**Map 4**).

Phenology: Not known.

Conservation status: Data Deficient DD. *H. lanugispinus* has not been found after its discovery by Ritter; amateurs have reported this species but its locality remains a secret amongst them, and the conservation status remains uncertain. Recent attempts to find this species in the field have not yielded results.

Comments:

After Ritter (1981) described *H. lanugispinus*, it has not been found again and therefore other biological aspects and the conservation status are still uncertain.

H. lanugispinus Ritter presents spines bearing white trichomes that give the cactus the woolly aspect reflected by its epithet. This character is being hypothesized as an autoapomorphy of probable high adaptative value. Further fresh material from the field is needed to prepare a complete description of this species, however, due to the very small size of the individuals, it is not surprising that this species has remained elusive for so long.

Map 4. *Haageocereus lanugispinus*= ○; *Haageocereus repens*=□; *Haageocereus tenuis*=△.

5. *Haageocereus platinospinus* (Werderm. & Backeb.) Backeb. in Backeb. & F. M. Knuth, Kaktus-ABC: 209 (1935, publ. 1936); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 391 (1958); Backeb., Die Cact. 2: 1234 (1960). *Cereus platinospinus* Werderm. & Backeb. in Backeb., Neue Kakteen: 76 (1931). Type locality: Peru, Arequipa, desertic areas (believed not to have been preserved). Lectotype (designated here): Backeb., Neue Kakteen: 76, photo on right side (1931).

H. pluriflorus Rauh & Backeb. in Backeb. Desc. Cact. Nov. [1]: 23 (1956, publ. 1957); Backeb., Die Cact. 2: 1185 (1960). Type: PERU, Arequipa, Majes valley, Hacienda Ongoro, 1000 m, 1956, *Rauh* K151 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1213, top fig. 1171 (1960). **Synon. nov.**

non Haageocereus fascicularis (Meyen) Ritter, Kakt. Südam. 3: 1125 (1980).

non Cereus fascicularis Meyen, A. Gartenztg 1: 211 (1833).

Habit semi-decumbent to erect, up to 0.5 m tall, branching at base; branches curved or upright, 4.0–6.8 cm diam., epidermis green to brownish; ribs 12–16, 5.0–19.0 × 4.0–7.0 mm. Areoles 5.0–8.0 × 3.0–7.0 mm, 2.1–10.0 mm apart, oval to circular, felt white and grey. Spines opaque, at first yellow and brown, later grey; central spines (0–)1–(2), 13.5–90.0 × 0.6–1.0 mm at base, ascending and descending; radial spines (12–)14–20, 4.6–10.0 × 0.3–0.6 mm. Flowers 6.0–8.0 × 4.2–6.0 cm; pericarpel 9.0–12.0 × 10.0–12.0 mm; tube 3.5–5.5 × 0.8–1.2 cm at base, widening towards apex to 2.0–2.4 cm diam., slightly curved, green, bearing few brownish yellow hair-spines emerging from the bract-scale axils; outer perianth-segments 17–29, 11.6–28.0 × 3.9–6.6 mm, reddish green; inner perianth-segments 12–18, 18.5–33.7 × 6.8–12.6 mm, white; nectar-chamber 6.0–14.4 × 4.2–5.0 mm, tubular; anthers 2.2–5.6 × 0.8–1.4 mm; style 40.0–61.0 × 1.4–1.7 mm; stigma-lobes 9–10, 2.6–4.0 mm; ovary locule 7.0–9.3 × 4.0–6.2 mm, circular to elliptic in longitudinal section. Fruit 3.2–5.0 × 2.5–3.8 cm, spherical to ovoid. Seeds broadly oval, medium-size, 1.61–1.73 × 1.02–1.19 × 0.97–1.0 mm, glossy; relief (SEM) convex; microrelief without cuticular striations; hilum

large, 0.76–0.81 mm, oblique, forming an angle of 55° with long axis of seed (**Fig. 6, Plates 3.1–3.3, 11.1–11.3**).

Examined material: PERU. AREQUIPA: Yura valley, hills surrounding town, 71°42'27.6''W, 16°14'53''S, 2470 m, 9 March 2004, *N. Calderón* 404 (Herb. B. G. La Molina); loc. cit., 71°42'22''W, 16°14'54.3''S, 2525 m, 9 March 2004, *N. Calderón* 401 (Herb. B. G. La Molina); loc. cit., road towards Huanca, 71°47'19.44''W, 16°14'49.02''S, 2357 m, 17 March 2004, *N. Calderón* 469 (Herb. B. G. La Molina); loc. cit., 71°42'22.3''W, 16°13'21.9''S, 2600 m, 1 April 2005, *N. Calderón* 447, 450 (Herb. B. G. La Molina); Tiabaya, Guayrondo chico, sandy and rocky hills, 71°36'14.8''W, 16°27'29.7''S, 2190 m, 10 March 2004, *N. Calderón* 408, 409, 410 (Herb. B. G. La Molina); TACNA: Tacna–Tarata road, arid hills, 70°6'15.9''W, 17°42'05.5''S, 2450 m, 6 April 2005, *N. Calderón* 456, 457, 458 (Herb. B. G. La Molina).

Habitat and Distribution: Found in rocky hillsides of valleys in southern Peru, being well represented in Arequipa and Tacna, 1000–2650 m (**Map 5**).

Phenology: *Flowers:* February, March and April; *Fruits:* March and April.

Conservation status: Endangered. EN[B1ab(ii,iii)]. The extent of occurrence is estimated to be 2469.6 km^2. It is known to exist at no more than four locations and continuing decline in the area of occupancy and the quality of habitats has been observed.

In most areas, populations grow healthily and abundantly, but in some places like Cerro Verde (Arequipa), much of the land is disturbed by mining activities, and by the extraction of rocks and other building materials.

Comments:

The species was first described by Werdermann and Backeberg (1931) but type-material was not preserved, therefore, the photograph published alongside the description is being designated as lectotype.

Ritter (1981) made the combination *Haageocereus fascicularis* for *Cereus fascicularis* Meyen (1833) for a cactus growing in Chapiquiña (Chile). The type-locality described by

Meyen (1833) in the Cordillera Tacna, would include the southern populations of *Haageocereus platinospinus* (Werderm. & Backeb.) Backeb. Nevertheless, neither Meyen (1833) nor Ritter's description (1981) match the characters of *H. platinospinus*, where the radial spine number is 10–20, while *H. fascicularis* (*Cereus fascicularis*) has 7–9 radial spines. In addition, the generic name *Weberbauerocereus* Backeb. (1942) is also based on *Cereus fascicularis* Meyen, being better to not use *H. fascicularis*, as explained before under the discussion presented for *H. chilensis*.

Haageocereus pluriflorus was created by Rauh & Backeberg (1957) but its type was not preserved, making necessary to designate a neotype for this taxon based on an illustration published later by Backeberg (1960). I consider *H. pluriflorus* a synonym of *H. platinospinus* because the only difference proposed by Rauh & Backeberg (1957) is the fact that *H. pluriflorus* has more numerous flowers. I have observed this character in the field, and concluded that flower number is not a constant character and is likely to be linked to the environment, not being enough to recognize these populations as different species.

Haageocereus platinospinus (Werderm. & Backeb.) Backeb. is characterized by its low height (up to 0.5 m), low radial spine number (10–20) and greyish spines (hence its epithet). *H. platinospinus* has conspicuous areoles and central spines, and ribs may present transversal folds of the epidermis around areoles, these characters being hypothesized as plesiomorphic.

In the Arequipa valley, above 2000 m, *Haageocereus platinospinus* lives together with other cacti like *Oreocereus hempelianus* (Gürke) Hunt, *Weberbauerocereus weberbaueri* (Vaupel) Backeb., *Opuntia corotilla* K.Schum., *Opuntia sphaerica* Först and *Corryocactus aureus* (Meyen) Hutchison. In Tacna, also above 2000 m, *H. platinospinus* lives with *Browningia candelaris* Britton & Rose, *Opuntia sp.* and *Corryocactus sp.*

Map 5. *Haageocereus platinospinus* = ●.

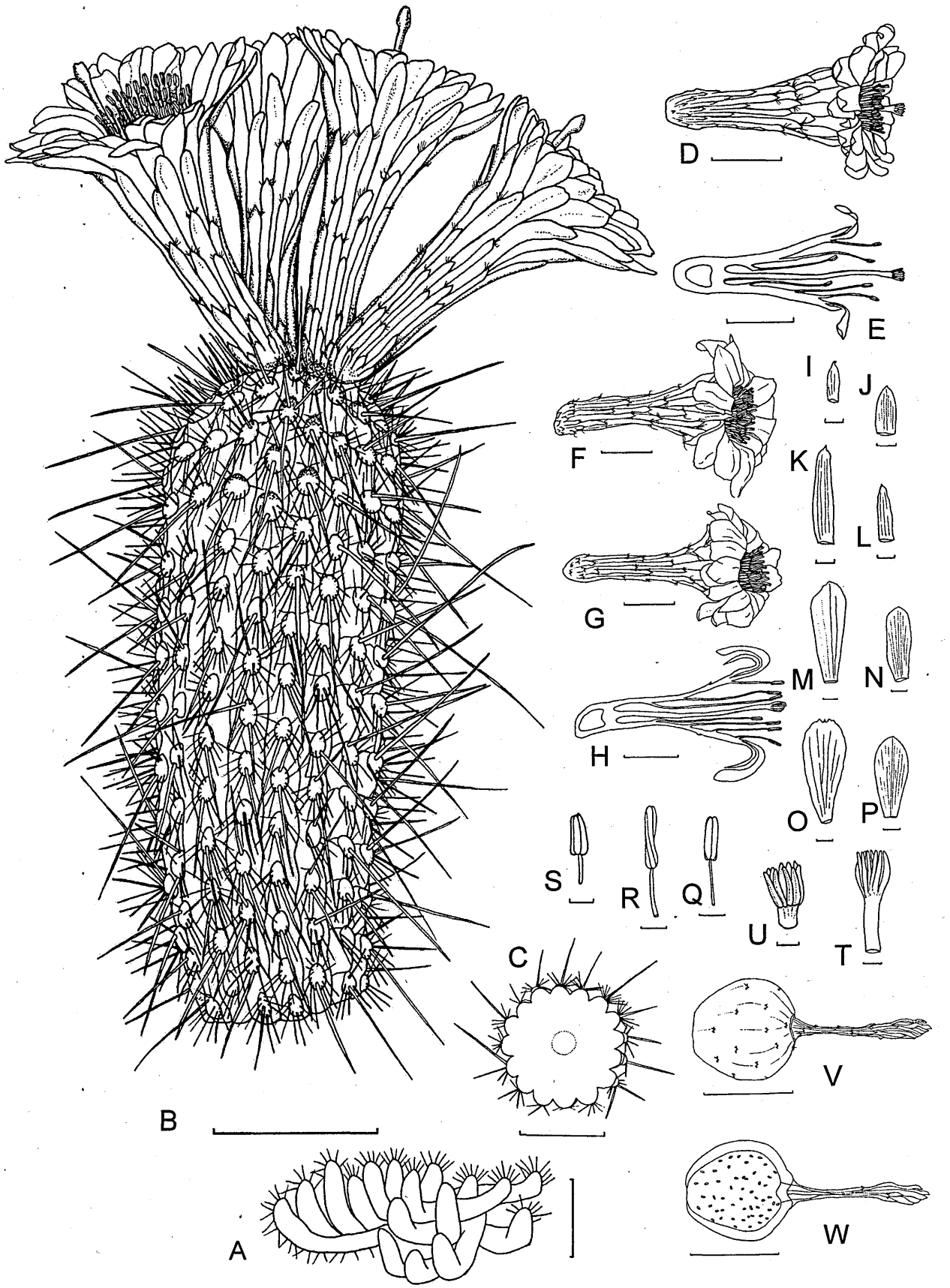


Fig. 6. *Haageocereus platinospinus* (A, C, *N. Calderón* 444; B, D, E, J, N, P, S, T, *N. Calderón* 447; F-I, K-M, O, Q, R, U, *N. Calderón* 450; V-W, *N. Calderón* 443); A, habit (scale=20cm); B, stem (scale=3cm); C, transverse section of stem (scale=3cm); D-H, flower, side view and longitudinal section (scale=2cm); I-L, bract-scales(scale=5mm); M-N, outer perianth segment (scale=5mm); O-P, inner perianth segment (scale=5mm);Q-S, anthers (scale=2mm); T-U,stigma lobes (scale=2mm); V-W, fruits, side view and longitudinal section (scale=3cm).

Plate 11. **11.1** *Haageocereus platinospinus*. *N. Calderón* 450, Yura valley. **11.2** *Ibid.*, *N. Calderón* 410, Tiabaya, in fruit. **11.3** *Ibid.*, *N. Calderón* 450, in flower.

6. *Haageocereus pseudomelanostele* (Werderm. & Backeb.) Backeb., Blätt. Kakt.-forsch. 1934(6): unpaged (1934); Backeb. & F. M. Knuth, Kaktus-ABC: 209 (1935, publ. 1936); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 426 (1958); Backeb., Die Cact. 2: 1226 (1960). *H. multangularis* var. *pseudomelanostele* (Werderm. & Backeb.) Ritter, Kakt. Südamer. 4: 1406 (1981). *Cereus pseudomelanostele* Werderm. & Backeb. in Backeb., Neue Kakteen: 74 (1931); Werderm., Fedde, Rep. Spec. Nov. 30: 61 (1932). Type locality: Peru, Lima, Rímac valley, by Cajamarquilla, in the Lima–La Oroya road (believed not to have been preserved). Lectotype (designated here): Backeb., Neue Kakteen: 75, photo (1931).

H. chosicensis (Werderm. & Backeb.) Backeb., Backeb. & F. M. Knuth, Kaktus-ABC, 207 (1936). *Cereus chosicensis* Werderm. & Backeb. in Backeb., Neue Kakteen: 74 (1931); Fedde, Rep. Spec. Nov. 30: 60 (1932); Krainz, Die Kakteen 1 (11): CVa, unpaged (1964). Type locality: Peru, Lima, by Chosica, in the Lima–La Oroya road, (believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1210, fig. 1168 (1960).

H. horrens Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957). Type: Peru, Trujillo, Km 720 Panamericana highway, in arid coastal hills, 1956, *Rauh* K68 (ZSS iso!). **Synon. nov.**

H. horrens var. *sphaerocarpus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ.1957). Type: Peru, Fortaleza river, Km 230, 1956, *Rauh* K48 (ZSS holo!). **Synon. nov.**

H. multangularis Ritter sensu, Kakt. Südamer. 4: 1400 (1981), nom. inval. (Art. 37.1, ICBN 2000) without type material.

H. pacalaensis Backeb., Die Cact. 2: 1202 (1960); Backeb. & F. M. Knuth, Kaktus-ABC: 412 (1935, publ. 1936); Backeb., Blätt. Kakt.-forsch. 1936(4): unpaged (1936). *Cereus tapalcalaensis* Backeb., Kakteenfreund 2(5): 54 (1933). Type locality: north of Peru, Malabrigo, (believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1204, fig. 1161 (1960). **Synon. nov.**

H. pacalaensis var. *longispinus* (Rauh & Backeb.) Krainz, Die Kakt. C. Va. (1962b). *H. laredensis* var. *longispinus* Rauh & Backeb. in Backeb. Die Cact. 2: 1195 (1960); Descr. Cact. Nov. [1]: 23 (1956, publ.1957). Type locality: Peru, Fortaleza valley, 500 m, (believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1200, fig. 1157 (1960). **Synon. nov.**

H. laredensis (Backeb.) Backeb. in Backeb. & F. M. Knuth, Kaktus-ABC: 208, 412 (1935, publ. 1936). *H. pacalaensis* var. *laredensis* (Backeb.) Krainz, Die Kakt. C. Va. (1962). *Cereus pseudomelanostele* var. *laredensis* Backeb., Kakteenfreund 2: 54 (1933). Type locality: north of Peru, close to Laredo, (believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1200, fig. 1156 (1960). **Synon. nov.**

H. pseudomelanostele subsp. *setosus* (Akers) Ostolaza, Zonas Aridas 7: 206 (2003). *H. pseudomelanostele* var. *setosus* (Akers) Backeb., Cact. Succ. J. (US) 23: 47 (1951). *Peruvocereus setosus* Akers, Cact. Succ. J. (US) 19(5): 68 (1947a). Type locality: Peru, south of Lima, Caracoles hills, (believed not to have been preserved). Lectotype (designated here): Akers, Cact. Succ. J. (US) 19(5): 67, fig. 41 (1947a).

H. pseudomelanostele var. *clavatus* (Akers) Backeb., Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 429 (1958), nom. inval. (Art. 33.2, ICBN 2000). *H. clavatus* (Akers) Cullmann, Kakt. And. Sukk. 8(12): 180 (1957), nom. inval. (Art. 33.2, ICBN 2000) given as a comb. nov., but without any indication of a basionym. *Peruvocereus clavatus* Akers, Cact. Succ. J. (US) 20(4): 55 (1948a). Type locality: Peru, Lima, north of Lurín river valley (believed not to have been preserved). Lectotype (designated here): Akers, Cact. Succ. J. (US) 20(4): 55, fig. 35 (1948a).

H. pseudomelanostele var. *chrysacanthus* (Akers) Ritter ex Krainz, Kat. ZSS 2: 65 (1967). *H. chrysacanthus* (Akers) Cullmann, Kakt. And. Sukk. 8(12): 180 (1957), nom. inval. (Art. 33.2, ICBN 2000). *Peruvocereus chrysacanthus* Akers, Cact. Succ. J. (US) 21(2): 45 (1949). Type locality: North of Lima, Km 226 of Panamericana highway, (believed not to have been preserved). Lectotype (designated here): Akers, Cact. Succ. J. (US) 21(2): 45, fig. 30 (1949).

Peruvocereus setosus var. *longicoma* Akers, Cact. Succ. J. (US) 19(6): 91 (1947b). Type locality: South of Lima, Caracoles hills, (believed not to have been preserved). Lectotype (designated here): Akers, Cact. Succ. J. (US) 19(6): 91, fig. 58 right (1947b). **Synon. nov.**

[*Cactus multangularis* Willd., Enum. Pl. Suppl.: 33 (1813). *Cereus multangularis* (Willd.) Haw., Suppl. Pl. Succ.: 75 (1819). *Binghamia melanostele* sensu (Vaupel) Britton & Rose, Cact. 2: 167 (1921) non *Cephalocereus melanostele* Vaupel (1913). *Binghamia multangularis* (Willd.) Britton & Rose, Cact. 4: 279 (1923). *Peruvocereus multangularis* (Willd.) Akers, Cact. Succ. J. (US) 22(6): 174 (1950). *H. akersii* Backeb. in Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 416 (1958), nom. inval. (Art. 36.1, 37.1, ICBN 2000) given as synonym of *Peruvocereus multangularis*. Type: believed not to have been preserved.].

Habit erect, up to 1.4(–1.7) m tall, branching at base; branches 4.0–8.0 cm diam., columnar, epidermis green; ribs 17–24, 6.0–11.0 × 2.0–3.5 mm, straight. Areoles 4.0–7.2 × 3.0–5.1 mm diam., 3.0–8.0 mm apart, oval to circular, felt white, yellow and grey. Spines opaque, yellow at first, later brownish and grey; central spines 0–2, 11.0–100.0 × 0.6–1.3 mm at base, ascending and descending; radial spines 21–56, 5.0–10.0 × 0.2–0.5 mm. Flowering areoles not differentiated. Flowers 5.0–10.0 × 2.5–4.25 cm; pericarpel 10.4 × 8.0–13.0 mm; tube 3.5–6.0 × 0.7–1.7 cm at base, widening towards apex to 1.5–2.7 cm diam., slightly curved, green, bearing short brown and yellow hair-spines emerging from the bract-scales axils; outer perianth-segments 12–20, 11.4–18.0 × 3.5–5.3 mm, greenish; inner perianth-segments 10–35, 10.7–18.0 × 3.8–6.6 mm, white; nectar-chamber 12.0–27.0 × 3.9–8.6 mm, tubular; anthers 1.6–5.0 × 0.5–1.1 mm; style 42.0–57.0 × 1.0–2.4 mm; stigma-lobes 9–13, 3.6–6.0 mm; ovary locule 6.0–8.5 × 3.5–7.0 mm, circular to elliptic in longitudinal section. Fruit 3.0–6.5 × 2.0–5.6 cm, spherical, pericarp red. Seeds broadly oval, medium-size, 1.26–1.40 × 0.89–1.03 × 0.69–0.75 mm, glossy; relief (SEM) convex; microrelief non-striated to weakly-striated; hilum large, 0.59–0.71 mm, oblique, forming an angle of 26°–54° with long axis of seed.

Habitat and Distribution: This taxon can be found in isolated arid areas and valleys in Lima, extending its range to the northern departments of Ancash, Lambayeque and La Libertad, 50–500(–780) m, and to the southern department of Ica, 1500–2000 m (**Map 6**).

Conservation status: Vulnerable. VU[A4c]. An inferred population size reduction of ≥30% over ten years, including both past and future time period, where the causes of its reduction have not ceased and a decline is observed in the area of occupancy, extent of occurrence and the quality of habitats (particularly those close to the vicinity of Lima).

Comments:

Britton & Rose (1920) misidentified this taxon as *Cephalocereus melanostele* Vaupel, which is the type of *Espostoa melanostele* (Vaupel) Borg., and created the genus *Binghamia* Britton & Rose, making the combination *Binghamia melanostele* (Vaupel) Britton & Rose. Later, Britton & Rose (1923) considered this species identical to *Cactus multangularis* Willd. (1809), based on a painting from Haworth's cacti living collection, and replaced *Binghamia melanostele* (Vaupel) Britton & Rose by *Binghamia multangularis* (Willd.) Britton & Rose. Later combinations have been made based on Willdenow's epithet multangularis, nevertheless, from its scant description and non-existent type, it is not possible to be certain which taxon actually *Cactus multangularis* Willd. refers to, and it is better left as a doubtful name (See **Appendix 2:** List of doubtful names attributed to the genus *Haageocereus*).

Werdermann and Backeberg (1931) did not accept *Bighamia* Britton & Rose as a genus and preferred to describe this species as *Cereus pseudomelanostele* establishing a relationship with the earlier but misplaced epithet of *Binghamia melanostele* (Vaupel) Britton & Rose. Later, Backeberg (1934) created the genus *Haageocereus*, making the combination *Haageocereus pseudomelanostele* (Werderm. & Backeb.) Backeb., which became the type species of the genus. As the genus *Binghamia* had been previously occupied by a genus of Algae (*Binghamia* Agardh 1894), the genus *Haageocereus* became widely used in the following years. In the absence of a type, the picture published with *Cereus*

pseudomelanostele Werderm. & Backeb. (1931) is being taken in this study to designate a lectotype.

Cereus chosicensis Werderm. & Backeb. (1931) lacks preserved type-material and no illustration was published with its description, bringing about the need to designate a neotype based on a photo published later by Backeberg (1960). *C. chosicensis* was later combined under *Haageocereus,* as *H. chosicensis* (Werderm. & Backeb.) Backeb. (1936c), and this name seems to be synonymous of *H. pseudomelanostele* because it shares most of the important diagnostic characters with *H. pseudomelanostele*, such as erect growth habit, numerous radial spines (30) and 19 ribs. *H. pseudomelanostele* and *H. chosicensis* were both described from nearby localities, at Rímac valley, which are not longer there because of housing. Nevertheless, Backeberg (1931) did not present any consistent difference between these names but the colour of flower, being reddish-lilac in *H. chosicensis* and white in *H. pseudomelanostele.* However this slight difference is not enough to consider *H. chosicensis* distinct at specific level and considering its type-locality is best placed as a synonym.

A number of taxa were described by Rauh & Backeberg for *Haageocereus* of central and northern localities of the Peruvian coast, such as *H. pacalaensis* Backeb. (1936c), *H. laredensis* Backeb. (1936c), *H. laredensis* var. *longispinus* Rauh & Backeb. (1957), *H. horrens* Rauh & Backeb. (1957) and *H. horrens* var. *sphaerocarpus* Rauh & Backeb. (1957). From these taxa, only *H. horrens* and *H. horrens* var. *sphaerocarpus* have types preserved and in the absence of types for the others, neotypes are being designated here from later illustrations published by Backeberg (1960). The slight differences among these taxa are related to the height, varying from 0.8–1.7 m tall, branch diameter (6.0–)7.0–8.5–(10.0) cm, rib number from 18–22, and numerous spines (40–45). All these characters fit within the variation recognized for *H. pseudomelanostele* subsp. *pseudomelanostele.* As result of the study of the protologues and available types, field observations in the type localities, further morphological and micro-morphological studies on seeds (SEM) from the type populations,

it is concluded that the names *H. pacalaensis, H. laredensis*, *H. laredensis* var. *longispinus, H. horrens,* and *H. horrens* var. *sphaerocarpus* are better placed as synonyms of *Haageocereus pseudomelanostele.*

Akers created the genus *Peruvocereus* (1947a) to describe a number of species, such as *P. setosus* Akers (1947a), *P. setosus* var. *longicoma* Akers (1947b), *P. clavatus* Akers (1948a), and *P. chrysacanthus* Akers (1949) and because he did not make types for these names, lectotypes are being designated here, based on the photos published within Akers's first descriptions. *P. setosus*, *P. setosus* var. *longicoma*, *P. clavatus* and *P. chrysacanthus* are mainly distinguished by presenting numerous bristle-spines, a character that has been observed to be variable in the field for populations of *Haageocereus pseudomelanostele*, and could well represent a form of this species. Photos available (lectotypes) and further field observation at the type localities of *P. setosus*, *P. setosus* var. *longicoma*, *P. clavatus*, and *P. chrysacanthus*, led to the conclusion that these taxa refer to *Haageocereus pseudomelanostele* subsp. *pseudomelanostele* and should be considered as its synonyms.

Ritter (1981) used *Cereus multangularis* Haw. (1819) to make the combination *Haageocereus multangularis* because he intended not to refer to *Cactus multangularis* Willd. (1813), or to any of the paintings subsequentely associated with this name (See **Appendix 2**: List of doubtful names attributed to the genus *Haageocereus*). According to Ritter, *Cereus multangularis* Haw. belonged to a different entity than *Cactus multangularis* Willd. In doing that, Ritter's combination excludes the type and is rendered invalid by lacking a type (Art. 37.1, ICBN 2000).

Haageocereus pseudomelanostele is characterized by its stems, undifferentiated flower-bearing areoles, slightly curved flower-tube, 17–24 ribs (the higher rib number for the genus) and 21–56 radial spines.

Haageocereus pseudomelanostele is subdivided in four subspecies: *H. pseudomelanostele* subsp. *pseudomelanostele*, *H. pseudomelanostele* subsp. *acanthocladus*, *H. pseudomelanostele* subsp. *carminiflorus* and *H. pseudomelanostele* subsp. *turbidus*.

Key to subspecies of *Haageocereus pseudomelanostele*

1. Areoles usually bearing long bristle-spines; inner perianth-segments white, sometimes pinkish; seeds small, 1.14–1.18 mm length (SEM) (central and northern Peru: Lima, Ancash, Lambayeque and La Libertad, 50–660 m) .....

   .....**6a. *H. pseudomelanostele* subsp. *pseudomelanostele***

   Areoles rarely bearing bristle-spines; inner perianth-segments white or reddish; seeds medium size, 1.26–1.40 mm length (SEM) (central and southern Peru: Lima and Ica valleys, 515–2000 m) **2**

2. Inner perianth-segments reddish (central Lima, Lurín and Santa Eulalia valleys, 930–1750 m) ..... **6c. *H. pseudomelanostele* subsp. *carminiflorus***

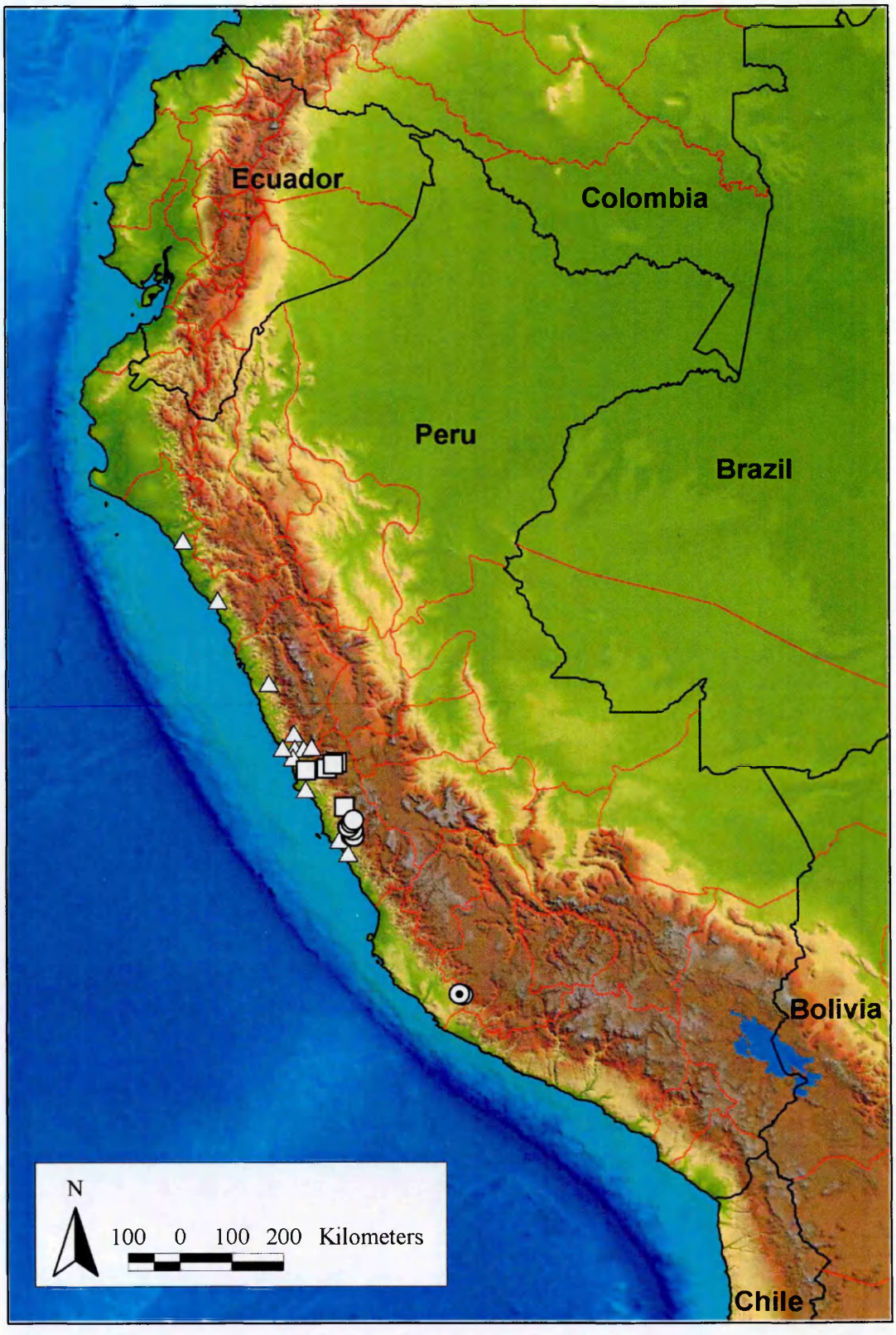
   Inner perianth-segments white (northern Lima and south-east of Ica) **3**

3. Fruits indehiscent (northern Lima: Chillón and Huaura valleys, 510–1980 m) .....

   ..... **6b. *H. pseudomelanostele* subsp. *acanthocladus***

   Fruits dehiscent (south-east Ica: Ica valley, 950–2000 m) .....

   .....**6d. *H. pseudomelanostele* subsp. *turbidus***



Map 6. *Haageocereus pseudomelanostele* subsp. *pseudomelanostele*=△; *Haageocereus pseudomelanostele* subsp. *acanthocladus*=□; *Haageocereus pseudomelanostele* subsp. *carminiflorus*=○; *Haageocereus pseudomelanostele* subsp. *turbidus*=⊙

6a. *Haageocereus pseudomelanostele* subsp. *pseudomelanostele*

Habit erect, up to 1.4(–1.7) m tall; branches straight, 4.0–7.0 cm diam.; ribs 18–24, 9.0 mm. Areoles 6.0–7.0 × 4.0–5.0 mm, 6.0 mm apart, bearing long bristle-spines. Central spines 1–2, 15.0–50.0 × 0.2–1.2 mm at base; radial spines 35–55, 5.0–15.0 × 0.2–0.4 mm at base. Flowers 4.0–7.5 cm; pericarpel 9.0–14.7 × 10.5–11.8 mm; tube 2.7–4.9 × 0.7–1.2 cm at base, widening towards apex to 1.75–2.1 cm diam.; outer perianth-segments 17–20, 10.7–15.3 × 4.0 mm, reddish and green; inner perianth-segments 24–27, 12.3–17.3.0 × 4.0–7.0 mm, pinkish, red or white; nectar-chamber 11.0–21.0 × 5.3–8.0 mm; anthers 2.3–2.4 × 1.0 mm; style 34.0–53.0 × 1.2–1.4 mm; stigma-lobes 10, 3.7–7.0 × 0.6 mm; ovary locule 6.0 × 4.8–10.0 mm, elliptic in longitudinal section. Fruit 4.0–4.5 × 5.0 cm, spherical to ovoid. Seeds broadly oval, medium-size, 1.14–1.18 × 0.79–0.90 × 0.62–0.70 mm, glossy; relief (SEM) convex; microrelief non-striated to weakly-striated; hilum large 0.34–0.68 mm, oblique, forming an angle of 44–64° with long axis of seed (**Fig. 7, Fig. 8: A–C; Plates 3.4–3.6, 12.1–12.4**).

Examined material: PERU. LIMA: Rímac valley, Lima–La Oroya road, Cajamarquilla, 500 m, 1 May 1980, *Carlos Ostolaza* 800065 (Herb. B. G. La Molina); loc. cit., 19 Nov. 1959, *Hoffmann* s/n (USM); Fortaleza valley, road towards Chasquitambo Km 40, 77°39'26.6''W, 10°21'55.9''S, 660 m, 4 Aug. 2005, *N. Calderón* 476 (Herb. B. G. La Molina); Pativilca valley, Km 239 Panamericana Norte, 77°51'6.0''W, 10°37'13.2''S, 250 m, 5 Nov. 2005, *N. Calderón* 338 (Herb. B. G. La Molina); loc. cit., road towards Ocros, 77°29'14.6''W, 10°37'47.7''S, 582 m, 6 Aug. 2005, *N. Calderón* 484 (Herb. B. G. La Molina); ANCASH: Casma-Huaraz road, 78°04'54''W, 09°30'33''S, 520 m, Nov. 2004, *N. Calderón* 361 (Herb. B. G. La Molina, seeds); LAMBAYEQUE: road towards Olmos, Km 722 Panamericana Norte, rocky hill, 79°33'53.8''W, 07°03'51.6''S, 50 m, Nov. 2004, *N. Calderón* 341 (Herb. B. G. La Molina); loc. cit., *G. Charles* 597.01 (Herb. B. G. La Molina, seeds).

Habitat and Distribution: This taxon can be found in very isolate arid areas and valleys in Lima, extending its range to the northern departments of Ancash, Lambayeque and La Libertad, 50–500(–780) m (**Map 6**).

Phenology: *Flowers:* December; *Fruits:* January.

Conservation status: Vulnerable. VU[B1ab(ii,iii,iv)]. The extent of occurrence is 17304.7 km^2, it is severely fragmented and continuing decline was observed in the area of occupancy and the quality of habitats and the number of subpopulations.

This subspecies has severely decreased in the localities where it used to predominate with habitat loss even worse for the last remaining localities surrounding Lima. For this reason, although it has an apparent wide distribution in central Peru, its situation is not free of concern.

Comments:

H. pseudomelanostele subsp. *pseudomelanostele* is characterized by areoles usually bearing long bristle-spines, small seeds (1.14–1.18) (SEM) and flowers with inner perianth-segments white to pinkish.

H. pseudomelanostele subsp. *pseudomelanostele* is sympatric with *H. acranthus* subsp. *acranthus* in Lima surrounding valleys, growing in association with *Tillandsia latifolia* Meyen (Bromeliaceae) and the very typical *Trixis cacalioides* D. Don (Asteraceae). Other cacti growing close to this subspecies in Lima are *Cleistocactus acanthurus* (Vaupel) Hunt and *Mila caespitosa* Britton & Rose. In the north, this subspecies can be found in sparse groups (Lambayeque) close to the coastal desert and, in dry valleys (Ancash) grows in association with *Neoraimondia arequipensis* (Meyen) Backeb, *Melocactus peruvianus* Vaupel and shrubs of *Trixis* sp. (Asteraceae).

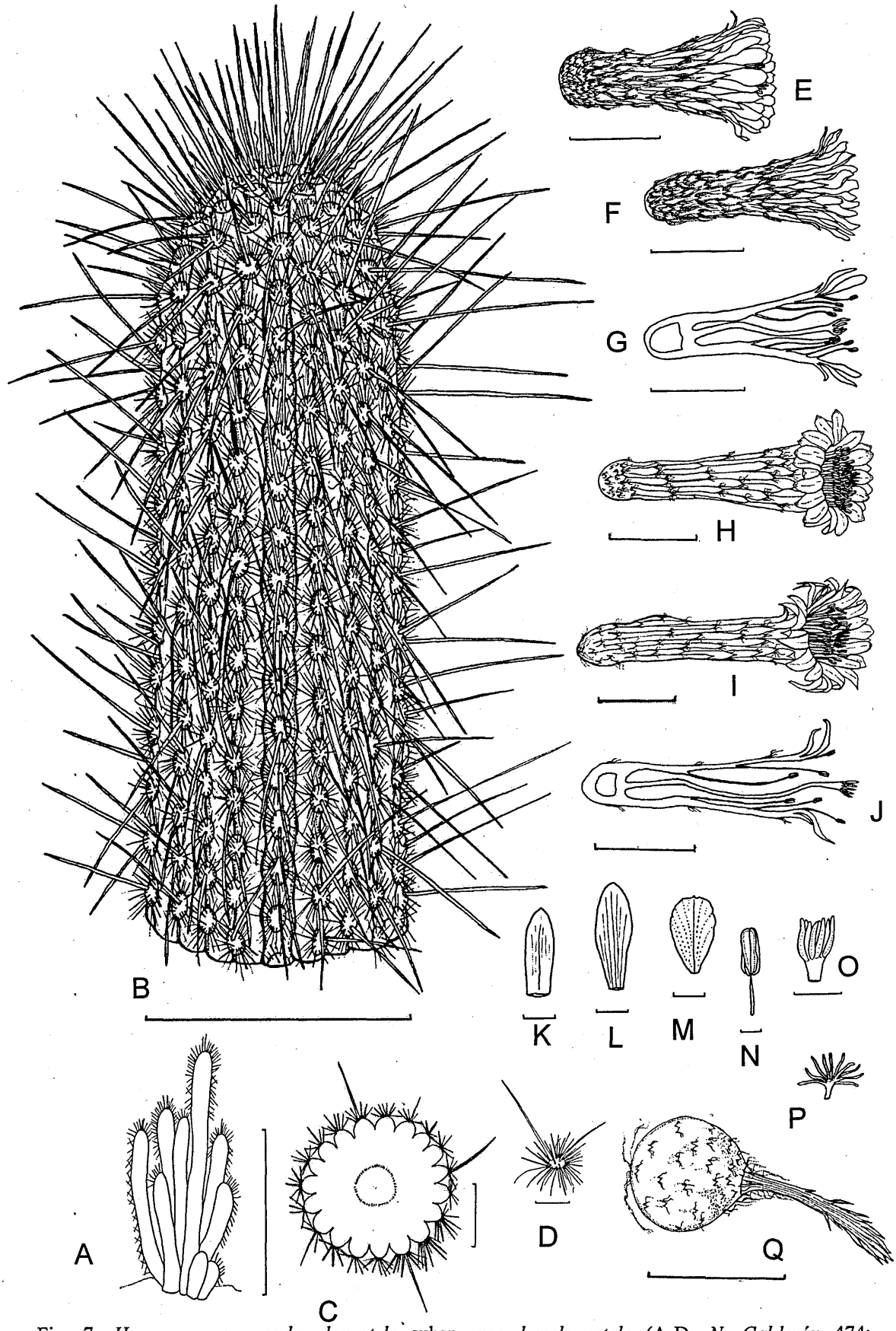


Fig. 7. *Haageocereus pseudomelanostele* subsp. *pseudomelanostele* (A-D, *N. Calderón* 474; E-G, K-O, *C. Ostolaza* s/n); *Haageocereus pseudomelanostele* subsp. *carminiflorus* (H,J,Q, *N. Calderón* 63; I,P, *N. Calderón* 175); A, habit (scale=50cm); B, stem (scale=5cm); C, transverse section of stem (scale=2cm); D, areole (scale=1cm); E-J, flower, side view and longitudinal section (scale=2cm); K, bract-scale(scale=5mm); L, outer perianth segment(scale=5mm); M, inner perianth segment(scale=5mm); N, anther (scale=1mm); O-P, stigma lobes(scale=5mm); Q, fruit (scale=3cm).

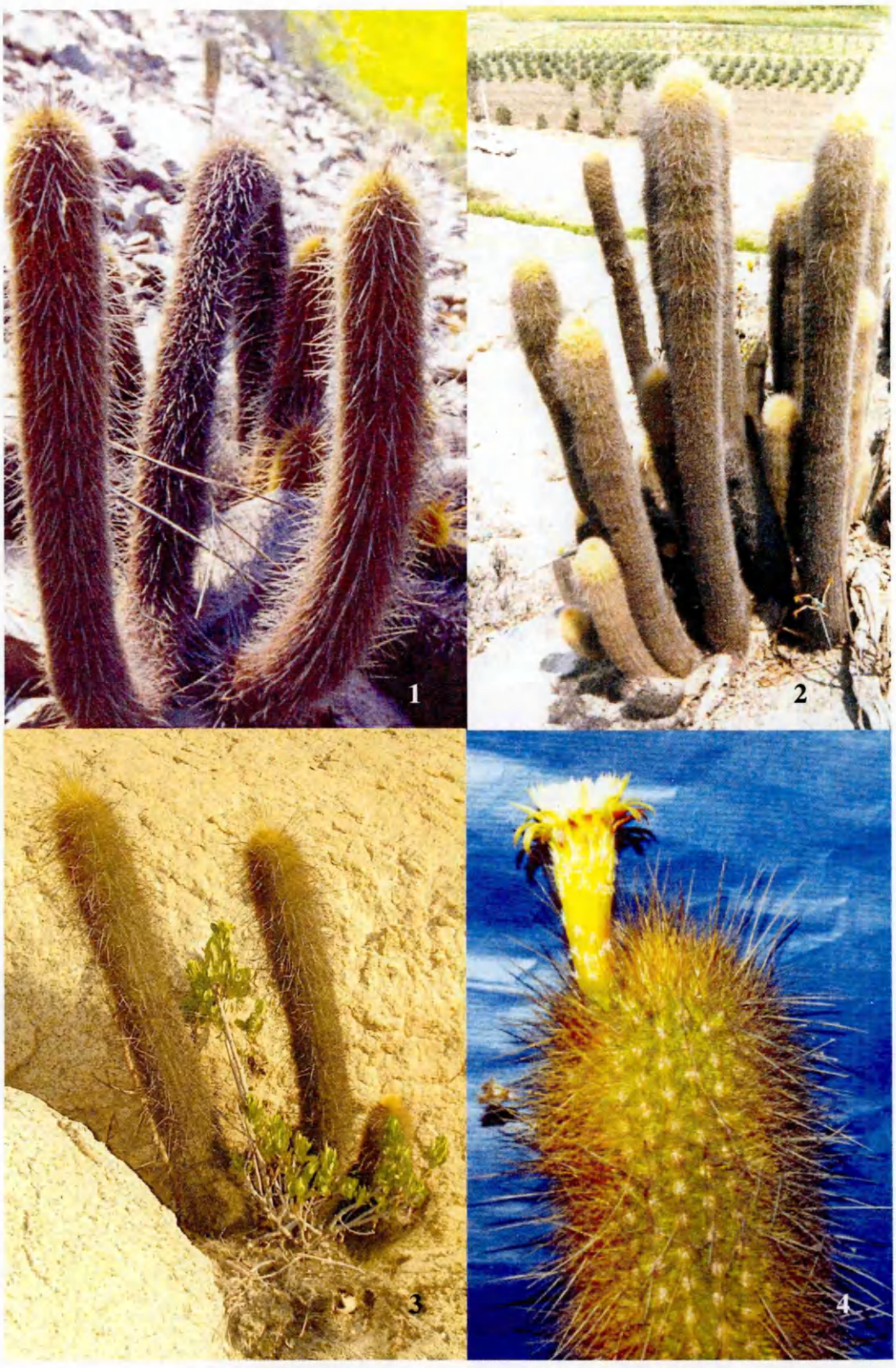


Plate 12. **12.1** *Haageocereus pseudomelanostele* subsp. *pseudomelanostele*. *N. Calderón* s.n., Chicama valley in La Libertad, 2003. **12.2** *Ibid.*, Picapiedra in the Lurín valley, 2001. **12.3** *Ibid.*, Fortaleza valley, 2005. **12.4** *Ibid., N. Calderón* 338, Pativilca valley, in flower.

6b. *Haageocereus pseudomelanostele* subsp. *acanthocladus* (Rauh & Backeb.) Ostolaza in Ostolaza et al. Brit. Cact. Succ. J. 21(2): 94 (2003). *H. acanthocladus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 23 (1956, publ. 1957); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 408 (1958); Backeb., Die Cact. 2: 1200 (1960). Type: Peru, Lima, Churín valley, Sayán, 900 m, 1956, *Rauh* K90 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: annex of photos, unpaged, fig. 85 (1960).

H. aureispinus Rauh & Backeb. in Rauh Beitr. Kenntn. Peruan. Kakt. veg.: 404 (1958). *H. pseudomelanostele* var. *aureispinus* (Rauh & Backeb.) Ostolaza, Brit. Cact. Succ. J. 14 (4):170 (1996). *H. pseudomelanostele* subsp. *aureispinus* (Rauh & Backeb.) Ostolaza, Cactaceae Consensus Initiatives 6: 9 (1998). Type: Peru, Lima, Chillón valley, Canta, 800–1000 m, 1956, *Rauh* K170 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: annex of photos, unpaged, fig. 86 (1960). **Synon. nov.**

H. pachystele Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ. 1957). Type: Peru, Lima, Churín valley, 900 m, 1956, *Rauh* K91 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1236, fig. 1199 (1960).

H. symmetros Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ. 1957). Type: Peru, Lima, Churín valley, 1200 m, 1956, *Rauh* K102 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1232, fig. 1195 (1960).

H. viridiflorus (Akers) Backeb., Die Cact.2: 1195 (1960). *Peruvocereus viridiflorus* Akers, Cact. Succ. J. (US) 19: 143 (1947e). Type locality: Peru, Chillón river, about 10 km above Santa Rosa de Quives (believed not to have been preserved). Neotype (designated here): Akers, Cact. Succ. J. (US) 19: 143, fig. 95 (1947e). **Synon. nov.**

?H. aureispinus var. *fuscispinus* Rauh & Backeb. in Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 407 (1958). Type: Peru, Lima, Canta (Chillón valley), 800–1000 m, 1956, *Rauh* K170b (HEID, believed not to have been preserved).

?H. rigidispinus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 26 (1956, publ. 1957). *H. aureispinus* var. *rigidispinus* Rauh & Backeb, Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 407 (1958), nom. inval. (Art. 33.2, ICBN 2000) based on *H. rigidispinus*. *H. aureispinus* var. *rigidispinus* (Rauh & Backeb.) Rauh & Backeb. in Backeb. Die Cact. 2: 1198 (1960). Type: Peru, Lima, Chillón valley, Canta, 800–1000 m, 1956, *Rauh* K170a (HEID, believed not to have been preserved).

Habit erect, up to 1.4 m tall; branches 5.8–7.5 cm diam.; ribs 17–22(–24), 6.0–11.0 mm. Areoles 4.0–7.2 × 3.0–5.1 mm diam., 3.0–8.0 mm apart. Central spines 0–2, 11.0–47.0 × 0.7–1.3 mm at base; radial spines (21–)25–56, 5.0–10.0 × 0.2–0.4 mm at base, yellow, brown, brownish red and grey. Flowers 7.3–7.6(–10.0) × 3.2–3.5 cm; pericarpel 12.0 × 9.0–11.0 mm; tube 4.3 × 0.8–1.1 cm at base, widening towards apex to 2.0–2.5 cm diam.; outer perianth-segments 20, 13.4–16.2 × 3.5–5.3 mm, greenish; inner perianth-segments 35, 12.0–18.0 × 5.5–6.6 mm, white; nectar-chamber 17.0–18.5 × 4.7–5.6 mm; anthers 2.7–4.2 × 0.5–1.1 mm; style 50.0–55.0 × 1.0 mm; stigma-lobes 11–13, 5.0–6.0 mm; ovary locule 8.0–8.5 × 5.0–7.0 mm, circular to elliptic in longitudinal section. Fruit 4.5–6.5 × 4.2–5.6 cm, spherical, indehiscent. Seeds broadly oval, medium-size, 1.26–1.29 × 0.98–1.03 × 0.74–0.75 mm, glossy; relief (SEM) convex; microrelief without cuticular striations; hilum large, 0.63–0.71 mm, oblique, forming an angle of 42°–54° with long axis of seed (**Fig. 8: E–G, K–O; Plates 4.4, 4.5, 13.1–13.3**).

Examined material: PERU. LIMA: Huaura valley, Sayán, 700 m, 9 June 2002, *N. Calderón* 250, 251, 252 (Herb. B. G. La Molina); loc. cit., Cerro Blanco, 900 m, 9 June 2002, *N. Calderón* 255, photo; loc. cit., road towards Cochamarca, 77°05'26.6''W, 10°58'15.3''S, 1520 m, 17 Feb. 2004, *N. Calderón* 372, 375 (Herb. B. G. La Molina); loc. cit., road towards Paccho, 76°58'38.5''W, 10°53'40.9''S, 1720 m, 18 Feb. 2004, *N. Calderón* 387 (Herb. B. G. La Molina); loc. cit., 76°58'40.3''W, 10°53'42.5''S, 1746m, 5 March 2005, *N. Calderón* 428, 434, 435, 438, 439, 440, 442, 442.1 (Herb. B. G. La Molina); Chillón valley, Umarcata

hill, Km 69 Lima–Canta road, 76°46'54''W, 11°37'23.4''S, 1260 m, 20 Sept. 2003, *N. Calderón* 333, 334, 335, 336 (Herb. B. G. La Molina).

Habitat and Distribution: Found in Huaura and Chillón valleys in central and northern Lima, 515–1750 m (**Map 6**).

Phenology: *Flowers:* June and July; *Fruits:* June, July and August.

Conservation status: Endangered. EN[B1ab(ii,iii)]. The extent of occurrence is estimated to be 2559.77 km^2; it is known to exist at no more than four locations and continuing decline was observed in the area of occupancy and the quality of habitats.

Comments:

This taxon was first described by Rauh & Backeberg (1957) for a cactus growing in the Huaura valley and, because type material was not preserved, a photograph published later by Backeberg (1960) is being proposed as neotype.

H. viridiflorus (Akers) Backeb. (1960), was first described by Akers (1947e) under the genus *Peruvocereus* for a species growing in the Chillón valley, which was distinguished by -sometimes- presenting a green to greenish-white flower; and in the absence of type-material, a lectotype is being designated here from the illustration published alongside the original description by Akers (1947e). According to the description, illustrations and study at the type locality *H. viridiflorus* is better recognized as a synonym of *H. pseudomelanostele* subsp. *acanthocladus.*

Rauh & Backeberg (1957, 1958) also described for the Huaura valley *H. pachystele* and *H. symmetros;* and for the Chillón valley, *H. aureispinus*, *H. aureispinus* var. *fuscispinus* and *H. rigidispinus*. As types were not preserved for any of these names, neotypes are being designated when illustrations are available, based on later photographs published by Backeberg (1960). According to the descriptions of all these names, they refer to erect plants of 17–24 number of ribs, areoles rarely bearing bristles but with (21–)25–56 radial spines, flowering areoles not clearly differentiated, bearing white flowers (inner perianth-segments)

and indehiscent fruits. All these characters fit well within the circumscription of *H. pseudomelanostele* subsp. *acanthocladus*. Field studies at the type-localities of *H. pachystele, H. symmetros* and *H. aureispinus* led to the conclusion that these names are synonyms of *H. pseudomelanostele* subsp. *acanthocladus*.

For the names *H. rigidispinus* Rauh & Backeb. (1957) and *H. aureispinus* var. *fuscispinus* Rauh & Backeb. (1958), which do not have any illustration available, it is difficult to be completely certain that they are synonyms of *H. pseudomelanostele* subsp. *acanthocladus*. Nevertheless, *H. rigidispinus* and *H. aureispinus* var. *fuscispinus* were described for the same type locality of *H. pseudomelanostele* subsp. *acanthocladus,* presenting similar characters to this subspecies.

H. pseudomelanostele subsp. *acanthocladus* is characterized by white flowers, areoles rarely bearing bristles-spines, seeds medium size (1.26–1.29 mm) and indehiscent fruits.

H. pseudomelanostele subsp. *acanthocladus* is sympatric with *H. acranthus* subsp. *backebergii* in the Chillón valley, and with *H. acranthus* subsp. *zonatus* in the Huaura, Fortaleza and Pativilca valleys. In all these valleys, it usually lives with *Espostoa melanostele* (Vaupel) Borg., *Neoraimondia arequipensis* subsp. *roseiflora* (Werderm. & Backeb.) Ostolaza, *Melocactus peruvianus* Vaupel, and other succulent plants such as *Cnidoscolus basiacanthus* (Pax & K. Hoffm.) J.F. Macbr. and *Jatropha macrantha* Müll. Arq. (both Euphorbiaceae). Other cacti living with this taxon in the Chillón valley are *Mila nealeana* Backeb., *Austrocylindropuntia pachypus* (K. Schum.) Backeb. and *Cleistocactus acanthurus* (Vaupel) Hunt.

Intergeneric hybrids between *H. pseudomelanostele* subsp. *acanthocladus* and *Espostoa melanostele* (×*Haagespostoa*) can be found in the Huaura valley, being more common towards Ancash department, where large populations of hybrids have been seen in the Fortaleza and Pativilca valleys.

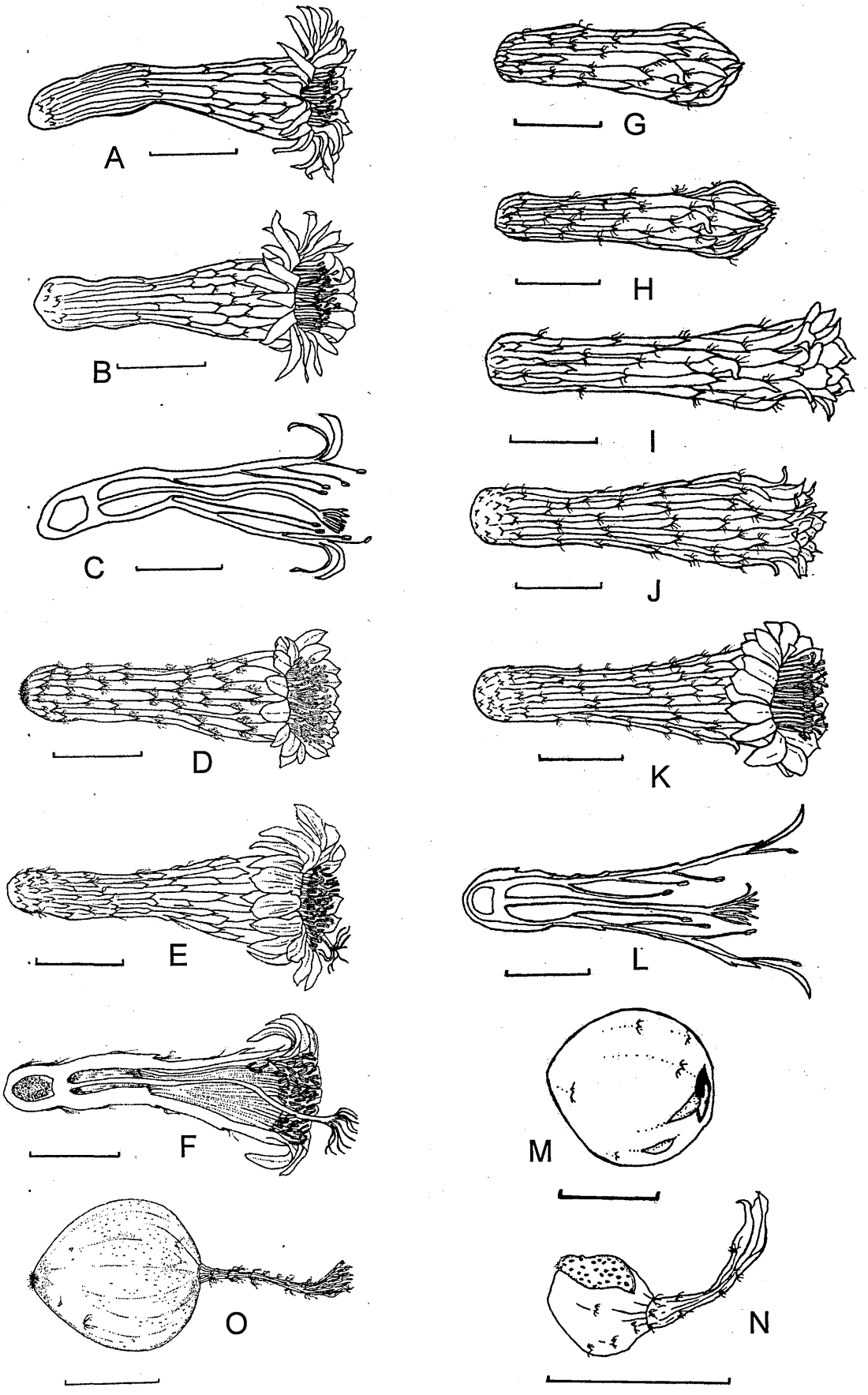


Fig. 8. *Haageocereus pseudomelanostele* subsp. *pseudomelanostele* (A-C, *N. Calderón* 338; D, *N. Calderón* 232); *Haageocereus pseudomelanostele* subsp. *acanthocladus* (E-G, K-O, *N .Calderón* 250); *Haageocereus pseudomelanostele* subsp. *turbidus* (G-L, *N. Calderón* 273; M-N, *N. Calderón* 276); A-L, flower, side view and longitudinal section (scale=2cm); M-O, fruits (scale=3cm).

Plate 13. **13.1** Habitat of *Haageocereus pseudomelanostele* subsp. *acanthocladus*. Paccho hills in the Huaura valley, 2005. **13.2** *Ibid.*, *N. Calderón* s.n., in fruit. **13.3** *Ibid.*, *N. Calderón* 255, in flower.

6c. *Haageocereus pseudomelanostele* subsp. *carminiflorus* (Rauh & Backeb.) Ostolaza, Cact. Consensus Initiatives 6: 9 (1998a). *H. pseudomelanostele* var. *carminiflorus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21 (1956, publ. 1957); ibid., Die Cact. 2: 1228 (1960); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 428 (1958); Ostolaza, Brit. Cact. Succ. J. (14) 4: 167 (1996). Type locality: Peru, Lima, Santa Eulalia valley, 1000 m, 1956, *Rauh* K20 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1229, fig. 1192 (1960).

Habit erect, up to 1.4 m tall; branches 4.0–5.0 cm diam.; ribs 18–23, 5.0–6.9 × 3.0–4.7 mm. Areoles 4.0–6.0 × 3.4–4.3 mm, 3.5–4.0 mm apart, oval to circular. Central spines 1–2, 18.0–40.0 × 0.6–1.1 mm at base; radial spines 40–50, 5.0–10.0 × 0.2–0.5 mm at base. Flowers 6.3–8.8 × 2.5–4.25 cm; pericarpel 10.5–13.0 × 8.0–13.0 mm; tube 3.5–6.0 × 0.7–1.4 cm at base, widening towards apex to 1.5–2.0 cm diam.; outer perianth-segments 12–19, 11.4–18.0 × 3.8–5.1 mm, reddish; inner perianth-segments 10–16, 10.7–16.5 × 3.8–5.1 mm, reddish; nectar-chamber 12.0–27.0 × 3.9–8.6 mm; anthers 2.6–5.0 × 0.7–0.9 mm; style 42.0–57.0 × 1.1–2.4 mm; stigma-lobes 9–11, 3.6–5.4 × 0.6–0.8 mm; ovary locule 6.0–7.5 × 3.5–5.5 mm, cylindric to elliptic in longitudinal section. Fruit 3.4–3.5 × 4.0–4.5 cm, spherical to ovoid, indehiscent, pericarp red. Seeds broadly oval, medium-size, 1.40 × 1.03 × 0.75 mm, glossy; relief (SEM) convex; microrelief without cuticular striations; hilum large, 0.66 mm, oblique, forming an angle of 26° with long axis of seed (**Plates 4.1–4.3, 14.5, 14.6**).

Examined material: PERU. LIMA: Lurín valley, Tinajas canyon, 76°39'50.3''W, 12°07'05.2''S, 1282 m, 23 Jan. 2002, *N. Calderón* 175a (Herb. B. G. La Molina); loc. cit., 24 July 2005, *N. Calderón* 470, 471 (Herb. B. G. La Molina); loc. cit., 76°37'9.7''W, 12°07'33.9''S, 1743 m, 24 July 2005, *N. Calderón* 472, 473, 475 (Herb. B. G. La Molina); Santa Eulalia valley, Barba Blanca, 76°37'37.4''W, 11°50'51.8''S, 1400 m, 11 Feb. 2003, *N. Calderón* 298a (Herb. B. G. La Molina); loc. cit., 19 Aug. 2005, *N. Calderón* 501.1, 501.2, 509 (Herb. B. G. La Molina).

Habitat and Distribution: Found in the Lurín and Santa Eulalia valleys, in central Lima, 930–1750 m (**Map 6**).

Phenology: *Flowers:* July and November; *Fruits:* August and December.

Conservation status: Endangered: EN[B1ab(ii,iii)+2ab(ii,iii)]. The extent of occurrence is estimated to be 186.3 km^2, and the Area of Occupancy is estimated to be 66.4 km^2, and it is known to exist at no more than two locations, and continuing decline was observed in the area of occupancy and the quality of habitats.

Comments:

This subspecies was first described as *Haageocereus pseudomelanostele* var. *carminiflorus* by Rauh & Backeberg (1957) for a population growing in the Santa Eulalia valley and, because type material was not preserved, a photograph published later by Backeberg (1960) is being used to designate a neotype.

H. pseudomelanostele subsp. *carminiflorus* is characterized by its reddish flowers, sometimes with the perianth-limb slightly zygomorphic, areoles rarely bearing bristles-spines and seeds medium size.

H. pseudomelanostele subsp. *carminiflorus* is sympatric with *H. acranthus* subsp. *backebergii* in Santa Eulalia valley, where it also lives with other cacti, such as *Austrocylindropuntia pachypus* (K. Schum.) Backeb., *Cleistocactus acanthurus* (Vaupel) Hunt and *Espostoa melanostele* (Vaupel) Borg., forming with the latter species the intergeneric hybrid ×*Haagespostoa*. In the Lurín valley, this taxon is also found growing with *H. acranthus* subsp. *backebergii*, and also grows with *E. melanostele* and froms hybrids.

6d. *Haageocereus pseudomelanostele* subsp. *turbidus* (Rauh & Backeb.) Ostolaza, Cact. Consensus Initiatives 6: 9 (1998a). *H. turbidus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 25 (1956, publ. 1957); Die Cact. 2: 1217 (1960); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 425 (1958); *H. multangularis* var. *turbidus* (Rauh & Backeb.) Ritter, Kakt. Südamer. 4: 1416 (1981). *H. pseudomelanostele* var. *turbidus* (Rauh & Backeb.) Ostolaza, Brit. Cact. Succ. J.: 16(3): 132 (1998c). Type locality: Peru, Ica, Nazca valley, 1200 m, 1956, *Rauh* K105 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1223, fig. 1185 (1960).

H. turbidus var. *maculatus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 25 (1956, publ. 1957). Type locality: Peru, Ica, Nazca valley, 1200 m, 1956, *Rauh* K110 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1224, fig. 1186 (1960).

Habit erect, up to 1.4 m tall; branches 5.0–8.0 cm diam., columnar, epidermis green; ribs 19, 7.0–11.1 × 2.0–3.5 mm, straight. Areoles 4.7–5.2 × 3.9–4.8 mm diam., 4.6–5.4 mm apart, oval to circular. Central spines 1–2, 50.0–100.0 × 0.7–1.0 mm at base; radial spines 35–45, 7.5–9.0 × 0.20 mm at base. Flowers 5.0–8.0 × 2.5 cm; pericarpel 10.4 × 9.0 mm; tube 5.5 × 1.1–1.7 cm at base, widening towards apex to 2.7 cm; outer perianth-segments reddish-green; inner perianth-segments 15.0 × 3.0 mm, white; nectar-chamber 15.2 × 8.2 mm; anthers 1.6 × 0.54 mm; style 45.7 × 1.6–2.2 mm; stigma-lobes 10, 7.0–8.0 mm; ovary locule 6.4 × 4.8 mm, cylindric to elliptic in longitudinal section. Fruit 3.0–4.0 × 2.0–3.0 cm, spherical, dehiscent, pericarp reddish. Seeds oval, medium-size, 1.35 × 0.89 × 0.69 mm glossy; relief (SEM) convex; microrelief without cuticular striations; hilum large, 0.59 mm, oblique, forming an angle of 39° with long axis of seed (**Fig. 8: G–L, M–N; Plates 4.6, 14.1–14.4**).

Examined material: PERU. ICA: Nazca, Km 30 Puquio–Nazca road, 1500 m, 26 May 2002, *N. Calderón* 273, 276 (Herb. B. G. La Molina).

Habitat and Distribution: Found in the rocky arid mountains of Nazca, 1200–2000 m (**Map 6**).

Phenology: *Flowers:* May; *Fruits:* May.

Conservation status: Critically Endangered. CR[B2ab(iii)]. The area of occupancy is less than 10 km^2. This subspecies is known to exist at no more than one location, and continuing decline has been observed in the quality of habitat.

Comments:

This subspecies was first described as *Haageocereus turbidus* by Rauh & Backeberg (1957) at the Nazca valley. Unfortunately, type material was not preserved and a photograph published later by Backeberg (1960) is being designated as neotype.

H. turbidus var. *maculatus* was described by Rauh and Backeberg (1957) but its type-material was not preserved. However, *H. turbidus* var. *maculatus* occurs together with *H. turbidus* and differs in spine colour. Such a character was observed in the field and proved to be rather variable, not granting the recognition of the population at a taxonomic level, therefore *H. turbidus* var. *maculatus* is here considered as a synonym.

H. pseudomelanostele subsp. *turbidus* is mainly distinguished by presenting dehiscent fruits, a unique feature for the genus, also uncommon in Trichocereeae.

This subspecies grows together with *Browningia candelaris* Britton & Rose and very little vegetation in this arid and rocky landscape.

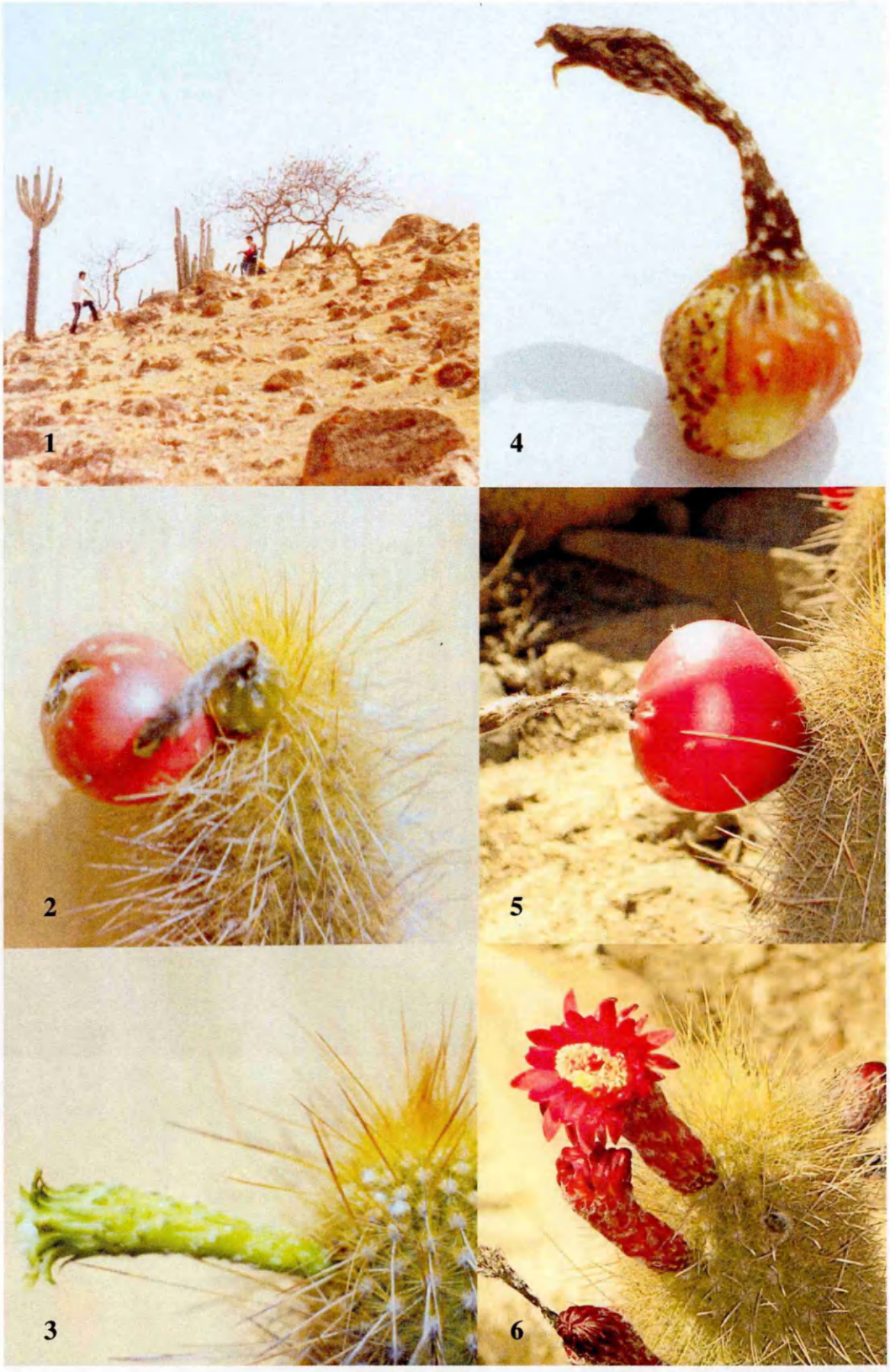


Plate 14. **14.1** Habitat of *H. pseudomelanostele* subsp. *turbidus*. Nazca desert in Ica, 2002. **14.2** *Ibid.*, *N. Calderón* 276, in fruit. **14.3** *Ibid.*, *N. Calderón* 273, in flower. **14.4** *Ibid.*, *N. Calderón* 276, in fruit. **14.5** *H. pseudomelanostele* subsp. carminiflorus *N. Calderón* 470, in fruit. **14.6** *Ibid.*, *N. Calderón* 475, in flower.

7. *Haageocereus repens* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 26 (1956, publ. 1957); Die Cact. 2: 1241 (1960); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 398 (1958). *H. pacalaensis* var. *repens* (Rauh & Backeb.) Krainz, Die Kakteen 1(12): CVa, unpaged (1962b). *H. pacalaensis* subsp. *repens* (Rauh & Backeb.) Ostolaza, Brit. Cact. Succ. J. 18 (3): 130 (2000). Type: Peru, La Libertad, sandy desert between Casma and Trujillo, 1956, *Rauh* K88 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1243, fig. 1208 (1960).

Habit semi-decumbent, branching at base; branches, 4.5–5.4(–8.0) cm diam., 1.0–2.0 m long., part of branches growing erect ≥20.0 cm above the ground, epidermis green; ribs 19–20. Areoles 4.0–5.0 × 2.0–3.0 mm, 5.0–10.0 mm apart, oval, felt grey. Spines opaque, at first yellow and brown, later grey; central spines 1(–2), 15.0–30.0 × 0.4–0.6 mm at base, ascending and descending; radial spines (25–)30–40, 5.0–10.0 × 0.2–0.3 mm at base. Flowering areoles not differentiated. Flowers 7.0 × 3.5 cm; tube markedly curved, green, bearing few hair-spines emerging from the bract-scale axils; outer perianth-segments reddish-brown; inner perianth-segments white; nectar-chamber 13.0 × 6.0 mm, tubular. Fruit ovoid. Seeds broadly oval, medium-size, 1.48 × 1.04 × 0.77 mm, semi-matt; relief (SEM) convex; microrelief with strong cuticular striations; hilum large, 0.64 mm, oblique, forming an angle of 42° with long axis of seed (**Fig. 9, Plates 5.1–5.3, 15.1–15.3**).

Examined material: PERU. LA LIBERTAD: South of Trujillo, Km 546 Panamericana highway, sandy desert, 78°56'40''W, 8°13'42.7''S, 130 m, 18 Nov. 2003, *N. Calderón* 358 (Herb. B. G. La Molina); loc. cit., *G. Charles* 254.01 (seeds, private collection).

Habitat and Distribution: Found in sandy desert in northern Peru, 130 m (**Map 4**).

Phenology: *Flowers:* November; *Fruits:* November.

Conservation status: Critically Endangered: CR[B2ab(ii,iii)]. The Area of occupancy is estimated to be less than 3 km^2; and it is known to exist only in a single location, and continuing decline has been observed in the area of occupancy and in the quality of habitat.

The habitat of *Haageocereus repens* is likely to disappear as a result of the agricultural pressure from the Chavimochic irrigation project for growing asparagus and other crops.

Comments:

The species was first described by Backeberg and Rauh (1957) but its material was either never preserved or subsequently lost. A neotype is being designated here with basis on an illustration published slightly later by Backeberg (1959).

H. repens was combined as *H. pacalaensis* var. *repens* (Rauh & Backeb.) Krainz (1962b), and later as *H. pacalaensis* subsp. *repens* (Rauh & Backeb.) Ostolaza (2000) because the growth habit was considered the one difference between the populations of *H. repens* Backeb. & Rauh (prostrate stems) and *H. pacalaensis* Rauh & Backeb. (erect stems).

During a study visit to the type locality, the species was observed growing semi prostrate, sometimes with few stems creeping, and with flowers with a markedly curved tube. The study of the seeds has shown a strong striate cuticle (SEM). All these characters contrast with the erect growing habit, slightly curved flowers and seeds without striations presented in *H. pacalaensis* Rauh & Backeb., suggesting that *H. repens* Rauh & Backeb. should be accepted at specific level. *H. pacalaensis* Rauh & Backeb., on the other hand, is being treated in this study as synonym of *H. pseudomelanostele* (Werderm. & Backeb.) Backeb.

H. repens is characterized by a semi-prostrate, instead of totally decumbent habit (hence its epithet), markedly curved flowers and strong striated cuticle of the seeds (SEM), these characters hypothesized as apomorphic.

No other plants are found growing in the same habitat and the closest populations of *H. pseudomelanostele* are found 20 km north-east, in the Moche valley.

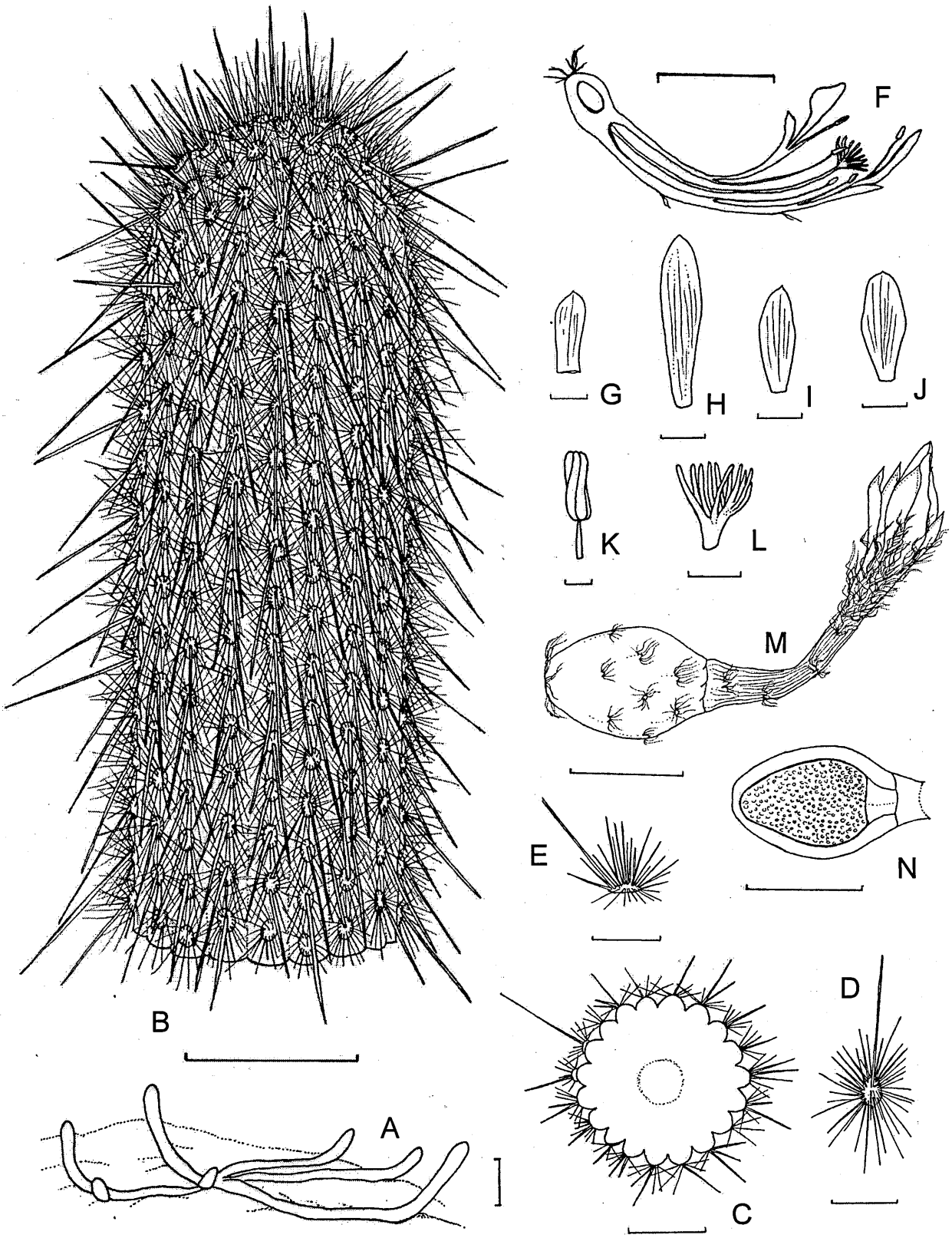


Fig. 9. *Haageocereus repens* (A-N, *N. Calderón* 358); A, habit (scale=20cm); B, stem (scale=3cm); C, transverse section of stem (scale=2cm); D-E, areoles (scale=1cm); F, flower (2cm); G, bract scale (scale=5mm); H, outer perianth segment (scale=5mm); I-J, inner perianth segment (scale=5mm); K, anther (scale=1mm); L, stigma lobes (scale=5mm); M-N, inmature fruits, side view and longitudinal section (scale=1.5cm).

Plate 15. **15.1** *Haageocereus repens. N. Calderón* s.n, South of Trujillo, 2003. **15.2** *Ibid., N. Calderón* 358. **15.3** *Ibid., N. Calderón* 358, in flower.

8. *Haageocereus tenuis* Ritter, Kakt. Südamer. 4: 1421 (1981); Ostolaza & Rauh, Kakt. And. Sukk. 41(2): 44 (1990). Type: PERU, Lima, between Chancay and Huacho, near Panamericana norte highway, July 1956, *Ritter* FR126e (U holo!).

H. australis f. *subtilispinus* Ritter, Kakt. Südam. 3: 1127 (1980). Type: Chile, Pisagua, Junín, 1954, *Ritter* FR126a (U holo!). **Synon. nov.**

Habit decumbent, branching at base and along the main stems, each individual occupying up to 2 m^2 area; branches prostrate with ascending apices up to 5.0–10.0 cm, 1.4–3.4 cm diam., 0.3–1.0 m long., epidermis green; ribs 12–15, 1.5–2.5 × 4.0–5.0 mm, straight. Areoles 1.6–2.9 × 1.2–2.0 mm, 2.0–4.0 mm apart, oval to circular, felt white and brownish. Spines opaque, light brown at first, later greyish, covered by trichomes visible with lens; central spines 1–2, 3.0–12.0 × 0.3–0.8 mm at base, ascending and descending; radial spines 28–35, 2.0–8.5 × 0.25–0.4 mm at base. Flowers (6.5–)8.0–11.5 × 6.0–8.0 cm; pericarpel 12.0–14.0 × 6.0–10.0 mm; tube 5.0–7.0 × 0.8–1.1 cm at base, widening towards apex to 1.8–2.25 cm, curved to markedly curved, reddish green, bearing short white trichomes emerging from the bract-scale axils; outer perianth-segments 10, 6.0–24.0 × 3.0–5.0 mm, reddish green; inner perianth-segments 17, 13.0–28.0 × 5.0–7.0 mm, white; nectar-chamber 18.0–26.0 × 3.0–4.0 mm, tubular, curved; anthers 2.5–3.0 × 0.4–0.8 mm; style 38.0–60.0 × 0.8–0.9 mm; stigma-lobes 9–11, 3.5 mm; ovary locule 4.0 × 8.0 mm, circular to elliptic in longitudinal section. Fruit 2.2–2.6 × 1.3–1.8 cm, spherical to ovoid, funicular pulp translucent pink. Seeds broadly oval, medium-size, 1.63 × 1.15 × 0.9 mm, semi-matt; relief (SEM) convex; microrelief with strong cuticular striations; hilum large, 0.83 mm, oblique, forming an angle of 40–45° with long axis of seed (**Fig. 10; Plates 5.4–5.6, 16.1–16.3**).

Examined material: PERU. LIMA: Halfway between Chancay and Huacho, at the Panamericana, July 1956, *Ritter* FR126e (U holo); Huaral, Km 118 of Panamericana norte highway, 77°27'12.5''W, 11°19'46''S, 376 m, 16 Feb. 2004, *N. Calderón* 364, 365, 369, 371 (Herb. B. G. La Molina); loc. cit., 4 March 2005, *N. Calderón* 419, 420 (Herb. B. G. La

Molina); loc. cit., 19 Sept. 2001, *N. Calderón* 138 (Herb. B. G. La Molina). CHILE: Pisagua, Junín, 1954, *Ritter* FR126a (U holo).

Habitat and Distribution: Found on the Pacific coastal desert: in Peru is located in northern Lima 274–380 m, and in Chile is reported for Junín, Pisagua (Map 4).

My observations of living plants of *H. tenuis* in Peru are based on populations found adjacent to the Panamericana norte highway Km 118, being highly probably the same location where Ritter collected the type. This area is a sandy esplanade, where the soil is composed by sand and mollusc-shell fragments that receive the constant sea breeze. Another small group of *H. tenuis* is found 1 km to the east of this location, on a small rocky hill.

This species may occur, far to the south, in the coast of Junín (Chile), according to Ritter's collection 126a (U) which he described as *H. australis* f. *subtilispinus* (1980). This collection constitutes the first record of *H. tenuis* in Chile.

Phenology: *Flowers:* January and February; *Fruits:* February and March.

Conservation status: In Peru, Critically Endangered: CR[B2ab(ii,iii,v)]. The area of occupancy is estimated to be 3 km^2 and population size to be of 252 individuals (Ceroni unpubl.). This species is known to exist only in a single location where continuing decline was observed in the area of occupancy, the quality of habitat and the number of mature individuals. The most evident threat for this species is the proximity to the Panamericana norte highway, which opens up a path where the wind blows plastic and paper residue (bottles, bags, etc.) into the desert, and even feathers from nearby chicken farms, covering the stems of *H. tenuis*. Other risk is further urban expansion along the busy highway. Currently, this species is being successfully conserved at La Molina University Botanic Garden as result of *ex situ* conservation activities this institution undertakes.

The current state of this species in Chile is unknown and further fieldwork is necessary to clarify if this species still exists in that place.

Comments:

Haageocereus tenuis was collected by Ritter in 1956 in one of his various expeditions to the Peruvian south coast, although the formal publication of the species only happened 25 years

later (Ritter 1981). Ostolaza & Rauh (1990) published a more complete diagnosis with reproductive material, including photographs of spine surface showing the presence of trichomes on the spines, a key character that this species only shares with *H. lanugispinus*.

H. australis f. *subtilispinus* Ritter (1980) was described for a locality in the coast of Junín (Chile). Study of the type and SEM of the seeds showed that *H. australis* f. *subtilispinus* has trichomes on the spines and seeds with microrelief strongly striated, in the same manner of *H. tenuis*. These characters being important for diagnosis, *H. australis* f. *subtilispinus* is proposed as a synonym of *H. tenuis*.

H. tenuis is characterized by prostrate individuals making very conspicuous groups expanding on the ground up to 2 m^2, and trichomes (visible with lens) on the spines, this latter character being hypothesized as an autoapomorphy, probably of high adaptative value. Its decumbent habit, the curved flower-tube, and seed microrelief with strong cuticular striations are considered as probable apomorphic characters. The pink funicular pulp of the fruits is very distinctive and unique within the genus.

The species epithet refers to its slender stems (1.4–3.4 cm diam.). In the field, these stems are found partially covered by sand and mollusc-shell fragments and, in some cases, by living snail colonies which do not seem to cause damage to the cacti.

In Peru, *H. tenuis* mostly lives in isolation from other plants, but its typical flat, sandy habitat can be also inhabited by annual herbs like *Stenomesson coccineum* (Amaryllidaceae). When growing close to rocky slopes, *H. tenuis* lives in the proximity of *Haageocereus pseudomelanostele* (Werderm. & Backeb) Backeb. and *Cleistocactus acanthurus* (Vaupel) Hunt.

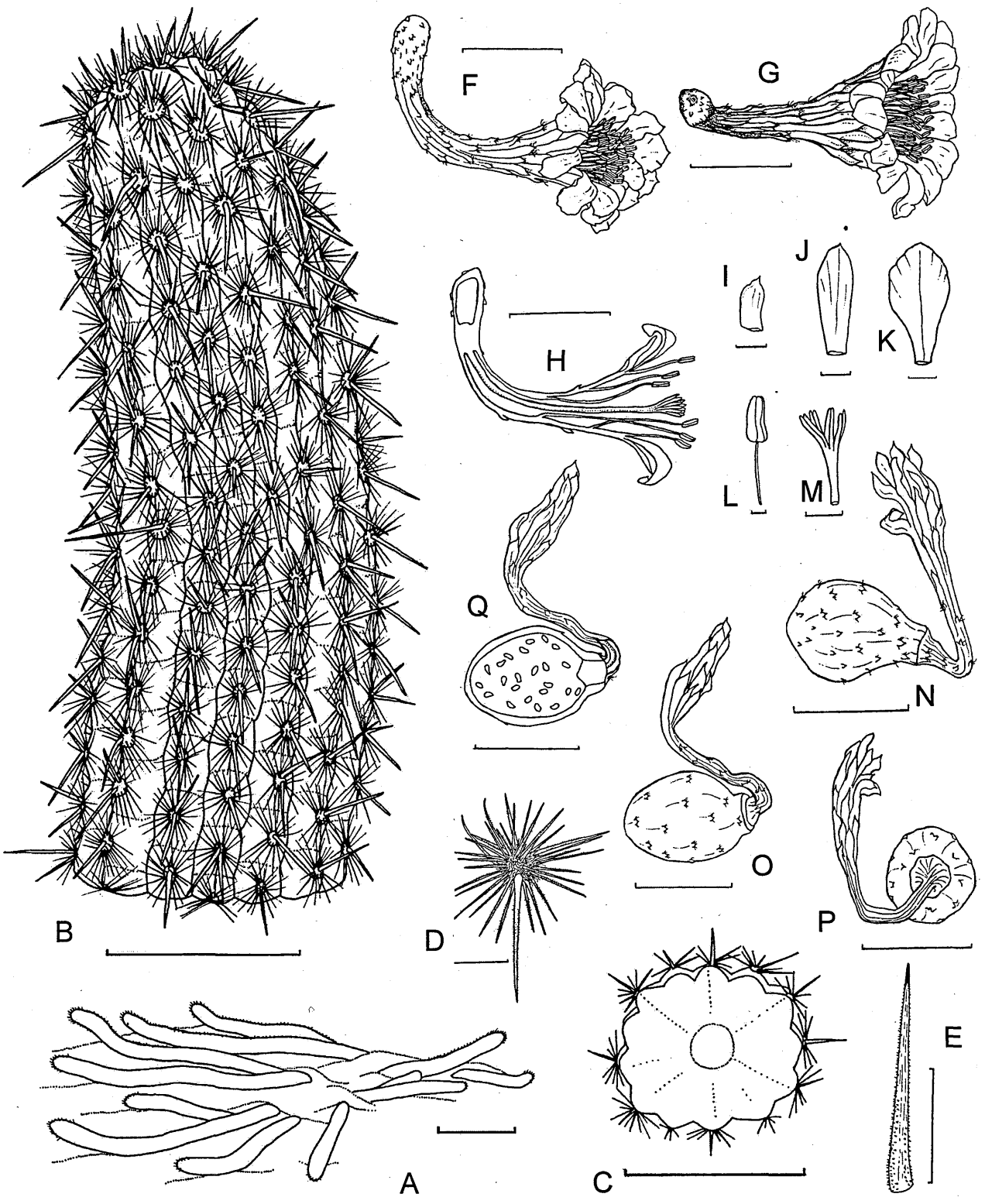


Fig. 10. *Haageocereus tenuis* (A-C,N-Q, *N. Calderón* 419; D-M, *N. Calderón* 364); A, habit (scale= 10cm); B, stem (scale=2cm); C, transverse section of stem (scale=3cm); D, areole (5mm); E, spine(scale= 5mm); F-H, flower, side view and longitudinal section (scale=2cm); I, bract-scale (scale=5mm); J, outer perianth segment (scale=5mm); K, inner perianth segment (scale=5mm); L, anther (scale=1mm);M, stigma lobes (scale=5mm); N-Q, fruits, side view, top view, and longitudinal section (scale=2cm).

Plate 16. **16.1** Habitat of *Haageocereus tenuis,* Huaral, north of Lima, 2005. **16.2** *Ibid.*, *Haageocereus tenuis*. *N. Calderón* s.n., in fruit. **16.3** *Ibid.*, *N. Calderón* 364, in flower.

9. *Haageocereus versicolor* (Werdem. & Backeb.) Backeb. in Backeb. & F. M. Knuth, Kaktus-ABC: 209 (1935, publ. 1936); Backeb., Blätt. Kakt.-forsch. 1936(4): unpaged (1936); Krainz, Die Kakteen 1(11): CVa, unpaged (1963); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 399 (1958); Backeb., Die Cact. 2: 1188 (1960). *Cereus versicolor* Werderm. & Backeb. in Backeb., Neue Kakteen: 81(1931); Werderm., Fedde. Rep. Spec. Nov. 30: 62. (1932). Type locality: Peru, Piura, by Morropón (believed not to have been preserved). Neotype (designated here): Peru. Piura, Morropón, 80°1'6.5''W 5°12'57.4''S, 129 m, 28 May 2005, *N. Calderón* 465 (MOL, Neotype).

H. icosagonoides Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 23 (1956, publ. 1957); ibid., Die Cact. 2: 1186 (1960). Type: Peru, Lambayeque, Saña valley, 500 m, 1956, *Rauh* K86 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1215, fig. 1174 (1960). **Synon. nov.**

H. icosagonoides f. *heteracanthus* Ritter, Kakt. Südam. 4: 1395 (1981). Type: Peru, Lambayeque, Saña valley, 500 m, *Ritter* FR169a. (U holo!) **Synon. nov.**

H. versicolor var. *catacanthus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 23 (1956, publ. 1957). Type: Northern Peru, close to Canchaque, 100 m, 1956, *Rauh* K71a (HEID, believed not to have been preserved). Neotype (designated here): Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 400, fig. 184-II (1958). **Synon. nov.**

H. versicolor var. *xanthacanthus* (Werderm. & Backeb.) Backeb. in Backeb. & F. M. Knuth, Kaktus-ABC: 210 (1935, publ. 1936). *Cereus versicolor* var. *xanthacanthus* Werderm. & Backeb. in Backeb. Neue Kakteen: 81 (1931). *H. versicolor* var. *xanthacanthus* Werderm. & Backeb. in Backeb. Blätt. Kakteenforsch. 1936-4: 3 (1936). Type locality: Peru, Piura, close to Serrán (believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1197, fig. 1153 (1960). **Synon. nov.**

?H. versicolor var. *humifusus* (Werderm. & Backeb.) Backeb. in Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 401 (1958); *H. humifusus* (Werderm. & Backeb.) Backeb. in Backeb. & F. M. Knuth, Kaktus ABC: 208 (1935). *Cereus versicolor* var. *humifusus* Werderm. &

Backeb. in Backeb. Neue Kakteen: 81 (1931). Type locality: Peru, Piura, close to Canchaque, 1500 m (believed not to have been preserved).

?H. versicolor var. *lasiacanthus* (Werderm. & Backeb.) Backeb. in Backeb. & F. M. Knuth, Kaktus-ABC:210 (1935, publ. 1936). *Cereus versicolor* var. *lasiacanthus* Werderm. & Backeb. in Backeb. Neue Kakteen: 81 (1931). Type locality: Peru, Piura, close to Carrasquillo (believed not to have been preserved).

?H. versicolor var. *aureispinus* Backeb. in Backeb. & F. M. Knuth, Kaktus-ABC: 210 (1935, publ. 1936); Cact. Succ. J. (US):47 (1951). Type locality: Peru, Piura, close to Despoblado, coast of Sechura desert (believed not to have been preserved).

?H. versicolor var. *fuscus* Backeb., Fedde Rep. Spec. Nov., 51: 62 (1942). Type locality: Peru, Piura, Salitrales-Talara (believed not to have been preserved).

Habit erect, branching at base, up to 1.7(–2.4) m tall; branches 2.0–8.0 cm diam., terete, epidermis green; ribs 16–18(–22), straight. Areoles oval to circular, felt reddish at first, later white and yellow. Spines opaque, reddish at first, later yellow and greyish; central spines 0–2, 10.0–25.0 × 0.5–0.9 mm at base, ascending and descending; radial spines 25–41, 4.0–10.0 × 0.25–10.0 mm at base. Flowering areoles of mature branches woolly, white, generally disposed in ring-like pseudocephalia around the stems, persistent. Flowers 5.0–9.0 cm, tube slightly curved, green, bearing long curly white trichomes and short hair-spines emerging from the bract-scale axils; outer perianth-segments reddish-green; inner perianth-segments white. Fruit 2.0–3.1 × 2.6–3.4 cm, spherical, pericarp greenish red. Seeds broadly oval, small to medium size, glossy; relief convex; microrelief non-striated to strongly-striated; hilum large (SEM).

Habitat and Distribution: Found in the *Seasonally dry forest* and valleys in northern Peru, 120–1670 m. This is the northern limit for the genus (**Map 7**).

Conservation status: Vulnerable: VU[B1ab(ii,iii)]. The extent of occurrence is 8062.5 km^2; it is known to exist at no more than seven locations and continuing decline has been observed in the area of occupancy and in the quality of habitats.

Comments:

The species was first described as *Cereus versicolor* by Werdermann and Backeberg (1931) but its type was not preserved. Later, Backeberg (1936c) combined the species under *Haageocereus*, including a photograph in this publication. Nevertheless, it is not clear whether the photograph presented in 1936, also appearing in Backeberg's work of 1960, actually belongs to the typical species or to *H. versicolor* var. *xanthacanthus*. Because of this possible confusion, a new specimen (*N. Calderón* 465, MOL) has been chosen as a neotype.

H. icosagonoides was created by Rauh & Backeberg (1957) and because its type was not preserved, a neotype is being proposed based on the illustration published later by Backeberg (1960). *H. icosagonoides* is distinguished by lacking a defined central spine. For the same locality of *H. icosagonoides*, Ritter (1981) published *H. icosagonoides* f. *heteracanthus* referring those plants with defined central spines. It became obvious through the field study that this character is widely variable within a population, therefore not being enough to justify recognition of taxa, and thus, *H. icosagonoides* and *H. icosagonoides* f. *heteracanthus* are better recognized as synonyms of *H. versicolor*.

H. versicolor var. *catacanthus* Rauh & Backebeberg (1957) was described for northern Peru, near Canchaque, and because its type was not preserved, an illustration published later by Rauh (1958) is being designated as neotype. The supposed difference of *H. versicolor* var. *catacanthus* was its central spines somewhat reddish, straight and descending. The same character was also found in the nearby populations of *H. versicolor*, at the Piura valley and, were not deemed to be enough to justify a taxonomic status; therefore, is better recognized as synonym.

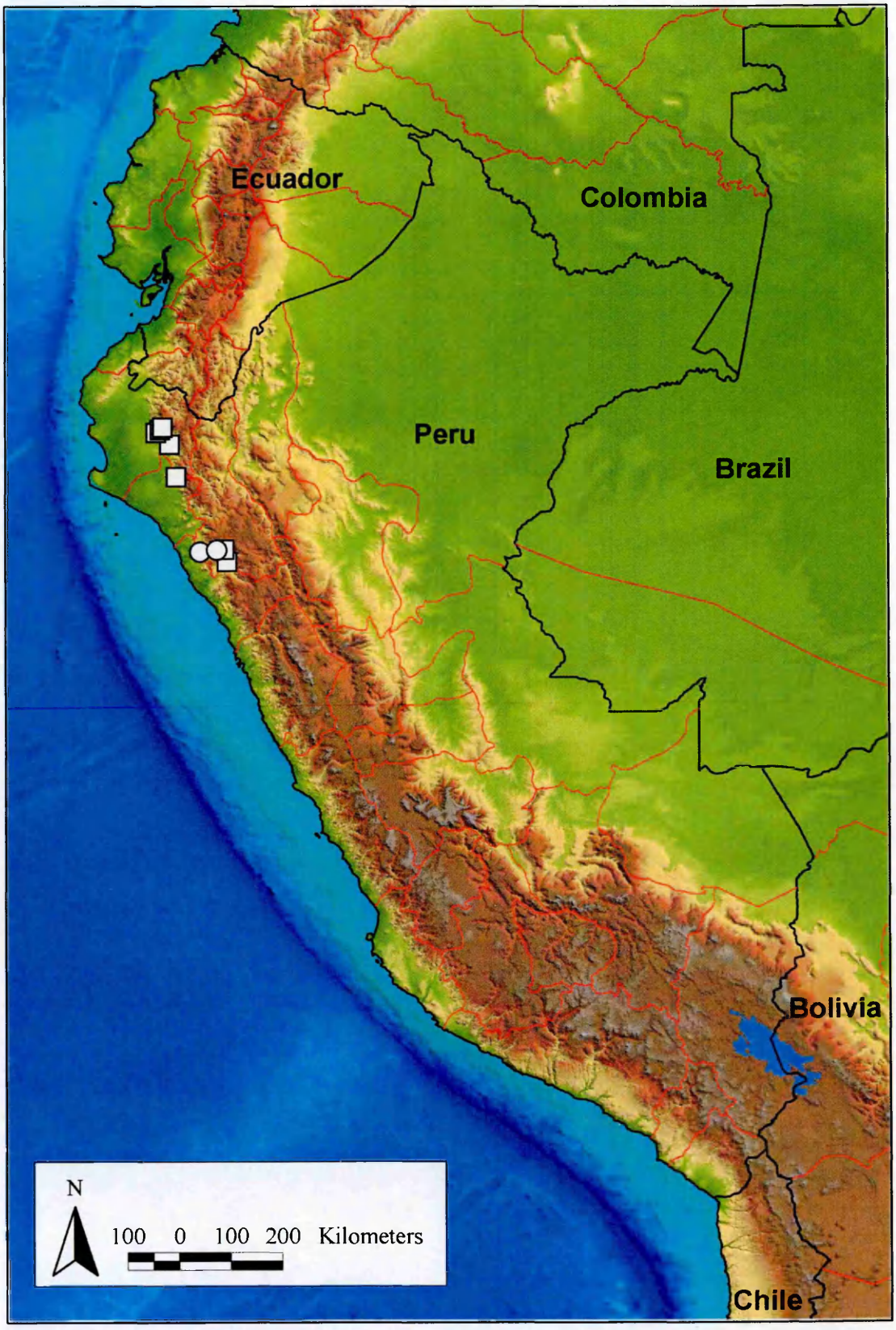
H. versicolor var. *xanthacanthus* (Werderm. & Backeb.) Backeb. (1936c) was distinguished from the typical variety by presenting few ribs (10–14) and 1–2 "stout" central spines, and

because the type-material was not preserved, an illustration published later by Backeberg (1960) is being designated as neotype. Backeberg indicated *C. versicolor* var. *xanthacanthus* grows in Despoblado, Cajamarquilla valley and close to Chilete at 500 m. According to recent field observations in the Piura valley and close to Chilete, variation in the length of central spines exists (to 40.0 mm long), and, although individuals with such a small number of ribs were not found, later illustrations of this taxon published by Backeberg (1960) do not show individuals with less than 15 ribs. For this reason, *C. versicolor* var. *xanthacanthus* is considered as synonym of *H. versicolor*.

Further names related to *H. versicolor*, such as *H. versicolor* var. *humifusus* (Werderm. & Backeb.) Backeb., *H. versicolor* var. *lasiacanthus* (Werderm. & Backeb.) Backeb., *H. versicolor* var. *aureispinus* Backeb., and *H. versicolor* var. *fuscus* Backeb., have no type-material preserved and were not illustrated. Nevertheless, the descriptions of these taxa show slight morphological differences in the colour, size and direction of the spines in comparison with *H. versicolor*. For these reasons, is probable that *H. versicolor* var. *humifusus, H. versicolor* var. *lasiacanthus*, *H. versicolor* var. *aureispinus* and *H. versicolor* var. *fuscus* Backeb. are actually synonyms of *H. versicolor*, nevertheless, in the absence of any previous material to make a neotype, these cacti are going to remain as possible synonyms of the *H. versicolor*.

H. versicolor shows "seasonal stem development" in its branches, where the new reddish areoles and spines contrast with the rest of the stem, which has yellow spines. Its specific epithet refers to this phenomenon. A distinctive and probably apomorphic character of this species is the ring-like pseudocephalium composed by the woolly flower-bearing areoles observed in mature individuals.

Haageocereus versicolor is here subdivided in two subspecies: *H. versicolor* subsp. *versicolor* and *H. versicolor* subsp. *pseudoversicolor*.



Map 7. *Haageocereus versicolor* subsp. *versicolor*=□; *Haageocereus versicolor* subsp. *pseudoversicolor*=○.

Key to subspecies of *Haageocereus versicolor*

Branches slender, 2.0–3.5(–5.0) cm diam.; seeds small size, microrelief strongly-striated (SEM) (Piura, Lambayeque and La Libertad, 119–1670 m; Cajamarca: Chilete, 900 m).....

..... **9a. *H. versicolor* subsp. *versicolor***

Branches thick, 4.0–8.0 cm diam.; seeds medium size, microrelief non-striated to weakly-striated (SEM) (Cajamarca: Jequetepeque valley, 250–620 m).....

..... **9b. *H. versicolor* subsp. *pseudoversicolor***

9a. *Haageocereus versicolor* subsp. *versicolor*

Habit up to 2.35 m tall; branches 2.0–3.5(–5.0) cm diam.; ribs 16–18(–22), 2.2–8.8 mm, straight. Areoles 2.3–4.2 × 2.4–4.6 mm, 2.4–5.2 mm apart. Central spines 0–2, 12.0–24.0(–40.0) mm; radial spines 4.0–9.0 mm. Flowers 5.8–6.8 × 3.1–5.0 cm; pericarpel 10.0–11.0 × 9.0–11.0 mm; tube 3.4–4.0 × 0.9–1.0 cm at base, widening towards apex to 1.8–2.0 cm diam., slightly curved, green; outer perianth-segments 13–17, 12.0–17.7 × 3.8–5.0 mm; inner perianth-segments 14–22, 17.0–18.3 × 5.7–7.5 mm; nectar-chamber 15.0–19.0 × 5.0–7.1 mm, tubular; anthers 2.9–4.6 × 2.0 mm; style 34.7–40.0 × 1.1–2.5 mm; stigma-lobes 10–11, 2.3–5.9 mm; ovary locule 6.5–7.0 × 5.6–6.4 mm, circular to elliptic in longitudinal section. Fruit (only immature fruit seen) 2.9–3.1 × 2.6–3.4 cm, spherical, pericarp green. Seeds broadly oval, small size, 1.09 mm × 0.92 × 0.73 mm, glossy; relief (SEM) convex; microrelief with strong cuticular striations; hilum large, 0.68 mm, oblique, forming an angle of 65° with long axis of seed (**Fig. 11, Plates 6.1–6.3, 17.1–17.3, 17.5**).

Examined material: PERU. PIURA: Morropón, 80°1'6.5''W, 5°12'57.4''S, 129 m, 28 May 2005, *N. Calderón* 465 (MOL, Neotype); ibid., *N. Calderón* 460.1, 462, 463, 464.1, 466, 467.1, 468 (Herb. B. G. La Molina); ibid., Piura valley, road towards Huancabamba, 79°47'19.3''W, 5°25'10.7''S, 180 m, 7 Nov. 2003, *N. Calderón* 347 (Herb. B. G. La Molina); LAMBAYEQUE: East of Olmos, 380 m, 6 Nov. 2003, *N. Calderón* 342 (Herb. B.

G. La Molina); CAJAMARCA: road towards Chilete, 78°50'10.8''W, 7°13'38.4''S, 950 m, 17 Nov. 2003, *N. Calderón* 351 (Herb. B. G. La Molina); LA LIBERTAD: Contumaza-Cascas road, 78°47'27''W, 7°26'10.8''S, 1670 m, 18 Nov. 2003, *N. Calderón* 355 (Herb. B. G. La Molina). LAMBAYEQUE: Saña valley, 500 m, *Ritter* FR169a (U holo).

Habitat and Distribution: Found in the *seasonally dry forest* and valleys in northern Peru, 120–1670m. This is the northern limit for the genus (**Map 7**).

Phenology: *Flowers:* November and May; *Fruits:* December and June.

Conservation status: Endangered EN[B1ab(ii,iii)]. The extent of occurrence is estimated to be 3981.78 km^2. It is known to exist at no more than six locations, and continuing decline observed in the area of occupancy and the quality of habitats.

The most evident threat for this species is the loss of habitat due to the construction of new roads and the subsequent transit activities. Goat shepherding has also been observed, representing a threat for this subspecies, as its branches are easily eaten by these animals.

Comments:

This subspecies lives together with *Armatocereus cartwrightianus* (Britton & Rose) Backeb., *Neoraimondia arequipensis* (Meyen) Backeb. and other deciduous plants typical of the seasonal dry forest, in a landscape dominated by *Prosopis* sp. (Leguminosae) which may also act as nurse-plant for the early stages of development of the cacti.

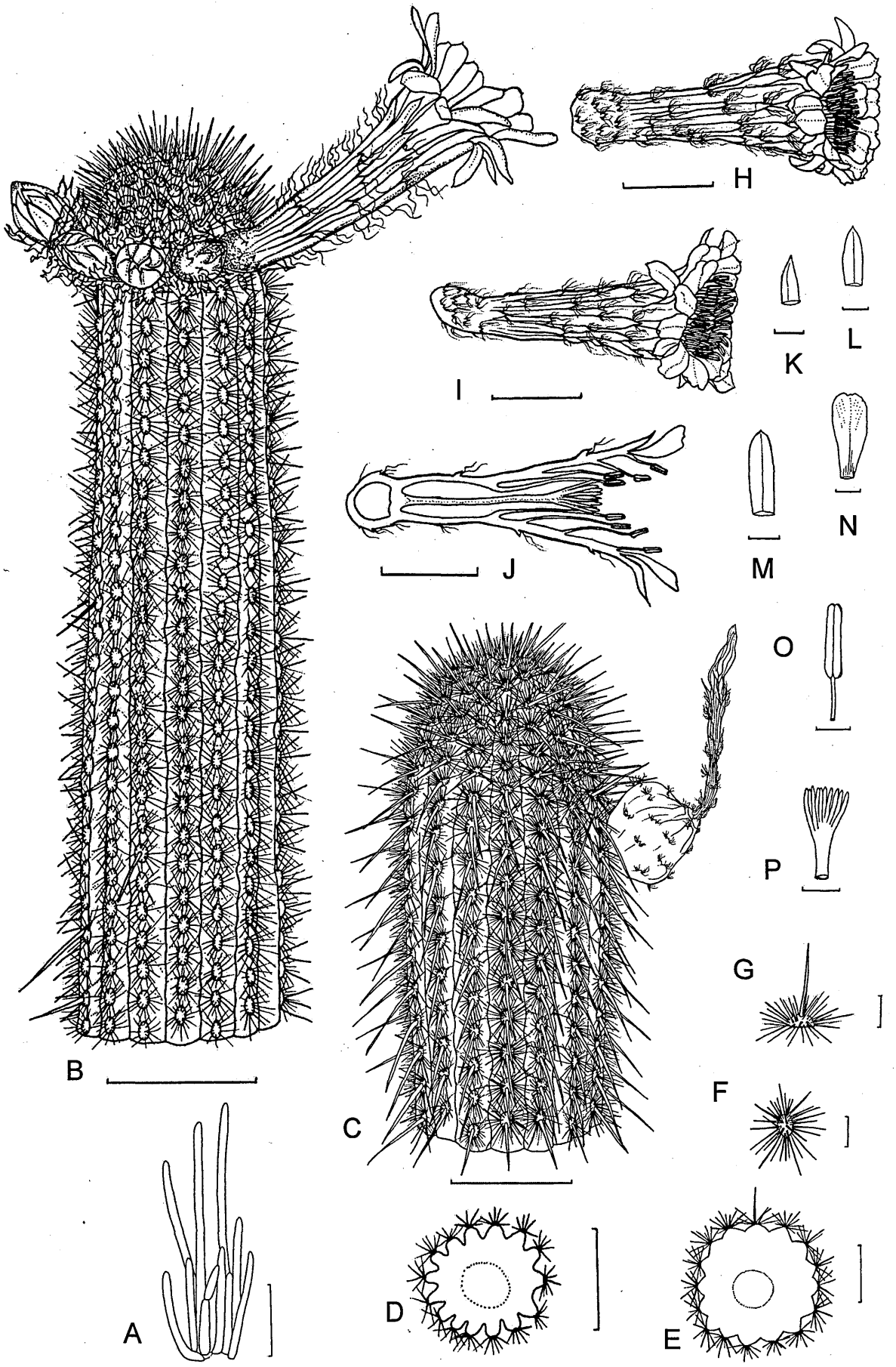


Fig. 11. *Haageocereus versicolor* subsp. *versicolor* (A-B, *N. Calderón* 465; C-G, *N. Calderón* 467; H-P, *N. Calderón* 468); A, habit (scale=50cm); B-C, stems (scale=3cm); D-E, transverse sections of stem (scale=2cm); F-G, areoles(scale=2cm); H-J, flower, side view and longitudinal section(scale=2cm); K-L, bract-scales(scale=5mm); M, outer perianthsegment (scale=5mm); N, inner perianth segment (scale=5mm); O, anther (scale=2mm); P, stigma lobes (scale=5mm).

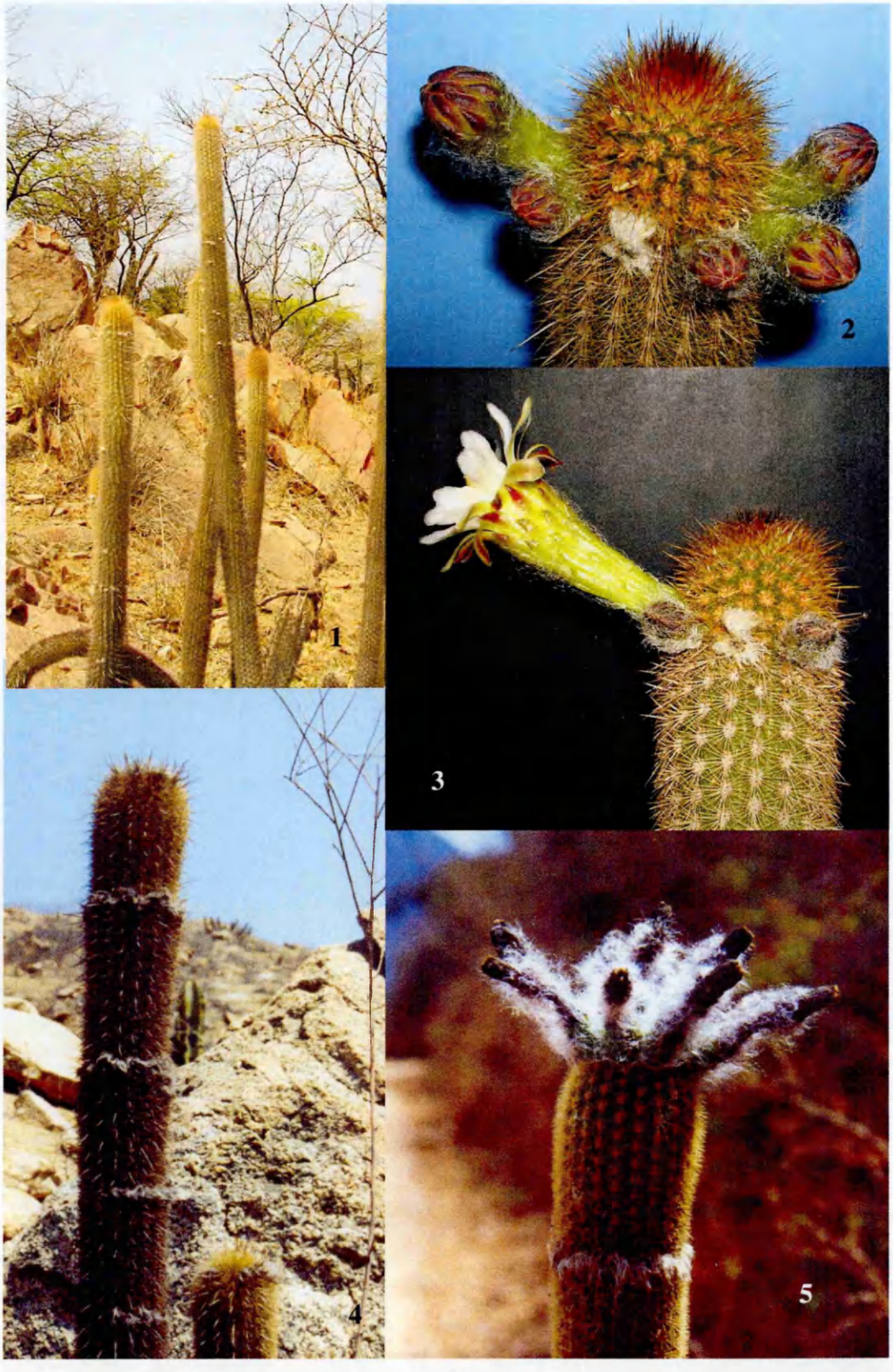


Plate 17. **17.1** *Haageocereus versicolor* subsp. *versicolor*. *N. Calderón* s.n., Morropón, 2005. **17.2** *Ibid.*, *N. Calderón* 465, in bud. **17.3** *Ibid.*, in flower. **17.4** *Haageocereus versicolor* subsp. *pseudoversicolor*. *N. Calderón* 340, Jequetepeque valley. **17.5** *Haageocereus versicolor* subsp. *versicolor*. *N. Calderón* 451, with immature fruits.

9b. *Haageocereus versicolor* subsp. *pseudoversicolor* (Rauh & Backeb.) N. Calderón comb. nov.

H. pseudoversicolor Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 23 (1956, publ. 1957); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 401 (1958); Backeb., Die Cact. 2: 1194 (1960). Type: Peru, Lambayeque, Saña valley, 100–200 m, 1956, *Rauh* K85 (HEID, believed not to have been preserved). Neotype (designated here): Backeb., Die Cact. 2: 1199, fig. 1155 (1960).

Habit up to 1.7 m tall; branches 4.0–8.0 cm diam.; ribs 18–19. Central spines 1–2, 12.3–30.0 mm; radial spines 10.0 mm. Flowers 5.0 cm long.; inner perianth-segments 15.0 × 6.0 mm; nectar-chamber 12.0mm; ovary locule 10.0 × 4.0 mm. Fruit 2.0–3.0 cm. Seeds broadly oval, medium-size, 1.45 × 1.04 × 0.75 mm, glossy; relief convex; microrelief non-striated to weakly-striated; hilum large, 0.75 mm, oblique, forming an angle of 48° with long axis of seed (SEM) (**Plates 6.4–6.5, 17.4**).

Examined material: PERU. CAJAMARCA: Jequetepeque valley, 79°15'19.3''W, 7°16'1.36''S, 250 m, 6 Nov. 2003, *N. Calderón* 340 (Herb. B. G. La Molina); ibid., Gallito Ciego (Irrigation project), 78°57'49.2''W, 7°14'1.10.8''S, 620 m, *G. Charles* 256.02 (seeds, private collection).

Habitat and Distribution: Found in Jequetepeque valley at Cajamarca in northern Peru, 250–620 m (**Map 7**).

Phenology: *Flowers:* November; *Fruits:* December.

Conservation status: Endangered: EN[B2ab(iii)]. The area of occupancy is estimated to be 21.81 km^2 and is known to exist at no more than two locations, and continuing decline observed in the quality of habitat.

Comments:

H. versicolor subsp. *pseudoversicolor* was first described by Rauh & Backeberg (1957) based on Rauh's collection K85, 1956, but this material was not preserved (or has been subsequently lost). Therefore, an illustration published later by Backeberg (1960) is being designated as a neotype for this subspecies.

The erect growing pattern, 18–19 ribs, central spines 1–2, 12.3–30.0 mm long, conspicuous flowering areoles and white flower are all within the variation accepted for the species but, on the other hand, few characters, like the stem diameter (to 8.0 cm) and the seed micromorphology (microrelief non-striated to weakly striated) distinguish this taxon from the typical species.

Occurring geographically close to the type-locality of *H. versicolor* subsp. *versicolor*, this taxon is not sympatric with other *Haageocereus* species. This subspecies lives together with *Neoraimondia arequipensis* (Meyen) Backeb., *Melocactus peruvianus* Vaupel and other plants like *Prosopis sp.* (Leguminosae).

PHYTOGEOGRAPHY

The phytogeographic knowledge of *Haageocereus* is based on the endemism, species richness and distribution patterns related to its habitat conditions.

Haageocereus species are distributed on the Pacific coast and the western slopes of the Andes, being mostly endemic to Peru, with two species also occurring in northern Chile. The middle Andean region of northern Chile, Bolivia and Peru, has been proposed as the probable centre of origin for the Cactaceae because a number of plesiomorphic basal groups are endemic to this geographic area (Wallace 2002). The most recent gene-based phylogenetic analysis suggests that at least the subfamilies Opuntioideae and Cactoideae [plus Maihuenioideae] could have this centre of origin, but the situation of Pereskioideae is more complex, and its origin is apparently partly centred on the Caribbean (Edwards et al. 2005).

In terms of species richness, *Haageocereus* has diversified mostly in central Peru, where *H. acranthus*, *H. lanugispinus*, *H. pseudomelanostele* and *H. tenuis* can be found. Occurring in the north are *H. repens* and *H. versicolor*, and in the south, *H. decumbens* and *H. platinospinus*. Cases of sympatry are found in central Peru, involving *H. acranthus* and *H. pseudomelanostele*, and between *H. pseudomelanostele* subsp. *pseudomelanostele* and *H. tenuis*.

Recent classifications of Peruvian vegetation and life zones have been produced (ONERN 1995, INRENA 1995, Brack et al. 2000); however, these classifications, although useful for some taxonomic groups, are not entirely accurate for describing cactus habitats because they are not subdivided and, for the purposes of this study, it is preferable to start with a broader concept of Peruvian natural regions. The three main Peruvian natural regions are the Coast, the Andes and the Tropical Forest, and *Haageocereus* is restricted to the Coast and the western Andes.

To describe *Haageocereus* habitats, terminology was taken and slightly modified from Weberbauer (1945) and Pennington et al. (2004). Among the vegetation formations recognised by Weberbauer, *Haageocereus* occurs in "coastal territories of deserts and lomas", "desert formation in the western Andes of southern Peru", "columnar cacti formation in the western Andes of southern Peru", "desert formation of the western basins in central Peru", "columnar cacti formation of the western basins in central Peru", and "western basins and inter-Andean valleys of northern Peru". Weberbauer (1945) also refers to a "piso del bosque pluviifolio" which corresponds to what Pennington et al. (2004) calls "seasonally dry forest". From these definitions, five types of habitat are recognised as follows:

Along the Pacific coast, *Haageocereus* is found between 50–900 m alt. in the following habitats:

1. The *Xerophytic Deserts* (XD), including arid areas of sandy slopes and rocky hills close to the sea, where ephemeral herbs (Lomas vegetation) or xerophytic plants like *Tillandsia* sp. (Bromeliaceae) may be present (**Plates 15.1, 16.1**).

2. The *Xerophytic Coastal Valleys* (XCV), which is a transitional area between the desert and the Andes and includes rocky hillsides of the lower courses of rivers draining to the Pacific, where woody shrubs like *Trixis cacaliodes* (Asteraceae) are rather common as well as the xerophytic *Tillandsia* sp. and other cacti, such as *Mila caespitosa* and *Cleistocactus acanthurus* (**Plates 7.1, 12.1, 12.2**).

In northern Peru, *Haageocereus* is found from the coastal plains, at around 120 m, to the Andes, at about 1800 m in:

3. The *Seasonally Dry Forest* (DF), essentially a woody vegetation, consisting of mostly deciduous trees and shrubs with or without a closed canopy and lacking a continuous grass layer, other cacti being present like *Neoraimondia arequipensis* subsp. *gigantea* and *Armatocereus carwrightianus*. Vegetation with *Prosopis* sp. (Leguminosae) is typical, as well as other trees such *Bougainvillea* sp. (Nyctaginaceae), *Ceiba* sp. (Bombacaceae),

Jacquinia sp. (Theophrastaceae), *Loxopterygium* (Anacardiaceae) and other genera of Leguminosae and Bignoniaceae (**Plate 17.1**).

In the western Andes, *Haageocereus* is found between 900–2800 m alt., forming part of the "Columnar cacti formation" (Weberbauer 1945) in the following habitats:

4. The *Xerophytic Formation of Central Andes* (XCA) including steep mountains and rocky hills ("canyons") close to the upper course of Pacific rivers, where xerophytic shrubs, such as *Cnidoscolus baciacanthus* and *Jatropha macrantha* (both Euphorbiaceae) are typical, growing with herbs and sometimes small trees such as *Schinus molle* (Anacardiaceae), *Acacia macracantha* (Leguminosae) and *Carica mito* (Caricaceae). Cactaceae communities are much more diverse here, with representatives of the genera *Armatocereus, Austrocylindropuntia, Browningia, Cleistocactus, Corryocactus, Espostoa, Melocactus, Mila, Neoraimondia, Opuntia* and *Weberbauerocereus* being present (**Plate 13.1**).

5. The *Xerophytic Formation of Southern Andes* (XSA), including rocky arid mountains and plateaux, where Cactaceae communities of *Browningia, Corryocactus, Neoraimondia,* Opuntioideae, *Oreocereus* and *Weberbauerocereus*, predominate among the very reduced herbaceous vegetation and shrubs (**Plate 11.1, 14.1**).

Taking into account their habitat spread, *H. pseudomelanostele* and *H. acranthus* have diversified with relatively more success than the other taxa, being present in most of the habitats identified for the genus (**Table 3**). In southern Peru the genus is mostly represented by *H. decumbens*, *H. platinospinus* and *H. chilensis*, whose habitats are more related to those of *H. acranthus* and *H. pseudomelanostele* than to the northern *H. versicolor.*

It is important to highlight the restricted distribution of *Haageocereus* to the western slopes of the Andes, while other genera of tribe Trichocereeae such as *Espostoa, Cleistocactus, Browningia* and *Weberbauerocereus,* which occasionally share the same habitat of different species of *Haageocereus.* These four genera occur and are more expressive on the eastern slopes of the Andes (including the so-called inter-Andean valleys). The formation of the

Andean mountain chain has made possible the immense variety and complexity of vegetation it comprises, where plesiomorphic groups of Trichocereeae occur to the east and west of the Andes, such as *Rauhocereus* (in Peru) and *Samaipaticereus* (in Bolivia). The latter genus has been taken as an example of a basal member of Trichocereeae for comparison with *Haageocereus*, as described in Chapter 1.

The present distribution of *Haageocereus*, west of the Andes, suggests that the diversification of *Haageocereus* could have been posterior to the formation of the Andes, contrasting to other more widespread genera, such as *Espostoa, Cleistocactus, Browningia* and *Weberbauerocereus*. Other examples of genera growing restricted to the western side of the Andes are represented by *Copiapoa* in Chile, *Mila* in Peru and *Eryocise* in Chile and Peru.

Table 3. Habitat types for *Haageocereus* including habitat preference codes: E=exclusive habitat for the taxon, NE= non-exclusive habitat for the taxon.

Habitat	Habitat E / NE	Taxon name	Sympatric species
Xerophytic Deserts (XD)	E	*H. decumbens*	none
	E	*H. repens*	none
	E	*H. tenuis*	*H. pseudomelanostele* subsp. *pseudomelanostele*
	NE	*H. acranthus* subsp. *acranthus* (also in XCV)	*H. pseudomelanostele* subsp. *pseudomelanostele.*
	NE	*H. pseudomelanostele* subsp. *pseudomelanostele* (also in XCV)	*H. acranthus subsp. acranthus* and *H. tenuis*
Xerophytic Coastal Valleys (XCV)	NE	*H. acranthus* subsp. *acranthus* (also in XD)	*H. pseudomelanostele* subsp. *pseudomelanostele*
	NE	*H. pseudomelanostele* subsp. *pseudomelanostele* (also in XD)	*H. acranthus subsp. acranthus*
Seasonally Dry Forest (DF)	E	*H. versicolor* subsp. *versicolor*	none
	E	*H. versicolor* subsp. *pseudoversicolor*	none
Xerophytic Formation, Central Andes (XCA)	E	*H. acranthus* subsp. *zonatus*	*H. pseudomelanostele* subsp. *acanthocladus*
	E	*H. acranthus* subsp. *backebergii*	*H. pseudomelanostele* subsp. *acanthocladus* or *H. pseudomelanostele* subsp. *carminiflorus*
	E	*H. pseudomelanostele* subsp. *acanthocladus*	*H. acranthus* subsp. *zonatus* or *H. acranthus* subsp. *backebergii*
	E	*H. pseudomelanostele* subsp. *carminiflorus*	*H. acranthus* subsp. *backebergii*
Xerophytic Formation, Southern Andes (XSA)	E	*H. pseudomelanostele* subsp. *turbidus*	none
	E	*H. platinospinus*	none

CONSERVATION

Overview

Cacti, like many other plants, are seriously threatened by habitat destruction, whether for the development of new agricultural land, for expanding urban areas, or for other human activities, such as road building and mining (Boyle & Anderson 2002). In this context, *Haageocereus* is a good example of a seriously threatened genus, most of its localities being in the proximity of growing cities and therefore, suffering constant human disturbance.

Conservation of cacti has been recognised as one of the urgent actions to be taken because of the ecological significance of this group, which comprises taxa of unique value, as judged by their endemism, varied ecological adaptations and their relative importance as environmental components.

International efforts towards the conservation of cactus species were established in 1984, when the Cactus and Succulent Specialist Group of the Species Survival Commission (SSC), a part of IUCN, was created. In 1997 this Specialist Group published the Cactus and Succulent Plants Conservation Action Plan (Oldfield 1997), compiling information about succulent plant groups, conservation measures, regional accounts, and action proposals, including one for Peru. The proposal for Peru recommended *Assessment of the in situ conservation requirements of succulents*, including: "assessment of extent to which the protected area system of Peru protects the habitats of endemic succulents, survey work being necessary to determine the degree of threat to populations of particular succulent species in the more mesic areas".

Conservation measures listed by the Cactus and Succulent Specialist Group also included international legislation (e.g. The Convention of Biological Diversity and The Berne Convention); trade controls by CITES authorities; and *in situ* and *ex situ* conservation actions.

While *in situ* and *ex situ* conservation measures are considered to be of high importance within the present work, trade based on wild-collected plants is not one of the concerns for *Haageocereus*.

In 2002, at the Conference of the Parties to the Convention on Biological Diversity (CBD), The Global Strategy for Plant Conservation was presented, targets of this Global Strategy include, for instance, that 60 per cent of the world's threatened species be conserved *in situ* by 2010. Therefore, in response to this aim, *in situ* conservation actions are also being presented in this study.

Conservation Assessments

In 1980, IUCN established criteria and categories of threat for assessing extinction risks to species. The IUCN Red List criteria were published in 1994 and a revised version in 2001. This later version is being used in the present study to assess categories of threat for *Haageocereus*. The categories of threat are: Extinct (Ex), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD).

For listing as Critically Endangered, Endangered or Vulnerable there is a range of quantitative criteria; meeting any one of these criteria qualifies a taxon for listing at that level of threat and each taxon should be evaluated against as many of the criteria as practicable.

Haageocereus species have been evaluated against the IUCN Red List criteria of "*geographic range*" in the form of area of occupancy and/or extent of occurrence, and -when appropriate- "*reduction of subpopulations*" of *Haageocereus*. The extent of occurrence and/or area of occupancy is stated within the treatment of taxa in Chapter 2. These estimations are based mainly on field studies and herbarium records made during the last five years.

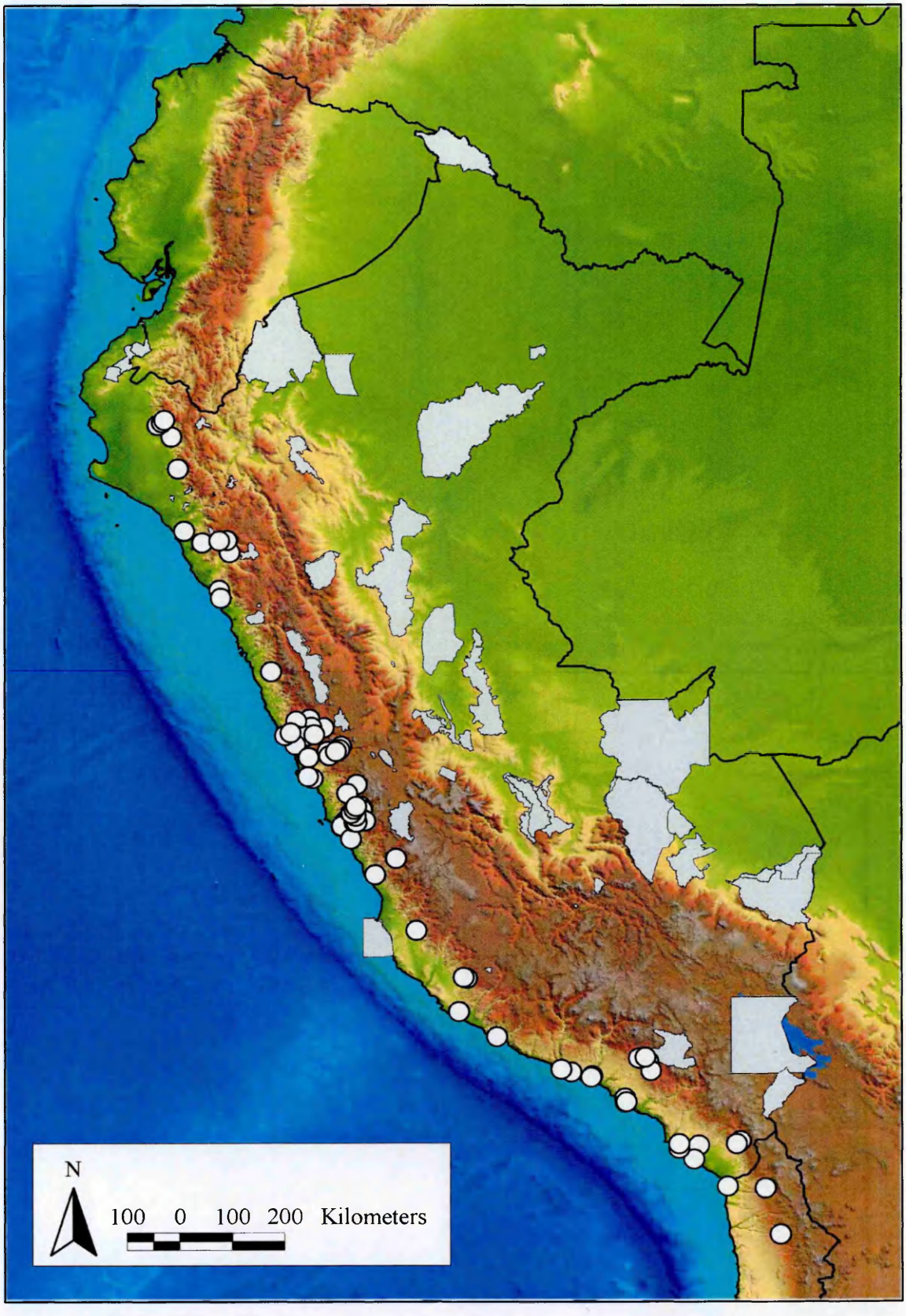
Both bibliographic records and personal observations in the field were fundamental for estimating the original distribution and the reduction of subpopulations for the species *H. acranthus* and *H. pseudomelanostele.* In general, *Haageocereus* localities are outside Peruvian national protected areas (**Map 8**) and recommendations towards the conservation of their habitats are being presented.

For estimating the area of occupancy at the only known locality of *H. tenuis*, the results of a recent field survey (Ceroni pers. comm. 2004) were incorporated. In the case of *H. repens*, which also has only one known population, the area of occupancy was inferred from direct observation. For the other species of *Haageocereus* occurring in Peru, which have more than one population known, their geographic range was estimated at the GIS Unit (RBG, Kew) where the area of occupancy and extent of occurrence was calculated automatically, using a specially designed software program. (**Map 9**).

Most *Haageocereus* species are categorized as CR, EN or VU (**Table 4**), for taxa existing at between one and ten localities, and also facing continuing decline, observed in the area of occupancy and the quality of habitat. Importantly, the loss of habitat, especially in arid areas, is a continuously increasing threat.

Conservation Actions and Recommendations

Modified habitats of *Haageocereus*, as those by the coast (*Xerophytic Deserts* and *Xerophytic Coastal Valleys*) are extremely difficult to recover based on the first author's observations in the past 5 years, but some alternative strategies can include *ex situ* conservation in botanical gardens, and possible re-introduction. In the case of *Haageocereus tenuis*, which is found only 13 km from the "Reserva Nacional de Lachay", it could be proposed to extent the area of this protected area to include the present species.



Map 8. Localities of *Haageocereus* = ○, and national protected areas (in grey).

Map 9. Application of IUCN Conservation assessment for *H. pseudomelanostele* subsp. *pseudomelanostele* using Geographic Range in the form of Extent of Occurrence (EOO: black-line polygon) and Area of Occupancy (AOO: red-lines squares).

The *Seasonally Dry Forest* has been receiving attention from researchers during the last few years (Centro de Datos para la Conservación-Univ La Molina, pers. comm.), towards the creation of a protected area. In this context, including some of the geographic range of *H. versicolor* is strongly recommended, as this species only grows in this vegetation type.

The *Xerophytic Formation of Central Andes* and *Southern Andes* are potentially excellent areas to be considered for *in situ* conservation and thus, to be included in the national system of protected areas. These environments include 6 taxa (**Table 3**) of *Haageocereus* and other important cacti. There are several reasons to recommend this initiative:

- There is no existing protected area covering these environments.
- These formations have some relatively untouched land not yet under direct human influence (e.g. farming, mining or other kind of exploitation of the resources in these habitats).
- These environments are included in the Status Survey and Conservation Action Plan-IUCN/SSC Cactus and Succulent Specialist Group (Oldfield 1997) within the Subdivisions I and II of the Andean Region of Peru (500–3500 m alt.) for being extremely rich in succulent plant species and with a high level of endemism.
- The conservation of part of these environments will enhance *target vii* of the Global Strategy for Plant Conservation (CBD 2002) for *conserving plant diversity,* i.e. that 60 per cent of the world's threatened species be conserved *in situ*.

According to field observations in the last five years, as well as *ex situ* conservation efforts undertaken at La Molina University Botanic Garden, specific actions and recommendations can be listed (See **Table 4**).

Table 4. IUCN Red List Categories for *Haageocereus* and Proposed protected areas and recommendations.

Taxon name	IUCN Red List Category [criteria]	Proposed actions recommended
Haageocereus acranthus	VU[A4c]	See below for subspecies.
Haageocereus acranthus subsp. *acranthus*	EN[B1ab(ii,iii,iv)]	Less than 50 individuals are protected at the Reserva Nacional de Lachay (Lima). Enhance current *ex situ* conservation efforts and establish *ex situ* gene banks to enable future re-introductions. Some *ex situ* conservation efforts have already been undertaken by La Molina Univ.
Haageocereus acranthus subsp. *backebergii*	EN[B1ab(ii,iii,iv)]	Establish a protected area in the surroundings of Umarcata and Orovel hills in the Chillón valley (Lima). Conservation in other localities in the Lurín valley, are also recommended to maintain genetic diversity.
Haageocereus acranthus subsp. *zonatus*	EN[B1ab(ii,iii)]	Establish a protected area in the surroundings of Paccho in the Huaura valley (Lima). Conservation in other localities in the Pativilca valley, is recommended.
Haageocereus decumbens	VU[B1ab(ii,iii,iv)]	Enhance current *ex situ* conservation and establish *ex situ* gene banks to enable future re-introductions.
Haageocereus platinospinus	EN[B1ab(ii,iii)]	Establish a protected area in the Yura valley (Arequipa).
Haageocereus pseudomelanostele	VU[A4c]	See below for subspecies.
Haageocereus pseudomelanostele subsp. *pseudomelanostele*	VU[B1ab(ii,iii,iv)]	Enhance current *ex situ* conservation. Some *ex situ* conservation efforts have been already undertaken by La Molina Univ.
Haageocereus pseudomelanostele subsp. *acanthocladus*	EN[B1ab(ii,iii)]	Establish a protected area in the surroundings of Paccho in the Huaura valley (Lima) and also in the surroundings of Umarcata and Orovel hills in the Chillon valley (Lima) to maintain genetic diversity.
Haageocereus pseudomelanostele subsp. *carminiflorus*	EN[B1ab(ii,iii)+ 2ab(ii,iii)]	Establish a protected area in the Tinajas canyon, in the Lurin valley (Lima).
Haageocereus pseudomelanostele subsp. *turbidus*	CR[B2ab(iii)]	Establish a protected area in the Nazca valley.
Haageocereus repens	CR[B2ab(ii,iii)]	Enhance current *ex situ* conservation. Some ex situ conservation efforts have been undertaken by the Univ. of Trujillo
Haageocereus tenuis	CR[B2ab(ii,iii,v)]	Site recommended for being included at the Reserva Nacional de Lachay (Lima). Some *ex situ* conservation efforts have been undertaken by La Molina Univ.
Haageocereus versicolor	VU[B1ab(ii,iii)]	See below for subspecies.
Haageocereus versicolor subsp. *versicolor*	EN[B1ab(ii,iii)]	Establish a protected area in the surroundings of Morropón (Piura).
Haageocereus versicolor subsp. *pseudoversicolor*	EN[B2ab(iii)]	Enhance current *ex situ* conservation activities.

CONCLUSIONS

Haageocereus has been regarded as a very complex genus in need of particular attention, and, although the present work recognizes only 9 species and 6 heterotypic subspecies, there are more than 100 names attributed to this genus. Most of these names reflected a very poor species concept, based on very few and variable characters. Type-material is also poor, if not lacking. Extensive field-work, morphological studies, as well as the outcomes from recent studies in the Cactaceae generally, have greatly contributed to clarify important biological, ecological and even possible evolutionary aspects of the genus *Haageocereus* and its species. The taxonomic and phytogeographic knowledge of *Haageocereus* is very important for making conservation assessments, and the development of recommendations towards a coherent conservation action plan. In this context, it is possible to present the following conclusions:

1. The delimitation of *Haageocereus* species in this work led to the first interpretation of their morphological characters within the complex tribe Trichocereeae. Morphological comparison of *Haageocereus* with a basal member of Trichocereeae, *Samaipaticereus,* represents the first attempt to elucidate the potential apomorphies of this genus.

2. As in many Cactaceae, typification of *Haageocereus* names, where types are unavailable, is based mainly on original illustrations, published as part of the protologues or in later publications, except for *H. versicolor,* where a specimen was designated as neotype. The herbarium records of *Haageocereus* species acquired for this work includes most of the Peruvian taxa recognised here (with the exception of *H. lanugispinus* and *H. chilensis*), all held at La Molina University (MOL).

3. The restricted distribution of *Haageocereus* to the Pacific drainage of the Andes together with the fact that other members of Trichocereeae, such as the allied genera *Espostoa* and

Cleistocactus, occur in inter-Andean valleys, leads to the hypothesis that *Haageocereus* could have originated after the formation of the Andean mountains and has been unable to radiate eastwards due to the altitude of the Andean range. In phytogeographic terms *Haageocereus* could be possibly a "modern genus" within the tribe, although further research is still needed, especially a gene-based phylogeny, is still needed to determine its exact position in the tribe.

4. The current situation of the habitats of *Haageocereus* is dramatic in terms of conservation, with all taxa listed under IUCN categories of threat. A list of reccomendations is presented, as a prerequisite to the future development of more detailed proposals to the appropriate Peruvian authorities. Habitats of *Haageocereus*, especially in the north (Piura) and south (Arequipa) of Peru are particularly suitable for the creation of protected areas, because of the biodiversity well-preserved in these beautiful landscapes. Universities are particularly encouraged to take part in *ex situ* conservation activities, through the incorporation of native and threatened species in their botanic gardens.

5. The present study presents essential information about the taxonomy, phytogeography and conservation of *Haageocereus* and, at the same time, provides research tools for their identification and further information towards a better comprehension of other Peruvian cacti. Further research in associated areas like reproductive biology, ecology and phylogenetics is especially important for a better comprehension of both *Haageocereus* and other the Peruvian cacti.

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GLOSSARY OF BOTANICAL TERMS USED IN *HAAGEOCEREUS*

areoles: are those felted structures, generally circular to oval, found on various parts of the plant, bearing spines, trichomes, hairs and -from their meristemal region- new shoots and the reproductive organs such as flowers and fruits.

bract-scales: are the scalelike appendages found on the pericarpel and flower-tube below the perianth-segments (Taylor & Zappi 2004), in Trichocereeae they subtend areoles bearing trichomes and hair-spines and may also become very conspicuous to decurrent podaria (*Haageocereus acranthus* subsp. *backebergii,* Plates 8.3 and 8.4).

bristle-spines: are true cactus spines, they are usually intergrading with the spines and are distinguished by being somewhat curved, translucent and thinner in diameter.

cephalium: is a modified part of the stem bearing abundant trichomes and/or spines and/or bristles, where the flowers and fruits develop. It can be very conspicuous growing lateral or apical, distinguishing the fertile region of stem from the rest of the plant.

flower-tube: is the hollow or partially hollow structure above the pericarpel which comprises fused floral and receptacular tissues, the latter on the exterior, often bearing bract-scales; the former within and subtending the perianth-segments at its apex (Taylor & Zappi 2004).

funicular pulp: is the term used for the either solid or semi-liquid pulp found within the pericarp of cactus fruits, surrounding the seeds, which is derived from the ovule funicles (Taylor & Zappi 2004).

hair-spines: are specialized true cactus spines (multicellular structures representing modified leaves) with a soft and often wooly, hairlike quality, often found on flowers of Trichocereeae. True areolar hairs are normally single-celled trichomes, short and felt-like, but sometimes longer and woolly (Taylor & Zappi 2004).

par-convex structures: (in seeds) are those projections, seen as appendages, of the testa-cell walls which can be classified in par-domed (*Haageocereus acranthus* subsp. *zonatus* Plate 1.5), par-conical, par-cylindrical and par-clavate, they differ from convex structures (relief) because only part of the cell wall is curved (Barthlott & Hunt 2000).

pericarp: is the fruit wall formed by the fusion of stem (receptacular) and floral tissues. The visible exterior is the stem component and may bear bract-scales, areoles, spines, bristle-spines, hairs, etc., or be almost or quite naked (Taylor & Zappi 2004).

pericarpel: is the structure comprising the lower part of the specialized stem or receptacle into which the ovary of the inverted cactus flower is sunken (Taylor & Zappi 2004).

podaria: are the swellings often subtending areoles that represent the points of attachment of leaves or bracts that have been lost, or almost lost, in the course of evolution of the highly succulent habit (Taylor & Zappi 2004).

pseudocephalium: is the region of the stem that resembles to a true cephalium, which also distinguishes the fertile part of the plant by bearing trichomes, bristles, etc. but without modifying the stem tissues. The pseudocephalium is by far less conspicuous than a true cephalium, i.e. the ring-like pseudocephalia (*Haageocereus acranthus* subsp. *zonatus,* Plate 9.4).

GLOSARIO DE TÉRMINOS BOTÁNICOS UTILIZADOS EN *HAAGEOCEREUS*

areoles — areolas: son aquellas estructuras afelpadas, generalmente circulares a ovaladas, localizadas sobre las costillas a lo largo del cuerpo de la planta. En las areolas se desarrollan las espinas (hojas modificadas), tricomas, pelos, y -de sus meristemos- nuevos brotes y los órganos reproductivos como flores y frutos.

bract-scales — brácteas escuamiformes: son los apéndices con forma de escamas localizados sobre el pericarpelo y tubo-floral, justo debajo de las piezas del perianto. En Trichocereeae subtienden a las areolas de las que brotan tricomas (unicelulares) y tricomas capiliformes (multicelulares) llegando a ser muy conspicuas en el caso de podaria decurrente (*Haageocereus acranthus* subsp. *backebergii*, Plates 8.3 and 8.4).

bristle-spines — espinas cerdosas: son espinas verdaderas que se encuentran intercalando con las espinas y se caracterizan por ser más delgadas, algo curvadas y translúcidas.

cephalium — cefalio: es la parte fértil y modificada del tallo caracterizada por dar origen a abundantes tricomas, espinas cerdosas, espinas y/o tricomas-capiliformes, donde se desarrollan las flores y los frutos, pudiendo ser muy conspicuo desarrollándose en forma lateral o apical al tallo.

flower-tube — tubo floral: es la estructura hueca o parcialmente hueca arriba del pericarpelo, formada por los tejidos florales y receptaculares fusionados, estos últimos tienen externamente brácteas escuamiformes mientras los primeros subtienden las piezas del perianto.

funicular pulp — pulpa funicular: es la pulpa sólida o líquida del interior de los frutos de cactus, como resultado de los funículos desarrollados que envuelven, nutren y protegen a las semillas.

hair-spines — espinas capiliformes: son verdaderas espinas de cactus especializadas, consisten en estructuras multicelulares con aspecto delicado y lanoso, se les encuentra frecuentemente en las flores de Trichocereeae. Se les diferencia de los pelos de las areolas porque estos últimos consisten en tricomas unicelulares.

par-convex structures — estructuras par-convexas: (en semillas) son aquellas proyecciones de las paredes de las células de la testa, vistas como apéndices, las cuales por su forma pueden ser clasificadas en par-domadas (*Haageocereus acránthus* subsp. *zonatus* Plate 1.5), par-cónicas, par-cilíndricas y par-clavadas, ellas difieren de las estructuras convexas (relieve) porque sólo una parte de la pared de la célula es curva.

pericarp — pericarpo: es la pared del fruto formada por la fusión de los tejidos receptacular (del tallo) y floral. La parte externa y visible constituye el componente receptacular del cual brotan brácteas escuamiformes, areolas, espinas, espinas-cerdosas, tricomas capiliformes, etc., o bien puede quedar desnudo del todo.

pericarpel — pericarpelo: es la estructura que envuelve al ovario ínfero, formada por la parte inferior del tejido receptacular.

podaria — podarios: son los engrosamientos que frecuentemente subtienden las areolas y representan los puntos de unión de las hojas o brácteas que han sido perdidas o casi perdidas en el curso de la evolución de los tallos con hábito extremadamente suculento.

pseudocephalium — pseudocefalio: es la región del tallo que se asemeja a un cefalio verdadero y también distingue la porción fértil de la planta (areolas) por presentar tricomas, espinas-cerdosas, etc. pero sin modificar los tejidos del tallo. El pseudocefalio es mucho menos conspicuo que un cefalio verdadero, por ejemplo, los pseudocefalios en forma anillada (*Haageocereus acranthus* subsp. *zonatus,* Plate 9.4).

List of names of *Haageocereus* (and *Peruvocereus*) possibly referring to ×*Haagespostoa*

The following taxa are believed to be names referring to hybrids between *Haageocereus* and *Espostoa*.

H. albisetatus (Akers) Backeb., Die Cact. 2: 1208 (1960); Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 414 (1958). *H. albisetatus* (Akers) Cullmann, Kakt. And. Sukk. 8(12): 180 (1957) *nom. inval.* (Art. 33.2, ICBN 2000), given as comb., but without any indication of a basyonym. ×*Haagespostoa albisetata* (Akers) Rowley, Nat. Cact. Succ. J. (UK) 37(3): 76 (1982). *Peruvocereus albisetatus* Akers, Cact. Succ. J. (US) 20(12): 184 (1948d). Type locality: Peru, Lima, Santa Eulalia valley, hills above valley (believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. albispinus (Akers) Backeb., Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 414 (1958); in Backeb., Die Cact. 2: 1210 (1960). *H. chosicensis* var. *albispinus* (Akers) Backeb., Cact. Succ. J.(US) 23(2): 47 (1951). *Peruvocereus albispinus* Akers, Cact. Succ. J. (US) 20(10): 154 (1948c). Type locality: Peru, Lima, Santa Eulalia valley.

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. albispinus var. *floribundus* (Akers) Backeb., Die Cact. 2: 1210 (1960). *Peruvocereus albispinus* var. *floribundus* Akers, Cact. Succ. J. (US) 20(10): 155 (1948c). Type locality: Peru, Lima, hills above Santa Eulalia river valley.

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. climaxanthus (Werderm.) Croizat, Cact. Succ. J. (US) 14(10–11): 148 (1942b). *Binghamia climaxantha* Werderm., Fedde, Rep. Spec. Nov. 42: 4 (1937a). ×*Haagespostoa climaxantha* (Werderm.) Rowley, Nat. Cact. Succ. J. (UK) 37(3): 76 (1982). Type: Peru, Lima, by Chosica, 1936, *Bloßfeld* 84 (B photo!).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. comosus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21 (1956, publ. 1957); Die Cact. 2: 1230 (1960). Type: Peru, Lima, Santa Eulalia valley, 1000 m, 1956, *Rauh* K27 (HEID, believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. dichromus var. *pallidior* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ.1957); Die Cact. 2: 1214 (1960). Type: Peru, Lima, Churín valley, 1700 m, 1956, Rauh K99 (HEID, believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *acanthocladus* and *Espostoa melanostele.*

H. divaricatispinus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 26 (1956, publ. 1957); Die Cact. 2: 1231 (1960). Type: Peru, Lima, Lurín valley, 500–1200 m, 1956, *Rauh* K176 (HEID, believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. pseudomelanostele subsp. *chryseus* D. Hunt, Cact. Systematics Initiatives 14: 17 (2002). Type: PERU, Ancash, Huallanca, *Ritter* FR147a (U holo!). *H. chryseus* Ritter, Kakt. Südam. 4: 1390 (1981). Type: Peru, Ancash, Santa valley, Huallanca, *Ritter* FR585 (U, syn) & FR147a. *Nom inval.* (Art. 37, ICBN 2000), based on two syntypes: *Ritter* FR585 and *Ritter* FR147a.

Parents: *H. pseudomelanostele* subsp. *acanthocladus* and *Espostoa nana.*

H. seticeps Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21 (1956, publ. 1957); Die Cact. 2: 1217 (1960). Type: Peru, Lima, Santa Eulalia valley, 1000 m, 1956, *Rauh* K43 (HEID, believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. seticeps var. *robustispinus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21 (1956, publ. 1957); Die Cact. 2: 1217 (1960). Type: Peru, Lima, Santa Eulalia valley, 1000 m, 1956, *Rauh* K37 (HEID, believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

H. zehnderi Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 23 (1956, publ.1957); Die Cact. 2: 1225 (1960). Type: Peru, Ancash, Santa valley, Huallanca, 1300 m, 1956, *Rauh* K67 (ZSS holo!).

Parents: *H. pseudomelanostele* subsp. *acanthocladus* and *Espostoa nana.*

Peruvocereus albisetatus var. *robustus* Akers, Cact. Succ. J. (US) 20(12): 186 (1948d). Type locality: Peru, Lima, Santa Eulalia valley, hills above valley (believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

Peruvocereus albicephalus Akers, Cact. Succ. J. (US) 19(10): 162 (1947f). Type locality: Peru, Lima, Santa Eulalia valley, hills above valley (believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

Peruvocereus albicephalus var. *armatus* Akers, Cact. Succ. J. (US) 19(10): 163 (1947f). Type: (believed not to have been preserved).

Parents: *H. pseudomelanostele* subsp. *carminiflorus* and *Espostoa melanostele.*

List of doubtful names attributed to the genus *Haageocereus*

Cactus multangularis Willd., Enum. Pl. Suppl.: 33 (1813). *Cereus multangularis* (Willd.) Haw., Suppl. Pl. Succ.: 75 (1819). *Binghamia melanostele* sensu (Vaupel) Britton & Rose, Cact. 2: 167 (1921) non *Cephalocereus melanostele* Vaupel (1913). *Binghamia multangularis* (Willd.) Britton & Rose, Cact. 4: 279 (1923). *Peruvocereus multangularis* (Willd.) Akers, Cact. Succ. J. (US) 22(6): 174 (1950). *H. akersii* Backeb., Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 416 (1958), nom. inval. (Art. 36.1, 37.1, ICBN 2000) given as synonym of *Peruvocereus multangularis.* Type: believed not to have been preserved.

According to the scant description and non-existent type of *Cactus multangularis* Willd., it is not possible to determine which taxon actually this name refers to. However, a later painting from a cultivated Haworth's plant of *Cereus multangularis* (Willd.) Haw. (dated

1824 and reproduced by Britton & Rose 1923, p. 279, fig. 255) led to the proliferation of later combinations using this specific epithet because of its priority as an earlier name.

Another "controversial" plant painting of *Cactus multangularis* Willd. (undated) is from Salm-Dyck (reproduced by Rowley 1999) which was also published by Leuenberger (2004) and, from his point of view, this species could be a synonym of *Weberbauerocereus johnsonii,* but to avoid further confusion *Cactus multangularis* should be rejected.

Cereus limensis Salm-Dyck, Allg. Gartenz 13(45): 353 (1845b). Type: believed not to have been preserved.

Because of the scant description and non-existent type it is not possible to attribute *Cereus limensis* to any known species of *Haageocereus*. However, Ritter made the combination *H. limensis* (*Nom. inval.* Art 37, ICBN 2000) because he considered it to be conspecific with *Cereus acranthus* Vaupel (1913) and in this manner, to recover the Salm-Dyck's old name. Existing doubts of the identity of *Cereus limensis*, this name is better left as doubtful.

H. acranthus var. *metachrous* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957); Die Cact. 2: 1177 (1960). Type: Peru, Ica, Pisco valley, 2000 m, 1955, *Rauh* K162 (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this name to any known species of *Haageocereus*.

H. albispinus var. *roseospinus* (Akers) Backeb., Die Cact. 2: 1211 (1960). *Peruvocereus albispinus* var. *roseospinus* Akers, Cact. Succ. J. (US) 20(10): 156 (1948c). Type locality: Peru, Lima, hills above Santa Eulalia river valley.

There is insufficient evidence to attribute this name to any known species of *Haageocereus*.

H. aticensis Ritter, Katalog H. Winter, (unpaged), 1958. *Nom. Inval.* (Art. 36.1, 37.1, ICBN 2000), published as provisional name (Eggli & Taylor 1991).

According to Ritter this taxon is equal to *H. subtilispinus* Ritter (1981 p. 1419). However, there is insufficient evidence to attribute this name to any known species of *Haageocereus.*

H. australis var. *acinacispinus* Rauh & Backeb. in Backeb. Desc. Cact. Nov.[1]: 25 (1956, publ. 1957). Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 392 (1958). Type: Peru, south, Km 697 Panamericana highway, rocky desert, 1956, *Rauh* K131 (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus.*

H. chosicensis var. *rubrospinus* (Akers) Backeb. Cact. Succ. J.(US) 23(2): 47 (1951). *H. rubrospinus* (Akers) Cullmann, Kakt. And. Sukk. 8(12): 180 (1957) *nom inval.* (Art. 33.2, ICBN 2000) based on *Peruvocereus rubrospinus* (Eggli & Taylor 1991). *H. chosicensis* fa. *rubrospinus* (Akers) Krainz, Die Kakt. C Va (1964). *Peruvocereus rubrospinus* Akers, Cact. Succ. J. (US) 19(8): 121 (1947d). Type locality: Peru, Lima, 300 m above Santa Eulalia river, western ridge.

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus.*

H. crassiareolatus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ.1957); Die Cact. 2: 1214 (1960). Type: Peru, Lima, Churín valley, 1200 m, 1956, *Rauh* K90b (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus.*

H. crassiareolatus var. *smaragdisepalus* Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 24 (1956, publ.1957); Die Cact. 2: 1214 (1960). Type: Peru, Lima, Churín valley, 1200 m, 1956, *Rauh* K94 (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. dichromus Rauh & Backeb. in Backeb. Descr. Cact. Nov.[1]: 24 (1956, publ.1957); Die Cact. 2: 1212 (1960). Type: Peru, Lima, Churín valley, 1200 m, 1956, *Rauh* K101 (HEID, believed not to have been preserved). *Haageocereus chosicensis* var. *dichromus* (Rauh & Backeb.) Ritter ex Krainz, Kat. ZSS 2: 64 (1967).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. elegans Ritter, Katalog H. Winter, (unpaged), (1957) nom. nud. *H. versicolor* var. *elegans* Ritter, Katalog H. Winter, (unpaged), (1957) nom. nud.

This is an invalid name that was later considered by Ritter as synonym of *H. icosagonoides* (Kakt. Südam. 4: 1422, 1981). However, there is insufficient evidence to link this name to any accepted species in this work.

H. fulvus Ritter, Kakt. Südam. 4: 1393 (1981). Type: Peru, Lima, Fortaleza valley, *Ritter* FR584 (ZSS only seeds!), believed not to have been preserved.

According to Ritter, this taxon and *H. acranthus* var. *fortalezensis* Rauh & Backeb. are synonyms. Nevertheless, there is insufficient evidence to attribute this taxon to any known species of *Haageocereus.*

H. fulvus var. *yautanensis* Ritter, Kakt. Südam.4: 1393 (1981). Type: Peru, Ancash, Yaután, *Ritter* FR 1067 (U holo!, ZSS seeds!).

The available evidence is insufficient to attribute this taxon to any known species of *Haageocereus.*

H. icensis (Backeb. ex) Ritter, Kakt. Südam. 4: 1394 (1981). Type: Peru, Ica, Canza Mine, 1953, *Ritter* FR146 (ZSS iso!).

The very poor type specimen and description are not enough evidence to attribute this taxon to any known species of *Haageocereus*.

H. longiareolatus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21 (1956, publ. 1957); Die Cact. 2: 1208 (1960). Type: Peru, Lima, Santa Eulalia valley, Chosica, 1000 m alt., 1956, *Rauh* K40 (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. multangularis var. *aureus* Ritter, Kakt. Südam.4: 1405 (1981). Based on Ritter 147d *Nom inval.* (Art. 36.1, ICBN 2000) published as provisional name (Eggli & Taylor 1991).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. pacalaensis var. *montanus* Ritter, Kakt. Südam. 4: 1417 (1981), nom. inval. (Art. 34.1, 36.1, ICBN 2000), published as provisional name, based on *Ritter* FR 294a.

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. peniculatus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21 (1956, publ.1957); Die Cact. 2: 1214 (1960). Type: Peru, Lima, Santa Eulalia valley, 1000 m, 1956, *Rauh* K40 (HEID, believed not to have been preserved).

According to Hunt (1999) this taxon is believed to be synonym of *H. albispinus* (Akers) Backeb. (*H. albispinus* is included in the list of names possibly referring to ×*Haagespostoa*). However, there is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. piliger Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 26 (1956, publ. 1957); Die Cact. 2: 1233 (1960). Type locality: Peru, Lima, Pachacámac, 100 m, 1956, *Rauh* K178 (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. pseudoacranthus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 23 (1956, publ. 1957); Die Cact. 2: 1176 (1960). Type: Peru, Lima, Lurín valley, 1000 m, 1956, *Rauh* K181 (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. salmonoideus (Akers) Cullmann, Kakt. And. Sukk. 8(12): 180 (1957) *Nom inval.* (Art. 33.2, ICBN 2000) given as comb. nov. but without any indication of a basyonym (Eggli & Taylor 1991). *H. salmonoideus* (Akers) Backeb. in Rauh, Beitr. Kenntn. Peruan. Kakt. veg.: 429 (1958). *Peruvocereus salmonoideus* Akers, Cact. Succ. J. (US) 19(7): 109 (1947). Type locality: Peru, Lima, Rímac canyon, 15 km above Chosica.

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. tenuispinus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 22 (1956, publ. 1957). Type: Peru, Ancash, Km 465 Panamericana highway, 30 km north of Pativilca, desertic hills, 1956, *Rauh* K89 (ZSS).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. smaragdiflorus Rauh & Backeb. in Backeb. Descr. Cact. Nov. [1]: 21 (1956, publ. 1957); Die Cact. 2: 1209 (1960). Type: Peru, Lima, Santa Eulalia valley, 1000 m alt., 1956, *Rauh* K40 (HEID, believed not to have been preserved).

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*.

H. zangalensis Ritter, Kakt. Südam. 4: 1424 (1981). Type: Peru, Cajamarca, Zangal–Chilete, 2000 m, *Ritter* FR1074 (U holo!).

The incomplete description without flowers nor fruits and very poor type prevent the attribution of this taxon to any known species of *Haageocereus*. Fieldwork carried out during this project failed to shed more light into the identity of this name.

Pygmaeocereus densiaculeatus Backeb., Descr. Cact. Nov. [3]: 12 (1963). Type: believed not to have been preserved.

There is insufficient evidence to attribute this taxon to any known species of *Haageocereus*, however Ritter (1981) believed it to belong with *Haageocereus lanugispinus*.

List of names of *Haageocereus* now placed in other genera

H. albus (Ritter) Rowley, Nation. Cact. Succ. J. 37(3): 76, 1982.

= ***Weberbauerocereus longicomus*** Ritter, in Hunt D., Cites Cactaceae Checklist: 282 (1999).

H. andinus Ritter, Backeberg's Descr. & Erort. Taxon.nomenklat. Fragen, 14, 1958. *Nom. Inval.* (Art. 36.1, 37.1, ICBN 2000) (published as provisional name.) (Eggli & Taylor 1991).

= ***Cleistocactus hystrix*** (Rauh & Backeb.) Ostolaza, as synonym in Hunt D. Cites Cactaceae Checklist: 171 (1999).

H. convergens Ritter, Katalog H. Winter, (unpaged), (1956) *Nom inval.* (Art. 36.1, 37.1, ICBN 2000) (1956, publ.1957). (Eggli & Taylor 1991).

= ***Cleistocactus acanthurus*** (Vaupel) Hunt **ssp. *acanthurus***, as synonym in Hunt. D., Cites Cactaceae Checklist: 170 (1999).

H. hystrix Ritter, Katalog H.Winter, (unpaged), (1958) *Nom inval.* (Art. 36.1, 37.1, ICBN 2000) published as provisional name (Eggli & Taylor 1991).

= ***Cleistocactus hystrix*** (Rauh & Backeb.) Ostolaza, as synonym in Hunt D. Cites Cactaceae Checklist: 171 (1999).

H. imperialis Ritter, Katalog H.Winter, (unpaged), (1958) *Nom inval.* (Art. 36.1, 37.1, ICBN 2000) published as provisional name (Eggli & Taylor 1991).

= ***Cleistocactus acanthurus*** (Vaupel) Hunt **ssp. *acanthurus***, as synonym in Hunt. D., Cites Cactaceae Checklist: 170 (1999).

H. montanus Ritter, Katalog H.Winter, (unpaged), (1958) *Nom inval.* (Art. 36.1, 37.1, ICBN 2000) published as provisional name (Eggli & Taylor 1991).

= ***Cleistocactus hystrix*** (Rauh & Backeb.) Ostolaza, as synonym in Hunt D. Cites Cactaceae Checklist: 171 (1999).

H. pacaranensis Ritter, Katalog H.Winter, (unpaged), (1958).

= ***Cleistocactus acanthurus*** (Vaupel) Hunt **ssp. *acanthurus***, as synonym in Hunt. D., Cites Cactaceae Checklist: 170 (1999).

H. paradoxus Rauh & Backeb., Descr. Cact. Nov. [1]: 21 (1956, publ.1957); Die Cact. 2: 1242, (fig.) (1959). Type: Peru, Lima, Santa Eulalia valley, 1000 m, 1956, Rauh K42 (HEID, believed not to have been preserved).

= ***Cleistocactus acanthurus*** (Vaupel) Hunt **ssp. *acanthurus***, as synonym in Hunt. D., Cites Cactaceae Checklist: 170 (1999).