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NOTES ON THE GENUS *CAIOPHORA* (LOASOIDEAE, LOASACEAE) IN CHILE AND NEIGHBOURING COUNTRIES

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Abstract. Ackermann, M. & M. Weigend. 2007. Notes on the genus *Caiophora* (Loasoideae, Loasaceae) in Chile and neighbouring countries. *Darwiniana* 45(1): 45-67.

This is the first revision for the representatives of the genus *Caiophora* (Loasaceae) in Chile. The genus is widely distributed in the Andes from Argentina/Chile in the South to Central Ecuador in the North, and comprises approximately 60 species. In Chile only five species are present, *Caiophora chuquitensis*, *C. cirsiifolia*, *C. coronata*, *C. deserticola* sp. nov. and *C. rosulata*. *Caiophora rosulata* is here subdivided into two subspecies: western Andean *C. rosulata* subsp. rosulata (present in northern Chile and southern Peru), and eastern Andean *C. rosulata* subsp. *taraxacoides*, stat. and comb. nov. Furthermore *C. superba* syn. nov. and *C. macrocarpa* syn. nov. are placed into synonymy under *C. chuquitensis*, and *C. rahmeri* syn. nov. is synonymized to *C. rosulata* subsp. *rosulata*. These five species comprise the complete range of growth forms known for the genus, i.e., subshrubs, cushion-forming herbs, acaulescent, rosulate herbs and vines. For all taxa a key and full morphological descriptions and synonymy are provided, including illustrations, notes on habitat, distribution, floral biology and chromosome numbers.

Keywords. *Caiophora*, Chile, chromosome number, high Andean flora, Loasaceae, morphology, pollination, taxonomy.

Resumen. Ackermann, M. & M. Weigend. 2007. Notas sobre el Género *Caiophora* (Loasoideae, Loasaceae) en Chile y países limítrofes. *Darwiniana* 45(1): 45-67.

Esta es la primera revisión del género *Caiophora* (Loasaceae) en Chile. El género comprende alrededor de 60 especies, y está ampliamente distribuido en los Andes, desde Argentina/Chile en el Sur, hasta el centro de Ecuador en el Norte. Se conocen solamente cinco especies de Chile: *Caiophora chuquitensis*, *C. cirsiifolia*, *C. coronata*, *C. deserticola* sp. nov. y *C. rosulata*. El material de *Caiophora rosulata* se divide entre dos subespecies, *C. rosulata* subsp. *rosulata* comb. nov., de los Andes Occidentales (presente en el norte de Chile y el sur de Perú, y *C. rosulata* subsp. *taraxacoides* stat. y comb. nov., de los Andes Orientales. Los nombres *C. superba* syn. nov. y *C. macrocarpa* syn. nov. son sinonimizados bajo *C. chuquitensis, y C. rahmeri* syn. nov., sinonimizado bajo *C. rosulata* subsp. rosulata. Estas cinco especies comprenden el rango completo de hábitos conocido para el género: sufrútices, hierbas perennes en forma de cojines, hierbas rosuladas acaules, y hierbas trepadoras. Proporcionamos una clave, descripciones morfológicas y la sinonimia completa para todos los taxones, incluyendo ilustraciones, notas sobre la distribución, el hábitat, la biología floral y números cromosómicos.

Palabras clave. *Caiophora*, Chile, Flora Alto Andina, Loasaceae, morfología, número cromosómico, polinización, taxonomía.

INTRODUCTION

The genus *Caiophora* C. Presl comprises about 60 species. It ranges from Central Argentina/Chile to central Ecuador with a single species in Uruguay and southern Brazil [*C. arechavaletae* (Urb.) Urb. & Gilg]. The genus is largely High Andean, and most taxa are restricted to elevations

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above 3000 m, ranging as high as 5000 m. The genus *Caiophora* forms a monophyletic group with clades of *Loasa* Adans. and *Scyphanthus* D. Don (Hufford et al., 2005; Weigend et al., 2004). Sleumer (1955) and Weigend (1997, 2000) made the first and preliminary attempts to organize and evaluate the numerous names published in the genus *Caiophora* since the studies by Urban & Gilg (1900, 1911), while some additional names were clarified in Weigend & Ackermann (2003). Many of the taxonomical problems in the genus stem from the fact that Urban & Gilg (1900) enthusiastically described new species on the basis of single, fragmentary specimens. However, a full-scale revision of the genus is still pending, and classification in the genus remains extremely problematical, due to the relative scarcity of clear morphological characters identifiable in herbarium specimens, the high degree of heterogeneity between populations of individual taxa as now recognized, and the abundance of interspecific hybrids (Sleumer, 1955). These complications are particularly true for Peru, where *Caiophora* is most diverse, and to a lesser extent for Bolivia. For Peru only one revision has been published (Macbride, 1941), which has been evaluated for the Checklist of that country (Schatz, 1996). These studies are based on a very superficial review of herbarium material only. Especially in Peru some species groups such as the *C. cirsiifolia*-group and *C. carduifolia*-group (Weigend & Ackermann, 2003) comprise numerous undescribed, often locally endemic taxa. In Chile the situation is less complex, with only a handful of relatively well defined species known. However, *Caiophora* is largely restricted to the North of Chile in the Region I, an area not well represented in herbaria due to the seasonality of its flora and the inaccessibility of the High Andean vegetation. Furthermore, the transport of organic material into the neighbouring Region is severely restricted for phytosanitary reasons, which provides a further inhibition for the collection of botanical specimens. Distribution limits are therefore not entirely clear. Another complication arises from the very incomplete locality data and absence of reliable numbering on the type collections by Philippi and Steinmann. Especially Philippi collected and described some specimens with nearly the same or without precise locality information (*C. superba* Phil. and *C. rahmeri* Phil. from Tarapacá) leading to confusion in both the literature and herbaria, as well as making the unequivocal identification of iso- and holotypes next to impossible. These problems are here addressed as best as possible.

In the present study, evaluation of species limits, i.e., morphological divergence typically present within relatively homogeneous species (and determined by ontogeny or ecology) versus morphological divergence sufficient to warrant the recognition of different taxa, is mostly derived from more than 15 field trips, mainly to Peru. Also, ca. 20 accessions of *Caiophora* taxa were taken into cultivation in Munich or Berlin to compare the variability of morphological characters from natural habitat with different ecological conditions, and an extensive amount of herbarium material was studied.

This study aims to provide well-defined names for the project of the "Checklist of the Southern Cone" (Weigend et al., forthcoming) and we here redefine the relevant taxa present there, reduce several names to synonymy and improve descriptions and illustrations. The following taxa are here reported for the flora of Chile: *Caiophora chuquitensis* (Meyen) Urb. & Gilg, *C. cirsiifolia* C. Presl, *C. coronata* (Gillies ex. Arn.) Hooker & Arn., *C. deserticola* Weigend & Mark. Ackermann, sp. nov. and *C. rosulata* (Wedd.) Urb. & Gilg subsp. *rosulata* comb. nov. and *C. rosulata* (Wedd.) Urb. & Gilg subsp. *taraxacoides* (Killip) Weigend & Mark. Ackermann stat. and comb. nov.

MATERIAL AND METHODS

The present study is based on field studies in southern Peru and from cultivation of several accessions at Munich and Berlin (vouchers at BSB, M, MSB). Specimens of the following herbaria were revised: B, BA, BM, BOLV, BR, BSB, CORD, CUZ, E, F, FR, G, GB, GOET, HBG, GH, HUSA, HUT, IBBA, K, L, LIL, LPB, LPZ, M, MA, MICH, MO, MSB, NY, OXF, P, PR, PRC, S, SI, SGO, TRIER, TUEB, UC, UMSS, U, US, USM, W, WU, Z, plus the online type collections of the Field Museum of Natural History (F, fm1.fieldmuseum.org/vrrc/index.php), New York Botanical Gardens (NY, www.nybg.org/bsci/herb/), Smithsonian Museum of Natural History (US, rave-

nel.si.edu/botany/types/) and the Herbarium of the University of Vienna (WU, herbarium.univie.ac.at/database/collections.htm). For identification and description of the different species we used the morphological characters of growth habit, leaf-size, flower-size, petal-size, nectar scale and staminode size and shape, and also the density of setae and trichomes (scabrid and glochidiate).

Chromosome counts were made from embryonic roots of germinating seeds (Petri culture dishes, on moist filter paper) or obtained from potted seedlings that were pre-treated in hydroxyquinoline for 1.5 hours, fixed in 95% ethanol-acetic acid (3:1 V/V), stained with aceto-orcein, and then squashed and counted. Additional counts were compiled from the literature.

Key to the Chilean species of *Caiophora*:

1. Acaulescent, rosulate plant. Capsule up to 16 mm long . . . . . .5. *C. rosulata*
1. Plants with well developed aerial shoot, shoots erect, decumbent or winding. Capsule over 20 mm long . . . . . .2.
2(1). Plants decumbent but leaves stiffly erect. Flowers on long, lax pedicels, geoflorous. Petals mostly white, cream, greenish-white (very rarely yellow or orange) . . . . . .3. *C. coronata*
2. Plants stiffly erect or winding. Flowers deflexed or pendulous. Petals orange, red or pale pink . . . . . .3.
3(2) Plants winding. Petals and nectar scales orange. Nectar scales keeled and never with three dorsal filaments (rarely one or two, and then inserted at scale apex) . . . . . .2. *C. cirsiifolia*
3. Plants erect. Petals orange, red or pink. Nectar scales white, usually not keeled and with three dorsal filaments inserted on middle or upper half of scale . . . . . .4.
4(3) Flowers penta- to heptamerous. Pedicel 20-30 (-70) mm (in anthetic and postanthetic flowers). Petals 15-25 mm long, pink. Abaxial leaf-surface nearly esetulose. Fruit conical . . . . . .4. *C. deserticola*
4. Flowers penta- to nonamerous. Pedicel 3-15 (-50) mm (in anthetic and postanthetic flowers). Petals 20-30 (-40) mm long, pink, bright orange or red, rarely white or yellow. Abaxial leaf-surface setose, fruit ovoid . . . . . .1. *C. chuquitensis*

1. Caiophora chuquitensis (Meyen) Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 301. 1900. *Loasa chuquitensis* Meyen, Reise Erde 1: 483. 1834. *Blumenbachia chuquitensis* (Meyen) Hook.f., Bot. Mag. 51: Tab. 6143. 1875. TYPE: Bolivia, Depto. La Paz, Prov. La Paz, Vic La Paz, 10000 ft, M. Bang 171 p.p. (neotype NY! designated by *M. Weigend, Sendtnera 4: 232.* 1997; isoneotypes BM!, E!, F!, GH!, MO, US!, W!). Figs. 1, 2.

Caiophora superba Phil., Anal. Mus. Nac. Chile 1891: 23. 1891, syn. nov. TYPE: Chile, I Región de Tarapacá, Tarapacá, *R. A. Philippi s.n.* (holotype SGO!; isotypes K!; WU!).

Caiophora horrida Urb. & Gilg, Mem. Torrey Bot. Club 3/3: 36. 1893. TYPE: Bolivia, near La Paz, M. Bang 171 p.p. (lectotype NY! designated by *M. Weigend, Sendtnera 4: 232*. 1997; isolectotypes BM!, E!, F!, GH!, MO, US!, W!).

Caiophora albiflora (Griseb.) Urb. & Gilg, in Engler and Prantl, Nat. Pflanzenfam. 3/6a: 119. 1894. *Caiophora heptamera* Wedd. var. *albiflora* Griseb., Symb. Fl. Argent. 139. 1879. TYPE: Argentina, Prov. Catamarca, Andalgalá, near Negrilla, *F. Schickendantz 149* (lectotype GOET! designated by *M. Weigend, Sendtnera 4: 232*. 1997; isolectotypes B destroyed, photo F, neg. nr. 10140, CORD).

Caiophora heptamera (Wedd.) Urb. & Gilg, in Engler and Prantl, Nat. Pflanzenfam. 6a: 119. 1894. *Loasa heptamera* Wedd., Chlor. And. 2: 218. 1857. TYPE: Bolivia, Depto. Potosi, *H. A. Weddell 4095* (holotype P!, photo F!, neg. nr. 38479).

Caiophora angustisecta Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 300. 1900. TYPE: Argentina. Prov. Salta: Cafayate, Cuesta del Arca, 3090 m, *C. Spegazzini 102321* (holotype B destroyed, photo F!, neg. nr. 10142; isotype LPS).

Caiophora lorentziana Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 289. 1900. TYPE: Argentina, Prov. Salta, Caldera, near Nevado del Castillo, *P. G. Lorentz & G. H. Hieronymus s. n.* (lectotype WU! designated by *M. Weigend Sendtnera 4: 234.* 1997).

Caiophora macrocarpa Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 285. 1900, syn. nov. TYPE: Argentina, Prov. Salta, Caldera, near Nevado del Castillo, *P. G. Lorentz and G. H. Hieronymus 49* (lectotype K! designated by *M. Weigend, Sendtnera 4: 234*.1997; isolectotypes B destroyed, photo F!, neg. nr.10156; G, GOET!).

Caiophora orbignyana Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 302 1900. TYPE: Bolivia, Potosí, *A. D´Orbigny 1436* (holotype BR!; isotypes G!, photo F!, neg. nr 24169, P!).

Caiophora sphaerocarpa Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 296. 1900. TYPE: Bolivia, La Paz, Larecaja, near Sorata, Arrilaya, Chuchu, 3800-4200 m, *G. Mandon 619 p.p.* (holotype P!, photo F!, neg. nr. 38498).

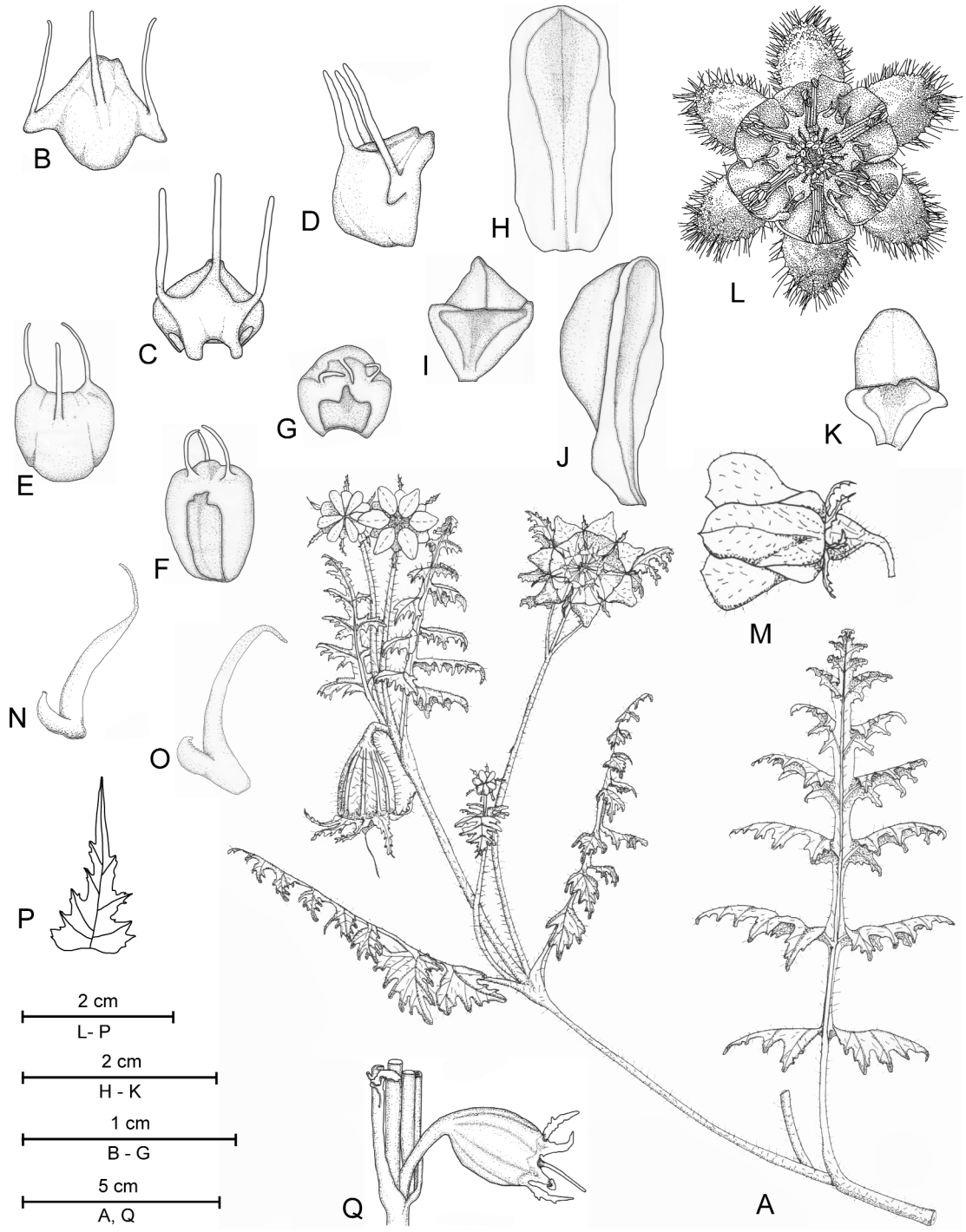

Fig. 1. *Caiophora chuquitensis*. **A,** growth habit. **B, E,** nectar scale, dorsal view. **C, G,** apical view. **D,** lateral view. **F,** ventral view. **H,** petal, dorsal view. **I, K,** apical view. **J,** lateral view. **L,** flower (drawn by H. Lünser, Berlin). **M,** lateral view.. **N-O,** staminodes. **P,** sepal. **Q,** fruit. **A** and **M,** drawn from cultivated plants in Munich *M. Weigend 3681* (MSB); **B-D, K, L, O, P,** from *M. Ackermann et al. 274* (BSB, HUSA, M); **E-J, N, Q,** from *F. Luebert 1720* (BSB, SGO).

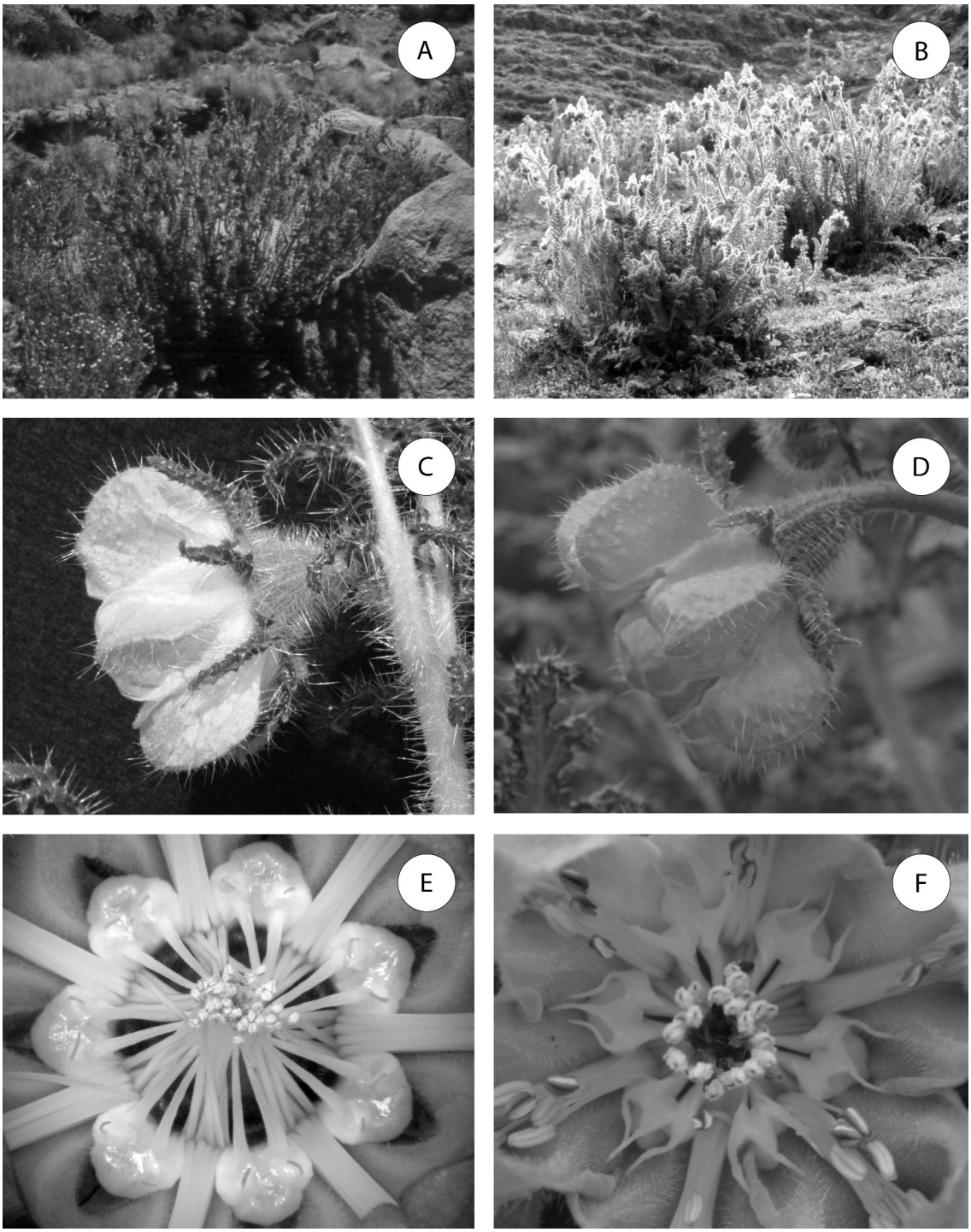

Fig. 2. *Caiophora chuquitensis.* **A,** natural habitat in Chile (Photo from F. Luebert) **B,** natural habitat in Peru. **C-F,** two different morphotypes, cultivated in Berlin. **C, D,** flower, lateral. **E, F,** nectar scales and staminodes. **A, C, E,** *F. Luebert 1720* (BSB, SGO): **B,** *M. Weigend & K. Weigend 2000/203* (HUSA, MSB, NY); **D, F,** *M. Ackermann et al. 274* (BSB, HUSA, M).

Caiophora fiebrigii Urb. & Gilg, Bot. Jahrb. Syst. 45: 470. 1911. TYPE: Bolivia, Tarija, Prov. Avilez, Puna Patanca, 3800 m, *K. Fiebrig 2603* (lectotype BM! designated by *M. Weigend, Sendtnera 4: 234*. 1997; isolectotypes B destroyed, photo F!, neg. nr. 10151; E!, G, HBG!, K!, L, M!, P!, U, US!, W!).

Perennial herbs to subshrubs (15-) 40-80 (-100) cm tall, with persistent basal leaf rosette from thick tap-root. Stems basally (for ca. 10-20 cm) lignescent and perennating, 4-20 mm thick, densely covered with setae 3-5 mm long, white, yellow or brown, and scabrid (0.2-0.5 mm long) and glochidiate trichomes (0.1-0.4 mm long). Basal leaves 10-15 (-25) cm long; laminas narrowly ovate, 70 x 30 to 150 x 45 (to 200 x 60) mm, pinnatisect (lower lobes generally free) with (6-) 9-12 (-14) lobes on each side; lobes narrowly ovate, up to 30 x 20 mm; lobe margins grossly serrate to pinnatifid to lobulate, with 5-8 serrations or lobules on each side; lobules up to 8 mm long, distal lobules usually recurved; adaxial leaf surface sparsely setose with stinging hairs 3-5 mm long and covered with scabrid trichomes up to 1 mm long; abaxial surface setose, very densely set with scabrid (up to 1 mm long) and glochidiate trichomes (up to 0.3 mm long). Inflorescences frondose, terminal, mono- or asymmetrical dichasia, rarely thyrsoids; with 3-7 flowers, with internodes 4-9 cm long; pedicels 3-15 (-50) mm long during anthesis. Flowers horizontal to deflexed, penta- to nonamerous. Calyx lobes spreading or deflexed, narrowly ovate-oblong to ovate-triangular, 9 x 2 to 11 x 3 mm, densely setose and covered with scabrid trichomes; margin coarsely serrate or dentate with 3-5 teeth on each side. Corolla widely balloon-shaped; petals erect, deeply cymbiform and sharply keeled, 20-30 (-40) mm long and 10 mm deep, dorsally setose and covered with scabrid and glochidiate trichomes; petals bright orange, red, pinkish, rarely yellow or white; apex blunt or acuminate. Stamens in 5-9 epipetalous fascicles, ca. 25 in number per fascicle each; filaments ca. 12-17 mm long, white; anthers ovoidal, pale yellow to orange, ca. 1 mm long. Nectar scales deeply cymbiform, white, hemispherical or keeled in dorsal view, ca. 5 x 6 to 7 x 8 mm; scale neck triangular or rounded, slightly thickened; with (rarely without) three filiform dorsal filaments up to 5 mm long, these sometimes basally widened, white with orange or red tip, inserted in the middle or in the upper third of scale back. Free staminodia L-shaped, 10-20 mm long, dorsally with spoon-shaped appendage ca. 5 x 2 mm, appendage sometimes papillose; apex of staminodia filiform and hook-shaped. Style terete, up to 25 mm long (towards the end of anthesis); ovary inferior, conical, with 3-5 placentae and numerous ovules. Fruit horizontal or deflexed; pedicels up to 50 mm long; capsule ovoidal, 20 x 10 to 30 x 25 mm, sometimes protracted into a short beak, opening with 3-5 longitudinal slits only; style persistent, up to 15 mm long (during anthesis), not accrescent in fruit; sepals accrescent, up to 20 mm long. Seeds numerous; testa deeply pitted, brown.

Geographical distribution and habitat. The species is distributed in Chile in Region II. (Marticorena et al., 1998), in Argentina in the provinces of Catamarca, Jujuy, Salta and Tucumán (Brücher, 1986, 1989; Sleumer, 1955), in Bolivia in the departments of Cochabamba, La Paz, Oruro, Potosi and Tarija (Weigend & Ackermann, forthcoming) and in Cuzco, Peru (Schatz, 1996). The elevational distribution ranges from (2500-) 3000-4500 m. This High Andean plant species is found on scree slopes, in corrals and at the base of dry stone walls, between rocks and in open grassland (Fig. 2A-B). *Caiophora chuquitensis* is pollinated by long-tongued bees and hummingbirds (Ackermann & Weigend, 2006; Harter, 1995; Coccuci & Sersic, 1998; Schlindwein, 2000).

Chromosome number. Sporophytic: 2n = 16 (incl. *C. macrocarpa*, Brücher 1986, 1989; own counts: *M. Ackermann et al. 274*).

Observations. *Caiophora chuquitensis* is a very heterogenous species with a wide range of morphological variations (Fig. 2A-F). Sizes of plants, laminas and flowers vary considerably. Leaf margins are typically recurved in nature, but may be flat in moist situations and in cultivation. Petal colour is typically bright orange and also red or pinkish, but specimens with yellow or white petals have been recorded. Nectar scales are either hemispherical or keeled, sometimes lacking dorsal filaments (Fig. 2E-F). Cultivated plants (specimen: *M. Ackermann et al. 274*) in the greenhouses in Berlin show that many of the characters used for species delimitation by Urban & Gilg (1900)

(plant size, presence or absence of dorsal filaments on nectar scales, degree of leaf dissection) vary between the wild collected plant and its offspring in cultivation and are thus not stable. Merosity, flower-size and fruit-size, which Sleumer (1955) and Urban and Gilg (1900) used to distinguish *C. heptamera* and *C. macrocarpa* are not fixed. Cultivated plants show that the first flower and fruit of the inflorescence is huge in comparison to the final ones and that merosity can decrease with the subsequent flowers. Density and occurrence of the different trichomes (scabrid and glochidiate) depend on seasonal and ecological factors. Leaves from plants cultivated in shade have few setae and flat laminas, whereas plants cultivated in sunshine have margins that are usually recurved. These observations lead us to synonymize *C. superba* and *C. macrocarpa* under *C. chuquitensis*. *Caiophora andina* Urb. & Gilg (Peru and Argentina) remains problematical and is only distinguished by its few-flowered inflorescences (one or two flowers) and the less deeply dissected leaves. Closely allied *C. mollis* (Griseb.) Urb. & Gilg (Bolivia and Argentina) can be distinguished by the lack of or scarcity of setae on the entire plant and the presence of long, white scabrid trichomes. *Caiophora rusbyana* Urb. & Gilg and *C. boliviana* Urb. & Gilg are characterized by capsules with a distinct conical beak.

Representative specimens examined

ARGENTINA. **Catamarca.** Depto. Andalgalá: Mina de Capillitas, subida el Cerro Yutuyaco, 3600-3900 m, 3-III-1952, *H. O. Sleumer 2739* (UC, US). **Jujuy.** Depto. Cochinoca: Cerro Jucahuasi, 4000 m, 5-III-1930, *S. Venturi 10371* (S). Depto. Humahuaca: Palca de Aparzo, 3700 m, 23o 10´ S, 065o 11´ W, 16-II-1997, *F. O. Zuloaga et al. 5948* (MO). Depto. Rinconada: Mina Pirquitas, 4200 m, III-1970, *H. Fabris and F. O. Zuloaga 7693* (P); Depto. Tilcara: Chorru Valley, near Tilcara, 4000 m, 13-II-1939, *E. K. Balls 6029* (E, K, UC, US). Depto. Yavi: Quebrada de Toquero, 3600 m, 21-XI-1963, *A. L. Cabrera 15370* (M). **Salta.** Depto. Rosario de Lerma, 3200 m, *S. Venturi 8131* (BM, GH, K, NY, US). Depto. Caldera: Potrero del Castillo, ascent to Nevado del Castillo via Mal Paso, 3700-3750 m, 15-III-1952, *H. O. Sleumer and F. B. Vervoorst* 2953 (US). Depto. Chicoana: Cuesta del Obispo, 2800 m, *A. L. Cabrera et al. 22021* (K). Depto. Orán: Cerro La Escalera, 3800 m, *A. Pierotti 1337* (GH). Depto. Poma: Cobres, 3500 m, 31-I-1944, *A. L. Cabrera 8333* (GH). Depto. San Antonio de los Pobres: Quebrada de Urcuro, 3700 m, 12-II-1945, *A. L. Cabrera 8687* (GH). Depto. Santa Victoria: near the village Santa Victoria, 2500-2800 m, 13-16-XII-1988, *J. L. Novara 8355* (M, S). **Tucumán.** Depto. Chicligasta: Estancia Las Pavas, 3000 m, 28-XI-1926, *S. Venturi 4655* (GH, US). Depto. Tafi: Cumbre de Chaquiril, 12-I-1945, *D. Olea 256* (BM, S).

BOLIVIA. **Cochabamba.** Prov. Quillacolllo: laderas de la cordillera sobre Tiquipaya y la comunidad de Laphia, 3750 m, 11-II-1990, *G. Navarro 1103* (BOLV). Prov. Tiraque: Kaspiconcha alto, Millumayo, 3950 m, 7-XII-1989, *R. Guillen 34* (BOLV). **La Paz.** Prov. Aroma: La Paz 75 km hacia al Sur y 10 km hacia al desvio a Sapahaqui, 17° S, 068° W, 4150 m, 18-I-1981, *S. Beck 6021* (MO, MSB). Prov. Bautista Saavedra: Charazani, Chajaya, 7-IV-1992, *P. Gutte 339* (LPB, LPZ). Prov. Inquisivi: 35 km de Caracollo-Leque Palca, 4 km hacia Cochabamba, sobre el camino nuevo asfaltado Tholopampa, 17° 35´ S, 066° 57´ W, 3950 m, 15-I-1995, *S. Beck 21725* (M). Prov. Los Andes: 6,6 km NW of Batallas on the principal road along Lake Titicaca, 16° 15´ S, 068° 33´ W, 3850 m, 5-II-1984, *J. C. Solomon 11442* (MO, US). Prov. Loayza: 9.8 km NW of Villa Loza on road towards Urmiri and Sapahaqui, 5-III-1993, *P. M. Petersen et al. 12679* (LPB). Prov. Murillo: al NW de La Paz, entre Lago Challapata y Lago Incachaca, 4300 m, 28-XII-1990, *S. Beck 17894* (MSB). Prov. Omasuyos: near Sircapaca, 3880 m, III-1982, *F. Casa & J. Molero 6464* (NY). Prov. Pacajes: Corocoro, 1 km east of town, 4050 m, 24-XI-1982, *T. Johns 82-58* (F, LPB, MICH, MO). Oruro. Prov. Sajama: de Turco 3 km hacia Curahurare de Carangas, 3880 m, 18-III-1992, *S. Beck 21050* (MSB). **Potosi.** Prov. Nor Chichas: Quechisla, XII-1931, *R. Cárdenas 49* (GH). Prov. Sud Chichas: 1 km before Macho Cruz, the pass across the Cordillera de Mochara from Tupiza to Tarija, 3700 m, 4-XII-1967, *B. B. Vuilleumier 405* (F, NY). Prov. Tomas Frias: Cerrania del Khare-Khare, arriba de la Ciudad de Potosi, a orrillas de

la Laguna Chalaviri, 4400 m, 4-II-1988, *Schulte 162a* (M). **Tarija.** Prov. Aviles: Tajzara cerca Patancas, 3650 m, 11-III-1986, *E. Bastión 1063* (LPB, MSB). Prov. Mendez: Abra entre Iscayachi y Cieneguillas, 3500 m, 27-XII-1985, *R. Ehrich 28* (LPB, MSB).

CHILE. **II Región de Antofagasta.** Prov. El Loa: Quebrada de Caspana, 5 km sur de Caspana, 3250 m, 18-II-2003, *F. Luebert 1720* (BSB).

PERU. **Cuzco.** Prov. Calca: road from Calca to Lares, after Rancal, 13° 10′ 26′′ S, 071° 57′ 55′′ W, 4000 m, 11-IX-2002, *M. Ackermann et al. 274* (BSB, HUSA, M). **Huancavelica.** Prov. Castrovirrayna: near Apacheta Grande, 4500 m, 28-XII-1974, *T. C. Plowman & W. Davis 4646* (USM).

2. Caiophora cirsiifolia C. Presl, Reliq. Haenk. 2: 42, plate 56. 1831. TYPE: Peru. Depto. Junin, Tarma?, *T. Haenke s.n*. (holotype PR!, photo PR!, neg. nr. 919; isotype PR!, photo PR!, neg. nr. 920). Figs. 3, 4A-B.

Caiophora sepiaria (Ruiz & Pav. ex G. Don) J. F. Macbr., Candollea 8: 23. 1940. *Blumenbachia sepiaria* Ruiz & Pav. ex G. Don, Gen. Hist. 3: 62. 1834. *Loasa sepiaria* Ruiz & Pav., Fl. peruv, in Anales Inst. Bot. Cavanilles 16: 420, tab. 449. 1958. TYPE: Ruiz & Pav., Fl. peruv, in Anales Inst. Bot. Cavanilles 16: tab. 449. 1958. (Lectotype designated by M. Weigend, Sendtnera 4: 227. 1997). Peru, Depto. Lima, Huacho, cerca Juncal, Mayobamba, *H. Ruiz & J. A. Pavón s.n*. (epitype MA! designated by M. Weigend, Sendtnera 4: 227. 1997, photo M!, fragment F!).

Caiophora preslii Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 1900: 306. TYPE: Peru. Depto. Lima, Matucana, cerca Matucana, "In vallibus cordillerum Peruvia", *T. Haenke s.n.* (holotype PR! nr. 24293).

Caiophora contorta auct. non (Descr.) Presl.

Perennial, winding herbs up to 2-5 m, without basal leaf rosette, with taproot and short underground rhizomes. Stems basally 2-4 mm thick, sparsely covered with stinging hairs (2-3 mm long), trichomes scabrid (up to 1 mm long) and glochidiate (0.3 mm long). Basal leaves with petioles 15-25 mm long; lamina (narrowly) triangular-ovate, 60 x 35 to 90 x 40 mm, apex acuminate, with proximal pair of leaflets sometimes free (basal leaves), pinnate-pinnatifid to bipinnatifid with (4-) 6-7 (-9) lobes on each side; lobes narrowly ovate, triangular, 7 x 4 to 15 x 7 (to 24 x 15) mm; margins grossly serrate to pinnatifid with 2-3 lobules/teeth on each side; lobules up to 4 mm long; adaxial leaf surface sparsely setose with stinging hairs up to 3 mm long and set with scabrid trichomes up to 1 mm long; abaxial leaf surface esetulose or with scattered stinging hairs mainly on major veins, up to 2 mm long, very densely covered with scabrid trichomes (up to 0.6 mm long) and glochidiate trichomes (ca. 0.3 mm long). Inflorescences frondose, winding anthoclades, terminal monochasia or very asymmetrical dichasia; internodes 5-25 cm, pedicels 20-30 (-60) mm long during anthesis. Flowers pendulous, pentamerous. Calyx lobes spreading, apically reflexed, narrowly triangular-ovate, 6 x 1 to 10 x 2 mm, sparsely setose and densely covered with scabrid trichomes, with margins coarsely serrate with 1-3 teeth on each side. Corolla saucer-shaped; petals deeply cymbiform, 13-20 mm long and 6-8 mm deep, setose and covered with scabrid and glochidiate trichomes, orange, petals laterally winged towards the base. Stamens in 5 epipetalous fascicles, 20-25 in number per fascicle; filaments ca. 10-12 mm long; anthers ovoid, pale yellow to brownish, ca. 1 mm long. Nectar scales deeply cymbiform, ca. 5 mm high, 6 mm wide and 6 mm deep, same colour as petals (orange), keeled in dorsal view; generally without dorsal filaments, scale neck thickened. Free staminodia L-shaped, 8-10 mm long, dorsally with a spoon-shaped, papillose (up to 1 mm) appendage ca. 3 x 1.5 to 4 x 2 mm. Style terete, up to 7 mm long (towards the end of anthesis); ovary inferior, conical to cylindrical, with 3 placentae with numerous ovules. Fruit deflexed, pedicel 30-40 (-70) mm long; capsule conical, (15-) 20-35 mm x 8-11 mm, twisted, opening with 3 longitudinal slits; style persistent, not accrescent in fruit; sepals accrescent, up to 10 mm long. Seeds numerous; testa deeply pitted, brown.

Geographical distribution and habitat. The species is part of a complex of several closely allied taxa mostly on the western slope of the Andes ranging from North Peru (Depto. Cajamarca) into North Chile (Region I). The plant from

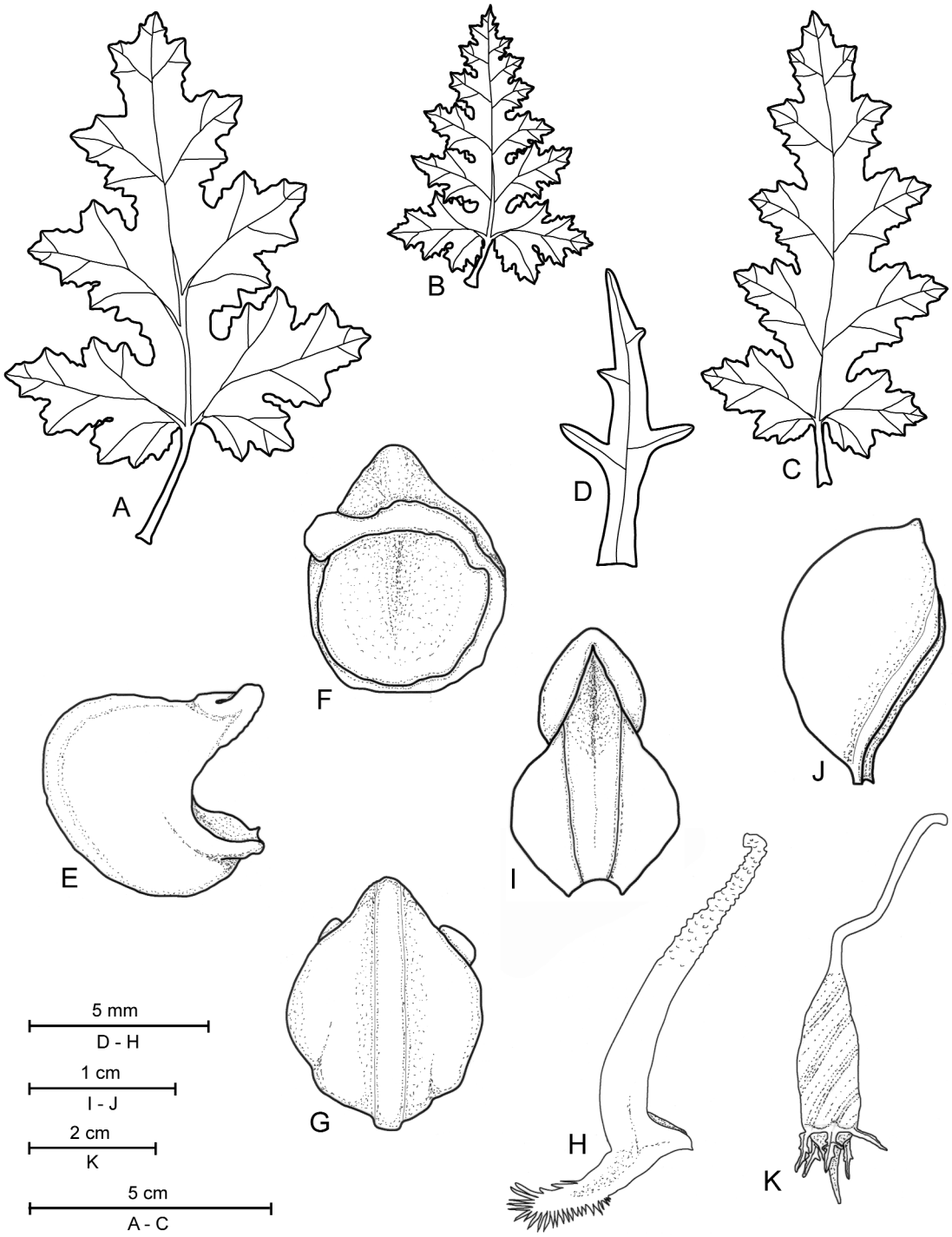

Fig. 3. *Caiophora cirsiifolia*. **A-C,** leaves. **D,** sepal. **E,** nectar scale, lateral view. **F,** ventral view. **G,** dorsal view. **H,** staminode. **I,** petal, ventral view. **J,** lateral view. **K,** fruit. **A, C-H, K,** *M. Ackermann et al. 420* (BSB, HUSA, **M,** USM, NY, F); **B, I, J,** *M. Ackermann et al. 555* (BSB).

North Chile is identical to our collections from South Peru and these in turn are close enough to the typical ones from Central Peru (Depto. Lima) to be included as one species without differentiat-

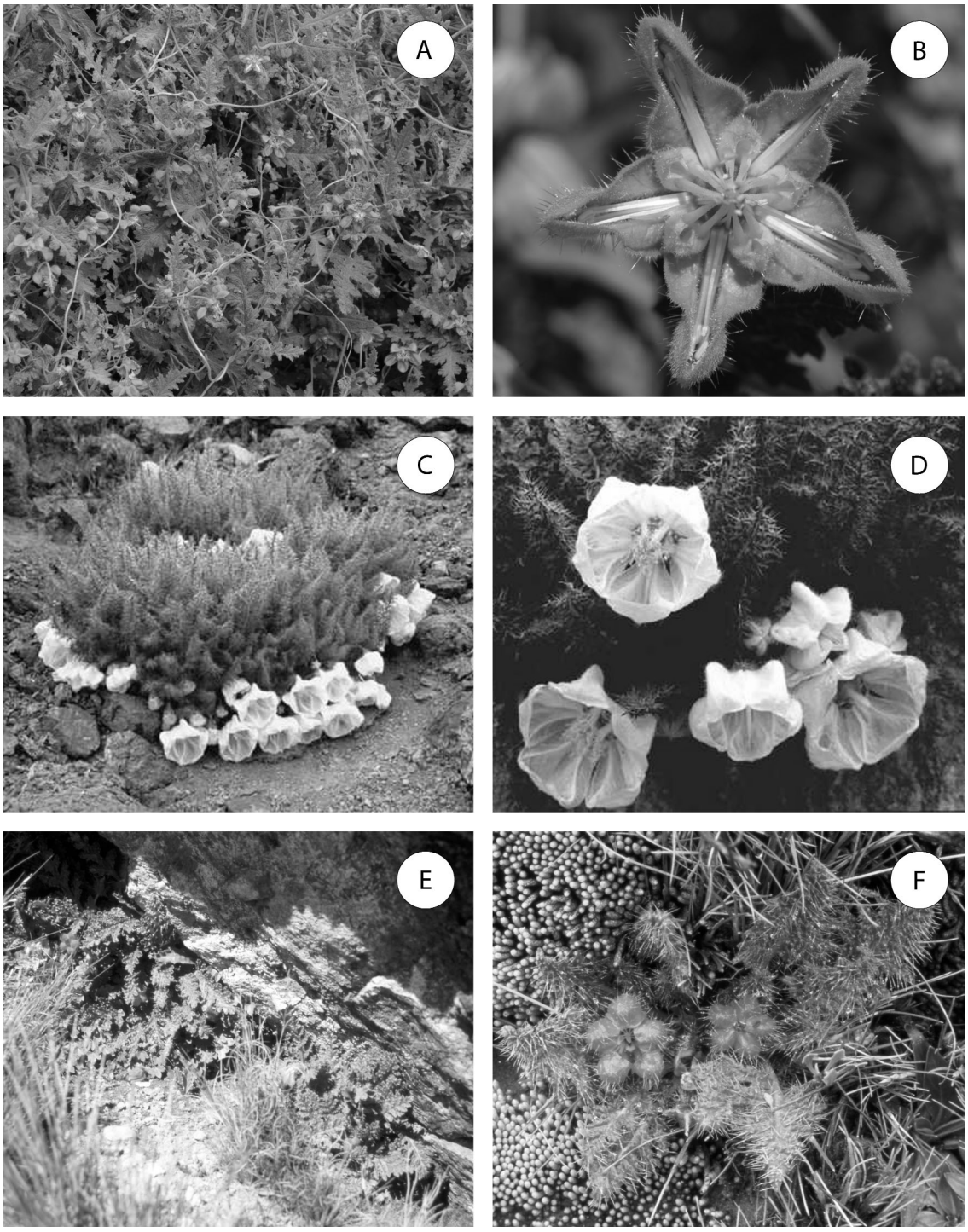

Fig. 4. *Caiophora cirsiifolia*. **A,** growth habit. **B,** flower. *Caiophora coronata*. **C,** growth habit. **D,** flowers (pictures from www.opuntiadelsur.de). *Caiophora rosulata* subsp. *rosulata*. **E,** habitat. **F,** growth habit. **A-B,** *M. Ackermann et al. 420* (BSB, HUSA, M, USM, NY, F); **E-F,** *M. Weigend & Ch. Schwarzer 7837* (BSB, HUSA, HUT, USM).

ing it at infraspecific level. The collections from the southern part of the range generally have smaller flowers and more deeply dissected leaves than those from Central Peru, but these differences largely vanish in cultivation, indicating that they simply reflect the generally drier conditions for plants growing in South Peru and Chile. *Caiophora cirsiifolia* ranges from elevations of 2400 to 3700 m and is usually found in dry scrub forest, hedges (Fig. 4A), road banks and dry stone walls. The flowers of *Caiophora cirsiifolia* are largely visited by long-tongued bees of the genera *Bombus* and *Centris* (Ackermann and Weigend, 2006).

Chromosome number. Chromosome counts of the southern *C. cirsiifolia* form are not available, but northwards in the adjacent departments our counts result in 2n =16 [Depto. Apurimac: *M. & K. Weigend 2000/392* (BSB, HUSA, M, USM), Depto. Ayacucho: *M. & K. Weigend 2000/341* (BSB, HUSA, M, USM)].

Observations. *Caiophora cirsiifolia* is a poorly documented species for Chile. There are only a few collections from Region I, of which we have seen a single specimen. We do not know whether the species is truly rare, or only undercollected, since Region I of Chile is particularly poorly documented. It certainly is a very common species e.g. in Depto. Arequipa, Moquegua and Tacna in Peru. It is the only winding species of *Caiophora* on the western side of the Andes south of the city of Arequipa.

Representative specimens examined

CHILE. **I Región de Tarapacá.** Prov. de Tarapacá: Belén, am Friedhof, ca. 3500 m, *J. Grau s.n.* (M).

PERU. **Arequipa.** Prov. Arequipa: Environment of Chiguata, east from Arequipa, 16° 24′ 20′′ S, 071° 22′ 38′′ W, 3100 m, 1-X-2002, *M. Ackermann et al. 420* (BSB, F, HUSA, M, NY, USM). Prov. Caylloma: Sibayo, 3500 m, IV-2002, *F. Caceres 2494* (BSB, HUSA). Prov. La Union: Dist. Puyca, arriba de Puyca, S 15°34.00′ W 72° 41.35′, 3562 m, 18-IX-1999, *V. Quipuscoa S. et al. 1591* (HUSA). **Moquegua.** Prov. Comás: Road from Arequipa to Puquina (Moquegua), between Arequipa and Pocsi, 16° 35′ 23′′ S, 071° 25′ 52′′ W, 3300-3400 m, 29-IV-2000, *M. Weigend et al. 2000/557* (HUSA, NY). Prov. General Sanchez Cerro: Omate, village Challoguaya above Omate, S16°38′42,5′′ W070°57′42,2′′, 2520m. 09-XII-2006, *M. Ackermann & F. Caceres 680* (BSB, HUSA, USM). Prov. Mariscal Nieto: Puquina, 3400 m, 21-IV-1967, *C. Vargas 19363* (BSB, CUZ). **Puno.** Prov. Moho: Dist. Moho, centro poblado de Huaraya, 3800-3900 m, 18-III-1997, *G. Arenas T. s/n* (HUSA). **Tacna.** Prov. Candarave: Volcan Yucamani, 3100-3400 m, 09-XII-1997, *M. I. La Torre 1956* (USM). Prov. Tarata: 16 km above Candarave on Mazo Cruz road (196 km west of Llave) 3680 m, 9-X-1997, *M. Weigend & H. Förther 97/797* (F, HUT, MO, MSB, NY, USM).

3. Caiophora coronata (Gillies ex. Arn.) Hook. & Arn., Bot. Misc. 3: 327. 1833. *Loasa coronata* Gillies ex Arn., Edinburgh J. Nat. Geogr. Sci. 3: 274. 1831. TYPE: Argentina, Mendoza, Andes of Mendoza, above Puente del Inca, Aguas del Cerro Pelado, *J. Gillies s.n.*, "anno 1821" (lectotype E! designated by *M. Weigend, Sendtnera 4: 235*. 1997; isolectotypes BM!, GH!, K!, OXF!). Figs. 4C-D, 5.

Caiophora pycnophylla Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 274. TYPE: Argentina, La Rioja, Famatina, Cueva de Pérez, 3700 m, *G. H. Hieronymus & G. Niederlein 388* (holotype B destroyed, photo F!, neg. nr. 10164; isotypes CORD, K!).

Caiophora absinthiifolia C. Presl, Reliq. Haenk.: 43, plate 57. 1831. TYPE: Chile, *T. Haenke s.n.* (holotype PRC, not located).

Perennial cushion-forming herb with spreading, decumbent stems and stiffly erect leaves, ca. 15-30 cm tall, 20-50 cm in diameter, with persistent basal leaf rosette. Stems rarely basally lignescent 3-5 mm thick, sparsely to densely covered with stinging hairs 3-4 mm long, scabrid trichomes (ca. 0.5 mm long) and glochidiate trichomes (0.1-0.3 mm long). Leaves 6-18 (-22) cm long; lamina oblong/ovate, 50 x 15 to 90 x 40 mm, pinnate-pinnatifid to bipinnatifid with 5-9 lobes on each side, proximal pair of leaflets often free; leaf lobes up to

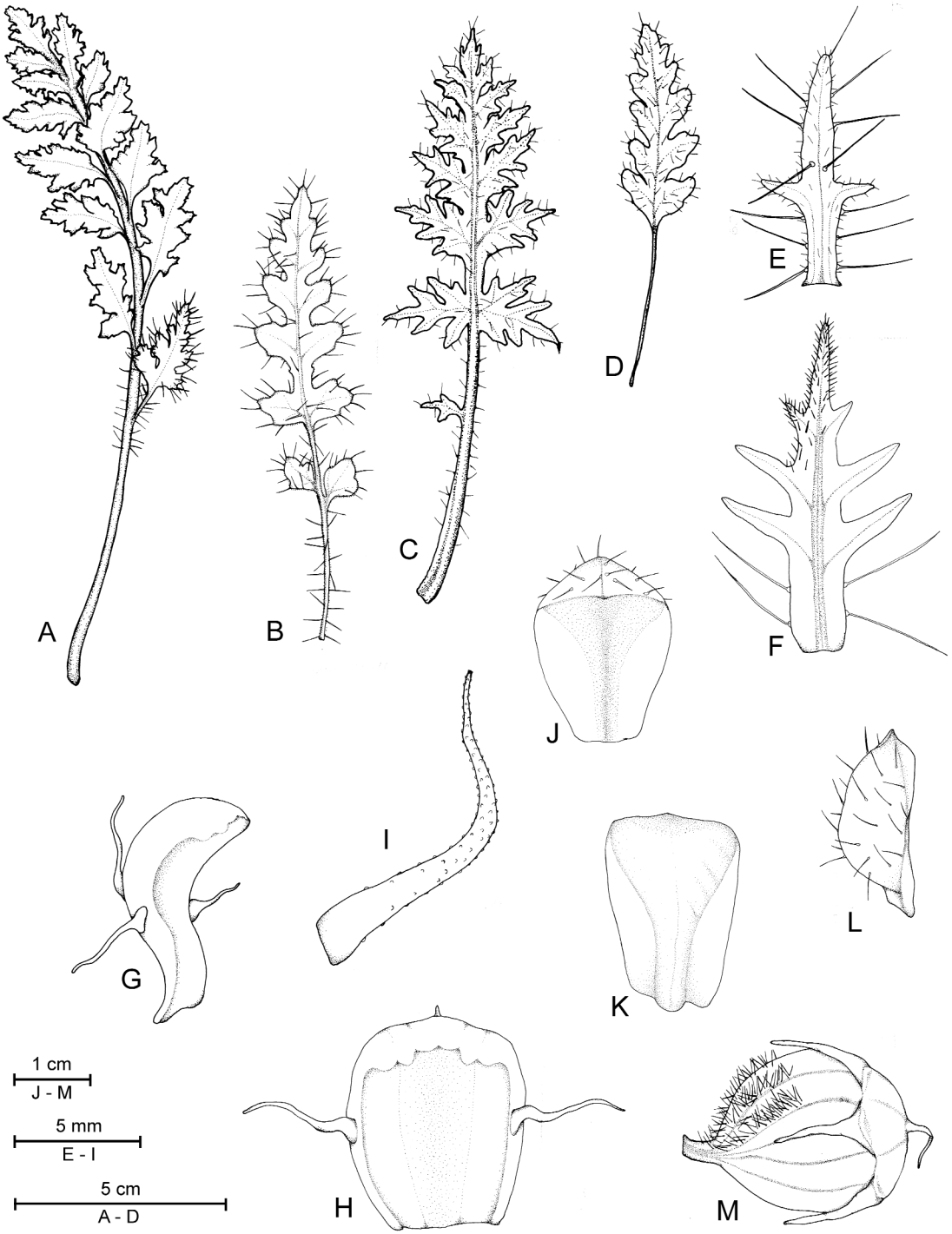

Fig. 5. *Caiophora coronata.* **A-D,** leaves. **E-F,** sepals. **G,** nectar scale, lateral view. **H,** ventral view. **I,** staminode. **J,** petal, ventral view. **K,** dorsal view. **L,** lateral view. **M,** fruit. A, *Meyen 4659* (NY, UC); **B, D, L,** *J. R. I. Wood 14626* (LPB); **G-K, M,** *T. H. Goodspeed & Y. Mexia 4611* (GH, UC); **C, E,** *M. Ackermann 60* (BSB); **F,** *E. Budin 7437* (UC); (drawn by C. Becker, Berlin).

22 x 15 mm; lobe margins reflexed, grossly serrate to pinnatifid with 2-4 (-6) lobules/teeth on each side, triangular to linear; adaxial leaf surface densely setose with stinging hairs 3-4 mm long, sparsely covered with scabrid trichomes up to 0.4 mm long; abaxial surface densely covered with glochidiate trichomes ca. 0.2 mm long; major veins both setose from stinging hairs 3-4 mm long and scattered scabrid trichomes ca. 0.3 mm long. Inflorescences frondose, terminal monochasia up to 10 cm long and with 2-5 flowers; internodes 1-3 cm, pedicels 2-12 cm long during anthesis. Flowers geoflorous, generally lying on the ground, oriented horizontally, pentamerous. Calyx lobes reflexed, narrowly triangular-linear, 8 x 1 to 15 x 2 mm, sparsely to densely setose and covered with scabrid trichomes; margin serrate to pinnatifid with (1-) 2-3 teeth/lobes on each side. Corolla bowl-shaped; petals deeply cymbiform, 20-30 mm long and 10-15 mm deep, dorsally setose and covered with scabrid and glochidiate trichomes, white, rarely cream, pale yellow, greenish or orange. Stamens in 5 epipetalous fascicles, 20-25 in number per fascicle; filaments ca. 15 mm long: anthers ovoid, pale yellow or brown, ca. 1.5 mm long. Nectar scales cymbiform to rectangular, white, ca. 4-5 x 5-8 mm, usually without dorsal filaments, sometimes with two or three white, filiform filaments up to 4 mm long, rising from the upper half of scale back. Free staminodia inflexed, 6-10 mm long, without appendage. Style terete, up to 12 mm long (towards the end of anthesis); ovary inferior, conical, with 3 placentae and numerous ovules. Fruit deflexed; pedicel 50-120 mm long; capsule globose to conical, slightly twisted, 20 (-40) x 18 (-25) mm, opening with 3-4 longitudinal slits; style persistent, not accrescent in fruit, sepals accrescent, up to 15 mm long. Seeds numerous; testa deeply pitted, brown.

Geographical distribution and ecology. The species is distributed in Chile from Santiago up to the Regions I and II (Arroyo et al., 1982; Marticorena et al., 1998, 2001), in Argentina from Mendoza up to Jujuy (Brücher, 1986, 1989; Sleumer, 1955) and in Bolivia in the southern departments Potosi and Tarija (Weigend, 1997). The elevational distribution ranges from (2000-) 2500-4500 (-5000) m, with elevation increasing from the South to the North. *Caiophora coronata* is found in at least seasonally dry habitats. It grows in corrals, at the base of rocks or in open habitats on scree slopes. (Fig. 4C). *Caiophora coronata* is pollinated by rodents, but is also visited by hymenoptera, hummingbirds and passerines (Coccuci and Sersic, 1998).

Chromosome number. Sporophytic 2n = 16 (Brücher 1986, 1989; Grau 1988). Huynh (1965) also published the same chromosome number for material collected in Depto. Puno, Peru, but we are confident that she counted chromosomes of *C. pentlandii*, distributed in that area (whereas *C. coronata* has not yet been recorded from Peru).

Observations. *Caiophora coronata* is the only decumbent species in the region and one of only two decumbent species in the genus. The other taxon is *C. pentlandii* (Graham) Loudon from South Peru, which also shares the same corolla shape and ecology, but has less deeply divided leaves, bright orange-red corollas and internodes in the inflorescences over 5 cm long. Nectar scales are hemispherical in contrast to cymbiform to rectangular nectar scales in *C. coronata.* Sleumer (1955) pointed out that in Argentina floral colour of *C. coronata* is often red, but yellow, white and cream are also common. Most of our investigated herbarium specimens and own observations in Chile (Region II) indicate white corollas (Fig. 4C-D). Moreover, Sleumer (1955) indicated the presence of interspecific hybrids of *C. coronata* with orange-flowered taxa in Argentina, so that orange and yellow flowered specimens of *C. coronata* may be the result of hybridization and/or introgression.

Representative specimens examined

ARGENTINA. **Catamarca.** Depto. Andalgalá: Cordillera Aconquija, 4400 m, 4-IV-1917, *P. Jörgensen 1857* (GH, NY, US). Depto. Antofagasta de la Sierra: Cuesta de Nacimientos, path to Laguna Blanca, 3100 m, 21-II-1974, *V. Legname and F. B. Vervoorst 58* (US). Depto. Tinogasta: Tres Quebradas, 4250 m, 27-III-1951, *F. B. Vervoorst 3227* (GH, NY, UC, US). **Jujuy.** Near Tilcara, Laguna Colorada, 13200 feet, 13-II-1939, *E. K. Balls 6069* (GH, UC, US). Depto. Cochinoca: Casabindo, 22o

59´ S, 066o 01´ W, 3540 m, *N. B. Deginani et al. 518* (MO). Depto. Humahuaca: Sierra del Aguila, 4000 m, III-1929, *S. Venturi 8722* (GH, US). Depto. Tilcara: Tilcara, II-1925, *S. Venturi 6550* (US). Depto. Tumbaya: Cerro Moreno, 4000 m, 3-II-1929, *S. Venturi 9456* (US). Depto. Santa Catalina: Cuesta de Toquero, 22o 06´ S, 65o 46´ W, 3570 m, 10-II-1995, *N. B. Deginani et al. 596* (MO). Dpto Humahuaca: Tres Cruces, 3700 m, 20-XI-1959, *H. Fabris & J. M. Marchionni 1784* (US). **La Rioja.** Depto. Famatina: Sierra de Famantina, Cueva de Perez, 3700 m, 26-IV-1951, *B. Sparre 8798* (W). **Mendoza.** Depto. Las Heras: Road Mendoza to Uspallata, 2700 m, 8-I-1936, *T. H. Goodspeed & Y. Mexia 4611* (GH, UC). **San Juan.** Depto. Iglesia: Between Los Manantiales and Plazeta del Peñón, path to El Paso del Espinacito, 11-I-1953, *A. Castellanos 15485* (US). **Tucuman.** Sierra de Cuejon, Los Chuscos, 4000 m, 11-I-1926, S. Venturi 6554 (US). Salta. Tres Morros, 3500-4000 m, *S. Vogel 565* (WU).

BOLIVIA. **Potosi.** Prov. Frias: On the descent from the pass to Laguna Mazuni coming from Potosi and Laguna Ulistia, Cordillera Kari Kari, 4600 m, 6-III-1999, *J. R. I. Wood 14626* (LPB). Prov. Quillaro: 4 km SW of Villacota on east facing slope above Lago, 3850-4130 m, 27-III-1993, *P. M. Peterson et al. 13118* (LPB). Prov. Sud Lipes: Cerro Tapaquillcha, 4600 m, 12-IV-1980, *M. Liberman 178* (LPB). **Tarija.** Prov. Aviles: Escayache near Tarija, 4000 m, 28-II-1904, *K. Fiebrig 2807* (BM, GH, PR).

CHILE. **II Región de Antofagasta.** Prov. Atacama: Cordillera de Porcuera, II-1866, *J. R. Figueroa s.n*. (GH). Prov. Loa: Guatin, cerca de San Pedro de Atacama, Quebrada Purifica, 22º 43.964´ S, 067º 59.996´ W, 3600 m, 10-III-2001, *M. Ackermann 123* (BSB). **III Región de Atacama.** Near Laguna Grande, 3100 m, *I. M. Johnston 5899* (GH, US). **IV Región de Coquimbo.** Prov. Coquimbo: Baños del Toro, 4000 m, XII-1923, *E. Werdermann 226* (BM, E, GH, UC, US). Prov. Elqui: Baños del Toro, just above Baños, 3300 m, 6-II-1939, *J. L. Morrison 17273* (GH). **Región Metropolitana.** Río Yeso, Laguna Pinguenes, 2500 m, 13-I-1945, *W. Biese 1018* (GH, NY). **V Región de Valparaíso.** San Felipe de Aconcagua: Near Portillo Station, 2800 m, 5-II-1936, *J. West 5247* (GH, US).

4. Caiophora deserticola Weigend & Mark. Ackermann, sp. nov. TYPE: Perú, Depto. Moquegua, Prov. General Sanchez Cerro, Between Puno and Moquegua, road down after junction with Lago Desaguadero road, 16° 59,539´ S, 070° 42,040´ W, 3900 m, 12-IV-2004, *M. Weigend & Ch. Schwarzer 7845* (holotype USM!; isotypes BSB!, M!, HUSA!, HUT!). Figs. 6, 7.

Suffrutex 20-100 cm altus. Caules basin teretes, lignosi. Folia opposita; lamina anguste ovata, profunde pinnatisecta, basi cordata, margine lobulata, lobis 4-8 in utrisque lateribus 40 mm longa et 30 mm lata, parce setosa. Petala rosea, profunde cymbiformia, 15-25 mm longa, 10-15 mm profunda, basi unguiculata, dense setosa et dorso pilis glochidiatis instructa. Squamae nectariferae ovatae, apicem versus emarginatae, albae, 5 mm longae, 8 mm latae, 5 mm profundae, basi incurvatae, apice conspicue incrassatae, leviter recurvae, dorso filis tribus 3-4 mm longis, filiformibus instructae.

Perennial herbs to subshrubs (20-) 40-80 (-100) cm tall; stems basally lignescent and perennating for ca. 10-30 cm, crowned with persistent leaf rosettes, (3-) 5-8 (-10) mm in diameter, densely covered with stinging hairs 3-4 mm long and glochidiate trichomes 0.1-0.3 mm long. Basal leaves (5-) 10-20 (-25) cm long; lamina narrowly ovate, 50 x 25 to 120 x 60 mm, pinnate-pinnatifid to bipinnatifid with (4-) 7-8 lobes on each side, with proximal pair of leaflets free; leaf lobes up to 40 x 30 mm; lobe margins grossly serrate to pinnatifid with 2-5 lobules/teeth on each side; adaxial leaf surface sparsely setose with stinging hairs 3-5 mm long and densely covered with scabrid trichomes up to 1 mm long; abaxial leaf surface esetulose or with scattered stinging hairs 3-5 mm long on major veins only, scattered scabrid trichomes on major veins, otherwise densely covered with glochidiate trichomes ca. 0.3 mm long. Inflorescences frondose, with terminal di- or monochasia, up to 30 cm long and with (3-) 5-8 (-10) flowers; internodes up to 11 cm long; pedicels 20-30 (-70) mm long during anthesis. Flowers horizontal to deflexed, penta- to heptamerous; calyx lobes spreading, apically reflexed, narrowly triangular-ovate, 10 x 1.5 to 17 x 3 mm, densely setose and covered with scabrid trichomes; margins coarsely serrate with 2-5 teeth on each side. Corolla balloon-shaped; petals deeply cymbiform, 15-25 mm

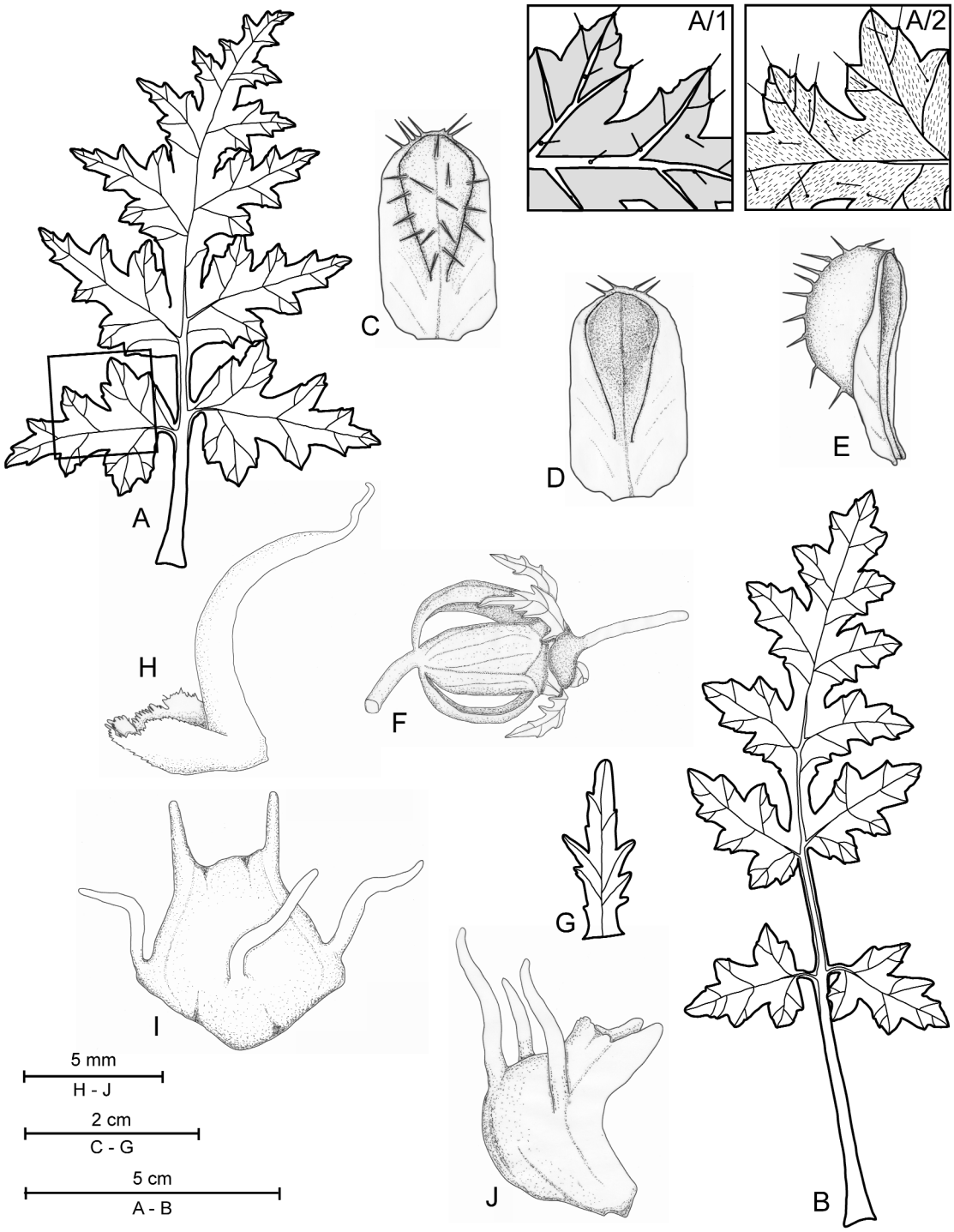

Fig. 6. *Caiophora deserticola.* **A-B,** leaves. **A/1,** abaxial surface. **A/2,** adaxial surface. **C,** petal, dorsal view. **D,** ventral view. **E,** lateral view. **F,** mature fruit. **G,** sepal. **H,** staminode. **I,** nectar scale, dorsal view. **J,** lateral view. **A-J,** *M. Weigend et al 7761* (BSB, HUSA, USM).

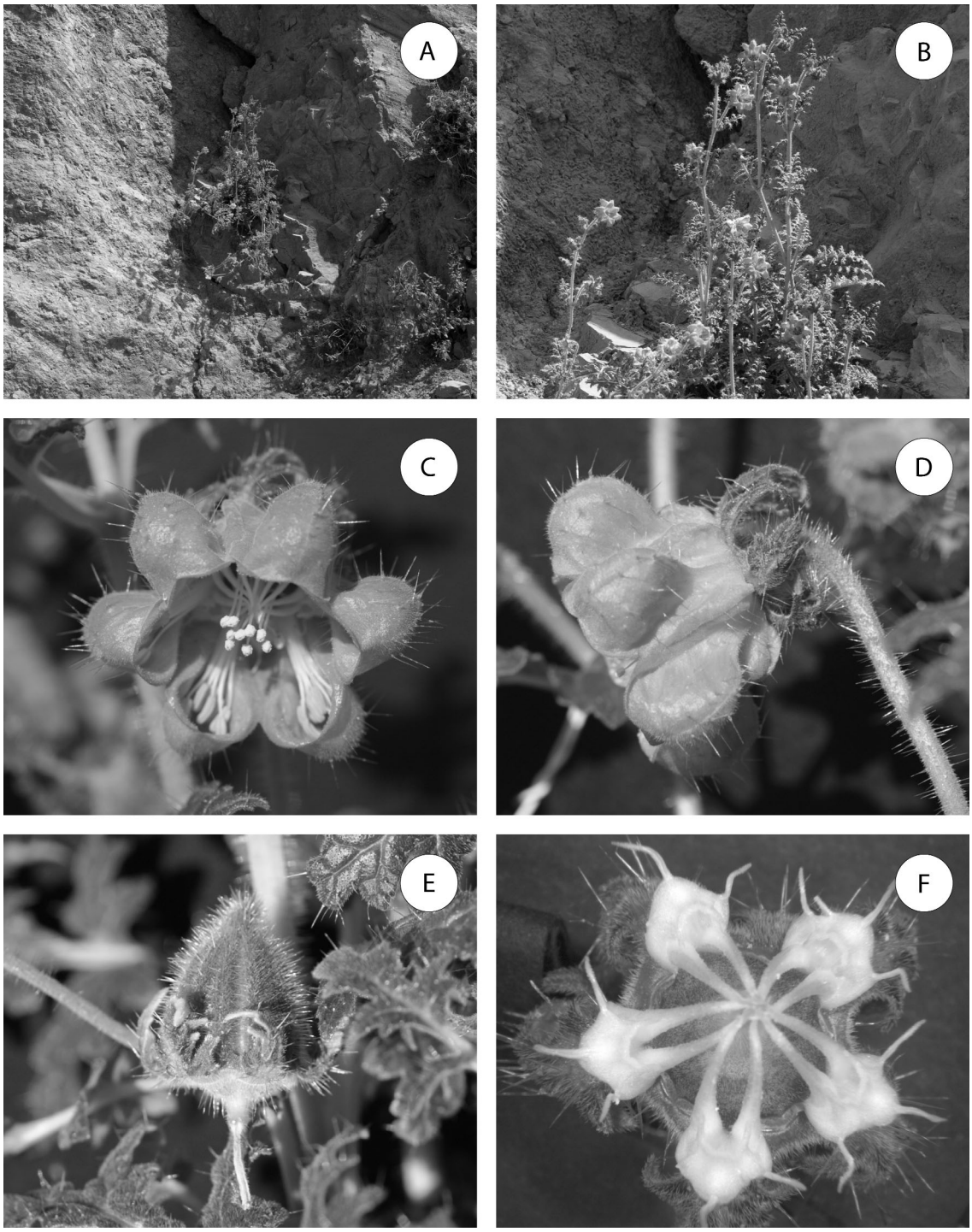

Fig. 7. *Caiophora deserticola.* **A-B,** natural habitat in Puno, Peru. **C-F,** photographs from cultivated plants in Berlin. **A,** habitat, **B,** growth habit. **C-D,** flower. **E,** young fruit. **F,** nectar scales and staminodes, petals and anthers removed. **A-F,** *M. Weigend et al 7761* (BSB, HUSA, USM).

long and 10-15 mm deep, dorsally setose and covered with scabrid and glochidiate trichomes, pink. Stamens in 5-7 epipetalous fascicles, 20-25 in number per fascicle; filaments ca. 17 mm long;

anthers ovoid, pale yellow, ca. 1-2 mm long. Nectar scales deeply cymbiform, white, hemispherical in dorsal view, ca. 5 x 8 mm, with usually three dorsal filiform filaments ca. 4-6 mm long (sometimes basally widened); dorsal filaments white with red tip, rising from central scale back. Free staminodia L-shaped, 12-15 (-18) mm long, dorsally with a spoon-shaped, papillose (0.2 mm long) appendage ca. 4 x 2 mm. Style terete, up to 25 mm long (towards the end of anthesis); ovary inferior, conical, with 3-5 placentae with numerous ovules. Fruit deflexed; pedicel 50 (-80) mm long; capsule conical, 25 x 15 mm, straight, opening with 3-5 longitudinal slits; style persistent, not accrescent, sepals accrescent, up to 20 mm long. Seeds numerous; testa deeply pitted, brown.

Geographical distribution and ecology. The species is known from the Region I in Chile and Arequipa, Moquegua and Tacna, plus contiguous parts of Puno in Peru. The elevational distribution ranges from 2400-3900 m. Of all known taxa of *Caiophora*, it grows in the most arid habitats, along roadsides, in crevices and between rocks and on scree slopes (Fig. 7A). Only *Centris* bees have been observed as flower visitors, but nectar parameters are close to proven hummingbird pollinated taxa (Ackermann and Weigend, 2006).

Chromosome number. Chromosome counts were not available.

Observations. This species was first collected by Weberbauer in 1925 (*A. Weberbauer 7468*) and then by Werdermann in 1926 (*E. Werdermann 1107*). Some of the latter specimens were annotated as a new taxon with the name *C. werdermannii* by Gilg, but this name was never published. Since the taxon is actually found in semi-desert habitats it is here named Caiophora deserticola. It is one of two suffrutescent species of the genus in Chile. All investigated specimens have penta- to heptamerous flowers, pink petals, and a pedicel of 20-30 (-70) mm (Fig. 7C and D), whereas in *C. chuquitensis* flowers are penta- to nonamerous, have red or orange petals, and pedicels are only 3-15 (-50) mm long. Also, *C. chuquitensis* is densely covered with stinging setae, whereas *C. deserticola* is sparsely setose. Lamina shape also differs: *Caiophora deserticola* is characterized by laminas with only one pair of free leaflets with up to 4-8 lobes on each side, and a flat leaf margin in contrast to *C. chuquitensis*, where more than one pair of leaflets can be free, the number of lobes is usually between 6-14 and the leaf margin is recurved.

Caiophora werdermannii Gilg., (in sched.) in herbaria M & S.

Representative specimens examined

CHILE. **I Región de Tarapacá.** Prov. Iquique: Cuesta de Usmagama, 19° 43′ 37′′ S, 069° 13′ 10′′ W, 3100 m, 11-XI-2002, *M. Muñoz-Schick 4296* (BSB, SGO). Prov. Tarapaca: Cordillera Japu, ca. 4200 m, III-1926, *E. Werdermann 1107* (B, E, GH, K, M, S, US).

PERU. **Puno.** Prov. Yunguyo: localidad de Yunguyo, zona desertica altiplano, 3890 m, 8-XII-2002, *F. Cáceres 2805* (BSB, HUSA). Moquegua. Prov. General Sanchez Cerro: Road from Arequipa to Omate, above Omate, Huarangao, Callejon de Omate, Cerro Cayranto, S16°37′00,7′′ W71° 04′00,5′′, 2875 m. 07-XII-2006, *M. Ackermann & F. Caceres 647* (BSB, HUSA, USM). Prov. Mariscal Nieto: Road Moquegua to Omate, 15° 59,587′ S, 070° 52,203′ W ′, 2744 m, 14-IV-2004, *M. Weigend & Ch. Schwarzer 7854* (BSB, USM, HUSA, HUT). **Tacna.** Prov. Candarave: Volcan Yucamani, 3100-3400 m, 09-XII-1997, *M. I. La Torre 1998* (USM). Prov. Palca: Comunidad de Vilavilani, cerca con la frontera con Chile, 413592 E, 8028761 N, 4145 m, 13-IV-2004, *I. Salinas & J. Frisancho 882* (USM). Prov. Tarata: 16 km above Candarave on Mazo Cruz road, 196 km west of Ilave, 3650 m, 9-X-1997, *M. Weigend &H. Förther 97/795* (F, MSB, USM).

5. Caiophora rosulata (Wedd.) Urb. & Gilg, In Engler and Prantl, Nat. Pflanzenfam. 3/6a: 119. 1894. *Loasa rosulata* Wedd., Chlor. And. II: 219. 1857. TYPE: Perú, Depto. Tacna, Tacora plateau, 4300 m, *H. A. Weddell s.n.* (holotype P!, photo F!, neg. nr. 38497). Figs. 4E-F, 8A-M.

Perennial acaulescent, rosulate herbs, 5-20 cm

tall. Shoot very short (rarely up to 3 cm long, internodes less than 5 mm), 2-4 mm thick, esetulose and covered with trichomes scabrid (0.5 mm long) and glochidiate (0.3 mm long). Leaves with petioles 10-50 (-80) mm long; lamina narrowly ovate to triangular-ovate, 20 x 17 to 140 x 60 mm, pinnate-pinnatifid to pinnatisect with 5-9 lobes on each side, with proximal pair of leaflets often free; leaf lobes up to 20 x 12 mm, margins grossly serrate to pinnatifid with 2-4 lobules/teeth on each side; adaxial leaf surface sparsely to densely setose with stinging hairs 3-5 mm long, and covered with scabrid trichomes up to 0.6 mm long; abaxial leaf surface esetulose or with scattered stinging hairs 2-3 mm long on major veins only, densely covered with scabrid trichomes 0.4 mm long and sparsely with glochidiate trichomes ca. 0.3 mm long. Flower erect to pendulous, arising on a ebracteate stalk directly from the leaf rosette (monochasium with condensed internodes), rarely subsessile or pedicel (2-) 3-10 (-20) cm long during anthesis, pentamerous. Calyx lobes reflexed or spreading, apically reflexed, narrowly linear to oblong, 6 x 1 to 10 x 1.5 mm, esetulose or sparsely setose and covered with scabrid trichomes 0.4 mm long; margin slightly serrate without or with 1-3 teeth on each side. Corolla bowl-, bell- or balloon-shaped; petals cymbiform, 13-18 mm long and 4-5 mm deep, dorsally setose and covered with scabrid and glochidiate trichomes, white, cream, yellow or orange. Stamens in 5 epipetalous fascicles, 10-15 in number per fascicle; filaments ca. 5-10 mm long; anthers ovoid, yellow, orange or brown, ca. 1 mm long. Nectar scales deeply cymbiform, white, hemispherical in dorsal view, ca. 3-6 x 2-4 mm; dorsal filiform filaments usually 3, ca. 2-3 mm long (sometimes basally widened), white, arising from the midlength to upper third of scale back. Free staminodia L-shaped, 5-6 mm long; appendage dorsal, spoon-shaped, papillose, ca. 1-2 x 0.3 mm. Style terete, up to 5 mm long (towards the end of anthesis); ovary inferior, conical, with 3 placentae with numerous ovules. Fruit erect to deflexed; pedicel 3-10 (-28) cm long; capsule globose, straight, up to 16 x 10 mm, opening with 3 longitudinal slits only; style persistent. Seeds numerous; testa deeply pitted, brown.

Geographical distribution and habitat. *Caiophora rosulata* subsp. *rosulata* is distributed in Chile in the Regions I and II (Type specimen, Marticorena et al., 1998; Teillier, 1999) and in Peru from Puno to Tacna (Macbride, 1941; Schatz, 1996). *Caiophora rosulata* subsp. taraxacoides is distributed in Argentina (Provinces Catamarca, Jujuy, La Rioja, Salta, Tucuman; Brücher, 1986, 1989; Sleumer, 1955) in Bolivia (Departments Cochabamba, La Paz, Oruro, Potosi) and Peru (Department Cuzco). The elevational distribution ranges from (3000-) 3500-4500 (-5000) m; it is the highest-growing representative of the family Loasaceae and one the highest growing angiosperms in the Andes. Its habitat in Peru experiences daily frost and thaw cycles, probably throughout the year. *Caiophora rosulata* is found at the bases of rocks and grass tussocks, protected from wind and changing temperatures and possibly receiving additional moisture from run-off (Fig. 4E). Autogamy or hummingbird-pollination are conceivable as pollination modes, but field observations are not available.

Chromosome number. Sporophytic: 2n = 16 (*C. rosulata* subsp. *taraxacoides*, Brücher 1986, 1989).

Key to the subspecies of *C. rosulata*

1. Leaves more or less erect. Flowers erect on a pedicel shorter than the leaves, flower balloon-shaped. . . . . .5a. *C. rosulata* subsp. *rosulata*

1. Leaves appressed to the ground. Flowers horizontal to pendulous on pedicel much longer than leaves, flower bowl- to bell-shaped. . . . . .5b *C. rosulata* subsp. *taraxacoides*

5a. Caiophora rosulata (Wedd.) Urb. & Gilg subsp. **rosulata**, in Engler and Prantl, Nat. Pflanzenfam. 3/6a: 119. 1894. *Loasa rosulata* Wedd., Chlor. And. II: 219. 1857. TYPE: Peru, Tacna, Tacora plateau, 4300 m, *H. A. Weddell s.n*. (holotype P!, photo F!, neg. nr. 38497). Figs. 4E-F, 8A-G.

Caiophora rahmeri Phil. syn. nov., Anal. Mus. Nac. Chile 1891: 23. 1891. TYPE: Chile, I Región de Tarapacá, Tarapacá, Huasco, 3900 m, *R. A. Philippi s. n*. (lectotype BM! here designated; isolectotype B destroyed, F neg. nr. 10165, SGO!, WU!).

Caiophora anemonoides Urban & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 277.

1900. TYPE: Chile, I Región de Tarapacá, Atacama, *J. Steinmann s.n.* (holotype B destroyed, photo F!, neg. nr. 10141).

Leaves more or less erect, oblong to triangular-ovate, 20 x 17 to 35 x 30 (-100 x 50) mm, longer than pedicel. Pedicel 2-3 (-9) cm long. Flowers erect; corolla balloon-shaped, orange or yellow. Nectar scales 3-4 mm long and 2-3 mm wide, membranous.

Observations. We have seen the Philippi collections of "*C. rahmeri*" from Tarapaca in BM, SGO and WU, both the BM and the WU specimens clearly correspond to the protologue (Philippi & Philippi, 1891) and are conspecific with *C. rosulata*. However, the fragmentary SGO specimen does not agree well with the diagnoses and cannot be identified satisfactorily at present.

Representative specimens examined

PERU. **Arequipa.** Prov. Arequipa: Cordillera entre Cotahuasi y Cailloma, 4500-4600 m, 26-III-1914, *A. Weberbauer 6881* (F, GH, USM). Prov. Caylloma: Nevado de Chachani, 5000 m, 22-III-1957, *W. Rauh-Hirsch P554* (F). Prov. Ramon Castilla: Orcopampa, alrededores de Cia. Minera Ares, 4700-4900 m, 31-II-2000 - 02-IV-2000, *A. Cano & N. Valencia 10097* (USM). **Moquegua.** Prov. Mariscal Nieto: between Puno and Moquegua, after Abra Loripongo and Humajalso, 16° 50′ 757′′ S, 070° 32′ 850′′ W, 4433 m, 12-IV-2004, *M. Weigend & Ch.Schwarzer 7840* (BSB, HUSA, HUT, USM). **Puno.** Prov. Puno: Between Puno and Abra Loripongo, before reaching Humajalso, 16° 34′ 09′′ S, 070° 22′ 31,9′′ W, 4606 m, 12-IV-2004. *M. Weigend & Ch. Schwarzer 7837* (BSB, HUSA, HUT, USM). **Tacna.** Prov. Tarata: Poma, carretera Tarata-Puno, Vilacota, 3900-4430 m, 04-XII-1997, *A. Cano 7950* (USM).

5b. Caiophora rosulata (Wedd.) Urb. & Gilg subsp. **taraxacoides** (Killip) Weigend & Mark. Ackermann, comb. & stat. nov. *Caiophora taraxacoides* Killip, J. Wash. Acad. Sci. 18: 92. 1928. TYPE: Argentina, Catamarca: Andalgalá, cerro Yutuyaco, *P. Jörgensen 1158* (holotype US!; isotypes BA, LIL, SI). Figs. 8H-M.

Caiophora acanthoides Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 286. 1900. TYPE: Argentina, Catamarca: Andalgalá, Campo Grande, below Cerro Yutuyaco, *F. Schickendantz 142* (lectotype GOET! designated by *M. Weigend, Sendtnera 4: 234*. 1997; isolectotypes B destroyed, photo F!, neg. nr. 10139, CORD).

Leaves appressed to the ground, oblong to triangular-ovate, 30 x 13 to 85 x 30 (-140 x 60) mm; pedicel 5-10 (-20) cm long, erect and longer than the leaves. Flowers horizontal to pendulous, bowl- to bell-shaped, white, cream, yellow or orange. Nectar scales 4-6 mm long and 3-4 mm wide, carnose.

Representative specimens examined

ARGENTINA. **Catamarca.** Depto. Andalgalá: subida al Cerro Yutuyaco desde Capillitas, lado S, arriba del Campo Grande, 3600-3800 m, 3-III-1952, *H. O. Sleumer 2722* (P, UC, US, W). **Jujuy.** Depto. Tumbaya: Cerro Moreno, 3400 m, 8-II-1929, *S. Venturi 9458* (US). Depto. Tilcara: Top of Chorru Valley, 4300 m, 12-II-1939, *E. K. Balls 6019* (E, K, UC, US). **Salta.** Depto. San Carlos: Cerro de Cachi, 3000 m, 13-III-1927, *S. Venturi 6999* (US). **Tucuman.** Depto. Chicligasta: Pueblo Viejo, 4000 m, 22-I-1925, *S. Venturi 6578* (US). Depto. Tafi: Sierra de Cajón, 4000 m, 17-II-1926, *S. Venturi 6571* (US).

BOLIVIA. **Cochabamba.** Prov. Arque: La Comuna, 4000 m, 9-II-1992, *P. Ibisch & P. Rojas 1116* (LPB). **La Paz.** Prov. Inquisivi: Pas height between Caxata and Quime, 4620 m, 8-I-1968, *B. B. Vuilleumier 478* (F). **Oruro.** Prov. Sajama: Unos 4 kms del pueblo, subiendo el valle del río Sururia, 18° 10′ S, 069° 00′ W, 4550 m, 10-IV-1995, *S. Beck 22356* (LPB, M). **Potosí.** Prov. Tomas Frias: Cerrania del Khare-Khare, arriba de la Ciudad Potosi, a orillas de la Laguna Chalaviri, 4400 m, 20-II-1988, *Schulte 162b* (M).

PERU. **Cuzco.** Prov. Espinar: Yauri, Pajonal de Puna, 14° 41′ S, 071° 16′ W, 4012 m, 9-V-2003, *L. Valenzuela et al. 2023* (BSB, MO). Prov. Urubamba: Chincheros, summit of Antakillqa, 4500 m, 20-I-1982, *E. W. Davis et al. 1706* (F, GH, USM).

Observations. *Caiophora rosulata* is one of the

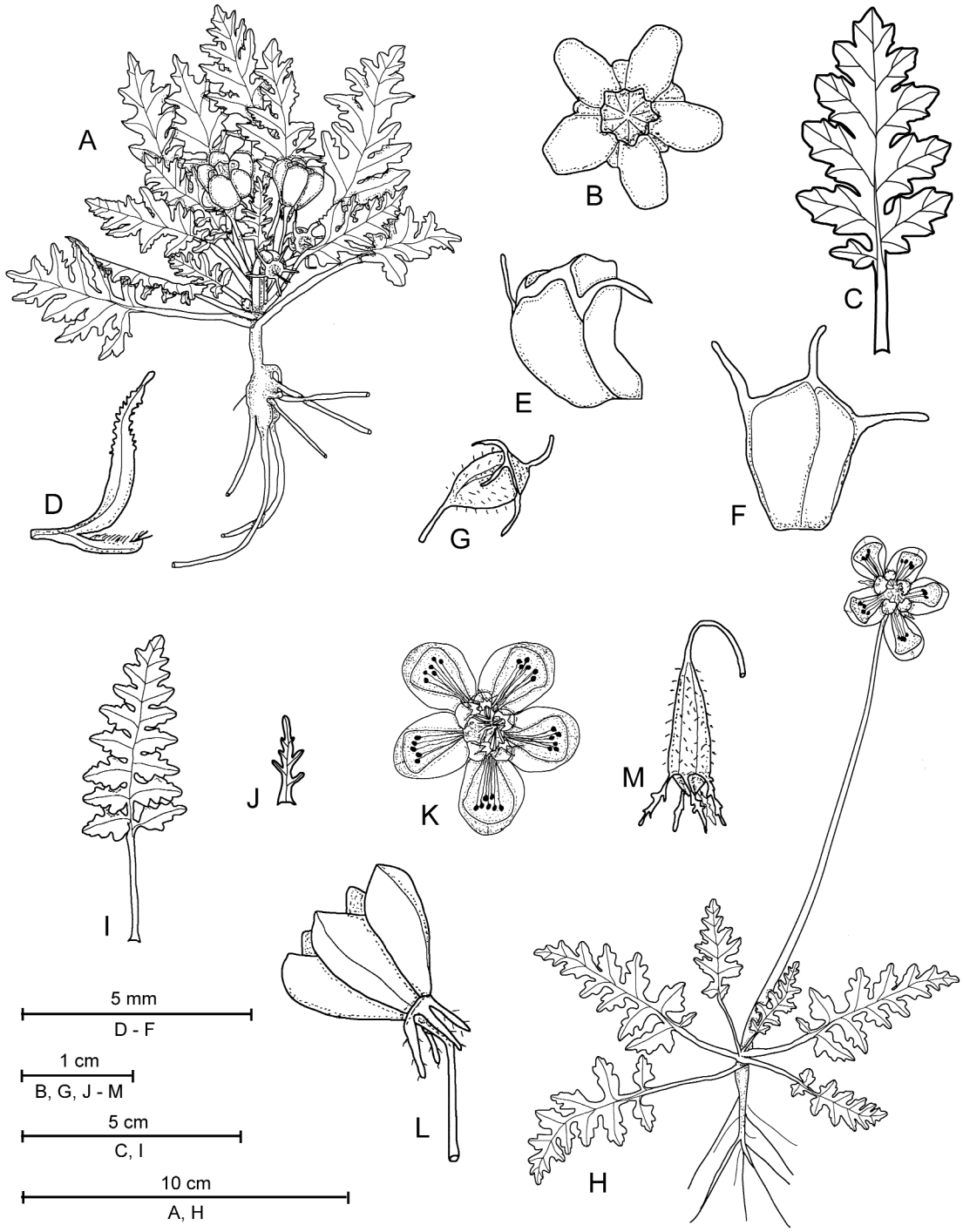

Fig. 8. *Caiophora rosulata* subsp. *rosulata*. **A,** growth habit. **B,** flower. **C,** leaf. **D,** staminode. **E,** nectar scale, lateral view. **F,** dorsal view. **G,** fruit. *Caiophora rosulata* subsp. *taraxacoides*. **H,** growth habit. **I,** leaf. **J,** sepal. **K,** flower. **L,** young flower, lateral view. **M,** fruit. **A-C,** *M. Weigend & Ch. Schwarzer 7837* (BSB, HUSA, HUT, USM); **D-G,** *D. Stafford 650* (BM, F, K); **H, K, L,** *C. Vargas 5578* (BSB, CUZ); **I,** *E. K. Balls 6019* (E, K, UC, US); **J,** *J. R. I. Wood 14595* (LPB); **M,** *P. Jörgensen 1158* (BA, LIL, SI, US).

three species within *Caiophora* sharing the rosulate growth habit. *Caiophora nivalis* Lillo and *C. pulchella* Urb. & Gilg (both Argentina) have extensive underground runners, very small leaf rosettes and nectar scales with well-developed dorsal calli, both of which are absent in *C. rosulata*. Also, the petals of *C. nivalis* are white, narrowly oblong and spreading, and the nectar scales yellow (personal communication and pictures: A. Wertlen, Berlin) and *C. pulchella* has a capsule opening with apical valves only and the nectar scales are more or less rectangular (Perez-Moreau & Crespo, 1992). Sleumer (1955) pointed out that he found a wide range of flower colours for the species (*C. rosulata* subsp. *taraxacoides*) in Argentina, ranging from red, orange, yellow to white. Our observations in South Peru confirm that *C. rosulata* subsp. *rosulata* has uniformly bright orange petals (Fig. 4E-F).

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INDEX OF COLLECTORS

Every specimen is cited alphabetically by the name of the first collector. The number in bracts indicates the species or subspecies investigated: *Caiophora chuquitensis* (1), *C. cirsiifolia* (2), *C. coronata* (3), *C. deserticola* (4), *C. rosulata* subsp. *rosulata* (5a) and *C. rosulata* subsp. *taraxacoides* (5b).

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