Studies on systematics, morphology and taxonomy of *Caiophora* and reproductive biology of Loasaceae and *Mimulus* (Phrymaceae)

Dissertation zur Erlangung des akademischen Grades des
Doktors der Naturwissenschaften (Dr. rer. nat.)
eingereicht im Fachbereich Biologie, Chemie, Pharmazie
der Freien Universität Berlin

vorgelegt von

Markus Ackermann
aus Buchen (Odenwald)

Berlin 2011

This work was carried out between 2002 and 2011
under the supervision of Prof. Dr. Maximilian Weigend
Institut für Biologie of the Freie Universität Berlin.

1st Reviewer: Univ.- Prof. Dr. Maximilian Weigend
2nd Reviewer: Univ.- Prof. Dr. Hartmut H. Hilger

Date of defence: 12.07.2012

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Cover illustration:

The cover inset shows a balloon-shaped funnel revolver flower of *Caiophora chuquitensis* from the High Andes. Nectar characters and floral morphology indicate it is hummingbird-pollinated. Within the monophyletic *Loasa*-*Caiophora* clade, switches from short-tongued bee- to hummingbird-pollination appear to have taken place over time. See Ackermann M, Weigend M. 2006. Annals of Botany 98(3): 503–514 http://aob.oxfordjournals.org/content/98/3.cover-expansion (Chapter 8).

1. Introduction

1.1. The family Loasaceae

The family Loasaceae is largely restricted to the Neotropics. The first taxa were named by Linné (1753) in “Species Plantarum” as *Gronovia scandens* (1753: 202) and *Mentzelia aspera* (1753: 516). In 1763 Adanson described the eponymic genus *Loasa* (1763). Several years later De Jussieu (1804) described the new family Loasaceae to unite the genera *Mentzelia* and *Loasa*. Since then, several new species and genera have been described. In 1900 Urban and Gilg divided the Loasaceae into three subfamilies: Gronovioideae, Mentzelioideae and Loasoideae. Several molecular studies (e.g. Moody et al., 2001; Hufford et al., 2003; Schenk and Hufford, 2010) largely confirm this subfamilial classification (compare current classification; tab 1.1).

In their monumental “Monographia Loasacearum” Urban and Gilg (1900) described more than 80 new species, and their work is still fundamental for taxonomic studies in Loasaceae. Since then, several new genera have been described: *Aosa* Weigend, *Chichicaste* Weigend, *Fuertesia* Urb., *Nasa* Weigend, *Plakothira* J.Florence, *Presliophytum* (Urb. & Gilg) Weigend, *Schismocarpus* S.F.Blake and *Xylopodia* Weigend (Urban, 1910; Blake, 1918; Florence, 1985; Weigend, 1996, 1997c, 2006; Weigend et al., 2006). When Weigend (1996, 1997a, b, c) began with his studies about Loasaceae, he revised numerous herbarium specimens and conducted several field trips to South America, that led to collections of unknown species. He and his co-authors described more than 60 new taxa and recombined some 70 taxa, most of them belonging in Loasaceae subfam. Loasoideae (e.g. Weigend, 1996, 1997a, c, 1998, 1999, 2000, 2001a, 2002a, 2004b, 2006, 2007; Weigend et al., 1998, 2003; Dostert and Weigend, 1999; Weigend and Ackermann, 2003; Rodríguez, 2008; Henning and Weigend, 2009, 2011; Henning et al., 2011). Today, Loasaceae comprises 20 genera with more than 300 species (Weigend, 2004c, 2010a).

The distribution of the family is largely restricted to the New World. The northernmost species are found in the genus *Mentzelia* (subfamily Mentzelioideae), ranging from Argentina/ Chile to the northern United States, whereas the southern distribution limit is formed by species of the genera *Loasa* and *Blumenbachia* (Fig. 1.1 C), distributed from Brazil to Patagonia (Chile and Argentina). The tribe Loaseae (subfam. Loasoideae) is restricted to Central and South America (Fig. 1.1 B) and the tribe Klaprothieae from northern Bolivia up to central Mexico (Fig. 1.1 A). There are only two genera outside of the Americas: *Kissenia* with two species in Africa (Dandy, 1926) and *Plakothira* with three species on Marquesas Islands (Florence, 1985). The subfamily Loasoideae, with 13 genera and more than 220 species (compare tab.

Subfamily	**Tribe**	**Genus**	**number of species**
Gronovioideae		*Cevallia* Lag.	1
		Fuertesia Urb.	1
		Gronovia L.	2
Loasoideae	Klaprothieae	*Klaprothia* Kunth	2
		Plakothira J.Florence	3
		Xylopodia Weigend	1
	Loaseae	*Aosa* Weigend	7
		Blumenbachia Schrad.	12
		Caiophora C.Presl	ca. 50
		Chichicaste Weigend	1
		Huidobria Gay	2
		Kissenia R.Br. ex T.Anderson	2
		Loasa Adans.	36
		Nasa Weigend	>100
		Presliophytum (Urb. & Gilg) Weigend	3
		Scyphanthus D.Don	1-2
Mentzelioideae		*Eucnide* Zucc.	13
		Mentzelia L.	80
		Schismocarpus S.F.Blake	1
Petalonychoideae		*Petalonyx* A.Gray	5

Table 1.1: Infrafamilial classification of Loasaceae (compiled from Hufford et al., 2003, 2005; Weigend, 1997c, 2004c, 2006; Weigend et al., 2004)

1.1), is the species-richest group within the family, with its centre of diversity in the Andes of Peru (Weigend, 2002b). *Nasa*, the largest genus within the subfamily, is most diverse in the Amotape-Huancabamba Zone (northern Peru: Weigend, 2002b; Weigend et al., 2004; Weigend and Gottschling, 2006; Henning et al., 2011). The second largest genus *Caiophora* shows its highest diversity from northern Peru to northern Argentina (Fig. 1.1 C). It has been shown that *Caiophora* is sister to the genus *Scyphanthus* and that both are sister to a clade formed by the genera *Loasa* and *Blumenbachia* (Moody et al., 2001; Hufford et al., 2003, 2005; Achatz, 2008; Schulz, 2009). This close relationship of *Scyphanthus* to *Caiophora* is confirmed by similar leaf-, flower- and fruit morphology [compare flowers of *Scyphanthus* (Fig. 1.4 A-B) with flowers of *C. arechavaletae* (Fig. 1.4 C), *C. pterosperma* (Fig. 1.4 F) and *C. stenocarpa* (Fig. 1.4 D)] and that both together are sister to a clade formed by the genera *Loasa* and *Blumenbachia* (Moody et al., 2001; Hufford et al., 2003, 2005; Weigend et al., 2004; Achatz, 2008; Schulz, 2009). The mediterranean Andes of central Chile (above 3000 m a.s.l.) are the southern distribution limit of *Caiophora*, where only two taxa (*C. rosulate* and *C. coronata*) have been recorded. *Scyphanthus*, endemic to central Chile, occurs around the southern limit of *Caiophora*, but at lower elevations (Fig. 1.1 C; 600-1600 m a.s.l.). *Scyphanthus* seems to be

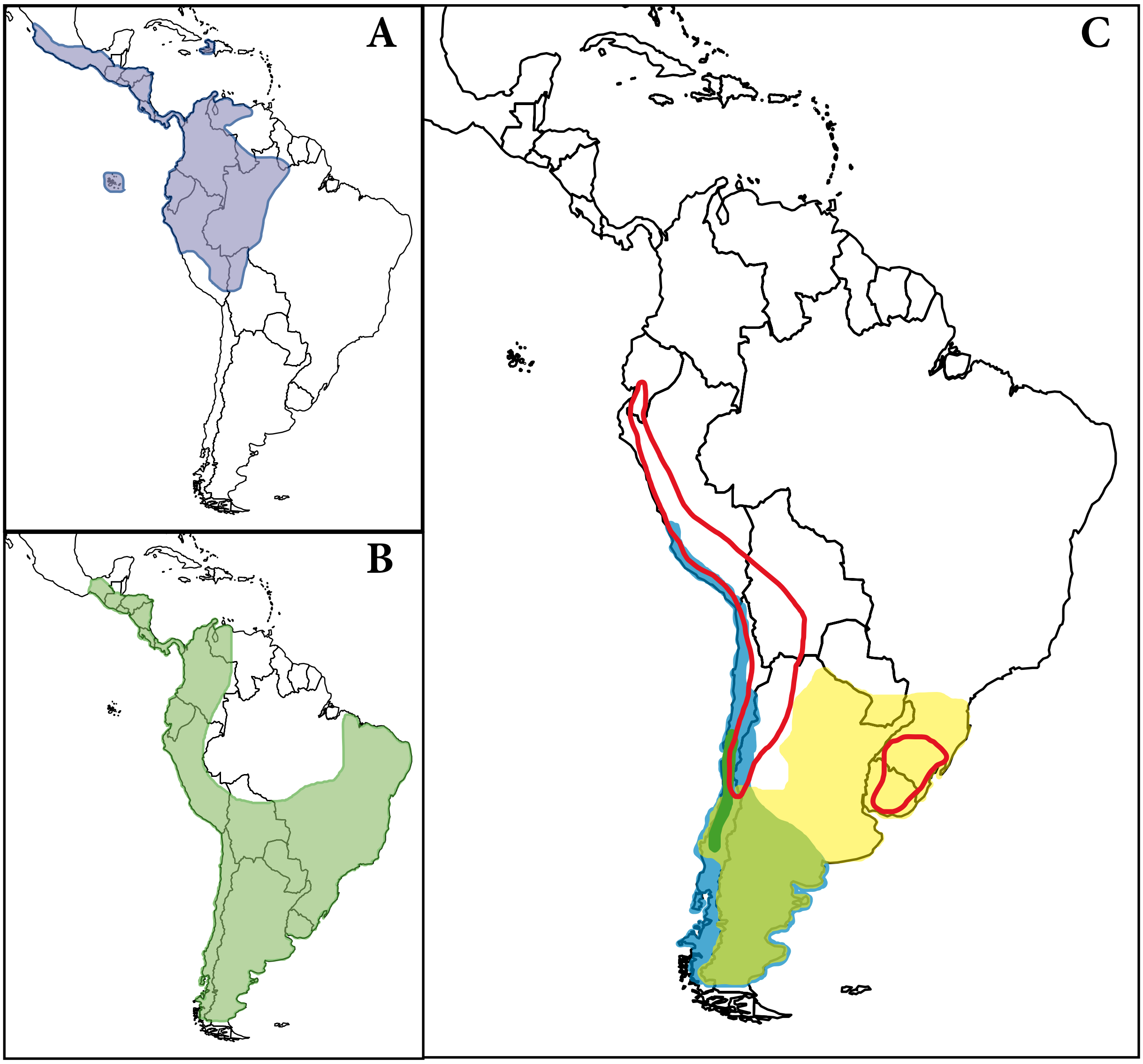

Fig. 1.1: Distribution of Loasaceae subfamily Loasoideae in Central and South America: A: Tribe Klaprothieae (*Klaprothia* and *Xylopodia*, except *Plakothira* from Marquesas Islands) B: Tribe Loaseae (*Aosa*, *Blumenbachia*, *Caiophora*, *Chichicaste*, *Huidobria*, *Loasa*, *Nasa*, *Presliophytum* and *Scyphanthus*; except *Kissenia* from Africa). C. „South Andean Loasas" a monophyletic clade out of the tribe Loaseae [*Blumenbachia* (blue), *Caiophora* (red), *Loasa* (yellow) and *Scyphanthus* (dark green); overlapping distribution of *Loasa* and *Blumenbachia* (light green)]. Distribution pattern compiled from herbarium specimens and literature data: Poston and Nowicke, 1990; Weigend, 2001, 2010a, b; Rodríguez and Weigend, 2007; Weigend et al., 2008; Weigend and Ackermann, forthc. (Map kindly provided by J. Mutke, Bonn).

adapted to a mediterranean climate. *Caiophora*, in contrast, prefers colder climates, with high day temperature and solar radiation and temperature up to ≤0°C during the night, even during the vegetative period. Its range begins at 2000 m a.s.l. and goes up to 5000 m a.s.l.

1.2. The genus *Caiophora*

The genus *Caiophora* was first described by Carol Boriwog Presl in “Reliquiae Haenkiana” (Presl, 1831) based on a specimen of *Loasa contorta*, which had been described by Desrousseaux (1789).

Caiophora species share several characters, but in general morphological diversity is high (Figs. 1.2 C-L, 1.3-1.10). *Caiophora* species are perennial herbs, except annual *C. arechavaletae*. The primary root is dominant (e.g. *C. carduifolia*, *C. chuquitensis*, *C. cirsiifolia*, Figs. 1.3 A-B) and depending on the species the secondary root can form tubers (e.g. *C. stenocarpa*, Fig. 1.3 C). Only a few species do have rhizomes (e.g. *C. contorta*, *C. andina*, *C. canarinoides*, Figs., 1.3 D-F). There are only few species with entire leaves (e.g. *C. aconquijae*, Fig. 1.3 G). In general all other known species do have pinnate (Fig. 1.3 H), ternate or bipinnatisect leaves (Fig. 1.3 I). The flowers are in terminal, symmetrical or asymmetrical dichasia, or are rarely borne from a rosette (e.g. Fig. 1.2 A: *C. rosulata*). Flowers are 5-7(-11)-merous, with red, orange, pink, yellow or white, cymbiform petals (Figs. 1.4 C-L, 1.5-1.6, 1.7 A-I), either with entire (most species) or dentate margin (Fig. 1.4 E). Sepals are entire (Fig. 1.7 J), entire with dentate margin (Fig. 1.7 K) or pinnatisect (Fig. 1.7 L). The staminodial complex consists of three outer, fused staminodes, building the nectar scale, either multicoloured (Fig. 1.8 A) or unicoloured (Figs. 1.8 H, I, K) and two inner free staminodes (Figs. 1.8 C, E, G, J, L). Presence (Figs. 1.8 A, B, D, F, G, H) or absence (Fig. 1.8 I, K) of the dorsal appendages on the back of the nectar scales is characteristic of some of the species group (compare tab. 1.2) as well as presence (Figs. 1.8 A; B, D, F) or absence of the double arch (Fig. 1.8 K). Dorsal appendages can be ligulate (Fig. 1.8 F), lanceolate or filiform (Figs. 1.8 A, B, D, G, H). Stamens are arranged in antesepalous fascicles, equalling the petals in number. The number of stamens ranges from 80-150. The stigma is always three-lobed. The fruit is an inferior capsule, cylindrical or subglobose, sometimes twisted, and opens with apical valves or longitudinal slits (Figs. 1.9 A-H), and always with three or four T- or Y-shaped placentae (Figs. 1.9 I-L). Seeds have a testa with fenestrated anticlinal walls. The chromosome number of all species is $2n = 16$.

Caiophora comprises more than 50 species, many yet undescribed. Weigend and Ackermann (2003) provided an informal infrageneric classification (Tab. 1.2) based on morphological characters, where ten groups are recognized. Classification of the species into these groups is straightforward, but differentiation among individual species can be quite demanding.

Caiophora contorta (Desr.) C.Presl is the northernmost species in the genus, being the only representative of *Caiophora* in Ecuador. The other ca. 50 species are distributed from northern Peru to central Chile and Argentina (Fig. 1.1 C), between (2000-)2500 and 4500(-5000) m a.s.l. Near Cuzco and La Paz (Bolivia) several species occur on both sides of the Andes. However, most species are endemic to one Andean slope (compare Rodríguez and

Table 1.2: Infrageneric groups of *Caiophora* with diagnostic characters (translated and modified from Weigend & Ackermann 2003)

group	habit	inflorescence	nectar scales colour	nectar scales structure	nectar scales dorsal filaments	corolla	petals	distribution	species
Caiophora nivalis-group	rosulate herbs, perennial	single flower in the rosette	whitish, neck brownish	thin with double arch on back	ligulate	wide spread	flat, margin serrate	Argentina	*C. nivalis* Lillo *C. pulchella* Urb. & Gilg
Caiophora arechavaletae-group	erect herbs, annual	erect inflorescence, sometimes winding	whitish, neck brownish	thin with double arch on back	ligulate	wide spread	flat, margin serrate	Uruguay, Brazil	*C. arechavaletae* (Urb.) Urb. & Gilg
Caiophora pterosperma-group	climbing herbs, perennial	winding inflorescence	whitish, neck brownish, reddish, greenish	thin with double arch on back	ligulate	wide spread	boot-shaped, margin serrate	Peru	*C. pterosperma* (Ruiz & Pav. ex G.Don) Urb. & Gilg *C. stenocarpa* Urb. & Gilg.
Caiophora chuquitensis-group	erect, lignified at base or rosulate, perennial	single flower in the rosette or erect inflorescences	white	thin with double arch on back	filiform, apical red	balloon-shaped	boot-shaped	Peru, Bolivia, Chile, Argentina	*C. andina* Urb. & Gilg *C. boliviana* Urb. & Gilg *C. chuquitensis* (Meyen) Urb. & Gilg *C. deserticola* Weigend & Mark. Ackermann *C. mollis* (Griseb.) Urb. & Gilg *C. rusbyana* Urb. & Gilg *C. rosulata* (Wedd.) Urb. & Gilg *C. scarlatina* Urb. & Gilg
Caiophora contorta-group	climbing herbs, perennial	winding inflorescence	white or orange	thin with double arch on back	filiform, apical red	balloon-shaped	boot-shaped	Ecuador, Peru	*C. contorta* (Desr.) K.Presl *C. grandiflora* (G.Don) Weigend & Mark. Ackermann
Caiophora coronata-group	decumbent herbs, perennial	decumbent inflorescence	white	thin, without double arch	without, rarely filiform	balloon-shaped or wide spread	boot-shaped	Peru, Bolivia, Chile, Argentina	*C. coronata* (Arn.) Hook. & Arn. *C. pentlandii* (Graham) Loudon
Caiophora clavata-group	climbing herbs, perennial	winding inflorescence	white or white with pink	thin with double arch on back	filiform, apical clavate	wide spread	boot-shaped	Bolivia, Argentina	*C. cernua* (Griseb.) Urb. & Gilg *C. chuquisacana* Urb. & Gilg (?) *C. clavata* Urb. & Gilg *C. dumetorum* Urb. & Gilg
Caiophora cirsiifolia-group	climbing or decumbent herbs, perennial	winding inflorescence	yellow or orange	thin, without double arch on back	without	wide spread to balloon-shaped	boot-shaped	Peru, Chile	*C. cirsiiifolia* K. Presl *C. peduncularis* (K.Presl) Weigend & Mark.Ackermann
Caiophora lateritia-group	climbing herbs, perennial	winding inflorescence	yellow or orange	thin, without double arch on back	apical ligulate and basally lanceolate, red	campanulate	ligulate to boot-shaped	Peru, Bolivia, Argentina	*C. aconquijae* Sleumer *C. buraeavii* Urb. & Gilg *C. canarinoides* (Lenné & C.Koch) Urb. & Gilg *C. hibiscifolia* (Griseb.) Urb. & Gilg *C. lateritia* Klotzsch *C. madrequisa* Killip *C. pediculariifolia* Killip *C. vargasii* Standl. & F.A.Barker
Caiophora carduifolia-group	climbing herbs, perennial	winding inflorescence	green, neck sometimes yellow or orange	carnose, without double arch on back	without	wide spread to balloon-shaped	profundos	Peru	*C. cinerea* Urb. & Gilg *C. carduifolia* K. Presl *C. macrantha* Killip *C. pachylepis* Urb. & Gilg *C. tenuis* Killip

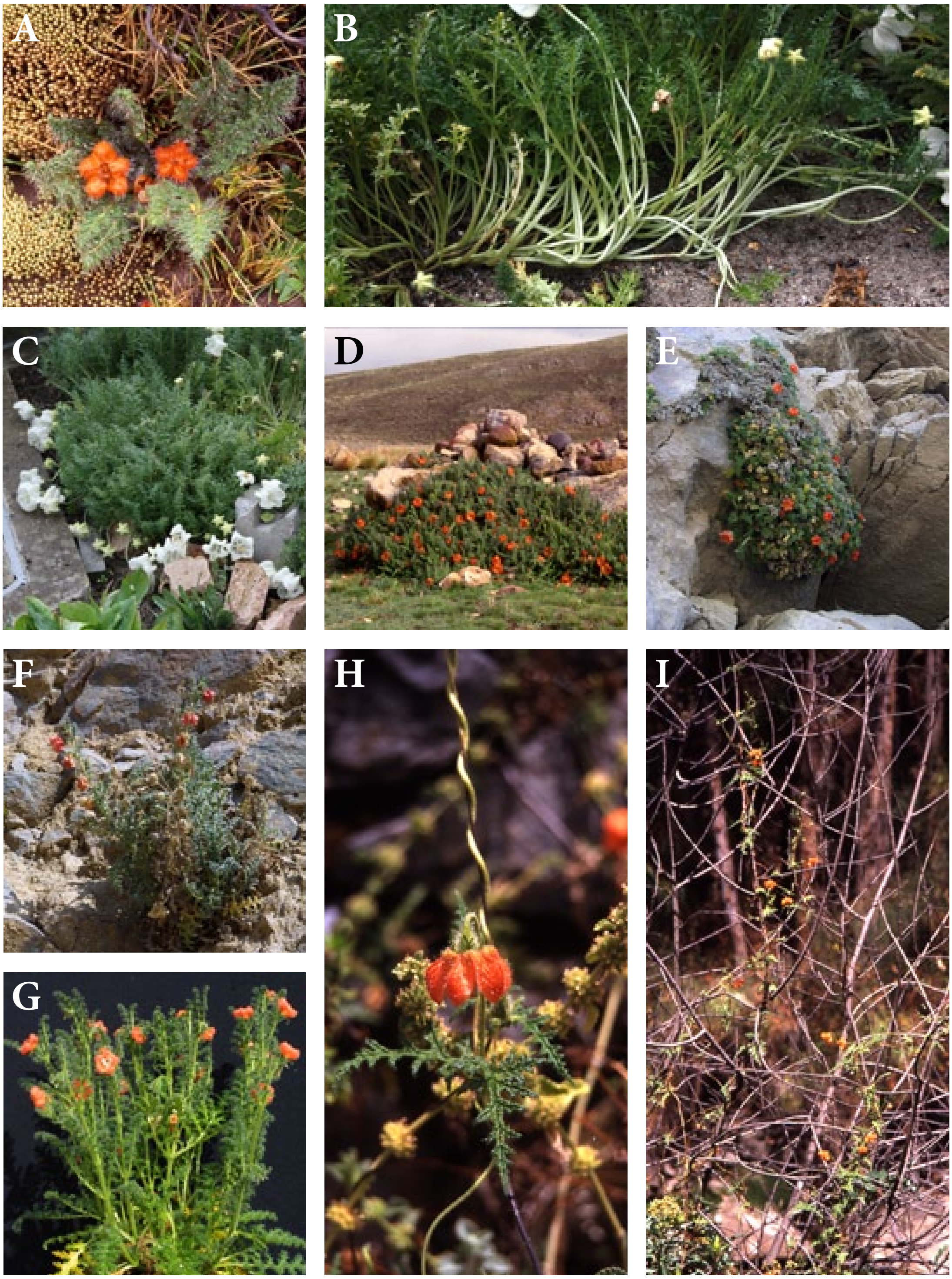

Fig. 1.2: Growth habit of *Caiophora* species — A: rosulate (*Caiophora rosulata* subsp. *rosulata*, photo M. Weigend); B-E decumbent (B-C: *C. coronata*, D: *C. pentlandii*, photo M. Weigend; E: *C. andina*); F-G: erect (F: *C. deserticola*; G: *C. chuquitensis*); H-I: scandent (*C. cirsiifolia*).

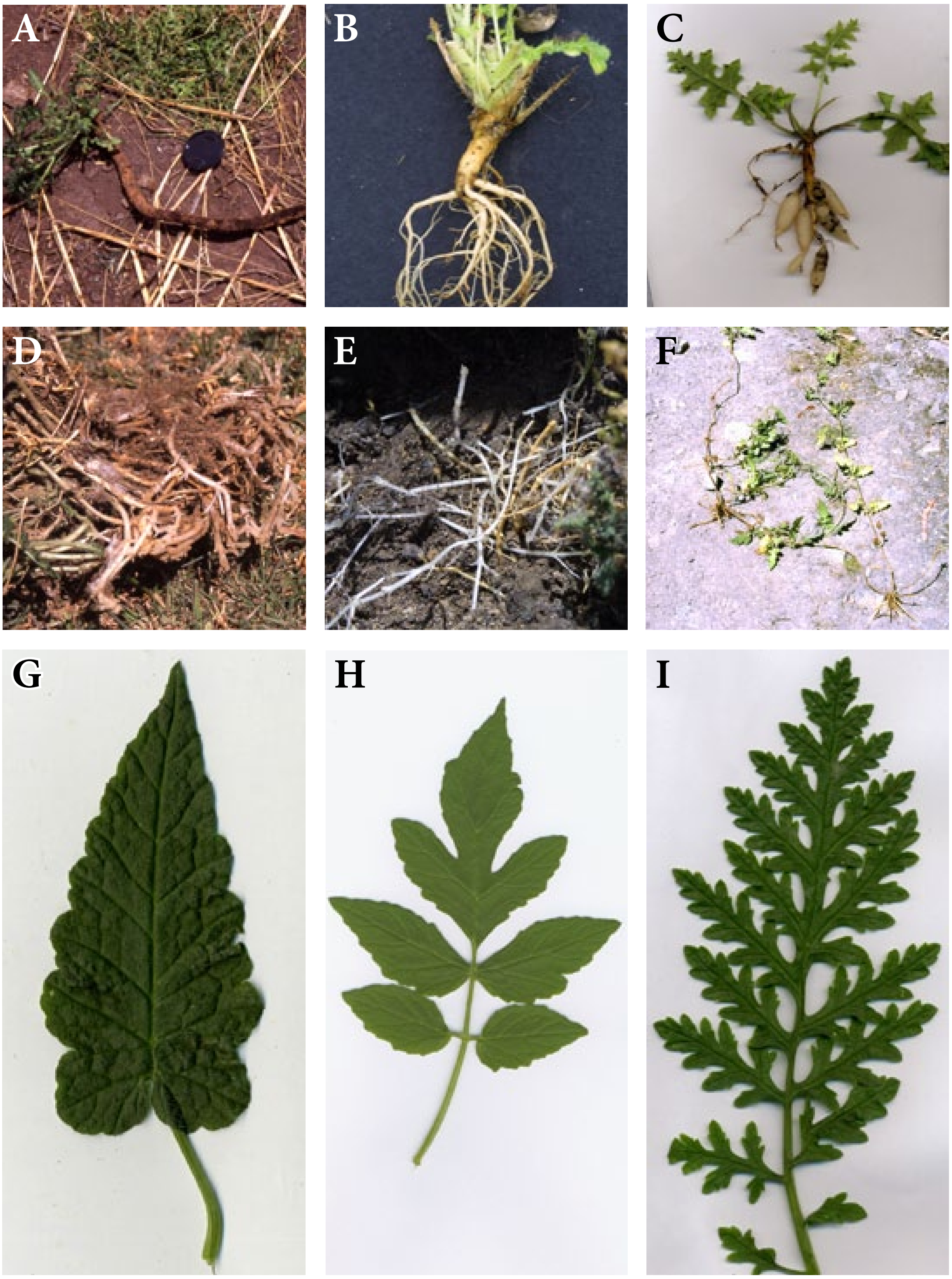

Fig. 1.3: Root system, rhizome and leaf shape — A-B: dominant primary root (A: *Caiophora carduifolia*, B: *C. chuquitensis*); C: secondary roots building tubers (*C. stenocarpa*, photo M. Weigend); D-E: rhizomes (D: *C. cirsiifolia*, E: *C. andina*, F: *C. canarinoides*); G-I: leaf shape — G: entire (*C.* sp. nov. ined, taxon belonging to *Caiophora lateritia*-group; compare Tab. 1.2); H: pinnate (*C. hibiscifolia*); I: pinnatisect (*C. arechavaletae*, photo M. Weigend).

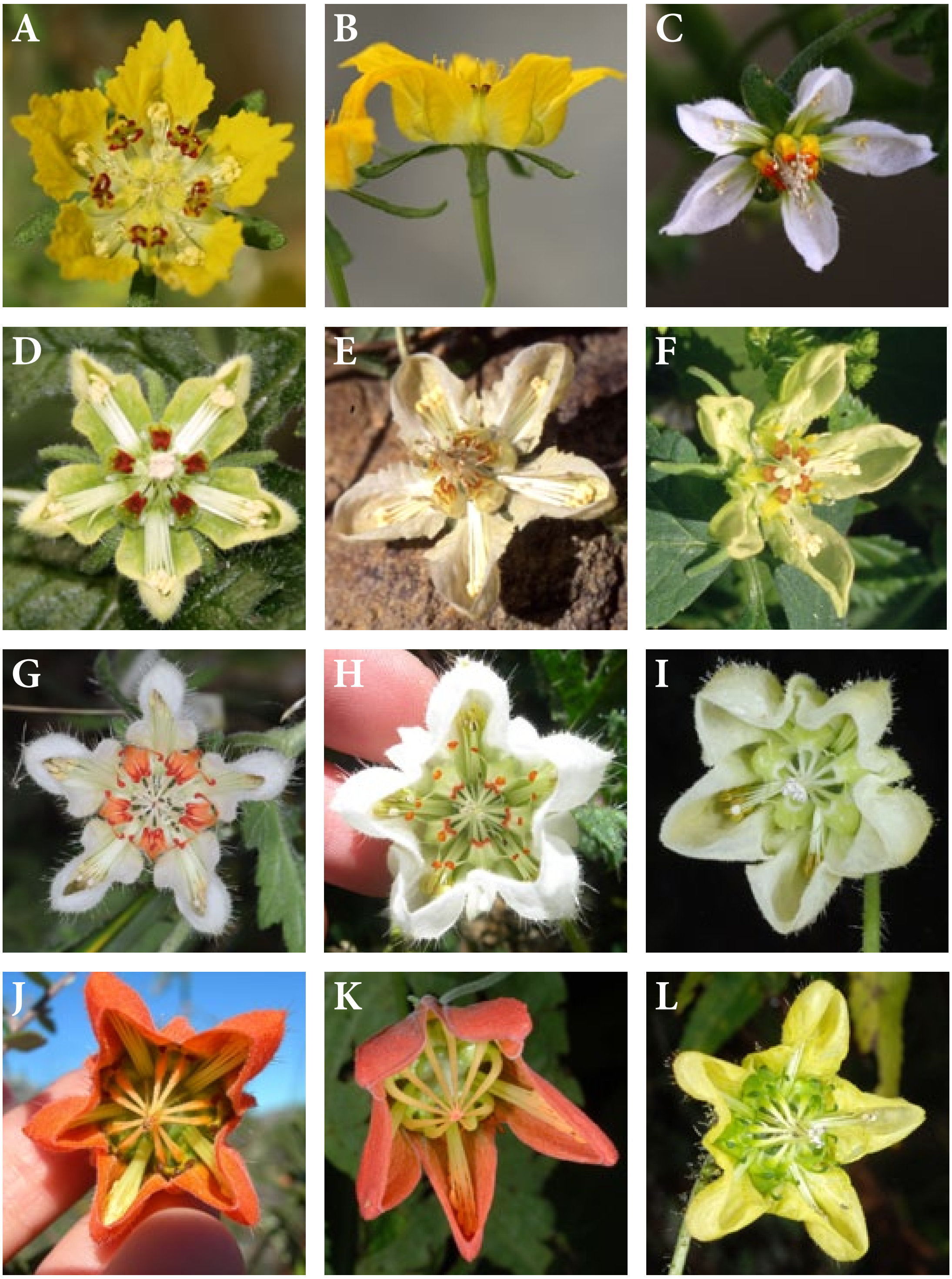

Fig. 1.4: *Scyphanthus* and *Caiophora* flowers — A-B: *Scyphanthus* (*S. elegans*); C-L: *Caiophora* — C: *Caiophora arechavaletae*-group (*C. arechavaletae*); D-F: *Caiophora pterosperma*-group (D: *C. stenocarpa*, E: *C.* sp. nov. ined., F: *C. pterosperma*); G-I: *Caiophora clavata*-group (G: *C. cernua*, H: *C. clavata*, I: *C. dumetorum*); J-L: *Caiophora lateritia*-group (J: *C. lateritia*, K: *C. hibiscifolia*, L: *C. aconquijae*). (Photo E-F: M. Weigend; G-L: M. Strelin, Argentina).

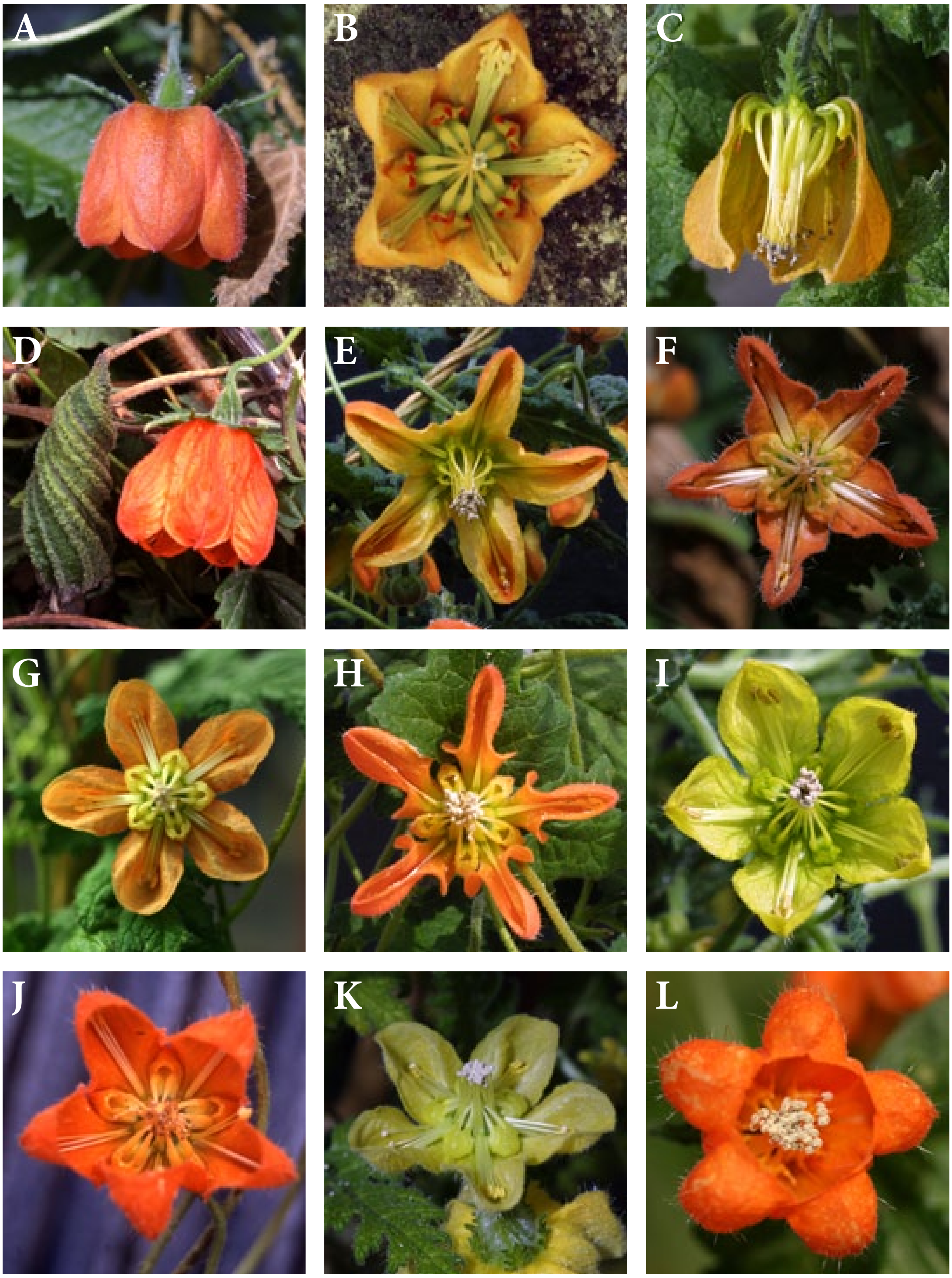

Fig. 1.5: *Caiophora* flowers — A-D: *Caiophora lateritia*-group (A: *C.* sp. nov. ined., B: *C. buraeavii*, photo M. Weigend, C: *C. canarinoides*, D: *C. madrequisa*, photo M. Weigend); E-K: *Caiophora cirsiifolia*-group (E-J: *C. cirsiifolia*, different morphotypes from Peru; E: Dept. Cajamarca - Prov. Contumaza, F: Dept. Arequipa - Prov. Arequipa, G: Dept. Lima - Prov. Lima, H: Dept. Ancash - Prov. Huaylas, I: Dept. Cajamarca - Prov. Santa Cruz, J: Dept. Lima - Prov. Yauyos. K: *C. peduncularis*); L: *Caiophora contorta*-group (*C. contorta*).

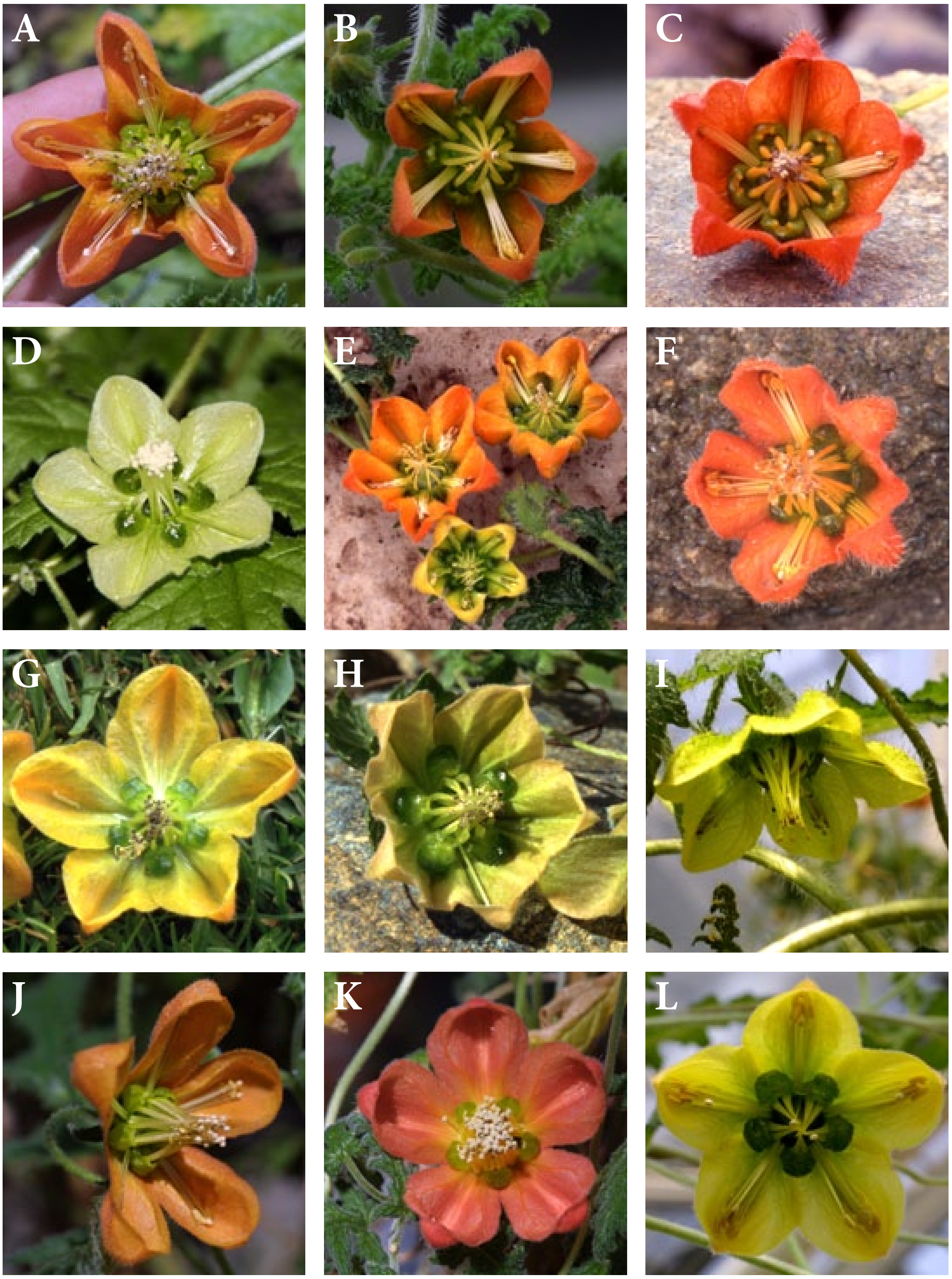

Fig. 1.6: *Caiophora* flowers — A-L: *Caiophora carduifolia*-group (A-J: *C. carduifolia*, different morphotypes from Peru. A: Dept. Cuzco - Prov. Cuzco, B: Dept. Cuzco - Prov. Paucartambo, C: Dept. Cuzco - Prov. Calca, D: Dept. Cuzco - Prov. Urubamba, E: Dept. Junin - Prov. Junin, F: Dept. Junin - Prov. Yauli, G: Dept. Huanuco - Prov. Dios de Mayo, H: Dept. Huanuco - Prov. Pachitea, I: Dept. Apurimac - Prov. Andahuaylas, J: Dept. Ayacucho - Prov. Huamanga; K: *C. cinerea*; L: *C. tenuis*). (Photo C, E-H: M. Weigend).

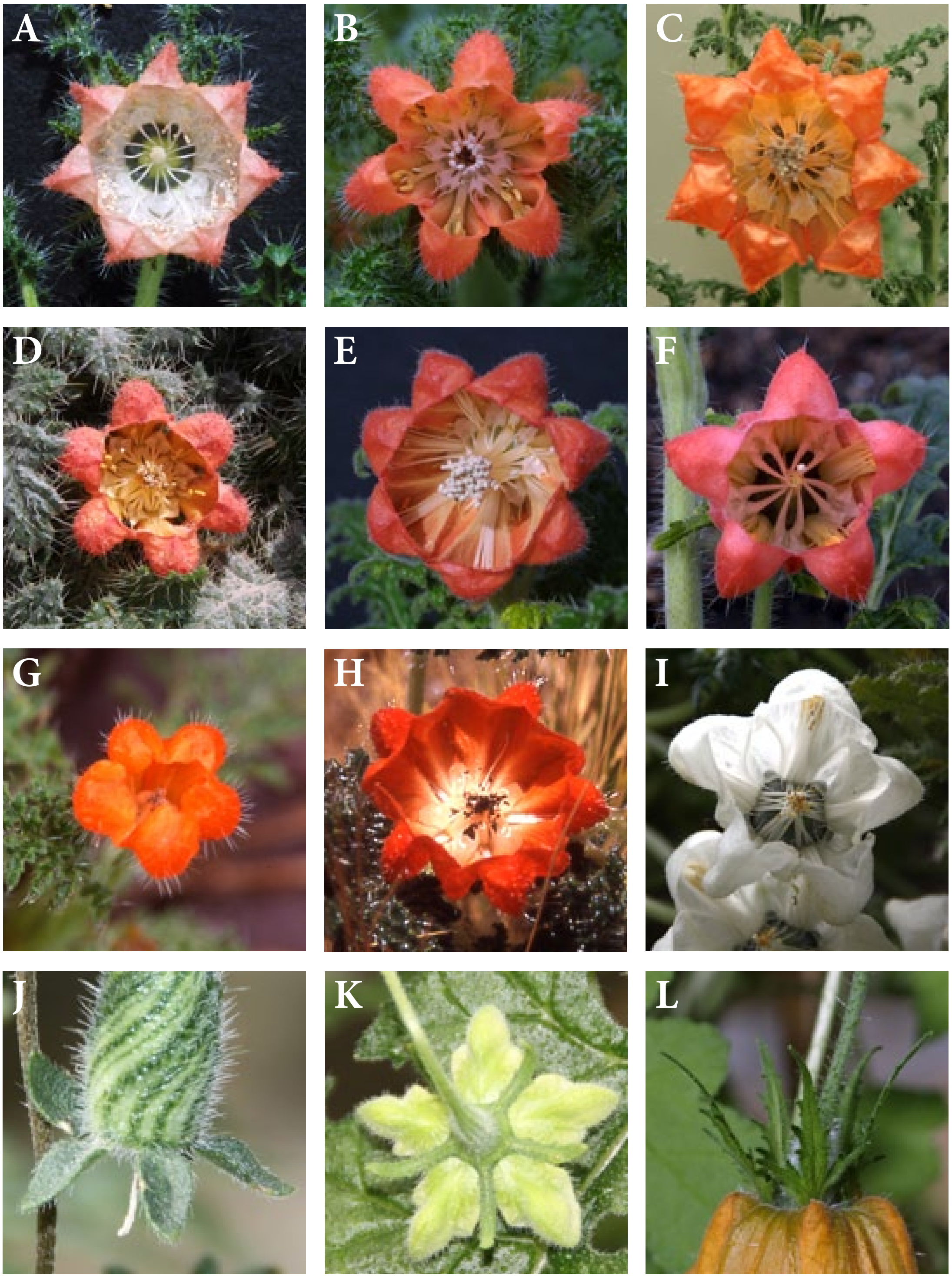

Fig. 1.7: *Caiophora* flowers and sepals — A-G: *Caiophora chuquitensis*-group (A: *C. chuquitensis* from Chile, B: *C. chuquitensis* from Peru, C: *C. chuquitensis* from Bolivia, D: *C. andina*, E: *C. scarlatina*, F: *C. deserticola*, G: *C. rosulata* subsp. *rosulata*); H-I: *Caiophora coronata*-group H: *C. pentlandii*, I: *C. coronata*). J-L: sepals — J: entire (*C. arechavaletae*); K: margin dentate (*C. carduifolia*); L: pinnatisect (*C. canarinoides*). (G-H: Photo M. Weigend).

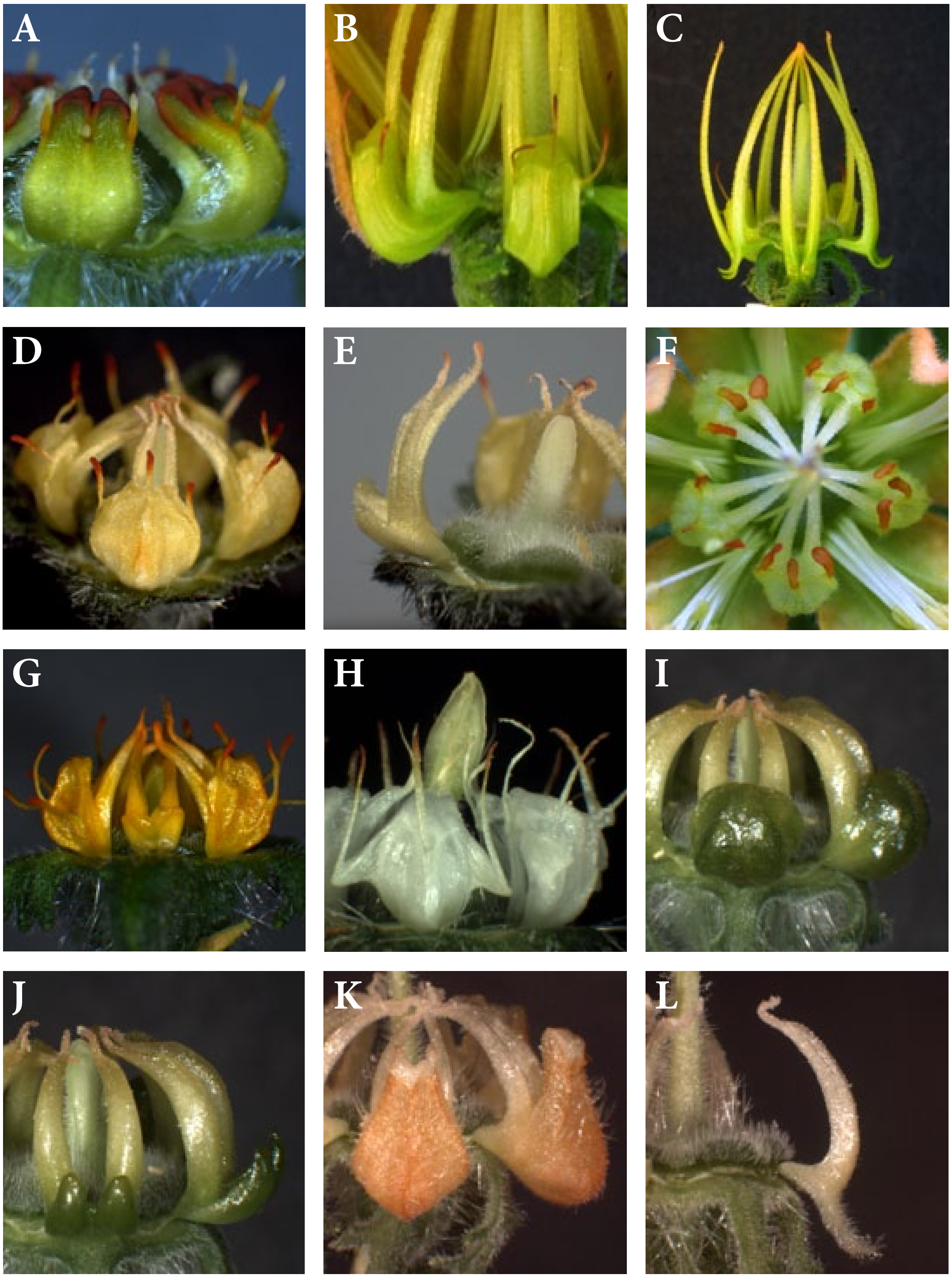

Fig. 1.8: Staminodial complex — A: *Caiophora stenocarpa*; multicoloured nectar scales with well developed double arch; B-C: *C. canarinoides* (B: nectar scales; C: staminodes); D-E: *C. grandiflora* (D: nectar scales; E: staminodes); F: nectar scales of *C. lateritia*. G: nectar scales and staminodes of *C. contorta*; H: nectar scales of *C. chuquitensis;* I-J: *C. carduifolia* (I: carnose nectar scales; J: staminodes); K-L: *C. cirsiifolia* (K: nectar scales; L: staminodes). (Petals, stamen and in Figs. C, E, G, J, and L nectar scales removed; D-E: photo L. Scherer, Berlin).

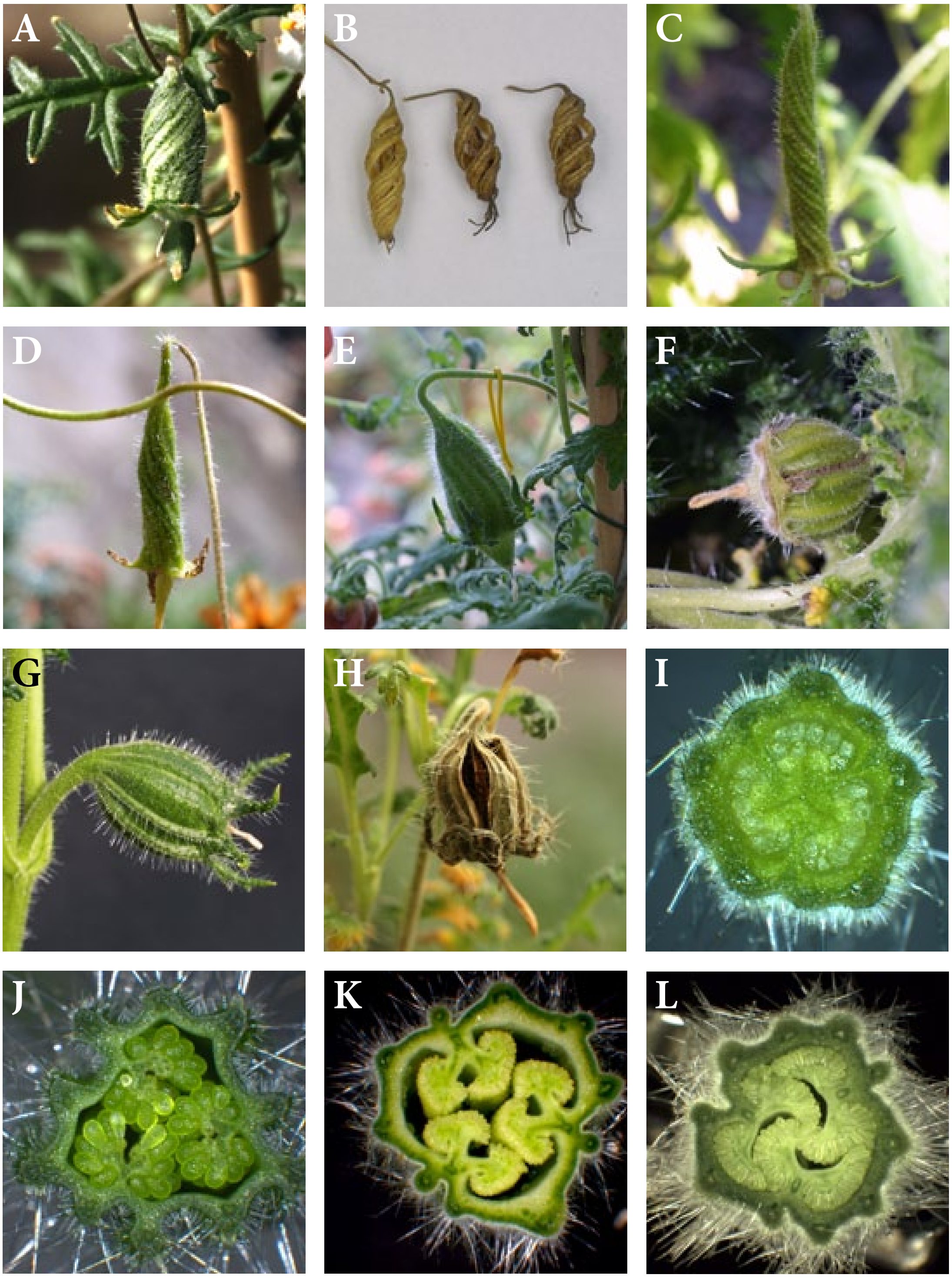

Fig. 1.9: Fruit shape and placentae — A-H fruit shape: A-D: fruit twisted (A: *C. arechavaletae*; B: *C.* sp. nov. ined, taxon belonging to *Caiophora lateritia*-group; C: *C. lateritia*, D: *C. cirsiifolia*); E-H: fruit not twisted (E: *C. cinerea*; F: *C. pentlandii* G: *C. chuquitensis*; H; *C. andina*); I-L shape of placentae — I: T-shaped (*C. stenocarpa*); J-L: Y-shaped (H: *C. arechavaletae*; J: *C. contorta*; K: *C. coronata*; L: *C. pentlandii*). B, H: fruit is opening with longitudinal slides. D, E: fruit with conical beak.

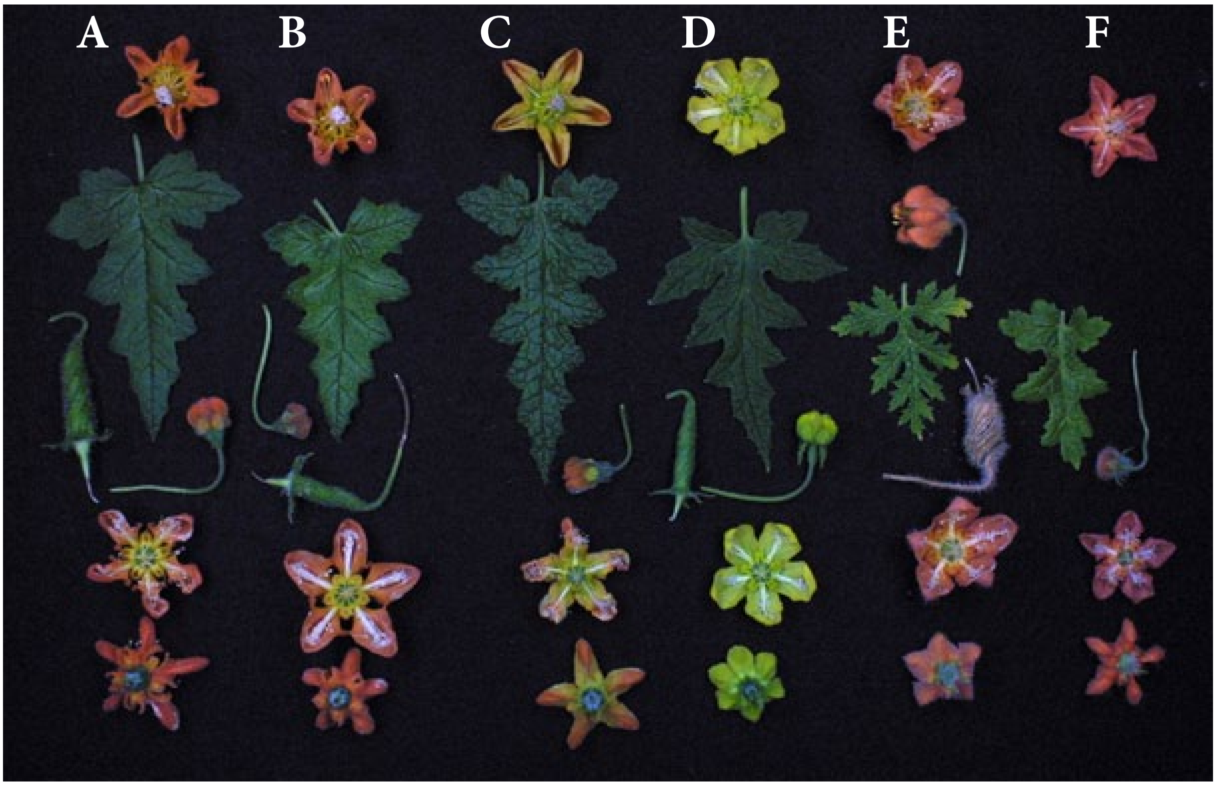

Fig. 1.10: Morphological diversity within cultivated *Caiophora cirsiifolia* from different localities in Peru (A-B: Dept. Ancash - Prov. Huaraz, C: Dept. Cajamarca - Prov. Contumaza, D: Dept. Cajamarca - Prov. Santa Cruz, E: Dept. Lima - Prov. Yauyos. F: Dept. Arequipa - Prov. Arequipa).

Weigend, 2007; Weigend et al., 2008; Weigend and Ackermann, forthc).

Alpha-taxonomy of *Caiophora* was and is the most problematical within Loasoideae. Several complications have been solved recently. Killip (1928), for example, described *Caiophora pauciseta* Killip based on a herbarium sheet with mixed individuals of two species (*Caiophora carduifolia* and *C. peduncularis*) and their corresponding hybrid (Weigend, 1997b; Weigend and Ackermann, 2003). Type specimens were designated and problems with old names without type locality or incomplete voucher information were solved (Weigend, 1997b; Weigend and Ackermann, 2003). But there are still numerous unsolved problems in alpha-taxonomy.

One central problem is that specimens have often been badly preserved. All *Caiophora* species are covered with stinging hairs. Preparing flowers and leaves for herbarium specimens, so that diagnostic characters are still visible, is not possible without physical pain and therefore often simply not done. But the main problem is the wide range of morphologically similar and intermediate morphotypes, especially in the *Caiophora cirsiifolia*-group (compare Figs. 1.5 E-K and fig. 1.10) and to a lesser degree in the *C. carduifolia*-group (compare Figs. 1.6 A-J and 1.11). Weigend (pers. com.) found several morphotypes at different elevations within the same

Fig. 1.11: Morphological diversity within cultivated *Caiophora carduifolia* from different localities in Peru (A-B: Dept. Apurimac - Prov. Andahuaylas, C-D: Dept. Ayacucho - Prov. Huamanga, E: Dept. Cuzco - Prov. Urubamba).

valley.

Cultivation of species within different temperature ranges (hot summer and moderate temperature during the winter in greenhouses) allowed recognizing that flower- and leaf shape and size can differ between seasons. Leaf size, structure and pubescence also differ significantly from summer to winter. Depending on the species and their natural habitat, leaves in winter tend to be smaller, more coriaceous and covered with glochidiate and scabrid trichomes and stinging setae, while summer leaves are larger, less pubescent and carnose (e.g. *C. chuquitensis*, *C. carduifolia*, *C. cirsiifolia* and *C. stenocarpa*). This indicates that specimens collected during different seasons may appear quite different at first glance. Several observations from Peru confirm this ontogenetic variability. In Southern Peru, for example, *C. cirsiifolia* is very common and represents a single morphotype (Figs. 1.5. F, 1.10 F). This taxon normally grows along hedges and stonewalls, but it also occurs along moist river and road banks, where growth habit and morphological characters differ from plants inhabiting drier areas. Temperature, solar radiation, soil composition and water availability influence plant growth, but this may not explain the large morphological variability observed in *Caiophora cirsiifolia*.

1.3. The Uplift of the Andes and the diversification of species

The uplift of the Andes started around 20 mya (Burnham and Graham, 1999). The final rise of the High Andes is dated to the Miocene, ca. 10 mya (e.g. Gregory-Wodzicki, 2000; Garzione et al., 2008; Picard et al., 2008; Hoorn et al., 2010). The uplift process of the southern and central Andes began in the South and continued up to the North. Several authors assume that colonization and radiation of Andean species generally followed the orogeny of the Andes (e.g. van der Hammen and Cleef, 1986; Hall, 2005; Ribas et al., 2007) or later (Pliocene and Pleistocene) through cyclical climate perturbations (Haffer, 1967; van den Elzen et al., 2001; Hoorn et al., 2010; Rull, 2011).

With the uplift of the Andes new habitats were created. Along with these changes, increasing isolation and the potential for diversification of species arose, which probably contributed to high local endemism in some Andean habitats (Gentry, 1986; Leimbeck et al., 2004; Hoorn et al., 2010; Antonelli and Sanmartin, 2011). It has been proposed that rapid diversification took place in the Andes (Gregory-Wodzicki, 2000; Jansson and Davies, 2008; Hoorn et al., 2010; Rull, 2011). Hughes and Eastwood (2006) postulated that the colonization of the cold upland habitats started in late Pliocene or early Pleistocene after the final Andean uplift. These high-elevation areas have been regarded as islands, where new habitats and unoccupied niches are frequent and rates and patterns of radiation and diversification are high (Böhle et al., 1996; Baldwin and Sanderson, 1998; Verheyen et al., 2003; Gavrilets and Vose, 2005; Hughes and Eastwood, 2006).

In the Amotape-Huancabamba zone the overlap of species from the southern and northern hemispheres, environmental heterogeny, fragmentation of forests and isolation of high-elevation mountains by dry interandean valleys led to high species diversity and endemism (Young and Reynel, 1997; Weigend, 2002b, 2004a). Stern et al. (2008) found out, that 25 (19%) of 133 *Solanum* species, distributed in the Amotape-Huancabamba zone are endemic. There are several other studies reporting high levels of endemism for the Amotape-Huancabamba zone, both in plants and animals (e.g. Weigend, 2002b, 2004a; Flanagan et al., 2005; Venegas et al., 2008; Struwe et al., 2009; Weigend et al., 2010; Jara-Munoz, 2011; Saerkinen et al., 2011; Samain et al., 2011).

Ecologically different conditions in the interandean valleys and in high-elevation habitats may cause pronounced niche differentiation in small areas. This may explain why several closely related, endemic species coexist in the Andes. It is assumed that species and morphotypes in *Caiophora* radiated recently, since nearly all species of *Caiophora* inhabit high elevations above 3000 m a.s.l., which is a geologically young habitat.

1.4. Pollination biology of Loasoideae (Loasaceae) and *Mimulus* (Phrymaceae)

Reproduction and as a consequence thereof recombination of genes is the aim of each living being. In plants, transfer of ripe pollen to receptive stigma is defined as pollination (King and Brooks, 1947). Pollination can either be abiotic (hydrophilous, anemophilous) or biotic (zoophilous). Within the Angiosperms (ca. 350,000 species, Paton et al., 2008) more than 80% of the species depend on biotic pollination (Ackerman, 2000; Ollerton et al., 2011). Ollerton et al. (2011) showed that species distributed in tropical communities depend more on animal-pollination (94%) than species in temperate-zone communities (78%). Biotic pollination is an interaction between animals and plants. Generally both, plants and animals benefit from pollination. The transfer of pollen by animals will increase the probability of outcrossing, the objective of the plant. The animal´s benefit is reward (e.g. pollen, nectar, oil, resin, perfume). The most common rewards are nectar and pollen. Outcrossing plant species produce more pollen and nectar than self-fertilizing species and outcrossing plants offering only pollen produce higher pollen-ovule ratios (P/O-ratio) than those with nectar and pollen or only nectar as reward (Cruden, 1977, 2000; Etcheverry and Aleman, 2005; own unpublished data about nectar production and P/O-ratio in Boraginaceae).

Species belonging to Loasoideae and *Mimulus* produce tiny up to large amounts of nectar (Loasoideae: Stiles and Freeman, 1993; Cocucci and Sersic, 1998. *Mimulus*: Vickery and Sutherland, 1994; Bradshaw et al., 1995; Cooley et al., 2008). Main pollinators for both groups are Hymenoptera and Trochilidae (e.g. Batalin, 1870; Robertson, 1895; Carpenter, 1976; Arroyo et al., 1985; Elisens and Freeman, 1988; Stiles and Freeman, 1993; Vickery and Sutherland, 1994; Schlindwein and Wittmann, 1997; Schlindwein, 2000; Medel et al., 2003, 2007; Botto-Mahan et al., 2004; Weigend and Gottschling, 2006; Cooley et al., 2008), but Diptera (Medel et al., 2003, 2007; Troncoso and Vargas, 2004; Devoto, 2006; Cooley et al., 2008) and Lepidoptera (butterflies and hawkmoths: Grant, 1993; Bradshaw et al., 1995; Medel et al., 2003, 2007; Ackermann and Weigend, 2006; Streisfeld and Kohn, 2007; compare photo at http://www.nhm.ac.uk/natureplus/message/6107#6107) also have been observed. Cocucci and Sersic (1998) additionally observed rodents and sunbirds visiting *Caiophora coronata*, the first report of possible rodent pollination in South America.

Urban (1886) was the first who described the thigmonastic stamen movement of six species of Loasoideae cultivated at Berlin Botanical Gardens. Little was known about natural pollination in Loasoideae when Schlindwein and Wittmann (1997) investigated pollinator behaviour of the bee *Bicolletes pampeana* (Colletidae) on *Caiophora arechavaletae* flowers in southern Brazil. Important for the bee and their trapping behaviour was, that *Caiophora arechavaletae* continuously offered pollen and nectar. They observed trap-lining behaviour of the bee and also triggered pollen presentation of *Caiophora arechavaletae* (Schlindwein and

Wittmann, 1997; Schlindwein, 2000). Since then, Henning investigated experimentally triggered resp. thigmonastic stamen movement in more than 20 species, and compared these data with observed flower visitors (Henning, 2006 and pers. comm.). In general, small flowers with spreading petals (in general bee-pollinated) present more stamina after triggered manipulation than large, campanulate or balloon-shaped flowers (in general hummingbird-pollinated). A wide range of flower visitors on different species of Loasoideae genera have been reported from the field (Weigend and Gottschling, 2006). Morphological diversity of flowers is high in *Caiophora*, but it is even more diverse in *Nasa* and *Loasa*. Weigend observed mainly small bees on small flowers and hummingbirds and/or large bees on large flowers. The visual signal (colour, floral size, floral shape), nectar production (amount of nectar and sugar, concentration, sugar composition, amino acids) and the amount of pollen offered varies widely and thus different pollinator guilds can be attracted, causing isolation through pollinator preferences, as has been postulated for other plant groups (e.g. Waser and Price, 1981; Grant, 1992; Vickery, 1992; Melendez-Ackerman et al., 1997; Altshuler, 2003; Castellanos et al., 2003; Fenster et al., 2004; Wilson et al., 2006; Nicolson, 2007; Perret et al., 2007; Campbell, 2008; Cooley et al., 2008; Smith et al., 2008; Thomson and Wilson, 2008; Smith, 2010; Venail et al., 2010).

Pollination in *Mimulus* is much better-known than in Loasaceae species (e.g Grant, 1993; Sutherland and Vickery, 1993; Vickery and Sutherland, 1994; Bradshaw et al., 1995; Fetscher and Kohn, 1999; Schemske and Bradshaw, 1999; Medel et al., 2003, 2007; Botto-Mahan et al., 2004; Carvallo and Ginocchio, 2004; Angert and Schemske, 2005; Streisfeld and Kohn, 2007; Cooley, 2008; Cooley et al., 2008; Cooley and Willis, 2009). Most of the studies have dealt with species from North America, where the genus has its centre of diversity with ca. 150-200 species (Beardsley and Olmstead, 2002). In Chile, there are ten closely-related species, and it is thus the second centre of diversity for *Mimulus* (Beardsley and Olmstead, 2002). Cooley et al. (2008) investigated pollinator behaviour in three Chilean species and in a hybrid swarm between two of them. Pollinators differ among these three species. *M. naiandinus* (pinkish corolla) and *M. luteus* (yellow corolla with red marks on the lower lip) are frequently visited by *Bombus dahlbomii*, whereas orange-coloured *M. cupreus* flowers are rarely visited. *M. naiandinus* and *M. luteus* produce relatively copious nectar, just like their interspecific hybrids. In contrast, *M. cupreus* only produced low amounts of dilute nectar, which does not seem to be suitable for *Bombus* and that may explain the view observations. Reward and visual signal isolate sympatric *M. cupreus* from *M. luteus* and *M. naiandinus*.

1.5. Hybridization in *Caiophora* and *Mimulus*

Hybridization is described by Arnold (1997, p. 3) as follows: “Natural hybridization involves successful mating in nature between individuals of two populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters." Arnold (1997) emphasizes that, this definition: (I) is independent of "any particular species concept, (II) that parental populations from which hybrid progeny derives do not have to be assigned to any taxonomic category, (III) that it is unnecessary to know the relative fitness of hybrids or adaptive norms (Stebbins, 1959) of parental types and (IV) the definition rests on straightforward empirical analyses to determine whether individuals involved in the putative hybridization event are drawn from populations that are recognizably different (Harrison, 1993) in at least one heritable character."

Under natural conditions isolating mechanisms prevent species to hybridize with others. Prezygotic isolation is defined as a mechanism preventing pollen transfer from one species to another (e.g. ecological, geographical, behavioural, mechanical, temporal and ethological isolation and gametic incompatibility). Postzygotic isolating mechanisms prevent development of seeds (zygotic mortality) or viability of the hybrid and their progeny [hybrid inviability, hybrid sterility, hybrid breakdown (e.g. Templeton, 1989; Rieseberg and Willis, 2007)].

In spite of isolating mechanisms, hybridization occurs throughout the animal and plant kingdoms (e.g. Emms and Arnold, 1997; Campbell et al., 1998; Sersic et al., 2001; Marhold et al., 2002; Gross et al., 2003; Stecconi et al., 2004; Tovar-Sanchez and Oyama, 2004; Wiens et al., 2006; Mavarez and Linares, 2008; Kimball and Campbell, 2009; Mallet, 2009). Seehausen (2004) discusses the probability of hybridization and adaptive radiation. He lists an example demonstrating that: "molecular gene mapping studies of hybrid species, together with the experimental creation of hybrid lines and computer simulations, …. demonstrated that homoploid hybrid speciation can be rapid, with no more than 25 generations required for stabilization of hybrid genomes (Ungerer et al., 1998)." For him "simulation models suggest that ecological separation from both parental species is essential (Mccarthy et al., 1995; Buerkle et al., 2000)" and several "empirical studies show that hybrid species usually differ ecologically from both parents by occupying different spatial, temporal or diet niches (DeMarais et al., 1992; Rieseberg, 1997; Giessler et al., 1999; Lexer et al., 2003)."

Few studies, compared to species-richness in the Andes, have reported hybrids and/or hybrid swarms (Berry, 1982; Hoshino and Berry, 1989; Sparre and Andersson, 1991; Graves, 2004; Smith and Baum, 2006; Alzate et al., 2008; Cooley et al., 2008; Soejima et al., 2008; Coloma et al., 2010; Watson and Flores, 2010; Masello et al., 2011). This may be due to the small number of existing hybrids, lack of taxonomical revisions or the difficulty to identify hybrids. Especially in the high mountains of the Andes, where accessibility is difficult, few plant specimens have been collected and the availability of material for studies is therefore restricted. In *Caiophora* (Sleumer, 1955; Brücher, 1986; 1989; M. Strelin, Argentina, pers. comm; own observations), as well as in Chilean *Mimulus* (Carvallo and Ginocchio, 2004; Cooley et al., 2008), natural hybrids have been observed.

As shown before, the Andes are young and high elevation habitats are presumably younger then 10 mya. It is assumed that *Caiophora* and also *Mimulus* species radiated and diversified recently after the final uplift of the Andes. Therefore it is expected, that High Andean *Caiophora* and *Mimulus* species are of young age and thus pre- and/or post-mating isolating mechanisms seem to be not fully developed.

1.6. Working hypothesis

The genus *Caiophora* is distributed in high elevations of the Andes in South America. Its closely related sister is the genus *Scyphanthus* in mediterranean Chile and both are related to *Loasa* in southern South America. The high Andes are of young origin. It is expected that *Caiophora* species radiated and diversified recently, after the final uplift of the Andes. Several species are narrowly endemic. Morpho- resp. ecotypes, especially within the *C. cirsiifolia*- and *C. carduifolia*-group may explain that morphological characters are not stabilized and can be the result of recent diversification processes or due to incomplete speciation. Isolating mechanisms may exist, but few observed, natural hybrids indicate that postzygotic isolating mechanisms have not fully developed.

If so, (I) the primary diversification of *Loasa* and *Scyphanthus* took place in temperate and mediterranean Chile and Argentina followed by a northwards expansion of *Caiophora*, (II) *Caiophora* species are geographically isolated, (III) postmating isolating mechanism do not exist in *Caiophora*, (IV) there are premating isolating mechanisms in Loasoideae taxa through pollinator preferences and (V) Similar isolating mechanisms are found in Chilean *Mimulus* species.

1.7. Objectives of this study

According to the hypotheses above the following questions have arisen and are discussed in this work:

1. What are the phylogenetic relationships of *Caiophora* and related genera out of the “South Andean *Loasa*” clade, and which morphological characters do they share?
2. How many species are recognized within the distribution range of Loasaceae genera and species in Argentina, Brazil, Bolivia, Chile, Paraguay and Uruguay?
3. Is experimental hybridization possible between different species of *Caiophora* and is progeny viable?

4. Are there different pollination syndromes in Loasaceae?
5. Does *Mimulus* show a similar lack of postmating isolating mechanisms as *Caiophora*?

1.8. Overview of the dissertation

This dissertation is a cumulative work of manuscripts in preparation, accepted or published. Therefore each manuscript is structured as a journal article.

Chapter 2-5 are about taxonomy and systematics in Loasaceae.

A preliminary phylogeny of the genera and lineages of Loasaceae subfam. Loasoideae is provided in Chapter 2. This investigation was conducted using the plastid trnl(UAA) intron. All genera and infrageneric entities were included in the analysis. The resulting phylogeny was used as basis for inferring hypothetical relationships within Loasoideae, with possible morphological apomorphies, mapped onto a cladogram. Geographical distribution patterns of the genera and entities are discussed.

Chapter 3 is a revision for the representatives of the genus *Caiophora* in Chile as a result of the study of herbarium specimens. In Chile five species of *Caiophora* can be recognised. One new species was described as *Caiophora deserticola* Weigend & Mark.Ackermann. *Caiophora rosulata* was subdivided in two subspecies: *C. rosulata* subsp. *rosulata* and *C. rosulata* subsp. *taraxacoides*. Several names were placed in the synonymy. A key to the species and full morphological descriptions, illustrations, distribution, floral biology and chromosome numbers are provided.

Two checklists for Loasaceae taxa were provided in chapter 4 and 5 based on revised herbarium specimens. In Chapter 4 seven genera and 67 species were recognized for Argentina, southern Brazil, Chile, Paraguay and Uruguay, 48 species of them are endemic and one species is introduced. In Chapter 5 four genera and 27 species are reported for Bolivia. Four of the species are endemic in Bolivia.

Anatomy and morphology of representatives out of the “South Andean *Loasa*” clade are analysed in Chapter 6.

Seed surface and cuttings were investigated using SEM and light microscopy. Morphology and anatomy of seeds are evaluated. Seed characters are discussed for affinities within and between lineages. Fruit shape and opening mechanisms as well as seed morphology and -weight are discussed and mapped on a cladogram.

Chapter 7-10 are about floral ecology and reproductive isolation.

In chapter 7 crossability of seven *Caiophora* species was examined in 37 different combinations. Flowers were hand-pollinated, developing fruits counted and seeds weighed. Germination rates were used to calculate the crossability index. Fruit set, seed weight and germination rates between parental species and hybrids are compared and discussed.

In chapter 8 nectar production, floral morphology and pollinator observations were investigated. Nectar amount and concentration were measured and sugar amount calculated. The obtained data were plotted in a ternary graph and compared to flower size and observed pollinators. Pollination syndromes were classified based on nectar production, flower-size and flower visitors.

In chapter 9 male fitness was tested to explain a complex reward portioning in *Nasa macrothyrsa*. Numbers of moved stamen were counted for thigmonastic and autonomous treatment per time interval. Using the same time interval nectar replenishment was measured repeatedly. Data and observed pollinator behaviour is discussed for generalized or specialized pollination syndrome.

Pollination biology of Chilean *Mimulus* species is explored in chapter 10. Nectar production per species was measured and compared with counted pollen- and ovule amounts and pollen-ovule ratio calculated as proxy for breeding system. For analyzing differences in floral display, tube length was measured as proxy for flower size and pictures were taken of UV-patterns and in visible light. Hand-pollination was carried out for intra- and interspecific crosses. Finally data were analyzed for pre- and postmating isolating mechanisms.

1.9. Literature

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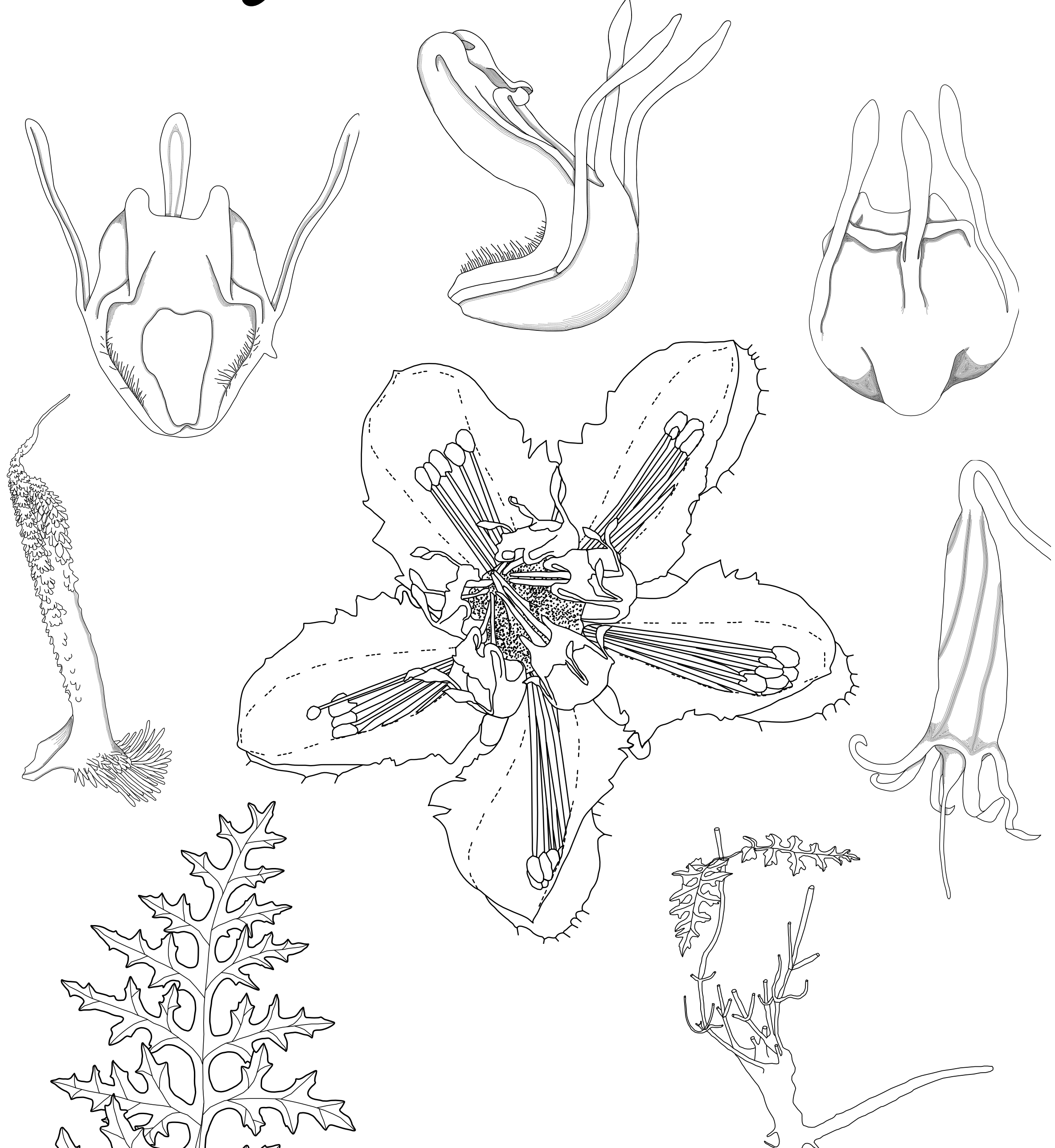

Caiophora sp. nov. (*Caiophora-pterosperma* group) from Peru

2. A preliminary phylogeny of Loasaceae subfam. Loasoideae (Angiospermae: Cornales) based on trnL(UAA) sequence data, with consequences for systematics and historical biogeography*

2.1. Abstract

The phylogeny of Loasaceae subfam. Loasoideae is investigated with sequences of the chloroplast trnL(UAA) intron, all genera and infrageneric entities are included in the analysis. Loasaceae subfam. Loasoideae is monophyletic, and the two most speciose, and monophyletic, clades (which account for approximately 90% of the species total) are *Nasa* and the so-called Southern Andean Loasas (*Blumenbachia*, *Caiophora*, *Loasa* s.str., *Scyphanthus*), but the phylogeny of the remainder is not completely resolved. The data underscore a basal position for *Chichicaste*, *Huidobria*, *Kissenia*, and Klaprothieae (*Xylopodia*, *Klaprothia*, *Plakothira*). High bootstrap support values confirm the monophyly both of Klaprothieae and *Presliophytum* (when expanded to include *Loasa* ser. *Malesherbioideae*). *Aosa* and *Blumenbachia* are not resolved as monophyletic, but have clear morphological apomorphies. Within *Nasa*, „*N.* ser. *Saccatae*“ is paraphyletic, and “*N.* ser. *Carunculatae*“ is polyphyletic. However, the *N. triphylla* group in „*N.* ser. *Saccatae*“ is a well-supported monophyletic group, as is *N.* ser. *Grandiflorae*. „*Loasa*“ in its traditional circumscription is paraphyletic, but *Loasa* s.str. (*L.* ser. *Macrospermae*, *L.* ser. *Deserticolae*, *L.* ser. *Floribundae*) is monophyletic. The remainder of „*Loasa*“ (*L.* ser. *Pinnatae*, *L.* ser. *Acaules*, *L.* ser. *Volubiles*) is probably closely allied to the essentially Patagonian-High Andean group comprising also *Scyphanthus* and *Caiophora*. These findings are congruent with morphology and phytogeography. *Nasa* seems to have undergone its primary radiation at moderate elevations (1500–2500 m) in the Andes of northern Peru (Amotape-Huancabamba Zone) and subsequently diversified into high elevations (above 4000 m) of the tropical Central Andes. South Andean Loasas appear to have undergone their primary diversification in the southern temperate and mediterranean regions of Chile and Argentina, with a subsequent northwards expansion of *Caiophora* into the high elevations of the tropical Andes. Hummingbird pollination has evolved independently from melittophily in High Andean clades of *Nasa* and *Caiophora*.

*The original publication is available at http://www.sciencedirect.com/ Published as: Weigend M, Gottschling M, Hoot S, Ackermann M. 2004. A preliminary phylogeny of Loasaceae subfam Loasoideae (Angiospermae: Cornales) based on trnL(UAA) sequence data, with consequences for systematics and historical biogeography. Organisms Diversity & Evolution 4: 73-90. doi.org/10.1016/j.ode.2003.12.001

Keywords: Loasaceae; High Andean clades; Floral morphology; Molecular systematics; *Nasa*; South Andean Loasas

2.2. Introduction

Loasaceae are medium-sized (ca. 300 spp.) and largely Neotropical plant family whose precise relationships among angiosperms have been controversially discussed. The last few years have brought enormous progress in this field, and the Loasaceae have been shown to be closely allied to Hydrangeaceae and firmly nested in Cornales (Hempel et al., 1995; Moody and Hufford, 2000). Morphological studies confirm this placement, and the similarity between some groups in Loasaceae and some groups in Hydrangeaceae (e.g. *Deutzia* Thunb., *Jamesia* Torr. & Gray, and *Philadelphus* L.) is indeed striking in varied character complexes such as seed morphology, flower morphology, indument morphology, phytochemistry, and leaf morphology (Weigend, 2004).

The subdivision of Loasaceae has also been controversially discussed (Davis and Thompson, 1967; Poston and Thompson, 1977; Weigend, 1997; Moody and Hufford, 2000). The mainly North American subfamilies Gronovioideae (*Cevallia* Lag., *Fuertesia* Urb., *Gronovia* L.), Mentzelioideae (*Eucnide* Zucch., *Mentzelia* L., *Schismocarpus* Blake), and Petalonychoideae (*Petalonyx* A.Gray) have been extensively studied, but these make up only about 1/3 of the family's species total. The subfamily that is by far the largest (over 200 spp.) and most diverse (morphologically, ecologically, and phytochemically), the Loasoideae, has been the subject of very few detailed studies, and these have usually been limited to the few commonly cultivated representatives, such as *Blumenbachia insignis* Schrad., *B. hieronymi* Urb., *Caiophora lateritia* Klotzsch, and *Nasa triphylla* (Juss.) Weigend subsp. *triphylla.*

Until recently, the only comprehensive study available was the „Monographia Loasacearum“ (Urban and Gilg, 1900) which was based nearly exclusively on herbarium material much of which was very poorly preserved. This study recognized a total of seven genera in Loasoideae (*Blumenbachia* Schrad., *Caiophora* C.Presl, *Kissenia* Endl., *Klaprothia* Kunth, *Loasa* Adans., *Sclerothrix* C.Presl, *Scyphanthus* D.Don), with „*Loasa*“ accounting for more than half of the species (83 of 153). The genera were grouped into three tribes, Kissenieae (*Kissenia*; 2 spp.), Klaprothieae (*Klaprothia*, *Sclerothrix*; 2 spp.), and Loaseae (*Blumenbachia*, *Caiophora*, „*Loasa*“, *Scyphanthus*; 149 spp.). „*Loasa*“ was circumscribed exclusively by the presence of fruits opening with apical valves, a truly plesiomorphic character also found in Mentzelioideae and outside of Loasaceae in the putative sistergroup Hydrangeaceae. Urban and Gilg (1900) wrote detailed studies on many aspects of morphology and studied Loasaceae with enormous accuracy, but in their subsequent classification they made little use of the numerous characters observed.

At species level, their decisions have been widely criticized as being too narrow (Darlington, 1934; Sleumer, 1956), and the generic concepts have also been challenged: *Sclerothrix* was reduced to synonymy under *Klaprothia* (Poston and Nowicke, 1990), and *Huidobria* Gay, which Urban and Gilg (1900) had treated as a subgenus in „*Loasa*", was re-instated at genus rank (Grau, 1997). However, because no detailed new studies are available, the treatments of Urban and Gilg (1900) have been largely followed, and only *Schismocarpus* Blake (subfam. Mentzelioideae) from southern Mexico and *Plakothira* Florence (subfam. Loasoideae, tribe Klaprothieae) from the Marquesas Islands in Polynesia have been described since the „Monographia Loasacearum".

Weigend (1997) made an attempt to arrive at a more natural classification of Loasaceae subfam. Loasoideae (Table 2.1) considering a wide range of morphological traits and character polarity. This study led to the segregation from „*Loasa*" of a total of four genera:

1. *Nasa* Weigend (short for „North Andean Loasas"; Urban and Gilg's groups *Loasa* ser. *Grandiflorae*, *L.* ser. *Saccatae*, *L.* ser. *Carunculatae*, *L.* ser. *Alatae*), for by now approx. 100 spp. mainly from the northern and central Andes;
2. *Aosa* Weigend, for the Brazilian and Hispaniolan representatives of „*Loasa*" (Urban and Gilg's groups *L.* ser. *Corymbosae*, *L.* ser. *Parviflorae*, *L.* ser. *Pusillae*);
3. *Presliophytum* (Urban and Gilg) Weigend (Urban & Gilg's *Loasa* subg. *Presliophytum*);
4. *Chichicaste* Weigend, for *Loasa grandis* Standl. (described after Urban & Gilg's studies).

Another systematic addition was the description of *Xylopodia* Weigend belonging to the Klaprothieae (discovered in northern Peru in 1997), and *Caiophora* was redefined by removing the two sections *Angulatae* and *Gripidea* to *Blumenbachia* (Weigend, 1997).

The Loaseae were informally segregated into two „grades": „Lower Loaseae", with a number of small genera characterized by relatively simple and upright flowers without thigmonastic stamens (*Chichicaste*, *Huidobria*, *Presliophytum*); and Higher Loaseae, comprising genera with more complex and usually pendulous flowers with thigmonastic stamens (*Aosa*, *Blumenbachia*, *Caiophora*, „*Loasa*", *Nasa*, *Scyphanthus*).

The Higher Loaseae divide into three clearly monophyletic assemblages: *Aosa*, *Nasa*, and a complex informally called South Andean Loasas comprising *Blumenbachia*, *Caiophora*, „*Loasa*", and *Scyphanthus*. Currently, South Andean Loasas remain largely unresolved, since they show reticulate patterns of variation in many characters and have not been studied in detail. *Caiophora* has recently been subdivided into species groups to make the large genus more manageable (Weigend and Ackermann, 2003). „*Loasa*" still contains one highly divergent entity, *L.* ser. *Malesherbioideae* (Table 2.1), which lacks the derived characters of *Loasa* s.str. and rather appears to be closely allied to *Presliophytum*. It is here treated separately (both species of *L.* ser. *Malesherbioideae* were available for analysis).

Table 2.1: Synopsis of the classification of Loasaceae subfamily Loasoideae, modified from Weigend (1997).

Loasaceae subfam. Loasoideae	Genus	Infrageneric entity	Acronym	Species total	Species studied	Distribution
Tribe Klaprothieae	*Klaprothia*	—		2	2	C & S America
	Plakothira	—		3	1	Marquesas Islands
	Xylopodia	—		1	1	N Peru
Tribe Loaseae	*Kissenia*	—		2	1	Africa
Lower Loaseae	*Chichicaste*	—		1	1	Panama & Costa Rica
	Huidobria	—		2	2	N Chile
	Presliophytum	—		3	2	Peru
	“Loasa”	ser. *Malesherbioideae*[a]	LoMa	2	2	N Chile
Tribe Loaseae	*Aosa*	ser. *Corymbosae*	AoCo	1	—	Brazil
Higher Loaseae		ser. *Pusillae*	AoPu	2	1	Brazil
		ser. *Parviflorae*	AoPa	4	2	Brazil & Hispaniola
	Nasa	ser. *Saccatae*	NaSc	29 (?)	11	Cordillera Mexico –Bolivia
		ser. *Carunculatae*	NaCa	4	2	Peru & S Ecuador
		ser. *Alatae*	NaAl	26 (?)	7	Colombia-Bolivia
		ser. *Grandiflorae*	NaGr	38 (?)	7	N Colombia to Peru
		N. venezuelensis group[b]		3	1	N Colombia & NW Venezuela
	“Loasa”	ser. *Acaules*	LoAc	1	1	Chile & Argentina (Andes)
		ser. *Deserticolae*	LoDe	2	2	N & C Chile (Costa)
		ser. *Floribundae*	LoFl	4	3	N & C Chile (Costa)
		ser. *Loasa*	LoLo	2	—	S Chile & Argentina
		ser. *Macrospermae*	LoMc	8 (?)	7	C & N Chile, Peru (Costa)
		ser. *Volubiles*	LoVo	4	2	S Chile
		ser. *Pinnatae*	LoPi	20 (?)	4	Chile & Argentina (Andes)
	Blumenbachia	sect. *Blumenbachia*	BlBl	4	2	Argentina–S Brazil
		sect. *Gripidea*	BlGr	3	1	S Brazil
		sect. *Angulatae*	BlAn	3 (4?)	3	S Chile & Argentina
	Scyphanthus		—	2	1	C Chile
	Caiophora[c]	*C. arechvaletae* group	CaAr	1	—	S Brazil–Uruguay
		C. carduiifolia group	CaCa	5	—	Peru
		C. chuquitensis group	CaCh	8	2	Peru–Argentina
		C. cirsiifolia group	CaCi	2	1	N Chile–Peru
		C. clavata group	CaCl	5	—	S Bolivia–N Argentina
		C. contorta group	CaCo	2	—	Ecuador–Peru
		C. coronata group	CaCr	2	—	Peru–Chile
		C. lateritia group	CaLa	8	1	Peru–Argentina
		C. nivalis group	CaNi	2	—	Argentina
		C. pterosperma group	CaPt	2	1	Peru
		C. rosulata group	CaRo	1	—	Peru–Argentina

? Not fully revised, numerous undescribed species.

a Here removed from *Loasa* based on molecular and morphological data.

b Not formalized, see Weigend (1997).

c Informal classification, see Weigend and Ackermann (2003).

Table 2.2: List of species and vouchers

DNA No.	Species	Classification	Collector/collection No. (herbarium)	Country of origin	GenBank Acc. No. (trnL)
1376	*Aosa rostrata* (Urb. & Gilg) Weigend	AoPu	Salino 3042 (M)	Brazil	AY285677
1289	*Aosa rupestris* (Gardner) Weigend	AoPa	Weigend 7138 (BSB, M)	Brazil	AY285678
590*	*Blumenbachia espigneira* Gay	BlAn	Weigend et al. 6816 (BRCO, BSB, M)	Argentina	AY285679
1384	*Blumenbachia exalata Weigend*	BlGr	Sehnem 3993 (B)	Argentina	AY285680
592*	*Blumenbachia insignis* Schrad.	BlBl	Weigend s.n. (M)	Argentina	AY285681
1384	*Blumenbachia latifolia* Cambess.	BlBl	Schwabe s.n. anno 1958 (B)	Argentina	AY285682
591*	*Blumenbachia prietea* Gay	BlAn	Weigend et al. 6823 (BRCO, BSB, M)	Argentina	AY285683
1385	*Blumenbachia sylvestris* Poeppig	BlAn	Weigend et al. 6807 (BRCO, BSB, M)	Argentina	AY285684
1342	*Caiophora andina* Urb. & Gilg	CaCh	Ackermann 360 (BSB, HUSA, M, USM)	Peru	AY285685
1341	*Caiophora chuquitensis* (Meyen) Urb. & Gilg	CaCh	M. & K. Weigend 2000/70 (M, NY, USM)	Peru	AY285686
1345	*Caiophora cirsiifolia* C.Presl	CaCi	Weigend et al. 5022 (BSB, HUT, M. USM)	Peru	AY285687
1357	*Caiophora madrequisa* (Killip)	CaLa	M. & K. Weigend 2000/191 (M, NY, USM)	Peru	AY285688
1356	*Caiophora* cf. *pterosperma* (Ruiz & Pav. ex G.Don) Urb. & Gilg	CaPt	Weigend et al. 5188 (BSB, HUT, M, USM)	Peru	AY285689
1293	*Deutzia discolor* Hemsley	Hydrangeaceae	Weigend 5615 (B 045-13-87-10/274, BSB)	China	AY285690
1292	*Deutzia rubens* Rehder	Hydrangeaceae	Weigend 5613 (B 103-26-74-80/1, BSB)	China	AY285691
1325	*Huidobria chilensis* Gay	Lower Loaseae	Ackermann 482 (BSB, CONC, M, SGO)	Chile	AY285692
1327	*Huidobria fruticosa* Phil.	Lower Loaseae	Dillon 8034 (F, M)	Chile	AY285693
1364	*Kissenia capensis* Endl.	Lower Loaseae	Greuter 2167 (B)	South Africa	AY285694
1348	*Klaprothia fasciculata* (C.Presl) Poston	Klaprothieae	Weigend et al. 5362 (BSB, HUT, M, USM)	Peru	AY285695
1349	*Klaprothia mentzelioides* Kunth	Klaprothieae	Henning & Schneider 276 (BSB, HUT, M, USM)	Peru	AY285696
1340	*Loasa acerifolia* Domb.	LoMc	Weigend et al. 6848 (BRCO, BSB, M, NY)	Chile	AY285697
1355	*Loasa asterias* Dusen	LoPi	Weigend et al. 6984 (BRCO, BSB, M, NY)	Argentina	AY285698
596*	*Loasa bergii Poepp.*	LoPi	Weigend et al. 6846 (BRCO, BSB, M, NY)	Argentina	AY285699
1354	*Loasa filicifolia* Poeppig	LoPi	Weigend et al. 6880 (BRCO, BSB, M, NY)	Argentina	AY285700
598*	*Loasa gayana* Urb. & Gilg	LoVo	Weigend et al. 7057 (BSB, M)	Chile	AY285701
1323	*Loasa heterophylla* Hook. & Arn.	LoMc	Weigend et al. 5920 (BSB, HUT, M, USM)	Chile	AY285702

1350	*Loasa lateritia* Gill.	LoAc	Werdermann 1342 (M)	Chile	AY285703
1367	*Loasa longiseta* Phil.	Lower Loaseae	Ehrhardt s.n. (M)	Chile	AY285704
1328	*Loasa malesherbioides* Phil.	Lower Loaseae	Wagenknecht 18509 (M)	Chile	AY285705
597*	*Loasa nana* Phil.	LoPi	Weigend et al. 7080 (BRCO, BSB, M, NY)	Argentina	AY285706
1339	*Loasa nitida* Desr.	LoMc	Weigend et al. 7346 (BSB, HUT, M, USM)	Peru	AY285707
1285	*Mentzelia albescens* Griseb.	Mentzeliodieae	Weigend et al. 6865 (BRCO, BSB, M, NY)	Argentina	AY285708
1286	*Mentzelia scabra* Kunth	Mentzelioideae	Weigend et al. 98/470 (F, HUT, M, USM)	Peru	AY285709
1375	*Nasa aeqatoriana* (Urb. & Gilg) Weigend	NaSc	Weigend & Jaramillo 3937 (M, QCNE)	Ecuador	AY285710
1236	*Nasa carunculata* (Urb. & Gilg) Weigend	NaCa	Weigend & Weigend 2000/363 (HUT, M, NY, USM)	Peru	AY285711
1335	*Nasa cymbopetala* (Urb. & Gilg) Weigend	NaGr	Weigend et al. 7458 (BSB, HUT, M, USM)	Peru	AY285712
1238	*Nasa driesslei* Weigend	NaAl	Henning & Schneider 243 (BSB, HUT, M, USM)	Peru	AY285713
1242	*Nasa ferruginea* (Urb. & Gilg) Weigend	NaSc	M. & K. Weigend 2000/199 (HUT, M, NY, USM)	Peru	AY285714
1351	*Nasa herzogii* (Urb. & Gilg) Weigend	NaAl	Müller 6596 (LPB)	Bolivia	AY285715
1378	*Nasa hornii* (Weigend) Weigend	NaGr	Weigend & Horn 3815 (M, QCNE)	Ecuador	AY285716
1365	*Nasa humboldtiana* (Urb. & Gilg) Weigend subsp. *obliqua* Dostert & Weigend	NaSc	Dostert 98/154 (F, HUT, MSB, USM)	Peru	AY285717
1374	*Nasa insignis* Weigend	NaGr	Dostert 98/161 (F, HUT, M, USM)	Peru	AY285718
1377	*Nasa jungiaefolia* (Weigend) Weigend	NaGr	Weigend & Horn 3838 (QCNE, M)	Ecuador	AY285719
1232	*Nasa laxa* (Killip) Weigend	NaSc	Weigend et al. 98/547 (F, HUT, M, USM)	Peru	AY285720
1239	*Nasa lenta* (Urb. & Gilg) Weigend	NaAl	Weigend et al. 5446 (BSB, HUT, M, USM)	Peru	AY285721
1240	*Nasa loxensis* (Kunth) Weigend	NaAl	Grant & Struwe 4063 (BSB)	Ecuador	AY285722
1330	*Nasa macrantha* (Urb. & Gilg) Weigend	NaGr	Weigend et al. 2000/816 (HUT, M, NY, USM)	Peru	AY285723
1329	*Nasa macrothyrsa* (Urb. & Gilg) Weigend	NaCa	Weigend et al. 97/s.n. (M, USM)	Peru	AY285724
1333	*Nasa magnifica* (Urb. & Gilg) Weigend	NaGr	Weigend et al. 97/468 (F, M, USM)	Peru	AY285725
1243	*Nasa poissoniana* (Urb. & Gilg) Weigend	NaSc	M. & K. Weigend 2000/208 (HUT, M, NY, USM)	Peru	AY285726
1237	*Nasa pteridophylla* Weigend subsp. *pteridophylla*	NaSc	Weigend et al. 97/307 (F, M, HUT, USM)	Peru	AY285727
1244	*Nasa raimondii* (Standley & Barkley) Weigend	NaSc	M. & K. Weigend 2000/167 (M, NY, USM)	Peru	AY285728
1353	*Nasa ramirezii* (Weigend) Weigend	NaSc	Weigend 3523C (COL, M)	Colombia	AY285729
1373	*Nasa rubrastra* (Weigend) Weigend	NaAl	Schwerdtfeger 22207 (M)	Ecuador	AY285730

1235	*Nasa solata* (Killip) Weigend	NaAl	Weigend & Dostert 98/259 (M, USM)	Peru	AY285731
1380	*Nasa trianae* (Urb. & Gilg) Weigend	NaAl	Weigend 3610 (COL, M)	Colombia	AY285732
–	*Nasa triphylla* (Juss.) Weigend subsp. *triphylla* (= *Loasa triphylla* Juss.)	NaSc	Erixon & Bremer 42 (UPS)	Ecuador	AJ430868
1246	*Nasa urens* (Jacq.) Weigend	NaSc	Weigend & Förther 97/542 (F, M, USM)	Peru	AY285733
1231	*Nasa vargasii* (J.F.Macbr.) Weigend	NaSc	M. & K. Weigend 2000/289 (HUSA, M, NY, USM)	Peru	AY285734
1366	*Nasa venezuelensis* (Steyerm.) Weigend	NaVe	Weigend 3604 (COL, M)	Venezuela	AY285735
1337	*Nasa weberbaueri* (Urb. & Gilg) Weigend	NaGr	Weigend & Dostert 98/261 (F, HUT, M, USM)	Peru	AY285736
1291	*Philadelphus pekinensis* Ruprecht	Hydrangeaceae	Weigend 5614 (B 270-16-96-10, BSB)	China	AY285737
1290	*Plakothira parviflora* Florence	Klaprothieae	Weigend s.n. (BSB, M, NTBG 970008)	Marquesas Islands	AY285738
1288	*Presliophytum arequipense* Weigend	Lower Loaseae	Weigend & Förther 97/848 (F, M, USM)	Peru	AY285739
1369	*Presliophytum heucheraefolium* Killip	Lower Loaseae	Weigend 7368 (BSB, HUT, M, USM)	Peru	AY285740
600*	*Scyphanthus elegans* D.Don	–	Grau & Ehrhart 2-093 (M)	Chile	AY285741
1287	*Xylopodia klaprothioides* Weigend	Klaptrothieae	Weigend et al. 97/450 (F, M, USM)	Peru	AY285742

DNA numbers follow an internal numbering code of the Institut für Biologie, Systematische Botanik und Pflanzengeographie, Freie Universität Berlin. Abbreviations for infrageneric taxa see Table 2.1. *Nasa triphylla* subsp. *triphylla* sequence from Bremer et al. (2002, as *Loasa triphylla* Juss.).

Some molecular data have already been published (matK: Moody and Hufford, 2000; matK and trnL-trnF: Hufford et al., 2003). While the principal results of these studies are largely congruent with the re-classification provided by Weigend (1997), we here aim at providing a more complete understanding of subfamily Loasoideae and especially its largest groups (*Nasa*, South Andean Loasas). The present study, using sequences from the chloroplast trnL(UAA) intron, addresses three primary aims: Firstly, molecular delimitation of the generic entities recognized in Weigend (1997), and relationships among them; secondly, identification of the lineages within the poorly understood South Andean Loasas; thirdly, recognition of infrageneric groupings in „*Loasa*“ and *Nasa*.

2.3. Material and methods

The plant material used in this study largely came from our own field collections over the past 10 years. Species were identified on the basis of all available literature, and are vouchered in herbaria as indicated in Table 2.2. A few taxa were only available from herbarium collections, samples of these were taken from specimens in the herbaria B, LPB, M, and MO.

A total of 77 species assigned to Loasaceae have been investigated (Table 2.2). Furthermore, 3 sequences from *Deutzia* and *Philadelphus* (Hydrangeaceae) were used for the user-specified outgroup comparison, they were treated as monophyletic in the molecular analysis. Only a small sample of species of *Caiophora* was included, since these showed minimal sequence divergence, and no internal resolution could be obtained with the marker chosen.

DNA extraction, PCR, purification and sequencing followed standard protocols, which are described in detail in Gottschling and Hilger (2001). Primers used for amplification and sequencing of the trnL(UAA) intron were those of Taberlet et al. (1991). The sequences were manually aligned using Se-Al v2.0a72 (Rambaut, 2001). The complete data matrix is available in NEXUS format on request.

Phylogenetic calculations were run on a Macintosh computer with the help of PAUP* 4.0b1 (Swofford, 1998). Parsimony trees were generated using heuristic searches, with gaps considered as informative based on the frequent occurrence of deletions and insertions in the trnL intron. The poly A region in the R-loop of the trnL secondary structure (Kuhsel et al., 1990) was excluded since it follows no phylogenetic pattern in Loasaceae. A bootstrap analysis (criterion = parsimony, BS) was estimated based on 350 replicates (addseq = random, nreps = 10, MaxTrees = 1000). A PUZZLE analysis (criterion = likelihood, P) was performed with 1000 quartet puzzling steps. Likelihood settings from the best-fit model were determined using the AIC criterion in Modeltest 3.06 (Posada and Crandall, 1998) (Fig. 2.1).

The trnL phylogeny is used as the basis for a hypothetical phylogeny of Loasoideae with possible morphological apomorphies mapped onto a cladogram (Fig. 2.7). The corresponding morphological characters are illustrated in Figs. 2.2–2.6.

2.4. Results

The aligned trnL data set was 536 bp in length. Of these sites, 113 (22%) were parsimony-informative (1.5 per taxon). The heuristic search found 13,284 most parsimonious trees, for which a strict consensus tree was computed (Fig. 2.1; L = 293; CI = 0.78, RI = 0.91). In the tree, bootstrap support values (BS; criterion = parsimony) and PUZZLE support values (P; criterion

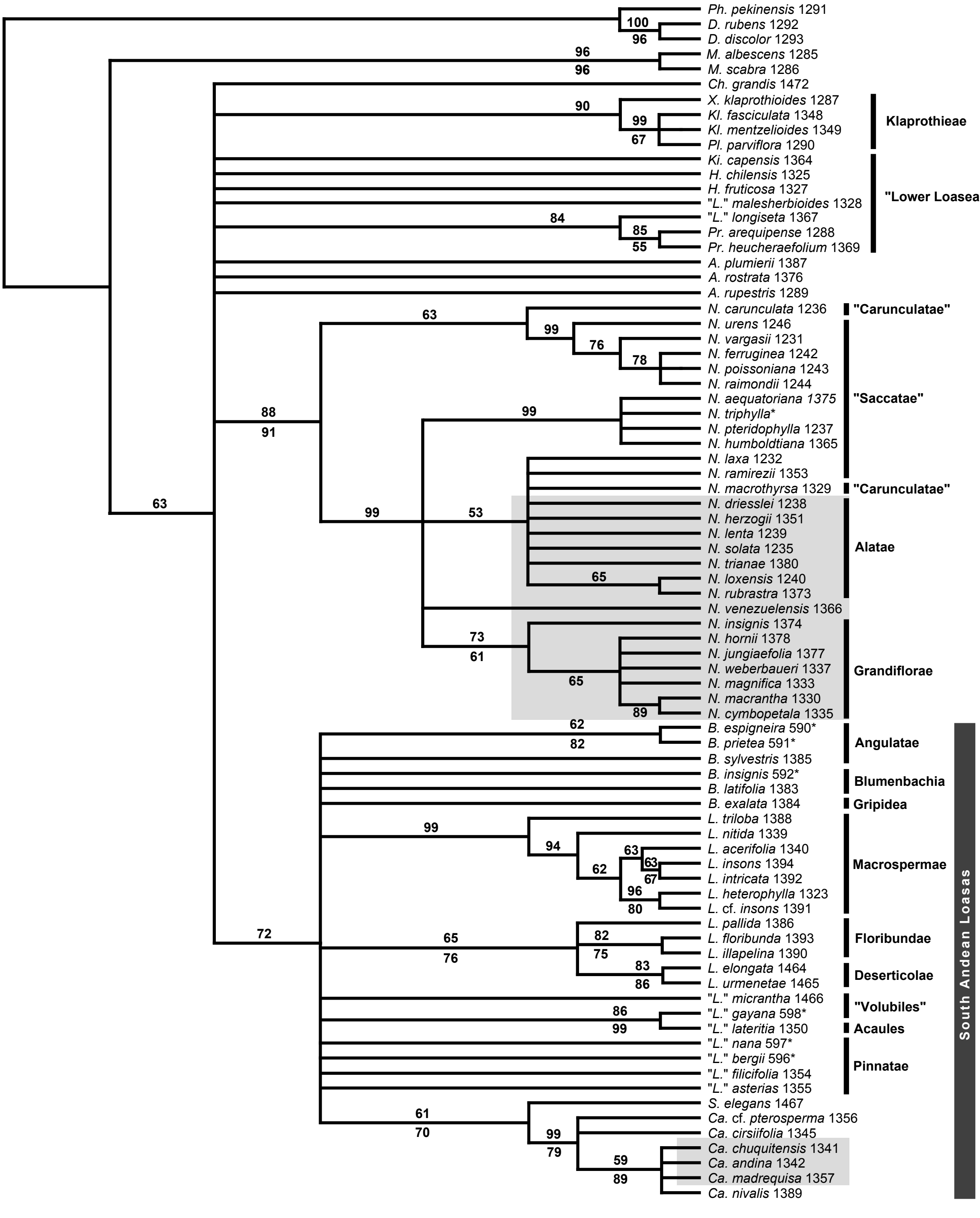

Fig. 2.1: Strict consensus tree of 13,284 most parsimonious trees (L = 293; CI = 0.78, RI = 0.91) of Loasoideae (with Mentzelioideae and Hydrangeaceae as outgroups), with bootstrap support values (above branches) and PUZZLE support values (below branches). Areas shaded in grey indicate the ornithophilous taxa (all other taxa in Loasoideae are melittophilous and/or autogamous).

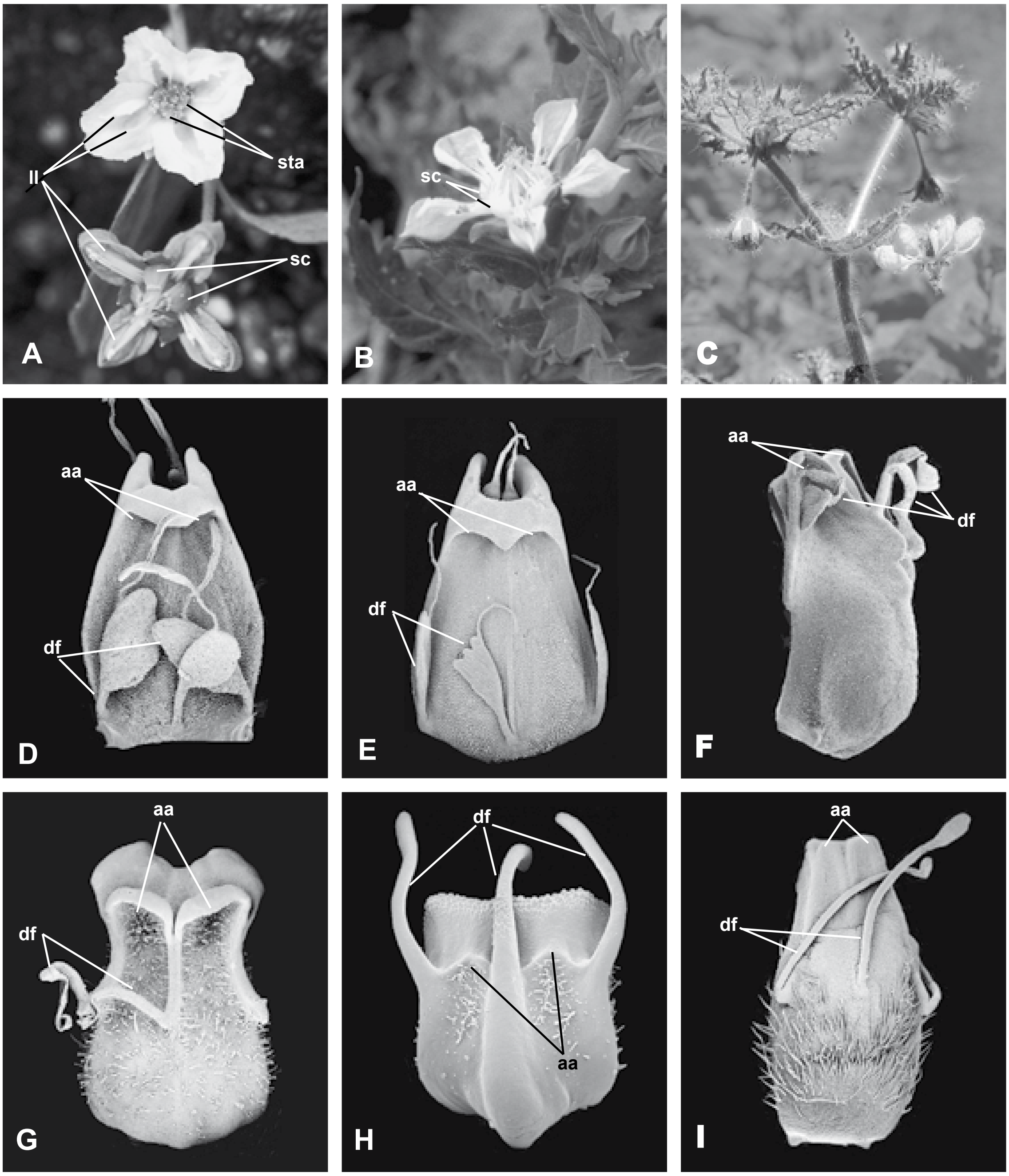

Fig. 2.2: Morphological characters in Loasoideae. (A) Flowers of *Xylopodia klaprothioides* (Weigend et al. 97/450C) and *Plakothira parviflora* (Weigend s.n.); note the apically free staminodes (sta) in *Plakothira* and the distinct floral scales (sc) in *Xylopodia*. Both species have longitudinal lamellae (ll) on their petals. (B) Erect flower of *Presliophytum incanum* (Weigend et al. 2000/695). (C) Pendulous flower of *Loasa insons* (LoMc, Weigend et al. 5913). (D) Floral scale of *Loasa acerifolia* (LoMc, Weigend et al. 6848) with double arch (aa) and flag-shaped dorsal filaments (df). (E) Floral scale of *Loasa nitida* (LoMc, Weigend et al. s.n.) with double arch (aa) and flag-shaped dorsal filaments (df). (F) Floral scale of ‘‘*Loasa*’’ *filicifolia* (LoPi, Weigend et al. 5880) with double arch (aa) and distally widened dorsal filaments (df). (G) Floral scale of *Caiophora pterosperma* (CaPt, Weigend & Dostert, 97/27) with double arch (aa) and distally widened dorsal filaments (df). (H) Young floral scale of *Caiophora canarinoides* (CaLa, Ackermann 402) with double arch (aa) and distally widened dorsal filaments (df). (I) Floral scale of ‘‘*Loasa*’’ *gayana* (LoVo, Weigend et al. 7057) with double arch (aa) and distally widened dorsal filaments (df).

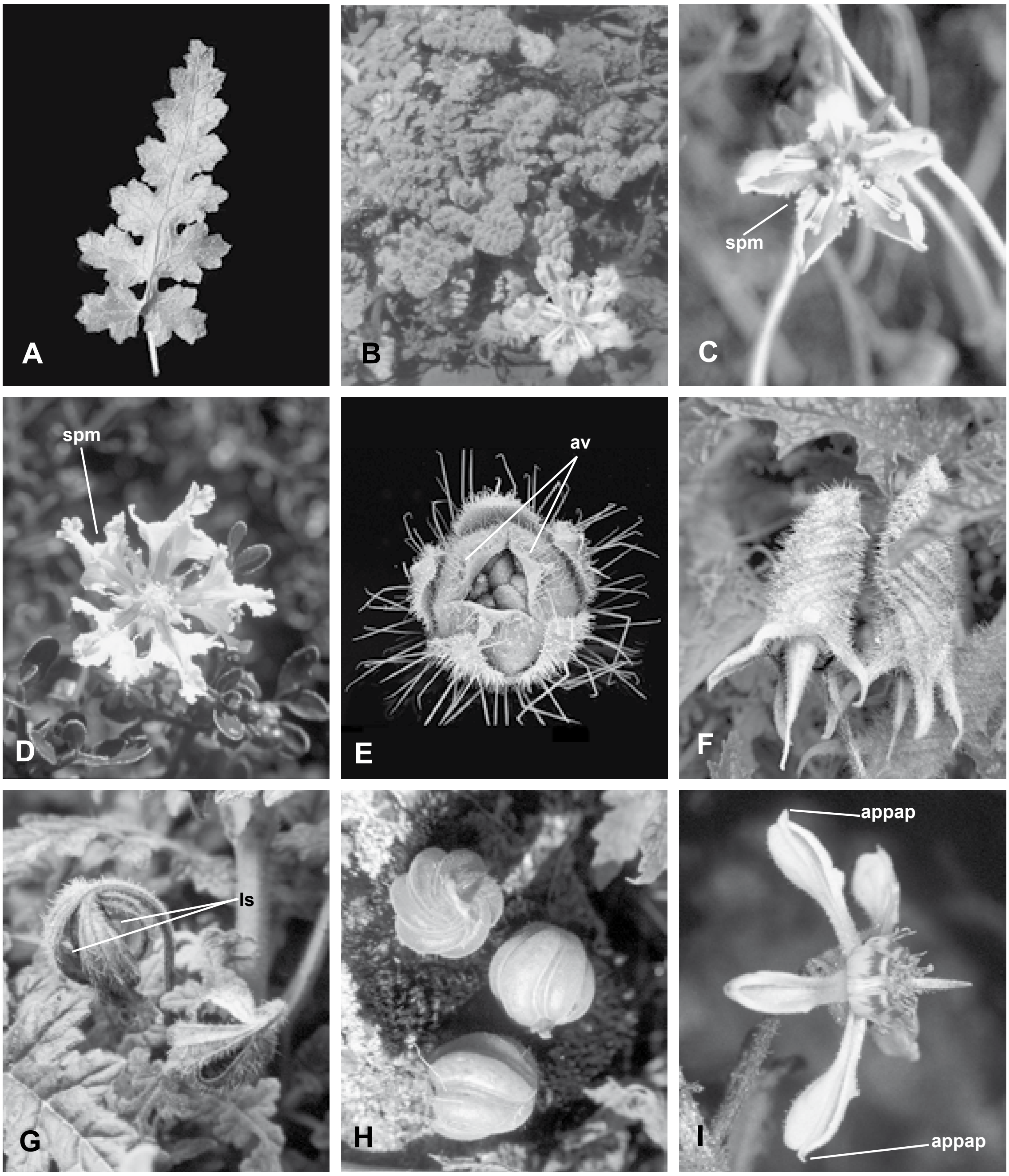

Fig. 2.3: Morphological characters in Loasoideae. (A) Shortly petiolate, deeply pinnatifid leaf of *Caiophora cirsiifolia* (CaCi, Weigend & Dostert, 97/194). (B) Shortly petiolate, deeply pinnatifid leaves of *Loasa nana* (LoPi, Weigend et al. 7080). (C) Serrate petal margin (spm) in the bee-pollinated flower of *Caiophora pterosperma* (CaPt, Weigend & Dostert, 97/27). (D) Serrate petal margin (spm) in "*Loasa*" *filicifolia* (LoPi, Weigend et al. 5880). (E) Capsule dehiscence with apical valves (av) in *Aosa rupestris* (Weigend, 7138). (F) Capsules twisted antidromously in *Caiophora carduifolia* (CaCa, Weigend et al. 5470). (G) Longitudinal dehiscence in capsules of *Caiophora scarlatina* (CaCh, M. & K. Weigend, 2000/108). (H) Capsules twisted anticlockwise in *Blumenbachia hieronymi* (BlBl, Weigend s.n.). (I) Hood-shaped, abruptly apiculate petals (appapp) in *Blumenbachia catarinensis* (BlBl, Foto C. Schlindwein).

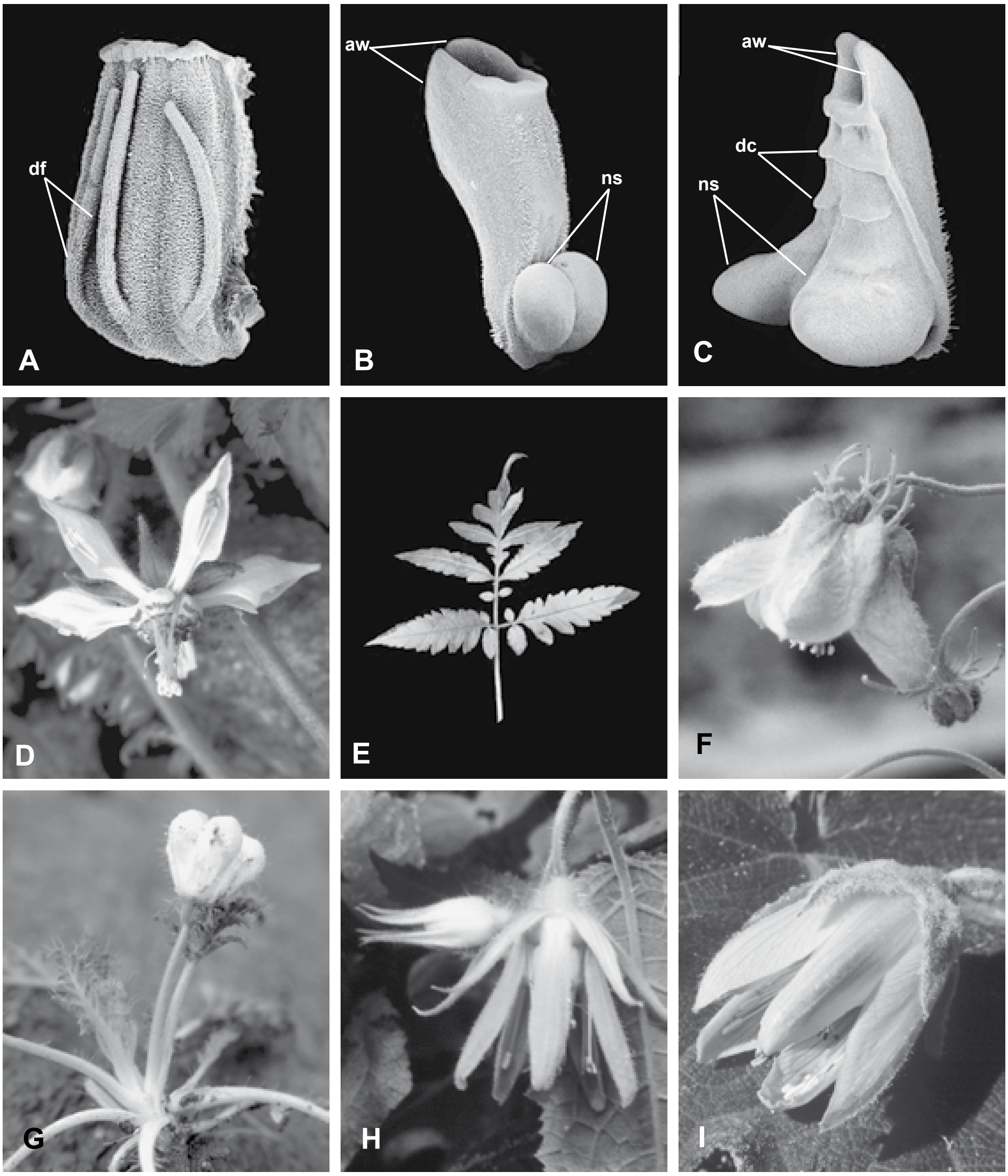

Fig. 2.4: Morphological characters in Loasoideae. (A) Floral scale of *Blumenbachia hieronymi* (BlBl, Weigend, s.n.) with basally inserted dorsal filaments (df). (B) Floral scale of *Nasa lenta* (NaAl, Weigend et al. 5446) with nectar sacs (ns) and apical wings (aw), dorsal filaments absent. (C) Floral scale of *Nasa urens* (NaSc, Weigend & Skrabal, 5889) with nectar sacs (ns), apical wings (aw), and dorsal calli (dc), dorsal filaments absent. (D) Pendulous flower of bee-pollinated *Nasa carunculata* (NaCa, Weigend et al. 5035). (E) Pinnate leaf of *Nasa aequatoriana* (*N. triphylla* group, NaSc, Weigend 3997). (F) Campanulate, hummingbird-pollinated flower of *Caiophora buraeavii* (CaLa, Kraus s.n., cultivated at Munich). (G) Campanulate, hummingbird-pollinated flower of *Caiophora rosulata* (CaCh, M. & K. Weigend, 2000/23). (H) Star-shaped, hummingbird-pollinated flower of *Nasa trianae* (NaAl, Weigend, 3610). (I) Campanulate, hummingbird-pollinated flower of *Nasa weberbaueri* (NaGr, Weigend & Dostert, 98/261).

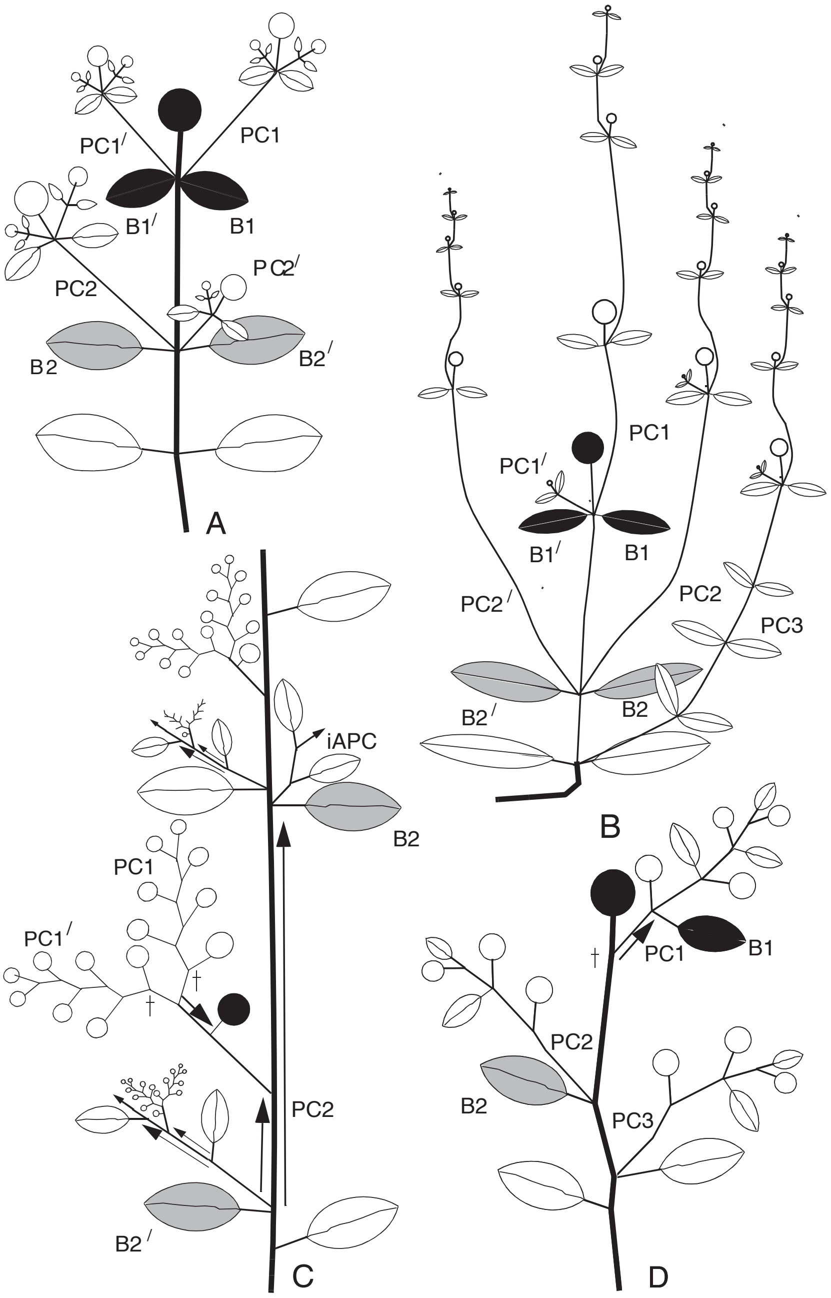

Fig. 2.5: Inflorescence architecture of Loasoideae (bracts and primary flower in distal dichasium black, next-lower bracts or pair of bracts grey; free arrows indicate metatopia). (A–B) Typical frondose inflorescences of *Loasa* s.str., *Caiophora* and *Scyphanthus* with non-recaulescent bracts (B, B/) and asymmetrically dichasial (A) to monochasial (B) paraclades. (C) Inflorescence of *Aosa* (*A. plumerii*, AoPa), both the ebracteose (w) distal dichasium and one bract (B2) are metatopically displaced onto paraclade 2 (PC2), distal paraclades strictly monochasial. (D) Frondose inflorescence of *Nasa* (*N. picta*, NaSc), one distal paraclade absent (w), the other strictly monochasial with one metatopic bract per flower.

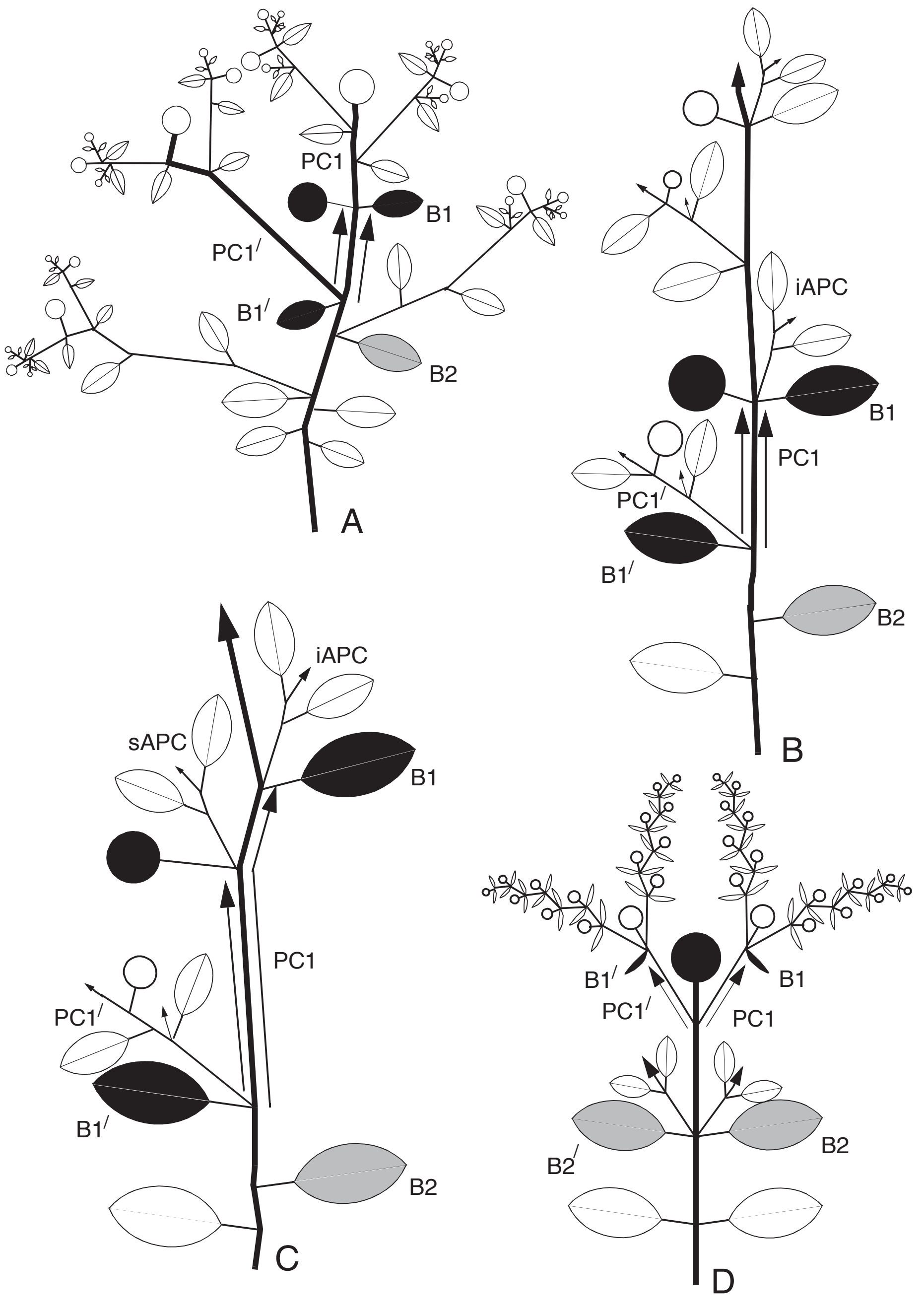

Fig. 2.6: Inflorescence architecture of Loasoideae (bracts and primary flower in distal dichasium black, next-lower bracts or pair of bracts grey; free arrows indicate metatopia). (A) Inflorescence of “*Loasa*” ser. *Malesherbioideae* (“*L.*” *longiseta*, LoMa), primary flower and one bract (B1) metatopic on one primary paraclade (PC1), PC1 moved into one line with primary axis. (B) Inflorescence of *Huidobria* (*H. chilensis*), as 6A, but with inferior accessory paraclades (iAPC). (C) Inflorescence of *Presliophytum* (*P. incanum*), as 6B, but with inferior and superior accessory paraclades (iAPC, sAPC). (D) Bracteose inflorescence of *Klaprothia mentzelioides*, distal paraclades once dichasial, second-order paraclades strictly monochasial, all bracts metatopic with their axillary products (if present).

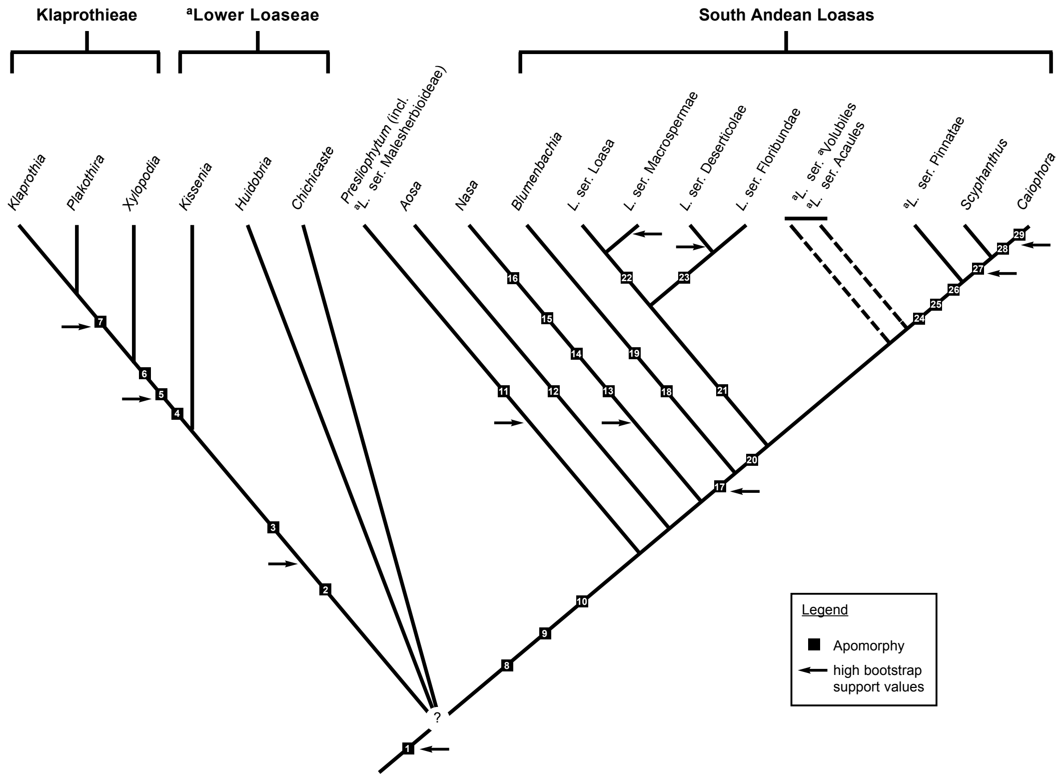

Fig. 2.7: Annotated cladogram of Loasoideae (for symbols see legend). (1) Staminodes united into antesepalous complexes (vs. absent or free). (2) Fruit wall strongly lignified (vs. not or weakly sclerified). (3) Inflorescences bracteose (vs. frondose or ebracteose). (4) Petals with longitudinal lamellae (Fig. 2.2A; vs. longitudinal lamellae absent). (5) Flowers tetramerous (Fig. 2.2A; vs. pentamerous). (6) Leaves opposite throughout (vs. alternate above). (7) Staminodes of floral scale free in distal part, apically lobed (vs. united to top, and entire). (8) Floral scales always of 3 united staminodes (vs. number variable or greater than 3). (9) Stamens thigmonastic (vs. with autonomous movement). (10) Flower scales strongly contrasting in colour (vs. white, yellow or greenish and more or less the same colour as petals). (11) Inflorescence with pronounced con- and recaulescence (Fig. 2.6; vs. metatopia absent or leading to different structure). (12) Inflorescences ebracteose (vs. bracteose or frondose). (13) Nectar scales with dorsal sacs (Fig. 2.4B and C; vs. sacs absent). (14) Nectar scales with well-developed apical wings (Fig. 2.4B and C; vs. wings absent or very short). (15) Each flower on paraclades with individual bract (Fig. 2.5D; vs. ebracteose or with 2 bracts). (16) 2n = 28 (vs. 2n = 12; 24, 26). (17) Metatopia in the inflorescence absent (or marginal recaulescence of bracts — Fig. 2.5A, B; vs. recaulescence with bracts moved to next flower). (18) Fruits twisted anticlockwise and with longitudinal dehiscence (Fig. 2.3H; vs. straight or twisted antidromously). (19) Petals apiculate (Fig. 2.3I; vs. petals acuminate). (20) Nectar scales with double arch on back (Figs. 2.2D and I; vs. double arch absent). (21) Complex hetero-oligomeric iridoids present (tricoloriside type, Weigend et al., 2000; vs. absent). (22) Dorsal filaments flag-shaped (Figs. 2.2D and E; vs. filiform or dorsoventrally flattened). (23) Thyrsoids basitonic, with alternate paraclades (vs. acrotonic and/or with opposite paraclades). (24) Leaves pinnatifid (to pinnate, bipinnate or bipinnatisect—Figs. 2.3A and B). (25) Leaves shortly petiolate (petiole less than 1/2 as long as lamina—Figs. 2.3A and B; vs. petiole equal to or longer than lamina). (26) Petal margins serrate (Figs. 2.3C and D; vs. margin entire). (27) Fruits with longitudinal sutures (Fig. 2.3G; vs. capsule opening with apical valves only). (28) 10-hydroxy-oleoside dimethyl ester present (vs. absent, Weigend et al., 2000). (29) Reduction of chromosome number (2n = 14; 16 vs. 2n = 24; 26).

= likelihood, calculated with the best-fit model: GTR+G model) are indicated.

Within the monophyletic Loasaceae subfam. Loasoideae (63 BS), the analysis of trnL sequences results in a basal polytomy involving eight unresolved single species, two minor clades (Klaprothieae, 90 BS; and *Presliophytum* including „*Loasa*“ *longiseta* from *L.* ser. *Malesherbioideae*, 84 BS), and two major and species rich clades (South Andean Loasas, 72 BS, comprising *Blumenbachia*, *Scyphanthus*, *Caiophora*, and the majority of „*Loasa*“; and *Nasa*, 88 BS, 91 P).

Within Klaprothieae, *Xylopodia* is sister to a clade comprising *Klaprothia* and *Plakothira* (monophyletic: 99 BS, 67 P), and PUZZLE analysis further indicates that *Klaprothia* may be paraphyletic with respect to *Plakothira* (*K. mentzelioides* as sister to *K. fasciculata* and *Plakothira parviflora*: 62 P). The two species of *Presliophytum* are retrieved as sister taxa (85 BS, 55 P) and appear to be closely allied to „*Loasa*“ *longiseta* (84 BS) as well as to „*L.*“ *malesherbioides* as a second species of *L.* ser. *Malesherbioideae*. The latter relationship receives support from the PUZZLE analysis (54 P).

The species remaining unresolved in the basal polytomy represent *Huidobria*, *Chichicaste*, and *Kissenia* from the „Lower Loasoideae“, and *Aosa* from the Higher Loaseae. Neither *Aosa* (3 of 7 species sampled) nor *Huidobria* (2 of 2) are retrieved as monophyletic, but their distinctness from „*Loasa*“ is evident. The same is true for monotypical *Chichicaste*.

Nasa is well supported (88 BS, 91 P) and falls into two clades comprising: (1) *N. carunculata* (Urb. & Gilg) Weigend (*N.* ser. „*Carunculatae*“) and some species of *N.* ser. „*Saccatae*“ (moderately supported: 63 BS); (2) the remainder of *N.* ser. „*Carunculatae*“ and *N.* ser. „*Saccatae*“, all of *N.* ser. *Grandiflorae* and *N.* ser. *Alatae*, and the *N. venezuelensis* group (99 BS). Within the second group, four more or less well-supported groups can be distinguished, of which the precise relationships are unresolved: (2a) *N. venezuelensis* (Steyerm.) Weigend, the only species of the *N. venezuelensis* group analyzed; (2b) the *N. triphylla* group (99 BS); (2c) *N.* ser. *Alatae* and a part of *N.* ser. „*Saccatae*“ (only low bootstrap support: 53 BS); (2d) *N.* ser. *Grandiflorae* (73 BS, 61 P).

The South Andean Loasas clade contains *Blumenbachia*, „*Loasa*“ (excl. ser. *Malesherbioideae*), *Scyphanthus*, and *Caiophora*. *Blumenbachia* is weakly supported as monophyletic in the PUZZLE analysis (50 P), but not in the bootstrap analysis, except for two of the taxa in *Blumenbachia* sect. *Angulatae* (63 BS, 84 P). In the parsimony tree, all species of „*Loasa*“ ser. *Pinnatae* („*L.*“ *bergii*, „*L.*“ *filicifolia*, „*L.*“ *nana*, „*L.*“ *asterias*) and one species of „*L.*“ ser. „*Volubiles*“ („*L.*“ *micrantha*) are found as a basal polytomy, with „*L.*“ *gayana* („*L.*“ ser. „*Volubiles*“) and“ *L.*“ *lateritia* („*L.*“ ser. *Acaules*) retrieved as sister taxa (86 BS, 99 P). However, all taxa sampled of „*L.*“ ser. *Pinnatae*, „*L.*“ ser. *Acaules*, „*L.*“ ser. „*Volubiles*“, *Scyphanthus*, and *Caiophora* constitute a monophyletic group in the PUZZLE analysis (67 P). *Scyphanthus* and *Caiophora* are invariably retrieved as sister taxa (61 BS, 70 P). There was little sequence variation in *Caiophora*. *Loasa* ser. *Macrospermae*, which was broadly sampled, is retrieved as a well-supported monophyletic group (99 BS), and the two closely allied series *Floribundae* (*L. illapelina, L. floribunda*, *L. pallida*; 53 P) and *Deserticolae* (*L. urmenetae*, *L. elongata*; 83 BS, 86 P) are identified as another monophylum (65 BS, 76 P).

2.5. Discussion

Systematics and plausibility of the molecular analyses

The trnL data confirm the conclusions of Weigend (1997) in showing the polyphyly of „*Loasa*“ sensu Urban and Gilg (1900) and in confirming the monophyly of the segregate genera *Nasa* and *Presliophytum*, of the re-defined genus *Caiophora* with the exclusion of two sections of *Blumenbachia* (*B.* sect. *Angulatae*, *B.* sect. *Gripidea*), and of tribe Klaprothieae. „*Loasa*“ remains paraphyletic (also indicated in Weigend, 1997), even after the exclusion of „*L.*“ ser. *Malesherbioideae*. These results are congruent with the data of Hufford et al. (2003), which also underscore the naturalness of *Caiophora*, *Presliophytum*, and *Nasa*, and the justification for the segregation of *Huidobria* and *Aosa* from „*Loasa*“. While the recent morphological classification of Weigend (1997) is thus largely vindicated, the infrageneric groups (i.e., sections and series) of the much older Urban and Gilg (1900) classification are also largely retrieved in *Loasa* s.str. (*L.* ser. *Deserticolae*, *L.* ser. *Macrospermae*, *L.* ser. *Floribundae*).

Klaprothieae (with *Xylopodia* as sister to *Klaprothia* and *Plakothira*) is identified as monophyletic by apomorphic characters such as longitudinal lamellae on the petals, tetramerous flowers (Figs. 2.2A and 2.7: characters 4, 5, 6), and strictly opposite, usually entire leaves (Fig. 2.7: character 7). The position of *Xylopodia* is crucial to understanding the evolution of Loasoideae flowers: It has antesepalous staminodes united into nectar scales, whereas the other Klaprothieae have distally free staminodes (Fig. 2.2A). Since all other Loasoideae have floral scales (and in all other subfamilies of Loasaceae staminodes are either free or absent) an apomorphic reversion, and not a retained ancestral character, is most parsimonious for *Klaprothia* and *Plakothira* in this respect. Hufford et al. (2003) retrieve the African genus *Kissenia* as sistergroup to Klaprothieae (not resolved in our analysis), which renders further support for this hypothesis, since *Kissenia* also has staminodes united into a distinct nectar scale. The close relationship between Neotropical *Klaprothia*, including *K.* (*Sclerothrix*) *fasciculata* (C.Presl) Poston as suggested by Poston and Nowicke (1990), and the Marquesas Islands endemic *Plakothira* is reflected in the phylogeny, and *Plakothira* may indeed have arisen from epizoochorous ancestors (*Klaprothia mentzelioides* has tardily dehiscent, burr-like capsules), with subsequent modifications due to the island environment (loss of dispersal mechanism, island woodiness). Although its position remains unresolved in the present analysis, *Kissenia* probably is the sistergroup of Klaprothieae (Hufford et al., 2003), since morphological characters such as strongly lignified fruits and bracteose inflorescences (Fig. 2.6D) can be regarded as synapomorphic (Fig. 2.7: characters 2 and 3).

Another aspect that is entirely congruent between the data presented here and those published by Hufford et al. (2003) is that the two species of *Huidobria* are not retrieved as monophyletic. They are essentially held together by the fact that the number of staminodes in the antesepalous groups is not fixed, but the same is true for Klaprothieae (whereas all other Loaseae have the apomorphic, fixed number of three staminodes; Fig. 2.7: character 8), indicating the plesiomorphic condition of this character state. Furthermore, both *Huidobria* species have a peculiar inflorescence morphology (Fig. 2.6D) which is, however, very similar to that found in *Presliophytum*. Grau (1997) discusses the profound differences between the two species of *Huidobria* regarding seed, leaf, and flower morphology. On balance, the available data suggest that the two species may indeed represent two only distantly related lineages.

The term „Lower Loaseae“ was informally introduced for *Chichicaste*, *Huidobria*, *Kissenia*, *Presliophytum* and “*Loasa*“ ser. *Malesherbioideae* (without indication of any close relationship), as a working concept to name the taxa lacking both thigmonastic stamens and colored floral scales (Weigend, 1997). However, green-house experiments by the present authors have recently shown that *Presliophytum* (*P. heucheraefolium*, *P. incanum*) does indeed show thigmonastic stamens, and at least one species (*L. malesherbioides*) has colored nectar scales. By definition, *Presliophytum* and ser. *Malesherbioideae* would thus have to be placed into Higher Loaseae, although molecular resolution is satisfactory neither in this analysis nor in Hufford et al. (2003). An expansion of *Presliophytum* s.l. to include „*L.*“ ser. *Malesherbioideae*, as was suggested in Hufford et al. (2003), is probably the sensible taxonomical consequence. *Presliophytum* s.l. is then held together by its peculiar inflorescence morphology with extreme metatopia (Figs. 2.6A, C and 2.7: character 11), leaf and seed characters.

The remaining taxa of Loasoideae (*Aosa*, *Blumenbachia*, *Caiophora*, „*Loasa*“ in a narrow sense, *Nasa*, and *Scyphanthus*) were united into Higher Loaseae, which are likely monophyletic based on apomorphies such as thigmonastic stamens and colored floral scales (Weigend, 1997; Fig. 2.7: characters 9 and10). The molecular results do not contradict this view if we include *Presliophytum* in this clade. The small Brazilian-Hispaniolan genus *Aosa* (6 spp.) is not retrieved as a clade, but shows various morphological characters (e.g., characteristic ebracteose inflorescences: Figs. 2.5C and 2.7: character 12) which render its monophyly likely.

Nasa is resolved as a well-supported monophyletic group in the present analysis as well as in Hufford et al. (2003, albeit with a smaller taxon sampling), and this is congruent with various unique morphological characters (presence of dorsal sacs and apical wings on the nectar scales: Figs. 2.4B and C; inflorescence morphology: Fig. 2.5D; karyology: $2n = 28$; Fig. 2.7: characters 13–16). The internal phylogeny of *Nasa* is partly resolved, with a basal dichotomy of a core clade comprising taxa of all five infrageneric groups and a smaller clade (*N. urens* group), but none of these clades are held together by any obvious morphological character. The *N. urens* group comprises a range of morphologically rather heterogenous species from *Nasa* ser. „*Saccatae*“ (*N. picta*, *N. chenopodiifolia*, *N. urens*, *N. vargasii*), the morphologically coherent *N. poissoniana* group (*N. ferruginea*, *N. poissoniana*, *N. raimondii*), and *N. carunculata*, the type species of *N.* ser. „*Carunculatae*“. *Nasa carunculata* has been considered as closely allied to *N. macrothyrsa*, primarily because of its strikingly similar habit (strongly branched shrubs; Weigend et al., 2003), but *N. macrothyrsa* is nested in the core clade, thus *N.* ser. „*Carunculatae*“ appears to be polyphyletic. The paraphyly of *Nasa* ser. „*Saccatae*“, previously postulated by Weigend and Rodriguez (2003), is again evident, involving at least three lineages. *Nasa* ser. „*Saccatae*“ was established by Urban and Gilg (1900) on the basis of annual habit, and flowers with spreading petals and contrastingly colored nectar scales (Fig. 2.4D), but these character states are clearly plesiomorphic for Higher Loaseae, since they are found in nearly all lineages (*Loasa*: Fig. 2.2C, *Caiophora*: Fig. 2.3C, *Blumenbachia*: Fig. 2.3I). Within the well-supported core clade in *Nasa*, two groups are strongly supported as monophyletic which are also well-circumscribed morphologically: the *N. triphylla* group from *N.* ser. „*Saccatae*“, which has deeply divided (trifoliolate to pinnate) leaves (Fig. 2.4E; Dostert and Weigend, 1999); and *N.* ser. *Grandiflorae*, a mostly High Andean lineage with erect wings on the floral scales and subcircular to peltate foliage leaves (Weigend and Rodriguez, 2002).

The South Andean Loasas sensu Weigend (1997) are retrieved with moderate support. They include nearly all the pre-1997 genera of Loaseae, namely *Blumenbachia*, *Caiophora*, „*Loasa*“, and *Scyphanthus*. The group is morphologically readily circumscribed on the basis of the absence of metatopia in its inflorescences (Figs. 2.5A, B and 2.7: character 17), whereas at least the bracts are metatopic in all other Loasaceae (indicating the plesiomorphic condition). All South Andean Loasas except *Blumenbachia* have a distinct double arch on the back of each nectar scale (Figs. 2.2D–I), and this uniqueness suggests the monophyly of the corresponding group (Fig. 2.7: character 20). *Blumenbachia* has been redefined by removing *B.* sect. *Angulatae* and *B.* sect. *Gripidea* from *Caiophora* (Weigend, 1997), and the distinctness from *Caiophora* of these two groups is clearly confirmed by molecular data from the present study. Like *Caiophora*, *Blumenbachia* has fruits with longitudinal dehiscence (Fig. 2.3H), but this character appears to be convergent, since the two groups differ profoundly in other aspects of morphology (e.g. scale morphology: Fig. 2.4A, petal morphology: Fig. 2.3I). Moreover, apart from the opening mode, actual fruit morphology is also quite different: In *Caiophora*, capsules are straight, and twisted antidromously if twisted at all (Fig. 2.3F), whereas those of *Blumenbachia* are always twisted, and twisted anticlockwise only (Figs. 2.3H and 2.7: character 18). The monophyly of *Blumenbachia* sensu Weigend (1997) is weakly supported in the quartet puzzling analysis (but not with the parsimony criterion). Hufford et al. (2003) did not address this problem, since they only included two species of sect. *Blumenbachia* (i.e., *Blumenbachia* sensu Urban and Gilg, 1900) in their analysis. However, all species of *Blumenbachia* share abruptly apiculate petals (Figs. 2.3I and 2.7: character 19), identical nectar scales (Fig. 2.4A), and capsules twisted anticlockwise (Fig. 2.3H), and are therefore likely to represent a monophyletic group in spite of the lack of molecular resolution. A sistergroup relationship between *Blumenbachia* and the remainder of the South Andean Loasas is plausible.

Within South Andean Loasas, two monophyletic clades with annual species of *Loasa* are clearly retrieved in the molecular tree: *L.* ser. *Macrospermae*, with extremely large and smooth seeds and very conspicuous, flag-shaped dorsal threads on their nectar scales (Figs. 2.2D, E and 2.7: character 22), and another clade comprising *L.* ser. *Floribundae* and *L.* ser. *Deserticolae*. The latter two groups show apomorphies in floral morphology (Urban and Gilg, 1900) and have identical inflorescences (basitonic thyrsoids with alternate paraclades, unique in Loasoideae; Fig. 2.7: character 23). Phytochemistry further indicates that all three series (*Deserticolae*, *Floribundae*, *Macrospermae*) probably share exclusive common ancestry, since they are the only groups containing a particular type of complex hetero-oligomeric iridoids (e.g., tricoloriside; Weigend et al., 2000; Fig. 2.7: character 21). *Loasa* ser. *Loasa*, the type section of the genus with only two species (*L. acanthifolia* Desr., *L. sclareifolia* Juss.), is morphologically closely allied to *L.* ser. *Macrospermae* and shares its two most striking characters (see above). *Loasa acanthifolia* was sequenced, but the trnL sequence has a very long delition (more than 250 bp in the alignment, representing helix 8 of the trnL secondary structure; Kuhsel et al., 1990). Because its inclusion thus eliminates many informative alignment positions, it had to be removed from the analysis. However, the close relationship between *L.* ser. *Loasa* and *L.* ser. *Macrospermae* is evident, thus the group comprising four series (*Deserticolae*, *Floribundae*, *Loasa*, *Macrospermae*) likely represents *Loasa* s.str. in the very narrowest sense.

The exact placement of „*L.*“ ser. *Pinnatae*, „*L.*“ ser. „*Volubiles*“, and “*L.*“ ser. *Acaules* remains unresolved in the bootstrap analysis, but the quartet puzzling analysis indicates a sistergroup relationship with the (well-supported) *Caiophora*/*Scyphanthus* clade, which is congruent with two unique morphological characters: the vast majority of species in these groups have deeply pinnatifid, very shortly petiolate leaves (Figs. 2.3A, B and 2.7: characters 24 and 25). In addition, „*L.*“ ser. *Pinnatae*, *Caiophora*, and *Scyphanthus* share the predominance of serrate petal margins (Figs. 2.3C, D and 2.7: character 26), the latter being entire in all other groups. *Scyphanthus* contains two annual herbs from the mediterranean climate in Chile, whereas *Caiophora* is a High Andean taxon containing over 50 species and ranging from Central Argentina into southern Ecuador, with a single annual species in Uruguay and SE Brazil. *Caiophora* and *Scyphanthus* were also retrieved as sister taxa in the analyses of Moody and Hufford (2000) and Hufford et al. (2003), and they are evidently closely allied since they share apomorphic characters. The fruits of *Scyphanthus* and *Caiophora* open both with apical valves and with longitudinal sutures (synapomorphic; Fig. 2.7: character 27; in the derived taxa of *Caiophora* the capsule apex remains coherent: Fig. 2.3G), whereas other Loasoideae typically have fruits opening with apical valves only (Fig. 2.3E). The monophyly of *Caiophora* sensu Weigend (1997) is based on karyology (2n = 14; 16) and phytochemistry (10-hydroxyoleoside-dimethyl ester; Weigend et al., 2000; Fig. 2.7: character 28), and is confirmed by the present analysis.

Historical biogeography

Some aspects of historical biogeography can be addressed on the basis of the data presented here, but the timing of divergence events appears to be impossible from the data available (see Table 2.1 for distribution areas). „*Huidobria*“ (N Chile), *Klaprothia* (Bolivia to Mexico), *Xylopodia* (N Peru: Amotape-Huancabamba Zone; Weigend, 2000), *Kissenia* (Africa), *Presliophytum* (NW Chile, W Peru), *Plakothira* (Marquesas Islands in Polynesia), and *Aosa* (Brasil and Hispaniola) are geographically widespread in the tropical regions primarily of South America, but they are completely absent from higher elevations and the temperate and mediterranean regions. They are found with a series of evident paleoendemics in the coastal deserts of western South America (*Presliophytum* and *Huidobria*), the rain forests of Central America (*Chichicaste*), in Africa (*Kissenia*), and Brazil (*Aosa*). Conversely, High Andean and southern temperate habitats have only been colonized by two, species-rich groups: the South Andean Loasas and *Nasa*.

Nasa is restricted to the American Cordillera, and the limits of its distribution coincide rather precisely with the limits of the tropical region (southern limit: Department Santa Cruz in Bolivia, northern limit: Province Chiapas in Mexico). *Nasa* ser. *Grandiflorae* is the only genuinely High Andean group (2500–4500 m). This monophylum is apparently derived from plants growing at lower elevations in the (paraphyletic) remainder of *Nasa*, such as the only coastal species (200–1000 m; *N. urens* (Jacq.) Weigend), various species from moderate elevations in inner-Andean valleys (<2500 m; *N. poissoniana*, *N. vargasii*), or cloud forest taxa (2000–3000 m; *N. triphylla* group, *N. laxa* (Killip) Weigend, *N. ramirezii* (Weigend) Weigend, *N.* ser. *Alatae*). The Amotape-Huancabamba Zone in N Peru and adjacent Ecuador seems to be the primary centre of diversification of *Nasa*, and ascent into the higher elevations as well as ecological diversification may have taken place largely in this region (Weigend, 2002).

Within the South Andean Loasas, it is also possible to trace geographical patterns: all species of *Loasa* s.str. (i.e. *L.* ser. *Loasa*, *L.* ser. *Macrospermae*, *L.* ser. *Deserticolae*, *L.* ser. *Floribundae*) are endemic to the mediterranean region or coastal desert of Chile, with only few species extending into similar habitats in Argentina or Peru; *Blumenbachia* is nearly exclusively south-east South American and is found in a wide arch from Brazil to Chile, with the morphologically most primitive group (*B.* sect. *Angulatae*) endemic to the southern Andes. The other groups of „*Loasa*“ („*L.*“ ser. *Acaules*, *„L.“* ser. „*Volubiles*“, *„L.“* ser. *Pinnatae*) are largely Patagonian. *Scyphanthus* is restricted to the mediterranean region of Chile. *Caiophora* is widespread at elevations above 3500m in the Andes (Argentinian Andes to Ecuador), but has its morphologically most primitive taxa (i.e., those most similar to *L.* ser. *Pinnatae* and *Scyphanthus*) in SW Brazil and Uruguay (*C. arechavaletae*), the Argentinian Andes (*C. pulchella*, *C. nivalis*), and at moderate elevations of the Peruvian Andes (*C. pterosperma* group). This distribution pattern indicates a primary radiation of the South Andean Loasas in the southern temperate and mediterranean zones. Subsequent dispersal and diversification, essentially of *Caiophora*, led to the current distribution patterns. Within South Andean Loasas, only *Caiophora* has High Andean groups, and it seems to have colonized the High Andean region from the south temperate zone.

In the colonization of tropical High Andean habitats by *Caiophora* and *Nasa*, two independent, alternative routes have thus been explored: *Caiophora* took the southern track by adaptation to temperate climate, whereas *Nasa* took the direct route with progressive adaptation to colder climates in the central Andes. In both groups, the widely open, contrastingly colored flowers typical for Loasoideae with melittophily (Figs. 2.2C, 2.3C, D, I and 2.4D) are ancestral, and they independently developed into superficially similar, much larger, orange or red, hummingbird-pollinated flowers (Figs. 2.1 and 2.4F –I) in their High Andean representatives only.

2.6. Acknowledgements

We would like to express our sincere gratitude to the National Tropical Botanical Gardens Hawaii (NTBG, Hawaii), Jon Ricketson (Missouri Botanical Gardens), St. Vogel (Institut für Botanik und Botanischer Garten der Universität Wien, Austria), J. Grau and Ch. Ehrhardt (Institut für Systematische Botanik München, Germany), J. Grant (Neufchatel, Switzerland), and L. Struwe (New Brunswick, USA) for leaf samples, as well as to the herbaria B, BSB, LPB, and M for access to and loans from their collections. We want to thank T. Hofreiter, M. Binder, T. Franke and H. Förther (Munich, Germany), N. Dostert, T. Henning and C. Schneider (Berlin, Germany), E. Rodriguez R. (Trujillo, Peru), A. Cano E. (Lima, Peru), G. Vobis, and C. Ezcurra (Bariloche, Argentina) for help in the field. We would like to thank Mrs. C. Müller and A. Biesek (Berlin) for the laboratory work. The funds kindly provided by the following institutions at various stages o the project are here gratefully acknowledged: Studienstiftung des Deutschen Volkes (1992–1997), Deutscher Akademischer Austauschdienst (1999–2000), Deutsche Forschungsgemeinschaft (Grant No. WE 2330/1, 2001–2003), Lewis B. and Dorothy Cullman Laboratory for Molecular Systematics Studies at the New York Botanical Garden (1999–2000), botconsult GmbH (1999-present).

2.7. Literature

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3. Notes on the genus *Caiophora* (Loasoideae, Loasaceae) in Chile and neighbouring countries*

3.1. Abstract

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, cushionforming 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.

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,

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*The original publication is available at http://www2.darwin.edu.ar/Publicaciones/Darwiniana/Vol45%281%29/d45_45-67.pdf. Published as: Ackermann M, Weigend M. 2007. Notes on the genus *Caiophora* (Loasoideae, Loasaceae) in Chile and neighbouring countriesDarwiniana 45: 45-67.

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.

3.2. 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 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 and Gilg (1900, 1911), while some additional names were clarified in Weigend and Ackermann (2003). Many of the taxonomical problems in the genus stem from the fact that Urban and Gilg (1900) enthusiastically described new species on the basis of single, fragmentary specimens. However, a fullscale 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 and 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.

3.3. 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, ravenel.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, leafsize, 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*

3.4. Results and discussion

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. 3.1, 3.2.

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).

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!).

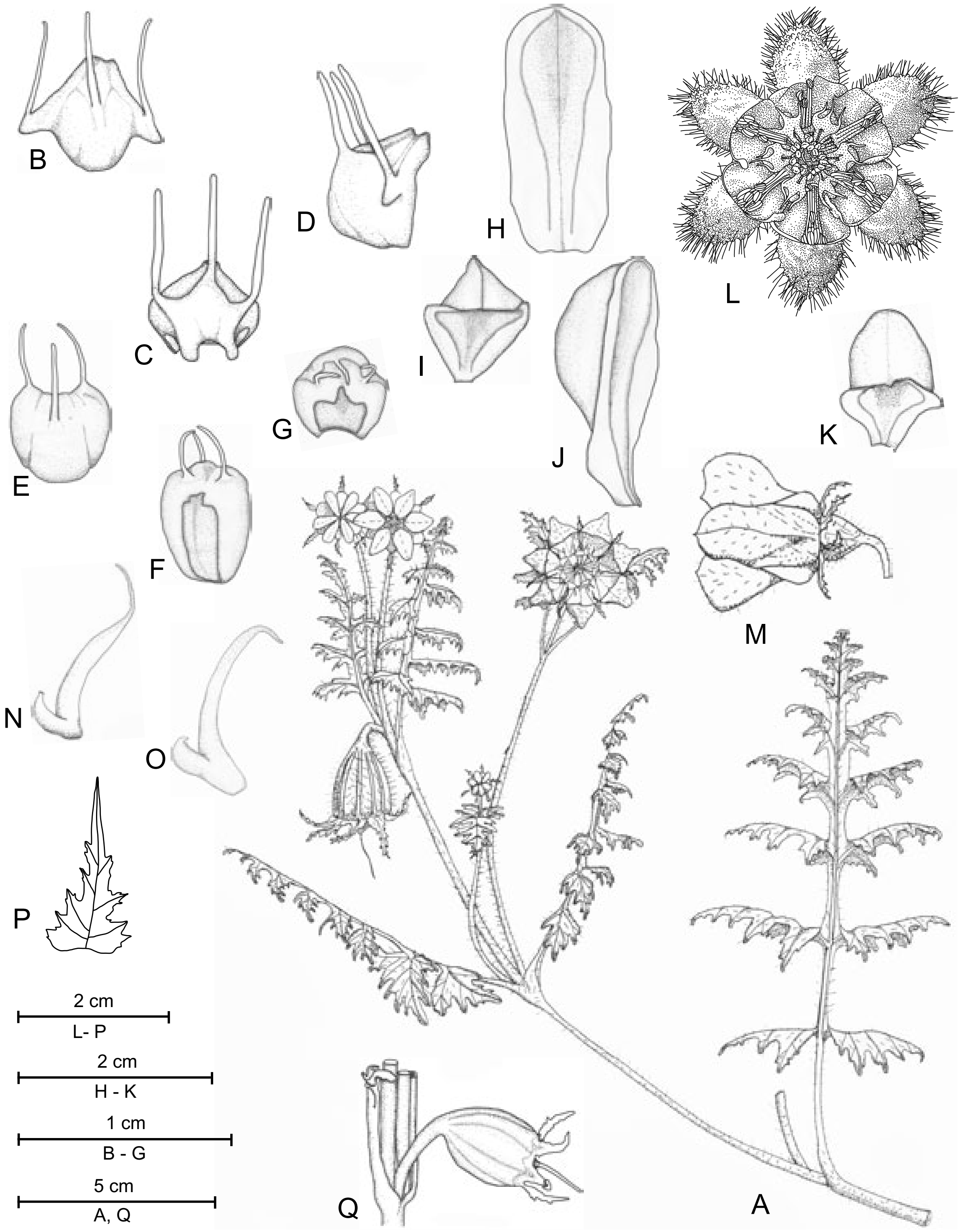

Fig. 3.1: *Caiophora chuquitensis*. **A,** growth habit. **B, E,** nectar scale, dorsal view. **C, G,** apical view. **D,** lateral view. **F,** ventral view. **H,** petal, dorsal view. **I, K,** apical view. **J,** lateral view. **L,** flower (drawn by H. Lünser, Berlin). **M,** lateral view.. **N-O,** 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. 3.2: *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).

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 Lshaped, 10-20 mm long, dorsally with spoonshaped 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 and 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. 3.2A-B). *Caiophora chuquitensis* is pollinated by long-tongued bees and hummingbirds (Ackermann and Weigend, 2006; Harter, 1995; Coccuci and 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. 3.2A-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. 3.2E-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 and 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, S 23°10´, W 065°11´, 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. Quillacollo: 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, S 17°35´, W 066°57´, 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, S 16°15´, W 068°33´, 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, S 13°10´26´´, W 071°57´55´´, 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. 3.3, 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) triangularovate, 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

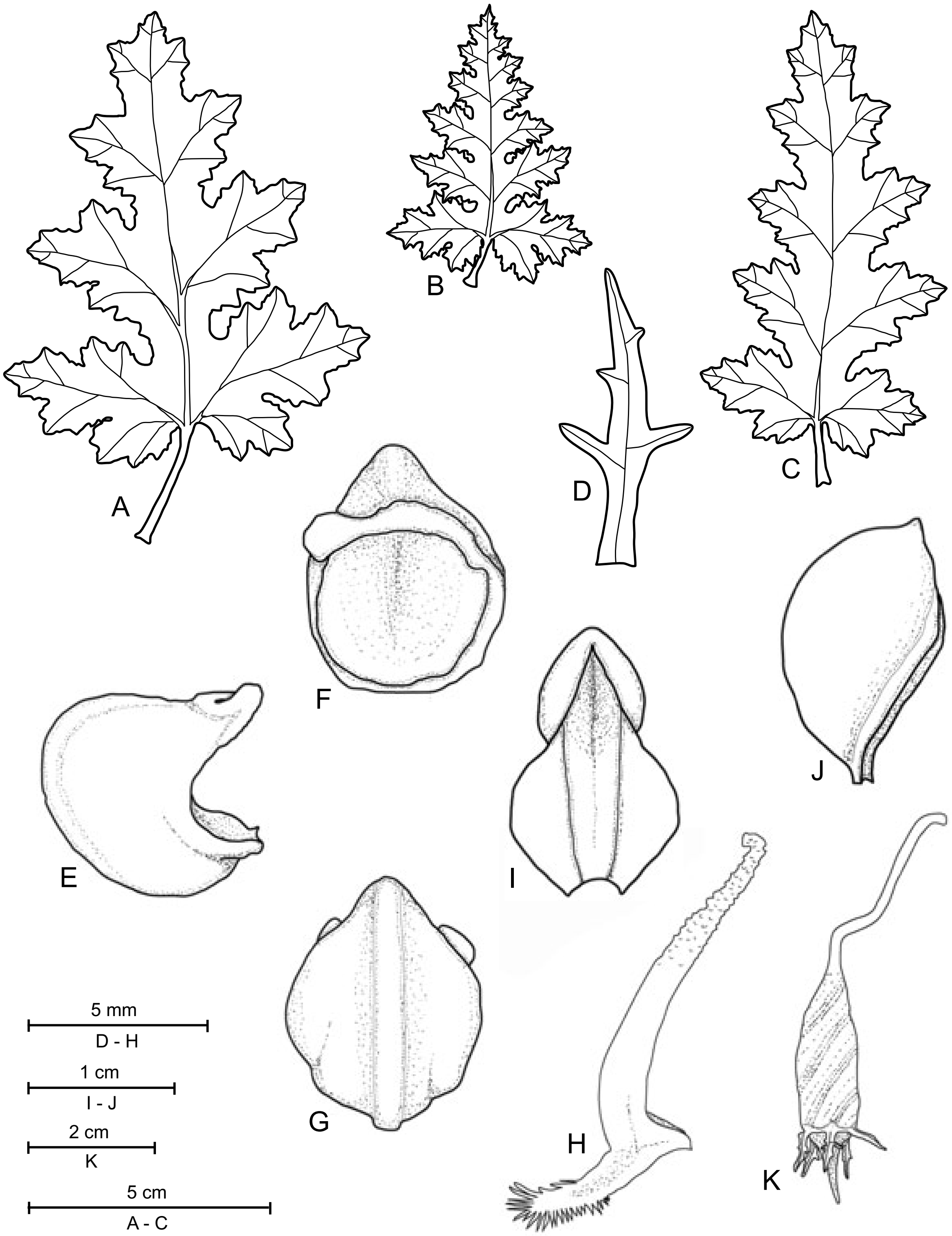

Fig. 3.3: *Caiophora cirsiifolia*. **A-C,** leaves. **D,** sepal. **E,** nectar scale, lateral view. **F,** ventral view. **G,** dorsal view. **H,** staminode. **I,** petal, ventral view. **J,** lateral view. **K,** fruit. **A, C-H, K,** M. Ackermann et al. 420 (BSB, HUSA, **M,** USM, NY, F); **B, I, J,** M. Ackermann et al. 555 (BSB).

Fig. 3.4: *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).

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 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 differentiating 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. 3.4A), 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, S 16°24´20´´, W 071°22´38´´, 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, S 16°35´23´´, W 071°25´52´´, 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. 3.4C-D, 3.5.

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 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

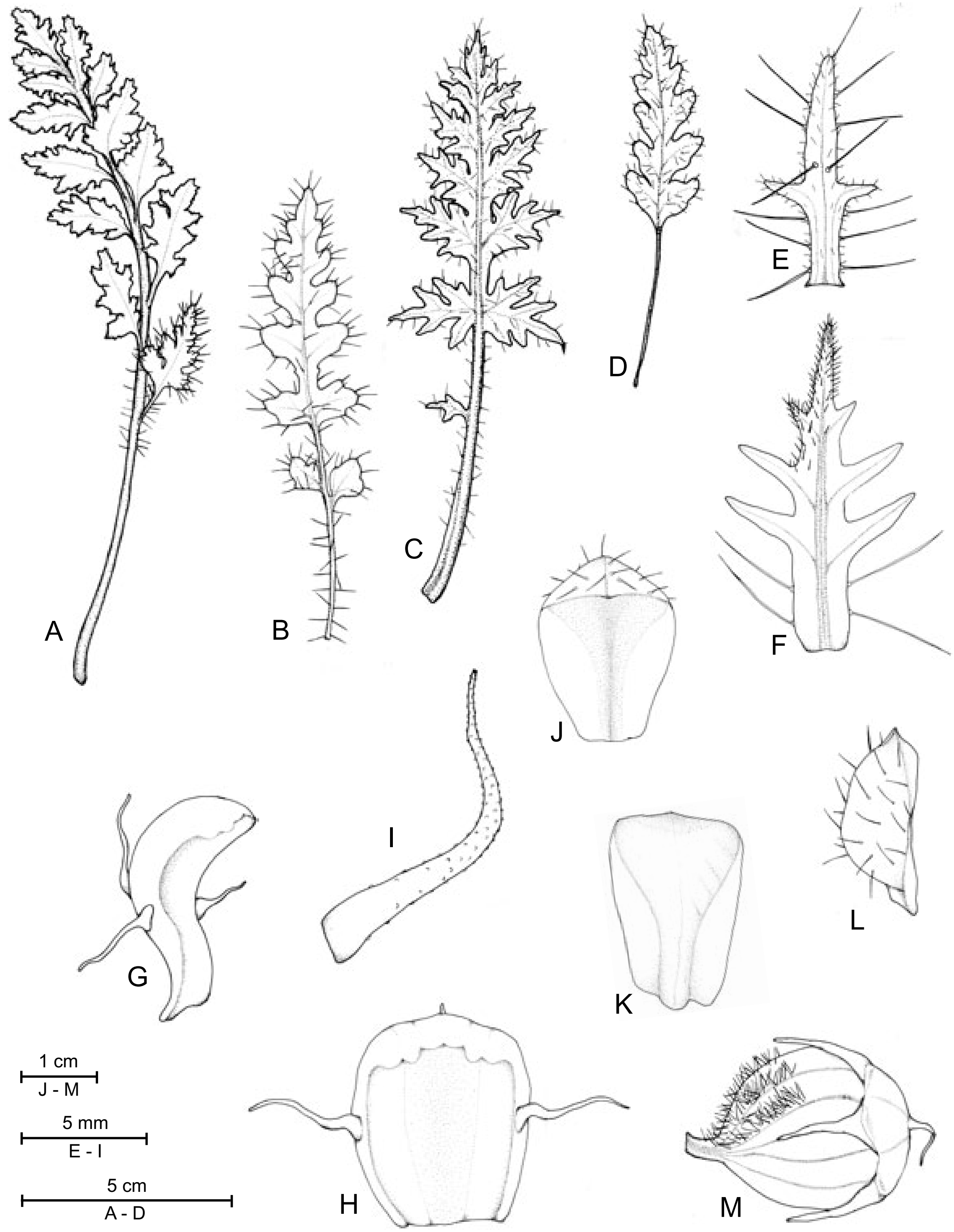

Fig. 3.5: *Caiophora coronata*. **A-D,** leaves. **E-F,** sepals. **G,** nectar scale, lateral view. **H,** ventral view. **I,** staminode. **J,** petal, ventral view. **K,** dorsal view. **L,** lateral view. **M,** fruit. A, Meyen 4659 (NY, UC); **B, D, L,** J. R. I. Wood 14626 (LPB); **G-K, M,** T. H. Goodspeed & Y. Mexia 4611 (GH, UC); **C, E,** M. Ackermann 60 (BSB); **F,** E. Budin 7437 (UC); (drawn by C. Becker, Berlin).

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. 3.4C). *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. 3.4C-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, S 22°59´, W 066°01´, 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, S 22°06´, W 65°46´, 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, S 22º43.964´, W 067º59.996´, 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, S 16°59.539´, W 070°42.040´, 3900 m, 12-IV-2004, M. Weigend & Ch. Schwarzer 7845 (holotype USM!; isotypes BSB!, M!, HUSA!, HUT!). Figs. 3.6, 3.7.

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 triangularovate, 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 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

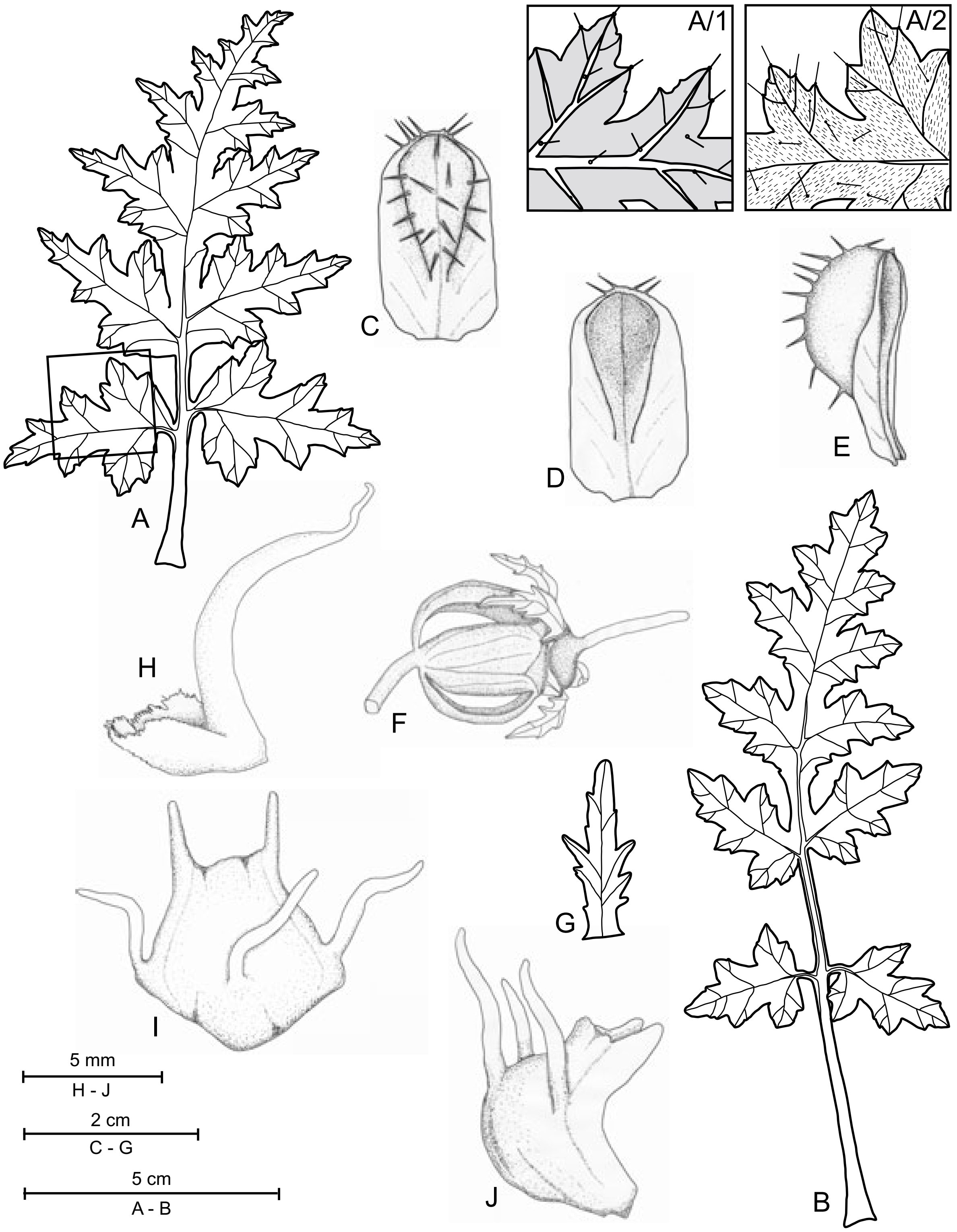

Fig. 3.6: *Caiophora deserticola.* **A-B,** leaves. **A/1,** abaxial surface. **A/2,** adaxial surface. **C,** petal, dorsal view. **D,** ventral view. **E,** lateral view. **F,** mature fruit. **G,** sepal. **H,** staminode. **I,** nectar scale, dorsal view. **J,** lateral view. **A-J,** M. Weigend et al 7761 (BSB, HUSA, USM).

Fig. 3.7: *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).

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. 3.7A). 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. 3.7C-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, 1 S 9°43´37´´, W 069°13´10´´, 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, S 15°59.587´, W 070°52.203´, 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. 3.4E-F, 3.8A-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

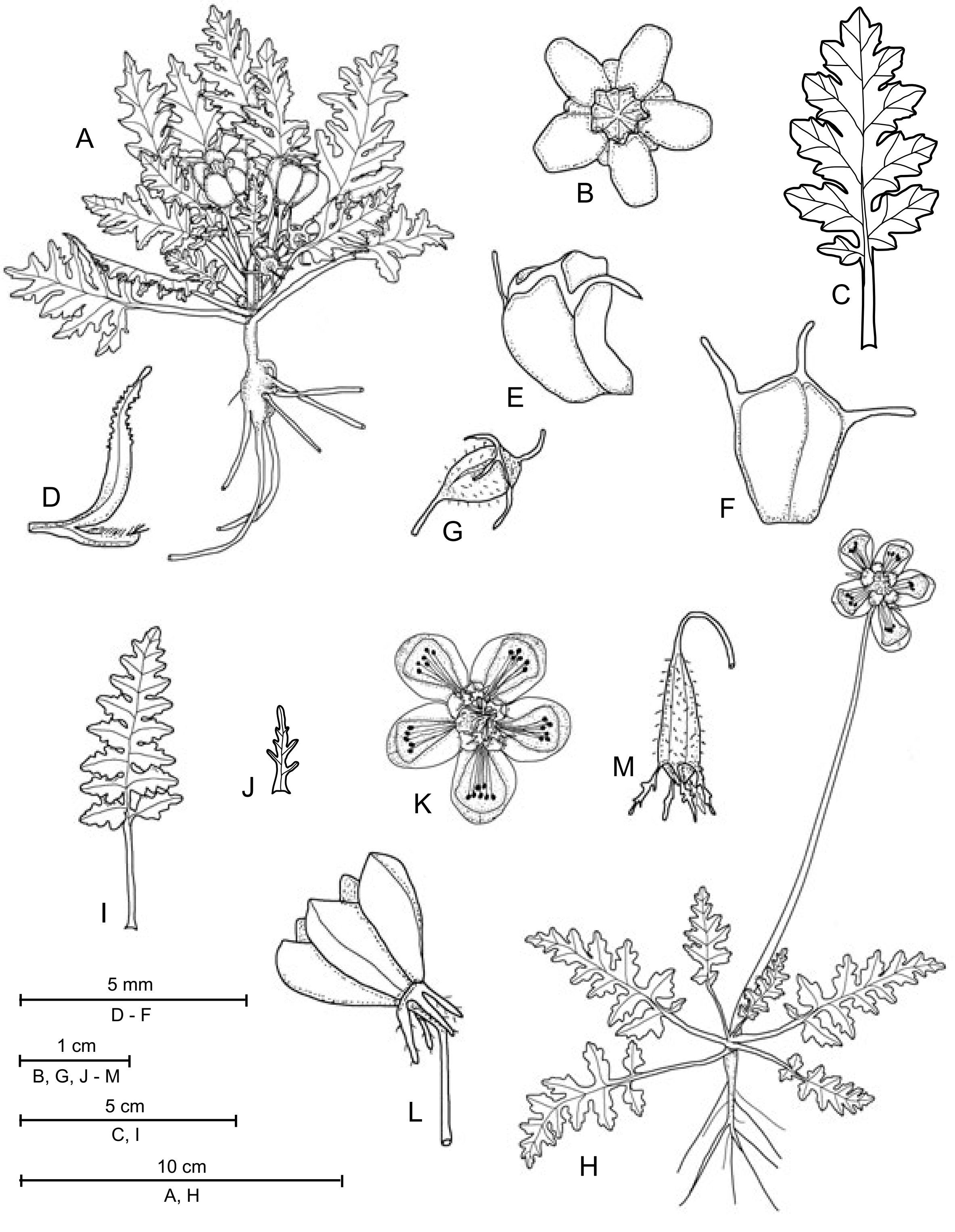

Fig. 3.8: *Caiophora rosulata* subsp. *rosulata*. A, growth habit. B, flower. C, leaf. D, staminode. E, nectar scale, lateral view. F, dorsal view. G, fruit. *Caiophora rosulata* subsp. *taraxacoides*. H, growth habit. I, leaf. J, sepal. K, flower. L, young flower, lateral view. M, fruit. A-C, M. Weigend & 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).

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 of 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. 3.4E). 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. 3.4E-F, 3.8A-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 triangularovate, 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 and 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, S 16°50´757´´, W 070°32´850´´, 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, S 16°34´09´´, W 070°22´31,9´´, 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. 3.8H-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, bowlto 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, S 18°10´, W 069°00´, 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, S 14°41´, W 071°16´, 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 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 and 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. 3.4E-F).

3.5. Acknowledgements

We would like to express our sincere gratitude to C. Becker and H. Luenser (Berlin) for providing some of the drawings, K. Gilmer, R. Langenberger, H. P. Thomas (http://www.opuntiadelsur.de, Germany), A. Wertlen (Berlin, Germany) and F. Luebert for pictures, H. H. Hilger for his support and helpful discussions, H. Förther (Munich, Germany), N. Dostert, T. Henning, O. Mohr, C. Schwarzer, K. Weigend (Berlin, Germany), F. Caceres (Arequipa, Peru), F. Luebert and M. Muñoz-Schick (Santiago, Chile) for help in the field and collecting specimens. We would like to thank the curators and directors of the following herbaria respectively for loans or access to their specimens: B, BA, BM, BOLV, BR, BSB, CORD, CUZ, E, F, FR, G, GB, GOET, HBG, GH, HUSA, HUT, IBBA, K, L, LIL, LPB, LPS, LPZ, M, MA, MICH, MO, MSB, NY, OXF, P, PR, PRC, S, SI, SGO, TRIER, TUEB, UC, UMSS, U, US, USM, W, WU, Z. Part of the study was supported by the Deutscher Akademischer Austauschdienst (DAAD), the Deutsche Forschungsgemeinschaft (DFG), the Lewis B. and Dorothy Cullman Program for Molecular Systematics Studies (The New York Botanical Garden), and botconsult GmbH, which are here gratefully acknowledged.

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Weigend M, Ackermann M. forthc. Loasaceae. In: Jörgensen PM, ed. The Catalogue of the Vascular Plants of Bolivia. St. Louis, Missouri Botanical Garden Press.

3.7. 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).

Ackermann, M. 60 (3), *123* (3), *274* (1), *420* (2), *555* (2), *642* (2), *646* (2), *647* (4), *680* (2); *Adeo, C. 11302* (5a); *Arakaki, M. 795* (4); *Arenas, G. s/n* (2), *4* (2), *151* (2).

Balls, E. K. 5884 (1), *6019* (5b), *6029* (1), *6069* (3); *Bang, M. 171* (1); *Barker 90* (1); *Barkley,* *F. A. 19AR863* (3); *Bastión, E. 656* (3), *1063* (1); *Beck, S. 6021* (1), *14321* (1), *17894* (1), *21050* (1), *21725* (1), *22356* (5b), *23831* (1), *26610* (1); *Biese, W. 1018* (3); *Blanchard, M. s/n* (2); *Boeke, J. 1364* (1); *Brooke, W. M. A. 5480* (5b); *Brücher, E. H. 832* (5b), *850* (1); *Buchtien, O. A. s.n. 1903* (3), *s.n. 1910* (1), *s.n. 1913* (1), *42* (1), *363* (1); *Budin, E. 7437* (3), *7464* (1), *7515* (3).

Cabrera, A. L. 7799 (1), *7827* (3), *8333* (1), *8687* (1), *15370* (1), *22021* (1); *Caceres, F. 576* (2), *867* (2), *1160* (2), *1514* (2), *2494* (2), *2805* (4), *3001* (4), *3002* (4), *3213* (2), *3252* (4); *Cárdenas, R. 49* (1), *3719* (1); *Cano, A. 7919* (2), *7950* (5a), *7984* (2), *8401* (5a), *10097* (5a); *Casa, F. 6464* (1); *Castellanos, A. 15485* (3), *15490* (3); *Castellón, A. s.n. 1914* (3); *Chapin 1102* (3); *Claren, F. 11298* (1); *Conrad, J. 2676* (5b); *Conway, W. M. 23* (1).

D´Orbigny, A. 1436 (1), *1441* (3); *Davidson, C. 3705* (1); *Davis, E. W. 1706* (5b); *De Avila, D. K. 59* (1); *Deginani, N. B. 518* (3), *596* (3); *Dillon, M. 4798* (4); *Doppelbaur, H. s.n. 1969* (1); *Dostert, N. 1024* (2); *Douglas s.n. 1892* (2).

Ehrich, R. 28 (1); *Elliot, S. 463* (3); *Emshwiller, E. 348* (1); *Eyerdam, W. J. 22176* (2); *Exp. Varsovia Polonia 31* (5a).

Fabris, H. 1784 (3), *7693* (1); *Feuerer, T 7459* (1); *Fiebrig, K. 2603* (1), *2807* (3), *3346* (1), *3347* (1); *Figueroa, J. R. s.n. 1866* (3); *Fisel, U. 139* (1); *Forster, W. s.n. 1953* (1); *Frangi, J. L. 32* (1); *Fries, K. R. E. 957* (3).

Garolera-Romero, A. s.n. (1); *Gay, C. s.n.* (3), *854* (3), *1621* (3); *Gillies, J. s.n. anno 1821* (3); *Goodspeed, T. H. 4611* (3); *Grandjot, K. 3798* (3); *Grau, J. s.n* (2); *Guillen, R. 34* (1); *Gutte, P. 339* (1).

Haenke, T. s.n. (3), s.n. (2), s.n. *PR 24293* (2); *Hensen, I. 1032* (1); *Hieronymus, G. H. 388* (3); *Hilger, H. H. ARG95/45* (1); *Hinckley, L.C 50* (2); *Hjerting, J. P. 1097* (5a); *Hohenacker, R. A. s.n.* (3); v. *D. Hoogte, L. 1856* (5b).

Ibisch, P. 1116 (5b); *Ihue U., Y. 2004-33* (2), *2004-108* (4); *Isern, J. 2019* (2).

Jewell 2 (5b); *Johns, T. 82-58* (1); *Johnston, I. M. 5899* (3), *6118* (3); *Jörgensen, P. 1157* (1), *1558* (5b), *1857* (3).

La Torre, M. I. 1812 (4), *1827* (2), *1956* (2), *1998* (4), *2420* (5a); *Legname, V. 58* (3); *Leuenberger, B. 3782* (3); *Liberman, M. 35* (5b), *178* (3), *Lillo, M. 4184* (1), *5513* (3); *Lobb, W. s.n.* (5b); *Lorentz, P. G. s.n. 1873* (1), *49* (1), *187* (1); *Lorini, J. s.n. 1979* (1); *Lourteig, A. 779* (3), *2603* (1); *Luebert, F. 1720* (1).

Malme, G. O. A. 2818a (3), *2963* (3); *Mancilla, R. 154* (1); *Mandon, G. 619* (1); *Meyer, T. 4659* (3), *4660* (1), *4661* (1), *33613* (3), *33614* (1), *33615* (1), *33616* (1), *33617* (3), *33618* (1); *Morrison, J. L. 17273* (3); *Müller 1825b* (2), *2089* (2), *2266* (5a), *3695* (2); *Muñoz-Schick, M. 4296* (4).

Naessany, L. 7 (1), *Navarro, G. 239* (1), *1103* (1); *Niethammer, G. s.n. 1951* (1); *Novara, J. L.*

8355 (1).

Olea, D. 256 (1), *257* (1); *Ostria, C. 69* (1).

Parodi, L. R. 7889 (3); *Peirano, A. s.n. 1934* (3), *10209* (3); *Pennell, J. W. 13262* (2), *13320* (5a); *Peterson P. M. 12679* (1), *13048* (3), *13118* (3); *Philippi R. A. s.n.* (5a), *s.n.* (3), *s.n.* (4), *s.n.* (1); *Pierotti, A. 1337* (1); *Plowman, T. C. 4646* (1); *Poston, M. 236* (2).

Quipuscoa S., V. 1591 (2).

Rauh-Hirsch, W. P554 (5a); *Reid s.n.* (3); *Renvoize, S. 3413* (1); *Rilke, S. 448* (1), *673* (1); *Rodriguez, M. s/n* (2), *Rodriguez, F. M. 445* (3), *1308* (1); *Roque, J. 1041* (2); *Ruiz, H. s.n* (2); *Ruthsatz, B. 797* (5b), *825* (5b).

Salinas, I. 882 (4); Sandeman, C. A. W. *3761* (2), *3910* (5a); *Schickendantz, F. 142* (5b), *149* (1); *Schlindwein, C. 1906* (1); *Schreiter, R. 5854* (1); *Schulte 162a* (1), 162b (5b); *Seler, E. 131* (1); *Sleumer, H. O. 2722* (5b), *2738* (1), *2739* (1), *2739a* (1), *2830* (1), *2831* (1), *2953* (1), *2954* (1), *3489* (1), *3495* (5b), *3667* (3), *3669* (1), *4099* (5b); *Solomon, J. C. 4876* (1), *5006* (1), *11442* (1), *16186* (1); *Solozarno, M. 25* (2); *Sparre, B. 1517* (3), *8798* (3); *Spegazzini, C. 102321* (1); *Spooner, D. M. 6579* (1); *Stafford, D. 597* (2), 650 (5a), *761* (5a), *816* (2); Steinmann, *J. s.n.* (5a); *Straw, R. 2287* (2), *2325* (5a), *2350* (2).

Tate, G. H. H. 1003 (1); *Tejada, M. 1* (5a), *5* (2); *Troll, C. 1901* (1), *2994* (5b).

Ulibarri, E. A. 713 (3).

Valenzuela, L. 2023 (5b); *Vargas, C. 5578* (5b), *8044* (2), *9275* (2), *10072* (1), *19363* (2); *S. Venturi 4413* (1), *4655* (1), *6550* (3), *6551* (3), *6552* (3), *6554* (3), *6571* (5b), *6578* (5b), *6579* (5b), *6999* (5b), *7007* (5b), *7642* (1), *8131* (1), *8722* (3), *9387* (3), *9456* (3), *9457* (3), *9458* (5b), *10070* (5b), *10135* (3), *10371* (1); *Vervoorst, F. B 3227* (3); *Viramonte, J. G. 4679* (1); *Vogel, S. 557* (1), *565* (3); *Vuilleumier, B. B. 405* (1), *447* (1), *478* (5b), 493 (3).

Wall, E. s.n. 1946 (3), *12* (3); *Walter, H. 684* (3); *Weberbauer, A. 6881* (5a), *7468* (4); *Weddell, H. A. s.n.* (5a), *s.n.* (2), *4095* (1); *Weigend, M. 97/795* (4), *97/797* (2), *97/802* (4), *2000/001* (2), *2000/023* (5a), *2000/203* (1), *2000/341* (2), *2000/392* (2), *2000/557* (2), *3680* (1), *3681* (1), *7754* (2), *7761* (4), *7837* (5a), *7840* (5a), *7845* (4), *7854* (4); *Werdermann, E. 226* (3), *1107* (2); *West, J. 5247* (3), *6084* (5b), *6090* (1), *6388* (1); *Wilczek, E. 407* (3); *Wolstenholme, G. E. 30* (1); *Wood, J. R. I. 7669* (1), *7880* (1), *14595* (5b), *14626* (3).

Ybert, J. P. 698 (1).

Zuloaga, F. O. 5948 (1).

4. Catalogue of the Vascular Plants of the Southern Cone (Argentina, Southern Brazil, Chile, Paraguay, and Uruguay): Loasaceae*

7 genera, 67 species, 48 endemic species, 1 introduced species.

Acrolasia bartonioides C. Presl = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

References: Darlington, J., 1934; Pérez-Moreau, R. L. & Crespo, S., 1988a.

Acrolasia bartonioides Gay, hom. illeg. = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Acrolasia elata Phil. = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz

Reference: Sleumer, H. O., 1955.

Acrolasia pinnatifida Phil. = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Acrolasia solieri Gay = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

References: Pérez-Moreau, R. L. & Crespo, S., 1988a.

Bartonia albescens Gillies ex Arn. = ***Mentzelia albescens*** (Gillies ex Arn.) Griseb.

References: Darlington, J., 1934; Pérez-Moreau, R. L. & Crespo, S., 1988a.

Bartonia sinuata C. Presl = ***Mentzelia albescens*** (Gillies ex Arn.) Griseb.

Reference: Darlington, J., 1934.

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*Published as: Weigend M, Grau J, Ackermann M. 2008. Loasaceae. In: Zuloaga FO, Morrone O, Belgrano MJ eds. Catalogue of the Vascular Plants of the Southern Cone (Argentina, Southern Brazil, Chile, Paraguay, and Uruguay). St. Louis, Mo., U.S.A., Missouri Botanical Garden Press.

4.1. *Blumenbachia* Schrad., nom. cons.

Number of species: 9, 5 endemic

Blumenbachia acaulis Phil. = ***Loasa lateritia* Gillies ex Arn.**

Reference: Urban, I. & Gilg, E., 1900.

Blumenbachia arechavaletae Urb. = ***Caiophora arechavaletae*** (Urb.) Urb. & Gilg

Reference: Weigend, M., 1997a.

Blumenbachia aspera (Vell.) Urb. = ***Blumenbachia eichleri*** Urb.

Reference: Weigend, M., 1997b.

Blumenbachia carduifolia (C. Presl) Ball = ***Caiophora carduifolia*** C. Presl

Reference: Weigend, M., 1997a.

Blumenbachia catharinensis Urb. & Gilg

References: Santos, E. & Fromm Trinta, E., 1985; Weigend, M., 1997a.
Winding herb. Annual or biannial. Endemic. 1300–1400 m.
Countries: BRA (RGS, SCA).
Reference example: BRA [Ule, E. H. G. 1486 (B, HBG)].

Blumenbachia cernua Griseb. = ***Caiophora cernua*** (Griseb.) Urb. & Gilg ex Kurtz

Reference: Weigend, M., 1997b.

Blumenbachia chuquitensis (Meyen) Hook. f. = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Weigend, M., 1997b.

Blumenbachia contorta Griseb., hom. illeg. = ***Caiophora clavata*** Urb. & Gilg

Reference: Sleumer, H. O., 1955.

Blumenbachia coronata (Gillies ex Arn.) Hieron. = ***Caiophora coronata*** (Gillies ex Arn.) Hook. & Arn.

Reference: Weigend, M., 1997b.

Blumenbachia dissecta (Hook. & Arn.) Weigend & J. Grau

Synonyms: *Blumenbachia espigneira* Gay, *Caiophora dissecta* (Hook. & Arn.) Urb. & Gilg, *Caiophora espigneira* (Gay) Urb. & Gilg, *Caiophora kurtzii* Urb. & Gilg, *Caiophora patagonica* Urb. & Gilg, *Loasa dissecta* Hook. & Arn., *Loasa patagonica* Speg., nom. illeg., *Loasa spegazzinii* Macloskie
References: Grau, J., 1988; Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic. 0–3500 m.
Countries: ARG (CHU, MEN, NEU, RNE, SCR); CHL (V, VI, VII, RME).
Reference examples: ARG [De Marco, N. 258 (SI)]; CHL [Meyen, 37 (B)].

Blumenbachia domeykoana Phil. = ***Blumenbachia silvestris*** Poepp.

Reference: Urban, I. & Gilg, E., 1900.

Blumenbachia eichleri Urb.

Synonyms: *Blumenbachia aspera* (Vell.) Urb., *Caiophora eichleri* (Urb.) Urb. & Gilg, *Caiophora scabra* (Miers) Urb. & Gilg var. *schenkiana* (Urb.) Urb. & Gilg, *Mentzelia aspera* Vell., hom. illeg.
References: Santos, E. & Fromm Trinta, E., 1985; Weigend, M., 1997a.
Winding herb. Annual. Endemic. 500–1200 m.
Countries: BRA (PAR, RGS, SCA).
Reference example: BRA [Smith, L. B. 5600 (NY, US)].

Blumenbachia espigneira Gay = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Blumenbachia hieronymi Urb.

Synonyms: *Blumenbachia multifida* Griseb., hom. illeg.
References: Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997a.
Herb. Annual or biannial. Native. 1900–2500 m.
Countries: ARG (COR, SLU).
Reference example: ARG [Pastore, A. L. 12 (SI)].

Blumenbachia insignis Schrad.

Synonyms: *Blumenbachia multifida* Ball, hom. illeg., *Blumenbachia multifida* Hook. f., *Blumenbachia palmata* (Spreng.) Cambess., *Blumenbachia parviflora* Gillies ex Hook.,

nom. nud., *Loasa muralis* Griseb., *Loasa palmata* Spreng.
References: Cabrera, A. L., 1966c; Di Fulvio, T. E., 1975; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955; Weigend, M., 1997a.
Herb. Biannial. Native. 0–500 m.
Countries: ARG (BAI, CAT, COR, ERI, LPA, MEN, MIS, RNE, SFE, SLU); BRA (RGS); URY (LAV, MON, ROC, SOR).
Reference examples: ARG [Pedersen, T. M. 11908 (SI)]; BRA [Jarenkow, J. A. 2741 (MBM)]; URY [Hertel, R. 719a (SI)].

Blumenbachia lateritia (Hook.) Griseb. = ***Caiophora lateritia*** Klotzsch

Reference: Weigend, M., 1997b.

Blumenbachia latifolia Cambess.

Synonyms: *Blumenbachia urens* (Vell.) Urb., *Loasa urens* Vell., hom. illeg.
References: Lillo, M., 1919b; Pensiero, J. F. & Gutiérrez, H. F., 2005; Santos, E. & Fromm Trinta, E., 1985; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997a.
Herb. Annual or biannial Native. 0–1000 m.
Countries: ARG (BAI, CHA, COS, ERI, FOR, JUJ, MIS, SFE, TUC); BRA (PAR, RGS, SCA); PRY (CAA, CEN, GUA, MIE); URY (ART, COL, LAV, MAL, RNO).
Reference examples: ARG [Morrone, O. 1305 (SI)]; BRA [Smith, L. B. 12557 (HBR, R, US)]; PRY [Pedersen, T. M. 6528 (SI)]; URY [Berro, M. B. 2707 (MVFA)].

Blumenbachia mitis Phil. = ***Blumenbachia silvestris*** Poepp.

Blumenbachia multifida Ball, hom. illeg. = ***Blumenbachia insignis*** Schrad.

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a.

Blumenbachia multifida Griseb., hom. illeg. = ***Blumenbachia hieronymi*** Urb.

References: Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900.

Blumenbachia multifida Hook. f. = ***Blumenbachia insignis*** Schrad.

Reference: Weigend, M., 1997a.

Blumenbachia nemorosa Phil. = ***Blumenbachia silvestris*** Poepp.

Reference: Urban, I. & Gilg, E., 1900.

Blumenbachia palmata (Spreng.) Cambess. = ***Blumenbachia insignis*** Schrad.

Reference: Weigend, M., 1997a.

Blumenbachia parviflora Gillies ex Hook., nom. nud. = ***Blumenbachia insignis*** Schrad.

Reference: Weigend, M., 1997a.

Blumenbachia prietea Gay

Synonyms: *Caiophora prietea* (Gay) Urb. & Gilg
References: Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900.
Herb. Perennial. Endemic. 1500–3000 m.
Countries: ARG (NEU, RNE); CHL (VI, VII, VIII, IX).
Reference examples: ARG [Boelcke, O. 14094 (BAA, BAB, SI)]; CHL [Gay, C. 2537 (P)].

Blumenbachia scabra (Miers) Urb.

Synonyms: *Blumenbachia scabra* (Miers) Urb. var. *schenkiana* Urb., *Caiophora scabra* (Miers) Urb. & Gilg, *Gripidea asperata* Miers, *Gripidea scabra* Miers
References: Santos, E. & Fromm Trinta, E., 1985; Weigend, M., 1997a.
Winding herb. Annual. Native. 0–600 m.
Countries: BRA (PAR, SCA).
Reference example: BRA [Hatschbach, G. 17414 (HB, HBR)].

Blumenbachia scabra (Miers) Urb. var. *schenkiana* Urb. = ***Blumenbachia scabra*** (Miers) Urb.

References: Santos, E. & Fromm Trinta, E., 1985; Weigend, M., 1997a.

Blumenbachia scandens Meyen = ***Blumenbachia silvestris*** Poepp.

Reference: Urban, I. & Gilg, E., 1900.

Blumenbachia sepiaria Ruiz & Pav. ex G. Don = ***Caiophora cirsiifolia*** C. Presl

Reference: Weigend, M., 1997b.

Blumenbachia silvestris Poepp.

Synonyms: *Blumenbachia domeykoana* Phil., *Blumenbachia mitis* Phil., *Blumenbachia nemorosa* Phil., *Blumenbachia scandens* Meyen, *Blumenbachia silvestris* Poepp. var. *australis* Urb. & Gilg, *Blumenbachia silvestris* Poepp. var. *leptocarpa* Speg., *Caiophora*

scandens Meyen & Klotzsch ex Walp., *Caiophora scandens* Meyen & Klotzsch ex Walp. var. *orientalis* Urb. & Gilg ex Kuntze, *Caiophora silvestris* (Poepp.) Urb. & Gilg, *Caiophora silvestris* (Poepp.) Urb. & Gilg var. l*eptocarpa* Urb. & Gilg, *Caiophora silvestris* (Poepp.) Urb. & Gilg var. *mitis* (Phil.) Urb. & Gilg, *Caiophora tomentosula* Urb. & Gilg, *Loasa ochagaviae* Phil., *Loasa scandens* Meyen, *Loasa volckmanni* Phil.
References: Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900.
Herb. Biannial or perennial. Endemic. 500–3000 m.
Countries: ARG (CHU, MEN, NEU, RNE); CHL (V, VI, VIII, IX, RME).
Reference examples: ARG [Cabrera, A. L. 32871 (SI)]; CHL [Poeppig, E. F. 858 (W)].

Blumenbachia silvestris Poepp. var. *australis* Urb. & Gilg = ***Blumenbachia silvestris*** Poepp.

Blumenbachia silvestris Poepp. var. *leptocarpa* Speg. = ***Blumenbachia silvestris*** Poepp.

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.

Blumenbachia urens (Vell.) Urb. = ***Blumenbachia latifolia*** Cambess.

Reference: Weigend, M., 1997a.

4.2. *Caiophora* C. Presl

Number of species: 16, 6 endemic

Caiophora absinthiifolia C. Presl = ***Caiophora coronata*** (Gillies ex Arn.) Hook. & Arn.

Reference: Weigend, M., 1997b.

Caiophora acanthoides Urb. & Gilg = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***taraxacoides*** (Killip) Weigend & M. Ackermann

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora aconquijae Sleumer

References: Sleumer, H. O., 1955; Weigend, M., 1997b.
Winding herb. Perennial. Endemic. 1500–2700 m.

Countries: ARG (CAT, TUC).
Reference examples: ARG [Sleumer, H. O. 2162 (BA, LP, P, SI, US, W), Sleumer, H. O. 2285 (SI)].

C*aiophora albiflora* (Griseb.) Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Weigend, M., 1997b.

Caiophora anemonoides Urb. & Gilg = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***rosulata***

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora angustisecta Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Weigend, M., 1997b.

Caiophora arechavaletae (Urb.) Urb. & Gilg

Synonyms: *Blumenbachia arechavaletae* Urb.
References: Weigend, M. & Ackermann, M., 2003; Weigend, M., 1997a.
Herb. Annual. Endemic. 0–500 m.
Countries: BRA (RGS); URY (MON).
Reference examples: BRA [Schlindwein, C. 1112 (TUEB)]; URY [Arechavaleta, J. 3425 (P, ZT)].

Caiophora boliviana Urb. & Gilg

References: Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997b.
Herb. Perennial. Native. 2000–3500 m.
Countries: ARG (SAL).
Reference example: ARG [Hunziker, J. H. 12352 (SI)].

[***Caiophora carduifolia*** C. Presl]

Synonyms: B*lumenbachia carduifolia (*C. Presl) Ball
Reference: Weigend, M. & Ackermann, M., 2003.
Notes: Species excluded from the project area.

Caiophora cernua (Griseb.) Urb. & Gilg ex Kurtz

Synonyms: *Blumenbachia cernua* Griseb., *Caiophora jörgensenii* I.M. Johnst., *Caiophora*

saltensis Urb. & Gilg, *Caiophora spegazzinii* Urb. & Gilg
References: Brücher, E. H., 1986; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997a, b.
Herb. Perennial. Endemic. 1000–3500 m.
Countries: ARG (CAT, COR, JUJ, LRI, SAL, SJU, SLU, TUC).
Reference example: ARG [Lorentz, P. G. 172 (GOET, K, SI)].

Caiophora chuquitensis (Meyen) Urb. & Gilg

Synonyms: *Blumenbachia chuquitensis* (Meyen) Hook. f., *Caiophora albiflora* (Griseb.) Urb. & Gilg, *Caiophora angustisecta* Urb. & Gilg, *Caiophora fiebrigii* Urb. & Gilg, *Caiophora heptamera* (Wedd.) Urb. & Gilg, *Caiophora heptamera* (Wedd.) Urb. & Gilg var. *albiflora* Griseb., *Caiophora lorentziana* Urb. & Gilg, *Caiophora macrocarpa* Urb. & Gilg, *Caiophora superba* Phil., *Loasa chuquitensis* Griseb., hom. illeg., *Loasa chuquitensis* Meyen, *Loasa heptamera* Wedd.
References: Ackermann, M. & Weigend, M., 2007; Brücher, E. H., 1986; Weigend, M., 1997b.
Herb or subshrub. Perennial. Native. 2500–4500 m.
Countries: ARG (CAT, JUJ, SAL, TUC); CHL (II).
Reference examples: ARG [Venturi, S. 4804 (SI)]; CHL [Luebert B., F. 1720 (SGO)].

Caiophora cirsiifolia C. Presl

Synonyms: *Blumenbachia sepiaria* Ruiz & Pav. ex G. Don, *Caiophora preslii* Urb. & Gilg, *Caiophora sepiaria* (Ruiz & Pav. ex G. Don) J.F. Macbr.
References: Ackermann, M. & Weigend, M., 2007; Weigend, M. & Ackermann, M., 2003.
Winding herb. Perennial. Native. 3500 m.
Countries: CHL (I).
Reference example: CHL [Grau, J. s.n. (M)].

Caiophora clavata Urb. & Gilg

Synonyms: *Blumenbachia contorta* Griseb., hom. illeg., *Caiophora tucumana* Urb. & Gilg
References: Brücher, E. H., 1986; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M. & Ackermann, M., 2003; Weigend, M., 1997a, b.
Herb. Native. 1500–4000 m.
Countries: ARG (CAT, JUJ, SAL, TUC).
Reference example: ARG [Lorentz, P. G. 694pp (B, CORD, G, GOET, K)].

Caiophora clavata Urb. & Gilg var. *dumetorum* (Urb. & Gilg) Sleumer = ***Caiophora dumetorum*** Urb. & Gilg

References: Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900.

[***Caiophora contorta*** (Desr.) C. Presl]

Synonyms: *Loasa contorta* Desr.
Reference: Weigend, M., 2000.
Notes: Species excluded from the project area.

Caiophora coronata (Gillies ex Arn.) Hook. & Arn.

Synonyms: *Blumenbachia coronata* (Gillies ex Arn.) Hieron., *Caiophora absinthiifolia* C. Presl, *Caiophora pycnophylla* Urb. & Gilg, *Loasa coronata* Gillies ex Arn.
References: Ackermann, M. & Weigend, M., 2007; Arroyo, M. T. K., Marticorena, C., Matthei, O. R., Muñoz-Schick, M. & Pliscoff, P., 2002; Brücher, E. H., 1986; Marticorena, C. & Quezada, M., 1985; Sleumer, H. O., 1955; Weigend, M. & Ackermann, M., 2003; Weigend, M., 1997b.
Herb. Perennial. Native. 2000–5000 m.
Countries: ARG (CAT, JUJ, LRI, MEN, SAL, SJU, TUC); CHL (II, III, IV, V, VIII, RME).
Reference examples: ARG [Hieronymus, G. H. E. W. 388 (B, CORD), Rodríguez, D. 35 (SI)]; CHL [Grandjot, G. F. 3798 (CONC)].

Caiophora deserticola Weigend & M. Ackermann

Reference: Ackermann, M. & Weigend, M., 2007.
Herb or subshrub. Perennial. Native. 2900–3700 m.
Countries: CHL (I).
Reference example: CHL [Muñoz-Schick, M. 4296 (SGO)].

Caiophora dissecta (Hook. & Arn.) Urb. & Gilg = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Caiophora dumetorum Urb. & Gilg

Synonyms: *Caiophora clavata* Urb. & Gilg var. *dumetorum* (Urb. & Gilg) Sleumer
References: Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997b.
Winding herb. Native. 2900–3900 m.
Countries: ARG (JUJ, LRI, MEN, SAL, TUC).
Reference examples: ARG [Sleumer, H. O. 3581 (SI), Spegazzini, C. L. 102168 (B, LPS)].

Caiophora eichleri (Urb.) Urb. & Gilg = ***Blumenbachia eichleri*** Urb.

Reference: Weigend, M., 1997a.

Caiophora espigneira (Gay) Urb. & Gilg = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Caiophora fiebrigii Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora heptamera (Wedd.) Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

References: Weigend, M., 1997b.

Caiophora heptamera (Wedd.) Urb. & Gilg var. *albiflora* Griseb. = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Weigend, M., 1997b.

Caiophora heptamera (Wedd.) Urb. & Gilg var. *mollis* Griseb. = ***Caiophora mollis*** (Griseb.) Urb. & Gilg

Reference: Weigend, M., 1997b.

Caiophora hibiscifolia (Griseb.) Urb. & Gilg

Synonyms: *Loasa hibiscifolia* Griseb.
References: Brücher, E. H., 1986; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997a.
Herb. Perennial. Native. 500–3000 m.
Countries: ARG (JUJ, SAL, TUC).
Reference example: ARG [Lorentz, P. G. 1028 (CORD, GOET)].

Caiophora jörgensenii I.M. Johnst. = ***Caiophora cernua*** (Griseb.) Urb. & Gilg ex Kurtz

Reference: Weigend, M., 1997b.

Caiophora kurtzii Urb. & Gilg = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Caiophora lateritia Klotzsch

Synonyms: *Blumenbachia lateritia* (Hook.) Griseb., *Caiophora platyphylla* Urb. & Gilg,

Loasa coccinea Loudon, nom. nud., *Loasa lateritia* Hook., nom. illeg., *Raphisanthe lateritia* (Hook.) Lilja
References: Brücher, E. H., 1986; Chiapella, J. & Ezcurra, C., 1999; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997a.
Winding herb. Perennial. Native. 0–3000 m.
Countries: ARG (CAT, JUJ, NEU, SAL, SDE, TUC).
Reference example: ARG [Hunziker, J. H. 12323 (SI)].

Caiophora lorentziana Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora macrocarpa Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora mollis (Griseb.) Urb. & Gilg

Synonyms: *Caiophora heptamera* (Wedd.) Urb. & Gilg var. *mollis* Griseb.
References: Grisebach, A. H. R., 1874; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997b.
Herb. Perennial. Endemic. 2000–4500 m.
Countries: ARG (CAT, LRI, SAL).
Reference example: ARG [Lorentz, P. G. 594 (CORD, GOET)].

Caiophora nivalis Lillo

References: Brücher, E. H., 1986; Lillo, M., 1919b; Sleumer, H. O., 1955; Weigend, M. & Ackermann, M., 2003; Weigend, M., 1997a.
Herb. Perennial. Endemic. 3500–4400 m.
Countries: ARG (CAT, JUJ, SAL, TUC).
Reference example: ARG [Lillo, M. 3090 (LIL)].

Caiophora patagonica Urb. & Gilg = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Caiophora platyphylla Urb. & Gilg = ***Caiophora lateritia*** Klotzsch

Reference: Weigend, M., 1997b.

Caiophora preslii Urb. & Gilg = ***Caiophora cirsiifolia*** C. Presl

Reference: Weigend, M. & Ackermann, M., 2003.

Caiophora prietea (Gay) Urb. & Gilg = ***Blumenbachia prietea*** Gay

References: Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.

Caiophora pulchella Urb. & Gilg

Synonyms: *Loasa pulchella* (Urb. & Gilg) R.L. Pérez-Mor. & Crespo
References: Pérez-Moreau, R. L. & Crespo, S., 1992; Weigend, M., 1997b.
Herb. Perennial. Endemic. 1900–4000 m.
Countries: ARG (MEN, SJU).
Reference example: ARG [Kiesling, R. 7350 (BAB, SI)].

Caiophora pycnophylla Urb. & Gilg = ***Caiophora coronata*** (Gillies ex Arn.) Hook. & Arn.

Reference: Weigend, M., 1997b.

Caiophora rahmeri Phil. = **Caiophora *rosulata*** (Wedd.) Urb. & Gilg subsp. ***rosulata***

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora rosulata (Wedd.) Urb. & Gilg subsp. ***rosulata***

Synonyms: *Caiophora anemonoides* Urb. & Gilg, *Caiophora rahmeri* Phil., *Loasa rosulata* Wedd.
References: Ackermann, M. & Weigend, M., 2007; Brücher, E. H., 1986; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 1997a.
Herb. Perennial. Native. 3500–4300 m.
Countries: CHL (I, II).
Reference example: CHL [Philippi, R. A. s.n. (BM, WU)].

Caiophora rosulata (Wedd.) Urb. & Gilg subsp. ***taraxacoides*** (Killip) Weigend & M. Ackermann

Synonyms: *Caiophora acanthoides* Urb. & Gilg, *Caiophora taraxacoides* Killip
References: Ackermann, M. & Weigend, M., 2007; Weigend, M., 1997b.
Herb. Perennial. Native. 3000–4800 m.
Countries: ARG (CAT, JUJ, SAL, TUC).
Reference example: ARG [Schickendantz, F. 142 (B, CORD, GOET)].

Caiophora saltensis Urb. & Gilg = ***Caiophora cernua*** (Griseb.) Urb. & Gilg ex Kurtz

Reference: Weigend, M., 1997b.

Caiophora scabra (Miers) Urb. & Gilg = ***Blumenbachia scabra*** (Miers) Urb.

References: Santos, E. & Fromm Trinta, E., 1985; Weigend, M., 1997a.

Caiophora scabra (Miers) Urb. & Gilg var. *schenkiana* (Urb.) Urb. & Gilg = ***Blumenbachia eichleri*** Urb.

References: Santos, E. & Fromm Trinta, E., 1985; Weigend, M., 1997a.

Caiophora scandens Meyen & Klotzsch ex Walp. = ***Blumenbachia silvestris*** Poepp.

References: Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.

Caiophora scandens Meyen & Klotzsch ex Walp. var. *orientalis* Urb. & Gilg ex Kuntze = ***Blumenbachia silvestris*** Poepp.

References: Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.

Caiophora sepiaria (Ruiz & Pav. ex G. Don) J.F. Macbr. = ***Caiophora cirsiifolia*** C. Presl

Reference: Weigend, M., 1997b.

Caiophora silvestris (Poepp.) Urb. & Gilg = ***Blumenbachia silvestris*** Poepp.

Caiophora silvestris (Poepp.) Urb. & Gilg var. *leptocarpa* Urb. & Gilg = ***Blumenbachia silvestris*** Poepp.

References: Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.

Caiophora silvestris (Poepp.) Urb. & Gilg var. mitis (Phil.) Urb. & Gilg = ***Blumenbachia silvestris*** Poepp.

Caiophora spegazzinii Urb. & Gilg = ***Caiophora cernua*** (Griseb.) Urb. & Gilg ex Kurtz

Reference: Brücher, E. H., 1986.

Caiophora superba Phil. = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora taraxacoides Killip = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***taraxacoides*** (Killip) Weigend & M. Ackermann

Reference: Ackermann, M. & Weigend, M., 2007.

Caiophora tomentosula Urb. & Gilg = ***Blumenbachia silvestris*** Poepp.

Caiophora tucumana Urb. & Gilg = ***Caiophora clavata*** Urb. & Gilg

Reference: Weigend, M., 1997b.

Grammatocarpus cumingii C. Presl = ***Scyphanthus elegans*** Sweet

Reference: Urban, I. & Gilg, E., 1900.

Grammatocarpus volubilis C. Presl = ***Scyphanthus elegans*** Sweet

Reference: Urban, I. & Gilg, E., 1900.

Gripidea asperata Miers = ***Blumenbachia scabra*** (Miers) Urb.

Reference: Weigend, M., 1997a.

Gripidea scabra Miers = ***Blumenbachia scabra*** (Miers) Urb.

Reference: Weigend, M., 1997a.

4.3. *Huidobria* Gay

Number of species: 2 endemic

Huidobria chilensis Gay

Synonyms: *Loasa chilensis* (Gay) Urb. & Gilg
Reference: Grau, J., 1997.
Shrub. Endemic. 0–1900 m.
Countries: CHL (II, III).
Reference example: CHL [Werdermann, E. 432 (SI)].

Huidobria fruticosa Phil.

Synonyms: *Loasa fruticosa* (Phil.) Urb. & Gilg
Reference: Grau, J., 1997.
Shrub. Endemic. 0–3700 m.
Countries: CHL (I, II, III).
Reference example: CHL [Ricardi, M. 320 (CONC)].

4.4. *Loasa* Adans.

Number of species: 33, 32 endemic, 1 introduced

Loasa acanthifolia Desr.

References: Baeza, C. M., Marticorena, C. & Rodríguez Ríos, R., 1999; Grau, J., 1988; Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a.
Herb. Perennial. Endemic. 1000 m.
Countries: ARG (NEU); CHL (VII, VIII, IX, X).
Reference examples: ARG [Crespo, S. 2391 (BAB)]; CHL [Behn, F. s.n. (SI), Grau, J. s.n. (M)].

Loasa acaulis (Phil.) Urb. & Gilg = **Loasa lateritia** Gillies ex Arn.

Loasa acerifolia Dombey ex Juss.

Synonyms: *Loasa furcata* Phil., *Loasa solaniifolia* Gay
References: Baeza, C. M., Marticorena, C. & Rodríguez Ríos, R., 1999; Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.
Herb. Annual. Endemic. 500–1000 m.
Countries: ARG (CHU, NEU, RNE); CHL (IV, VII, VIII, IX, X).
Reference examples: ARG [Diem, J. 1736 (SI), Diem, J. s.n. (SI)]; CHL [Montero, 7746 (CONC)].

Loasa acutiloba Urb. & Gilg = ***Loasa pinnatifida*** Gillies ex Arn.

Loasa alba D. Don = ***Loasa prostrata*** Gillies ex Arn.

Loasa aldunatea Gay = ***Loasa pallida*** Gillies ex Arn.

Loasa alpina (Poepp.) Urb. & Gilg = ***Loasa volubilis*** Dombey ex Juss.

Loasa amabilis Urb. & Gilg = ***Loasa volubilis*** Dombey ex Juss.

Loasa aphanantha Urb. & Gilg = ***Loasa heterophylla*** Hook. & Arn.

Loasa argentina Urb. & Gilg

Synonyms: *Loasa patagonica* Urb. & Gilg, nom. nud., *Loasa pinnatifida* Gillies ex Arn. var. *gracilis* Speg.
Reference: Crespo, S. & Pérez-Moreau, R. L., 1981.
Herb. Perennial. Endemic. 0–2500 m.
Countries: ARG (CHU, MEN, NEU, RNE, SCR); CHL (XI, XII).
Reference examples: ARG [Boelcke, O. 12879 (SI), Boelcke, O. 13759 (BAB, SI)]; CHL [Rentzell, I. 6184 (SI)].

Loasa arnottiana Gay

References: Grau, J., 1988; Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic. 0–1800 m.
Countries: CHL (IV).
Reference examples: CHL [Gay, C. 347 (P), Grau, J. s.n. (M)].

Loasa artemisiifolia Poepp. ex Urb. & Gilg = ***Loasa volubilis*** Dombey ex Juss.

[*Loasa asterias* Sleumer, hom. illeg.]

Notes: Dubious name.

Loasa asterias Dusén = ***Loasa bergii*** Hieron.

Loasa barneoudii Gay = ***Loasa heterophylla*** Hook. & Arn.

Reference: Grau, H. R. J., 1996.

Loasa bergii Hieron.

Synonyms: *Loasa asterias* Dusén, *Loasa karraikensis* Macloskie, *Loasa petrophila* Urb., nom. nud., *Loasa urbanii* A. Soriano, *Scyphanthus stenocarpus* Hicken, hom. illeg.
References: Cabrera, A. L., 1966c; Crespo, S. & Pérez-Moreau, R. L., 1981; Marticorena, C. & Quezada, M., 1985; Sleumer, H. O., 1955.
Herb. Perennial. Endemic. 0–2500 m.
Countries: ARG (BAI, CHU, MEN, NEU, RNE, SCR); CHL (XI, XII).
Reference examples: ARG [Cabrera, A. L. 33139 (SI)]; CHL [Rentzell, I. 6184 (SI)].

Loasa bertrandii Phil. = ***Loasa elongata*** Hook. & Arn.

Loasa bridgesii Urb. & Gilg = ***Loasa pinnatifida*** Gillies ex Arn.

Loasa bryoniifolia Schrad. ex DC. = ***Loasa tricolor*** Ker Gawl.

Loasa caespitosa Phil.

Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic. 2900–3500 m.
Countries: CHL (III, IV, V, RME).
Reference example: CHL [Ricardi, M. 2938 (CONC)].

Loasa chilensis (Gay) Urb. & Gilg = ***Huidobria chilensis*** Gay

Reference: Grau, J., 1997.

Loasa chillana Urb. & Gilg = ***Loasa pinnatifida*** Gillies ex Arn.

Loasa chuquitensis Griseb., hom. illeg. = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Loasa chuquitensis Meyen = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Weigend, M., 1997b.

Loasa coccinea Loudon, nom. nud. = ***Caiophora lateritia*** Klotzsch

Reference: Weigend, M., 1997b.

Loasa contorta Desr. = ***Caiophora contorta*** (Desr.) C. Presl

Reference: Weigend, M., 2000.

Loasa coronata Gillies ex Arn. = ***Caiophora coronata*** (Gillies ex Arn.) Hook. & Arn.

Reference: Weigend, M., 1997b.

Loasa dissecta Hook. & Arn. = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Loasa elongata Phil., nom. nud. = ***Loasa heterophylla*** Hook. & Arn.

Reference: Grau, H. R. J., 1996.

Loasa elongata Hook. & Arn.

Synonyms: *Loasa bertrandii* Phil., *Loasa urmenetae* Phil.
Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic. 0–700 m.
Countries: CHL (II, III, IV).
Reference example: CHL [Ricardi, M. 2067 (CONC)].

Loasa filicifolia Poepp. = ***Loasa pinnatifida*** Gillies ex Arn.

Loasa floribunda Hook. & Arn.

Synonyms: *Loasa floribunda* Hook. & Arn. var. *brachysepala* Urb. & Gilg
References: Arroyo, M. T. K., Marticorena, C., Matthei, O. R., Muñoz-Schick, M. & Pliscoff, P., 2002; Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic.
Countries: CHL (IV, V, RME).
Reference examples: CHL [Cuming, H. 670 (B), Morrison, J. L. 16892 (SI)].

Loasa floribunda Hook. & Arn. var. *brachysepala* Urb. & Gilg = ***Loasa floribunda*** Hook. & Arn.

Loasa fruticosa (Phil.) Urb. & Gilg = ***Huidobria fruticosa*** Phil.

Reference: Grau, J., 1997.

Loasa furcata Phil. = ***Loasa acerifolia*** Dombey ex Juss.

Reference: Urban, I. & Gilg, E., 1900.

Loasa gayana Urb. & Gilg

Synonyms: *Loasa sagittata* auct. non Hook. & Arn.
Reference: Marticorena, C. & Quezada, M., 1985.
Winding herb. Perennial. Endemic. 0–500 m.
Countries: CHL (IX, X).
Reference example: CHL [Hollermayer, A. 815 (B)].

Loasa heptamera Wedd. = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg

Reference: Weigend, M., 1997b.

Loasa heterophylla Hicken, hom. illeg. = ***Loasa tricolor*** Ker Gawl.

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a.

Loasa heterophylla Hook. & Arn.

Synonyms: *Loasa aphanantha* Urb. & Gilg, *Loasa barneoudii* Gay, *Loasa elongata* Phil., nom. nud., *Loasa insons* Poepp. var. *prostrata* Poepp., *Loasa parviflora* Phil., hom. illeg., *Loasa subandina* F. Phil.
References: Grau, H. R. J., 1996; Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic. 1700–2600 m.
Countries: ARG (MEN); CHL (IV, V, VII, RME).
Reference examples: ARG [Spegazzini, C. L. 18710 (LP)]; CHL [Marticorena, A. 608 (CONC)].

Loasa hibiscifolia Griseb. = ***Caiophora hibiscifolia*** (Griseb.) Urb. & Gilg

References: Brücher, E. H., 1986; Sleumer, H. O., 1955; Weigend, M., 1997b.

Loasa humilis Phil.

Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic. 3000 m.
Countries: CHL (VII).
Reference example: CHL [Philippi, R. A. 1747 (SGO)].

Loasa ignea Phil. = ***Mentzelia scabra*** Kunth subsp. ***chilensis*** (Gay) Weigend

Reference: Weigend, M., 2007.

Loasa illapelina Phil.

Synonyms: *Loasa illapelina* Phil. var. *laciniata* (Phil.) Urb. & Gilg, *Loasa leucantha* Phil.
Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic. 0–100 m.
Countries: CHL (IV).
Reference example: CHL [Jiles P., C. 3936 (CONC)].

Loasa illapelina Phil. var. *laciniata* (Phil.) Urb. & Gilg = ***Loasa illapelina*** Phil.

Loasa incurva Crespo & R.L. Pérez-Mor.

Reference: Pérez-Moreau, R. L. & Crespo, S., 1983.
Herb. Perennial. Endemic. 2000–2500 m.
Countries: ARG (MEN, NEU).
Reference example: ARG [Boelcke, O. 13881 (BAA, BAB, SI)].

Loasa insons Poepp.

Synonyms: *Loasa intricata* Gay, *Loasa meyeniana* Walp., *Loasa tricolor* Ker Gawl. var. *insons* (Poepp.) Urb. & Gilg, *Loasa tricolor* Ker Gawl. var. *mendocina* Urb. & Gilg
References: Marticorena, C. & Quezada, M., 1985; Teillier A., S., 2003.
Herb. Annual. Endemic. 1200–2300 m.
Countries: ARG (MEN); CHL (IV, V, VI, VII, RME).
Reference examples: ARG [Wilczek, E. 406 (Z)]; CHL [Zoellner, O. 7659 (CONC)].

Loasa insons Poepp. var. *prostrata* Poepp. = ***Loasa heterophylla*** Hook. & Arn.

Reference: Grau, H. R. J., 1996.

Loasa intricata Gay = ***Loasa insons*** Poepp.

Reference: Grau, H. R. J., 1996.

Loasa karraikensis Macloskie = ***Loasa bergii*** Hieron.

Loasa kurtzii Urb. & Gilg = ***Loasa sigmoidea*** Urb. & Gilg

Loasa lateritia Hook., nom. illeg. = ***Caiophora lateritia*** Klotzsch

Reference: Weigend, M., 1997b.

Loasa lateritia Gillies ex Arn.

Synonyms: *Blumenbachia acaulis* Phil., *Loasa acaulis* (Phil.) Urb. & Gilg
References: Grau, J., 1988; Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900.
Herb. Perennial. Endemic. 1300–3000 m.
Countries: ARG (MEN, NEU); CHL (IV, VII, VIII, IX).
Reference examples: ARG [Boelcke, O. 13775 (BAA, BAB, SI)]; CHL [Werdermann, E. 1342 (SI)].

Loasa leucantha Phil. = ***Loasa illapelina*** Phil.

Reference: Urban, I. & Gilg, E., 1900.

Loasa longiseta Phil.

Synonyms: *Loasa sessiliflora* Phil.
Reference: Marticorena, C. & Quezada, M., 1985.
Subshrub. Endemic. 200–2300 m.
Countries: CHL (III, IV).
Reference example: CHL [Ricardi, M. 557 (CONC)].

Loasa malesherbioides Phil.

References: Grau, J., 1988; Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1991b.
Herb. Annual. Endemic. 1400–3500 m.
Countries: ARG (SJU); CHL (II, III).
Reference examples: ARG [Kiesling, R. 7489 (BAB, SI)]; CHL [Zöllner, O. 4955 (CONC)].

Loasa martinii Phil.

Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic. 0–800 m.
Countries: CHL (IX, X).
Reference example: CHL [Sparre, B. B. 313 (CONC)].

Loasa meyeniana Walp. = ***Loasa insons*** Poepp.

Reference: Urban, I. & Gilg, E., 1900.

Loasa micrantha Poepp.

Synonyms: *Loasa remyi* Gay
References: Arroyo, M. T. K., Matthei, O. R., Marticorena, C., Muñoz-Schick, M., Pérez, F. & Humaña, A. M., 2001[2000].
Herb. Annual. Endemic. 200–800 m.
Countries: CHL (VI, VII, VIII, IX, RME).
Reference example: CHL [Arroyo, M. T. K. 994995 (CONC, SGO)].

Loasa multifida Gay

Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic. 300–1100 m.
Countries: CHL (III, IV).
Reference example: CHL [Jiles P., C. 3483 (CONC)].

Loasa muralis Griseb. = ***Blumenbachia insignis*** Schrad.

Reference: Sleumer, H. O., 1955.

Loasa nana Phil.

References: Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.
Herb. Perennial. Endemic. 1500–3000 m.
Countries: ARG (NEU, RNE); CHL (IX, X).
Reference examples: ARG [Burkart, A. 9633 (SI)]; CHL [Marticorena, C. 1329 (CONC)].

Loasa nemoralis Phil. = ***Loasa sclareifolia*** Juss.

Loasa nitida Desr.

References: Grau, J. & Bayer, E., 1994; Weigend, M., 1998.
Herb. Annual. Introduced. 0–500 m.
Countries: CHL (I, II).
Reference example: CHL [Grau, J. 4978 (CONC, M, SGO)].

Loasa ochagaviae Phil. = ***Blumenbachia silvestris*** Poepp.

Reference: Urban, I. & Gilg, E., 1900.

Loasa pallida Gillies ex Arn.

Synonyms: *Loasa aldunatea* Gay
References: Arroyo, M. T. K., Marticorena, C., Matthei, O. R., Muñoz-Schick, M. & Pliscoff, P., 2002; Marticorena, C. & Quezada, M., 1985.
Subshrub. Endemic. 1400–3200 m.
Countries: CHL (III, IV, V, RME).
Reference example: CHL [Jiles P., C. 4728 (CONC)].

Loasa palmata Spreng. = ***Blumenbachia insignis*** Schrad.

Reference: Weigend, M., 1997a.

Loasa paradoxa Urb. & Gilg

Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic. 2900–3500 m.
Countries: CHL (V, RME).
Reference example: CHL [Gay, C. 225 (B)].

[***Loasa parviflora*** Schrad. ex DC.]

References: Sleumer, H. O., 1955; Weigend, M., 1997a.
Notes: Species excluded from the project area.

Loasa parviflora Phil., hom. illeg. = ***Loasa heterophylla*** Hook. & Arn.

Loasa patagonica Speg., nom. illeg. = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Loasa patagonica Urb. & Gilg, nom. nud. = ***Loasa argentina*** Urb. & Gilg

Reference: Crespo, S. & Pérez-Moreau, R. L., 1981.

Loasa petrophila Urb., nom. nud. = ***Loasa bergii*** Hieron.

Loasa pinnatifida Gillies ex Arn.

Synonyms: *Loasa acutiloba* Urb. & Gilg, *Loasa bridgesii* Urb. & Gilg, *Loasa chillana* Urb. & Gilg, *Loasa filicifolia* Poepp., *Loasa poeppigiana* Urb. & Gilg, *Loasa tripartita* Urb. & Gilg
Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic.
Countries: ARG (NEU); CHL (VI, VII, VIII, IX, X, RME).
Reference examples: ARG [Boelcke, O. 11586 (SI)]; CHL [Marticorena, C. 867 (CONC)].

Loasa pinnatifida Gillies ex Arn. var. *gracilis* Speg. = ***Loasa argentina*** Urb. & Gilg

Reference: Crespo, S. & Pérez-Moreau, R. L., 1981.

Loasa placei Lindl.

Synonyms: *Loasa tricolor* Ker Gawl. var. *placei* (Lindl.) Urb. & Gilg
Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Annual. Endemic. 300–1000 m.
Countries: CHL (III, IV, V, VI, RME).
Reference example: CHL [Grandjot, G. F. 3006 (CONC)].

Loasa poeppigiana Urb. & Gilg = ***Loasa pinnatifida*** Gillies ex Arn.

Loasa prostrata Gillies ex Arn.

Synonyms: *Loasa alba* D. Don, *Loasa prostrata* Gillies ex Arn. var. *cumingii* Hook. & Arn., *Loasa tricolor* Ker Gawl. var. *prostrata* (Gillies ex Arn.) Urb. & Gilg
Reference: Grau, H. R. J., 1996.
Herb. Annual. Endemic. 900–2500 m.
Countries: CHL (IV, V, VI, RME).
Reference examples: CHL [Marticorena, A. 669 (CONC), Morrison, J. L. 17278 (SI)].

Loasa prostrata Gillies ex Arn. var. *cumingii* Hook. & Arn. = ***Loasa prostrata*** Gillies ex Arn.

Reference: Grau, H. R. J., 1996.

Loasa pulchella (Urb. & Gilg) R.L. Pérez-Mor. & Crespo = ***Caiophora pulchella*** Urb. & Gilg

Loasa remyi Gay = ***Loasa micrantha*** Poepp.

Reference: Urban, I. & Gilg, E., 1900.

Loasa rosulata Wedd. = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***rosulata***

Reference: Weigend, M., 1997b.

Loasa sagittata Hook. & Arn.

Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic.
Countries: CHL (X).
Reference example: CHL [Cuming, H. 60 (B)].

Loasa sagittata auct. non Hook. & Arn. = ***Loasa gayana*** Urb. & Gilg

Loasa scandens Meyen = ***Blumenbachia silvestris*** Poepp.

References: Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.

Loasa sclareifolia Juss.

Synonyms: *Loasa nemoralis* Phil., *Loasa sclareifolia* Juss. var. *brachycarpa* Urb. & Gilg, *Loasa sclareifolia* Juss. var. *inermis* Urb. & Gilg, *Loasa sclareifolia* Juss. var. *nemoralis* (Phil.) Urb. & Gilg
References: Marticorena, C. & Quezada, M., 1985; Rossow, R. A., 1993b.
Herb. Biannial o perennial. Endemic. 0–2000 m.
Countries: ARG (NEU); CHL (III, IV, V, VI, VII, VIII, IX, RME).
Reference examples: ARG [Rossow, R. A. 4537 (BAB, BAF)]; CHL [Marticorena, C. 1256a (CONC)].

Loasa sclareifolia Juss. var. *brachycarpa* Urb. & Gilg = ***Loasa sclareifolia*** Juss.

Loasa sclareifolia Juss. var. *inermis* Urb. & Gilg = ***Loasa sclareifolia*** Juss.

Loasa sclareifolia Juss. var. *nemoralis* (Phil.) Urb. & Gilg = ***Loasa sclareifolia*** Juss.

Loasa sessiliflora Phil. = ***Loasa longiseta*** Phil.

Loasa sigmoidea Urb. & Gilg

Synonyms: *Loasa kurtzii* Urb. & Gilg

References: Arroyo, M. T. K., Marticorena, C., Matthei, O. R., Muñoz-Schick, M. & Pliscoff, P., 2002; Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic. 2000–3300 m.
Countries: ARG (MEN); CHL (III, IV, VII, RME).
Reference examples: ARG [Burkart, A. 14163 (SI, US)]; CHL [Grandjot, G. F. 3576 (SI)].

[*Loasa simoni* Phil.]

Reference: Urban, I. & Gilg, E., 1900.
Notes: Dubious name.

Loasa solaniifolia Gay = ***Loasa acerifolia*** Dombey ex Juss.

Reference: Urban, I. & Gilg, E., 1900.

Loasa spegazzinii Macloskie = ***Blumenbachia dissecta*** (Hook. & Arn.) Weigend & J. Grau

Loasa subandina F. Phil. = ***Loasa heterophylla*** Hook. & Arn.

Reference: Grau, H. R. J., 1996.

Loasa tricolor Ker Gawl.

Synonyms: *Loasa bryoniifolia* Schrad. ex DC., *Loasa heterophylla* Hicken, hom. illeg.
References: Luebert, B. F. & Muñoz-Schick, M., 2005; Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900.
Herb. Annual. Endemic. 0–1500 m.
Countries: ARG (MEN, NEU, SJU); CHL (III, IV, V, RME).
Reference examples: ARG [Boelcke, O. 14404 (BAA, BAB, SI)]; CHL [Werdermann, E. 38 (SI)].

Loasa tricolor Ker Gawl. var. *insons* (Poepp.) Urb. & Gilg = ***Loasa insons*** Poepp.

Loasa tricolor Ker Gawl. var. *mendocina* Urb. & Gilg = ***Loasa insons*** Poepp.

References: Grau, H. R. J., 1996; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.

Loasa tricolor Ker Gawl. var. *placei* (Lindl.) Urb. & Gilg = ***Loasa placei*** Lindl.

Reference: Grau, H. R. J., 1996.

Loasa tricolor Ker Gawl. var. *prostrata* (Gillies ex Arn.) Urb. & Gilg = ***Loasa prostrata*** Gillies ex Arn.

Reference: Grau, H. R. J., 1996.

Loasa triloba Dombey ex Juss.

References: Grau, J., 1988; Marticorena, C. & Quezada, M., 1985; Weigend, M., 1998.
Herb. Annual. Endemic. 0–1700 m.
Countries: CHL (III, IV, V, VI, VII, VIII, IX).
Reference example: CHL [Hellwig, F. H. s.n. (M)].

Loasa tripartita Urb. & Gilg = ***Loasa pinnatifida*** Gillies ex Arn.

[*Loasa unguiculata* Urb. & Gilg]

Notes: Dubious name.

Loasa urbanii A. Soriano = ***Loasa bergii*** Hieron.

Loasa urens Jacq. = ***Nasa urens*** (Jacq.) Weigend

Reference: Weigend, M., 1998.

Loasa urens Vell., hom. illeg. = ***Blumenbachia latifolia*** Cambess.

Reference: Weigend, M., 1997a.

Loasa urmenetae Phil. = ***Loasa elongata*** Hook. & Arn.

Loasa volckmanni Phil. = ***Blumenbachia silvestris*** Poepp.

Reference: Urban, I. & Gilg, E., 1900.

Loasa volubilis Dombey ex Juss.

Synonyms: *Loasa alpina* (Poepp.) Urb. & Gilg, *Loasa amabilis* Urb. & Gilg, *Loasa artemisiifolia* Poepp. ex Urb. & Gilg, *Loasa volubilis* Dombey ex Juss. var. *alpina* Poepp.

Reference: Marticorena, C. & Quezada, M., 1985.
Herb. Perennial. Endemic. 100–2600 m.
Countries: CHL (V, VII, VIII, IX, RME).
Reference example: CHL [Poeppig, E. F. 852 (G, M, P, W)].

Loasa volubilis Dombey ex Juss. var. *alpina* Poepp. = **Loasa volubilis** Dombey ex Juss.

4.5. *Mentzelia* L.

Number of species: 5, 2 endemic

Mentzelia albescens (Gillies ex Arn.) Griseb.

Synonyms: *Bartonia albescens* Gillies ex Arn., *Bartonia sinuata* C. Presl, *Nuttallia albescens* (Gillies ex Arn.) Standl.
References: Cabrera, A. L., 1966c; Darlington, J., 1934; Grisebach, A. H. R., 1874; Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a; Sleumer, H. O., 1955.
Herb. Biannial. Endemic. 0–2500 m.
Countries: ARG (BAI, CAT, COR, LPA, LRI, MEN, NEU, RNE, SJU, SLU, TUC); CHL (III, IV, V, RME); URY (SOR).
Reference examples: ARG [Kiesling, R. 4819 (SI)]; CHL [Werdermann, E. 101 (C, F, M, SI)]; URY [Berro, M. B. 2708 (MVFA)].

Mentzelia andina I.M. Johnst., hom. illeg. = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a.

Mentzelia andina Urb. & Gilg = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Mentzelia aspera L.

References: Darlington, J., 1934; Sleumer, H. O., 1955; Weigend, M., 2000.
Herb. Annual. Native. 500–2000 m.
Countries: ARG (JUJ, MEN, SAL, TUC).
Reference example: ARG [Krapovickas, A. 1661 (SI)].

Mentzelia aspera Vell., hom. illeg. = ***Blumenbachia eichleri*** Urb.

Reference: Weigend, M., 1997a.

Mentzelia bartonioides (C. Presl) Urb. & Gilg

Synonyms: *Acrolasia bartonioides* C. Presl, *Acrolasia bartonioides* Gay, hom. illeg., *Acrolasia pinnatifida* Phil., *Acrolasia solieri* Gay, *Mentzelia andina* I.M. Johnst., hom. illeg., *Mentzelia andina* Urb. & Gilg, *Mentzelia citrina* Urb. & Gilg, *Mentzelia haenkei* A. Gray, *Mentzelia pinnatifida* (Phil.) Urb. & Gilg, *Mentzelia pinnatifida* (Phil.) Urb. & Gilg var. *uniseriata* Hauman, *Mentzelia pinnatifida* Sleumer, hom. illeg., *Mentzelia solieri* (Gay) Urb. & Gilg ex Urb.
References: Darlington, J., 1934; Marticorena, C. & Quezada, M., 1985; Pérez-Moreau, R. L. & Crespo, S., 1988a.
Herb. Annual. Endemic. 2000–4000 m.
Countries: ARG (MEN, NEU, SJU); CHL (III, IV).
Reference examples: ARG [Kiesling, R. 7549 (SI)]; CHL [Philippi, R. A. 734 (US)].

Mentzelia chilensis Gay = ***Mentzelia scabra*** Kunth subsp. ***chilensis*** (Gay) Weigend

Reference: Weigend, M., 2007.

Mentzelia chilensis Griseb., hom. illeg. = ***Mentzelia scabra*** Kunth subsp. ***cordobensis*** (Urb. & Gilg ex Kurtz) Weigend

Reference: Darlington, J., 1934.

Mentzelia chilensis Gay var. *atacamensis* Urb. & Gilg = ***Mentzelia scabra*** Kunth subsp. ***atacamensis*** (Urb. & Gilg) Weigend

Reference: Weigend, M., 2007.

Mentzelia citrina Urb. & Gilg = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a.

Mentzelia cordobensis Urb. & Gilg ex Kurtz = ***Mentzelia scabra*** Kunth subsp. ***cordobensis*** (Urb. & Gilg ex Kurtz) Weigend

Reference: Weigend, M., 2007.

Mentzelia fendleriana Urb. & Gilg = ***Mentzelia scabra*** Kunth subsp. ***chilensis*** (Gay) Weigend

Reference: Weigend, M., 2007.

Mentzelia grisebachii Urb. & Gilg = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz

Reference: Weigend, M., 2007.

Mentzelia haenkei A. Gray = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Mentzelia ignea (Phil.) Urb. & Gilg = ***Mentzelia scabra*** Kunth subsp. ***chilensis*** (Gay) Weigend

Reference: Weigend, M., 2007.

Mentzelia jujuyensis Sleumer = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz

Mentzelia parviflora Monticelli = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz

Mentzelia parvifolia Urb. & Gilg ex Kurtz

Synonyms: *Acrolasia elata* Phil., *Mentzelia grisebachii* Urb. & Gilg, *Mentzelia jujuyensis* Sleumer, *Mentzelia parviflora* Monticelli, *Mentzelia parvifolia* Urb. & Gilg ex Kurtz var. *transiens* Sleumer
References: Darlington, J., 1934; Monticelli, J. V., 1938; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900.
Herb. Native. 0–3500 m.
Countries: ARG (CAT, CHA, COR, FOR, JUJ, LPA, LRI, MEN, SAL, SDE, SFE, SJU, SLU, TUC).
Reference example: ARG [Hunziker, J. H. 12488 (MO, NY, SI)].

Mentzelia parvifolia Urb. & Gilg ex Kurtz var. *transiens* Sleumer = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz

Mentzelia pinnatifida (Phil.) Urb. & Gilg = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Mentzelia pinnatifida Sleumer, hom. illeg. = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a.

Mentzelia pinnatifida (Phil.) Urb. & Gilg var. *uniseriata* Hauman = ***Mentzelia bartonioides*** (C.

Presl) Urb. & Gilg

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a.

Mentzelia scabra Kunth subsp. ***atacamensis*** (Urb. & Gilg) Weigend

Synonyms: *Mentzelia chilensis* Gay var. *atacamensis* Urb. & Gilg
References: Darlington, J., 1934; Weigend, M., 2007.
Subshrub. Endemic. 0–3000 m.
Countries: CHL (II, IV).
Reference example: CHL [Werdermann, E. 798 (E, G, M, SI, Z)].

Mentzelia scabra Kunth subsp. ***chilensis*** (Gay) Weigend

Synonyms: *Loasa ignea* Phil., *Mentzelia chilensis* Gay, *Mentzelia fendleriana* Urb. & Gilg, *Mentzelia ignea* (Phil.) Urb. & Gilg
References: Darlington, J., 1934; Weigend, M., 2007.
Shrub or subshrub. Native. 0–3000 m.
Countries: CHL (IV).
Reference example: CHL [Jiles P., C. 1888 (CONC, M)].

Mentzelia scabra Kunth subsp. ***cordobensis*** (Urb. & Gilg ex Kurtz) Weigend

Synonyms: *Mentzelia chilensis* Griseb., hom. illeg., *Mentzelia cordobensis* Urb. & Gilg ex Kurtz
References: Darlington, J., 1934; Di Fulvio, T. E., 1967; Sleumer, H. O., 1955; Urban, I. & Gilg, E., 1900; Weigend, M., 2007.
Subshrub. Endemic. 500–2000 m.
Countries: ARG (COR, JUJ, SAL, TUC).
Reference example: ARG [Lorentz, P. G. 265 (BA, GOET, K)].

Mentzelia solieri (Gay) Urb. & Gilg ex Urb. = ***Mentzelia bartonioides*** (C. Presl) Urb. & Gilg

Reference: Pérez-Moreau, R. L. & Crespo, S., 1988a.

4.6. *Nasa* Weigend

Number of species: 1

Nasa urens (Jacq.) Weigend

Synonyms: *Loasa urens* Jacq.
Reference: Weigend, M., 1998.
Herb. Annual. Native. 0–100 m.
Countries: CHL (II).
Reference example: CHL [Jaffuel, F. 2566 (CONC)].

Nuttallia albescens (Gillies ex Arn.) Standl. = ***Mentzelia albescens*** (Gillies ex Arn.) Griseb.

Reference: Darlington, J., 1934.

Raphisanthe lateritia (Hook.) Lilja = ***Caiophora lateritia*** Klotzsch

Reference: Weigend, M., 1997b.

4.7. *Scyphanthus* Sweet

Number of species: 1, 1 endemic

Scyphanthus elegans Sweet

Synonyms: *Grammatocarpus cumingii* C. Presl, *Grammatocarpus volubilis* C. Presl, *Scyphanthus stenocarpus* (Poepp.) Urb. & Gilg
Reference: Marticorena, C. & Quezada, M., 1985.
Winding herb. Annual or biannial Endemic. 800–1600 m.
Countries: CHL (IV, V, VI, VII, VIII, IX, RME).
Reference example: CHL [Worth, C. R. 16544 (SI)].

Scyphanthus stenocarpus (Poepp.) Urb. & Gilg = ***Scyphanthus elegans*** Sweet

Scyphanthus stenocarpus Hicken, hom. illeg. = ***Loasa bergii*** Hieron.

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4.9. Abbreviations

auct. non = name erroneously applied. ex = indicates that the author listed after the “ex” is the author of the validly published name but who attributed that name to the author listed before the “ex.” f. = form. nom. illeg. = illegitimate name, a later homonym. nom. cons. = name conserved in the International Code of Botanical Nomenclature. nom. illeg. = illegitimate name. nom. nud. = name not accompanied by a valid description. subsp. = subspecies. var. = variety.

Acronyms used in the Catalogue to designate the countries and provinces/states/departments/ regions

Argentina (ARG): Buenos Aires (BAI), Catamarca (CAT), Chaco (CHA), Chubut (CHU), Córdoba (COR), Corrientes (COS), Entre Ríos (ERI), Formosa (FOR), Jujuy (JUJ), La Pampa (LPA), La Rioja (LRI), Mendoza (MEN), Misiones (MIS), Neuquén (NEU), Río Negro (RNE), Salta (SAL), San Juan (SJU), San Luis (SLU), Santa Cruz (SCR), Santa Fe (SFE), Santiago del Estero (SDE), Tucumán (TUC).

Brasil (BRA): Paraná (PAR), Rio Grande do Sul (RGS), Santa Catarina (SCA).

Chile (CHL): Región I – Tarapacá (I), Región II – Antofagasta (II), Región III – Atacama (III), Región IV – Coquimbo (IV), Región V – Valparaíso (V), Región VI – O’Higgins (VI), Región VII – Maule (VII), Región VIII – Bío Bío (VIII), Región IX – Araucanía (IX), Región X – Los Lagos (X), Región XI – Aisén (XI), Región XII – Magallanes(XII), Región Metropolitana deSantiago (RME).

Paraguay (PRY): Caazapá (CAA), Central (CEN), Guairá (GUA), Misiones (MIE).

Uruguay (URY): Artigas (ART), Colonia (COL), Lavalleja (LAV), Maldonado (MAL), Montevideo (MON), Río Negro (RNO), Rocha (ROC), Soriano (SOR).

5. Catalogue of the Vascular Plants of Bolivia: Loasaceae*

5.1. Loasaceae Juss., Ann. Mus. Natl. Hist. Nat. 5: 21. 1804.

4 genera, 27 species, 5 endemic species.

5.2. *Caiophora* C. Presl, Reliq. Haenk. 2: 41. 1831.

16 species, 4 endemic species.

In the protologue Presl (1831) described the genus as *Caiophora* with “ i “, but Urban & Gilg (1900) changed it to *Cajophora* written with “ j “. This form was used afterwards. Here we use the original form.

Caiophora andina Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 287. 1900.

> Synonyms: *Loasa heptamera* var. *chelidonifolia* Wedd., *Caiophora mandoniana* Urb. & Gilg.
> References: Foster, R. C. (1958), Weigend, M. (1997).
> Habit: Herb. Status: Native. Elevation: 3500-4500 m. Region: Altiplano. Vegetation Zone: Humid puna, Dry puna.
> Distribution: Cochabamba, La Paz, Oruro.
> Voucher specimen: D.M. Spooner & García 6506 (LPB, TEX). Type specimen: Mandon 620 p.p. (LT: G, IT: NY, P, S).

Caiophora boliviana Urb. & Gilg in Engl. & Prantl, Nat. Pflanzenfam. 3(Ab. 6a): 119. 1894.

> References: Foster, R. C. (1958), Weigend, M. (1997).
> Habit: Herb. Status: Native. Elevation: 2000–4500 m. Region: Altiplano. Vegetation Zone:

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*To be published as: Weigend M, Ackermann M. forthc. Loasaceae. In: Jörgensen PM ed. The Catalogue of the Vascular Plants of Bolivia. St. Louis, Missouri Botanical Garden Press.

Dry puna.
Distribution: Tarija.
Voucher specimen: E. Bastián 546 (LPB, MSB). Type specimen: R.W. Pearce s.n. (LT: K).

Caiophora buraeavii Urb. & Gilg ex Rusby, Mem. Torrey Bot. Club 3(3): 37. 1893.

References: Rusby, H. H. (1893), Foster, R. C. (1958), Weigend, M. (1997).
Habit: Herb. Vine. Status: Endemic. Elevation: 2500–4000 m. Region: Andes. Vegetation Zone: Yungas, Paramo Yungeno.
Distribution: Chuquisaca, Cochabamba, La Paz.
Voucher specimen: D.M. Spooner et al. 6633 (LPB, TEX, WIS). Type specimen: M. Bang 1156 (LT: M; IT: BM, E, HUH, NY, US).

Caiophora canarinoides (Lenné & C. Koch) Urb. & Gilg in Engl. & Ptantl, Nat. Pflanzenfam. 3(6a): 119. 1894.

Synonyms: *Illairea canarinoides* Lenné & C. Koch, *Loasa canarinoides* (Lenné & C. Koch) Britton, *Caiophora macrophylla* Rusby.
References: Foster, R. C. (1958), Adolfo María, H. (1966), Weigend, M. (1997).
Habit: Herb. Vine. Status: Native. Elevation: 2500–4000 m. Region: Andes. Vegetation Zone: Yungas, Paramo Yungeno.
Distribution: Chuquisaca, Cochabamba, La Paz, Tarija.
Voucher specimen: S.G. Beck 18744 (LPB, MSB).

Caiophora cernua (Griseb.) Urb. & Gilg, Rev. Mus. La Plata, Secc. Bot. 5: 291. 1893.

Synonyms: *Blumenbachia cernua* Griseb.
References: Foster, R. C. (1958), Weigend, M. (1997).
Notes: Reported by R. C. Foster (1958), but we have not seen material from Bolivia. It is possible that there is confusion with *C. chuquisacana*, or *C. cernua* is only present in the extremely south of the country.

Caiophora chuquisacana Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 322. 1900.

Synonyms: *Caiophora kuntzei* Urb. & Gilg.
References: Foster, R. *C.* (1958), Weigend, M. (1997).
Habit: Herb. Vine. Status: Endemic. Elevation: 2500–4000 m. Region: Andes. Vegetation Zone: Montane Chaqueno forest.
Distribution: Chuquisaca, Cochabamba.
Voucher specimen: N. Ritter & J.R.I. Wood 1498 (LPB, MO). Type specimen: Orbigny

1242 (HT: P; IT: W).

Caiophora chuquitensis (Meyen) Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 301. 1900.

Synonyms: *Loasa chuquitensis* Meyen, *Blumenbachia chuquitensis* (Meyen) Hook. f., *Caiophora albiflora* (Griseb.) Urb. & Gilg, *Caiophora angustisecta* Urb. & Gilg, *Caiophora fiebrigii* Urb. & Gilg, *Caiophora heptamera* (Wedd.) Urb. & Gilg, *Caiophora heptamera* Wedd. var. *albiflora* Griseb., *Caiophora horrida* Urb. & Gilg, *Caiophora lorentziana* Urb. & Gilg, *Caiophora macrocarpa* Urb. & Gilg, *Caiophora orbignyana* Urb. & Gilg, *Caiophora sphaerocarpa* Urb. & Gilg. *Caiophora superba* Phil., *Loasa heptamera* Britton.
References: Rusby, H. H. (1893), Foster, R. C. (1958), Weigend, M. (1997), Serrano, M. & J. Terán (2000), Ackermann, M. & M. Weigend (2007).
Habit: Herb. Status: Native. Elevation: 3500–5000 m. Region: Altiplano. Vegetation Zone: Humid puna. Dry puna.
Distribution: Chuquisaca, Cochabamba, La Paz, Oruro, Tarija.
Voucher specimen: S.G. Beck 17894 (LPB, MSB).

Caiophora cinerea Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 301. 1900.

References: Foster, R. C. (1958), Weigend, M. (1997).
Notes: Synonym of *C. carduifolia* C. Presl – the type of *C. cinerea* was attributed to Bolivia, but it comes from Peru, Department Junín. *C.* cinerea is not confirmed for Bolivia.

Caiophora cirsiifolia C. Presl, Reliq. Haenk. 2: 42. 1831.

Synonyms: *Caiophora sepiaria* (Ruiz & Pavón ex G. Don) Macbr., *Caiophora preslii* Urb. & Gilg.
References: Foster, R. C. (1958), Weigend, M. (1997), Weigend, M. & M. Ackermann (2003), Ackermann, M. & M. Weigend (2007).
Notes: Reported for Bolivia by R. C. Foster (1958), but restricted to Peru and Chile.

Caiophora contorta (Desr.) C. Presl, Reliq. Haenk. 2: 42. 1831.

References: Foster, R. C. (1958), Lopez (1995), Saravia (1996), Weigend, M. (1997).
Notes: Reported for Bolivia, but restricted to Ecuador and Peru. The material cited by Saravia (1996) belongs to an undescribed species.

Caiophora coronata (Gillies ex Arn.) Hook. & Arn., Bot. Misc.. 3: 327. 1833.

Synonyms: *Loasa coronata* Gillies ex Arn., *Caiophora absinthiifolia* C. Presl, *Caiophora*

pycnophylla Urb. & Gilg.
References: Foster, R. C. (1958), Weigend, M. (1997), Ackermann, M. & M. Weigend (2007) .
Habit: Herb. Status: Native. Elevation: 3000– >5000 m. Region: Andes, Altiplano. Vegetation Zone: Dry puna.
Distribution: Potosi, Tarija.
Voucher specimen: E. Bastián 656 (LPB).

Caiophora dumetorum Urb. & Gilg, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 309. 1900.

Synonyms: *Caiophora clavata* var. *dumetorum* (Urb. & Gilg) Sleumer.
References: Sleumer, H. (1955), Weigend, M. (1997).
Habit: Herb. Vine. Status: Native. Elevation: 2500–4000 m. Region: Andes. Vegetation Zone: Tucuman-Bolivian forest, Montane Chaqueno forest.
Distribution: Potosi, Tarija.
Voucher specimen: D.M. Spooner & García 6580 (LPB, TEX, WIS).

Caiophora hibiscifolia (Griseb.) Urb. & Gilg in Engl. & Prantl, Nat. Pflanzenfam. 3(6a): 119. 1894.

Synonyms: *Loasa hibiscifolia* Griseb.
References: Weigend, M. (1997).
Habit: Herb. Vine. Status: Native. Elevation: 1000–3000 m. Region: Andes. Vegetation Zone: Dry Chaqueno forest.
Distribution: Cochabamba, La Paz, Santa Cruz, Tarija.
Voucher specimen: J.C. Solomon 11204 (LPB, MO).

Caiophora lateritia Klotzsch, Allg. Gartenzeitung 6: 329. 1838.

Synonyms: *Loasa lateritia* Hook., *Caiophora platyphylla* Urb. & Gilg., *Blumenbachia lateritia* (Hook.) Griseb.
References: Weigend, M. (1997), González et al. (1999).
Habit: Herb. Vine. Status: Native. Elevation: 500–2500 m. Region: Andes. Vegetation Zone: Dry Chaqueno forest.
Distribution: Chuquisaca, Santa Cruz, Tarija.
Voucher specimen: S.G. Beck 11466 (LPB, M).

Caiophora mollis (Griseb.) Urb. & Gilg in Engl. & Prantl, Nat. Pflanzenfam. 3(Abt. 6a): 119. 1894.

Synonyms: *Caiophora heptamera* var. *mollis* Griseb.
References: Weigend, M. (1997).
Habit: Herb. Status: Native. Elevation: 3000–4000 m. Region: Andes. Vegetation Zone: Dry Valleys.
Distribution: Chuquisaca, Cochabamba, Tarija.
Voucher specimen: J.R.I. Wood & M. Serrano 14488 (LPB, MO).

Caiophora pedicularifolia Killip, J. Wash. Acad. Sci. 18: 95. 1928.

References: Foster, R. C. (1958), Weigend, M. (1997).
Habit: Herb. Vine. Status: Endemic. Elevation: 3000–4500 m. Region: Andes. Vegetation Zone: Yungas, Paramo Yungeno.
Distribution: La Paz.
Voucher specimen: S.G. Beck et al. 21872 (LPB, M). Type specimen: Buchtien 2898 (HT: US; IT: HUH, NY).

Caiophora pentlandii (Paxton ex Graham) G. Don ex Loudon, Encycl. Pl. (new ed., 1855). 2: 1438. 1855.

Synonyms: *Loasa pentlandii* Paxton ex Graham, *Caiophora lechleri* Urb. & Gilg.
References: Weigend, M. (1997).
Notes: Not reported for Bolivia, but probably present near Titicaca Lake.

Caiophora rosulata (Wedd.) Urb. & Gilg subsp. ***taraxacoides*** (Killip) Weigend & Mark. Ackermann in Darwiniana 45(1): 45-67. 2007.

Synonyms: *Loasa rosulata* Wedd., *Caiophora acanthoides* Urb. & Gilg, *Caiophora taraxacoides* Killip.
References: Foster, R. C. (1958), Weigend, M. (1997), Ackermann, M. & M. Weigend (2007).
Habit: Herb. Status: Native. Elevation: 4000– >5000 m. Region: Altiplano. Vegetation Zone: Humid puna, Dry puna.
Distribution: Cochabamba, La Paz, Oruro, Potosi, Tarija.
Voucher **specimen:** M. Liberman 35 (L, LPB, M, MO).

Caiophora rusbyana Urb. & Gilg, Mem. Torrey Bot. Club 3(3): 35. 1893.

References: Rusby, H. H. (1893), Foster, R. C. (1958), Weigend, M. (1997).
Habit: Herb. Status: Endemic. Elevation: 2000–4500 m. Region: Andes. Vegetation Zone: Dry Valleys.
Distribution: Chuquisaca, Cochabamba, La Paz, Potosi.

Voucher specimen: S.G. Beck 6174 (LPB, MO). Type specimen: M. Bang 1142 (LT: E; IT: B destroyed, BM, HUH, K, MO, NY, US, W).

Caiophora scarlatina Urb. & Gilg, Bot. Jahrb. Syst. 45: 470. 1911.

References: Weigend, M. (1997).
Habit: Herb. Status: Native. Elevation: 3000–4500 m. Region: Andes. Vegetation Zone: Dry Valleys.
Distribution: La Paz, Santa Cruz.
Voucher speci**men:** J.P. Schmitt et al. 172 (LPB, MSB).

5.3. *Gronovia* L., Sp. pl.: 202. 1753.

1 species.

Gronovia scandens L., Sp. pl.: 202. 1753.

References: Foster, R. C. (1958).
Notes: Reported by R. C. Foster (1958), but without citing a voucher. Presence of the species possible in dry, tropical forests of Bolivia.

5.4. *Klaprothia* Kunth in Humb. Nov. Gen. Sp. (folio ed.). 6: 96. 1823.

2 species.

Klaprothia fasciculata (C. Presl) Poston, Syst. Bot. 15: 677. 1990.

Synonyms: *Sclerothrix fasciculata* C. Presl.
References: Urban, I. & W. Gilg (1900), Foster, R. C. (1958), Weigend, M. (2000).
Habit: Herb. Status: Native. Elevation: 1000–2000 m. Region: Andes. Vegetation Zone: Yungas.
Distribution: La Paz.
Notes: Reported by Urban, I. & W. Gilg (1900), material not seen.

Klaprothia mentzelioides Kunth in Humb. Nov. Gen. Sp. (quarto ed.). 6: 123, t. 537. 1823.

References: Foster, R. C. (1958), Weigend, M. (2000).
Habit: Herb. Status: Native. Elevation: 1000–3000 m. Region: Andes. Vegetation Zone:

Paramo Yungeno.
Distribution: Cochabamba.
Voucher specimen: Davidson 5175 (MO).
Notes: Only one specimen seen, but probably widely distributed in Cochabamba and La Paz.

5.5. *Mentzelia* L., Sp. Pl. 1: 516. 1753.

3 species.

Mentzelia aspera L., Sp. Pl. 1: 516. 1753.

Synonyms: *Mentzelia fragilis* Huber, *Mentzelia corumbaensis* Hoehne, *Mentzelia triloba* Ruiz & Pav. ex E.A. López.
References: Foster, R. C. (1958), López, A. (1995), Serrano, M. & J. Terán (2000), Weigend, M. (2000, 2007).
Habit: Herb. Status: Native. Elevation: 500–1500 m. Region: Lowlands, Andes. Vegetation Zone: Semideciduo Chiquitano forest, Dry Chaqueno forest, Montane Chaqueno forest.
Distribution: Chuquisaca, Cochabamba, La Paz, Santa Cruz.
Voucher specimen: Gutte & B. Herzog 595 (LP, LPB).

Mentzelia parvifolia Urb. & Gilg ex Kurtz, Revista Mus. La Plata, Secc. Bot. 5: 289. 1893.

Synonyms: *Acrolasia elata* Phil., *Mentzelia grisebachii* Urb. & Gilg, *Mentzelia jujuyensis* Sleumer, *Mentzelia parvifolia* var. *transiens* Sleumer.
References: Sleumer, H. (1955), Foster, R. C. (1958), Adolfo María, H. (1966), Weigend, M. (2007).
Habit: Herb. Status: Native. Elevation: 2000–3000 m. Region: Andes. Vegetation Zone: Dry Valleys.
Distribution: Chuquisaca, Cochabamba, Potosi, Tarija.
Voucher specimen: Torrico & Peca 496 (LPB, M, MSB).
Notes: The three species recognized by Sleumer (1955) do not represent more than slight modifications of a very common type. We reject them in favor of one heterogeneous species.

Mentzelia scabra Kunth subsp. ***chilensis*** (Gay) Weigend, Ann. Missouri Bot. Gard. 94: 677. 2007.

Synonyms: *Mentzelia chilensis* Gay, *Mentzelia fendleriana* Urb. & Gilg, *Mentzelia ignea*

(Phil.) Urb. & Gilg, *Loasa ignea* Phil., *Mentzelia soratensis* Urb. & Gilg.

References: Rusby, H. H. (1893), Foster, R. C. (1958), Adolfo María, H. (1966), López, A. (1995), López, R. P. (2000), Weigend, M. (2000, 2007).

Habit: Subshrub. Shrub. Status: Native. Elevation: 1000–3500 m. Region: Andes. Vegetation Zone: Montane Chaqueno forests, Dry Valleys.

Distribution: La Paz, Potosi, Santa Cruz, Tarija.

Voucher specimen: S.G. Beck 18724 (LPB, M).

Notes: This subspecies is widely distributed and shows a wide range morphological diversification.

Mentzelia scabra Kunth subsp. ***boliviana*** Weigend, Ann. Missouri Bot. Gard. 94: 674.

References: Weigend, M. (2007).

Habit: Subshrub. Shrub. Status: Native. Elevation: 2000--3500 m. Region: Andes. Vegetation Zone: Montane Chaqueno forests, Dry Valleys.

Distribution: Chuquisaca, Cochabamba, Tarija.

Voucher specimen: S. G. Beck & R. Seidel 14597 (HT: LPB; IT: M). Type specimen: S. D. Smith & S. Leiva G. 411 (F, HAO, LPB, MO).

5.6. *Nasa* Weigend, *Nasa* Conq. S. Amer. 214. 1997.

2 species, 1 endemic species.

Nasa ferruginea (Urb. & Gilg) Weigend, Arnaldoa. 5(2): 164. 1998.

Synonyms: *Loasa ferruginea* Urb. & Gilg.

References: Foster, R. C. (1958), Weigend, M. (1998), Weigend, M. (2001).

Habit: Herb. Status: Native. Elevation: 3000–3500 m. Region: Andes. Vegetation Zone: Unknown.

Distribution: La Paz.

Voucher specimen: B. Herzog 755 (LP).

Nasa herzogii (Urb. & Gilg) Weigend, Novon. 11(1): 153. 2001.

Synonyms: *Loasa herzogii* Urb. & Gilg.

References: Foster, R. C. (1958), Weigend, M. (2001).

Habit: Herb, Subshrub. Status: Endemic. Elevation: 2000–3000 m. Region: Andes. Vegetation Zone: Yungas, Paramo Yungas.

Distribution: Santa Cruz.

Voucher specimen: Müller & Heinrichs 6596 (LPB). Type specimen: B. Herzog 2277 (LT: L; IT: B destroyed, photo F, neg. no. 10195, S).

5.7. Literature

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Weigend M, Ackermann M. 2003. Los nombres antiguos en el genero *Caiophora* (Loasaceas subfam. Loasoideae) y una clasificacion infragenerica preliminar. Arnaldoa 10: 75-94.

5.8. List of Synonyms:

Acrolasia

elata Phil. = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz

Blumenbachia

cernua Griseb. = ***Caiophora cernua*** (Griseb.) Urb. & Gilg
chuquitensis (Meyen) Hook. f. = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
lateritia (Hook.) Griseb. = ***Caiophora lateritia*** Klotzsch

Caiophora

absinthiifolia C. Presl = ***Caiophora coronata*** (Gillies ex Arn.) Hook. & Arn.
acanthoides Urb. & Gilg = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***taraxacoides*** (Killip) Weigend & Mark. Ackermann
anemonoides Urb. & Gilg = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***rosulata***
albiflora (Griseb.) Urb. & Gilg **=** ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
angustisecta Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
clavata var. *dumetorum* (Urb. & Gilg) Sleumer = ***Caiophora dumetorum*** Urb. & Gilg
fiebrigii Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
cinerea Urb. & Gilg = ***Caiophora carduifolia*** C. Presl
heptamera (Wedd.) Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
heptamera Wedd. var. *albiflora* Griseb. **=** ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
heptamera var. *mollis* Griseb. = ***Caiophora mollis*** (Griseb.) Urb. & Gilg
horrida Urb. & Gilg **=** ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
kuntzei Urb. & Gilg = ***Caiophora chuquisacana*** Urb. & Gilg

lechleri Urb. & Gilg = ***Caiophora pentlandii*** (Paxton ex Graham) G. Don ex Loudon
lorentziana Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
macrocarpa Urb. & Gilg **=** ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
macrophylla Rusby = ***Caiophora canarinoides*** (Lenné & C. Koch) Urb. & Gilg
mandoniana Urb. & Gilg = ***Caiophora andina*** Urb. & Gilg
orbignyana Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
platyphylla Urb. & Gilg = ***Caiophora lateritia*** Klotzsch
preslii Urb. & Gilg = ***Caiophora contorta*** (Desr.) C.Presl
pycnophylla Urb. & Gilg = ***Caiophora coronata*** (Gillies ex Arn.) Hook. & Arn.
rahmeri Phil. = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***rosulata***
sepiaria (Ruiz & Pavón ex G. Don) Macbr = ***Caiophora cirsiifolia*** C. Presl
sphaerocarpa Urb. & Gilg = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
superba Phil. **=** ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
taraxacoides Killip . **=** ***Caiophora*** **rosulata** (Wedd.) Urb. & Gilg subsp. ***taraxacoides*** (Killip) Weigend & Mark. Ackermann

Illairea

canarinoides Lenné & C. Koch = ***Caiophora canarinoides*** (Lenné & C. Koch) Urb. & Gilg

Loasa

canarinoides (Lenné & C. Koch) Britton = ***Caiophora canarinoides*** (Lenné & C. Koch) Urb. & Gilg
chuquitensis Meyen = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
coronata Gillies ex Arn. = ***Caiophora coronata*** (Gillies ex Arn.) Hook. & Arn.
ferruginea Urb. & Gilg = ***Nasa ferruginea*** (Urb. & Gilg) Weigend
heptamera Britton = ***Caiophora chuquitensis*** (Meyen) Urb. & Gilg
heptamera var. *chelidonifolia* Wedd. = ***Caiophora andina*** Urb. & Gilg
herzogii Urb. & Gilg = ***Nasa herzogii*** (Urb. & Gilg) Weigend
hibiscifolia Griseb. = ***Caiophora hibiscifolia*** (Griseb.) Urb. & Gilg
ignea Phil. = ***Mentzelia scabra*** Kunth
lateritia Hook. = ***Caiophora lateritia*** Klotzsch
pentlandii Paxton ex Graham = ***Caiophora pentlandii*** (Paxton ex Graham) G. Don ex Loudon
rosulata Wedd. = ***Caiophora rosulata*** (Wedd.) Urb. & Gilg subsp. ***rosulata***

Mentzelia

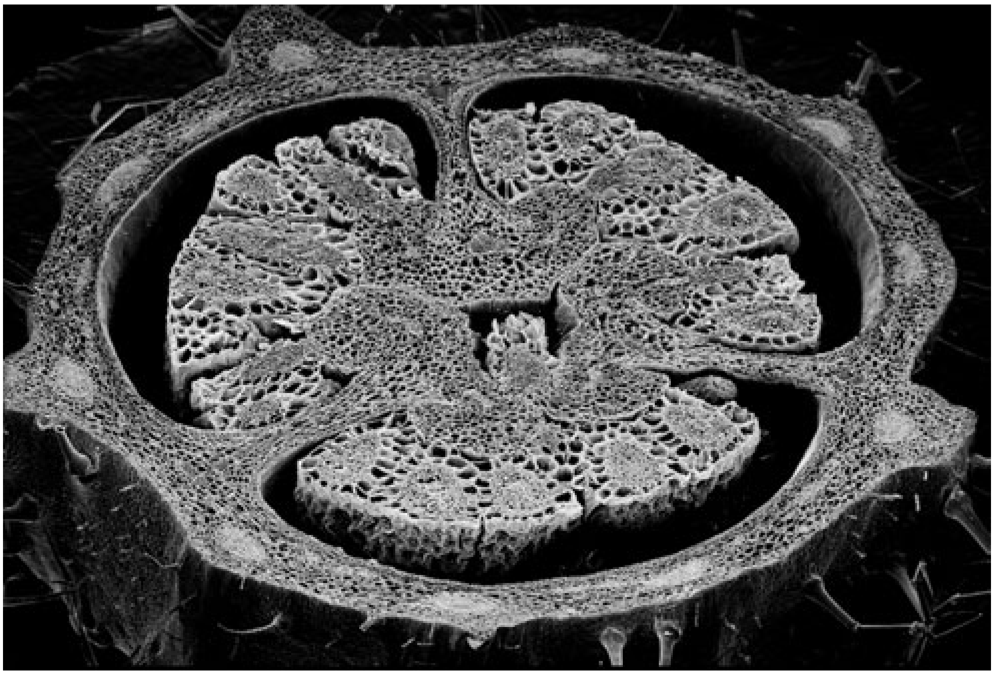
chilensis Gay = ***Mentzelia scabra*** Kunth Kunth subsp. **chilensis** (Gay) Weigend
cordobensis Urb. & Gilg ex Kurtz = ***Mentzelia scabra*** Kunth subsp. ***cordobensis*** (Gay) Weigend
cordifolia Dombey ex Urb. & Gilg = ***Mentzelia scabra*** Kunth subsp. ***grandiflora*** (Gay) Weigend
corumbaensis Hoehne = ***Mentzelia aspera*** L.

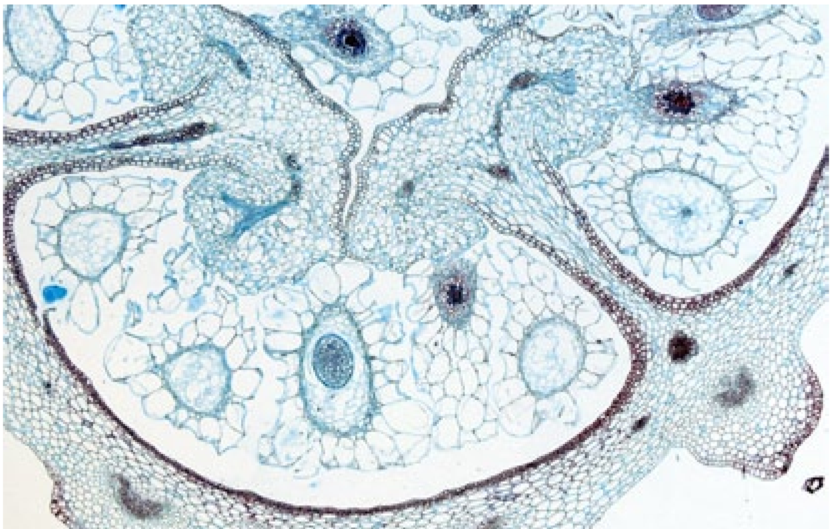
fendleriana Urb. & Gilg = ***Mentzelia scabra*** Kunth subsp. ***chilensis*** (Gay) Weigend
fragilis Huber = ***Mentzelia aspera*** L.
grisebachii Urb. & Gilg = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz
ignea (Phil.) Urb. & Gilg = ***Mentzelia scabra*** Kunth subsp. ***chilensis*** (Gay) Weigend
jujuyensis Sleumer = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz
parvifolia var. *transiens* Sleumer = ***Mentzelia parvifolia*** Urb. & Gilg ex Kurtz
soratensis Urb. & Gilg = ***Mentzelia scabra*** Kunth subsp. ***chilensis*** (Gay) Weigend
triloba Ruiz & Pav. ex E.A. López = ***Mentzelia aspera*** L.

Sclerothrix

fasciculata C. Presl = ***Klaprothia fasciculata*** (C. Presl) Poston

Anatomy and Morphology





Caiophora stenocarpa Urb. & Gilg: transversial fruit section. on top SEM, below LM

6. The seeds of Loasaceae subfam. Loasoideae (Cornales) II: Seed morphology of „South Andean Loasas“ (*Loasa*, *Caiophora*, *Scyphanthus* and *Blumenbachia*)*

6.1. Abstract

South Andean Loasas (*Blumenbachia*, *Caiophora*, *Loasa*, *Scyphanthus*) are a monophyletic group of taxa within Loasaceae subfam. Loasoideae, comprising some 100 species, 49 of which are investigated here. They retain a many-layered testa in the mature seeds and usually have passive transfer testas with complex, spongiose wall outgrowths. Additional modifications concern the undulations of the testa epidermis, presence or absence of the outer periclinal wall, secondary sculpturing, the presence or absence of spines, warts and finally spongiose structures on the anticlinal walls of the testa epidermis and the inner periclinal wall. Seeds of the widespread “deeply pitted” type are plesiomorphic, while various subclades of South Andean Loasas have derivations underscoring their relationships and confirming the relationships found with molecular markers and other morphological characters. The genus *Blumenbachia* has either seeds with a many-layered testa forming longitudinal lamellae (sect. *Angulatae*), or balloon seeds with a loose outer testa layer and spongiose wall outgrowths on the inner periclinal walls (sect. *Blumenbachia* and sect. *Gripidea*) and is clearly monophyletic. *Loasa* s.str. (ser. *Loasa*, ser. *Macrospermae*, ser. *Floribundae*, ser. *Deserticolae*) is characterized by the presence of a subterminal hilum or hilar scar and one subgroup (ser. *Loasa*, ser. *Macrospermae*) by very large and heavy seeds with a collapsed testa. *L.* ser. *Pinnatae*, ser. *Acaules*, ser. *Volubiles*, *Scyphanthus* and *Caiophora* share more or less one seed types with minor modifications. Within *Caiophora* various derivations are observed, of which the gradual loss of the secondary sculpture of the inner periclinal wall is the most striking one. Anemochoria is the most widespread dispersal mechanism in South Andean Loasas and is achieved in at least five structurally different ways.

Keywords: Seed morphology; Anemochoria; Many-layered testa; Loasaceae; Transfer testa

*The original publication is available at http://www.sciencedirect.com/science/journal/03672530. Published as: Weigend M, Gröger A, Ackermann M. 2005. The seeds of Loasaceae subfam. Loasoideae (Cornales) II: Seed morphology of “South Andean Loasas” (*Loasa, Caiophora, Scyphanthus* and *Blumenbachia*). Flora 200: 569-591. doi.org/10.1016/j.flora.2005.06.009

6.2. Introduction

Loasoideae is the largest subfamily of Loasaceae (13 genera, ca. 2/3rds of the species total – Weigend, 1997) and is unequivocally monophyletic (Moody and Hufford, 2000; Weigend et al., 2004a). Its centre of diversity is in Andean South America and the group falls into a number of small, and relatively isolated genera (e.g., *Huidobria*, *Chichicaste*, *Aosa*, *Klaprothia*) and two large monophyletic complexes, the genus *Nasa* (>100 spp.) and the South Andean Loasas (ca. 100 spp.; Weigend et al., 2004a; Weigend, 2004). South Andean Loasas comprise the genera *Blumenbachia*, *Caiophora*, *Scyphanthus* and *Loasa* (sensu Weigend, 1997; Fig. 6.1). Phylogenetic resolution within this group is, however, still unsatisfactory and an attempt to resolve some of the key questions was made recently (Weigend, 1997). The concepts proposed there have been heavily criticized by Hufford et al. (2003), but are in agreement with published data, as far as taxon sampling carries. Irrespective of that controversy, some groupings are now clear (Weigend et al., 2004a) and the current understanding of the relationships is

genera	Infrageneric entities	acronym	ssp. total	ssp. investigated
Loasa	Ser. *Acaulis*	LoAc	1	1
	Ser. *Deserticolae*	LoDe	2 ?	2
	Ser. *Floribundae*	LoFl	4	2
	Ser. *Loasa*	LoLo	2 ?	1
	Ser. *Macrosperma*	LoMc	8	4
	Ser. *Volubilis*	LoVo	4	3
	Ser. *Pinnatae*	LoPi	20 ?	9
Blumenbachia	Sect. *Blumenbachia*	BlBl	4	4
	Sect. *Gripidea*	BlGr	3	3
	Sect. *Angulatae*	BlAn	3	3
Scyphanthus	-	-	2 ?	2
Caiophora	*C. arechavaletae*-group	CaAr	1	1
	C. carduifolia-group	CaCa	5 ?	5*
	C. chuquitensis-group	CaCh	8 ?	5*
	C. cirsiifolia-group	CaCi	2 ?	2*
	C. clavata-group	CaCl	5	3
	C. contorta-group	CaCo	2 ?	2*
	C. coronata-group	CaCr	2	2
	C. lateritia-group	CaLa	8 ?	4*
	C. nivalis-group	CaNi	2	1
	C. pterosperma-group	CaPt	2 ?	2*

Fig. 6.1: Synopsis of the classification of South Andean Loasas, modified from Urban and Gilg (1900) and Weigend (1997) ([1]informal classification see Weigend and Ackermann, 2003; *multiple accessions of divergent morphotypes in individual taxa, ? not revised, species number doubtful).

summarized in Fig. 6.2. The South Andean Loasas fall into two large sister clades, the *Loasa–Blumenbachia* clade (*Blumenbachia* with *Loasa* s.str.: *Loasa* ser. *Loasa*, ser. *Floribundae*, ser. *Deserticolae*, ser. *Macrospermae*) on the one hand and the *Caiophora* clade (*Caiophora* and *Scyphanthus*, *Loasa* ser. *Pinnatae*, ser. *Acaules*, ser. *Volubiles)* on the other. Within these clades, *Blumenbachia* is sister to L*oasa* s.str. *Loasa* ser. *Volubiles* and ser. *Acaules* are sister to a clade including ser. *Pinnatae*, *Scyphanthus* and *Caiophora*, and ser. *Pinnatae* is in turn sister to *Scyphanthus* and *Caiophora*. This arrangement is in agreement with overall morphology, and thus with some generic re-arrangements made in Weigend (1997), namely the removal of *Caiophora* sect. *Gripidea* and *Angulatae* to *Blumenbachia*. However, contrary to these results, seed morphology has been used as a character to argue for a close relationship between *Caiophora* sect. *Gripidea* and *Angulatae* and *Caiophora* s.str. by Hufford (1988) in support of the taxonomy proposed by Urban and Gilg (1900).

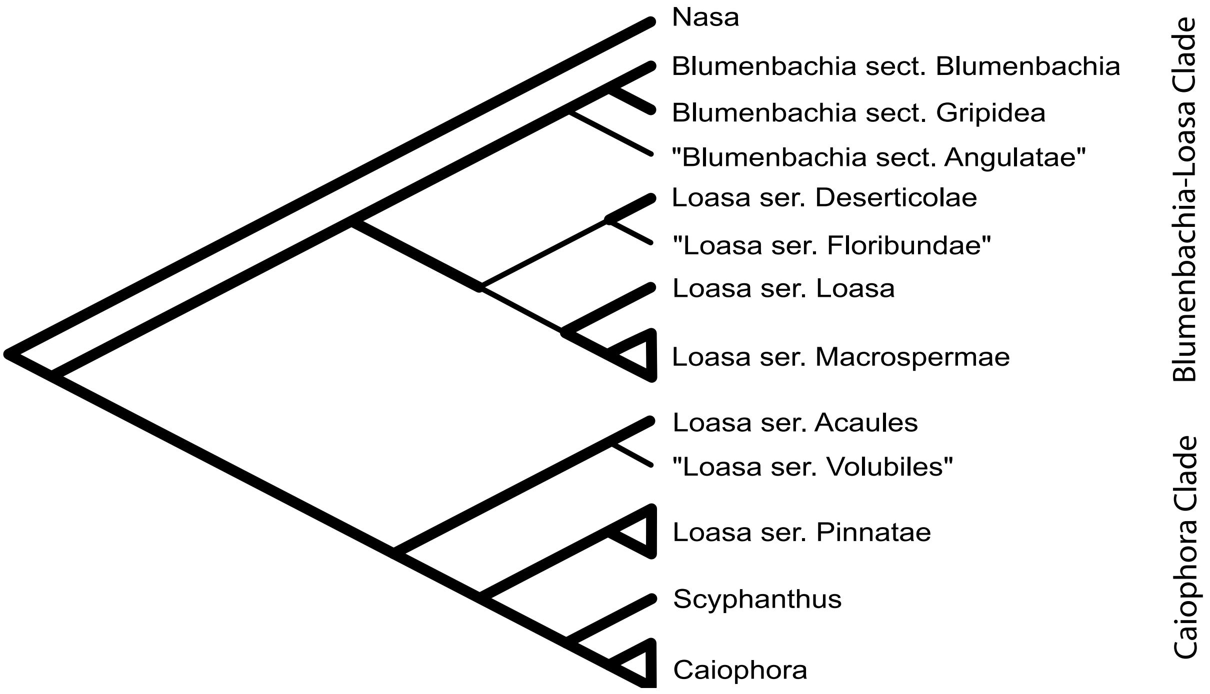


Fig. 6.2: Hypothetical phylogeny of South Andean Loasas based on Weigend et al. (2004a) and Hufford et al. (2003), thin lines: clades inferred from morphology without clear molecular support.

The aim of the current study is to investigate seed morphology and anatomy of South Andean Loasas, in order to elucidate character polarity and to look for morphological characters to refine the picture obtained with molecular characters. This will hopefully help to clarify, e.g., whether there are real similarities between the groups in *Blumenbachia* and *Caiophora* as indicated by Hufford (1988), which would of course have to be interpreted as homoplasious in view of our current phylogenetic understanding.

Seed morphology of Loasaceae has not so far been extensively studied, and the only genera which have been subject to surveys are *Mentzelia* (Hill, 1976) and *Eucnide* (Hufford, 1988). *Eucnide* turned out to be rather uniform in seed morphology, whereas *Mentzelia* showed a wide range of morphotypes, which largely coincided with previously described infrageneric groupings. The most relevant seed morphological study in the context of Loasaceae is a study of the seed morphology of Hydrangeaceae (Hufford, 1995), since the Hydrangeaceae are considered as a sister group of the Loasaceae (Moody and Hufford, 2000; Weigend, 2004). Generally, information on the seeds of Loasaceae and Hydrangeaceae is poorly documented, and Tweddle et al. (2003) list information on 1000 seed weights, oil content and germination data for only 17 taxa of Loasaceae (1 sp. *Petalonyx*, 1 sp. *Cevallia*, 3 spp. *Caiophora*, 12 spp. *Mentzelia*). Additional data on seed weights, fatty acid composition, seed release mechanisms and dispersal agents have been published recently (Aitzetmüller et al., 2004; Weigend et al., 2004b). The morphological and anatomical data presented here should be seen in the context of that latter article and the discussion will aim at bringing these two lines of evidence together.

In spite of the relative scarcity of detailed data, there is a long history of using seed morphology in the systematics of Loasoideae: Ruiz and Pavon y Jimenez (1958, written ca. 1800) described a *Loasa pterosperma* [= *Caiophora pterosperma* (Ruiz and Pavon) Urb. & Gilg] with reticulately winged seeds from Peru, referring to and illustrating such a fine detail as the secondary sculpture of the inner periclinal walls. Miers (1866) provided the first and the most comprehensive ever overview over seed morphology in Loasaceae and described the Brazilian genus *Gripidea* [= *Blumenbachia* sect. *Gripidea* (Miers) Urb.] on the basis of its peculiar seed morphology. He also studied the anatomy of the seeds and was the only scientist to recognize the profound differences between the seeds of *Caiophora* on the one hand and *Blumenbachia* and *Gripidea* on the other, by emphasizing that the latter two taxa have a loose outer seed coat, whereas this seed coat is firmly attached in *Caiophora*, quite apart from structural differences. Seed morphology has also been used at the infrageneric level: Urban and Gilg (1900) defined *Caiophora* sect. *Angulatae* [= *Blumenbachia* sect. *Angulatae* (Urb.) Weigend] entirely by its seed morphology and illustrated seeds of most genera, albeit not always correctly and in less detail than Miers (1866). The 20th century brought very little advance in the knowledge of seed morphology or anatomy of Loasoideae, and few of the detailed observations on secondary sculpture, anticlinal wall fenestration and the presence of a many-layered testa made by Miers (1866) were taken up in subsequent studies. Hardly any new structures were discovered and only a confirmation of known structures by scanning electron microscope (SEM) was carried out, e.g., the undulated, fibrous testa of *Blumenbachia*, which had been beautifully analyzed and illustrated in Miers (1866, Table 28, 12–17, 27–33) was illustrated with SEM photographs in Hufford (1988, Figs. 37–38, 41–41). The SEM studies of Poston and Nowicke (1990) and Hufford (1988) compared small sample sizes and did not come to any clear conclusions on Loasoideae systematics. However, a more central problem of the study by Hufford (1988) is the low quality of the seeds – apparently most seeds had been taken from herbarium material and were either immature and/or had been badly damaged in specimen preparation for the herbarium and/or seed preparation for the SEM. Most of the seeds show peculiar invaginations and compressions, indicating that the endosperm had collapsed for some reason. The poor quality of the seed material used in Hufford (1988) also rendered a detailed observation of secondary structure impossible and not even hand sections were used to elucidate structural detail, so that he failed to distinguish the transfer structures on the inner periclinal wall of *Caiophora* from the granular secondary sculpture of the outer periclinal wall in *Presliophytum*. A wider survey on the micromorphology of the seeds of 65 species of Loasoideae seeds was generated by one of us (Gröger, 1990), but that study has not been published and its results are incorporated here.

For Loasoideae we therefore basically have to take up the thread at the level which Miers (1866) had reached and look at both the external morphology and the anatomical details of the seeds. Here, special emphasis is placed on demonstrating the structural diversity of Loasoideae seeds, and on placing this diversity into an ecological and phylogenetic context. In this article we address the relationships between the closely related South Andean genera *Blumenbachia*, *Caiophora*, *Loasa* and *Scyphanthus*. The emphasis is on generic and infrageneric groups and near-comprehensive sampling has been carried out for the large genera (all sections and series of *Loasa*, *Blumenbachia* and *Caiophora*) to test the homogeneity of the structures observed in various representatives. In *Caiophora* problems at the α-taxonomic level still abound (Weigend, 1997) and the species are here treated in the sequence of informal groupings as recently proposed (Weigend and Ackermann, 2003). Wherever possible, multiple accessions of the vaguely defined species were studied, to provide a sound basis for the interpretations offered.

6.3. Material and methods

Seed material

Seed samples were mostly collected directly from wild or cultivated plants. The seeds were taken from fully mature capsules, which are recognized by opening of the sutures (usually apical valves) of the fruit and the dark colouration of the testa. Seed material was available from a total of 11 field trips to South America (Peru, Ecuador, Chile, Argentina, Venezuela, Colombia), and from material kindly provided by Prof. Dr. J. Grau and Dr. Ch. Ehrhardt (Institut für Systematische Botanik München, Germany). Very few additional samples were removed from herbarium sheets, and these were also previously checked for maturity and structural integrity under a dissecting microscope. A complete list of the vouchers specimens and the investigations they were used for is given in Appendix A.

Storage

No controlled storage conditions were maintained for the seeds. They were kept in paper bags in the office with temperature fluctuating between 18 and 20°C most of the year and temperatures reaching highs of over 30°C for extended periods of time in summer. Humidity was mostly low (<30%), but reaching highs of ca. 90% in the humid summer months.

Microscopy

For microscopy the seeds were pre-examined under a dissecting microscope to check for maturity and possible contamination (fungal hyphae, dirt). For SEM the seeds were sputter coated with gold or platinum and subsequently viewed and photographed in a LEO VP 438 SEM at a voltage of 15 kV. To ensure that the seed morphology encountered under the SEM is typical of the respective genera or infrageneric groups a light microscopical survey of additional species was undertaken, especially for the larger genera (representatives of all species groups in the large genera *Nasa*, *Caiophora*, *Loasa*, all species in the small genera *Scyphanthus*, *Chichicaste*, *Presliophytum*, *Huidobria*, *Blumenbachia*, *Aosa*). Under the dissecting microscope most details visible under the SEM can be discerned, but cannot be photographed. Hand sections for the SEM were carried out with a razor blade on seeds mounted onto double-sided adhesive tape. Since the finer details of testa morphology may be obscured by oil smears in the hand sections, these were in some cases pre-treated with pure acetone to remove oil and then air-dried before mounting and sputter coating.

Descriptions

Morphological terminology follows Boesewinkel and Bouman (1984) and Werker (1997) wherever possible, but the term „primary sculpture” is here restricted to the outline and dimensions of the testa epidermis cells, while the anticlinal walls and outer periclinal walls are treated separately, since they show a wealth of differentiations, some of which are only visible in section and should therefore not be included in the primary sculpture. „Secondary sculpture” theoretically includes cuticular sculptures, secondary wall thickenings and cell wall inclusions (Boesewinkel and Bouman, 1984). In Loasoideae both cuticular sculptures and secondary wall thickenings are found, but cell wall inclusions appear to be absent. A crucial character for the morphological descriptions is a form of secondary sculpturing of the anticlinal walls, which is called „fenestration” here. These fenestrations are quite variable and a set of terms is here introduced to describe them. The „windows” are transparent under the LM and bright under the SEM, alternating with darker and thicker structures (latticework). The latticework between the individual windows is well visible both under the LM (Figs. 6.12.5–6.12.7), SEM (e.g., Figs. 6.7.1– 6.7.12) and the TEM (Figs. 6.12.8 and 6.12.9). Fenestrations show a wide morphological diversity; sometimes there is a single row of more or less regular fenestrations (Figs. 6.7.10 and 6.7.11), sometimes there are numerous rows separated by relatively wide (*Caiophora pulchella*) or very narrow (e.g., Figs. 6.9.1–6.9.9) thick-walled parts and sometimes only the „frames” are thick-walled (total fenestration, Figs. 6.10.11, 6.10.12 and 6.11.1–6.11.9). The latticework usually frames the individual windows completely (complete fenestration, Figs. 6.8.11 and 6.8.12), but sometimes it is irregular and ends blindly in the windows (incomplete fenestration, Figs. 6.7.8 and 6.8.2). In some taxa all fenestrations are more or less circular or polyhedral and of one size (regular fenestration, Fig. 6.8.11), in other taxa the fenestrations are different and/or irregularly shaped (irregular fenestration, Figs. 6.10.2–6.10.8). Also, the latticework is usually continuous with the secondary sculpture of the inner periclinal wall of the testa cells (Figs. 6.7.9 and 6.7.12), rarely is it separated from it by a distinct ledge (Fig. 6.5.8). Tertiary sculpturing is often present in the form of granular or echinate sculpturing, on the outer periclinal wall (if present), the anticlinal and the inner periclinal wall (e.g., Figs. 6.7.8 and 6.7.9). These show gradual transitions to increasingly branched (Figs. 6.5.11 and 6.5.12), or regularly reticulate (Fig. 6.4.7) and finally densely spongiose, rather diffuse structures (Figs. 6.12.11 and 6.12.12). Complex, spongiose structures are interpreted here as passive transfer structures (Diane et al., 2002).

6.4. Results

The sequence of descriptions here largely follows the perceived phylogenetic relationships in South Andean Loasas as proposed in Weigend et al. (2004a). The infrageneric groupings follow the classification by Urban and Gilg (1900) as modified by Weigend (1997). The aim is to unite the taxa sampled into more or less homogeneous groups, in order to be able to compare these groups to each other. These data are then interpreted on the basis of our current phylogenetic understanding in the discussion. The two heterogeneous and seed morphologically diverse genera *Blumenbachia* and *Loasa* are subdivided into their constituent sections and series. These species groups as used here are largely natural entities, which can be shown readily on the basis of a range of other morphological characters and the molecular data so far available. The only exceptions are *Loasa* ser. *Volubiles*, which is paraphyletic to the monotypic ser. *Acaules* (*L. lateritia*), ser. *Floribundae* which belongs to *Loasa* s.str. but may be polyphyletic, and *Blumenbachia* sect. *Angulatae*, which is also rather heterogeneous and may be the paraphyletic basal group in *Blumenbachia*.

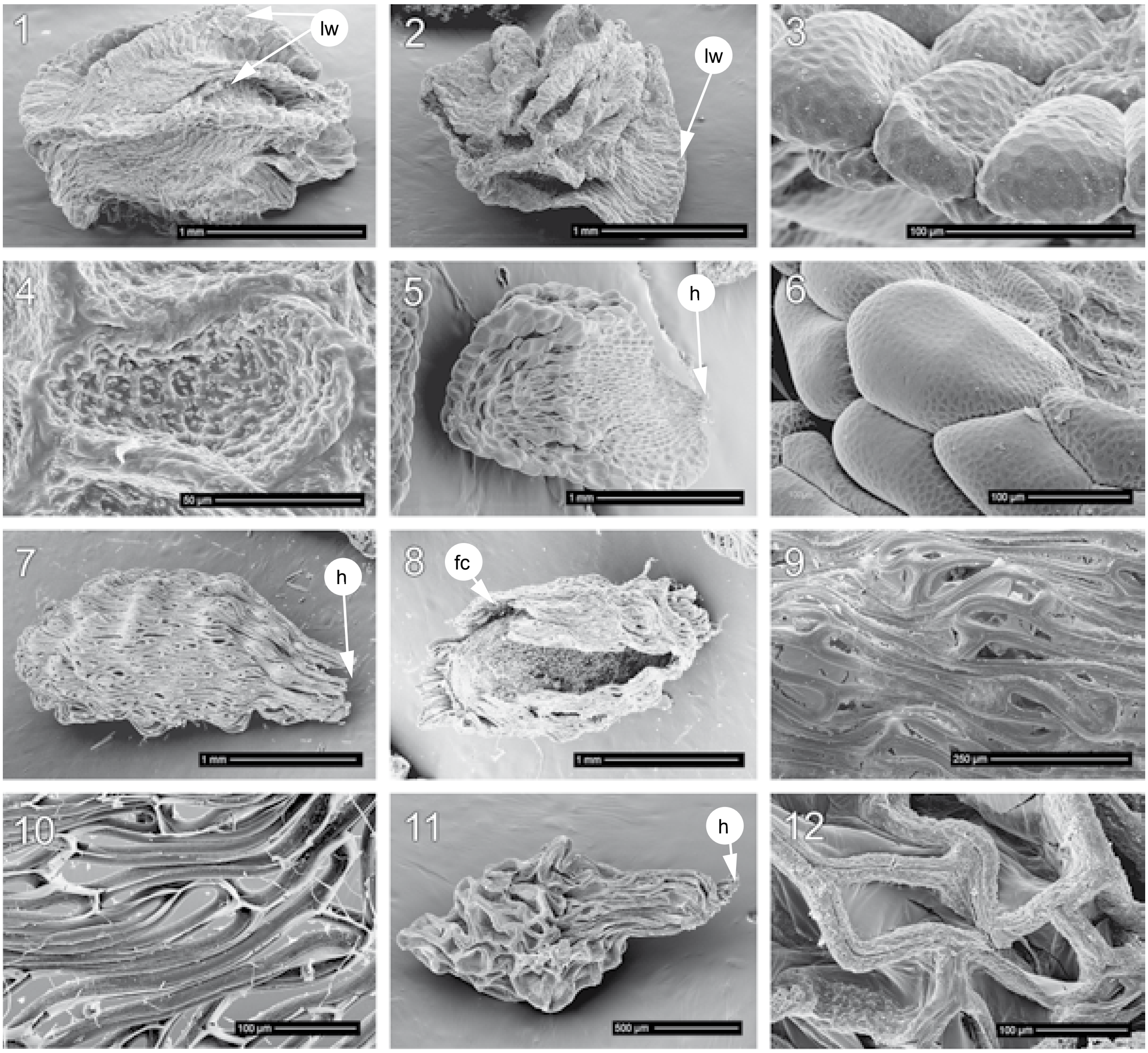


Fig. 6.3: Seed morphology of *Blumenbachia*. (1–3). *B. silvestris* (BlAn *) (Weigend et al. s.n.). (1) Entire seed, lateral view. (2) Entire seed, chalazal pole. (3) Testa epidermis. (4) *B. prietea* (BlAn, Weigend et al. 6823), testa cell. (5, 6) *B. espigneira* (BlAn, Weigend et al. 6816). (5) Entire seed. (6) Testa epidermis. (7–10) *B. hieronymi* (BlBl, Weigend s.n.). (7) Entire seed, note obliquely equatorial undulations. (8) Entire seed, outer testa layer partially removed. (9) Outer testa layer. (10) Outer testa layer, view from the inside. (11, 12) *B. exalata* (BlGr, Sehnem 3886). (11) Entire seed. (12) Individual testa cell, central part of seed (all SEM, fc – fibrouos coat = apices of anticlinal walls plus outer periclinal walls, h = hilum, lw = longitudinal wing; *abbreviations of infrageneric groups see Fig. 6.1 and Appendix A).

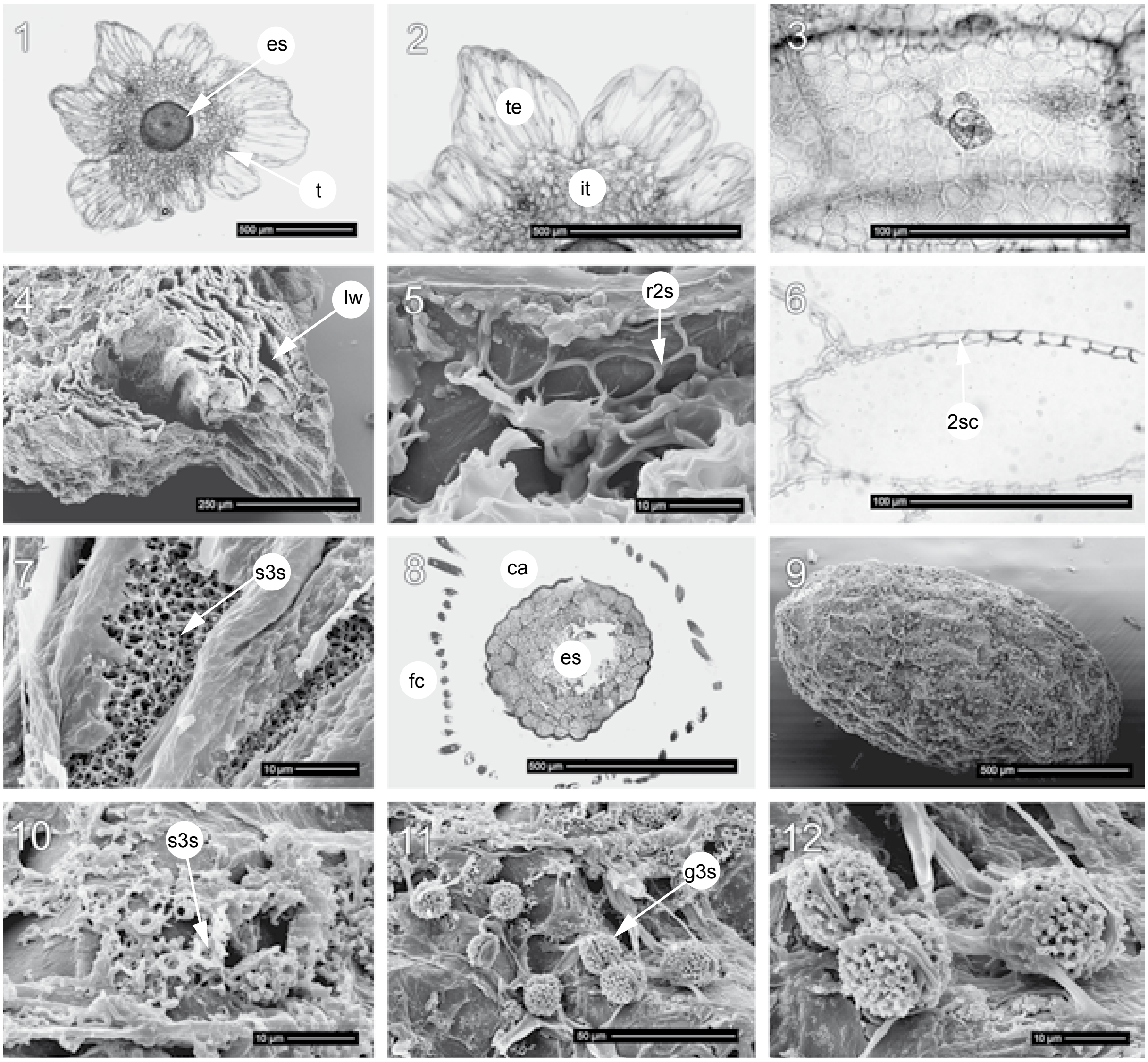


Fig. 6.4: Seed anatomy of *Blumenbachia*. (1–3) *B. prietea* (BlAn, Weigend et al. 6879), transverse section of immature seed (LM). 1. Overview of many-layered testa, and endosperm. (2) Testa. (3) Individual testa cell. (4–6) *B. silvestris* (BlAn, Weigend et al. 6999), mature seed, transverse section. (4) Longitudinal testa-wings (SEM). (5) Inner periclinal wall of innermost testa layer (SEM). (6) Testa epidermis cell in transverse section (LM). (7) *B. exalata* (BlGr, Sehnem 3886), mature seed, inner periclinal wall of testa epidermis (SEM). (8–12) *B. hieronymi* (BlBl, Weigend s.n.), mature seed. (8) Transverse section through seed (LM). (9) Central part of seed (endosperm covered with inner periclinal walls, SEM). (10–12) Transfer structures from the inner periclinal walls (SEM) (ca = cavity, es = endosperm, fc = fibrouos coat, g3s = globose tertiary sculpture, it = inner testa layers, lw = longitudinal wing, r2s = reticulate secondary sculpture, s3s = spongiose tertiary sculpture, t = testa, te = testa epidermis).

Blumenbachia **sect.** ***Angulatae*** (Figs. 6.3.1–6.3.6 and 6.4.1–6.4.6)

Blumenbachia sect. *Angulatae* consists of three vegetatively rather divergent species in Patagonia, all three species, *B. espigneira* Gay, *B. silvestris* Poepp., and *B. prietea* Gay were investigated. There are no conspicuous differences in their seed morphology.

Shape and size: Irregularly ovoidal and laterally flattened and approximately 2000 µm long and 1500–1800 µm wide, with 20–30 testa cells end to end; both the chalazal and the micropylar poles protracted into short beaks, overall surface is very irregularly structured with longitudinal lamellae or wings formed by the many-layered testa only (Figs. 6.4.1, 6.4.2 and 6.4.4). Primary sculpture: Polyhedral with testa epidermis cells ca. 60–70 µm long and 50–60 µm wide. Outer periclinal walls: Persistent, largely convex (Figs. 6.3.3 and 6.3.6), rarely concave (Figs. 6.3.4 and 6.3.5), with reticulate secondary sculpturing. Anticlinal walls: No structural differentiation between the anticlinal and the periclinal walls, all identical in thickness and structure, usually reticulate and finely granular (Figs. 6.3.4–6.3.6). Anticlinal walls as such cannot be differentiated. Secondary sculpture: All testa cell walls of the inner and outer layers show very regular reticulations ca. 10 µm wide and the walls in between are ca. 0.5 µm wide (Figs. 6.4.3 and 6.4.5). Tertiary sculpture: Absent. Inner testa cell layers: 5–7 layers, fully developed and smaller than cells of testa epidermis, structurally identical to testa epidermis cells (Figs. 6.4.1–6.4.2).

Blumenbachia **sect.** ***Blumenbachia*** (Figs. 6.3.7–6.3.10 and 6.4.8–6.4.12)

Blumenbachia sect. *Blumenbachia* consists of four very closely related species in Argentina, Uruguay, Paraguay and Brazil. Three species (*B. hieronymii* Urb., *B. insignis* Schrad., *B. latifolia* Camb.) were investigated, congruent literature data are available on the other species (*B. catarinensis* Urb. & Gilg – Urban and Gilg, 1900). Section *Blumenbachia* is closely allied to *Blumenbachia* sect. *Gripidea*, which differs marginally in leaf shape, habit, and seed morphology.

Shape and size: Irregularly ovoidal, approximately 2000 µm long and 1000 µm wide (Fig. 6.3.7), with 7–9 testa cells end to end, poles tapering, the elongation of the chalazal pole (ca. 600–800 µm) typically longer than that of the micropylar pole (ca. 400 µm), outer part of testa epidermis completely free from the inner testa layers (Fig. 6.4.8). Primary sculpture: Reticulate,cells narrow, ca. 1000 µm long and 100 µm wide, testa shows irregular oblique-equatorial undulations. Anticlinal walls: Ruptured in the proximal, thin portion so that the outer periclinal wall and the apex of the anticlinal walls form a loose, fibrous seed coat (Figs. 6.3.8 and 6.4.8), distal portion of the anticlinal wall conspicuously thickened and ca. 40 µm wide and slightly granular (Figs. 6.3.9 and 6.3.10). Outer periclinal walls: Persistent, concave,

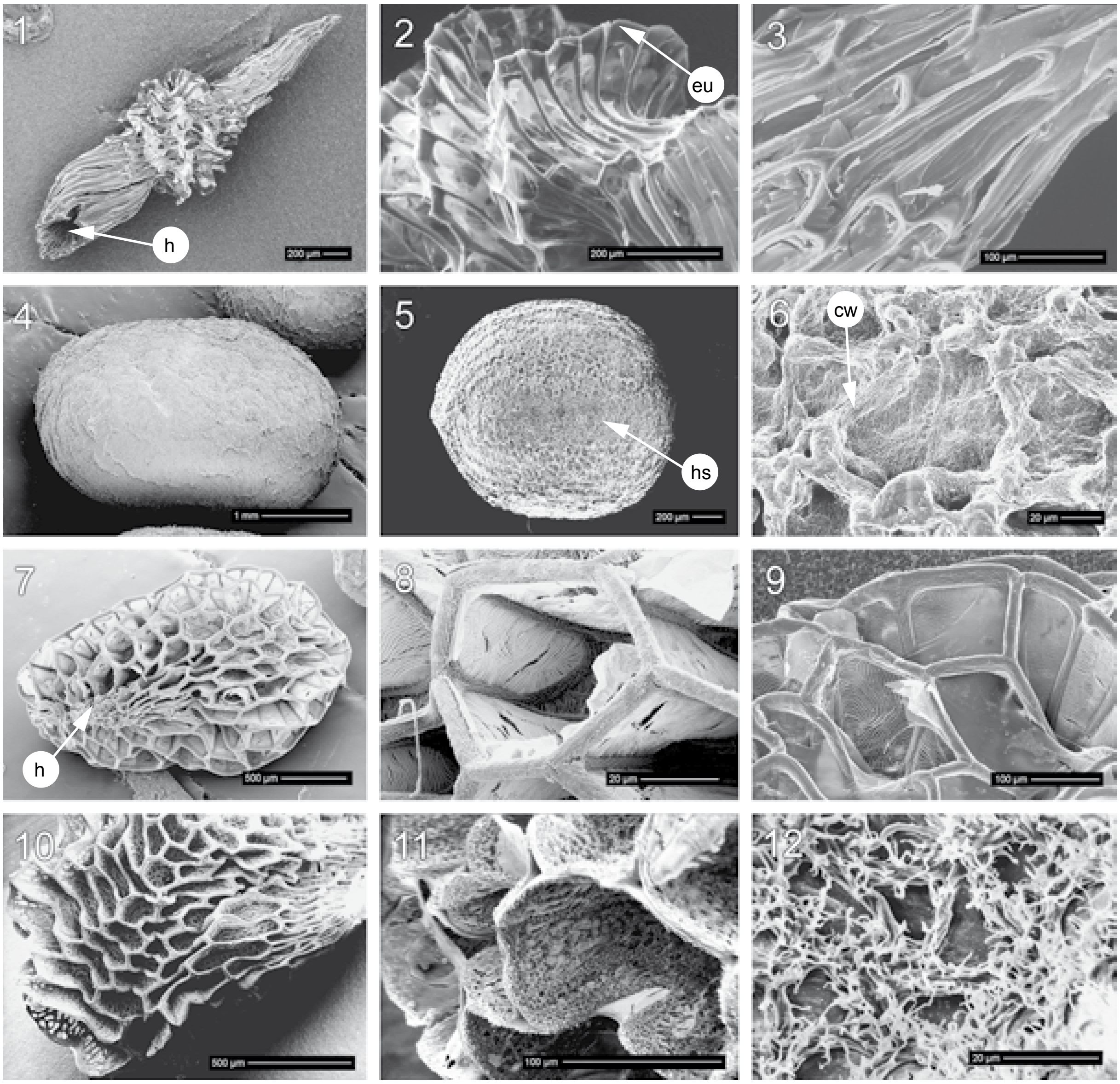


Fig. 6.5: Seed morphology of *Blumenbachia* sect. *Gripidea*, *Loasa* ser. *Macrospermae*, *L*. ser. *Deserticolae*, *L*. ser. *Floribundae*. (1–3) *B. eichleri* (BlGr, Schlindwein 610). (1) Entire seed, oblique lateral view. (2) Central part of seed. (3) Outer testa layer on wing. (4) *L. heterophylla* (LoMc, Jiles 6448), entire seed. (5, 6) *L. nitida* (LoMc, Weigend et al. 7346). (5) Entire seed, wide note distinct hilar scar (hs). (6) Individual testa cell. (7, 8) *L. urmentea* (LoDe, King s.n.). (7) Entire seed, note subterminal hilar region. (8) Individual testa cell. (9) *L. elongata* (LoDe, Rechinger and Rechinger 63390), testa cells. (10) *L. floribunda* (LoFl, Montero 296), part of seed. (11–12) *L. pallida* (LoFl, Bayer 655). (11) Testa cells. (12) Inner periclinal wall, note spongiose transfer structures on reticulate secondary sculpture (all SEM, cw = collapsed wall, eu = equatorial undulations, h = hilum, hs = hilar scar, tw = terminal wings).

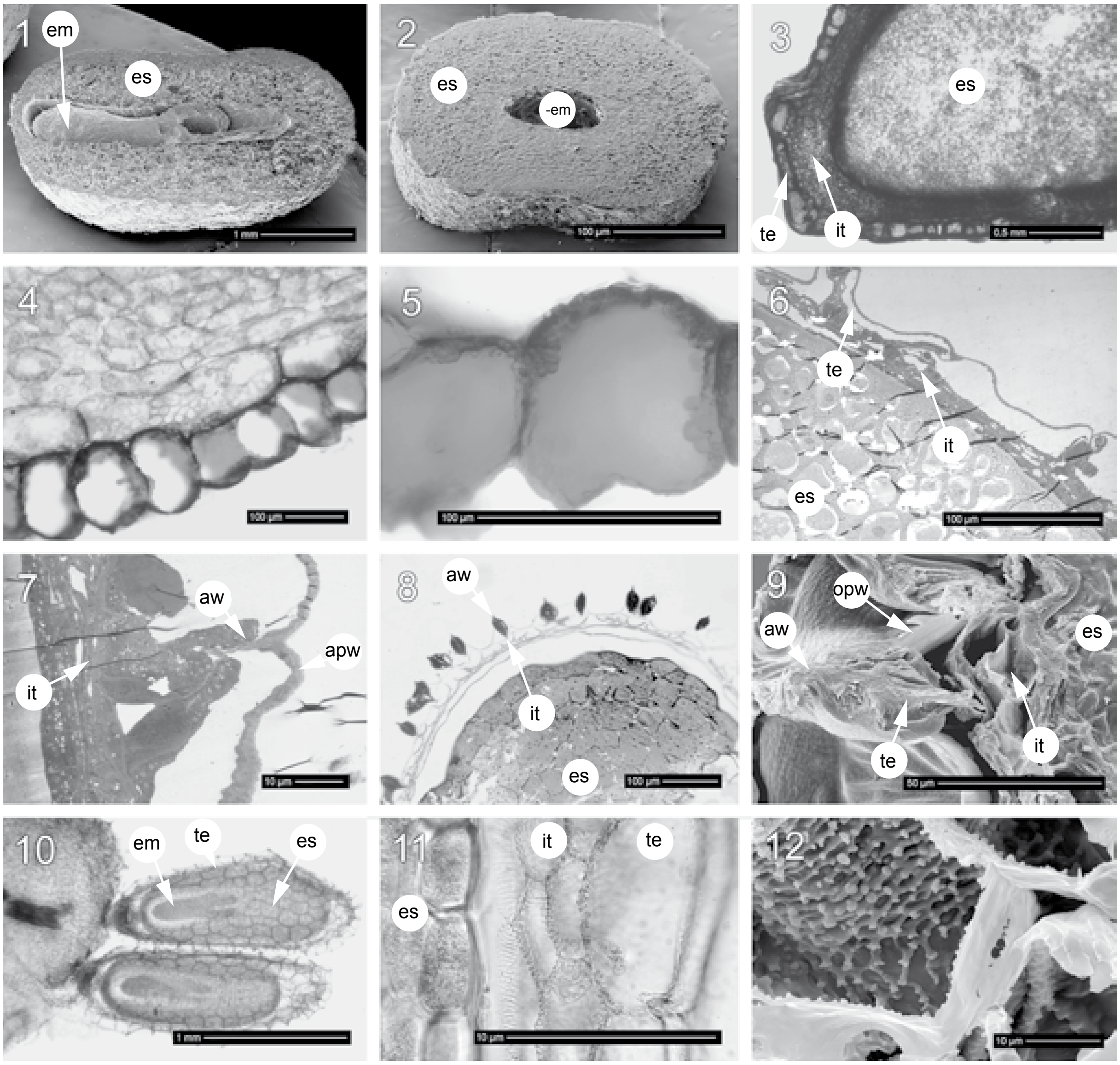


Fig. 6.6: Seed anatomy of *Loasa* ser. *Macrospermae*, *L.* ser. *Loasa*, *L.* ser. *Volubiles* and *L.* ser. *Pinnatae.* (1) *L. heterophylla* (LoMc, Jiles 6448), longitudinal section of seed with note massive endosperm (SEM). (2) *L. acerifolia* (LoMc, Weigend et al. 6848), transverse sections through seed (SEM). (3–5) *L. acanthifolia* (LoLo, Weigend et al. 6924), longitudinal section of young seed (LM). (3) Hilar pole. (4) Detail of testa. (5) Testa epidermis. (6–7) *L. nitida* (LoMc, Weigend et al. 2000/901), mature seed (TEM). (6) Endosperm and testa. (7) Detail of testa with anticlinal and periclinal walls. (8) *L. gayana* (LoVo, Weigend et al. 7057), transverse section of mature seed with 3-layered testa (LM). (9) *L. martinii* (LoVo, Montero 7905), transverse section of mature seed, 3-layered testa, massively thickened anticlinal wall (SEM). (10–12) *L. asterias* (LoPi, Weigend 6991), young seeds. (10). Two young seeds (LM). (11) Detail of 3–4-layered testa with secondary sculpturing in young seed (LM). (12) Details of secondary sculpturing (SEM). (aw = anticlinal wall, es = endosperm, em = embryo, em = embryo removed, it = inner testa layers, opw = outer periclinal wall, te = testa epidermis).

smooth, often partially ruptured. Inner testa cell layers: 5–7 layers, largely collapsed in mature seed (compare Corner, 1976). Secondary sculpture: Absent. Transfer structures: Reticulate, spongiose transfer structures cover part of the inner periclinal walls (Fig. 6.4.10), but most of the transfer structures are in the shape of glomerules (Figs. 6.4.11 and 6.4.12), which appear to consist of two flatfooted hemispheres (Fig. 6.4.11, see also Corner, 1976).

Blumenbachia sect. ***Gripidea*** (Figs. 6.3.11, 6.3.12, 6.4.7 and 6.5.1–6.5.3)

Blumenbachia sect. *Gripidea* consists of three closely related winding herbs from Uruguay and Brazil, two of them (*B. eichleri* Urb. and *B. exalata* Weigend) were analyzed, literature data are available on the third species [*B. scabra* (Miers) Urb. – Miers, 1866; Urban, 1889]. The two well-known species *B. scabra* and *B. eichleri* have very similar seeds, while those of *B. exalata* Weigend (Weigend, 1997) differ clearly. Traditionally the group was allied to *Caiophora* (together with *B.* sect. *Angulatae*, Urban and Gilg, 1900), but was transferred to *Blumenbachia* (Weigend, 1997), because of the extreme similarity in both flower and inflorescence characters.

Shape and size: Pear-shaped in *B. exalata*, and ca. 1400 µm long and 400–500 µm wide, the micropylar pole is undifferentiated, chalazal pole protracted into a short, truncate wing ca. 500 µm long and 400 µm wide (Fig. 6.3.11); with two empty, polar wings each ca. 1300 µm long and 4000 µm long overall in *B. scabra* and *B. eichleri*, the wing at the micropylar pole wider (ca. 670 µm) and open at the end, whereas the wing at the chalazal pole is tapering and only ca. 100 µm wide (Fig. 6.5.1), with 9–12 testa cells end to end. Primary sculpture: Central part of the seed with widely and irregularly reticulate testa (cell diam. ca. 450–500 µm), anticlinal walls ca. 400 µm high and ca. 30 µm wide, with parallel, equatorially orientated cell rows which form distinct, elevated ridges (undulations) with their equatorial walls (Fig. 6.5.2) in *B. eichleri* and *B. scabra*, wings with long and narrow testa epidermis cells (1000 x 100 µm, Fig. 6.5.3). Anticlinal walls: Very thin and often partially ruptured in the proximal portion (compare *B.* sect. *Blumenbachia*), distal portion conspicuously thickened and ca. 40 µm wide and slightly granular. Outer periclinal wall: Persistent, concave, smooth, often irregularly ruptured. Inner testa cell layers: 1–3 layers, collapsed in mature seed. Secondary sculpture: Absent. Tertiary sculpture: Irregularly spongiose–reticulate sculpturing (compare *Blumenbachia* sect. *Blumenbachia*) on the inner periclinal walls (Fig. 6.4.7).

Loasa ser. ***Loasa*** (syn. ***Loasa*** ser. ***Acanthifoliae***) and ***Loasa*** ser. ***Macrospermae*** (Figs. 6.5.4–6.5.6 and 6.6.1–6.6.7)

Loasa ser. *Loasa* and ser. *Macrospermae* are two closely allied groups of *Loasa* largely restricted to Chile with 10–20 species, four species of ser. *Macrospermae* (*L. nitida* Desr., *L.*

heterophylla Hook. & Arn., *L. acerifolia* Domb., *L. tricolor* Ker.Gawl.) and one (of possibly two) species of ser. *Loasa* (*L. acanthifolia* Desr.) were investigated and they show rather uniform seed morphology. They both have very large and heavy seeds (compare Weigend et al., 2004b).

Shape and size: Globose (Fig. 6.5.5) to ovoidal (Fig. 6.5.4) seeds and ca. 1600–4000 µm in diameter, usually with very conspicuous raphe ca. 1600 µm long and 400 µm wide (Fig. 6.5.5), cell borders are too indistinct to clearly count cell numbers (Fig. 6.5.6). Primary sculpture: Indistinctly shallowly reticulate, testa cells polyhedral to subcircular and ca. 45 µm in diameter (Fig. 6.5.6). Anticlinal walls: Low, poorly differentiated, ca. 10 µm wide, irregularly thickened (visible only in section – Figs. 6.6.4–6.6.7). Outer periclinal walls: Persistent, largely collapsed onto the inner periclinal wall (Fig. 6.6.6). Inner testa cell layers: 8–10 layers (Figs. 6.6.3 and 6.6.4), largely collapsed in mature seed (Figs. 6.6.6 and 6.6.7). Secondary sculpture: Usually not observed under the SEM due to the thickness of the outer periclinal wall, but well visible in *Loasa triloba* Domb., otherwise outer periclinal walls irregularly folded and rugose, inner testa layers with reticulate secondary sculpture in young seeds (Fig. 6.6.4). Tertiary sculpture: Not observed.

Loasa ser. ***Deserticolae*** (Figs. 6.5.7–6.5.9)

This is a probably monotypical series of annual, decumbent to ascending herbs restricted to Chile (Urban and Gilg, 1900). Material corresponding to the two illdefined species, *L. urmenetae* Phil. and *L. elongata* Phil., was available for analysis and their seeds are morphologically indistinguishable.

Shape and size: Irregularly ovoidal, ca. 2500 µm long and 1500 µm wide, micropylar pole rounded, but the seeds with subterminal, poorly developed hilum (raphe) ca. 400 µm long and 150 µm wide (Fig. 6.5.7), with 10–13 testa cells end to end. Primary sculpture: Reticulate, cells polyhedral, 180–250 µm long and ca. 100–200 µm wide. Anticlinal walls: Well developed, ca. 150–200µm high, ca. 30 µm wide, distally thickened (Fig. 6.5.8) and slightly granulose, with complete fenestration (Figs. 6.5.7–6.5.9). Outer periclinal walls: Absent in mature seeds. Inner testa cell layers: 1–3 layers, of small, but not collapsed cells. Secondary sculpture: Irregular reticulations on the inner periclinal walls, the fenestrations of the anticlinal walls show a fine striate, vermicelli-sculpture. Tertiary sculpture: Clear, spongiose transfer structures are not found, but the secondary sculpture of all testa layers shows granular–- echinate wall outgrowths.

Loasa ser. ***Floribundae*** (Figs. 6.5.10–6.5.12)

This is a group of four decumbent to ascending, mostly annual species restricted to Chile (Urban and Gilg, 1900); two of which, *L. floribunda* Hook. & Arn. and *L. pallida* Gill. ex Arn., were

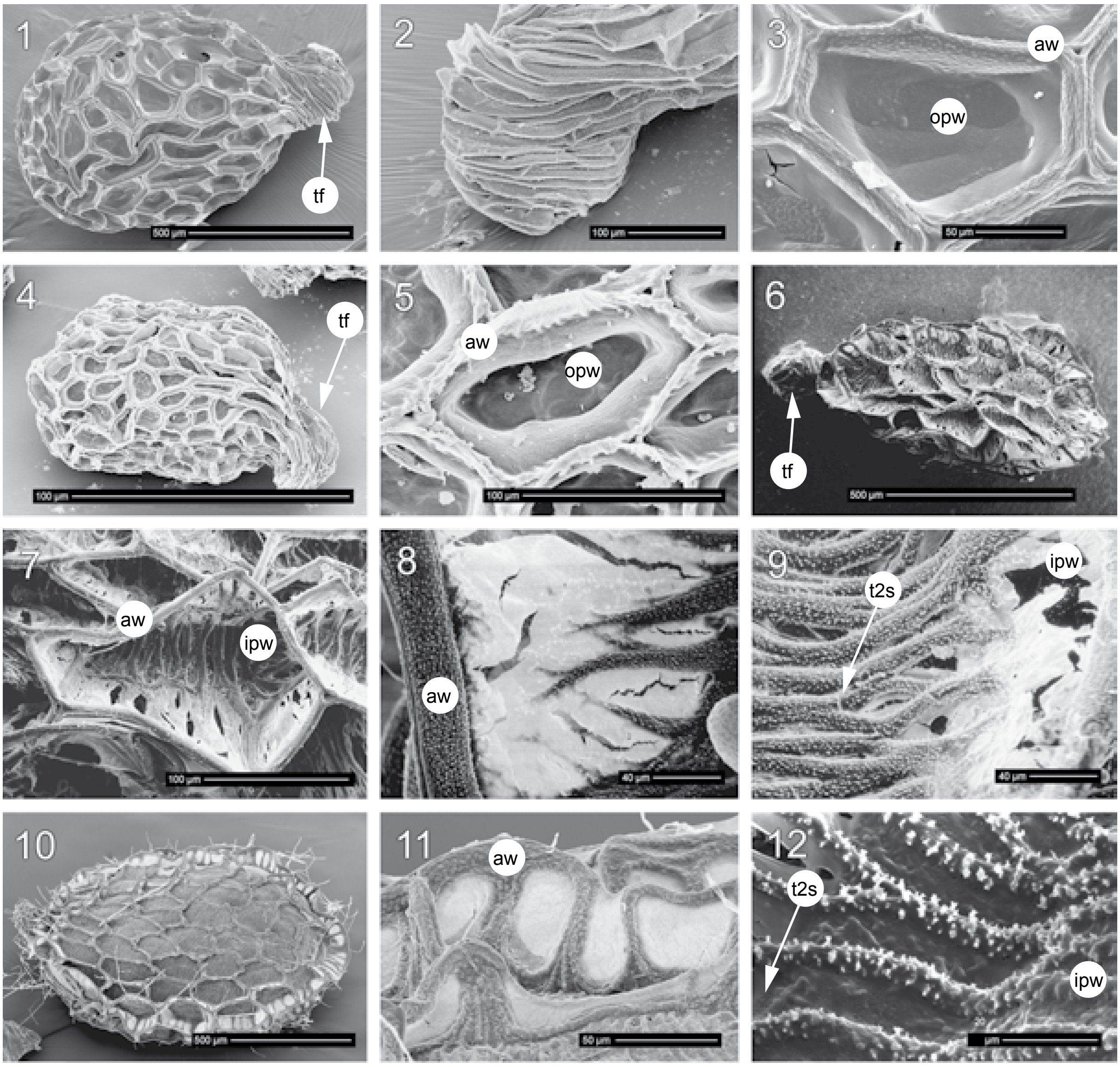


Fig. 6.7: Seed morphology of *Loasa* ser. *Volubiles* and *Scyphanthus*. (1–3) *L. gayana* (LoVo, Weigend et al. 7057). (1) Entire seed. (2) Funicular pole, note twisted testa cells. (3) Individual testa cell. (4, 5) *L. martinii* (LoVo, Montero 7905). (4) Entire seed. (5) Individual testa cell. (6–9) *L. micrantha* (LoVo, Po¨ ppig s.n.). (6) Entire seed, note funicular pole with slightly twisted testa cells. (7) Individual testa cell. (8) Anticlinal wall, note the not anastomosing secondary sculpture between ‘‘windows’’. (9) Transverse secondary sculpture. (10, 11) *Scyphanthus stenocarpus* (Aravena 33318), entire seed. (11) Anticlinal wall. (12) *Scyphanthus stenocarpus* (Buchtien 361), detail of transverse secondary sculpture. (all SEM, aw = anticlinal wall, ipw = inner periclinal wall, opw = outer periclinal wall, tf = twisted hilar cone, t2s = transverse secondary sculpture).

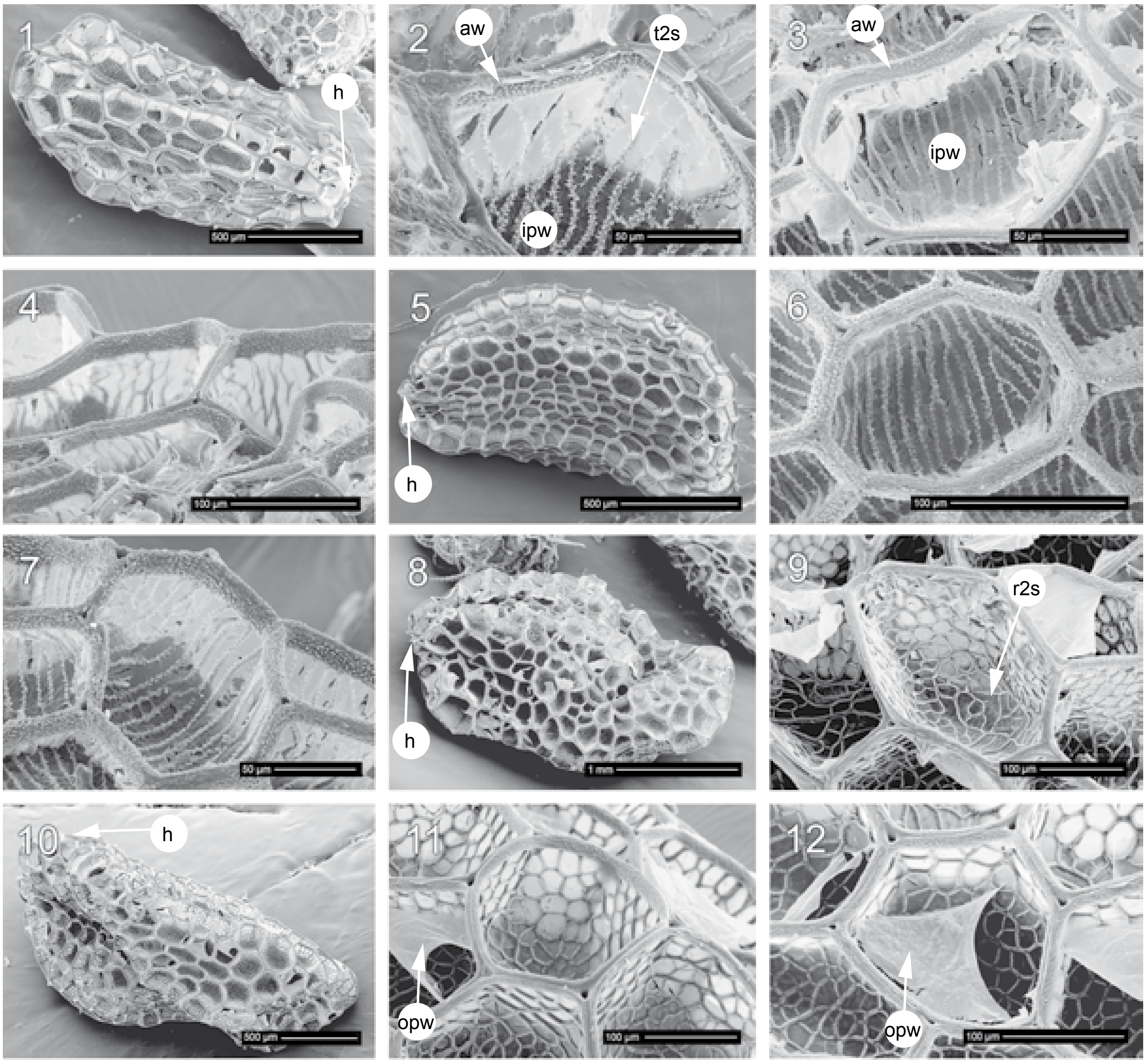


Fig. 6.8: Seed morphology of *Loasa* ser. *Pinnatae*. (1, 2) *L.* asterias (LoPi, Weigend et al. 6991). (1) Entire seed. (2) Part of testa cell, note transverse to transverse-reticulate secondary sculpture extending onto anticlinal walls. (3, 4) *L. bergii* (LoPi, Weigend et al. 6899). (3) Individual testa. (4) Anticlinal wall with incomplete fenestration. (5–7) *L. filicifolia* (LoPi, Weigend 6933). (5) Entire seed. (6) Individual testa cell. (7) Anticlinal walls. (8, 9) *L. paradoxa* (LoPi, Sparre and Constance 10897). (8) Entire seed. (9) Individual testa cell, note ± regularly reticulate, granular secondary sculpture. (10–12) *L. nana* (LoPi, Weigend et al. 7080). (10) Entire seed. (11) Testa cell, note regular, reticulate secondary sculpture. (12) Partially broken outer periclinal wall (all SEM, aw = anticlinal wall, h = hilar pole, ipw = inner periclinal wall, opw = outer periclinal wall, r2s = reticulate secondary sculpture, t2s = transverse secondary sculpture).

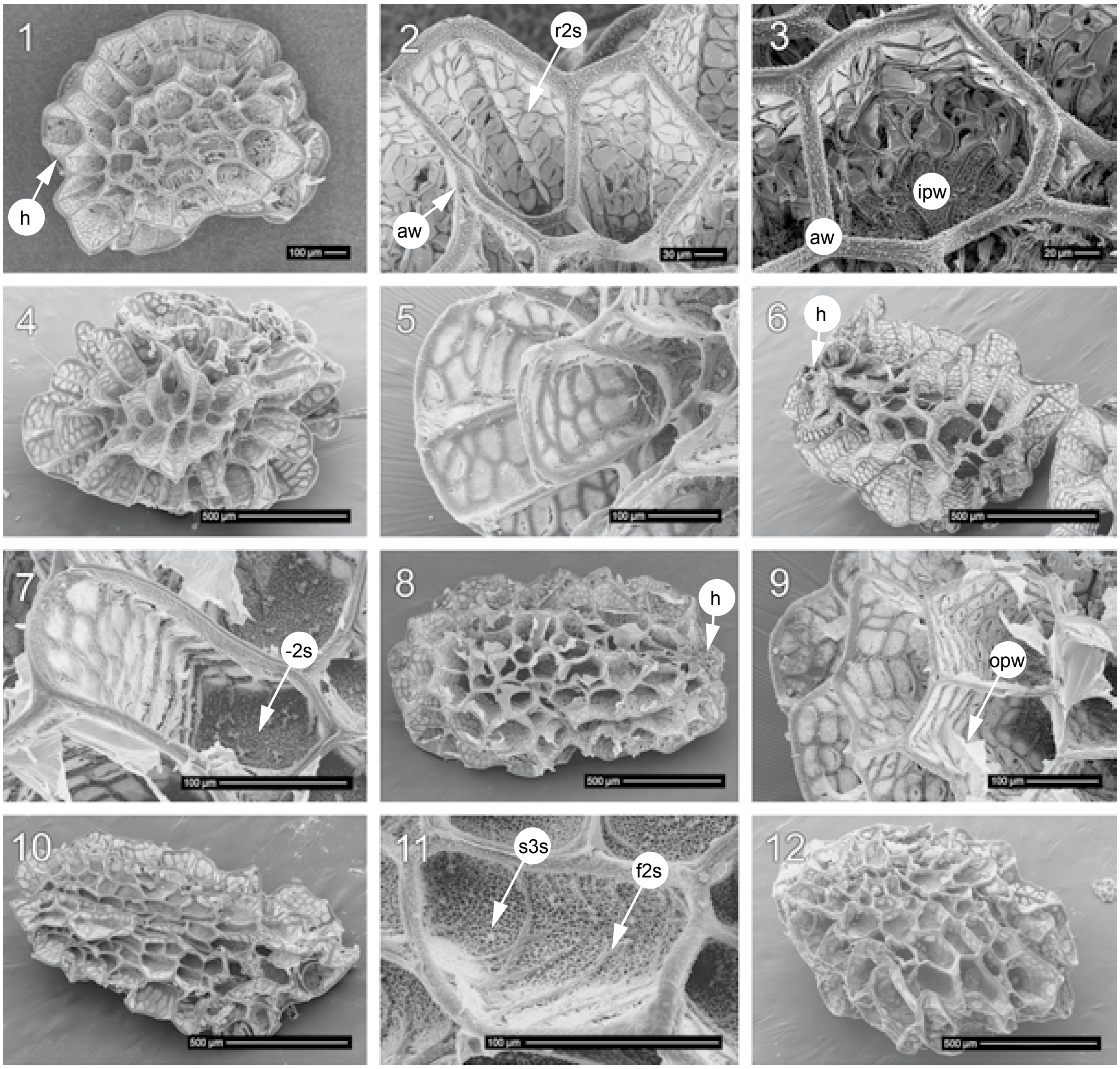


Fig. 6.9: Seed morphology of *Caiophora*. (1–3) *C. arechavaletae* (CaAr, Schlindwein 397). (1) Entire seed. (2) Individual testa cells, note reticulate secondary sculpture. (3) Individual testa cell. (4, 5) *C. pentlandii* (CaCr, Weigend and Förther 97/783). (4) Entire seed, outer periclinal wall absent. (5) Testa cells. (6, 7) *C. coronata* (CaCr, Ackermann 123). (6) Entire seed. (7) Testa cells, note fragmented secondary sculpture and spongiose transfer structures on inner periclinal wall with. (8, 9) *C. superba* (CaCh, Weigend and Förther 97/802). (8) Entire seed. (9) Testa cells. (10, 11) *C. andina* (CaCh, Kraus s.n.). (10) Entire seed. (11) Testa cell. (12) *C. scarlatina* (CaCh, M. & K. Weigend 2000/108), entire seed (all SEM, aw = anticlinal wall, f2s = fragmented secondary sculpture, h = hilar pole, ipw = inner periclinal wall, opw = outer periclinal wall, r2s = reticulate secondary sculpture, s3s – spongiose tertiary sculpture, -2s– absent secondary sculpture).

available for analysis and both of which are virtually identical with respect to seed morphology.

Shape and size: Irregularly ovoidal, ca. 2500 µm long and 1500 µm wide, micropylar pole is rounded, but the seeds have a subterminal, poorly developed hilum (raphe) ca. 400 µm long and 150 µm wide, with 15–20 testa cells end to end. Primary sculpture: Reticulate, cells polyhedral and 100–150 µm long and ca. 80–150 µm wide. Anticlinal walls: Well developed, ca. 100 µm high, ca. 30 µm wide, distally thickened (Fig. 6.5.11) and slightly granulose. Proximal part with complete, irregular fenestration. Outer periclinal walls: Absent in mature seeds. Inner testa cell layers: 1–3 layers, of small, but not collapsed cells. Secondary sculpture: Present in the form of irregular reticulations on the inner periclinal walls and the anticlinal walls. Tertiary sculpture: Clear, spongiose transfer structures are not found, but the secondary sculpture of all testa layers shows long, branched wall outgrowths (Fig. 6.5.12).

Loasa ser. ***Volubiles*** (Figs. 6.6.8, 6.6.9 and 6.7.1–6.7.9)

This is a group of only four of winding species restricted to Chile (Urban and Gilg, 1900). Three species, *L. gayana* Urb. & Gilg, *L. micrantha* Poepp. and *L. martinii* Phil., were available for analysis, the fourth species, *L. sagittata* Hook. & Arn. from Chiloe, has apparently not yet been collected in fruit.

Shape and size: Irregularly ovoidal, ca. 1000–1200 µm long and 600–700 µm wide, micropylar pole rounded, but seeds with a usually very conspicuous, slightly twisted hilum 200 µm long and wide (Figs. 6.7.1, 6.7.2 and 6.7.6), with 7–10 testa cells end to end. Primary sculpture: Reticulate, testa cells polyhedral and 150–200 µm long and ca. 100 µm wide. Anticlinal walls: Low, or well developed, ca. 10–30 µm wide, distally thickened (Figs. 6.6.8, 6.6.9 and 6.7.8). with (*L. martini* – Fig. 6.7.5) or without (*L. gayana* – Fig. 6.7.3) indistinct apical ornamentation, proximal part with irregular, incomplete fenestrations (Figs. 6.7.7 and 6.7.8). Outer periclinal walls: Persistent and collapsed onto the inner periclinal wall (*L. martinii*, *L. gayana* – Figs. 6.7.1–6.7.5), or absent in mature seed (*L. micrantha* – Figs. 6.7.6 and 6.7.7), smooth and without sculpturing. Inner testa cell layers: 1–3 layers, of small, but not collapsed cells (Figs. 6.6.8 and 6.6.9). Secondary sculpture: Irregular, transverse striations ca. 3 µm wide and 6–8 µm apart (Fig. 6.7.7), but usually obscured by the persistent outer periclinal wall. Secondary sculpture of inner periclinal walls is continuous with the latticework of the anticlinal walls. Tertiary sculpture: Spongiose transfer structures present, additionally, the secondary sculpture of all testa layers shows granular–echinate wall outgrowths (Fig. 6.7.9).

Fig. 6.10 continued: (12) Testa cell, anticlinal wall with irregular, scabrid SSC leading to very large, irregular fenestrations of only 1–2 per wall (SEM, f2s = fragmented secondary sculpture, h = hilar pole, -2s= absent secondary sculpture, lw = longitudinal wing).

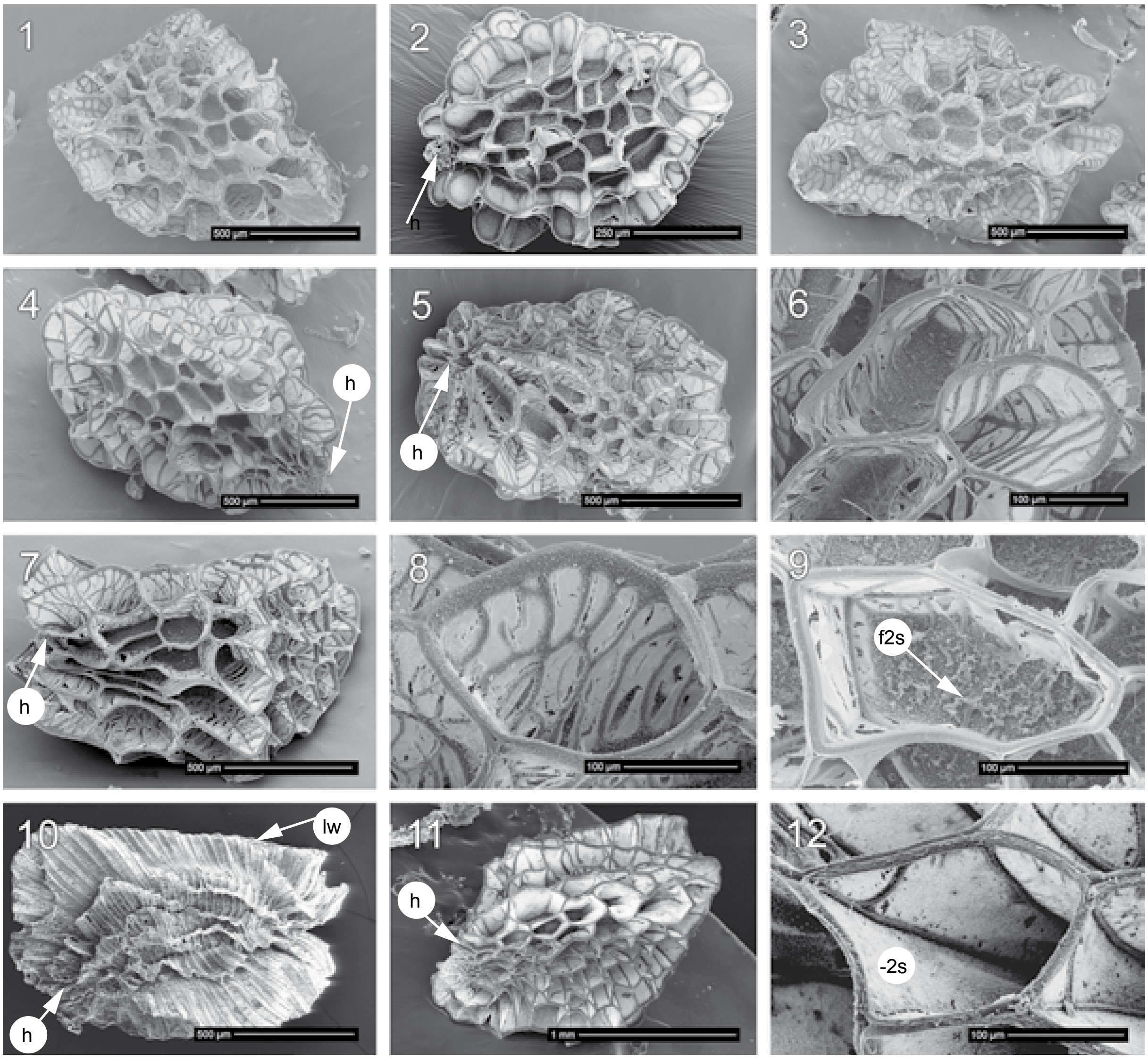


Fig. 6.10: Seed morphology of *Caiophora*. (1) *C. carduifolia* (CaCa, M. & K. Weigend 2000/326), entire seed, outer periclinal wall largely absent, anticlinal wall with irregularly reticulate, scabrid secondary sculpture (secondary sculpture = SSC) leading to large, irregular fenestrations. (2) *C. cernua* (CaCl, Sleumer 37), entire but immature seed, outer periclinal wall absent, anticlinal wall with scarcely developed scabrid SSC and incomplete fenestrations, inner periclinal wall with spongiose transfer structures, without SSC. (3) *C. cirsiifolia* (CaCi, Weigend et al. 97/464), entire seed, outer periclinal wall absent, anticlinal wall with irregularly reticulate, scabrid SSC leading to large, irregular fenestrations. (4) *C. cirsiifolia* (CaCi, Weigend et al. 97/314), entire seed, outer periclinal wall absent, anticlinal wall with irregularly reticulate, scabrid SSC leading to very large, incomplete fenestrations. (5, 6) *C. grandiflora* (CaCo, Weigend and Dostert 97/31). (5) Entire seed, outer periclinal wall absent. (6) Testa cells, anticlinal wall with irregularly reticulate, scabrid SSC leading to very large, incomplete fenestrations, inner periclinal walls with spongiose transfer structures, with fragmentary SSC. (7–9) *C. contorta* (CaCo, Weigend et al. 97/323). (7) Entire seed, outer periclinal wall absent. (8) Testa cells, anticlinal wall with irregularly reticulate, scabrid SSC leading to very large, irregular fenestrations. (9) Testa cell, inner periclinal walls with spongiose transfer structures and much fragmented SSC. (10) *C. pterosperma* (CaPt, Weigend and Dostert 97/29), entire seed, outer periclinal wall absent, anticlinal walls in one plane extremely high, with transverse SSC and spongiose walls. (11, 12) *C.* cf. *pterosperma* (CaPt, Weigend et al. 5118). (11) Entire seed, outer periclinal wall absent.

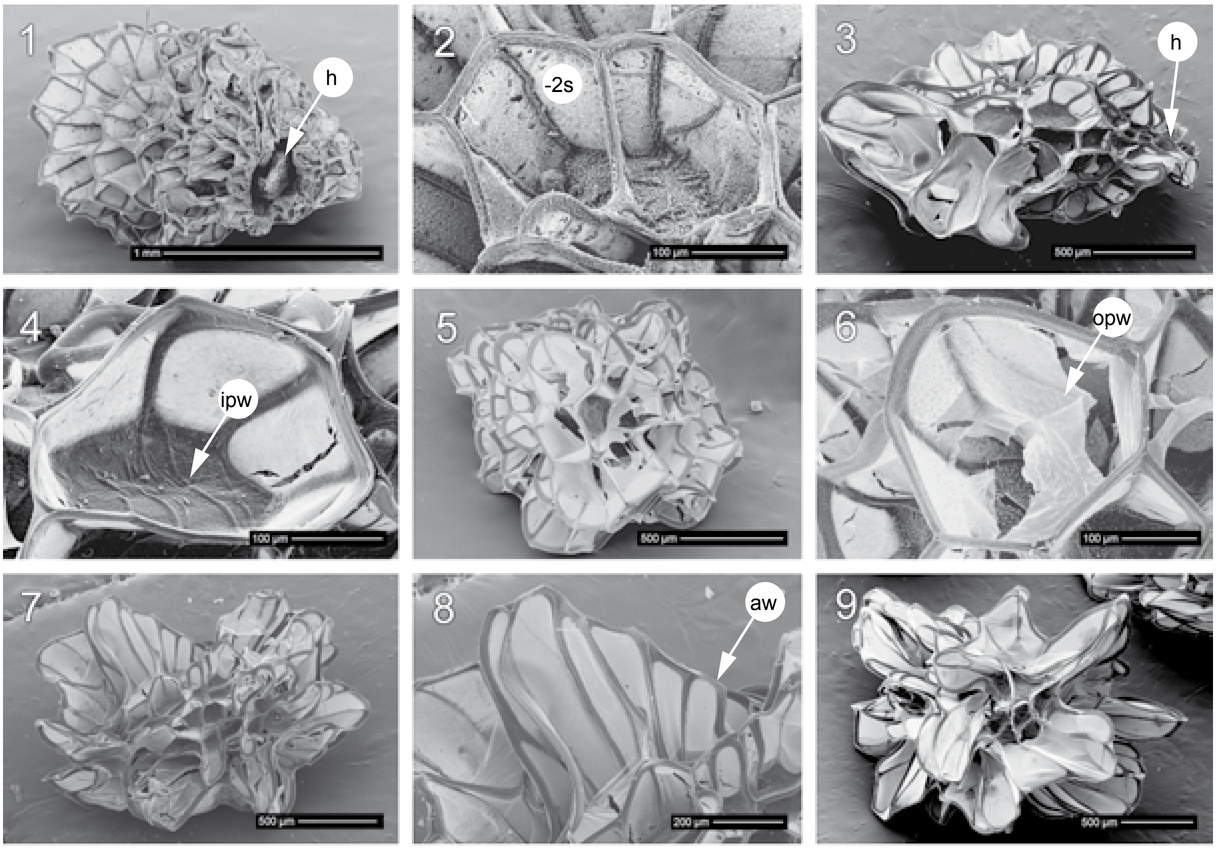


Fig. 6.11: Seed morphology of *Caiophora*. (1, 2) *C. buraeavii* (CaLa, Kraus s.n.). (1) Entire seed. (2) Testa cells, note the total fenestration. (3, 4) *C. canarinoides* (CaLa, Ackermann 375). (3) Entire seed, outer periclinal walls absent or present as concave ‘‘sails’’. (4) Individual testa cell. (5, 6) *C. madrequisa* (CaLa, M. & K. Weigend 2000/101). (5) Entire seed. (6) Individual testa cell. (7, 8) *C. madrequisa* (CaLa, M. & K. Weigend 2000/301). (7) Entire seed. (8) High anticlinal walls with total fenestration. (9) *C. madrequisa* (CaLa, Ackermann 356), entire seed, note absence of secondary sculpture on inner periclinal walls without (all SEM, aw = anticlinal wall, h = hilar pole, ipw = inner periclinal wall, opw = outer periclinal wall, -2s= absent secondary sculpture).

Scyphanthus (Figs. 6.7.10–6.7.12)

Scyphanthus is a genus of winding herbs, consisting of possibly two Chilean species (Urban and Gilg, 1900). Both currently accepted taxa, *S. stenocarpus* Urb. & Gilg and *S. elegans* D.Don, were analyzed and have an identical seed morphology.

Shape and size: Irregularly ovoidal and ca. 1000–1500 µm long and 700–800 µm wide, micropylar pole rounded, but seeds with conspicuous hilum ca. 130 µm long and wide, with 8–10 testa cells end to end. Primary sculpture: Reticulate (Fig. 6.7.10), cells polyhedral, 200–250 µm long and ca. 100–150 µm wide. Anticlinal walls: Low on two „flat” sides of the seeds, much higher in a broad zone in one longitudinal plane, higher walls ca. 50–75 µm high and 5–10 µm wide, distally thickened, proximal part with one row of regular, complete fenestrations (Fig.

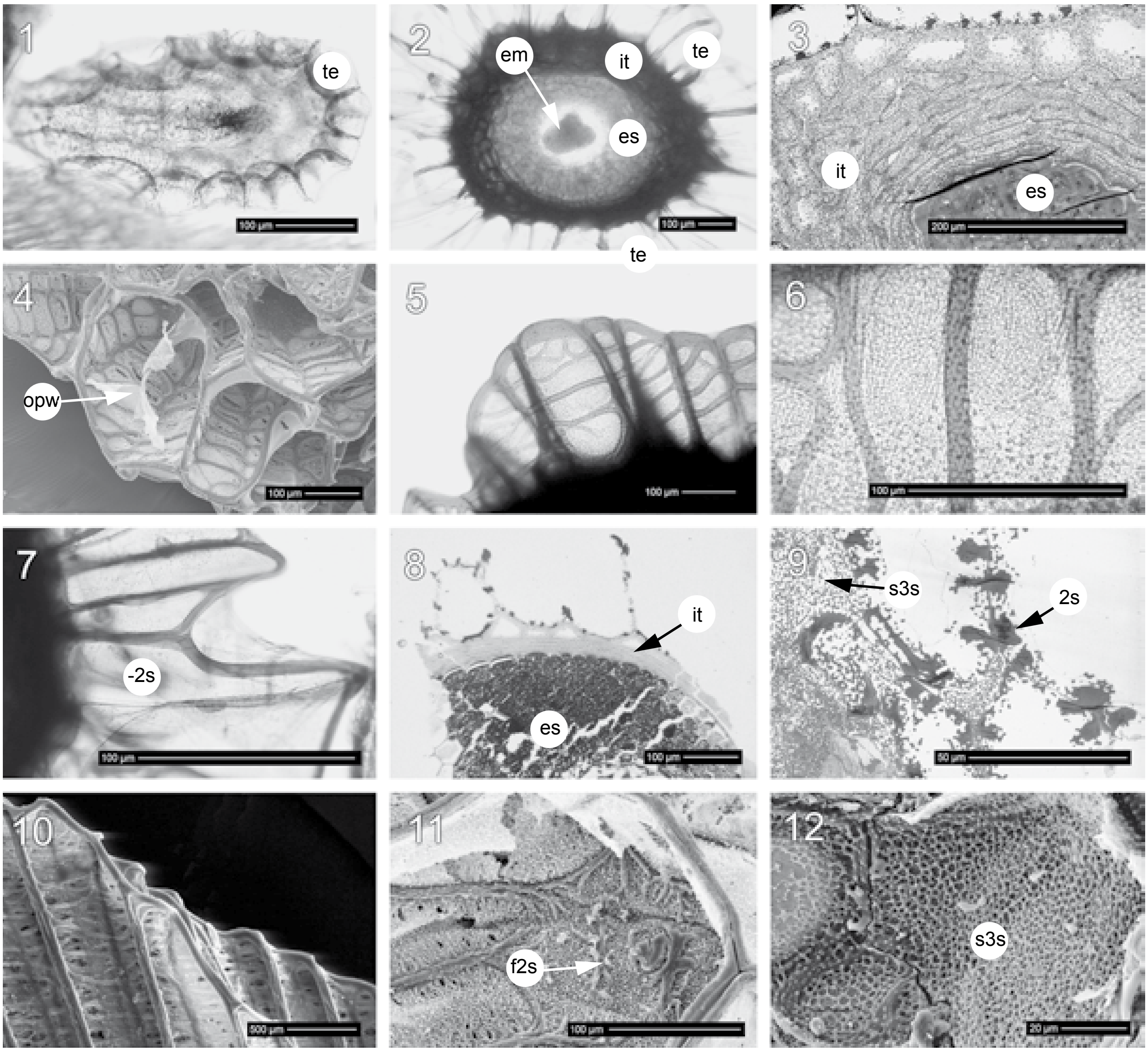


Fig. 6.12: Seed anatomy of *Caiophora*. (1) *C. pterosperma* (CaPt, Weigend et al. 5484), young seed with haustoria and developing testa epidermis (LM). (2) *C. madrequisa* (CaLa, M. & K. Weigend 2000/240), transverse section of immature seed (LM). (3) *C. cirsiifolia* (CaCi, Weigend et al. 97/465), transverse section of mature seed (TEM). (4) *C. carduifolia* (CaCa, Weigend et al. 2000/326), testa epidermis cells (SEM). (5, 6) *C. carduifolia* (CaCa, Weigend et al. 5415), anticlinal walls of immature seed (LM). (7) *C. cirsiifolia* (CaCi, Dostert 98/156), immature seed (LM). (8, 9) *C. cirsiifolia* (CaCi, Weigend et al. 97/465), mature seed (TEM). (8) Many-layered transfer-testa and endosperm. (9) Details of anti- and periclinal walls of transfer testa. (10) *C. pterosperma* (CaPt, Weigend and Dostert 97/29), mature seed, detail of anticlinal wall with lattice-like wall outgrowths (SEM). (11) *C.* cf. *pterosperma* (CaPt, Weigend et al. 5118), mature seed (SEM). (12) *C. madrequisa* (CaLa, Ackermann 356), mature seed (SEM) (em = embryo, es = endosperm, f2s = fragmented secondary sculpture, it = inner testa layers, opw = outer periclinal wall, s3s = spongiose tertiary scultpure, te = testa epidermis, -2s= absent secondary sculpture, 2s = secondary sculpture).

6.7.11). Outer periclinal walls: Persistent and collapsed onto the inner periclinal wall, occasionally absent in mature seeds. Inner testa cell layers: 1–3 layers, of small, but not collapsed cells. Secondary sculpture: Irregular, transverse striations ca. 3 µm wide and 6–8 µm apart (Fig. 6.7.12), usually obscured by the persistent outer periclinal wall. Secondary sculpture of inner periclinal walls is continuous with the latticework of the anticlinal walls. Tertiary sculpture: Spongiose transfer structures present, additionally secondary sculpture of all testa layers with granular–echinate wall outgrowths (Fig. 6.7.12).

Loasa **ser.** ***Acaules***

Loasa ser. *Acaules* is a probably monotypical series from the Patagonian Andes. *L. lateritia* Gill. ex Arn. shows close morphological resemblance to *Loasa* ser. *Pinnatae* and ser. *Volubiles*.

Shape and size: Irregularly ovoidal, ca. 2000–2500 µm long and 1600 µm wide, chalazal pole rounded, micropylar pole slightly protracted into a cylindrical hilum, with 10–15 testa cells end to end. Primary sculpture: Reticulate, cells polyhedral, 100–250 µm long and ca. 80–160 µm wide. Anticlinal walls: Very well developed, 200–300 µm high, distally thickened and 5–10 µm wide, slightly granulose, with total fenestration. Outer periclinal walls: Usually completely absent on mature seeds, occasionally, remnants present. Inner testa cell layers: Not investigated. Secondary sculpture: The inner periclinal walls with sinuose–reticulate secondary sculpture, lumina 15–40 µm wide, not continuous with fenestration of anticlinal walls, since these show total fenestration. Tertiary sculpture: Not investigated.

Loasa **ser.** ***Pinnatae*** (Figs. 6.6.10–6.6.12 and 6.8.1–6.8.12)

Loasa ser. *Pinnatae* is a southern Andean and Patagonian species group, which is strikingly homogeneous. Urban and Gilg (1900) recognized 20 species, but there are probably a lot less. Nine species representing all morphological types in the group were analyzed (*L. filicifolia* Poepp., *L. asterias* Dusen, *L. paradoxa* Urb. & Gilg, *L. nana* Phil., *L. bergii* Hieron., *L. volubilis* Domb., *L. artemisiifolia* Poepp., *L. poeppigiana* Urb. & Gilg, *L. sigmoidea* Urb. & Gilg).

Shape and size: Irregularly ovoidal, ca. 1500–2200 µm long and 600–1000 µm wide, both poles more or less rounded, with 9–17 testa cells end to end. Primary sculpture: Reticulate (Figs. 6.8.1, 6.8.5 and 6.8.8), cells polyhedral, 140–300 µm long and ca. 100–200 µm wide. Anticlinal walls: Very well developed, 100–150 µm high, distally thickened and 5–10 µm wide, slightly granulose, proximal part with one row of irregular, incomplete (Figs. 6.8.2 and 6.8.4) or irregular, complete (Fig. 6.8.7), or to up to four rows of regular, complete fenestrations (Figs. 6.8.9 and 6.8.11). Unequal compression is probably the reason for the observation of „longitudinal wings” in *Loasa bergii* Hieron. by Hufford (1988), which are simply the anticlinal walls which

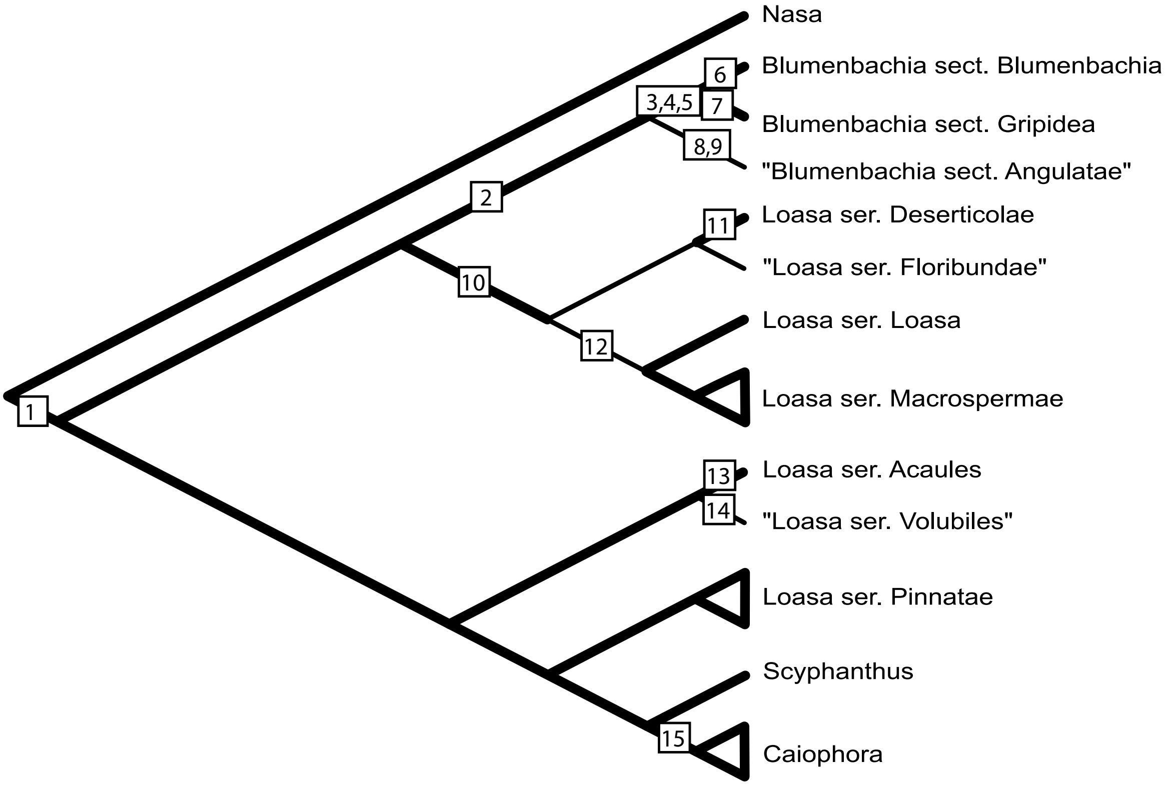


Fig. 6.13: Seed morphology mapped onto a cladogramm. Numbers refer to presumably apomorphic characters states (probably paraphyletic groups in quotation marks; abbreviations for infrageneric groups). (1) Testa with many cell-layers in mature seed; (2) seeds with testa with longitudinal or equatorial undulations; (3) outer testa walls (apex of anticlinal wall and outer perclinal wall) forming a loose outer coat (balloon seeds); (4) all testa cells or only the ones on terminal wings very narrow and spirally twisted; (5) testa epidermis, at least in central part, with equatorial undulations; (6) inner periclinal walls of testa epidermis with globose transfer structures; (7) seeds with 1 or 2 terminal wings; (8) apex of anticlinal walls not thickened, all testa layers more or less identical in shape and sculpture; (9) testa epidermis with longitudinal undulations (wings); (10) hilum or hilar scar subterminal or lateral; (11) secondary sculpture very finely striate; (12) testa epidermis collapsed in mature seeds, anticlinal walls undifferentiated; (13) anticlinal walls with total fenestration; (14) hilar cone spirally twisted. (15) Secondary sculpture of inner periclinal wall reduced to lost.

remained intact in one plane but were compressed on both sides of the seeds. Our seeds of the species showed anticlinal walls of equal heights in all directions. Outer periclinal walls: Usually completely absent on mature seeds, occasionally, remnants present (Fig. 6.8.12). Inner testa cell layers: 1–3 layers, of small, but not collapsed cells. Secondary sculpture: The inner periclinal walls with more or less strongly anastomosing transverse striations (Figs. 6.8.11, 6.8.2 and 6.8.6) ca. 3–4 µm wide and 8–10 µm apart or a irregular to regular reticulation with lumina 15–25 µm wide (Figs. 6.8.9 and 6.8.11), secondary sculpture of inner periclinal walls continuous with the latticework of the anticlinal walls. Tertiary sculpture: Spongiose–reticulate transfer structures are found on the inner testa layers (Fig. 6.6.12), the secondary sculpture of

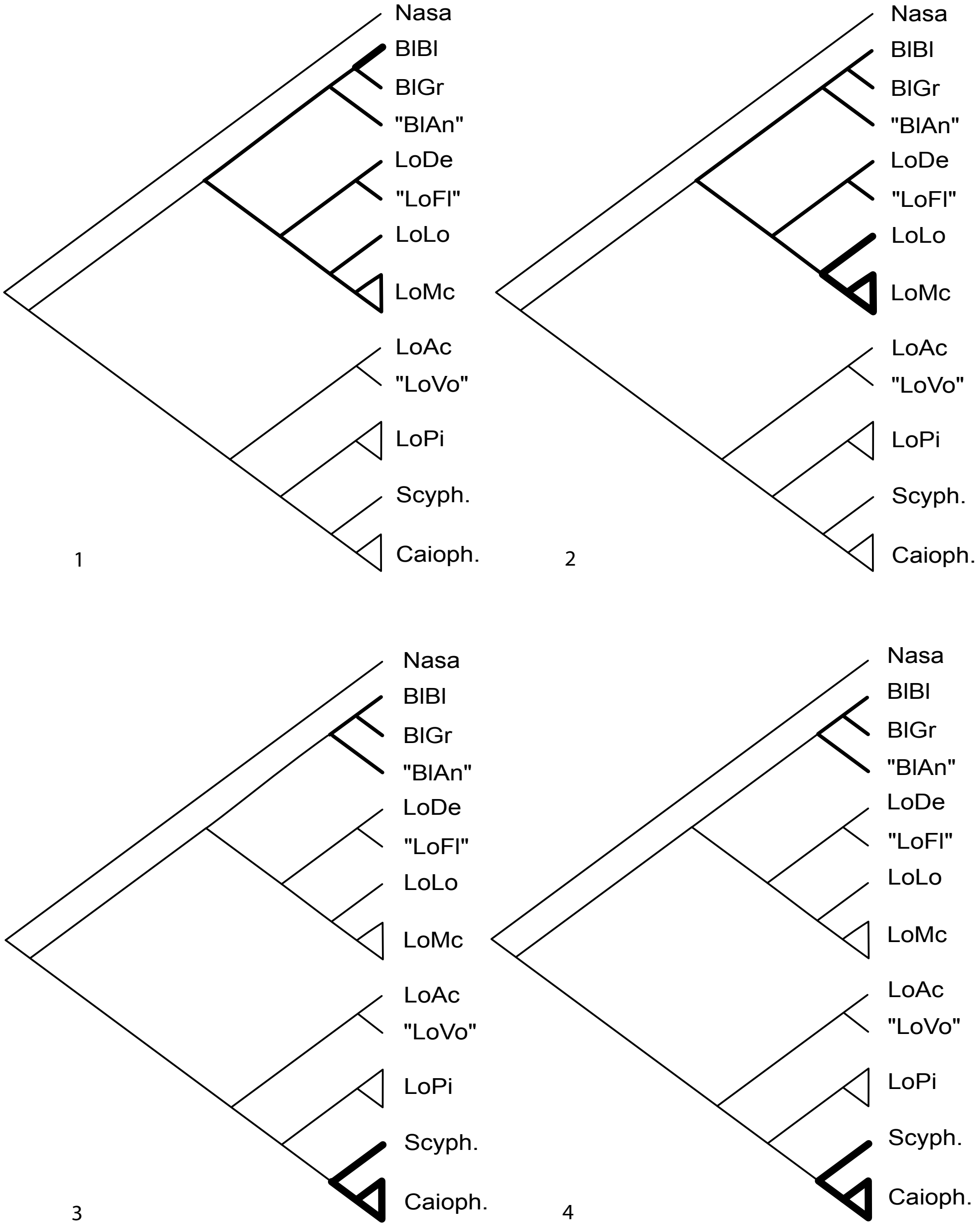


Fig. 6.14: Seed weights and fruit morphology and opening mode mapped onto a cladogramm (data from Weigend et al., 2004b). (1) Fruit opening mechanism. Fine line: capsules reversibly xerochasious; medium line: capsules irreversibly xerochasious or with irregular timing (tardily closing upon wetting); thick line: capsule not xerochasious. (2) Thousand seed weight (tsw), divided into classes. Thin line: tsw 0.1–0.5 g; medium line: tsw 0.5–1 g; thick line tsw >10 g. (3) Fruit opening mode. Fine line: septicidal, apical valves; medium line: septifragous, longitudinal (6 sutures) dehiscence with coherent apex; thick line: septicidal, longitudinal (3 sutures) and apical dehiscence. (4) Fruit shape. Thin line: straight; medium line: twisted anticlockwise only; thick line: (straight or) twisted anticlockwise (abbreviations for infrageneric groups: BlBl = *Blumenbachia* section *Blumenbachia*, BlGr = *Blumenbachia* section *Gripidea,* BlAn = *Blumenbachia* section *Angulatae*, LoDe = *Loasa* ser. *Deserticolae*, LoFl = *Loasa* ser. *Floribundae*, LoLo = *Loasa* ser. *Loasa*, LoMc = *Loasa* ser. *Macrospermae*, LoAc = *Loasa* ser. *Acaules*, LoMc = *Loasa* ser. *Volubiles*, LoPi = *Loasa* ser. *Pinnatae*, Scyph. = *Scyphanthus*, Caioph. = *Caiophora*).

the inner periclinal walls shows granular–echinate, sometimes branched wall outgrowths (Fig. 6.8.2).

Caiophora (Figs. 6.9.1–6.9.12, 6.10.1–6.10.9, 6.11.1–6.11.12 and 6.12.1–6.12.12)

The mostly high-Andean genus *Caiophora* is alpha-taxonomically the most complex and least understood group in Loasaceae. There are probably over 50 species, ranging from Ecuador to N Argentina and N Chile, with most species in Peru and Bolivia. The group can be informally divided into species groups according to habit, leaf and flower morphology (Weigend and Ackermann, 2003). Nearly all taxa were available for analysis and a selection representing the most important forms is here presented.

Shape and size: Very irregularly shaped, mostly ovoidal and angled and slightly compressed, sometimes with long protracted wings in (+/–) one plane, (750–) 1000–1500 (–2000) µm long and 500–1500 µm wide, poles not differentiated and difficult to see in the mature seed, with 8–12 testa cells end to end. Primary sculpture: Reticulate (e.g., Figs. 6.9.1 and 6.10.2), cells polyhedral and 100–200 µm long and wide. Anticlinal walls: Usually lower on two „flat” sides of the seeds, much higher in a broad zone in on longitudinal plane, height typically differing by a factor 2–3 (particularly well visible in *C. pterosperma* with heights differing by a factor 10), 50–100 (–750) µm high, distally thickened and 5–10 µm wide, slightly granulose, fenestration extremely variable, largely group-specific: regular fenestrations in 7–9 rows with polygonal to circular windows (*C. arechavaletae* group, *C. coronata* group, *C. chuquitensis* group, *C. nivalis* group, Figs. 6.9.1–6.9.12), or irregular fenestrations in 1–3 rows and very irregular windows, sometimes incompletely fenestrated (*C. carduifolia* group, *C. contorta* group, *C. cirsiifolia* group, *C. clavata* group, one species of the *C. pterosperma* group, Figs. 6.10.1–6.10.9, 6.10.11 and 6.10.12), or total fenestration (Figs. 6.11.1–6.11.9), then often anticlinal wall extremely long and irregular (*C. lateritia* group). One taxon [*C. pterosperma* (G.Don) Urb. & Gilg – Fig. 6.10.10] with very high anticlinal walls with a single row of extremely high fenestrations. One taxon (*C. pulchella* Urb. & Gilg) with 4–6 rows of windows and these perfectly circular and separated by wide latticework (> than windows diameter). Outer periclinal walls: Usually completely absent on mature seeds, occasionally, remnants present and collapsed (Figs. 6.10.3 and 6.10.6). Inner testa cell layers: 3–8 layers, of small, but not collapsed cells (Fig. 6.12.3). Secondary sculpture: The inner periclinal walls with strongly fragmented secondary sculpture (Figs. 6.9.3, 6.9.11, 6.10.9, 6.11.2 and 6.11.4), sometimes secondary sculpture completely absent (Fig. 6.11.12). If present, the secondary sculpture of the inner periclinal walls continuous with the latticework of the anticlinal walls (Figs. 6.9.3 and 6.10.10). Tertiary sculpturing: Spongiose–reticulate (transfer) structures on the inner periclinal wall, and all inner testa layers (Figs. 6.12.3, 6.12.9 and 6.12.12), sometimes also on the anticlinal walls (Figs 6.12.10).

6.5. Discussion

General patterns: A deeply pitted testa without outer periclinal walls in the mature seed and with reticulate or transverse secondary sculpturing seems to represent the ancestral condition in South Andean Loasas, since it is nearly universally found in South Andean Loasas and widespread in the outgroups. Secondary sculpture is absent only in the mature seeds of ser. *Macrospermae* and ser. *Loasa*, but is found here in young, immature seeds, indicating that reticulate secondary sculpture is the plesiomorphic condition for this entire clade. A many-layered testa is present in nearly all South Andean Loasas and is secondarily reduced in the mature seeds of one monophyletic group (*Loasa* ser. *Loasa* and ser. *Macrospermae*) but has not so far been found in any other group of Loasaceae and likely represents an important apomorphy of South Andean Loasas. Also, the outer periclinal wall, if present, is always smooth and not granular as in other Loasoideae. Echinate to spongiose tertiary sculpture is found in most South Andean Loasas and may represent another apomorphy. We interpret spongiose tertiary sculpturing as passive transfer structures to accelerate water uptake of the seed (compare Diane et al., 2002).

Apart from these common features, seed morphology in South Andean Loasas is very variable, but largely follows the groupings found with other morphological characters and molecular markers. Figs. 6.13 and 6.14 show some character states presented here and the characters of seed weight and fruit morphology (Weigend et al., 2004b) mapped onto the hypothetical phylogeny of South Andean Loasas.

South Andean Loasas fall into two clades, the *Blumenbachia*–*Loasa* clade and the *Caiophora* clade, which are, however, not clearly retrieved by seed morphology. The *Blumenbachia*–*Loasa* clade shows a distinct trend towards heavier seeds than both the outgroup and the *Caiophora* clade (Fig. 6.14.2) and towards a loss of xerochasious capsules (Fig. 6.14.1). The former culminates in the very heavy seeds of *Loasa* ser. *Loasa* and ser. *Macrospermae*, the latter in the irreversibly xerochasious or non-xerochasious capsules of some species of ser. *Macrospermae* (e.g., *L. nitida* Desr.) and all *Blumenbachia* species. *Blumenbachia* as defined here (i.e., including the sections *Gripidea* and *Angulatae*) is held together by capsule shape and opening mode (Figs. 6.14.3 and 6.14.4), while sharing no derived character states with the *Caiophora* clade or *Caiophora* itself. Hufford (1988) argued for close similarity between the seeds of *B. eichleri* (sect. *Gripidea*) and *Caiophora lateritia* and *C. macrocarpa*, while he considers the seeds of *B. insignis* (sect. *Blumenbachia*) to be very different. This is very difficult to understand, since all informative characters are nearly identical between *B. eichleri* and *B. insignis*, while differing widely between both *Blumenbachia* species and *Caiophora* (e.g., balloon seeds with persistent outer periclinal wall vs. deeply pitted seeds without outer periclinal wall, presence vs. absence of narrow, spirally twisted testa epidermis cells and equatorial undulations) – the close affinity between the two sections of *Blumenbachia* cannot sensibly be doubted (Figs. 6.13 and 6.14.1–6.14.4). *Blumenbachia* exalata from sect.

Gripidea with a single terminal wing bridges the small remaining gap between the other two taxa of *Gripidea* (with two terminal wings) and sect. *Blumenbachia* (without wings). The sections *Blumenbachia* and *Gripidea* themselves are likely monophyletic since they again have unique and apparently apomorphic features (Fig. 6.13), such as the peculiar globose tertiary sculpturing of sect. *Blumenbachia* and the (1–) 2 terminal wings of sect. *Gripidea*. The initial suspicion that the globose structures in sect. *Blumenbachia* might be of fungal origin could not be confirmed: they were observed on both seeds from wild collections of three species and from cultivated plants of two species and on FAA-material of barely mature fruits, which would imply an unlikely degree of contamination. *Blumenbachia* sect. *Angulatae*, another group that has traditionally been placed into *Caiophora* (not investigated in Hufford, 1988), is more problematical, since its seed morphology is quite distinct from the rest of *Blumenbachia* and indeed all other Loasoideae. Its testa epidermis has an often convex outer periclinal wall (lost, or concave in all other taxa) with reticulate secondary sculpturing (smooth in all other taxa), the anticlinal cell walls are homogenous (apically thickened in all other taxa) and the testa forms unique, irregular, longitudinal wings. However, these derivations are universal in sect. *Angulatae* and paraphyly of that group is somewhat unlikely. While the three sections as such can thus be readily defined, there are no clear seed morphological apomorphies for the genus *Blumenbachia* as such, unless we accept the presence of testa undulations (in the form of equatorial undulations, respectively, longitudinal wings) as synapomorphic, irrespective of their orientation.

The *Loasa* s.str. subclade is supported by the presence of a subterminal to lateral hilum or hilar scar in all taxa investigated, whereas all other Loasaceae investigated so far have terminal hilum or hilar cone, so that this character state can probably be considered as apomorphic. It falls into two clear seed morphological groups: The seeds of ser. *Deserticolae* and *Floribundae* are rather small (1000 seed weight <1 g) and deeply pitted with fenestrate anticlinal walls, closely conforming to the plesiomorphic condition in South Andean Loasas, and are thus not supported as a monophyletic group by seed morphology. Secondary sculpture in ser. *Deserticolae* is finely striate–undulate, which is unique in Loasoideae, but this series may be monotypic, so that this is only of alpha-taxonomical relevance. Conversely, *Loasa* ser. *Loasa* and ser. *Macrospermae* have a unique seed morphology for the family with their very large and heavy seeds (Fig. 6.14.2; tsw 11–24 g and ca. 10 x as heavy as the largest seed outside these groups in Loasoideae; Weigend et al., 2004b) and a many-layered testa where both the outer and the inner layers collapse completely in the mature seed, leading to a very poorly structured seed surface (whereas at least the outer testa cells retain their structural integrity in all other Loasoideae) and thus share a very well-defined apomorphic condition.

The *Caiophora* clade has relatively small (tsw 0.1–0.46 g; Weigend et al., 2004b), deeply pitted seeds with fenestrate anticlinal walls, usually without outer perclinal walls in the mature seeds, and in this seems to have retained the ancestral condition of South Andean Loasas. Within the *Caiophora* clade some individual species and groups have derived character states: The seeds of ser. *Volubiles* have a twisted hilar cone quite unlike other Loasoideae, and are thus well characterized, but lack any other morphological derivations. *Loasa lateritia* (ser. *Acaules*) lacks this twisted hilar cone and has anticlinal walls with complete fenestration (versus incomplete fenestration in *Volubiles*), so that the affinity between ser. A*caules* and ser. *Volubiles* found in molecular data is not retrieved in seed morphology. *Loasa* ser. *Pinnatae*, *Scyphanthus* and *Caiophora* all have secondary sculpturing on the inner periclinal walls continuous with that of the anticlinal walls, and lack the outer periclinal walls in the mature seed. Most species of *Caiophora*, *Scyphanthus* and ser. *Pinnatae* have nearly identical seeds, with only *Caiophora* having some additional derived types in some of its subgroups. The seeds of *L.* ser. *Pinnatae* always have extremely well developed and regular secondary sculpturing, and the taxa investigated can be subdivided into two groups, a group with reticulate secondary sculpture and complete fenestration (*L. paradoxa*, *L. nana*) and a group with transverse secondary sculpture and incomplete to complete fenestration (*L. asterias*, *L. filicifolia*, *L. bergii*). Incidentally, these two groups are also united by characters of habit and habitat: *L. nana* and *L. paradoxa* are decumbent herbs from high elevations (>1800 m), while *Loasa asterias*, *L. bergii* and *L. filicifolia* are winding or erect herbs from lower elevations (50–1600 m). *Scyphanthus* is apparently the sister group to *Caiophora*, and within *Caiophora* an ancestral complex of various rather isolated species groups (*C. pterosperma*, *C. nivalis*, *C. coronata*, *C. chuquitensis*, *C. arechavaletae*) can be distinguished from more derived groups (*C. carduifolia*, *C. cirsiifolia*, *C. contorta*, *C. lateritia*). *Caiophora pterosperma*, which may represent one of the earliest extant lineages in *Caiophora*, still has the same type of secondary sculpturing on the inner periclinal wall as *Scyphanthus*, i.e., complete transverse ribs, and also has a single row of, albeit very high, fenestrations like those of *Scyphanthus*. In all other investigated species of *Caiophora* the anticlinal walls have either numerous rows of (often irregular or incomplete) fenestrations, or total fenestration. Further, and most importantly, the secondary sculpturing of the inner periclinal wall is fragmented, reduced, or lost, thus representing a unique condition in Loasoideae underscoring the naturalness of this group of taxa within *Caiophora*. Within *Caiophora* the groups defined by floral and vegetative morphology are largely retrieved by the finer details of seed morphology: A gross-morphologically heterogeneous assemblage of species groups (*C. arechavaletae* group, *C. coronata* group, *C. chuquitensis* group, *C. nivalis* group) have regular fenestrations in 7–9 rows and windows which are +/– polygonal to circular in outline. This more or less closely resembles a type also found in *L.* ser. *Pinnatae* and probably representing the plesiomorphic condition, since these species groups variously represent ancestral character states in other aspects of morphology such as rosulate habit, erect growth, straight capsules, and capsules with apical instead of longitudinal dehiscence. *C. pulchella* (*C. nivalis* group) has anticlinal walls with small, perfectly round fenestrations, which are not found in any other taxon investigated. This underscores a high degree of isolation of this taxon, which, together with *C. nivalis*, also has straight capsules opening with apical valves (and not longitudinal slits as all other species of *Caiophora*). It has therefore been placed in *Loasa* by recent authors (Perez-Moreau and Crespo, 1992). The presence of spongiose transfer structures and the absence of regular secondary sculpturing on the inner periclinal wall clearly indicate that this taxon indeed does belong to *Caiophora* as probably one of the most basal extant lineages of the genus. The winding species groups with more derived floral morphology (*C. carduifolia* group, *C. contorta* group, *C. cirsiifolia* group, *C. clavata* group) typically show very irregular fenestrations in 1–3 rows, whereas the most derived seed type with extremely unequal anticlinal walls forming long, oblique sails is restricted to the *C. lateritia* group, which is also defined by a very derived floral morphology. The outer periclinal wall is usually always absent from the mature seeds of *Caiophora*, but in this particular group it is often still present and spans the oblique lumina of the testa cells like a thin, white tarpaulin.

Dispersal: Most seeds of South Andean Loasas are anemochorous, irrespective of their exact morphology (Weigend et al., 2004b), and are not hydrochorous – with the only possible exception of *Blumenbachia silvestris* (sect. *Angulatae*). Interestingly, anemochoria is achieved by different morphological structures in the various groups. Small, deeply pitted seeds are widespread and represent the ancestral condition (*Loasa* ser. *Deserticolae*, ser. *Floribundae*, ser. *Pinnatae*, ser. *Acaules*, ser. *Volubiles*, *Scyphanthus*, most *Caiophora*). „Wings” of some type arose four times: (i) from longitudinal undulations of a many-layered testa (*Blumenbachia* sect. *Angulatae*), (ii) from the protraction of the anticlinal walls in only one longitudinal plane into sails (*Caiophora pterosperma*), (iii) from the irregular protraction of anticlinal walls into sails (*C. lateritia* group) and (iv) from the formation of terminal „air sacs” by the polar portions of the testa (*Blumenbachia* sect. *Gripidea*). Sections *Gripidea* and *Blumenbachia* additionally have balloon seeds, where the apex of the anticlinal wall together with the outer periclinal wall forms a loose, fibrous coat, enclosing air around the much smaller central part of the seed and thus lowering specific weight. Only *Loasa* ser. *Loasa* and ser. *Macrospermae* have terminally lost the ability for wind dispersal, and have developed remarkably large, smooth and heavy seeds, a phenomenon likely correlated to substrate (Weigend et al., 2004b).

All taxa with anemochorous seeds have reversibly xerochasious capsules restricting seed release to dry and windy conditions (Weigend et al., 2004b), with the only exception of *Blumenbachia* (not xerochasious) and some *Loasa* s.str. (often irreversibly xerochasious). In *Blumenbachia*, the fruits themselves are very light and occasionally tardily dehiscent (and primarily dispersed as a unit – sect. *Blumenbachia*).

6.6. Acknowledgements

We would like to express out sincere gratitude to the herbaria B, BSB, F, M, NY, P, SGO, TUEB, UC, W for access to and loans of their collections. We want to thank Dr. H. Förther (Munich, Germany), N. Dostert, T. Henning, and C. Schneider (Berlin, Germany), Eric Rodriguez R. (Trujillo, Peru), A. Cano E. (Lima, Peru), G. Vobis and C. Ezcurra (Bariloche, Argentina) for help in the field. We would like to thank Mr. H. Lünser (Berlin) for arranging the photographic plates, Dr. E. Facher and Dr. R. Melzer (Munich), and Mrs. Ch. Grüber (Berlin) for help with the SEM work. The funds kindly provided by the following institutions at various stages of the project are here gratefully acknowledged: Studienstiftung des Deutschen Volkes (for M. Weigend: 1992–1997), Deutscher Akademischer Austauschdienst (for M. Weigend: 1999–2000), Deutsche Forschungsgemeinschaft (Grant No. WE 2330/1, 2001–2003), Lewis B. and Dorothy Cullman Laboratory for Molecular Systematics Studies at the New York Botanical Garden (for M. Weigend: 1999–2000), botconsult GmbH (1999–present).

6.7. Literature

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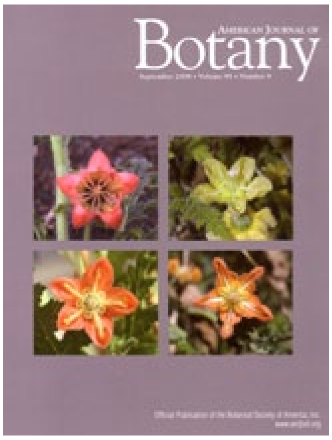
Floral ecology and hybridization



Cover Illustration:

Flowers of three Peruvian species of *Caiophora* (Loasacae subfam. Loasoideae) and a natural hybrid (bottom left: *C. cirsiifolia* C.Presl × *C. deserticola* Weigend & Mark.Ackermann, raised in Berlin from seeds from a plant of *C. deserticola* in Omate in southern Peru [top left]). Hybrid formation is the result of secondary contact of the parental species due to human impact: the maternal population of *C. deserticola* grows in a dry, high Andean habitat, whereas the paternal *C. cirsiifolia* populations (bottom right) are usually found in more humid areas at lower elevations. Localized populations of *C. cirsiifolia*, however, are found in higher, drier habitats where hedges and irrigation channels provide a suitable habitat for this species. In these areas, populations of the two usually allopatric species are neighbors, permitting cross-pollination and consequently interspecific hybridization. In experimental inter- and intraspecific crosses between morphologically and ecologically differentiated taxa, all species of *Caiophora* tested were highly interfertile. Crossability indices were generally higher in the progeny from interspecific crosses than from intraspecific crosses, indicating a marked heterosis effect and the possible presence of an inbreeding depression in the parental populations. Hybridization is thus expected to occur wherever human impact brings different taxa of *Caiophora* into secondary contact. Intensifying agriculture and new road construction are common in the Andes, likely increasing the levels of secondary contact and interspecific hybridization in *Caiophora*, thus threatening the genetic integrity of the *Caiophora* species and probably of other Andean taxa with a similar lack of crossing barriers. See Ackermann et al. 2008. American Journal of Botany 95: 1109-1121 http://www.amjbot.org/content/95/9.cover-expansion (Chapter 7).

7. Hybridization and crossability in *Caiophora* (Loasaceae subfam. Loasoideae): Are interfertile species and inbred populations results of a recent radiation?*

7.1. Abstract

Interspecific hybridization is considered a possible mechanism of plant diversification. The Andes are a hotspot of biodiversity, but hybridization in Andean taxa has so far not been investigated intensively. The current study investigates crossability in *Caiophora* (Loasaceae subfam. Loasoideae) by experimental interspecific hybridization of seven different species. Hand pollination was undertaken, developing fruits counted, thousand (seed) grain weights, and seed viability were examined. Cross pollination led to some fruit set in 36 of the 37 different combinations. Overall fruit set was virtually identical irrespective of the combination of parental plants. Mean germination rates were much higher in hybrid seeds, indicating a marked heterosis effect and the possible presence of an inbreeding depression in the source populations: In experimental hybridization the divergent taxa of *Caiophora* behave like isolated, inbred populations of a single species. Allopatry and different habitat preferences seem to be the key factors keeping the (interfertile) taxa of *Caiophora* apart in the apparent absence of both postmating isolating mechanisms and obvious isolating mechanisms in phenology and floral biology. Interspecific hybrids reported from the wild appear to be the result of secondary contact due to human impact.

Key words: Andes; *Caiophora*; heterosis; hybridization; Peru; postmating isolating mechanisms; Loasaceae.

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*The original publication is available at http://www.amjbot.org/. Published as: Ackermann M, Achatz M, Weigend M. 2008. Hybridization and crossability in *Caiophora* (Loasaceae subfam. Loasoideae): Are interfertile species and inbred populations results of a recent radiation? American Journal of Botany 95: 1109-1121. doi: 10.3732/ajb.2007403

7.2. Introduction

Species limits are usually defined by some type of reproductive isolation, either premating or postmating (McDade, 1995; Rieseberg and Carney, 1998; Rieseberg et al., 2006). Artificial hybridization experiments have thus been used in the past to infer relationships between different taxa via the degree of postmating reproductive isolation (e.g., Janczewski, 1907; Meurman, 1928; Keep, 1962; Beckmann, 1979; Wilson, 1980; McDade and Lundberg, 1982; den Nijs and Visser, 1985; Freyre et al., 2005; Mráz and Paule, 2006). It is expected that the degree of crossability between members of the same taxon is higher than crossability between different taxa (Elisens, 1989; Motley and Carr, 1998). Following a strict biological species concept, intraspecific crosses should result in full seed set with fully viable seed and viable and fertile offspring, while interspecific crosses should either not lead to seed set or to nonviable seed or the F1 generation should be sterile. In reality, some degree of crossability between taxa is often present, and the „crossability index“ for fruits/seeds has been proposed as a measure for the degree of reproductive isolation (McDade and Lundberg, 1982). Elisens (1989) showed that crossability within species was close to 1, roughly 10 times as high as crossability between congeneric species and 100 times as high as between species of different genera in an extensive hybridization experiment in Scrophulariaceae (Scrophulariaceae – Anthirrhineae, Maurandyinae, involving 17 species in four genera). Crossability indices for other parameters of postmating reproductive isolation can be calculated in the same manner for data such as seed/ hybrid viability or hybrid fertility (pollen viability, F1 seed set). Even if interspecific hybridization leads to seed set, the hybrid seeds should have lower germination rates and/or higher seedling mortality and/or F1 sterility compared to the parental taxa (Janczewski, 1907; Keep, 1962; den Nijs and Visser, 1985; Ramsey et al., 2003). In very general terms, the crossability index, based on any of the described parameters, should be or 1 (or close to 1) between freely interbreeding and fully interfertile populations, whereas it should be <1 between different taxa, if their taxonomic segregation is justified.

However, those hybrid plants that do develop frequently display heterosis, i.e., high survivorship and/or vigorous growth and development, irrespective and independently of their reduced fertility (Grant, 1975; Rieseberg and Carney, 1998; Ramsey et al., 2003). Heterosis and crossability are partly independent of each other: crosses between geographically closer vs. more distant populations in two forest tree species (of the genera *Shorea* and *Syzygium*, Stacy, 2001) showed that cross-fertility peaked at distances of 1–10 km between stands and was lower at higher distances (i.e., between different forest patches), but marked hybrid vigor was observed only in hybrids obtained from between-forest crosses in *Shorea*.

The majority of hybridization studies has been carried out in North America (e.g., Wyatt, 1990; Emms and Arnold, 1997; Campbell, 2003; Ramsey et al., 2003; Hochwender and Fritz, 2004; Burgess et al., 2005), Hawaii (e.g., Kim and Carr, 1990; Wagner et al., 1990; Whitkus, 1998; Caraway et al., 2001; Carr, 2003) and Europe (Ghazanfar, 1989; Bleeker 2002, 2003,

Table 7.1: Main morphological and ecological characters of *Caiophora* accessions from Peru used in the hybridization experiment, classified according to species group and section. (Abbreviations in parentheses in column 1 are those used for species group in the text.)

Classification according to							Color					
species group[a]	*Caiophopora* section[b]	Species[c]	Growth habit	Basal leaf rosette at flowering	Flower merosity	Corolla shape	Corolla	Floral scales	Floral scales, – dorsal filaments	Fruit	Altitudinal (m a.s.l.)	Habitat
C. carduifolia (CA)	*Orthocarpae*	*C. carduifolia* (AP)	winding herb	-	5	bowl	yellow	green	absent	twisted	2500–3500	andean scrub
C. chuquitensis (CH)	*Orthocarpae*	*C. deserticola* (MO)	erect shrublet	+	7–8	ballon	pink	white	present	straight	3000–3500	andean scrub
C. chuquitensis (CH)	*Orthocarpae*	*C. chuquitensis* (CU1)	erect herb	+	7–8	balloon	orange	white	present	straight	3500–4500	puna
C. cirsiifolia (CIR)	*Orthocarpae*	*C. cirsiifolia* (CA1)	winding herb	-	5	bowl	yellow	yellow	absent	twisted	1000–2000	cloud forest
C. cirsiifolia (CIR)	*Orthocarpae*	*C. cirsiifolia* (AN)	winding herb	-	5	saucer	orange	pale orange	absent	twisted	2500–3500	andean scrub
C. cirsiifolia (CIR)	*Orthocarpae*	*C. cirsiifolia* (CA2)	winding herb	-	5	bowl	orange	white	present	twisted	2500–3500	andean scrub
C. lateritia (LA)	*Platypetalae* [b]	*C. madrequisa* (PU)	winding herb	-	5	balloon	orange	pale orange	present	twisted	2000–3000	cloud forest
C. lateritia (LA)	*Platypetalae*	*C. canarinoides* (PU)	winding herb	-	5	bell	orange	yellow	present	twisted	2000–3000	cloud forest
C. coronata (CO)	*Dolichocarpae*	*C. pentlandii* (PU)	decumbent herb	+	5	bowl	red	white	absent	straight	3400–4500	puna

Notes:

+ present; – absent;

[a] Based on Weigend and Ackermann (2003).;

[b] Described after Urban and Gilg (1900), but would fall into *Platypetalae* by their definition.

[c] Abbreviation after plant names indicate department of origin in Peru; see Appendix B.

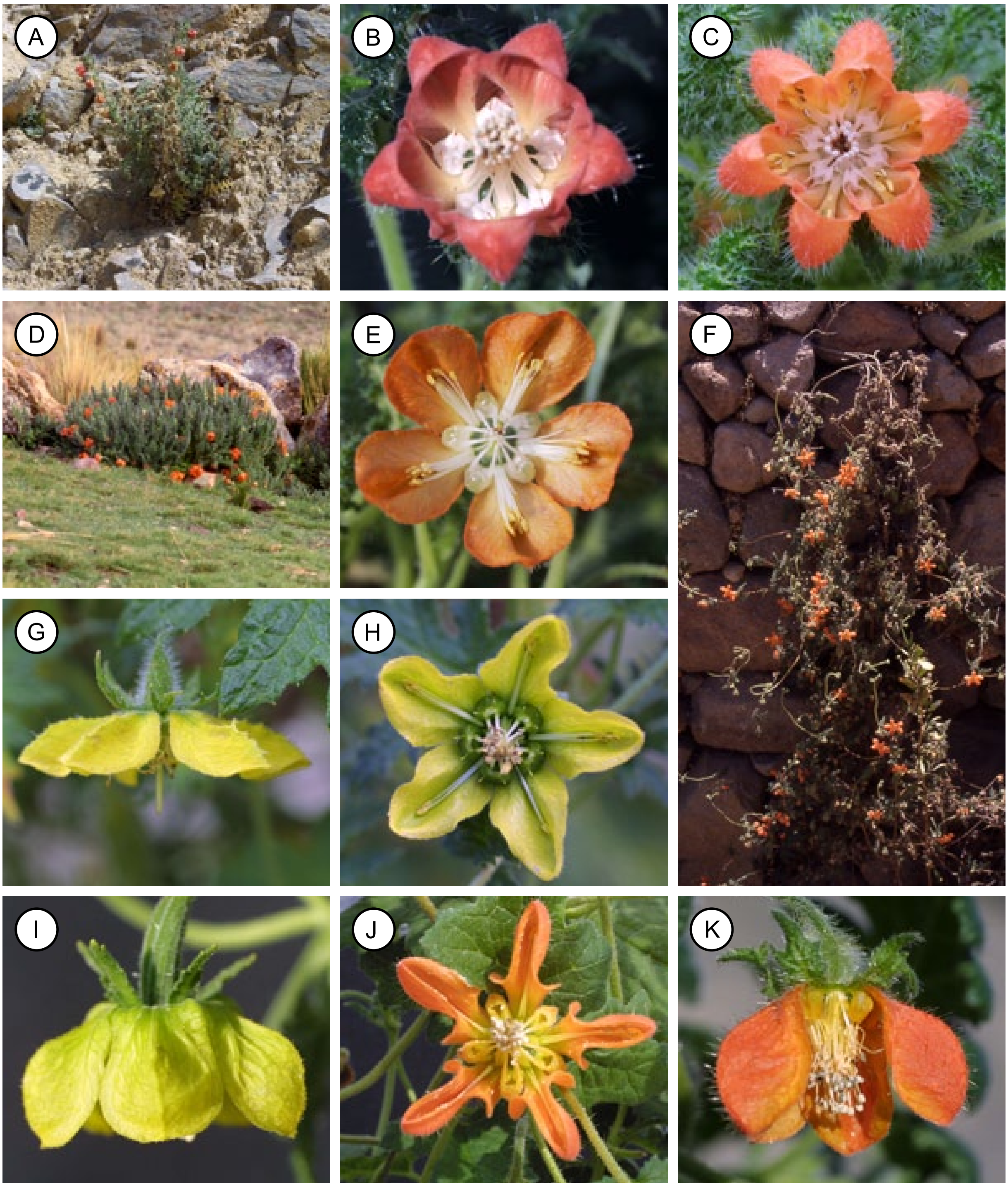

Fig. 7.2: Parental species used for inter- and intraspecific crosses (see App. 7.1. for voucher details, boldface: infrageneric group from Table 7.1). (A, B) *Caiophora deserticola* (MO, **CH**). (A) Erect shrublet in natural habitat, Depto. Moquegua. (B) Balloon-shaped, pinkish corolla; nectar scales (= NSC) white, with filiform filaments. (C) *C. chuquitensis* (CU1, **CH**), balloon-shaped, orange corolla, NSC white with filiform filaments. (D, E) *C. pentlandii* (PU, **CO**). (D) Decumbent plant in natural habitat in Depto. Puno. (E) Bowl-shaped, orange corolla, NSC white, generally without filaments. (G, H) *C. carduifolia* (AP, **CA**) winding herb with bowl-shaped, greenish-yellow corolla, NSC green, sometimes with filiform filaments. (F, I–K). *C. cirsiifolia* (**CIR**); four different morphotypes, all winding herbs with keeled NSC and without filaments. (F) *C. cirsiifolia* (AR)

b; Choler et al., 2004, Bleeker and Matthies, 2005; Mráz and Paule, 2006; Bleeker et al., 2007), Few experimental studies have been published from other regions such as Andean South America (Freyre et al., 2005), a particular hotspot of biodiversity. However, putative interspecific hybrids in the field have been reported from several South American plant groups (e.g., *Calceolaria*: Molau, 1988; Brücher, 1989; Sérsic et al., 2001; *Fuchsia*: Berry, 1982; Hoshino and Berry, 1989; *Passiflora*: Fischer, 2004).

The current study focuses on the genus *Caiophora* (ca. 50 spp.) of Loasaceae subfam. Loasoideae. It is the second largest genus of the subfamily (the largest is *Nasa* with > 100 spp.) and distributed from central Argentina/Chile to southern Ecuador at altitudes ranging from 2000 to 4500 m a.s.l. *Caiophora* is monophyletic and has strong morphological differentiation, especially in floral morphology and function, but also in growth habit and vegetative morphology (Weigend, 1997a, b; Ackermann and Weigend, 2006). Molecular data have so far been unable to resolve the phylogeny of the genus (Weigend et al., 2004b) and the genus is therefore informally divided into several „species groups“ (Weigend and Ackermann, 2003), based on a range of morphological characters (Table 7.1; Figs. 7.1, 7.2A, F, H, J, L, M, O; habit, petal and floral scale morphology, fruit shape). Within the species groups, the individual taxa are differentiated by minor details of flower color and morphology and leaf dissection, but are more or less homogeneous with respect to floral scale morphology, fruit morphology, and growth habit, so that species delimitation is difficult in *Caiophora*. Molecular data published so far indicate that sequence divergence is low in *Caiophora* compared to other genera of Loasaceae (trnL-trnF, psbA-trnH: Hufford et al. 2003, 2005; trnL UAA, ITS1: Weigend et al., 2004b; Weigend and Gottschling, 2006), and the numerous taxa may go back to a relatively recent radiation. Many of the currently recognized species are widely polymorphic and fall into numerous local races, differing in characters such as floral color and morphology, fruit size, leaf morphology, and growth habit (Weigend, 1997b; Weigend and Ackermann, 2003; Ackermann and Weigend, 2007). Flower ecology of Loasaceae subfam. Loasoideae has been studied intensively (Harter, 1995; Schlindwein, 1995, 2000; Wittmann and Schlindwein, 1995; Schlindwein and Wittmann, 1997; Ackermann and Weigend, 2006; Weigend and Gottschling, 2006), revealing a range of floral types and pollination syndromes. However, in *Caiophora* only a relatively small range of syndromes has been reported, with mixed pollination by hummingbirds and long-tongued bees in the majority of taxa (Ackermann and Weigend, 2006).

Several interspecific hybrids have been reported from the genus *Caiophora* (Table 7.2), while no hybrids have been documented in the literature for the much larger and more widespread genus *Nasa* nor for other genera in Loasoideae. Sleumer (1955) was the first to report hybridization in *Caiophora* and named a total of three putative hybrids from northern

Fig. 7.1 continued: bowl- to saucer shaped corolla and orange petals and NSC. (I) *C. cirsiifolia* (CA2) with bowl-shaped corolla and yellow petals and NSC. (J) *C. cirsiifolia* (CA1) with saucer- to bowl-shaped corolla and winged, orange petals and NSC. (K) *C. cirsiifolia* (AN) with balloon-shaped corolla and orange petals and NSC.

Argentina. Brücher (1986, 1989) also reported interspecific hybrids between various winding species of *Caiophora* in northwestern Argentina and southern Bolivia, especially between *C. lateritia* (Hook.) Klotzsch, *C. aconquijae* Sleumer, and *C. hibiscifolia* (Griseb.) Urb. & Gilg. More recently, the type collection of *Caiophora pauciseta* Killip [= *C. peduncularis* (C.Presl) Weigend and Mark.Ackermann] was recognized as coming from a hybrid population between *C. peduncularis* (C.Presl) Weigend and Mark.Ackermann and *C. carduifolia* C.Presl, including both parental species plus intermediate specimens (Weigend and Ackermann, 2003). In the past 15 years, we carried out a total of 65 wk of field studies in Andean South America, leading to > 200 collections of *Caiophora*. These include several collections that we assume to represent interspecific hybrids (Table 7.3, Fig. 7.2G, I, K, N), since they are morphologically intermediate between their putative parental taxa, both of which are present in the collection area in all cases (Fig. 7.2F, H–J, L, M, O). All putative interspecific hybrids in *Caiophora* appeared to have normally developed capsules and seeds. In the literature data and our own observations, 11 apparently fertile interspecific hybrids are thus reported for *Caiophora*, all of them hybrids between widely divergent species (mostly belonging to different species groups as defined in Weigend and Ackermann, 2003). However, as Rieseberg and Wood (2006, p. 6) pointed out, „The lack of association between contemporary hybridization and taxonomic difficulties may be an artifact of the difficulty of recognizing hybrids where taxa are not distinct to begin with.“ This may hold true for *Caiophora*, for which hybrids between the various „species“ or local races of the *C. cirsiifolia*, *C. carduifolia*, or *C. chuquitensis* groups would be difficult to identify in the field and next to impossible to recognize in the herbarium.

The observations on putative interspecific hybrids in *Caiophora* from the field were the starting point of the current study. Artificial crosses in the greenhouse were performed to address the following questions: Is hybridization between different species and different species groups indeed possible in *Caiophora* (especially between the groups from which putative hybrids have been reported in the field)? Are there differences in crossability between pollination within the same population, between closely allied taxa (species from the same species group respectively different geographical races of *C. cirsiifolia*) and between species from different species groups? What is the viability of the seeds of crosses between and within accessions/species? Can we find an explanation for the incidence of the interspecific hybridization observed in *Caiophora* in the field?

7.3. Materials and methods

Sampling

Putative interspecific hybrids are known from most groups of *Caiophora*. Our own observations include putative hybrids between the *C. chuquitensis* and the *C. cirsiifolia* or *C. carduifolia* species groups (Table 7.3) and a hybrid between the *C. cirsiifolia* and *C. carduifolia* species groups (Weigend and Ackermann, 2003). We therefore included representatives of these three species groups in our experiment. Additionally, two representatives of the *C. lateritia* species group and one of the *C. coronata* group were included because putative hybrids between species of these groups have been reported (Sleumer, 1955; Brücher, 1986, 1989). Three different geographical races of *C. cirsiifolia* (Fig. 7.1I–K) were also included in the experiment. This sampling should enable us to compare the crossability between more distantly to more closely allied taxa.

Experimental crosses

Voucher data for all accessions used in this study are summarized in Appendix B Abbreviations for the departments were added to the name throughout text, figures, and tables to indicate the source location of each accession. Seeds were collected in the wild, each seed lot was mixed from several seed capsules from different plants for each accession, and thus each accession represents a population subsample. We will refer to „accessions“ for these subsamples and infer conclusions about the populations in the discussion based on these population subsamples. All plants were cultivated in the greenhouse in Berlin in the same compartment and thus under identical conditions (lighting, temperature, soil, pot size). The same individual plants were used for both inter- and intraspecific crosses. Artificial interspecific and intraspecific crosspollinations were done in April – May 2004. Reciprocal crosspollinations were carried out between seven species of *Caiophora* (one represented by three different morphotypes), representing five different species groups sensu Weigend and Ackermann (2003). All species of *Caiophora* are proterandrous, but of all the *Caiophora* species so far cultivated (ca. 25 species and multiple different morphotypes) require hand-pollination in the absence of pollinators: fruit set was not observed in any of the several hundred flowers that were not hand-pollinated. Only one species so far cultivated [*C. contorta* (Desr.) C.Presl] is self-pollinating. *Caiophora contorta* was not used for crosses, i.e., none of the *Caiophora* taxa used in the experiment is self-pollinating. Flowers used as pollen recipients were nevertheless emasculated before anther dehiscence (Fig. 7.2B) to avoid accidental self-pollination during manipulation. Also, greenhouse windows were closed, precluding pollinator activity during the experiments. A total of 230 flowers were hand-pollinated (Table 7.4): In six species (including *C. cirsiifolia* with three morphotypes), 20 flowers each were used (five flowers each for pollination with pollen from three other species and five for intraspecific pollination, 120 flowers total). In the other two species, 45 flowers each were used (five flowers each for hybridization with eight other species and five for intraspecific pollination, 90 flowers total). When flowers reached the carpellate phase (fully developed stigma, Fig. 7.2C), they were dusted twice with

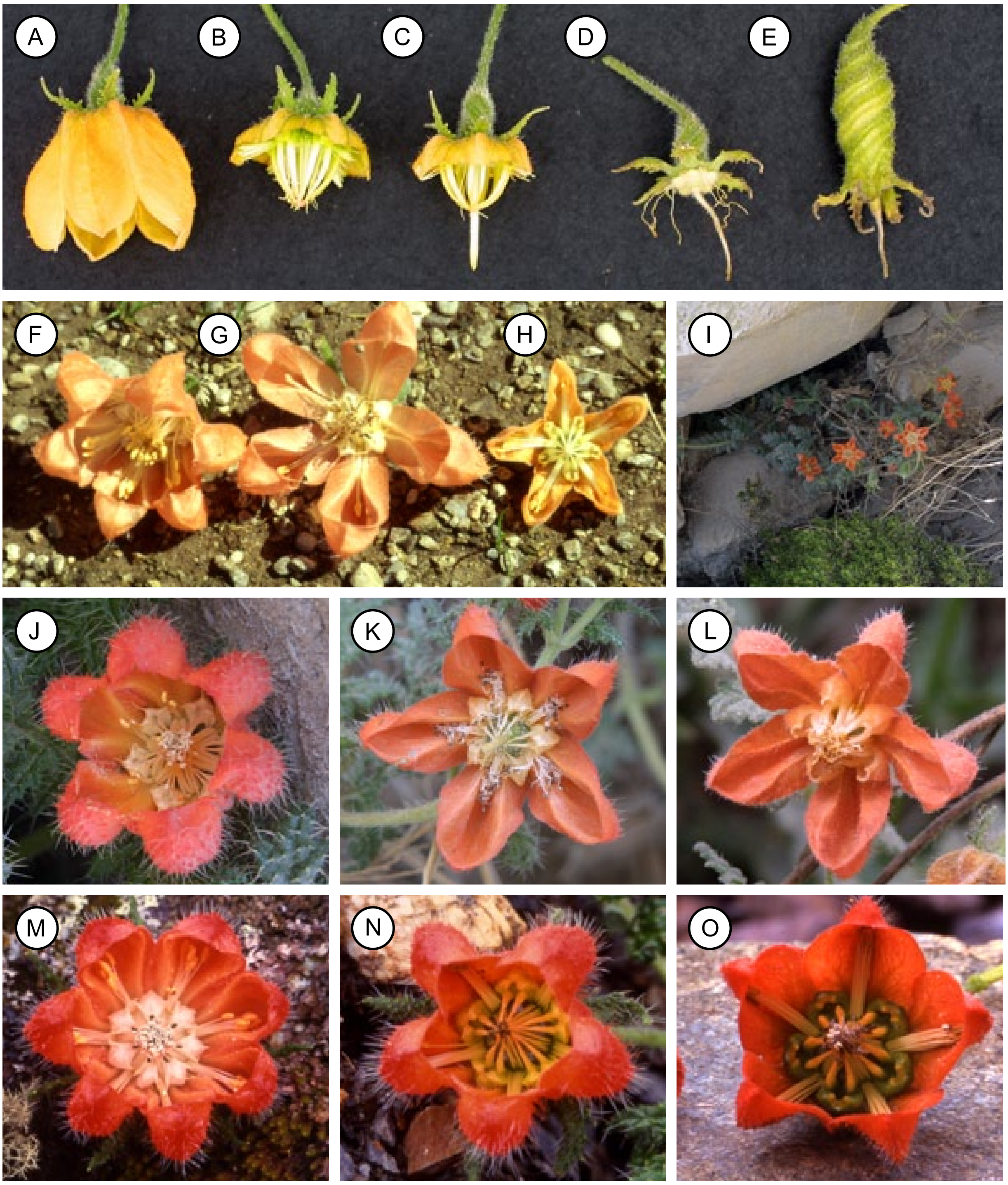

Fig. 7.3: Floral morphology and putative hybrids in *Caiophora* (see Table 7.3 for voucher details, boldface: infrageneric group from Table 7.1). (A–E) Floral morphology (= **FL**) and developmental stages for cross pollination in *C. canarinoides* (PU, **LA**). (A) Campanulate, yellowish-orange corolla, nectar scales (= NS) yellow, with long filaments. (B) emasculated flower at early anthesis. (C) Emasculated flower, carpellate phase. (D) Abortive fruit. (E) Well-developed fruit, just before maturity. (F–H) Putative hybrid *C. cirsiifolia* x *C. deserticola* (TA) and its parental taxa. (F) *C. deserticola* (TA, **CH**); **FL**: corolla balloon-shaped, pink, NS white with long white filaments. (G) Intermediate specimen, corolla half spreading with NS of *C. deserticola*. (H) *C. cirsiifolia* (TA, **CIR**); **FL**: corolla bowl-shaped, orange, NS yellowish-orange, keeled, without, or with short filaments. (I–L)

dehisced anthers of the pollen donor on consecutive days. Each flower was then marked with a colorcoded wire. Capsules matured after four to six weeks (Fig. 7.2E). Maturity is recognizable by the color change (green to yellow/brown) and the opening of longitudinal sutures. Fully developed capsules were counted and collected in paper bags. With the start of summer, especially with high temperatures and the onset of acariasis, some of the taxa [*C. carduifolia* (AP) and *C.* cf. *madrequisa*, to some degree *C. canarinoides*] began to die, producing few or no mature capsules (Fig. 7.2D), which led to the loss of some fruits (from both interspecific and intraspecific pollination).

Table 7.2: Interspecific hybrids in *Caiophora* reported in the literature (species group according to Weigend and Ackermann, 2003; CA = *Caiophora carduifolia* group, CH = *C. chuquitensis* group, CIR= *C. cirsiifolia* group, CL = *C. clavata* group, CO = *C. coronata* group, LA = *C. lateritia* group); ! = specimen seen.

hybrid	species groups	voucher	Literature
C. chuquitensis (Meyen) (Gillies ex. Arn.) Hooker & Arn. x *C. clavata* Urb. & Gilg	CH, CL	Argentina, Prov. Tucuman, Vervoorst 3309 (LIL), Hjerting 9835 (LIL), Lillo 4186 (NY!), Lillo 4183 (NY!).	Sleumer 1955
C. coronata (Gillies ex. Arn.) Hooker & Arn. x *C. chuquitensis* (Meyen) (Gillies ex. Arn.) Hooker & Arn.	CO, CH	Argentina, Prov. Salta, Seumer 3717 (LIL); Sleumer 4065 (LIL). Prov. Jujuy, Meyer 33614 (HUH!).	Sleumer 1955
C. coronata (Gillies ex. Arn.) Hooker & Arn. x *C. mollis* (Griseb.) Urb. & Gilg	CO, CH	Argentina, Prov. Catamarca, Sleumer & Vervoorst 2610 (LIL, US!).	Sleumer 1955
C. hibiscifolia (Griseb.) Urb. & Gilg x *C. aconquijae* Sleumer	LA, LA	E-Bolivia, NO-Argentina	Brücher 1986, 1989
C. hibiscifolia (Griseb.) Urb. & Gilg x *C. lateritia* (Hook.) Klotzsch	LA, LA	E-Bolivia, NO-Argentina	Brücher 1986, 1989
C. laterita (Hook.) Klotzsch x *C. aconquijae* Sleumer	LA, LA	E-Bolivia, NO-Argentina	Brücher 1986, 1989
C. carduifolia C.Presl x *C. peduncularis* (C.Presl) Weigend & Mark.Ackermann	CA, CIR	Peru, Depto. Junín, Kalenborn 48 pro parte (US, F, GH, MO, NY!).	Weigend & Ackermann 2003

Fig. 7.2 continued: Putative hybrid *C. andina* × *C. cirsiifolia* (AR) and its parental taxa. (I) Habits of ascending *C. andina* × *C. cirsiifolia* (AR). (J) *C. andina* (AR, **CH**) **FL**: corolla balloon-shaped, reddish, NS white with long white filaments. (K) Intermediate specimen, corolla bowl-shaped, orange, with pale orange, keeled NS, and long, pale-orange filaments. (L) *C. cirsiifolia* (TA, **CIR**) **FL**: corolla bowl-shaped, orange, NS orange, keeled, without filaments. (M–O) Putative hybrid *C. chuquitensis* × *C. carduifolia* (CU) and its parental taxa. (M) *C. chuquitensis* (CU2, **CH**) **FL**: corolla balloon-shaped, orange, NS white with long white filaments. (N) Intermediate specimen, corolla balloon-shaped, orange, with pale green-yellow NS without or only short filaments, shape of NS similar to *C. chuquitensis* (CU2). (O) *C. carduifolia* (CU, **CA**); **FL**: bowl-shaped, orange corolla, NS green, keeled, without or only with short filaments.

Table 7.3: Putative hybrids and parental taxa as observed in the field and their habitats and altitudinal ranges (mean altitude: arithmetic mean from all collections revised, number of specimens revised is given as n)

Taxon[a]	Species group*	Voucher	Habitat	Mean altitude and distribution range (m a.s.l.)	Population size
C. andina Urb. & Gilg (AY)	CH	M. & K. Weigend 2000/374	Under rocks in puna (natural vegetation)	4138 (3300–5000; N = 50)	Locally abundant
C. andina Urb. & Gilg x *C. carduifolia* C.Presl (AY)		M. & K. Weigend 2000/376	Old dry stone wall in abandoned farmstead (anthropogenic)	4040	Individual plant
C. carduifolia C.Presl (AY)	CA	M. & K. Weigend 2000/377	Upper ranges of cloud forest (natural vegetation)	3550 (2300–4400; N = 59)	Locally abundant
C. andina Urb. & Gilg (AR)	CH	M. Ackermann et al. 641	Under rocks in puna (natural vegetation)	4138 (3300–5000; N = 50)	Locally abundant
C. andina Urb. & Gilg x *C. cirsiifolia* C.Presl (AR)		M. Ackermann et al. 642	Under rocks on roadbank (anthropogenic)	4300	Individual plant
C. cirsiifolia C.Presl (AR)	CI	M. Ackermann et al. 643	Upper ranges of dry Andean scrub (natural vegetation)	3269 (2400–4300; N = 49)	Locally abundant
C. carduifolia C.Presl (CU)	CA	M. & K. Weigend 2000/178	Upper ranges of dry Andean scrub (natural vegetation)	3550 (2300–4400; N = 59)	Locally abundant
C. carduifolia C.Presl x *C. chuquitensis* (Meyen) Urb. & Gilg (CU)		M. & K. Weigend 2000/184	Under rocks on roadbank (anthropogenic)	4300	Individual plant
C. chuquitensis (Meyen) Urb. & Gilg (CU2)	CH	M. & K. Weigend 2000/185	Under rocks in puna (natural vegetation)	4050 (3250–5000; N = 53)	Locally abundant
C. deserticola Weigend & Mark.Ackermann (TA)	CH	Weigend & Förther 97/795	Dry rocks faces and scree slopes (natural vegetation)	3274 (2380–4200; N = 22)	Locally abundant
C. cirsiifolia C.Presl x *C. deserticola* Weigend & Mark.Ackermann (TA)		Weigend & Förther 97/796	Road bank next to hedges and scree slope (anthropogenic)	3680	Individual plant
C. cirsiifolia C.Presl (TA)	CI	Weigend & Förther 97/797	Upper ranges of Andean scrub (natural vegetation)	3269 (2400–4300; N = 49)	Locally abundant

Notes: Abbreviations for species group, see Table 7.1

[a] Abbreviation after plant names indicate department of origin in Peru; see Appendix B.

Fruit set

Table 7.4 summarizes the data on cross pollination and fruit set. All normally developed fruits contained normally developed seeds. Percentage fruit set was obtained by dividing the number of mature fruits by the number of cross pollinations attempted. The overall number of crosses performed was too low for a meaningful comparison, so crossability indices were only calculated for the three different overall data sets: (1) Percentage fruit set from cross pollination within individual accessions (P = parent). (2) Percentage fruit set from cross pollination between closely allied taxa (geographical races of the same species, different species from the same species group; F1 = hybrid). (3) Percentage fruit set from cross pollination between species from different species groups (F1 = hybrid). Crossability indices were obtained by dividing the percentage fruit set obtained in (2) respectively (3) by the figure obtained in (1). The following formula was used to obtain crossability indices of fruit set: CI = (Σ % fruit set F1) / (Σ (% fruit set P1 + % fruit set P2) /2).

Seed masses

Mature seeds from capsules resulting from cross pollination and the seeds of the parental species were investigated for seed mass. One hundred seeds were counted out and weighed with a Sartorius R2000D laboratory balance and calculated as thousand grain weight (tgw). Means and standard deviation (SD) are given for ease of comparison.

Seed germination

One hundred seeds from each crossing experiment were germinated by placing them onto moist filter paper in sealed plastic petri-dishes (Whatmann’s No.1 filter paper moistened with water, kept in daylight at ca. 18–21° C). Germination was measured by counting and removing the germinated seeds in the course of the subsequent three weeks, after which no further germination was observed. Germination rates were tabulated and crossability indices calculated from them. Crossability indices for seed viability were obtained for the three types of cross pollination specified (see fruit set) and calculated by dividing the germination rate obtained from crosses between species/accessions (Σ germ. F1) by the mean germination rate of seeds obtained from the corresponding cross-pollination between individuals from the same accession (Σ (germ. P1 + germ. P2) /2). The following formula was used to obtain crossability indices for germination data: CI = (Σ germ. F1) / (Σ (germ. P1 + germ. P2) /2).

7.4. Results

Fruit set

Experimental crosses between both closely allied and widely divergent species of *Caiophora* (parental species: Figs. 7.1, 2A, 2F) were equally successful (Table 7.4). A total

Table 7.4: Fruit formation in experimental crosses of inter- and intraspecific pollination in *Caiophora* (first number: number of capsules obtained, second number: number of flowers pollinated, crosses between morphotypes of *C. cirsiifolia* highlighted in boxes).

species group*		CA	CH	CH	CIR	CIR	CIR	LA	LA	CO				
	species	*C. carduifolia* (AP)♂	*C. deserticola* (MO) ♂	*C. chuquitensis* (CU1) ♂	*C. cirsiifolia* (CA1) ♂	*C. cirsiifolia* (AN) ♂	*C. cirsiifolia* (CA2) ♂	*C. madrequisa* (PU) ♂	*C. canarinoides* (PU) ♂	*C. pentlandii* (PU) ♂	Same accession	Same species group, diff. species Same species group, diff. acc.	Different species group	mature capsules/ pollinated flowers
CA	*C. carduifolia* (AP) ♀				1/2[a]	2/5[a]			2/5[a]		2/5[a]		5/12	7/17
CH	*C. deserticola* (MO) ♀	4/5		2/5	3/5	4/5	3/5[b]	3/5	1/5	0/4	2/5	2/5	18/34	22/44
CH	*C. chuquitensis* (CU1) ♀	4/5	5/5			5/5					4/5	5/5	9/10	18/20
CIR	*C. cirsiifolia* (CA1) ♀	4/5	5/5			3/5					5/5	3/5	9/10	17/20
CIR	*C. cirsiifolia* (AN) ♀	5/5	5/5	5/5	5/5		5/5	5/5	5/5	5/5	5/5	10/10	30/30	45/45
CIR	*C. cirsiifolia* (CA2) ♀	5/5	4/5			5/5					5/5	5/5	9/10	19/20
LA	*C. madrequisa* (PU) ♀	3/3[a]	1/5			1/3[a]					2/4[a]		5/11	7/15
LA	*C. canarinoides* (PU) ♀	3/4[a]	4/5			3/4[a]					4/5		10/13	14/18
CO	*C. pentlandii* (PU) ♀	5/5	4/5			4/5					4/5		13/15	17/20
total												**7/10**		
											33/44	**18/20**	**108/145**	**166/219**
												total 25/30		
%											**0.75**	**0.83**	**0.74**	**0.76**
CI												**1.1**	**1**	

Notes: Abbreviations for species group, see Table 7.1; CI = crossability index; % = percentage of mature capsules.

[a] Plant died before capsule matured.

[b] Small fruits with few, but normally developed seeds.

[c] Abbreviation after plant names indicate department of origin in Peru; see Appendix B.

Table 7.5: Thousand grain weight (tgw) of *Caiophora* seeds, including the seeds obtained from crosses. For parental species the mean tgw is for seeds collected from natural populations in Peru (NP) and cultivated seeds. For hybrids (boldfaced), tgw and mean value and standard deviation (SD) are given.

species group*	Maternal taxon[a]	Paternal taxon[a]	tgw	Mean tgw ± SD
CA	*C. carduifolia* (AP) NP		0,166	
	C. carduifolia (AP)	*C. carduifolia* (AP)	0,090	0,128
	C. carduifolia (AP)	*C. cirsiifolia* (CA1)	**0,151**	**0,134 ± 0,0280**
	C. carduifolia (AP)	*C. cirsiifolia* (AN)	**0,102**	**SD = 20,9%**
	C. carduifolia (AP)	*C. canarinoides* (PU)	0,150	
CH	*C. deserticola* (MO) NP		0,149	
	C. deserticola (MO)	*C. deserticola* (MO)	**0,175**	**0,162**
	C. deserticola (MO)	*C. carduifolia* (AP)	**0,252**	**0,189 ± 0,0535**
	C. deserticola (MO)	*C. chuquitensis* (CU1)	**0,125**	**SD = 28,3%**
	C. deserticola (MO)	*C. cirsiifolia* (CA1)	**0,233**	
	C. deserticola (MO)	*C. cirsiifolia* (AN)	**0,242**	
	C. deserticola (MO)	*C. madrequisa* (PU)	**0,139**	
	C. deserticola (MO)	*C. canarinoides* (PU)	**0,184**	
	C. deserticola (MO)	*C. cirsiifolia* (CA2)	**0,146**	
CIR	*C. cirsiifolia* (AN) NP		0,218	
	C. cirsiifolia (AN)	*C. cirsiifolia* (AN)	0,194	0,206
	C. cirsiifolia (AN)	*C. carduifolia* (AP)	**0,233**	**0,193 ± 0,0281**
	C. cirsiifolia (AN)	*C. deserticola* (MO)	**0,213**	**SD = 14,6%**
	C. cirsiifolia (AN)	*C. chuquitensis* (CU1)	**0,186**	
	C. cirsiifolia (AN)	*C. cirsiifolia* (CA1)	**0,197**	
	C. cirsiifolia (AN)	*C. madrequisa* (PU)	**0,141**	
	C. cirsiifolia (AN)	*C. canarinoides* (PU)	**0,188**	
	C. cirsiifolia (AN)	*C. pentlandii* (PU)	**0,174**	
	C. cirsiifolia (AN)	*C. cirsiifolia* (CA2)	**0,212**	
CIR	*C. cirsiifolia* (CA2) NP		0,440	
	C. cirsiifolia (CA2)	*C. cirsiifolia* (CA2)	0,353	0,397
	C. cirsiifolia (CA2)	*C. carduifolia* (AP)	**0,318**	**0,318 ± 0,0130**
	C. cirsiifolia (CA2)	*C. deserticola* (MO)	**0,331**	**SD = 4,1%**
	C. cirsiifolia (CA2)	*C. cirsiifolia* (AN)	**0,305**	
CO	*C. pentlandii* (PU) NP		0,166	
	C. pentlandii (PU)	*C. pentlandii* (PU)	0,203	0,185
	C. pentlandii (PU)	*C. carduifolia* (AP)	**0,204**	**0,177 ± 0,0318**
	C. pentlandii (PU)	*C. deserticola* (MO)	**0,142**	**SD = 18,0%**
	C. pentlandii (PU)	*C. cirsiifolia* (AN)	**0,185**	
LA	*C. canarinoides* (PU) NP		0,174	
	C. canarinoides (PU)	*C. canarinoides* (PU)	0,134	0,154
	C. canarinoides (PU)	*C. carduifolia* (AP)	**0,158**	**0,146 ± 0,0108**
	C. canarinoides (PU)	*C. deserticola* (MO)	**0,137**	**SD = 7,4%**
	C. canarinoides (PU)	*C. cirsiifolia* (AN)	**0,143**	

Note:

* Abbreviations for species group, see Table 7.1.

[a] Abbreviation after plant names indicate department of origin in Peru; see Appendix B.

of 37 crosses between different geographical races or species were attempted, usually with each individual accession serving once as pollen donor and once as pollen recipient for any given combination. Thirty-six of the crosses resulted in fully developed capsules; only one interspecific combination did not lead to fruit set (*C. deserticola* × *C. pentlandii*). Fruit set from cross pollination between species from different species groups (74%) and between individuals of the same accession (75%) was virtually identical (CI: 1). The (fewer) cross pollinations between closely allied taxa led to marginally higher fruit set (83%, CI: 1.1).

Seed masses

Seed masses from inter- and intraspecific pollination in *Caiophora* are summarized in Table 7.5. They show only minor differences. Mean values for seed masses of the parental species obtained from cultivation and collected in the wild are close to the mean values for hybrids with the same maternal accession. Standard deviations (of tgw) for hybrids with the same maternal accession range between 4.1 and 28.3%, means of the maternal accession are usually within the range of this hybrid SD. Seed mass variation of a factor two (in viable seeds) is common within individual species/populations of Loasoideae (Weigend et al., 2004a), so that all seeds obtained appeared to be normally developed.

Germination

The germination results of *Caiophora* seeds obtained from interspecific and intraspecific pollination (Table 7.6) confirm that most of the seeds were normally developed and viable. Crossability indices [CI = Σ germ. F1 / (Σ (germ. P1 + germ. P2) /2)] obtained from the germination rates of hybrid seeds range from 0 to 21.5. Seeds resulting from cross-pollination between different species/accessions generally had higher germination rates than those from intraspecific crosspollination. Overall germination rate was 56% in seeds from cross pollination between species from different species groups and 46% in seed obtained from crosses between geographical races/closely allied species. Conversely, average germination is only 19% in seeds obtained from cross pollination within the same accession. Overall crossability indices calculated on the basis of seed germination are thus 3.02 for crosses between species from different groups and 2.49 for crosses between geographical races/ closely allied species. Crossability indices were higher than 1 in 25 sets of hybrid seeds (two-thirds of the sample), i.e., viability was higher in seeds obtained from hybridization than in seeds from same-accession pollination. Only 11 interspecific combinations (one-third of the sample) yielded seed that was less viable or equally viable as seeds from same-accession pollination (CI ≤ 1). Some of the highest germination rates were obtained with hybrid seeds from crosses between remotely

Table 7.6: Number of seeds germinated (of 100 seeds) and crossability index (CI) of seeds obtained from cross-pollinated flowers in *Caiophora* (Crosses between morphotypes of *C. cirsiifolia* highlighted in bold squares).

species group		CA	CH	CH	CIR	CIR	CIR	LA	LA	CO				
	species	*C. carduifolia* (AP) ♂	*C. deserticola* (MO) ♂	*C. chuquitensis* (CU1) ♂	*C. cirsiifolia* (CA1) ♂	*C. cirsiifolia* (AN) ♀	*C. cirsiifolia* (CA2) ♂	*C. madrequisa* (PU) ♂	*C. canarinoides* (PU) ♂	*C. pentlandii* (PU) ♂	Same accession	*same species group, diff. species, Same species, diff. Acc.*	different species group	Totel germinated seeds/ number of seeds
CA	*C. carduifolia* (AP) ♀				5 (CI 1)	0 (CI 0)			94 (CI 6.7)		10/100		99/300	109/400
CH	*C. deserticola* (MO) ♀	95 (CI 3.5)		55 (CI 2.5)	87 (CI 4)	84 (CI 1.3)	83 (CI 3.1)	90 (CI 3.9)	96 (CI 3.1)		44/100	*55/100*	535/600	634/800
CH	*C. chuquitensis* (CU1) ♀	63 (CI 12.6)	7 (CI 0.3)			32 (CI 0.8)					0/100	*7/100*	95/200	102/400
CIR	*C. cirsiifolia* (CA1) ♀	34 (CI 6.8)	14 (CI 0.6)			2 (CI 0.1)					0/100	*2/100*	48/200	50/400
CIR	*C. cirsiifolia* (AN) ♀	92 (CI 2)	71 (CI 1.1)	91 (CI 2.2)	72 (CI 1.8)		96 (CI 2.1)	97 (CI 2.3)	98 (CI 2.2)	59 (CI 1.4)	81/100	168/200	508/600	757/900
CIR	*C. cirsiifolia* (CA2) ♀	78 (CI 8.2)	90 (CI 3.4)	74 (CI 16.4)							9/100		242/300	251/400
LA	*C. madrequisa* (PU) ♀	0 (CI 0)	0 (CI 0)		0 (CI 0)						2/100		0/300	2/400
LA	*C. canarinoides* (PU) ♀	36 (CI 2.6)	3 (CI 0.1)		0 (CI 0)						18/100		39/300	57/400
CO	*C. pentlandii* (PU) ♀	85 (CI 12.1)	46 (CI 1.9)	43 (CI 21.5)							4/100		174/300	178/400
											168/900	62/200 170/300 Total of 232/500	1740/3100	2140/4500
% G											0,19	0,46	0,56	0,48
CI overall											-	2,49	3.02	

Notes:

* Abbreviation for species group, see Table 7.1; crossability index: CI = (Σ germ. F1) / (Σ (germ. P1 + germ. P2) /2); %G = percentage of germinated seeds. [a] Abbreviation after plant names indicate department of origin in Peru; see Appendix B.

Table 7.7: Asymmetrical crossing barriers: Comparison of germination rates of some hybrids in relation to pollen recipient/donor (boldfaced: hybrid combination also documented in the wild in Peru; CI = crossability index; %G = percentage of germinated seeds).

Female parent[a]	Male parent[a]	Germination rate (CI)	Germination rate (CI)	Female parent[a]	Male parent[a]
C. deserticola (MO)	*C. chuquitensis* (CU1)	55 (CI 2.5)	7 (CI 0.3)	*C. chuquitensis* (CU1)	*C. deserticola* (MO)
C. deserticola (MO)	**_C. cirsiifolia_ (CA1)**	**87 (CI 3.9)**	**14 (CI 0.6)**	**_C. cirsiifolia_ (CA1)**	**_C. deserticola_ (MO)**
C. deserticola (MO)	*C. madrequisa* (PU)	90 (CI 3.9)	0 (CI 0)	*C. madrequisa* (PU)	*C. deserticola* (MO)
C. deserticola (MO)	**_C. cirsiifolia_ (AN)**	**84 (CI 1.3)**	**71 (CI 1.1)**	**_C. cirsiifolia_ (AN)**	**_C. deserticola_ (MO)**
C. deserticola (MO)	*C. canarinoides* (PU)	96 (CI 3.1)	36 (CI 2.6)	*C. canarinoides* (PU)	*C. deserticola* (MO)
C. cirsiifolia (AN)	**_C. carduifolia_ (AP)**	**92 (CI 2.1)**	**0 (CI 0)**	**_C. carduifolia_ (AP)**	**_C. cirsiifolia_ (AN)**
C. cirsiifolia (AN)	*C. cirsiifolia* (CA1)	72 (CI 1.8)	2 (CI 0.1)	*C. cirsiifolia* (CA1)	*C. cirsiifolia* (AN)
C. cirsiifolia (AN)	*C. chuquitensis* (CU1)	91 (CI 1.1)	32 (CI 0.8)	*C. chuquitensis* (CU1)	*C. cirsiifolia* (AN)
C. cirsiifolia (CA1)	**_C. carduifolia_ (AP)**	**34 (CI 6.8)**	**5 (CI 0.5)**	**_C. carduifolia_ (AP)**	**_C. cirsiifolia_ (CA1)**
C. cirsiifolia (CA2)	**_C. deserticola_ (MO)**	**90 (CI 3.4)**	**83 (CI 3.1)**	**_C. deserticola_ (MO)**	**_C. cirsiifolia_ (CA2)**
C. carduifolia (AP)	*C. canarinoides* (PU)	94 (CI 6.7)	36 (CI 2.6)	*C. canarinoides* (PU)	*C. carduifolia* (AP)

[a] Abbreviation after plant names indicate department of origin in Peru; see Appendix B.

related species (compare Table 7.1, *C. deserticola* × *C. canarinoides*: 96%, *C. deserticola* × *C. carduifolia*: 95%). Conversely, same-accession cross pollination yielded seeds with low germination rates in some cases (e.g., *C. pentlandii*: 4%, *C. cirsiifolia* (CA1): 0%, *C. chuquitensis*: 0%, *C. madrequisa*: 2%).

7.5. Discussion

Possibility of interspecific hybridization

Caiophora can be freely hybridized across species and species groups. Successful hybridization between divergent lineages (such as the *C. cirsiifolia* and the *C. chuquitensis* group) inferred from field observations (Tables 7.2, 7.3) is confirmed as possible by the experimental data. Fruit set obtained in inter- and intraspecific crosses is nearly identical, and postmating isolating mechanisms are apparently absent in *Caiophora*. The high crossability of *Caiophora* is in line with the conclusion of Ellstrand et al. (1996), that natural hybridization is more prevalent in outcrossing perennials. However, at present there is no evidence for the presence of reproductive modes stabilizing hybridity „such as agamospermy, vegetative spread, or permanent odd polyploidy” (Ellstrand et al., 1996, p 5090.). Germination rates of hybrid seeds on average far exceed the germination rates of seed from within-accession cross-pollination, which can be seen as a case of hybrid vigor (Grant, 1975). The crossability indices calculated from seed germination further indicate that hybrids between highly divergent parental species have germination rates that are identical to or higher than those between closely allied taxa. Viability, vigor, and/or fertility of the F1 plants are usually reduced in interspecific hybrids between distantly related taxa (Sawant, 1958; Keep, 1962; Goldschmidt, 1964; den Nijs and Visser, 1985; Rieseberg and Carney, 1998; Burke and Arnold, 2001; Sérsic et al., 2001), whereas heterosis (hybrid vigor) is expected in crosses between geographical races of individual species (Grant, 1975). A high crossability index (≥ 1) and a marked heterosis effect are expected in crosses between isolated, inbreeding populations of individual taxa (Fenster and Galloway, 2000; Sheridan and Karowe, 2000; Weller et al., 2005; Busch, 2006; Heliyanto et al., 2006). Thus, in our hybridization experiment, all taxa and accessions of *Caiophora* behaved like isolated, inbred populations of a single species, with overall crossability indices based on seed germination > > 1. This is particularly striking because in other studies crossability decreased with increasing geographical distance between populations of the same species within a relatively narrow geographical range (Wyatt, 1990; Stacy, 2001) or allopatric populations of the same morphospecies had high degrees of reproductive isolation (Grundt et al., 2006). Germination rates are partly dependent on the choice of the pollen donor/pollen recipient, and some (weak) asymmetrical crossing barriers are apparently in place (compare Tiffin et al., 2001): The figures show striking differences in the CIs of individual taxon combinations, depending on the choice of the male and female parent. Thus, the germination rates of seeds obtained from *C. deserticola* × *C. madrequisa* have a CI of 3.9 with *C. deserticola* as female parent, but a CI of 0 with *C. madrequisa* as female parent; similar trends can be observed in other species combinations (Table 7.7).

Premating isolating mechanism and the causes of hybridization in nature

Data published by Ackermann and Weigend (2006) indicate that the pollination biology of the species groups here investigated is little differentiated; most taxa fell into a group pollinated by long-tongued bees and/or hummingbirds, and pollinator specificity is likely low. Accidental interspecific cross pollination is likely to occur where more than one species is found in a single area. There is direct observational evidence for two species sharing the same pollinator in the case of *C. deserticola* and *C. cirsiifolia* in Moquegua, where both species are visited and apparently pollinated by the same species of *Centris* (long-tongued bees, Apidae; Ackermann and Weigend, 2006). Incidentally, an interspecific hybrid has been documented between these two species in the same region (Table 7.3). Neither does phenology provide an isolating mechanism in *Caiophora* because all species have their peak flowering time at the end of the rainy season in the Andes (ca. March – May in Peru). Ecogeographic isolation remains the only obvious premating isolating mechanism in *Caiophora*; there is usually geographical and/or altitudinal segregation between different species of *Caiophora*, both between and within species groups. Altitudinal distributions of species usually overlap slightly across their geographical range (compare Tables 7.1, 7.3), but in any given region different species are not usually found at the same elevation. In many cases there is additional ecological differentiation, with, e.g., the erect (suffruticose) species of the *C. chuquitensis* group found in shallow, often open soils and the winding species of other groups largely restricted to scrub and scrub forest. Table 7.3 gives habitats and the elevational ranges of the parental taxa and the habitat and elevation at which the putative hybrids were collected. In three of the four cases, the hybrids were found far above the mean altitudinal range of one of the parental species and in the range of the second parental species. In these three cases, hybrids were found near roads coming from lower elevations with natural stands of the other („azonal“) parent, so that both disturbance and seed transport by man may have played a role in hybrid formation. The fourth case of hybridization reported apparently also goes back to human impact. Both C*. deserticola* and *C. cirsiifolia* are abundant in Depto. Moquegua at the same elevations, but whereas *C. deserticola* is a shrubby species restricted to rock faces and dry scree slopes, *C. cirsiifolia* is a winding species restricted to moister parts of the scrub-forest, usually in gullies and near seepage areas, so that isolation is maintained under natural conditions. The hybrid was collected in a place where agricultural terraces had been built right into a dry scree slopes with natural stands of *C. deserticola*. The terraces were fenced with hedges and irrigated and provided an excellent manmade habitat for *C. cirsiifolia*, so that the two species grew less than 5 m apart.

7.6. Conclusion

Hybrids in *Caiophora* are readily produced even between morphologically divergent species groups, differing in floral and growth morphology, distribution, and ecology. Postmating isolating mechanisms are apparently absent. Taxa are primarily kept apart by ecogeographical isolation. Secondary contact from human impact leads to hybrid formation, while under natural conditions the efficiently wind-dispersed seed of *Caiophora* (Weigend et al., 2004a, 2005) may ensure the occasional contact between different taxa. Problems with taxon delimitation in *Caiophora* are likely at least partly due to the presence of specimens with „mixed“ or „intermediate” morphological characters as a result of hybridization and possibly introgression. The low sequence divergence observed in *Caiophora* (Hufford et al., 2003, 2005; Weigend et al., 2004b) correctly reflects a close relationship and possibly recent radiation of *Caiophora* in the Andes. However, the morphological and ecological differences between taxa clearly argue that they largely behave as distinct lineages under natural conditions and should be kept taxonomically separate. Many natural populations of *Caiophora* are short-lived and isolated and often have few individuals, which may explain the relatively low seed viability of same-population cross-pollinated seeds, indicating that at least some natural populations of *Caiophora* are subject to inbreeding depression. The high degree of interspecific crossability of *Caiophora* is possibly best compared to similar observation made on recently diverged species of island floras (Wagner et al., 1990; Motley and Carr, 1998). Hughes and Eastwood (2006, p. 10334) demonstrated an extraordinary rate of speciation resulting in a large number of geographically isolated, but closely related species of the genus *Lupinus* in the high Andes and called this phenomenon an „island radiation on a continental scale.“ A similarly rapid allopatric „island radiation“ may have taken place in Andean *Caiophora*, also leading to morphologically highly distinct, but young and, in this case, (still?) interfertile lineages. Further studies on the F2 and F3 generations are now under way to investigate the occurrence of a possible hybrid breakdown and the stability of novel characters or character combinations in subsequent generations to understand the possible role of hybridization in the evolution of the genus.

7.7. Acknowledgement

The authors express their gratitude to L. Rieseberg (Vancouver) and S. Renner (Munich) for helpful comments on the manuscript. The authors thank A. Cano and M. I. La Torre (Lima, Peru), F. Luebert (Santiago, Chile), E. Rodríguez (Trujillo, Peru), N. Salinas (Cuzco, Peru), H. Förther (München, Germany), N. Dostert, T. Henning, D. Kollehn, O. Mohr, C. Schwarzer and K. Weigend (Berlin, Germany) for help in the field and collecting; Prof. Dr. H. H. Hilger for space and funds for this study. Funds kindly provided by the following institutions are gratefully acknowledged: Studienstiftung des Deutschen Volkes, Deutscher Akademischer Austauschdienst, Lewis B. and Dorothy Cullman Laboratory for Molecular Systematics Studies at the New York Botanical Garden, Deutsche Forschungsgemeinschaft (Grant-nr.WE 2330/1), botconsult GmbH.

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8. Nectar, Floral Morphology and Pollination Syndrome in Loasaceae subfam. Loasoideae (Cornales)*

8.1. Abstract:

Background and Aims: Loasaceae subfam. Loasoideae are mostly distributed in South America (sea-level to over 4500 m) with a wide range of animals documented as pollinators. Our aim is to investigate correlations between nectar parameters, flower morphology, pollination syndrome and phylogeny.

Methods: Nectar was collected from 29 species from seven genera in the subfamily. Concentration and volumes were measured and amount of sugar calculated. Correlation of nectar data were plotted in a ternary graph and nectar characteristics compared to flower visitors, floral morphology and phylogenetic data.

Key Results: Sugar concentrations are generally higher than reported for most plant families in the literature. The species investigated can be roughly grouped as follows: Group I: plants with ca. 1.5 (—3.5) µl nectar with (40—) 60—80 % sugar and 0.19—2 mg sugar/flower; with small, white, star-shaped corollas, pollinated by short-tongued bees, Groups II/III/IV: plants with mostly orange, balloon-, saucer-, bowl- or bell-shaped corollas: Group II: plants with ca. 9—14 µl nectar with 40—60 % sugar and 4—10 mg sugar/flower; mostly visited by long-tongued bees and/or hummingbirds, Group III: plants with 40—100 µl nectar with 30—40 % sugar and 14—36 mg sugar/flower, mostly visited by hummingbirds, and Group IV: geoflorous plants with 80—90 µl with 10—15 % sugar and 8.5—12 mg sugar//flower, presumably visited by small mammals. Groups II and III include species visited by bees and/ or hummingbirds.

Conclusions: Pollinator switches from short-tongued bees via long-tongued bees to hummingbirds appear to have taken place repeatedly in the genera *Nasa*, *Loasa* and *Caiophora*. Changes in nectar amount and concentration appear to evolve rapidly with little phylogenetic constraint.

Keywords: nectar, pollination, *Caiophora*, *Loasa*, *Nasa*, Loasaceae, short-tongued bees, long-tongued bees, Colletidae, Apidae, Anthophoridae, rodents, ornithophily.

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*The original publication is available at http://aob.oxfordjournals.org/. Published as: Ackermann M, Weigend M. 2006. Nectar, floral morphology and pollination syndrome in Loasaceae subfam. Loasoideae (Cornales). Annals of Botany 98: 503-514. doi: 10.1093/aob/mcl136

8.2. Introduction

Nectar production and composition are understood to be crucial factors influencing flower visitation and consequently pollinator preferences for particular plant species (e.g. Baker and Baker, 1982; Endress, 1994). Certain pollinator species show a distinct preference for particular nectar types (e.g. Baker, 1975; Bolten and Feinsinger, 1978; Bolten et al., 1979; Baker and Baker, 1983; Heyneman, 1983; Zimmermann, 1983; Blem et al., 2000; McDade and Weeks, 2004). Thus, there is general agreement, that sugar concentration in hummingbird pollinated flowers is generally lower (20–26% sugar; Hainsworth and Wolf, 1972; Baker, 1975; Cruden et al., 1983) than in insect-pollinated flowers (>30% sugar; rarely up to 80 %). Further differences have been reported between 'lowland hummingbird nectar' and 'highland hummingbird nectar', with highland nectar less concentrated and hence less viscous, but present in higher volumes such that these flowers present roughly the same caloric value (Hainsworth and Wolf, 1972; Baker, 1975). Heinrich and Raven (1972) and Forcone et al. (1997) argue that energetic reward for pollinators in habitats with low temperatures is higher than in areas with high temperatures. Cruden et al. (1983) claim that the nectar volume of flowers pollinated by 'large bees' (e.g. *Bombus*, *Xylocopa*, *Centris*) has to be significantly higher than that of flowers pollinated by 'small bees' (e.g. *Colletes*, *Apis*). Because bee pollination seems to phylogenetically precede hummingbird pollination in most plant groups [e.g. Scrophulariaceae: tribe Antirrhineae (Elisens and Freeman, 1988; Ghebrehiwet et al., 2000); *Penstemon* (Wilson et al., 2006); *Mimulus* (Fishman et al., 2002; Beardsley et al., 2003); Gesneriaceae: tribe Sinningieae (Perret et al., 2001, 2003)], scientists have variously addressed the question as to how the transition from 'typical' bee nectar to 'typical' hummingbird nectar took place. Bolten and Feinsinger (1978) argue that the relatively low sugar concentration in hummingbird nectar is not due to a preference for lower sugar concentrations by hummingbirds, but rather serves to render the flowers less attractive to bees. One crucial problem of many of the data sets published on the relationship between nectar and pollination is the comparison of nectar and pollinator data including taxa from distantly related plant groups. Differentiating between adaptive responses and possible phylogenetic constraints is thus difficult. There have been two major studies attempting to elucidate the evolution of nectar characteristics and pollination syndromes within presumably monophyletic plant groups, albeit without an explicit phylogenetic framework. The study on Scrophulariaceae (now Plantaginaceae) Tribe Antirrhineae (20 North American species; Elisens and Freeman, 1988) concentrated on sugar composition, i.e. the relative percentages of different sugars in the nectar, while giving no data on absolute nectar volumes, sugar concentrations or absolute sugar amounts. The study on Gesneriaceae Tribe Sinningieae (45 Neotropical species; Perret et al., 2001) provides data on sugar concentration, and sugar composition, but not on overall nectar production. Both studies show correlations between pollination syndromes and nectar composition, but in neither case is an explicit correlation of pollination syndrome to quantitative nectar features clarified.

The present study intends to compare nectar and pollination syndromes in Loasaceae subfam. Loasoideae, a monophyletic, largely Neotropical plant group of approx. 200 species, with its centre of diversity in the Central Andes (Weigend, 2004a) and with considerable variability in their floral morphology and pollination biology (Urban, 1886, 1889, 1892; Urban and Gilg, 1900; Brown and Kaul, 1981; Weigend, 2004a; Weigend et al., 2004). Representatives of this group are found in many different ecosystems ranging from tropical to temperate rainforests, from coastal lomas formations in the Atacama desert up to 4500m in the Andes. The phylogeny of this group has been largely clarified (Hufford et al., 2003, 2005; Weigend et al., 2004). Taxa of subfamily Loasoideae share a complex floral morphology: the heterochlamydeous, polyandrous flowers have a highly differentiated androecium with antesepalous stamina modified into staminodial complexes alternating with antepetalous fascicles of (10–28) fertile stamens (Urban, 1886; Weigend, 2004a, Weigend and Gottschling, 2006). The staminodial complexes typically consist of two free, inner staminodia, and three outer, fused staminodia forming the so-called nectar scale. All flowers of Loasoideae are primarily nectar flowers, and pollen presentation is typically triggered by the manipulation of the nectar scale during nectar extraction by the flower visitor (Schlindwein, 2000). Nectar is secreted from the receptacle through antesepalous, inframarginal stomata into the nectar scales, where nectar is stored (Urban, 1886, 1892; Weigend and Rodriguez, 2003; Weigend, 2004b). The nectar is thus hidden from the flower visitor and only accessible through the opening between the apex of the floral scale and the free staminodia, by manipulating the floral scale and tilting it outwards. This functional floral morphology has been described as ‘tilt-revolver flower’ (Weigend and Gottschling, 2006). While this general pattern is fairly universal in Loasoideae, there are major differences in the size and coloration of the overall flower and also in the shape and size of the nectar scales (Weigend et al., 1998, 2003, 2004; Dostert and Weigend, 1999; Rodriguez and Weigend, 1999; Weigend, 2000a, b, 2001, 2004b; Weigend and Rodriguez, 2002, 2003; Weigend and Ackermann, 2003; Weigend and Gottschling, 2006). In some taxa the opening of the much larger floral scales is widened and nectar can be accessed without moving the floral scale. This flower type has recently been described as ‘funnel-revolver flower’ (Weigend, 2004b). Tilt-revolver flowers are characterized by producing very small amounts of very viscous nectar from very small nectaries (Weigend and Rodriguez, 2003), whereas funnel-revolver flowers produce larger amounts of less viscous nectar from much larger nectaries (Weigend, 2004b). Some functional morphological aspects have thus been clarified, but both pollination data and nectar analysis are still scarce for the family.

Pollinator observations have been published for 29 species (from eight genera: *Aosa*, *Blumenbachia, Caiophora*, *Eucnide*, *Loasa*, *Mentzelia*, *Nasa* and *Scyphanthus*) from the USA, Chile, Argentina and Brazil (Linsley and Hurd, 1959; Thompson and Ernst, 1967; Brown and Kaul, 1981; Keeler, 1981; Arroyo et al., 1982; Stiles and Freeman, 1993; Harter, 1995; Harter et al., 1995; Schlindwein, 1995, 2000; Wittmann and Schlindwein, 1995; Forcone et al., 1997; Schlindwein and Wittmann, 1997; Cocucci and Sérsic, 1998; Medan et al., 2002; Villagrán et al., 2003; Sargent and Otto, 2004; Troncoso and Vargas, 2004), and the reports include various groups of bees (long-tongued bees: Anthophoridae, Apidae, Megachilidae, Mellitidae; short-tongued bees: Colletidae, Halictidae), wasps (Ichneumonidae), flies (Syrphidae), moths (Sphingidae), hummingbirds (Trochilidae), passerines (Emberizidae, Tyrannidae) and small mammals (Muridae), i.e. a considerable range of very different pollinator groups. However, a large proportion of the taxa in Loasoideae are apparently primarily visited by short-tongued bees of a particular group (Colletidae; see Wittmann and Schlindwein, 1995; Weigend, 2004a; Weigend et al., 2004). Ornithophilous taxa in *Nasa* and *Caiophora* can be shown to represent derived and largely high Andean clades in originally melittophilous genera from intermediate elevations (Weigend et al., 2004; Weigend and Gottschling, 2006). Nectar analyses had so far been published for only three species of Loasoideae from Argentina and Costa Rica (Stiles and Freeman, 1993; Forcone et al., 1997; Cocucci and Sérsic, 1998). However, Loasaceae subfam. Loasoideae have their centre of diversity, both in terms of taxic richness and morphology, in the Central Andes (Weigend, 2000b, 2002, 2004a–c), and no data sets on either pollinators or nectar have been published from that region.

The present paper intends to fill this gap and provide an overview of nectar composition in subfam. Loasoideae. Nectar composition was studied in cultivated plants under flower visitor exclusion. In *Caiophora* there are several taxonomically unresolved species complexes comprising closely allied species with differences in floral colour and size (Weigend and Ackermann, 2003). Multiple accessions from these groups, representing different floral morphologies, were studied to investigate possible differences in pollination and nectar composition. In Andean South America the main pollinator groups for Loasoideae are long-tongued and short-tongued bees and hummingbirds, with a single report of small mammals. Assuming that nectar composition correlates with pollinator taxon, a wide range of different nectar types would be expected. The observations on nectar composition are also compared with phylogenetic data compiled from published phylogenies (Weigend et al., 2004; Hufford et al., 2005; Weigend and Gottschling, 2006) to investigate whether there have been multiple convergent changes of nectar composition in the evolution of subfam. Loasoideae. The aims are: (a) to clarify the characteristics of nectar produced by Loasoideae; (b) to provide flower visitor data for additional groups in Loasaceae subfam. Loasoideae from the full range of habitats from the Pacific coast to the high Andean region; (c) to correlate quantity and quality of nectar with overall floral morphology and flower visitors; and (d) to investigate a possible phylogenetic constraints versus adaptive responses on the basis of published systematic and phylogenetic data

8.3. Materials and Methods

Plant material

Field studies were carried out in Argentina, Chile, Colombia, Ecuador, Peru and Venezuela, where pollinator observations were realized and habitat, growth habit and morphological data were obtained (approx. 200 collections of *Nasa*; approx. 200 collections of *Caiophora*; several collections of *Blumenbachia*, *Loasa*, *Presliophytum* and *Xylopodia*). Approx. 60 species of Loasaceae subfam. Loasoideae were brought into cultivation in the greenhouses at the Institut für Biologie, Freie Universität Berlin (February 2003 to December 2005). Seeds were sown into standard soil for seedlings and later potted into clay pots (potting soil: 2 parts mature leaf compost, 1 part peat). In winter (October–April) artificial light was used in the greenhouses (12 h, high pressure sodium lamps: Philips SON-T AGRO 400 W). High Andean and south temperate taxa *Caiophora*, *Nasa dillonii*, *N. macrothyrsa* and *Loasa sclareifolia* were cultivated with night-time temperatures of 5–15 C and daytime temperatures of 15–25 C; all other species were grown at night-time temperatures of 18–20 C and daytime temperatures of 20–25 C. Cultivation in the greenhouses permitted nectar samples to be obtained under fairly standardized conditions eliminating possible effects of, for example, altitudinal differences, water stress, ambient air humidity (Corbet et al., 1979a, b; Plowright, 1981; Bertsch, 1983; Zimmermann, 1988; Carroll et al., 2001; Pacini et al., 2003). The measurements obtained document the amount and composition of nectar produced in the absence of flower visitors. There are several lines of evidence that argue that the samples obtained from the plants cultivated for this research represent a good proxy to natural conditions:

(a) Published nectar data based on samples collected in nature agree with the present analysis of closely allied species: The field data on *Caiophora coronata* (Cocucci and Sérsic, 1998) are similar to greenhouse data on the closely allied *C. pentlandii* (Table 8.1 and Fig. 8.1). Field data on *Nasa speciosa* (Stiles and Freeman, 1993) and *Caiophora nivalis* (investigated by A. Wertlen) are also close to data for allied taxa from the greenhouse.

(b) The few measurements of nectar volume that were taken in nature [*Caiophora carduifolia* (3), 200–235 µl; *C. carduifolia* (4), 105–215 µl; *C. carduifolia* (5), 110–600 µl; *C. carduifolia* (6), 135–200 µl; *C. chuquitensis*, 10–185 µl; *C. pentlandii* (2), 210– 490 µl; *Nasa urens*, 02–20 µl] are close to those obtained from cultivation, but generally lower, probably due to pollinator visits (excluded in the greenhouse).

(c) There is close agreement between floral morphology, pollinator spectra documented in the wild and nectar composition, so that there is no reason to believe that nectar data are grossly aberrant.

(d) Kaczorowski et al. (2005) found that *Nicotiana* L. section *Alatae*, species with hummingbird-pollinated flowers show similar nectar composition under greenhouse conditions and in

Table 8.1: Nectar parameters (means ± s.d.), pollinators, morphological pattern and elevational distribution of Loasaceae subfam. Loasoideae from South America.

Group	Species	No. (in fig. 8.1)	Elevation (m)	PL (mm)	Corolla shape	FT	Pollinator	n	Nectar amount (µl)	Concen-tration (%)	Sugar amount (mg)
I	*A. rupestris*	1	0—2500 (*—3000)	5	Star-shaped	T	Co!	16	0.75 ± 0.64	51.25 ± 17.05	0.34 ± 0.22
	B. hieronymi	2		12	Star-shaped	T	Co! + Le! + Be! + Hu!	36	0.91 ± 0.70	72.95 ± 13.03	0.68 ± 0.57
	B. insignis	3		15	Star-shaped	T	Co! + Meg! + Hal!	7	0.34 ± 0.19	66.76 ± 18.35	0.24 ± 0.18
	C. nivalis[3]	4		11	Star-shaped	T	Be	15	0.71 ± 0.51	40.18 ± 7.57	0.26 ± 0.16
	L. gayana	5		16	Star-shaped	T	Be	16	0.74 ± 0.65	63.55 ± 15.27	0.41 ± 0.25
	N. moroensis	6		14	Star-shaped	T	Co!	17	1.70 ± 0.99	57.23 ± 13.83	0.99 ± 0.63
	*N. picta**	7		15	Star-shaped	T	Co! + Bo!	6	0.55 ± 0.28	83.00 ± 4.10	0.46 ± 0.24
	N. poissoniana	8		14	Star-shaped	T	Co	16	1.47 ± 0.82	66.51 ± 10.21	0.95 ± 0.54
	N. triphylla ssp. *flavipes*	9		15	Star-shaped	T	Co	7	2.14 ± 1.45	51.40 ± 22.05	1.03 ± 0.70
	N. triphylla ssp. *triphylla*	10		18	Star-shaped	T	Co	6	0.67 ± 0.15	68.62 ± 12.24	0.45 ± 0.13
	N. cf. *triphylla* spec nov.	11		15	Star-shaped	T	Co	6	1.62 ± 0.70	62.30 ± 8.17	0.98 ± 0.40
	N. urens	12		18	Star-shaped	T	Co!	9	3.66 ± 2.03	51.13 ± 4.07	1.87 ± 1.02
	N. vargasii	13		16	Star-shaped	T	Co!	16	1.04 ± 1.23	65.94 ± 11.84	0.68 ± 0.79
	P. arequipensis	14		16	Star-shaped	T	Le! + Xy! + Hu!	1	1.20	16.30	0.20
	*X. klaprothioides**	15		11	Star-shaped	T	Co!	18	0.28 ± 0.19	69.67 ± 7.90	0.19 ± 0.13
II	*N. dyeri* ssp. *australis*	16	0—1500	20	Star-shaped	T	Co!	11	9.88 ± 6.04	39.77 ± 9.45	3.85 ± 2.17
	L. sclareifolia	17		18	Saucer-shaped	T	Co	11	9.36 ± 1.28	62.16 ± 5.77	5.79 ± 0.77
	P. incanum	18	0—2500	17	Star-shaped	T	Co! + Le! + Be! + Hu!	22	14.34 ± 4.60	55.50 ± 7.05	7.94 ± 2.58
	C. cirsiifolia (1)	19	2500—3500	19	Saucer-shaped	T	Ce! + Bo!	7	11.43 ± 7.34	65.71 ± 3.15	7.35 ± 4.31
	C. cirsiifolia (2)	20		21	Bowl-shaped	T	Ce!	6	17.33 ± 11.31	58.58 ± 6.18	10.27 ± 7.02
	C. cirsiifolia (3)	21		17	Bowl-shaped	T	Ce! +Bo!	29	11.97 ± 6.51	44.14 ± 9.52	4.97 ± 2.30
	C. grandiflora (1)	22		18	Balloon-shaped	T	Hu! + Bo!	10	11.41 ± 7.98	44.00 ± 22.93	4.70 ± 3.00
	C. grandiflora (2)	23		18	Balloon-shaped	T	Hu! + Bo!	11	11.36 ± 4.65	49.68 ± 18.05	5.30 ± 2.25

	C. lateritia	24		20	Bowl-shaped	F	Hu	5	9.70 ± 5.37	63.40 ± 2.38	6.09 ± 3.28
III	*L. acanthifolia*	25		18	Bowl-shaped	T	Bo! + Co!	6	46.83 ± 17.57	54.00 ± 9.52	25.41 ± 11.35
	N. dillonii	26		29	Bell-shaped	F	Hu?	40	53.18 ± 23.35	31.40 ± 6.28	17.10 ± 8.98
	N. olmosiana	27		25	Balloon-shaped	F	?	65	54.17 ± 21.38	29.38 ± 5.89	15.88 ± 7.12
	P. heucheraefolium	28		25	Star-shaped	T	Xy	17	50.06 ± 13.38	38.06 ± 8.04	19.71 ± 9.05
	C. canarinoides	29		40	Bell-shaped	F	Hu!	14	50.32 ± 24.02	41.73 ± 12.97	21.15 ± 11.75
	C. carduifolia (1)	30		21	Bowl-shaped	T	Hu!	11	69.59 ± 35.21	34.14 ± 14.46	24.96 ± 20.09
	C. carduifolia (2)	31		23	Bowl-shaped	T	Hu!	7	75.86 ± 32.18	49.00 ± 7.30	35.91 ± 12.75
	C. chuquitensis	32		22	Balloon-shaped	F	Hu!	6	101.83 ± 28.47	32.47 ± 9.74	31.62 ± 8.79
	C. cirsiifolia (4)	33		30	Saucer-shaped	T	Ce! + Bo!	19	42.53 ± 14.12	44.47 ± 10.14	19.02 ± 7.37
	C. cf. *superba*	34		26	Balloon-shaped	F	Ce!	19	51.03 ± 24.32	29.91 ± 9.67	14.08 ± 6.00
	C. cf. *madrequisa*	35		18	Bell-shaped	F	Hu	8	45.44 ± 22.03	41.19 ± 8.62	17.90 ± 7.56
	*N. macrothyrsa***	36		32	Star-shaped	T	Xy! + Co!	64	75.13 ± 28.98	32.39 ± 10.61	24.04 ± 11.51
	N. speciosa[2]	37		55	Bell-shaped	F	Hu!	8	36.00	18.83	6.78
IV	*C. coronata*[1]	38		30	Bowl-shaped	F	Ma! + Be! + Hu! + Pa!		79.90 ± 39.65	14.88	11.90
	C. pentlandii (1)	39		30	Bowl-shaped	F	Ma?	18	87.39 ± 25.53	9.78 ± 2.05	8.61 ± 3.23
	C. pentlandii (2)	40		30	Bowl-shaped	F	Ma?	9	79.78 ± 54.21	12.90 ± 3.00	10.19 ± 6.66

[PL = petal length. FT = floral type (see also fig.8.3), N = number of investigated flowers. Group: I = short-tongued bee-pollinated, II = long-tongued bee and hummingbird-pollinated, III = hummingbird-pollinated, IV = mammal-pollinated. Genus names: *A. = Aosa*, *B. = Blumenbachia*, *C. = Caiophora*, *L. = Loasa*, *N. = Nasa*, *P. = Presliophytum*, *X. = Xylopodia*. Floral type: T = tilt-revolver flower sensu Weigend and Gottschling 2006, F = funnel-revolver flowers sensu Weigend 2004b. Pollinator: Be = bee, *Bo = Bombus*, *Ce = Centris*, Co = colletids, Hal = Halictidae, Hu = Hummingbird, Le = Lepidoptera, Ma = Mammals, Meg = Megachilidae, Pa = Passerines, *Xy = Xylocopa*. ! = direct observation in the field, Abbreviation + ? = doubtful, ? = unknown. Literature data: [1] = Cocucci and Sérsic, 1998; [2] = Stiles and Freeman, 1993; [3] = unpublished data from A. Wertlen, 2003.]

the field.

(e) Several studies of nectar composition across a larger group of closely allied species used greenhouse experiments (Elisens and Freeman, 1988; Perret et al., 2001).

Total nectar amount of individual flowers

The entire amount of nectar present in each flower was harvested by inserting micro-capillaries between the two staminodia and the floral scale (micro capillaries: 1- and 2-µl Microcaps; Drummond Scientific Co., Broomall, PA, USA; 5, 10 and 25-µl Duran Ringcaps; Hirschmann Laborgeräte, Eberstadt, Germany). Nectar was harvested twice from each floral scale within 5 min to obtain the full amount of nectar. Brix measurements were then made with a handheld refractometer (neoLab-Handrefraktometer Universal; 10–80% Brix). Small amounts of nectar (mostly highly concentrated and therefore highly viscous as in all species of group I) was pipetted into 1 µl distilled water on the refractometer for measurements and the concentration was calculated for the original amount.

Nectar from 607 flowers (1597 flowers mean per species, 1423 s.d.) from 31 species (including three subspecies, 37 accessions in total) of seven genera (*Aosa*, *Blumenbachia*, *Caiophora*, *Loasa*, *Nasa*, *Presliophytum* and *Xylopodia*) was analysed, including multiple accessions of heterogeneous species complexes such as the *Caiophora cirsiifolia*- and *C. carduifolia*-aggregates. A complete list of the accessions used for the nectar analysis including all authors of plant names is given in the Appendix C. Multiple accessions of individual species are differentiated by Arabic numerals in brackets behind the species and name throughout the text and in the appendix C. Nectar data were all taken during the first half of the staminate phase to ensure that the data are comparable. Sugar concentration (%) and nectar volume (µl) were measured and total sugar production (mg) calculated for the individual flowers. Mean values and standard deviations were calculated for all flowers of one accession. To visualize the correlation between the three data sets (total amount of nectar, total amount of sugar and sugar concentration) the percentage of each value (mean value) was calculated relative to the total amount of nectar data (µl nectar +% sugar + mg sugar = 100 %) and these data then plotted, with Sigmaplot (for windows vers. 80, SPSS Inc. 2002) in a ternary plot. This plot is here favoured over a two-dimensional plot, since it pulls the individual data sets apart much more clearly and is thus better suited to illustrate the divergence of nectar characteristics. Two data sets published elsewhere were included in the ternary plot (*Nasa speciosa* = as '*Loasa spectabilis*', Stiles and Freeman, 1993; *Caiophora coronata*, Cocucci and Sérsic, 1998) and also the unpublished data set of *Caiophora nivalis*, analysed in Argentina by Anna Wertlen (Institut für Biologie, Neurobiologie, Freie Universität Berlin, Germany).

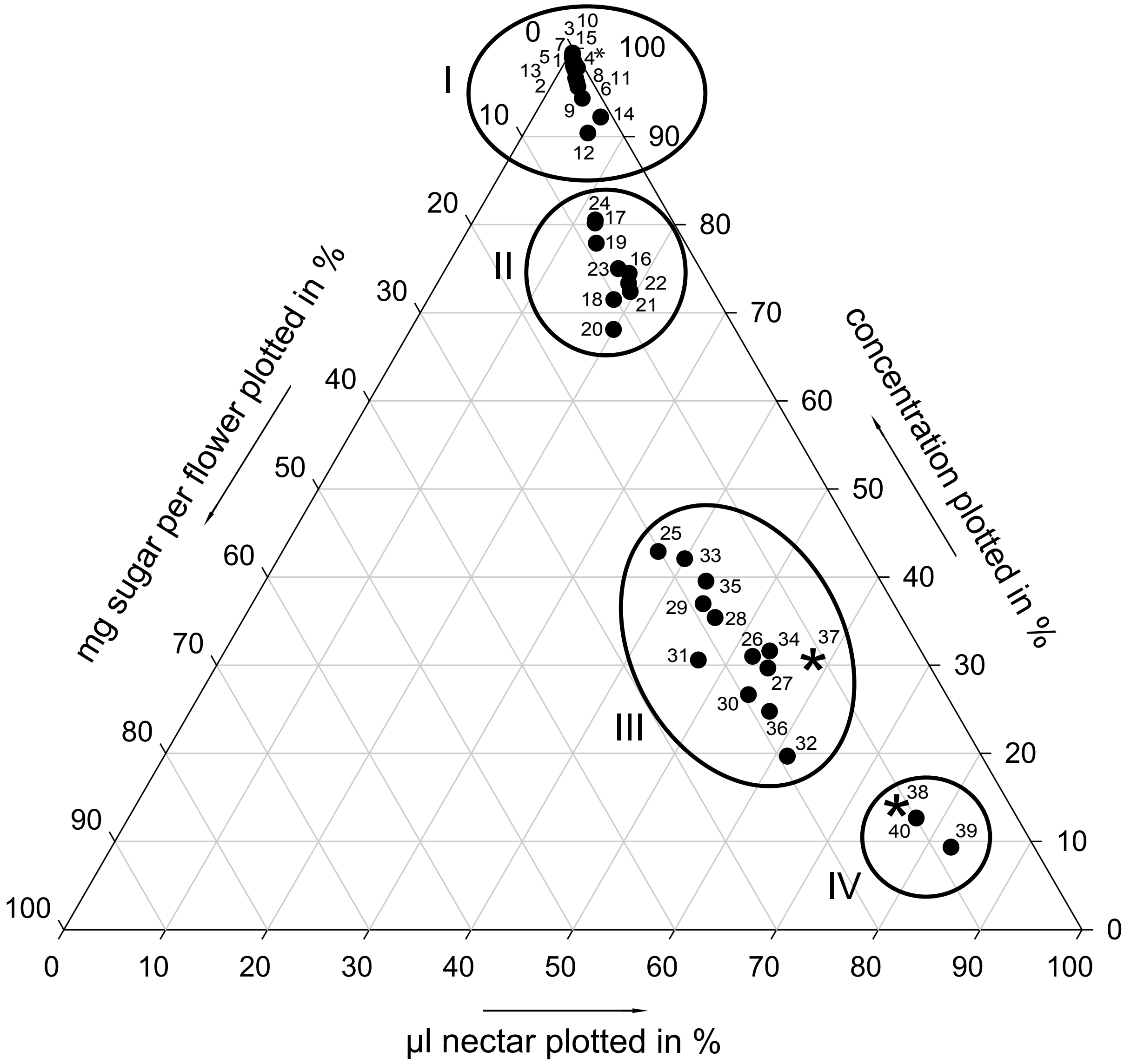
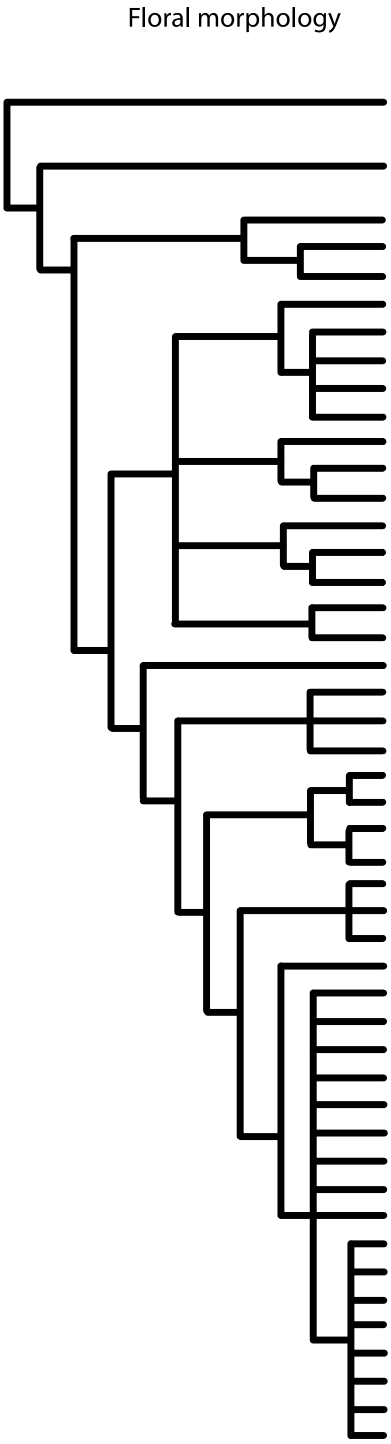


Fig. 8.1: Ternary plot illustrating the relationships between nectar production (NP), sugar concentration (SC) and sugar production (SP) of some species of Loasaceae subfam. Loasoideae (data set from table 8.1 is plotted in percentages, numbers and groups I—IV in diagram correspond to numbering and grouping in Tab. 8.1), e. g. *Blumenbachia hieronymi*, No. 2 in Table 8.1: original data: 0,91 NP + 72,95 SC + 0,68 SP = 100 % = — calculated percentage: = 1.22 % (NP) + 97,87 % (SC) + 0,91 % (SP). Four groups are recognizable: I) SC high, NP and SP low; II) SC, NP and SP between groups I and III; III) SC lower than in group II, NP and SP high; IV) SC very low, NP high and SP lower than in group III. [* = published data from Cocucci and Sérsic 1998 (No. 38); Stiles and Freeman 1993 (No. 37) and unpublished data from A. Wertlen 2003 (No. 4)].



Species	"Nectar group"	Corolla-shape	Floral type
Mentzelioideae	?		
H. fruticosa	(I)	star	T
H. chilensis	(I)	star	T
X. klaprothioides	I	star	T
K. fasciculata	(I)	star	n.a.
N. picta	I	star	T
N. cf. triphylla ssp. nov.	I	star	T
N. triphylla ssp. flavipes	I	star	T
N. triphylla ssp. triphylla	I	star	T
N. dyeri ssp. australis	II	star	T
N. urens	I	star	T
N. vargasii	I	star	T
N. poissoniana	I	star	T
N. macrothyrsa	III	star	T
N. dillonii	III	bell	F
N. olmosiana	III	balloon	F
N. moroensis	I	star	T
N. speciosa	III	bell	F
A. rupestris	I	star	T
P. arequipensis	I	star	T
P. incanum	II	star	T
P. heucheraefolium	III	star	T
B. hieronymii	I	star	T
B. insignis	I	star	T
L. acanthifolia	III	bowl	T
L. sclareifolia	II	saucer	T
L. gayana	I	star	T
L. nana	(I)	star	T
L. bergii	(I)	star	T
S. elegans	(I)	star	T
C. nivalis	I	star	T
C. carduifolia (1)	III	bowl	T
C. carduifolia (2)	III	bowl	T
C. cirsiifolia (1)	II	saucer	T
C. cirsiifolia (2)	II	bowl	T
C. cirsiifolia (3)	II	bowl	T
C. cirsiifolia (4)	III	saucer	T
C. grandiflora (1)	II	balloon	T
C. grandiflora (2)	II	balloon	T
C. canarinoides	III	bell	F
C. cf. madrequisa	III	bell	F
C. lateritia	II	bowl	F
C. cf. superba	III	balloon	F
C. chuquitensis	III	balloon	F
C. coronata	IV	bowl	F
C. pentlandii (1)	IV	bowl	F
C. pentlandii (2)	IV	bowl	F

Fig. 8.2: Consensus phylogeny of Loasaceae subfam. Loasoideae (based on Hufford et al., 2005; Weigend et al., 2004; Weigend and Gottschling, 2006) with nectar groups, corolla shape (corresponding to tab. 8.1 and fig. 8.3) and flower type (T = tilt-revolver flowers, F = funnel-revolver flowers, see also tab. 8.1). Clades with less than 50 bs in these three studies collapsed. [Genus names: *A. = Aosa*, *B. = Blumenbachia*, *C. = Caiophora*, *H. = Huidobria*, *K. = Klaprothia, L. = Loasa*, *N. = Nasa*, *P. = Presliophytum*, *S. = Scyphanthus*, *X. = Xylopodia*. Nectar group I—IV (see tab. 8.1, fig. 8.1): ? many *Mentzelia* species with pollen flowers and no nectar, representative data on nectariferous taxa not available. (I) tiny amounts of highly viscose nectar observed, but no measurements available. n.a. = not applicable].

Pollinator observations

Qualitative data on flower visitors were obtained in Peru and Ecuador (see Table 8.1 for observations and Appendix C. for dates and localities), observation times typically ranged from 60 to 90 min per species and location and were performed in clear weather only (typically between 0900–1200 h and 1600–1800 h). Hymenopteran flower visitors were captured and determined by D. Wittmann (Institut für Landwirtschaftliche Zoologie und Bienenkunde der Universität Bonn, Germany) and C. Schlindwein (Universidade Federal de Pernambuco, Departamento de Botanica, Brazil), where the insects are also deposited. Determination to species was usually not possible, but the taxonomy of the visitors is given to family rank. Hummingbird observations were noted in the field book as means of documentation without identification to species.

Correlates of nectar production

Floral morphology, elevational distribution and pollinator observations are summarized in Table 8.1 to permit a direct comparison of nectar composition to the other data sets. Figure 8.2 provides a consensus diagram of Loasaceae subfam. Loasoideae based on various published phylogenies (Weigend et al., 2004; Hufford et al., 2005; Weigend and Gottschling, 2006) where each species analysed is assigned to a ‘nectar group’ and gross floral morphology (based on Weigend, 2004b; Weigend and Gottschling, 2006).

8.4. Results

Total nectar amount

Table 8.1 summarizes the data on nectar quantities, concentrations and sugar amounts. The amounts of nectar secreted per flower range from 0.3 to 100 µl, the concentrations from 10–83% and the total amounts of sugar provided per flower from 0.19 to 36 mg. These widely variable data can be roughly grouped into four classes (correlation of the data visualized in Fig. 8.1 in the form of a ternary plot). The amounts of nectar are discontinuously distributed and measurements mostly fall into the following ranges: group I, 0.3–15(–35) µl (1.19 µl mean, 0.87 s.d.); group II, 9–14(–17) µl (11.86 µl mean, 2.54 s.d.); groups III and IV, 40–100 µl (III, 57.84

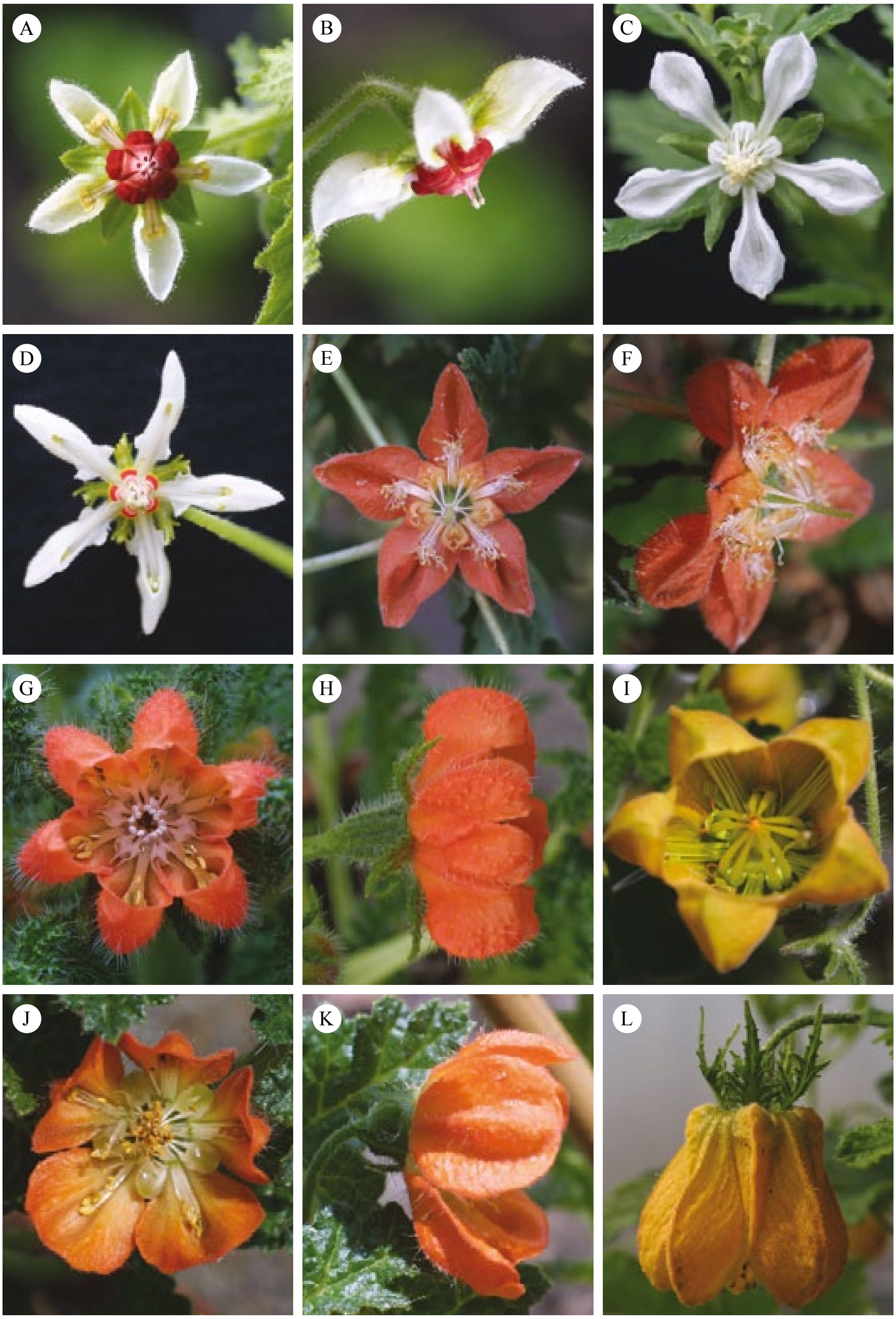


Fig. 8.3: Flower morphology in Loasaceae subfam. Loasoideae. A—F: tilt-revolver flowers; A—D: star-shaped flowers: A—B: *Nasa moroensis*, C: *Presliophytum incanum*, D: *Blumenbachia insignis*; E—F: saucer-shaped flower of *Caiophora cirsiifolia* (1); G—K: funnel-revolver flowers; G—H: balloon-shaped-flower of *Caiophora chuquitensis*. I, L: bell-shaped flower of *Caiophora canarinoides*; J—K: bowl-shaped flower of *Caiophora pentlandii*.

µl mean, 17.99 s.d.; IV, 82.36 µl mean, 4.36 s.d.). Roughly the same groups are retrieved from sugar concentration [group I, (40–)60–80% (59.12% mean, 15.89 s.d.); group II, 40–60(–65)% (53.66% mean, 9.57 s.d.)] but those taxa with 50–100 µl of nectar per flower fall into two subgroups with widely different concentrations [group III, 30–40(–55)% (36.69% mean, 9.35 s.d.); group IV, 10–15% (12.52% mean, 2.57 s.d.)]. These patterns are reflected in the overall amount of sugar offered by the flowers, which falls into group I, 0.19–2 mg (065 mg mean, 046 s.d.); group II, 4–10 mg (6.25 mg mean, 1.97 s.d.); group III, 14–36 mg (2223 mg mean, 651 s.d.); and group IV, 8.5–12 mg (9.40 mg mean, 1.12 s.d.).

Altitudinal distribution, floral morphology and pollinators

The four nectar groups retrieved from nectar data roughly correspond to the morphological and ecological data. The corolla shapes as here defined are illustrated in Fig. 8.3. Floral display depends on both flower shape and petal length (Fig. 8.3 and Table 8.1; mean value and s.d. for petal lengths: group I, 14.07 ± 3.28; group II, 18.67 ± 1.41; group III, 28.00 ± 10.11; group IV, 30.00). Bowl-shaped flowers have a much larger floral display than star-shaped flowers with the same petal length. Petal size in combination with corolla shape is therefore here used as a proxy for display size. In general terms there is more nectar in (a) more closed flower types (versus more open), and flowers with (b) larger (versus smaller) petals. Also, highly concentrated nectar in small amounts (group I) is found only in tilt-revolver flowers and very dilute nectar in huge amounts (group IV) only in funnel-revolver flowers. Group II nectar is more often found in tilt-revolver flowers than in funnel-revolver flowers (six versus three taxa) and group III nectar is found roughly as often in tilt-revolver as in funnel-revolver flowers (six versus seven taxa).

Group I: mainly low-elevation plants (mostly <2500 m) with relatively small, typically white, star-shaped flowers [petals approx. (5–)12–18 mm long; Table 8.1 and Fig. 8.3A–D]. Flowers of this group are predominantly visited and pollinated by short-tongued bees, mostly colletid bees. Only *Nasa picta* and *Xylopodia klaprothioides* range into higher elevations.

Group II: mid-elevation plants (2500–3500 m) often with larger, more closed, mostly orange or red flowers (petals approx. 17–21mm long; Table 8.1 and Fig. 8.3E, F, bell-, balloon-, saucer- or bowl-shaped). Both long-tongued bees and hummingbirds have been documented as flower visitors of that group. The only taxa which are aberrant in pollinator visitor (colletid bees) and elevational distribution (0–1500m) for this group are *Loasa sclareifolia*, *N. dyeri* ssp. *australis* and *Presliophytum incanum*.

Group III: mostly high elevation plants (3000–4000 m) and a few species from low elevations (500–1500 m), with some of the largest flowers in the subfamily, flowers are largely closed and orange, red or rarely yellow (petals up to 55 mm long; Table 8.1 and Fig. 8.3G–I, L, bell-, bowl- or balloon-shaped). Only exceptions are *Nasa macrothyrsa* and *Presliophytum* *heucheraefolium* from lower elevations with white, star-shaped flowers. Hummingbirds are likely to be the most important flower visitors of this group, but long-tongued bees (*Centris*, *Bombus* and *Xylocopa*) have also been observed, often on the same plant species.

Group IV: only two decumbent high elevation taxa (>3500 m) with large petals (approx. 30mm long; Table 8.1 and Fig. 8.3J, K), either white or orange-red bowl-shaped flowers (similar to types also found in group III). While it has not been possible to document flower visitors in the field, there is one publication indicating that small rodents may be the principal pollinators for one of the two taxa (*C. coronata*; Cocucci and Sérsic, 1998).

8.5. Discussion

Overall nectar and sugar production in relation to pollination syndrome

Sugar concentrations here reported are generally higher than most literature data (both for bee- and hummingbird pollinated flowers; Baker, 1975; Bolten and Feinsinger, 1978; Bolten et al., 1979; Pyke and Waser, 1981; Cruden et al., 1983; Heyneman, 1983; Forcone et al., 1997; Galetto et al., 1998; Bernardello et al., 2000; Blem et al., 2000; Chalcoff et al., 2006; Wilson et al., 2006) and this may be an idiosyncratic phenomenon of Loasaceae. Group III may be predominantly hummingbird-pollinated, but the hummingbird-pollinated taxa studied here have unusually high sugar concentrations in the nectar (Table 8.1 and Fig. 8.1, nos 29, 31, 33 and 35, 30–55% as compared with the ‘typical’ 20–26 %; Baker, 1975; Cruden et al., 1983). Heinrich and Raven (1972) and Forcone et al. (1997) argue that ‘highland hummingbird nectar’ should be less viscous and less concentrated, but this is apparently not true in Loasaceae. Higher than typical sugar concentrations in flowers pollinated by hummingbirds have also been found for hummingbird nectar by Kaczorowski et al. (2005) in *Nicotiana* sect. *Alatae*. This might be due to the high Andean habitat and the therefore high energy requirements of the birds: Heinrich and Raven (1972) and Forcone et al. (1997) argue that, in low temperatures, energetic rewards for hummingbirds must be higher than in high temperatures. Higher concentrations in this group of taxa may also be due to the fact that the flowers of at least some of the taxa concerned [e.g. *Caiophora* cf. *superba*, *C. cirsiifolia* (4), *Loasa acanthifolia*, *Nasa macrothyrsa* and *Presliophytum heucheraefolium*] are often also visited by long-tongued bees and there may be no reason for the plant to exclude them as flower visitors (Bolten and Feinsinger, 1978). Interestingly, there is a single data set from an ornithophilous species of *Nasa* from Costa Rica (*N. speciosa*; Stiles and Freeman, 1993) which has the typical, relatively low sugar concentration of hummingbird nectar (Heinrich and Raven, 1972; Forcone et al., 1997).

Pollination, nectar and elevation

Comparing the four groups defined above, it becomes apparent that there is a trend towards higher nectar volume and higher total amount of sugar per flower at increasing elevations, i.e. bird- and mammal-pollinated taxa are largely high-Andean (groups III and IV), whereas the taxa pollinated by short-tongued bees are found at low and intermediate elevations (group I). At elevations above approx. 3500m only the two genera *Nasa* and *Caiophora* are present in the Andes, and both with species where hummingbird pollination predominates among the taxa.

Evolution of nectar characteristics and pollination syndromes

Figure 8.2 shows a phylogeny of Loasoideae together with the assignment of terminal taxa to nectar group and gross floral morphology. It appears that group I nectar represents the plesiomorphic condition and this agrees with the previously published hypothesis that pollination by short short-tongued bees (especially colletid bees) is the plesiomorphic condition in the subfamily (Weigend et al., 2004; Weigend and Gottschling, 2006). Evolution towards higher amounts of more dilute nectar appears to have happened several times: (a) at least twice in *Nasa* (in the *Nasa triphylla* group and at least once in the *N. macrothyrsa–N. speciosa* clade); (b) in *Presliophytum*; (c) in the *Blumenbachia–Loasa acanthifolia* clade; and (d) at least once in the *Loasa gayana–Caiophora* clade.

The transitions towards more dilute nectar took place without a transition towards funnel-revolver flowers in the *Blumenbachia–Loasa acanthifolia* clade and *Presliophytum*. It seems to be phylogenetically correlated with the transition from tilt-revolver flowers to funnel-revolver flowers in the *Loasa gayana–Caiophora* clade and in the *Nasa macrothyrsa–N. speciosa* clade. The nectar and pollinator data here presented show that the repeated morphological transformations of Loasoideae flowers from small, bee-pollinated flowers to large, bird-pollinated flowers (Weigend et al., 2004; Weigend and Gottschling, 2006; see also corolla shapes and petal lengths in Table 8.1) were likely preceded by changes in nectar composition. The evolution of a different nectar type ('nectar group') as a means of recruiting different pollinators seems to be a rapid process in relative terms. There are considerable differences in nectar production between closely allied taxa with morphologically very similar flowers (*Nasa triphylla* group, *C. carduifolia* complex, *C. cirsiifolia* complex). Vastly different forms of nectar production can apparently evolve with relative ease and nectar production (in terms of both absolute amounts and concentration) appears to evolve more rapidly than functional floral morphology in Loasaceae subfam. Loasoideae.

8.6. Acknowledgements

We would like to express out sincere gratitude to M. Achatz, P. Beckers, G. Brokamp, N. Cusimano, G. Fröhlich, S. Grossmann, T. Henning, P. Kramer, B. Nordt, N. Nürk, N. Poser, E. Scherer, C. Schneider, C. Schwarzer and A. Tais (Berlin, Germany) for obtaining nectar from flowers and measuring sugar concentration. We would like to thank Natalie Cusimano (Berlin, Germany) for help with calculating the ternary graphs with Sigma Plot, Anna Wertlen (Berlin, Germany) for the data set from *Caiophora nivalis*, as well as Natalie Hempel de Ibarra (Berlin, Germany) for methodological advice and helpful discussions. We thank A. Cano and M. I. La Torre (Lima, Peru), Eric Rodriguez (Trujillo, Peru), N. Salinas (Cuzco, Peru), G. Vobis and C. Ezcurra (Bariloche, Argentina), H. Förther (München, Germany), N. Dostert, T. Henning, D. Kollehn, O. Mohr, C. Schwarzer and K. Weigend (Berlin, Germany) for help in the field and collecting seeds. We thank D. Wittmann (Institut für Landwirtschaftliche Zoologie und Bienenkunde der Universität Bonn, Germany) and C. Schlindwein (Universidade Federal de Pernambuco, Departamento de Botânica, Brazil) for identifying the captured hymenopteran pollinators. The funds kindly provided by the following institutions at various stages of the project are gratefully acknowledged: Studienstiftung des Deutschen Volkes (1992–1997), Deutscher Akademischer Austauschdienst (1999–2000), Lewis B. and Dorothy Cullman Laboratory for Molecular Systematics Studies at the New York Botanical Garden (1999–2000), Deutsche Forschungsgemeinschaft (Grant-nr.WE 2330/1, 2001–2003), botconsult GmbH (1999–present).

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9. Reloading the revolver – male fitness as a simple explanation for complex reward partitioning in *Nasa macrothyrsa* (Loasaceae, Cornales)*

9.1. Abstract

Reward partitioning and replenishment and specific mechanisms for pollen presentation are all geared towards the maximization of the number of effective pollinator visits to individual flowers. An extreme case of an apparently highly specialized plant–pollinator interaction with thigmonastic pollen presentation has been described for the morphologically complex tilt-revolver flowers of *Caiophora arechavaletae* (Loasaceae) pollinated by oligolectic *Bicolletes pampeana* (Colletidae, Hymenoptera). We studied the floral biology of *Nasa macrothyrsa* (Loasaceae) in the field and in the glasshouse, which has very similar floral morphology, but is pollinated by polylectic *Neoxylocopa* bees (Apidae, Hymenoptera). We investigated the presence of thigmonastic anther presentation, visitor behaviour (pollinators and nectar robbers), co-ordination of pollinator visits with flower behaviour and the presence of nectar replenishment. The aim of this study was to understand whether complex flower morphology and behaviour can be explained by a specialized pollination syndrome, or whether alternative explanations can be offered. The results showed that *Nasa macrothyrsa* has thigmonastic pollen presentation, i.e. new pollen is rapidly (<<10 min) presented after a pollinator visit. Nectar secretion is independent of removal and averages 7–14 μL/h. The complex flowers, however, fail to exclude either native (hummingbirds) or introduced (honeybees) nectar robbers, nor does polylectic *Neoxylocopa* actively collect the pollen presented. The findings do not support a causal link between complex flower morphology and functionality in Loasaceae and a highly specialized pollination. Rapid pollen presentation is best explained by the pollen presentation theory: the large proportion of pollinators coming shortly after a previous visit find little nectar and are more likely to move on to a different plant. The rapid presentation of pollen ensures that all these valuable 'hungry pollinators' are dusted with small pollen loads, thus increasing the male fitness of the plant by increasing the likelihood of siring outcrossed offspring.

Additional keywords: asymmetric specialization – hungry pollinator – nectar replenishment – pollen presentation.

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*'The definitive version is available at www3.interscience.wiley.com Published as: Weigend M, Ackermann M, Henning T. 2010. Reloading the revolver - male fitness as a simple explanation for complex reward partitioning in *Nasa macrothyrsa* (Loasaceae, Cornales). Biological Journal of the Linnean Society 100: 124-131. DOI: 10.1111/j.1095-8312.2010.01419.x

9.2. Introduction

Floral rewards are crucial for pollinator attraction, and pollen and nectar are the most common rewards for pollinators. To encourage repeated visits, rewards must be replenished at ecologically relevant frequencies (Engel and Irwin, 2003; Castellanos et al., 2006). Nectar is commonly replenished in flowers and may be available throughout anthesis, in spite of repeated removal by flower visitors (Aizen and Basilio, 1998; Valtueña et al., 2007), and overall nectar production may be adjusted to higher and lower visitation rates (Vickery and Sutherland, 1994; Castellanos et al., 2002; Hernández-Conrique et al., 2007). In contrast, pollen cannot be replenished, as the number of anthers present and the amount of pollen contained in them is fixed long before anthesis. However, particular mechanisms have evolved to improve male fitness to receptive stigmas. Pollen presentation theory explains pollen presentation in terms of male fitness (Lloyd and Yates, 1982; Harder and Thomson, 1989, Thomson 2003, Castellanos et al., 2006). One crucial aspect is that not all pollen can be removed by an individual flower visitor. This can be ensured by, for example, sequential maturation of anthers of individual flowers (‘packaging’), or by providing the anther only with a small opening, releasing pollen in small portions (‘dispensing’; Lloyd and Yates, 1982; Harder and Thomson, 1989; Thomson et al., 2000). A particularly complex case of pollen partitioning by packaging has been described from the largely neotropical Loasaceae subfamily Loasoideae. These plants have proterandrous tilt-revolver flowers with 80–100(–120) stamens in five groups, with the stamens initially enclosed in pockets formed by the petals (Fig. 9.1 A; Weigend and Gottschling, 2006). The five stamen groups alternate with five boat-shaped staminodial complexes. Staminodial complexes consist of an outer, deeply boat-shaped nectar scale (open at the apex and towards the inside of the flower) and two free staminodes closing the inside of the scale. Seen from above, the apical openings of these floral scales form a circle like the holes in the drum of a revolver (Fig. 9.1 E). Individual anthers mature over several days and one-by-one move into the centre of the flower, where they dehisce and present their pollen (Fig. 9.1 B, C). Nectar is secreted into the scales (Fig. 9.1 F), and bees probe each scale to harvest its nectar. Most importantly, in *Caiophora arechavaletae* (and some other species of *Blumenbachia* and *Caiophora*), stamen movement can also be triggered by nectar-harvesting bees (Schlindwein and Wittmann, 1997; Schlindwein, 2000). Only oligolectic females of the short-tongued bee *Bicolletes pampeana* (Colletidae) pollinate these flowers. These bees return to the individual flower shortly after the first visit (c. 5 min) to harvest the pollen presented as a result of the previous manipulation of the nectar scales (Schlindwein and Wittmann, 1997). The complex floral morphology, the difficult access to the nectar, frequent documentation of colletids as pollinators and, especially, the triggered pollen presentation seem to point to a specialized (and possibly exclusive) relationship between tilt-revolver flowers and short-tongued, oligolectic colletid bees (Schlindwein and Wittmann, 1997; Schlindwein, 2000). However, Ackermann and Weigend (2006) and Weigend and Gottschling (2006) reported a wide range of bees and other insects as flower visitors for different species of Loasaceae with tilt-revolver flowers from several distantly related genera, casting doubt on a direct causal link between complex flowers and specialized pollination.

The Andean genus *Nasa* is the largest genus of Loasaceae (> 100 species), and about one-half of its species have tilt-revolver flowers as described above (Weigend and Gottschling, 2006). It is unknown whether species of *Nasa* also possess triggered (thigmonastic) stamen movement, whether nectar is replenished in these tilt-revolver flowers and whether nectar replenishment (if present) is triggered by flower visits. We therefore investigated the floral function and ecology of *Nasa macrothyrsa*, a shrubby species, narrowly endemic to the provinces of San Miguel and Contumazá, Department of Cajamarca, in northern Peru (Weigend et al., 2003). Its flowers are larger but structurally similar to those of *C. arechavaletae*. In contrast with *C. arechavaletae*, *N. macrothyrsa* is mainly visited by large carpenter bees (*Neoxylocopa lachnea* Moure, 1951, observed in several populations across the distribution area of the species; Ackermann and Weigend, 2006) and produces a large amount of nectar (under visitor exclusion 75.13 ± 28.98 µL nectar per flower, 32.39 ± 10.61% sugar, 24.04 ± 11.51 mg sugar per flower; Ackermann and Weigend, 2006). We investigated whether this species, with carpenter bees as presumably less specialized pollinators (Raju and Rao, 2006), showed the same complex pattern of reward partitioning and presentation, and whether the pollen/reward replenishment was paralleled by correspondingly timed flower visits. We aimed at a detailed picture of flower behaviour. How long are the phases of anthesis in *N. macrothyrsa* and are its flowers self-pollinated? Is stamen movement also thigmonastic? Is nectar replenished, and is nectar replenishment influenced by flower visits? What is the timing of flower visits? Does reward accumulation (pollen and nectar) in some way correspond to the observed visitor frequencies?

9.3. Material and methods

Plant material and cultivation

Observations on the flowers of *N. macrothyrsa* were made on plants in their natural habitat [Peru: Depto. Cajamarca, Prov. Contumazá, Contumazá; on a rocky slope next to the road, surrounded by cloudforest remnants. 2681 m, 12.6.2008, T. Henning & J. Schulz 32 (USM)]. Seeds collected on a previous collection trip had been used to raise plants of this species in the glasshouse [voucher: M. Weigend et al. 7471 (B, M, USM, HUT)]. Seeds were sown into standard sowing soil (Compo Sana). Seedlings were pricked out as soon as the cotyledons were fully developed into 5-cm clay pots filled with the same soil, and then repotted into successively larger clay pots [potting soil: two parts mature leaf compost, one part peat, fertilized with a mixed inorganic–organic fertilizer (Garten- and Gemüsedünger, ASB Grünland, H. Aurenz GmbH) and basalt powder (Neudorffs Urgesteins Mehl, W. Neudorff GmbH KG)]. Plants were

Fig. 9.1: Flower of and flower visits on *Nasa macrothyrsa*. A, Flower, note the numerous stamens reflexed into the hooded petals. B, Flower in the staminate phase, with red and white floral scales and stamens in the centre of the flower. C, Stamen moving from the petal on the upper right into the flower centre. D, Nectar overflowing (along style) in the absence of flower visitors. E, Staminodial complexes with apical openings of the floral scale (access to the nectar). F, Staminodial complexes, lateral view, nectar visible through semi-transparent nectar scales. G, Honeybee robbing nectar, holding on to the petal base and accessing nectar scale from the side without touching anthers or stigma. H, I, Carpenter bee holding onto other nectar scales and inserting proboscis into one floral scale to remove nectar. K, Abdomen of carpenter bee dusted with pollen; note the filaments in the centre of the flower and the triggered stamen moving from the left.

kept outdoors in light shade during the summer (May–October) and moved into the glasshouse in winter (November–April). Flowering took place between November and February when the plants were kept in the glasshouse with artificial lighting (12 h, high-pressure sodium lamps: Philips SON-T AGRO 400 W) and temperatures of 10–15 °C at night and 20–25 °C during the day (closely resembling the temperature regime in the natural habitat).

Glasshouse experiments

Flower longevity was investigated by marking individual flowers and recording the phases of anthesis (incipient anthesis, staminate phase, carpellate phase, shedding of petals/anthers, N = 20). Overall stamen number per flower was recorded (N = 29). Self-pollination was investigated by marking individual flowers and then either leaving them unmanipulated (N = 30, selfing) or hand-pollinating by dehisced anthers from other flowers (N = 28, pollination) and subsequently recording fruit set. Flowers were not bagged, as experiments were carried out in winter (November–February) without pollinator activity.

Nectar replenishment was studied in flowers in the middle staminate phase. At the beginning of the experiment, the entire amount of nectar present in each flower was removed by insertion of graded microcapillaries (microcapillaries: 5-, 10- and 25-µL Duran Ringcaps, Hirschmann Laborgeräte, Eberstadt, Germany) into the nectar scales. The amount of nectar replenished was then studied by harvesting and measuring the nectar five times after fixed intervals, once at the end of the experiment. Sugar concentrations were calculated from Brix measurements made for each flower separately with a hand-held refractometer (neoLab-Handrefraktometer Universal; 10–80% Brix). A first experiment was carried out in December 2005 (five intervals of 30 min, total 150 min, N = 18; one interval of 150 min, N = 8); a second experiment was carried out on the same plants in December 2008 (five intervals of 60 min, total 300 min, N = 26; one interval of 300 min, N = 16). Mean nectar production was calculated for each interval (30 min and 60 min) and compared with the longer interval (150 min and 300 min).

Stamen movement was studied in December 2008 by marking flowers and cutting off mature stamens already present in the centre of the flower 1 h before the first stimulation experiment. Twenty flowers were used for the experiment with a control group of ten flowers. Five consecutive 30-min intervals between stimuli were chosen, based on field observations indicating an average interval between two visits to individual flowers of c. 25 min. Stamen movement was triggered by slight bending of all five nectar scales outwards with a dissecting needle, thus imitating a pollinator visit. Stamen movement from the reflexed into the upright position takes c. 1.5–3 min, so that the 30-min interval between stimuli was further subdivided into 5-min subintervals for recording purposes. Autonomous stamen movement was observed in an unmanipulated control group. Each flower and every flower manipulation were treated statistically as a single event, comparable with a single pollinator visit in the natural habitat.

Field observations

Field observations were carried out in June 2008 on a large population (several dozen plants with several hundred open flowers) near Contumazá (see above). Flowers were individually marked and flower visits were recorded. A total of 30 flowers was watched during two observation periods of 150 min each (12 June 2008, 14:30–17:00 h; 13 June 2008, 10:00–12.30 h). Visitor intervals and the type of visitor were recorded. If a flower was visited twice within the same minute, an interval of 30 s was arbitrarily assigned. Voucher specimens of visiting insects were caught at the end of the observation period for determination purposes. Hummingbird visits were recorded without determination of species or vouchering.

Statistics

In stamen movement, the triggered flowers and the control group are independent samples and the data (number of stamens moved at a given time) are not normally distributed. The general tendency of stamen movements was tested for significance using the nonparametric Mann–Whitney U-test. Nectar secretion was tested for significant differences by comparing only the total amount of nectar per flower secreted during the time of the experiment. The data were first tested for normality using the Kolgomorov–Smirnov test (normal distribution given in all cases). Then, a t-test was performed to compare the nectar values produced per flower in the repeatedly probed and control flowers. The resulting P values (exact significance, two-tailed) are given in parentheses. Datasets were prepared using Microsoft Excel (Microsoft Corp.); statistical analyses were performed using SPSS 9.0 (SPSS Inc.) for Windows. Graphs were calculated with SigmaPlot 8.0 (SPSS Inc.) and graphically processed with Adobe Illustrator CS (Adobe Systems Inc.).

9.4. Results

Flower longevity and self-pollination

Unmanipulated flowers were open for c. 5 days (5.21 ± 0.58 days) and were in the staminate phase for c. 4 days (3.83 ± 0.42 days). Individual flowers possessed ≥100 stamens each (104.69 ± 11.32). Flowers were not self-pollinated; unpollinated flowers set no fruit in the

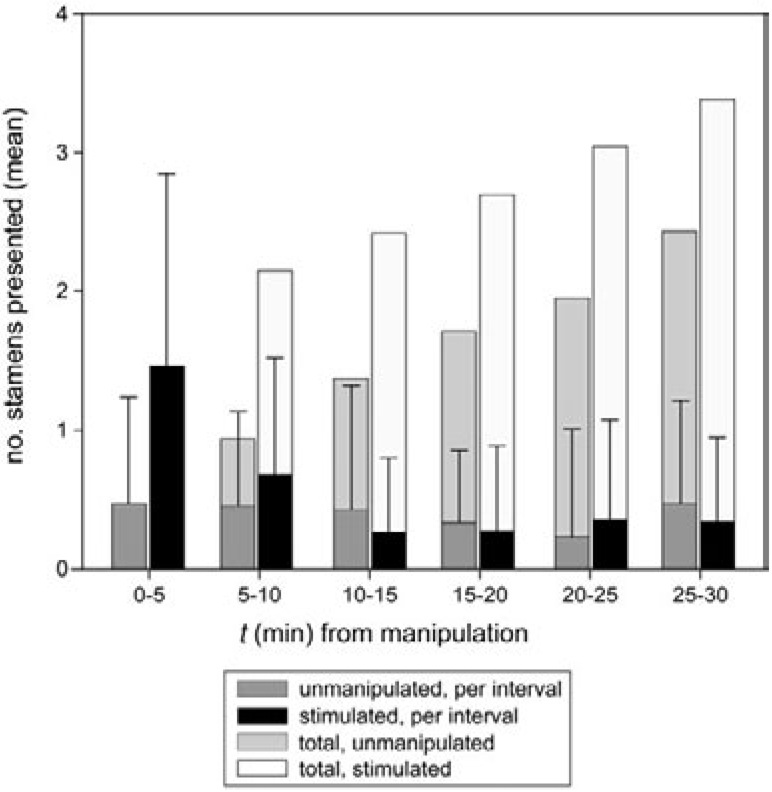

Fig. 9.2: Autonomous and triggered stamen movement in flowers of *Nasa macrothyrsa*. Dark bars, number of stamens moving per stimulus and interval; light bars, sum of stamens present in the centre of the flower after each interval at a given interval after the stimulus.

glasshouse (N = 30, all abortive), but 85% of hand-pollinated flowers set fruit (N = 28, resulting in 25 capsules with viable seed).

Nectar replenishment

Unmanipulated flowers in the middle staminate phase contained 84.23 ± 33.34 µL of nectar with a concentration of 44.38 ± 3.72% (30-min experiment), and 17.56 ± 7.48 µL of nectar with a concentration of 53.96 ± 5.77% (60-min experiment). Nectar replenishment was found to take place in both experiments (2005, 2008), but nectar secretion was clearly higher in 2005 than in 2008. In the 30-min experiment, individual flowers produced 0.15 ± 0.04 µL of nectar per minute with a concentration of 25.17 ± 2.73%, corresponding to 0.04 ± 0.02 mg sugar per minute. In the 60-min experiment, individual flowers produced 0.07 ± 0.02 µL of nectar per minute with a concentration of 22.86 ± 2.47%, corresponding to c. 0.02 ± 0.005 mg sugar per minute. There was no significant difference in nectar secretion between the flowers sampled at intervals of 30 and 60 min compared with the flowers sampled after 150 and 300

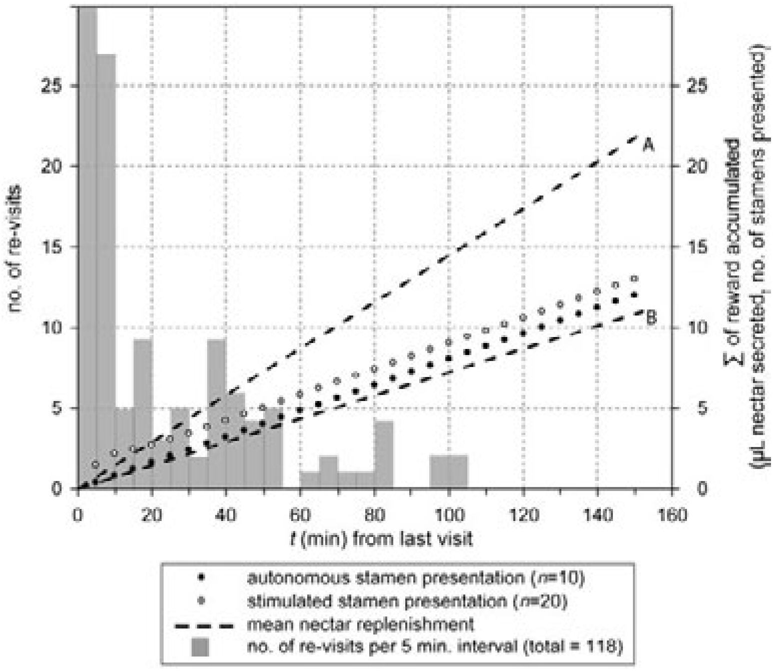

Fig. 9.3: Flower visits and reward accumulation. Absolute number of second visits to individual flowers and reward available per flower at a given time (t) after previous visit: nectar A, 30-min experiment (2005); nectar B, 60-min experiment (2008). The majority of visitors come very soon after a previous visit and (presumably) reward depletion.

min (60 min: N = 25, blind = 16, T = 0,794, d.f. = 39, P = 0432; 30 min: N = 18, blind = 8, T = 0,793, d.f. = 24, P = 0435). Accumulated nectar measured at the beginning of the experiment had a much higher sugar concentration than the freshly secreted nectar produced during the experiment. Nectar production/replenishment appears to be independent of nectar removal in the time frame relevant to this study. Indeed, flowers do not cease to produce nectar if nectar is not removed, and floral scales eventually overflow with nectar dripping out of the flower (Fig. 9.1 D).

Thigmonastic stamen movement

Autonomous stamen presentation was studied in unmanipulated flowers in the glasshouse (5 x 30-min intervals on 10 flowers = 50; Fig. 9.2). An average of 2.44 ± 0.72 stamens every 30 min (one interval) moved into the centre of the flower. Simulated pollinator visits (tilting of the floral scales in intervals of 30 min, 5 x 30-min intervals on 20 flowers = 100) led to a highly significant increase in stamen presentation (P = 0.007, Mann–Whitney-U-test), with an average of 3.39 ± 0.79 stamens every 30 min (Fig. 9.2). Most of the thigmonastic stamen movement occurred soon after the stimulus (63% in the first 10 min).

Flower visits in nature

During the observation period, a total of 136 individual flower visits were recorded, with *Neoxylocopa* as the most frequent visitor (77 visits, 52.03%, Fig. 9.1 H–K), followed by (non-native, introduced) honeybee *Apis mellifera* (59 visits, 39.86%, Fig. 9.1 G) and hummingbirds (12 visits, 8.11%). *Apis* and hummingbirds usually failed to touch anthers or stigma (and did not collect pollen in the flowers) and are unlikely to pollinate. Only *Neoxylocopa* bees collected nectar as described for *Bicolletes* bees in *C. arechavaletae* (Schlindwein and Wittmann, 1997), that is by inserting their proboscis into each floral scale (Figs 9.1H, I) whilst pollen was deposited on their abdomen (Fig. 9.1 K). *Neoxylocopa* did not actively remove pollen from the anthers. All flowers were visited at least twice during the observation period, with 4.93 ± 2.43 visits per flower and intervals between visits ranging from 0.5 to 105 min, with a mean interval of 24.78 ± 26.55 min between visits (Fig. 9.3). However, data were heavily skewed towards shorter intervals, and the median time lapse between visits to individual flowers was only 11 min because of a very high percentage of bee visits after less than 10 min (48.31% total; 60.61% in *Neoxylocopa*, 48.93% in *Apis*, 33.30% in hummingbirds).

9.5. Discussion

The flowers of *N. macrothyrsa* require pollination to set fruit. The field data presented here, in conjunction with the data from other populations presented in Ackermann and Weigend (2006), show that *Neoxylocopa lachnea* is the principal flower visitor and likely pollinator of *N. macrothyrsa*. There is thus no exclusive relationship between tilt-revolver flowers and Colletid bees. *Neoxylocopa* bees expertly manipulate the complex flowers, extracting nectar from all five nectar scales, whilst their abdomen is dusted with pollen from the mature anthers in the centre of the flower. Conversely, honeybees and hummingbirds evidently act as nectar robbers, without effecting pollination. The flowers show a highly complex pattern of reward/ pollen partitioning and timing: the numerous anthers are autonomously (slowly) or thigmonastically (more rapidly) presented in the centre of the flower, the nectar is distributed over five nectar scales, which increases handling time for the visitor, and nectar is continuously replenished in the five nectar scales. The nectar replenished after visits has a relatively low sugar concentration of c. 22–25%, compared with accumulated nectar in flowers that have not recently experienced a visit.

The flowers of *N. macrothyrsa* have an extended staminate phase (four-fifths of anthesis duration), especially when compared with polyandrous flowers of other genera of Loasaceae with less complex floral morphology: In *Mentzelia*, flowers are usually open for a single morning with all pollen (from a similarly large number of anthers) dispensed in a few hours (subfamily

Mentzelioideae; Weigend, 2008). *Nasa macrothyrsa* pollen is presented in small portions (a few anthers at a time), and this can be considered as an extreme case of 'packaging'. Taking the length of the staminate phase from the glasshouse (3.83 ± 0.41 days, c. 12 h daylight, similar to natural conditions) and superimposing the visitor frequency in the field (average interval 24.78 ± 26.55 min), we would expect an average of over 100 flower visits overall for each flower during the staminate phase alone (multiplying visitor frequency from the field with floral longevity from the glasshouse), nearly half by the legitimate pollinator *Neoxylocopa*. As a result of sequential anther maturation and rapid thigmonastic pollen presentation, the vast majority of visitors will be dusted with small amounts of pollen throughout the staminate phase. Harder and Wilson (1994) argued that 'the most effective (pollen) dispensing schedule allows dynamic adjustment of removal to the prevailing frequency of visits experienced by individual plants' – this is clearly the case in *N. macrothyrsa*, where anther presentation is triggered by flower visits. Conversely, the carpellate phase in *N. macrothyrsa* is only c. 1 day and, from experimental pollination in the glasshouse, it would seem that a single pollinator visit will be sufficient for full seed set. Pollen presentation in *N. macrothyrsa* can be strongly accelerated by pollinator visits, ensuring the rapid replenishment of pollen during periods of high visitor activity. In the field, most (60.61%) flowers visited by *Neoxylocopa* received a second visit within the first 10 min. Thigmonastic pollen presentation ensures that fresh pollen is already available after this short time period, but visitors will only receive a very minor amount of nectar (<0.7–1.5 µL). Overall attractiveness (i.e. amounts of pollen and nectar available in the individual flower) gradually increases with time from the last visit as a result of reward accumulation (Fig. 9.3), ensuring that some of the flowers of *N. macrothyrsa* visited by *Neoxylocopa* offer a very large amount of nectar and pollen, making it a rewarding resource. In particular, nectar is then available in large quantities and at higher sugar concentrations. Pollinators encountering little or no nectar in an individual flower appear to be more likely to leave the inflorescence or the plant concerned and move on to a different individual (Cresswell, 1990; Biernaskie et al., 2002; Johnson et al., 2004; Jersákova and Johnson, 2006). Thus, the 'best' pollinators for *N. macrothyrsa* are those visitors coming soon after a previous flower visit, as they will receive little nectar and are thus more likely to move on to a different plant. Moreover, bees receiving a heavy pollen load from individual flowers are much more likely to groom (i.e. move the pollen into the scopae for transport) than bees receiving a smaller pollen load (Harder, 1990). Pollen is then no longer available for pollination. Thus, depositing small amounts of pollen on all visitors is the most efficient way of dispensing pollen in terms of male fitness. Small amounts of pollen presented whilst nectar is depleted should be most likely to sire out-crossed offspring because of these idiosyncrasies of bee behaviour. Accelerated pollen presentation will be advantageous, irrespective of pollinator species, in a reward-limited system, and probably increases male fitness.

Schlindwein and Wittmann (1997) viewed the parallelism between pollen presentation and bee behaviour in *B. pampeana* on *C. arechavaletae* as an extreme case of a specialized pollination syndrome. The data presented here argue that this may be a classical case of asymmetric specialization, which is probably common in plant–pollinator systems (Vázquez and Aizen, 2004). *Bicolletes pampeana* is apparently specialized on *C. arechavaletae*, but *C. arechavaletae* is probably not dependent on *B. pampeana*. Evidence from the cultivation of other similar species of *Caiophora* shows that European bumblebees (*Bombus*) and honeybees (*Apis*) are perfectly capable of learning to manipulate the complex tilt-revolver flowers and of efficiently pollinating these flowers. There is no need to explain the complex morphology and behaviour of tilt-revolver flowers in general by the specialized behavioural pattern of particular species of Colletid bee (as presumably highly specialized pollinators). Even unspecialized and ineffective visitors, such as introduced honeybees, are not successfully excluded and are perfectly capable of exploiting floral rewards in spite of the complex flower morphology. We argue that thigmonastic pollen presentation in tilt-revolver flowers is a mechanism to increase male fitness by making maximum use of the 'hungry pollinator'. Which animal species ultimately becomes the dominant visitor/pollinator species is determined by the complement of potential pollinator species present in a given locality and the competition between them (Herrera, 2005). Complex reward partitioning and timing, together with rapid and repeated pollen presentation, probably ensure a high degree of outcrossing, even under interference from native (hummingbirds) and introduced (honeybees) nectar robbers, as in the system studied here.

9.6. Acknowledgements

Funds provided for the field studies by Deutscher Akademischer Austauschdienst, Nachwuchsförderungsgesetz and botconsult GmbH are gratefully acknowledged. We also thank Joana Schulz and Franziska Weber (Freie Universität Berlin, Germany) for help with data collection. Comments on the manuscript by Peter K. Endress and one anonymous reviewer are gratefully acknowledged. The experiments comply with the current laws of the countries in which they were performed.

9.7. Literature

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10. Chilean *Mimulus* (Phrymaceae) – premating isolating mechanisms and floral ecology of flashy coloured Monkey flowers*

10.1. Introduction

The monkey-flower, *Mimulus*, is a subcosmopolitan genus of the family Phrymaceae, (Beardsley and Olmstead, 2002; Bremer et al., 2009; Olmstead et al., 2001). Grant (1924) subdivided *Mimulus* into two subgenera and ten sections. Some 150-200 species are known, most of them distributed in North America, the primary centre of diversity (ca. 75%; Beardsley and Olmstead, 2002). A second centre of diversity is found in Chile with ten species.

The phenotypic diverse genus *Mimulus* has been used for the past decade as a model system for investigations into e.g. speciation genetics (Bleiweiss, 2001; Bradshaw et al., 1995; Sweigart et al., 2006), the evolution of mating systems (Willis, 1993; Leclerc-Potvin and Ritland, 1994; Fishman et al., 2002; Sweigart and Willis, 2003), inbreeding depression (Carr and Dudash, 1996; Dudash and Carr, 1998; Marriage and Kelly, 2009; O'Halloran and Carr, 2010) and ecological adaptations (Angert and Schemske, 2005; Hall et al., 2010; Macnair, 1983). There are only few studies of South American *Mimulus*, primarily dealing with the *Mimulus luteus* complex from Chile, concentrating on flower colour and pollinator preferences (Medel et al., 2003; 2007; Botto-Mahan et al., 2004; Carvallo and Ginocchio, 2004; Cooley et al., 2008; 2011; Cooley and Willis, 2009).

Four of the Chilean species correspond to *Mimulus* sect. *Simiolus* Green and *M. bridgesii* to sect. *Paradanthus* Grant. The section *Simiolus* is divided in six species complexes, all distributed in the Americas. The Chilean taxa correspond to the *M. luteus* complex, characterized by yellow corolla with red spots and/or tetraploid chromosomes (e.g. *M. cupreus*, *M. depressus*, *M. luteus* and *M. naiandinus;* Vickery et al., 1968; Hughes and Vickery, 1974; Beardsley and Olmstead, 2002; Cooley et al., 2008; Cooley and Willis, 2009) and to the heteroploid *M. glabratus* complex (e.g. *M. glabratus*; Tai and Vickery, 1970; Alam and Vickery, 1973; Argue, 1981). The majority of these are self-compatible (Ritland and Ritland, 1989; Wu et al., 2008). Most taxa of sect. *Simiolus* are interfertile (Vickery, 1978) and autogamous. Chromosome counts indicate that numbers within the section are variable (Tab. 10.1; Tai and Vickery, 1970; Vickery,

*Manuscript in preparation; chapter included with the permission of the co-authors: Ackermann M, Karabascheva G, Martinez-Harms J, Weigend W. (in prep.). Chilean *Mimulus* (Phrymaceae) – premating isolating mechanisms and floral ecology of flashy coloured Monkey flowers.

Table 10.1. Sectional belonging, morphology, distribution, life cycle and chromosome number of investigated *Mimulus* taxa. Superscript belonging to literature as follows: 1 = Grant, 1924; 2 = Beardsley et al., 2004; 3 = Cooley et al., 2008; 4 = Tai and Vickery, 1970; 5 = Vickery, 1995; 6 = Cooley and Willis, 2009; 7 = Medel et al., 2007; 8 = Grant, 1993; 9 = Streisfeld and Kohn, 2007.

species	*M. bridgesii* Clos	*M. cupreus* Regel	*M. glabratus* A.Gray	*M. luteus* L.	*M. naiandinus* J.M.Watson & C. von Bohlen	*M. aridus* (Abrams) A.L. Grant	*M. aurantiacus* Curtis
section	*Paradanthus* Grant[1]	*Simiolus* Greene[2]	*Simiolus* Greene[2]	*Simiolus* Greene[2]	*Simiolus* Greene[3]	*Diplacus* Gray[2]	*Diplacus* Gray[2]
country	Chile	Chile	Chile	Chile	Chile	USA	USA
region	VII Region	VII Region	Region Metropolitana	Region Metropolitana	VII Region	California	California
locality	Pelarco, Libueno	Laguna Maule	La Parva	Embalse Yeso	Vilches Alto, El Morillo	San Diego	Los Angeles
elevation (m)	280-320	2300	1800-3200	1400-2900	1000-2000		
voucher	M. Weigend 9320	M. Weigend 9317	M. Weigend 9319	M. Weigend 9321	M. Weigend 9318	M. Weigend 9449	M. Weigend 9392
chromosome number	n = 46 (expacted[4])	n = 31[5]	n = 15, 30, 31, 46[5]	n = 30, 31, 32[5]	n = 32[6]	n = 10[5]	n = 10[5]
life cycle	annual	annual	annual	annual	annual	perennial	perennial
growth habit	decumbent to erect, up to 20 cm high	erect, 20-50 cm high	decumbent, up to 10 cm high	erect, 20-50 cm high	erect, 30-70 cm high	erect, 20-50 cm high	erect, up to 100 cm high
flower size	up to 2,5 cm	up to 4 cm	up to 2 cm	up to 5,5 cm	up to 7 cm	3,5 - 5,5 cm	4,0 - 5,5 cm
petals	cordate	emarginate	emarginate	emarginate	emarginate	rounded, sometimes slightly notched	unequal, upper ones cordate, margins undulate
flower colour	yellow	orange to red	yellow	yellow	lower lip white to pale pink, others parts pink	pale yellow	orange with white margins
nectar guide	fance yellow with red spots	fance yellow	fance yellow with few red spots	fance yellow with few, red spots	fance pale yellow with pink spots	fance yellow	fance white and orange

1995; Cooley and Willis, 2009). All species share similar gross flower morphology (compare fig.10.1), with pentamerous, zygomorphic and hermaphroditic flowers with four anthers and superior, bilocular ovary with numerous ovules (Wu et al., 2008). However, corollas vary widely in colouration and size. The stigma is thigmonastic and bilobate (Newcombe, 1922). Fruits are epigynous and bearing amounts of seeds in bilocular capsules.

Due to the final geologically young uplift of the Andes (Miocene, Gregory-Wodzicki, 2000; Picard et al., 2008; Hoorn et al., 2010), the current distribution of the species is also influenced through migrations and ice ages. Several recent studies indicate that many Andean species groups are comparatively young (*Caiophora*: Ackermann et al., 2008; *Calceolaria*: Ehrhart 2000; Cosacov et al., 2009; *Lupinus*: Hughes and Eastwood, 2006; Clements et al., 2008; *Heliotropium*: Luebert et al., 2011; *Fuchsia*: Berry et al., 2004). Hybridization has been reported in some groups, especially in man-made areas with secondary contact of previously allopatric taxa (Molau, 1981, 1988; Ackermann et al., 2008).

In Chile a natural hybrid swarm is known of *M. luteus* and *M. naiandinus* and one between varieties of *M. luteus* (Carvallo and Ginocchio, 2004; Cooley et al., 2008). Cooley et al. (2008) cross-pollinated several species and subspecies out of the *M. luteus* group (*M. cupreus* x *M. luteus* var. *variegatus* and *M. luteus* var. *luteus* x *M. luteus* var. *variegatus*) and demonstrated that hybrids are fertile up to the F2 generation (Cooley, 2008; Cooley and Willis, 2009; Cooley et al., 2011). Another example is a cultivated, established hybrid in Scotland from *Mimulus luteus* x *M. cupreus*, known as *Mimulus* x *maculosus* W. Bull ex T. Moore (Stace et al., 2011). The occurrence of natural hybrids indicates that pre- and postzygotic barriers are weak or absent, at least in the three species involved. However, all three species concerned are morphologically similar in corolla size and have always been considered as very closely related.

Premating isolating mechanisms generally ensure that pollen is not transferred to the stigma (King and Brooks, 1947). The most common mode within the plant kingdom is pollination through animals. It is known, that both concentration and amount of nectar, but also accessibility of the flower are the main factors which do demand pollinator visits. As postulated before, quality and quantity of reward influences pollinator guilds (Baker and Baker, 1983; Nicolson, 2007 and lit. cited). In general terms, floral display correlates to nectar production between closely related taxa with smaller flowers producing less nectar than larger flowers (Spira, 1980; Galetto and Bernardello, 2004; Rebolledo R. et al., 2004; Kaczorowski et al., 2005). Additionally, biomass of the flower correlates with nectary size and can be used to predict nectar quantity within related taxa. With increasing biomass (and nectary size) nectar amount also increases (Weryszko-Chmielewska and Masierowska, 2003; Nicolson, 2007; Amela Garcia and Gottsberger, 2009).

For *Mimulus* a wide range of pollinators have been reported (Batalin, 1870; Grant, 1993; Vickery and Sutherland, 1994; Bradshaw et al., 1995; Medel et al., 2003; 2007; Botto-Mahan et al., 2004; Cooley et al., 2008) including hummingbirds, Hymenoptera (*Bombus, Centris, Corynura, Megachile, Melissoptila, Mesonychium*), Lepidoptera (*Argyrophorus,* *Faunula, Hylephila, Hyles, Tatochila, Vanessa, Yramea*) and Diptera (*Bombyliidae, Eristalis, Hypodinerus, Melanostoma*). While the different species do have variable floral displays as mentioned before, display size may correlate to nectar production; pollinators may distinguish species through visual signals and reward. Cooley et al. (2008) investigated colour preferences, nectar production and visitation rates of *Bombus dahlbomii* in Chile. They found out that within the natural hybrid swarm and their parental taxa (*M. luteus* x *M. naiandinus*) the main visitor *Bombus dahlbomii* does not have colour preferences in the parental taxa and their hybrid progeny. Furthermore, they also investigated pollinator visitation rates for *Mimulus cupreus*, of which a yellow and an orange morphotype are known. Cooley et al. (2008) showed that both morphotypes had much lower visitation rates of the common pollinator *Bombus dahlbomii* than observed for *M. luteus* in the same area. This proves that reward (tiny amounts of dilute nectar) or visual signals of *M. cupreus* are not attractive to *B. dahlbomii*. Cooley et al. (2008) found out that between the yellow morph and *M. luteus* no differences are found in visual attraction. UV reflectance, anthocyanin pigmentation and also corolla pigmentation is very similar to *M. luteus´s*. They also observed few Bombyliidae on *M. cupreus* flowers. Dinkel and Lunau (2001) postulate, that Diptera are also attracted by visual guide lines. This may explain the Bombyliidae visits on *M. cupreus* observed by Cooley et al. (2008), but not the large numbers of normally developed fruits.

Cruden (1977) investigated breeding systems based on the number of pollen and ovules produced per flower. The P/O-ratio calculated is used to classify breeding systems (cleistogamy 4.7±0.7, obligate autogamy 27.7±3.1, facultative autogamy 168.5±22.1, facultative xenogamy 796.6±87.7, and xenogamy 5859.2±936.5). Plitmann and Levin (1990) showed that in Polemoniaceae the P/O-ratios are generally higher (compare also Lindsey, 1982; Preston, 1986). Ritland and Ritland (1989) published P/O-ratios indicating, that seven of eight closely related, small flowered taxa in the North American *M. guttatus* complex are obligately autogamous and only one is cleistogamous.

Since the Chilean species differ widely in corolla colour, display size and observed pollinators, it is expected that they correspond to different breeding systems and pollination modes and if so, premating isolating mechanisms may exist.

The focus of this work lies on the reproductive isolating mechanisms of five Chilean *Mimulus* species out of different species complexes and sections. Therefore we investigated colour patterns, floral display size, nectar production and pollen/ovule-ratio (P/O-ratio), and compared then to published pollinator observations. Finally we cross-pollinated five species out of two different species groups and tested selfing ability and crossability. Two Californian monkey flowers (sect. *Diplacus*), reportedly pollinated by Sphingidae, were analyzed as reference for reward and P/O-ratio.

10.2. Materials and methods

Five Chilean *Mimulus* species (Phrymaceae, Scrophulariaceae s.l.) were chosen for this investigation. All material used in our study was collected in the wild (Tab. 10.1) and cultivation took place at the Institut für Biologie, Freie Universität Berlin, Germany, where the voucher were also deposited (BSB). All investigated Chilean species are morphologically differentiated through colour and size of their flowers (Tab. 10.1, fig. 10.1). Additionally, two Californian sphingophilous species (*M. aridus* and *M. aurantiacus*) were investigated as reference for nectar production, P/O-ratio and *M. aurantiacus* also for UV-patterns.

Seeds were sown out in standard soil for seedlings and later potted into clay pots with a mixture of compost and peat (2:1), fertilized with standard fertilizer (Garten- and Gemüsedünger, ASB Grünland, H. Aurenz GmbH) and basalt powder (Neudorffs Urgesteins Mehl®, W. Neudorff GmbH KG). Cultivation of the Chilean species took place from March to July 2010 and for the Californian species from January to April 2011, in the same greenhouse compartment und therefore under identical conditions (lighting, temperature, soil, pot size). To exclude artificial pollination by insects and wind, windows and doors were closed during the experiment.

UV-patterns

Flowers were evaluated with respect to their patterns of ultraviolet light (UV) reflectance. To this end UV exposures of whole flowers were taken, using a digital camera EOS 10D (Canon USA Inc., Lake Success, NY, USA) especially modified for this purpose. The camera in combination with a quartz lens (105 mm, UV-Nikkor, Nikon, Tokyo, Japan) and a filter (Baader Venus U-Filter, Baader Planetarium, Mammendorf, Germany) made it possible to expose the digital sensors of the camera to UV light only. The filter used consisted of a Schott UG11 substrate with dielectric coating which totally blocked wavelengths in the visible and infrared parts of the spectrum while transmitting light exclusively between 300 and 400 nm. Additionally photos were taken in the human-visible range.

As a proxy for floral display size, corolla and tube length were measured. Mean and standard deviation were calculated for each character and species.

Nectar production and floral size

The entire amount of nectar present in each flower was harvested by inserting micro-capillaries into the floral tube (micro capillaries: 1-µL Microcaps; Drummond Scientific Co., Broomall, PA, USA and 5-µL Duran Ringcaps; Hirschmann Laborgeräte, Eberstadt, Germany).

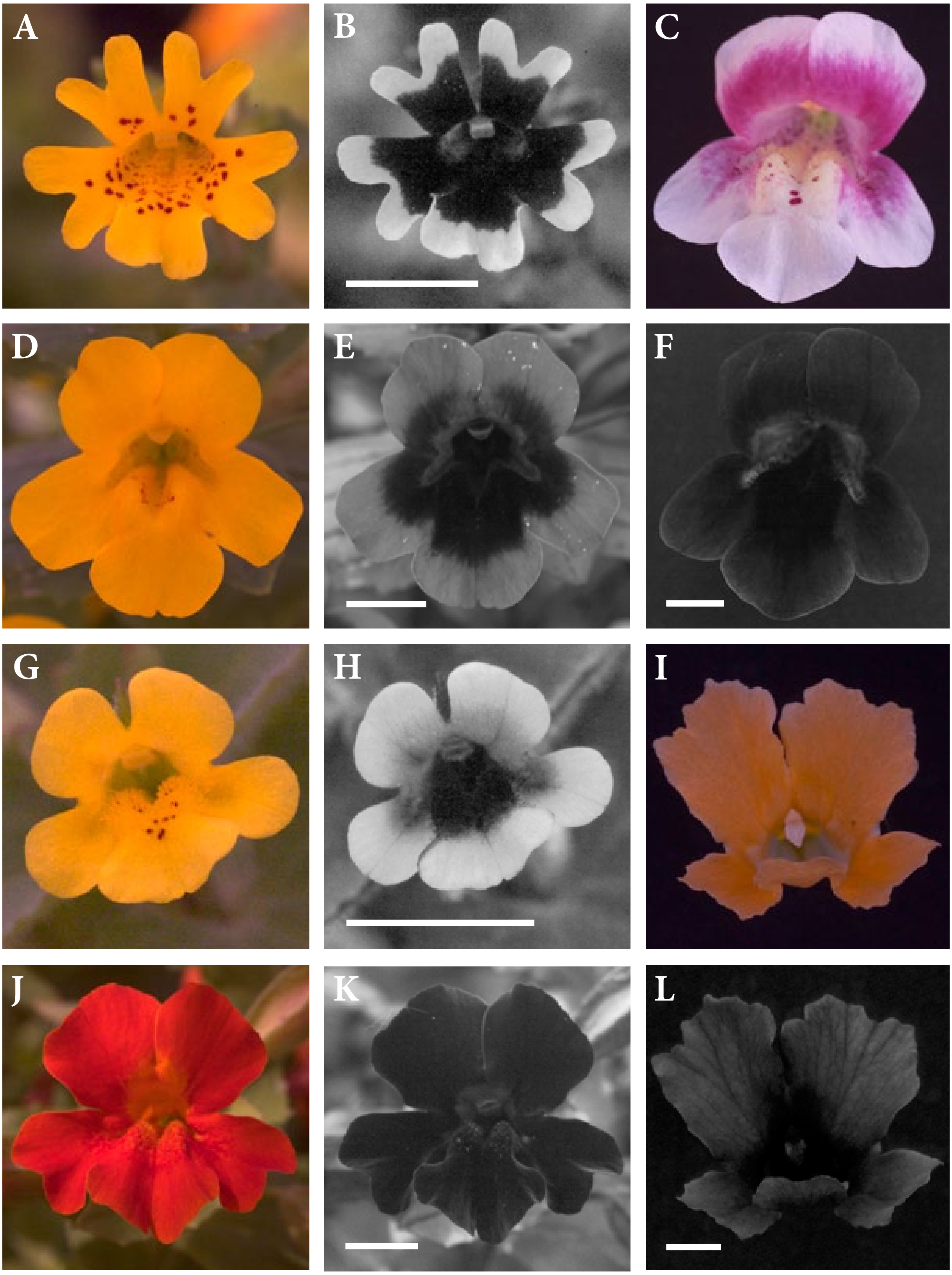

Fig. 10.1. Floral images in visible (VL) and ultraviolet light (UV). A-B: *Mimulus bridgesii*; C, F: *M. naiandinus*; D-E: *M. luteus*; G-H: *M. glabratus*; I-L: *M. aurantiacus*; J-K *M. cupreus*. [The UV-images (10.1 B, E, F, H, K, L) are transformed into black and white; scale bar corresponds to 1 cm].

We investigated nectar amount and concentration of five flowers per plant and from five individual plants per species. Brix measurements were taken with a handheld refractometer (neoLab-Handrefraktometer Universal; 10–80% Brix) and sugar amount was calculated. The relationship of nectar production from the investigated and reported species was plotted in a ternary graph (compare Ackermann and Weigend 2006 for details):

amount nectar : concentration : amount sugar = 100

Pollen number and Pollen-ovule ratio (P/O-ratio)

The stamens of ten flowers per species were cut off and all four stamens of a single flower were transferred into an Eppendorf tube. Flowers/anthers were used in an early ontogenetic phase when pollen sacs still were closed to ensure that all pollen grains were available. A mixture of 100 µl Glycerol [C3H5(OH)3] and 100 µl water were added to the dried stamens and then mixed for two minutes with a laboratory mixer mill (Retsch: MM 200). Afterwards the tubes were placed in an ultrasonic bath (Bandelin: Sonorex Rk 52) for another 15 minutes to ensure that all pollen grains were successfully separated from the anthers and evenly dispersed. Immediately before counting, the tubes were vortexed again. The number of pollen was counted using a Haemocytometer (Fuchs-Rosentahl counting chamber). In the glass microscope slide a chamber is engraved with a grid consisting of 16 squares of 1 mm² each. Five of these squares were chosen randomly before the first sample (20 µl of the solution) was transferred to the Haemocytometer. The volume of five squares is 1 µl. All pollen grains within the five squares were counted and the total number of pollen grains per flower calculated. Mean value and standard deviation were calculated. Ovules were counted using the same method. For calculation of the P/O-ratio the number of pollen grains/flower was divided through the number of ovules/flower (Cruden, 1977).

Experimental pollination

Experiments concerning breeding system, selfing- and crossing ability were carried out with five flowers each, from different plants for each treatment (Tab. 10.2). Pre-anthetic flower buds were carefully opened and emasculated to avoid self-pollination. The stigma is two-lobed and sensitive. Stigmatic receptivity is recognizable by the spreading of the stigmatic lobes. Lobes close again immediately after pollination (Dudash and Ritland, 1991; Fetscher and Kohn, 1999). As control five flowers/species were emasculated without pollination and five flowers/species were unmanipulated to test selfing ability. Hand pollination was carried out upon stigma receptivity and pollination success was controlled by checking the closure of the stigmatic lobes. Flowers were then marked with colour coded wire. Fruit set was recorded and

Table 10.2. Fruit formation of inter- and intraspecific crosses in *Mimulus* (first number represent capsules obtained, second number flowers pollinated; UM = unmanipulated; E= emasculated).

	M. bridgesii	*M. cupreus*	*M. glabratus*	*M. luteus*	*M. naiandinus*	UM	UM + E
M. bridgesii	5/5	5/5	5/5	5/5	5/5	5/5	0/5
M. cupreus	5/5	5/5	5/5	5/5	5/5	5/5	0/5
M. glabratus	5/5	5/5	5/5	5/5	5/5	5/5	0/5
M. luteus	5/5	5/5	5/5	5/5	5/5	5/5	0/5
M. naiandinus	5/5	5/5	5/5	5/5	5/5	5/5	0/5

mature capsules were harvested individually. Capsule maturity was recognizable by a colour change from green to brown ca. four weeks after pollination.

10.3. Results

Display size, visible and UV-patterns

The measured tube length of the flowers ranged from 1.15 to 5.15 cm and all over corolla length from 1.8-6.29 cm. Flowers of all Chilean species show different patterns of UV reflectance (Fig. 10.1). Apart from *M. aurantiacus*, the throat of all investigated species showed moderate UV reflectance. *Mimulus bridgesii*, *M. glabratus* and *M. luteus*, all with yellow corolla and with some red marks on the lower lip, show a dark UV-light absorbing region in the central part of the limb, whereas the distal, peripheral parts of the limb are UV reflecting. The UV reflecting and UV absorbing parts of the corolla are sharply delimited in *M. bridgesii*, but have a diffuse transition in *M. glabratus* and *M. luteus*. *M. cupreus* and *M. naiandinus* are UV-absorbing over the entire limb and only parts of the throat are UV reflecting. In *Mimulus cupreus*, the UV reflecting area of the throat appears yellow to the human eye, whereas all other parts of the corolla are orange. In white-pinkish flowers of *M. naiandinus*, the UV-reflecting part of the throat appears as a mixture of pale yellow, white and pink to the human eye. *Mimulus aurantiacus* reflects UV on the whole corolla limb and on the stigma.

Nectar production

Selfcompiled and investigated nectar data are tabulated in table 3. In our experiments two of the Chilean species (*M. bridgesii* and *M. cupreus*) contained only traces of nectar. The remaining species showed measurable amounts of nectar, with generally low concentrations

Table 10.3. Flower sizes, nectar production, pollen and ovule number and P/O-ratio (means and s.d.) of seven *Mimulus* taxa (N = number of measurements; n.d. = not detectable)

.

species	N	*M. bridgesii*	*M. cupreus*	*M. glabratus*	*M. luteus*	*M. naiandinus*	*M. aridus*	*M. aurantiacus*
Corolla-length (cm)	10	2.07 ± 0.26	3.86 ± 0.33	1.80 ± 0.13	4.84 ± 0.60	6.29 ± 0.61	6.08 ± 0.29	4.60 ± 0.33
Floral tube length (cm)	10	1.15 ± 0.14	1.91 ± 0.22	1.20 ± 0.09	3.03 ± 0.53	3.91 ± 0.36	5.15 ± 0.29	2.38 ± 0.12
Nectar volume (µl)	25	n.d.	n.d.	0.35 ± 0.14	3.34 ± 2.75	3.75 ± 1.96	11.83 ± 5.41	1.76 ± 0.81
Concentration (%)	25	n.d.	n.d.	11.50 ± 4.85	21.94 ± 10.60	22.72 ± 8.84	28.00 ± 4.45	38.85 ± 5.93
Sugar amount (mg)	calc.	n.d.	n.d.	0.04 ± 0.02	0.54 ± 0.27	0.70 ± 0.29	3.12 ± 1.04	0.67 ± 0.31
Pollen per flower	10	6050 ± 1319	30250 ± 9551	5741 ± 2425	66229 ± 20566	60029 ± 18206	41617 ± 18414	63286 ± 38216
Seeds per capsule	10	146.67 ± 64.75	144.17 ± 48.42	273.33 ± 124.72	76.82 ± 47.45	212.08 ± 138.6	139.46 ± 49.62	137.67 ± 19.76
P/O-ratio	calc.	41.25	209.82	21.00	862.13	283.05	298.42	459.69

(Chilean *Mimulus*: 11.5-22.72%, North American *Mimulus*: 28.00 resp. 38.85%). The amount of nectar ranges from 0.35-3.75 µl and the amount of sugar between 0.04-0.70 mg in the Chilean species and 1.76 resp. 11.83 µl and 0.67 resp. 3.12 mg in the North American species. Four main groups have been detected (Table 10.4. incl. published data): 1. flowers without or not detectable tiny amounts of nectar (*M. bridgesii*), 2. flowers producing small amounts of nectar and sugar (0.11-0,35 µl/flower, 0.01-0.04 mg/flower) in low concentrations (9-11.5%; *M. glabratus*, *M. cupreus*), 3. moderate amounts of nectar and sugar (1.07-3.75 µl/flower, 0.13-0.8 mg/flower) in low concentrations [(11-)20-50%; *M. aurantiacus, M. guttatus, M. lewisii, M. luteus, M. luteus x M. naiandinus, M. naiandinus*] and 4. large amounts of nectar and sugar (5,42- 50,78 µl/flower, 0,95-10,55 mg/flower) in low concentrations (17-28%; *M. aridus, M. cardinalis, M. eastwoodiae, M. nelsonii, M. rupestris, M. verbenaceus*).

The results achieved indicate that there is a positive correlation between nectar amount and floral display size. With increasing tube length the amount of nectar increases (Fig. 10.2; R2 = 0.8448; p < 0.0001), while correlation of overall corolla length and nectar amount is not significant (R2 = 0.4832; p = 0.0121).

P/O-ratio

Pollen numbers per flower range from 5,741 to 63,286 (Factor 11). The ovule number (76.82-212.08; factor 3.5) is less variable. The resulting P/O-ratios range from 21 to 862. Comparing the pollen and ovule production with floral display size, the small flowers of *M. glabratus* (1.20 cm tube length) produce the highest number of ovules (273) and the lowest

Table 10.4. Observed pollinators and nectar production of own investigated *Mimulus* taxa and data used from literature. Numbers (no.) correspond to numbering in ternary plot (literature data for pollinator observations: 1 = Grant 1993, 2 = Bradshaw et al. 1995, 3 = Vickery and Sutherland 1994, 4 = Cooley et al. 2008; 5 = Medel et al. 2003, 2007; 6 = Batalin 1870; for nectar production: 3 = Vickery and Sutherland 1994, 4 = Cooley et al. 2008; own data).

species	No.	nectar group	flower visitor	nectar volume (µl)	concentration (%)	sugar amount (mg)	cited in
M. aridus	1	4	Sphingidae	11,83 ± 5,41	28,00 ± 4,45	3,12 ± 1,04	1, own data
M. aurantiacus	2	3	Sphingidae (*Hyles lineate*)	1,76 ± 0,81	38,85 ± 5,93	0,67 ± 0,31	1, 2, own data
M. bridgesii	3	1		n.d.	n.d.	n.d.	own data
M. cardinalis	4	4	hummingbirds	50,78 ± 13,71	20,78 ± 3,54	10,55 ± 25,79	3
M. cupreus	5	2	*Bombus dahlbomii*, Bomiliidae	0,11 ± 0,032	9 ± 2,8	0,01 ± 0	4
M. eastwoodiae	6	4		6,41 ± 2,58	18,97 ± 7,27	1,22 ± 0,41	3
M. glabratus	7	2		0,35 ± 0,14	11,50 ± 4,85	0,04 ± 0,02	own data
M. guttatus	8	3	bees	1,27 ± 0,88	11,21 ± 3,91	0,13 ± 0,07	6, own data
M. luteus x *M. naiandinus*	9	3	*Bombus dahlbomii*,	1,6 ± 0,15	50,2 ± 2,4	0,8 ± 0,03	4
M. lewisii	10	3	*Bombus*	1,54 ± 0,81	33,05 ± 11,74	0,51 ± 0,02	2, 3
M. lewisii	11	3	*Bombus*	2,29 ± 3,52	13,72 ± 8,53	0,31 ± 0,05	2, 3
M. luteus	12	3	Apoidea (*Centris*, *Melissoptila*, *Megachile*, *Bombus dahlbomii*, *Mesonychium*, *Corynura*) Diptera (*Hypodinerus*, *Melanostoma*, *Eristalis*) Lepidoptera (*Hylephila*, *Yramea*, *Vanessa*, *Tatochila*, *Faunula*, *Argyrophorus*) hummingbirds	1,07 ± 0,11	20,43 ± 0,85	0,22 ± 0,01	4, 5,
M. luteus	13	3		3,34 ± 2,75	21,94 ± 10,60	0,54 ± 0,27	own data
M. l. var. *luteus*	14	3		1,7 ± 0,13	47,3 ± 1,9	0,8 ± 0,03	4
M. l. var. *variegatus*	15	3		1,7 ± 0,23	35,5 ± 1,97	0,6 ± 0,03	4
M. naiandinus	16	3	*Bombus dahlbomii*	3,75 ± 1,96	22,72 ± 8,84	0,70 ± 0,29	4, own data
M. nelsonii	17	4	hummingbirds	19,26 ± 9,44	17,92 ± 4,55	3,45 ± 3,71	3
M. rupestris	18	4	hummingbirds	5,42 ± 3,02	17,53 ± 7,64	0,95 ± 0,29	3
M. verhenaceus	19	4	hummingbirds	42,49 ± 13,67	17,32 ± 1,61	7,36 ± 18,05	3
M. nelsonii	17	4	hummingbirds	19,26 ± 9,44	17,92 ± 4,55	3,45 ± 3,71	3
M. rupestris	18	4	hummingbirds	5,42 ± 3,02	17,53 ± 7,64	0,95 ± 0,29	3
M. verhenaceus	19	4	hummingbirds	42,49 ± 13,67	17,32 ± 1,61	7,36 ± 18,05	3

number of pollen (5741) and consequently have the lowest P/O-ratios (21). Similar results are found in *M. bridgesii* (tube length: 1.15 cm, 6,050 pollen grains, 147 ovules and P/O-ratio: 41) but the ovule number is only half that of *M. glabratus*. The remaining five species do produce larger amounts of pollen (30,250-66,229, 5-11 times more) and only ≤ ¼ of ovules (77-212, tab. 10.3) and consequently its P/O ratio is higher, ranging from 209-862.

Experimental pollination

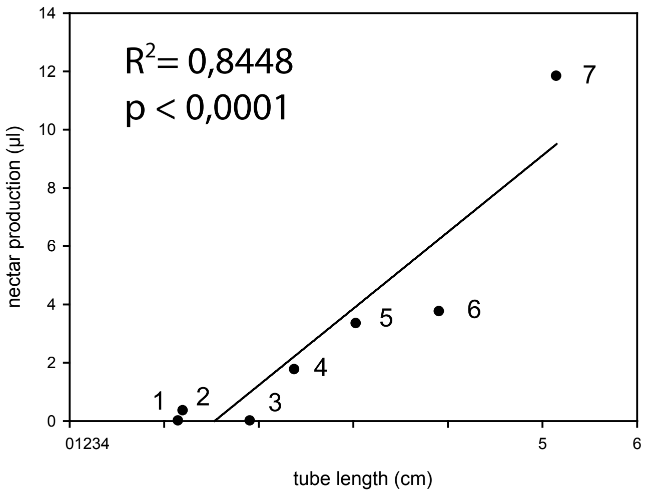

Fig. 10.2. Tube length plotted against nectar production, number corresponding to species in table 10.3.

All pollination treatments and the unmanipulated flowers resulted in full fruit set and morphologically normally developed seeds. The emasculated and non-pollinated flowers (negative control) showed no fruit set.

10.4. Discussion

UV-patterns

All *Mimulus* investigated showed UV-patterns. UV-patterns as well as its colouration in visible light differ among the investigated species. Especially in *M. luteus* and *M. naiandinus* the UV-patterns in the throat can be interpreted as nectar guides. Comparing UV-signals with flower size (compare fig. 10.1; flowers with scale bar), it is obvious that signals in larger flowers will be better perceived. In the case of orange-red *M. cupreus* flowers, UV-signals are weak, but several authors postulate that bees can recognize red flowers or can learn to recognize them (Kevan, 1983; Martinez-Harms et al., 2010; Rodriguez-Girones and Santamaria, 2004). Cooley et al. (2008) investigated colour preferences and visitation rates of *B. dahlbomii* within a natural hybrid swarm, their parental taxa (*M. luteus* and *M. naiandinus*) and a nearby *M. cupreus* population. Their results showed that *B. dahlbomii* prefers yellow flowers of *M. luteus* or the pink flowers of *M. naiandinus* as well as those of their hybrids (none with orange flowers) over the orange flowers of *M. cupreus*. These observations suggest that differences found in flowers reward or visual signals between *M. cupreus* and *M. luteus* might affect their attractiveness to insect pollinators. Previous reports about *M. luteus* have not revealed patterns of UV reflectance by their flowers. The here presented data suggest, that differences in flower colour between the yellow morphs of *M. cupreus* and *M. luteus* might exist. If this is the case, *B. dahlbomii* could learn to associate differences in the amount of reward with flowers colour, which in turns would explain the differences in visitation rate reported for *B. dahlbomii* on the flowers of these two species.

Nectar production

The investigated *Mimulus* taxa are morphologically well separated in floral size and display. Therefore it is not surprising that nectar production is different in concentration, nectar- and sugar amount. Literature data for *Mimulus* (Tab. 10.4, including own dataset) show that nectar production in hummingbird-pollinated species (and sphingophilous *M. aridus*) is high, whereas concentration is low, in contrast to mainly insect-pollinated species (and sphingophilous *M. aurantiacus*) where nectar concentration is either very low (9-11%) or moderate (20-50%). Published data indicates that bees in general do prefer highly concentrated nectar (e.g. Forcone et al., 1997, Ackermann and Weigend 2006; Nicolson, 2007 and lit. cited), but measurements of *Mimulus* nectar investigated elsewhere do show similar results in amount of nectar and also in concentration (Cooley et al., 2008; Medel et al., 2003).

Using the same system as Ackermann and Weigend (2006) two major groups can be detected in the ternary plot (Fig. 10.3): species of group 1 represent insect-pollinated taxa (subdivided in group II and III); group 2 (group IV in the ternary graph) only hummingbird-pollinated species and *Mimulus aridus*, pollinated by Sphingidae. Our results for nectar production, compared with observed pollinators (Tab. 10.4) do confirm that *M. luteus* and *M. naiandinus*, visited by *Bombus dahlbomii*, are located in group one. This group is postulated as mainly visited by short- and long-tongued bees (Ackermann and Weigend, 2006). Surprisingly two of the taxa with UV-patterns (*M. bridgesii* and *M. cupreus*) do not produce nectar or only very tiny amounts. It is postulated that UV-patterns attract pollinators (e.g. Lunau and Maier, 1995), but here it seems, that either pollinators are attracted by other characters or these species are selfing. Comparing proboscis length of *Bombus dahlbomii* of 9.86 mm (Rebolledo R. et al., 2004) with tube length of the Chilean *Mimulus* taxa, accessibility to the nectar seems to be limited by tube length. Only *M. glabratus*, *M. bridgesii* and *M. cupreus* show tube sizes in the range of the proboscis length. Flower shape, especially throat width (compare fig. 10.1), of the remaining taxa seem to be wide enough for Bombus to have access to the nectar. Pollinator frequencies confirm that (Cooley et al., 2008). *M. bridgesii* and *M. cupreus* did not show any nectar production in our experiment, but Cooley et al. (2008) have shown that *M. cupreus* produce 0.11 µl nectar with a concentration of 9% in cultivated plants in North Carolina, USA, similar to the nectar production observed in our *M. glabratus*, but certainly very low amounts and concentration for pollination by *B. dahlbomii*. Additionally, they observed a small number of Bombyliidae visiting *M. cupreus* flowers in Chile. Little is known about Bombyliidae preferences on nectar amount and concentration. Few authors report that amount is little, ranging from 0.05-0.7 µl (Armbruster et al., 2006; Gomez et al., 2008; Johnson and Dafni, 1998; Johnson and Midgley, 1997; Ortiz et al., 2000) and the concentration is between 35-42% (Ortiz et al., 2000). Regarding to our results, nectar concentration seems to be very low for Bombyliidae preferences. P/O-ratio, few observed Bomyliidae and full fruit set (Cooley et al., 2008) indicate, that *M. cupreus* is a self-pollinating species.

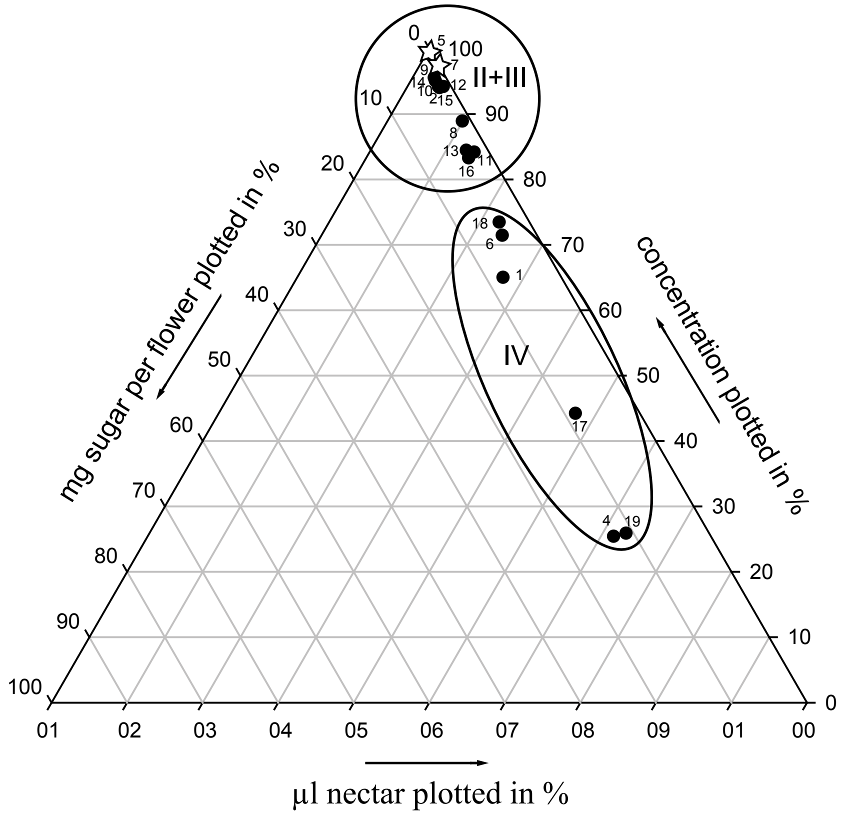

Fig. 10.3. Ternary plot illustrating the relationship between nectar production, sugar concentration and sugar production of Chilean *Mimulus* species and data obtained from literature. Numbering is corresponding to table 10.4. Group I: not included in the ternary plot - without nectar production. Group II: low amounts of nectar with low concentration (marked with asterisks; No. 5 and 7). Group III: moderate nectar amount with higher concentrations. Group IV: large amount of nectar with low concentration. Species out of group II and III are mainly insect pollinated and those of group IV hummingbird pollinated.

P/O-ratio

The five *Mimulus* taxa used for pollination experiments and also the two Californian taxa, used as additional reference for another pollination syndrome, differ in pollen- and ovule number and, as a conclusion, in P/O-ratio. Following the concept of Cruden (1977) that P/O-ratio increases with the degree of outcrossing (see also Charnov, 1979; Charlesworth and Charlesworth, 1981; Mazer and Delesalle, 1998) leads to the fact that *M. glabratus* and *M. bridgesii* are obligately autogamous, whereas *M. aridus*, *M. aurantiacus*, *M. cupreus* and *M. naiandinus* are facultatively autogamous and only *M. luteus* is facultatively xenogamous. The hybridization yielded full seed-sets (cross-pollinated and self-pollinated). This does support our results that within the investigated taxa obligate xenogamous species are missing (full seed set in unmanipulated flowers). In general, autogamous flowers are characterized by smaller flowers which are less open and do offer less reward than their xenogamous relatives (Sicard and Lenhard, 2011). There is a similar trend found in the taxa here investigated (compare flower sizes with P/O ratios tab. 3, fig. 10.1, 10.4), but the two species with the largest flowers (*M. aridus* and *M. naiandinus*) show lower P/O-ratios than the smaller flowered *M. luteus*. P/O-ratios found for *M. naiandinus* and *M. cupreus* are similar, but flower size and nectar production differ significantly. Only regarding the nectar and pollen production, *M. naiandinus* seems to be adapted to animal-pollination, whereas *M. cupreus* do not produce any nectar and only half of the pollen number. Flower colour and size, both together indicate possible animal pollination, as it was postulated before (Cooley et al., 2008; Cooley and Willis, 2009). *M. luteus*, with the highest pollen number is producing the lowest number of ovules, and *M. glabratus* show the reverse trend. *M. guttatus*, which is very similar in growth habitat and flower morphology to *M. luteus*, is supported as melittophilous (Batalin, 1870) and facultative xenogamous (Sutherland and Vickery, 1993; Willis, 1993; Fishman et al., 2001) and therefore we assume that *M. luteus* is melittophilous, too, whereas Medel et al. (2007) observed a wide range of Hymenoptera, but also Diptera, Lepidoptera and one hummingbird species as visitor. Several studies about *M. luteus* do show, that nectar concentration, colour and size of nectar guides and corolla, differ between populations resp. subspecies (Medel et al., 2003, 2007; Cooley et al., 2008). Therefore it is likely that P/O-ratio may be different between local populations or morphotypes and may explain why some of the large flowered species do not produce higher P/O-ratios and higher nectar amounts.

Experimental pollination

All cross-pollinated combinations led to full fruit set, except emasculated and unmanipulated flowers (negative control). Regarding the chromosome counts (Tai and Vickery, 1970; Vickery,

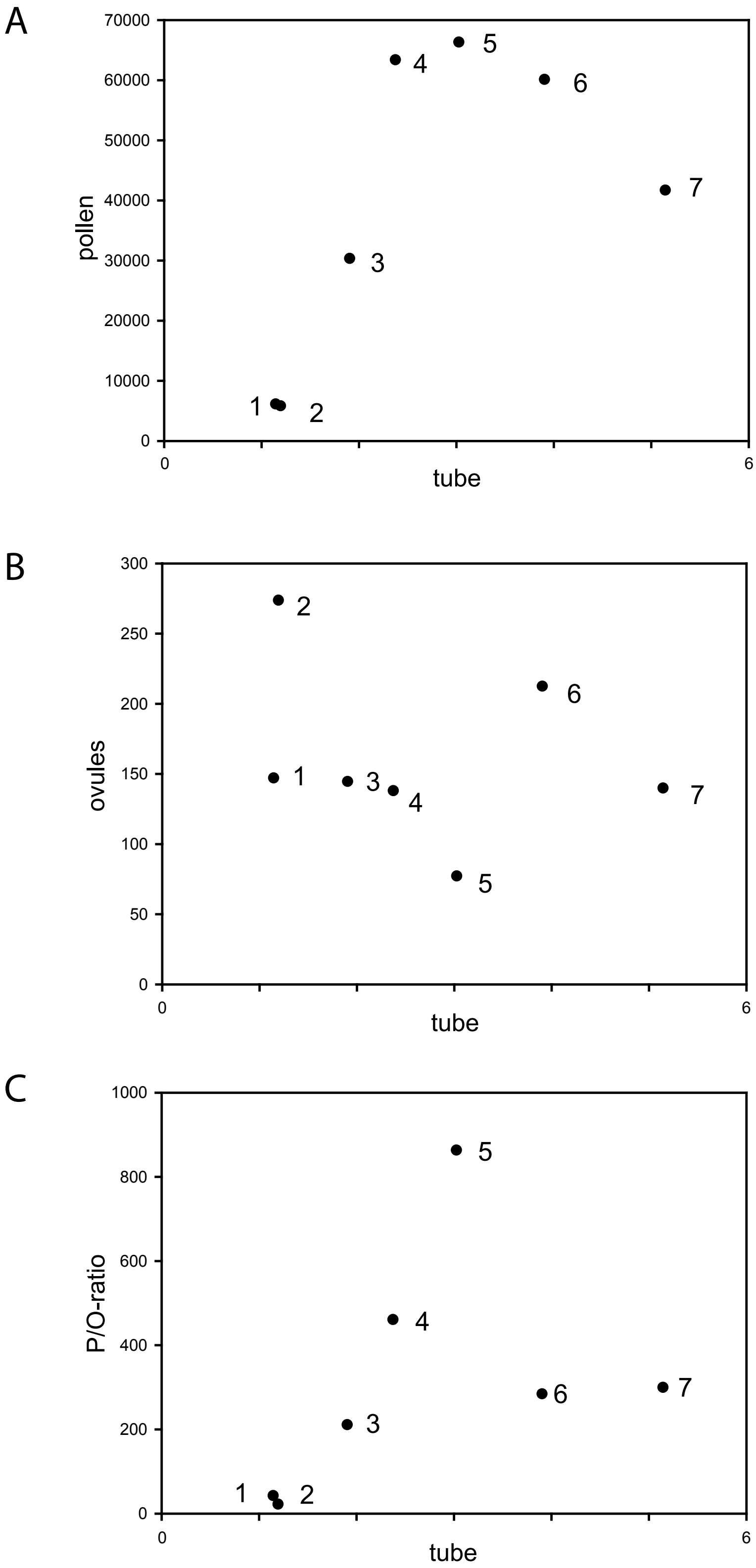

Fig. 10.4. A: Scatter plot of tube length and pollen number, B: Scatter plot of tube length and ovule number, C: Scatter plot of tube length and P/O-ratio (Numbering is corresponding to species in table 10.3).

1995; Cooley and Willis, 2009) it is surprising, that postzygotic barriers do not seem to exist, for at least some of the species. This is also substantiated by documented natural hybrids in literature (Carvallo and Ginocchio, 2004) and hybridization experiments (*M. luteus* var. *luteus* x *M. luteus* var. *variegatus* and. *M. cupreus* x *M. luteus* var. *variegatus*; Cooley and Willis, 2009)

The P/O-ratio of *M. cupreus* is low and it is classified as facultative autogamous (Cruden, 1977). Cooley et al. (2008) showed that both, the yellow and the orange morphotype of *M. cupreus* are developing lots of fruits filled with seeds. This raises the question if *M. cupreus* is always self-pollinated. Self-pollination in visual attractive plants for a pollinator is not unusual: Chen et al. (2009) observed in *Gesneria citrina*. a yellow, hummingbird pollinated species from Puerto Rico, elongation of the stamen in absence of pollinators, so that pollen can reach stigma height and self-pollinate. There are several other examples of self-fertilizing showy flowered taxa known (e.g. *Schizanthus*: Perez et al., 2009; *Datura*: Motten and Antonovics, 1992, both Solanaceae). Facultative selfing of attractive and reward producing species seems to be a plausible explanation if pollinators are infrequent. In our case, we do expect that the pollinator *B. dahlbomii* does have preferences in amount and concentration of nectar and UV-patterns allow differentiation within the species (compare Cooley et al. 2008, low visitation frequency and low nectar production in *M. cupreus*). But maybe the few observed visits on *M. cupreus* flowers (with successful pollination?) can be enough to exchange genetic information, which does prevent inbreeding depression.

10.5. Conclusions

Nectar production data of the investigated taxa and those obtained from literature are different in amount and concentration. Tube length and nectar amount do correlate with our data set, as far as nectar was produced, and could be used to estimate nectar production. Two major pollinator groups can be found – one comprising species pollinated by hummingbirds and one by bees. The bee group is divided in two subgroups – one with low amounts of nectar and low nectar concentration and the other one with moderate amounts of nectar and manifested higher nectar concentration. The remaining taxa do not belong to one of the postulated pollinator groups, since they do not produce nectar. The Chilean taxa differ in floral colour, size and UV-patterns. The observed pollinator *Bombus dahlbomii* does show preferences in colours and UV-patterns and was observed visiting flowers with nectar concentrations of 20-50%. Therefore it is not surprising that in co-occurring populations of *Mimulus luteus*, *M. naiandinus* and *M. cupreus* hybrids of sympatric taxa, with similar nectar production and UV-patterns can be found (*M. luteus* x *M. naiandinus*). The pollen/ovule-ratio indicates that species tested are facultative or obligate autogamous, except *M. luteus* which is facultatively xenogamous. Species with small flowers are obligately autogamous and with increasing flower size the P/O-ratio tends to increase, too. Our observations indicate that self-fertilization in *M. aurantiacus* and *M. aridus* (sect *Diplacus*) do not occur whereas the tested selfing ability of *M. luteus* (sect *Simiolus*) has produced positive results. Members of *M. luteus*- and *M. glabratus*-complex can easily be cross-fertilized within and among the species complexes. The fruit set, filled with seeds indicates that postzygotic isolating mechanisms do not exist, but occurrence of only few known natural hybrids demonstrate that premating barriers, especially nectar and colour preferences of *B. dahlbomii* must exist. Literature data confirm that, because only a single natural hybrids swarm of interspecific taxa has been observed (Cooley et al., 2008).

10.6. Literature

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11. Conclusions

11.1. Morphology, Taxonomy and Systematics

The genus *Caiophora* belongs to Loasaceae subfam Loasoideae. The relatives of *Caiophora* are found in the so called “South Andean *Loasa*” group comprising, besides *Caiophora*, the genera *Blumenbachia*, *Loasa* s.str. and *Scyphanthus* (Chapter 2). Several morphological characters confirm this close affinity (compare S*cyphanthus* and *Caiophora* flowers and nectar scales in figs. 1.4 A-F and seed morphology in chapter 6). A well resolved phylogeny is not available, but the close relationship of the “South Andean Loasa” group was confirmed by recent investigations (Hufford et al., 2005; Achatz, 2008; Schulz, 2009).

All representatives of the “South Andean *Loasa*” group are characterized by the absence of metatopia in the inflorescence, which is found in its sister clade with the remaining Loaseae (Fig. 2.7). Within “South Andean *Loasa*”, the missing double arch on the floral scales of *Blumenbachia* separates it from the remaining genera of this informal group. This clade is not well supported, but several morphological characters allow distinguishing series within *Loasa* s.str. Three *Loasa* series, *L.* ser *Acaulis*, *L.* ser. *Pinnatae*, *L.* ser. *Volubiles*, morphologically form a monophyletic group along with *Caiophora* and *Scyphanthus* (Fig. 2.7). Here exact placement of the *Loasa* series remains uncertain, but Achatz (2008) demonstrated that *L.* ser. *Acaulis* and *L.* ser. *Volubiles* are sister to each other and these are sister to *L.* ser. *Pinnatae* and all of them are sister to *Scyphanthus* and *Caiophora*. All investigated members out of *L.* ser*. Acaulis*, *L.* ser. *Pinnatae*, *L.* ser. *Volubiles*, *Caiophora* and *Scyphanthus* are characterized by a secondary sculpturing on the inner periclinal walls (Chapter 6). Taxa belonging to the three *Loasa* series have short petiolated, pinnatifid (to pinnate, bipinnate or bipinnatisect) leaves, and petals with serrate margins (Figs. 2.3 B, D), which also are to be found in S*cyphanthus* and some *Caiophora* species. Their seeds are morphologically very similar to each other and are adapted to wind dispersal (Chapter 6). Several morphological characters support the close relationship of *Caiophora* and *Scyphanthus* (e.g. fruit is opening with longitudinal sutures and/or apical valves, nectar scales with dorsal filaments arising immediately above the double arch if present, leaves pinnate to bipinnatisect, dichasial anthocladal inflorescences with opposite pairs of frondose bracts; compare chapter 2). Especially species out of the *Caiophora pterosperma*-group (*C. stenocarpa* and *C. pterosperma*) show similar morphological characters compared with its sister genus *Scyphanthus* (Figs. 1.4 A, B, D-F; multicoloured nectar scales, petal margins serrate, pinnatifida resp. pinnatisect leaves, etc.).

The distribution of the genera is overlapping in the southern range of *Caiophora* in Central Chile (Fig. 1.1 C). The morphologically most primitive group within *Blumenbachia* (*B.* sect.

Angulatae) is endemic to the southern Andes. The *Loasa* series (*L.* ser *Acaulis*, *L.* ser. *Pinnatae*, *L.* ser. *Volubiles*) are mostly distributed in Patagonia. The latitudinal distribution of *Scyphanthus* overlaps with the southern limit of *Caiophora* in mediterranean Chile (Fig. 1.1). It can therefore be suggested that the "South Andean *Loasa*" clade originated in the mediterranean and the temperate regions of Chile. The most primitive taxa of *Caiophora*, similar in their morphology to *L.* ser. *Pinnatae* and to *Scyphanthus*, are distributed in Brazil/Uruguay (*C. arechavaletae*), in Argentina (*C. nivalis*, *C. pulchella*) and Peru (*C. pterosperma*-group). It is expected that the group evolved in mediterranean resp. temperate South America and *Caiophora* migrated with the uplift of the Andes to the north and radiated there.

Caiophora comprises around 35 described and accepted species and one subspecies, some of them endemic to small areas (Chapter 3, 4 and 5; Weigend, 1996; Rodríguez and Weigend, 2007). In general, species out of the genus *Caiophora* are mostly distributed at high elevations of the Andes ranging from south-central Ecuador to central Argentina and Chile. Several taxa are still undescribed. In chapter 3 the representatives of *Caiophora* from Chile were revised and based on the material studied, one new species was described as *Caiophora deserticola* Weigend & Mark.Ackermann (Figs. 3.6 and 3.7), a sub-shrub distributed in northern Chile and southern Peru. Today, five species are known to Chile: *C. chuquitensis*, *C. cirsiifolia*, *C. coronata*, *C. deserticola* and *C. rosulata*. All of them are also distributed in neighbouring countries. *Caiophora superba* and *C. macrocarpa* were placed in synonymy of *C. chuquitensis*, and *C. rahmerii* was placed in synonymy of *C. rosulata* subsp. *rosulata*, which occurs only on the western slopes of the Andes. The status of its close relative *C. taraxacoides* was changed to *C. rosulata* subsp. *taraxacoides*. The clarification of species limits and their distribution in Chile was the basis of the treatment of both the Checklist of the Southern Cone (Chapter 4) and the Checklist of Bolivia (Chapter 5). The large number of herbarium specimens revised allowed a delimitation of the species and evaluation of their distribution patterns. Both checklists provide for the first time a list of known Loasaceae species for the whole area, including synonyms, altitudinal distribution and general information about growth habit.

11.2. Floral ecology and hybridization

Species of Loasaceae, and to a lesser extent of *Mimulus*, are divergent in floral morphology. Especially in Loasoideae there are many brightly coloured species, differing in flower size, -shape and -functionality. The wide range of differences in floral morphology and observed pollinators, as well as the very few known natural hybrids indicate that isolating mechanisms do exist. A large part of this dissertation focuses on pollinator preferences and their impact on reproductive biology (Chapter 8-10).

Reward is the major factor for plants to attract pollinators and to encourage flower visits. In general, it is expected that small flowers with low amounts of nectar will attract other pollinators than large flowers producing large amounts of nectar. Additionally, accessibility of reward and display size influence pollinators visits (Thomson et al., 2000; Perret et al., 2001; Beardsley et al., 2003; Castellanos et al., 2003; Wilson et al., 2004; Galliot et al., 2006; Nicolson, 2007; Smith et al., 2008; Smith, 2010). In Loasaceae flowers, nectar is secreted and accumulated into nectar scales (Chapter 8 and 9). With increasing flower size resp. petal length, nectar scale size is increasing, too. *Mimulus* taxa (Chapter 10) secrete and accumulate nectar at the base of the tube. As shown in figure 10.2 for *Mimulus*, nectar amount increases with increasing tube length. Flowers of Loasoideae taxa show a similar trend for the obtained groups: small flowers do produce tiny amounts of nectar and large flowers produce large amounts of nectar (compare petal length; table 8.1). Especially flower size limits accessibility to the reward, for example nectar hidden at the base of long floral tubes or nectar scales can only be accessed by legal pollinators with appropriate bill or tongue length.

All Loasoideae species so far investigated and most of the Chilean *Mimulus* produce measurable nectar amounts and are thus attractive for many pollinators. Differences in the amounts of nectar and sugar offered as well as nectar concentrations are indicating attractiveness to different pollinator guilds (Chapter 8 and 10). Several studies about nectar production of closely related taxa largely confirm, that amount of reward and concentration is similar for the same pollinator guild and different between pollinator guilds (Thomson et al., 2000; Ando et al., 2001; Perret et al., 2001; Beardsley et al., 2003; Galliot et al., 2006; Smith and Baum, 2006; Smith et al., 2008; Goldberg, 2009; Agostini et al., 2011). To visualize the differences in nectar production, amount of nectar and sugar as well as nectar concentration measurements are transformed and plotted in a ternary graph. This method was here used for the first time to evaluate differences in nectar quality and quantity between closely related taxa under pollinator exclusion. The grouping based on nectar characters corresponds to different pollinator guilds (Figs. 8.1 and 10.3; short-tongued and long-tongued bees, hummingbirds and rodents) with different energetic requirements (compare Nicolson, 2007 and literature cited). Evaluation of the phylogenetic relationships of the species studied in Loasoideae indicates several shifts from bee- to hummingbird pollination. There are several samples known in literature with similar shifts between closely related species from bee to hummingbird pollination and it is expected, that reward (in general nectar), accessibility to the nectar (e.g. tube length, corolla shape) can act as an isolating mechanism for sympatric species (Kay and Schemske, 2003; Castellanos et al., 2004; Kay et al., 2005; Wilson et al., 2006; Whittall and Hodges, 2007; Thomson and Wilson, 2008; Kay and Sargent, 2009; Schlumpberger, 2011; Wester and Classen-Bockhoff, 2011).

Pollen is the second factor playing a role in attracting pollinators. In *Nasa macrothyrsa* reward presentation is a continuous process, in the number of anther (amount of pollen) presented as well as in the amount of nectar secreted (Chapter 9). In natural systems standing crop values of flowers from the same plant are varying, influenced by previous pollinator visits and different flower ages. Pollinators are generally offered a small amount of reward (nectar and pollen), which makes a visit worthwhile. The pollen presentation theory explains this behaviour: offering always small amounts of pollen supports, that shortly after a previously visit other pollinators will come and find nothing or little nectar and pollen and are more likely to move on to another plant (Lloyd and Yates, 1982; Harder and Thomson, 1989; Thomson, 2003; Castellanos et al., 2006). It therefore is important that the total amount of reward presented is sufficient to satisfy the energetic need of the pollinator, if that is not the case the pollinator will move to other species. After each visit the pollinator is dusted with pollen and is carrying the pollen load from plant to plant. This will increase outcrossing and the potential fitness of the population.

Based on molecular and taxonomical studies more and more hybrids have been detected in the Andes (e.g. Berry, 1982; Molau, 1988; Smith and Baum, 2006; Cooley et al., 2008). For *Caiophora* several man-made hybrids are known in nature (Chapter 7). Along with the construction of new roads, seeds can be accidentally dispersed and established (see Chapter 6: light, wind dispersed *Caiophora* seeds). Through these changes in distribution patterns, species can come in secondary contact with other species sharing the same pollination syndrome. Pollinators do not distinguish between species if reward is in their preferred range, as is the case of eco-geographically isolated *Caiophora chuquitensis* and *C. carduifolia* in Peru. For both species nectar production is high (>50µl) and nectar concentration is in the range of hummingbirds (30-35 %), the legal pollinator for both. Exactly for these two species a hybrid is known, growing along roadsides and indicating that prezygotic and/or postzygotic isolating mechanisms are not fully developed.

The hybridization experiment presented demonstrates that postmating isolating mechanism do not exist, neither in *Caiophora* nor in *Mimulus* (Chapter 7 and 10). Germination rates of the hybrid seeds confirm the lack of any hybridization barriers in *Caiophora*. Additional unpublished data show for both genera, that the F1 generation is also viable and fertile. This suggests that natural hybrid swarms can establish themselves. Nevertheless, the low numbers of hybrids observed in nature, for both *Caiophora* and *Mimulus*, indicates that at least some degree of premating isolating mechanism must exist, while hybridization seems to be a rare event in the investigated taxa and that most of the species are normally allopatric (Chapter 7 and 10).

Nectar production demonstrates that at least in *Caiophora cirsiifolia* several populations differ in floral morphology, amount of nectar and sugar and nectar concentration and thus attract different pollinators (Chapter 8). Recent observations by T. Henning (pers. comm.) confirm the assumption, that the northernmost populations of *C. cirsiifolia*, producing large amounts of nectar, are visited by hummingbirds, while morpho- and ecologically different populations southwards are visited by bees. If individuals of these populations come in secondary contact, pollinators can separate them through their nectar preferences (prezygotic isolation). In *Mimulus* it was shown that experimentally obtained F2-hybrids from *M. lewisii* (bee pollinated, producing small amounts of nectar) and *M. cardinalis* (hummingbird pollinated, producing large amounts of nectar) differ in their nectar production (low up to large amounts of nectar) and their concentration of petal anthocyanins and petal carotenoids. Individuals with large amounts of nectar (compared to parental bee-pollinated *M. lewisii*) are more likely to be visited by hummingbirds than those with low amounts (Schemske and Bradshaw, 1999). Similarly to that increasing petal anthocyanins and petal carotenoids decrease bee visitation rate, too. Reward and visual signal are isolating the individuals of the hybrid swarm.

Similar results of hybridization experiments and nectar investigations in *Caiophora* and *Mimulus* (Chapter 7 and 10) indicate that pollinators are attracted by species with bright coloured flowers, through both visual signal and the quality and quantity of the reward. Being outside of the preference range of the pollinator would lead to discrimination and thus to a reproductive disadvantage (compare Schemske and Bradshaw, 1999; Beardsley et al., 2003; Bradshaw and Schemske, 2003). If isolation is incomplete and reward of both putative parental taxa is in the preference range of the pollinator, hybridization may be expected.

Comparing the altitudinal distribution of *Caiophora*, generally above 2500 m a.s.l. with the calculated age of 10 mya of the high Andes (Gregory-Wodzicki, 2000; Garzione et al., 2008; Picard et al., 2008; Hoorn et al., 2010), it may be assumed that adaptation to high-elevation habitats occurred recently. Additionally, all related genera are distributed in southern South America. Migrations in the Andes may have been common during the Pliocene and Pleistocene. It can be assumed that *Caiophora* originated in the temperate resp. mediterranean region of Chile/Argentina and migrated recently northwards. It is expected that diversification took place in high elevations of the Central Andes, where for example all of the morphotypes of *Caiophora carduifolia* (South to Central Peru) and *C. cirsiifolia* (Central Peru) are distributed. Similar migration trends from the South northwards are found for example in *Calceolaria* (Cosacov et al., 2009). The wide range of morphospecies e.g. within *C. carduifolia* and *C. cirsiifolia*, the absence of a postzygotic isolating mechanism and the young age of the high Andes, where *Caiophora* is distributed, leads to the conclusion that *Caiophora* radiated recently as shown for other species (Pennington et al., 2010; Särkinen et al., in press).

Especially in the High Andes were accessibility was precarious and development started only recently, eco-geographical isolation of previously allopatric species is being disturbed. Through man-made secondary contact, previously allopatric species sharing the same pollinator come in contact and hybridization can take place.

Some questions are answered, but some still remain open and will be addressed to future work. First of all, for *Caiophora* new species are to be described. A revision, comprising all species is needed. Further on it has to be clarified with molecular techniques, how the genera within the Loasoideae are related. There are many data, morphological, anatomical and ecological, which need to be discussed and interpreted in a phylogenetic context.

Within Loasoideae some pollinator shifts are known and indication of ancestral condition is difficult. Molecular studies may facilitate interpretation. Hybridization and pre- and postmating isolating mechanism are still of interest, especially for taxa in *Caiophora*, sharing morphological characters with *Scyphanthus*, which are expected as ancestral species. It will be fascinating to investigate pre- and/or postmating isolating mechanisms among the genera.

11.3. Literature

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Summary

The genus *Caiophora* belongs to Loasaceae subfam. Loasoideae. The species are mainly distributed in high elevations of the Andes. Their distribution ranges from Chile/Argentina up to southern Ecuador and from 2500 up to 5000 m a.s.l. Around 50 species are known, some of them endemic to small areas.

In Chapter 2 a preliminary phylogeny of the genera and lineages of Loasaceae subfam. Loasoideae is provided. All genera and infrageneric entities are included in the analysis, using the plastid trnl(UAA) intron. The resulting phylogeny is used as basis for inferring hypothetical relationships within subfam. Loasoideae, the possible morphological apomorphies are mapped onto a cladogram. The closest relatives of *Caiophora* are taxa from the so called "South Andean *Loasa*" clade. Besides *Caiophora* the clade comprises the genera *Blumenbachia*, *Loasa* s.str. and *Scyphanthus.* Their close relationship is corroborated by several morphological characters. Their geographical distribution overlaps in mediterranean Chile. It is expected that the "South Andean *Loasa*" clade evolved in mediterranean resp. temperate South America and *Caiophora* migrated with the uplift of the Andes to the North and radiated there.

The first revision of the Chilean *Caiophora* taxa is provided in chapter 3. *Caiophora deserticola* Weigend & Mark.Ackermann was described as a new species for science and several names were placed in synonymy. A key, full morphological description, distribution, notes about ecology, chromosome numbers and illustrations are given for all Chilean representatives.

In chapter 4 and 5 checklists for Loasaceae genera and species from southern South America are presented. Based on revised herbarium specimens and analysed literature, synonyms, habitat, elevational distribution, occurrence in countries and their departments are given for all investigated taxa. In Chapter 4 seven genera and 67 species are recognized for Argentina, southern Brazil, Chile, Paraguay and Uruguay, 48 of them are endemic in the area and one species is introduced. In Chapter 5 five genera and 27 species are reported for Bolivia; four of them are endemic.

Morphology of seed surfaces and seed anatomy are explored in Chapter 6 for all genera belonging to the "South Andean *Loasa*" clade. Representatives of *Scyphanthus*, from nearly all sections of the genera *Blumenbachia* and *Loasa* and from all informal species groups of *Caiophora* are analysed. SEM and light microscopy are used to analyse seed morphology and anatomy. Seed characters are compared for affinities within and between lineages. Dispersal mechanisms, as well as seed morphology and -weight are discussed and mapped on a cladogram.

To test postmating isolating mechanisms, seven *Caiophora* species were cross-pollinated in 37 species combinations (Chapter 7). Flowers of species belonging to the same - but also among different - species groups were hand-pollinated. Developing fruits were counted and seeds weighed. Seeds were sown and their germination rate determined. The crossability index was calculated as a proxy for fitness. Germination rates and crossability indexes indicate that hybrid progeny of the F1-generation is viable and most of the combinations show higher fitness (crossability index >1) compared to their parental species. High fruit- and seed sets and germination rates of hybrid progeny clearly indicate that postmating isolating mechanisms in *Caiophora* fail.

Species belonging to Loasaceae are divergent in floral morphology. Flower size, -shape and -colour as well as flower functionality differ between the investigated genera and species. The wide range of morphological differences concerning flowers, observed pollinators belonging to Hymenoptera, Diptera, Lepidoptera, Trochilidae and Mammalia and only few documented hybrids indicate that taxa belonging to subfamily Loasoideae are ecologically isolated by pollinator preferences.

In chapter 8 nectar production of Loasaceae flowers from seven genera and 31 species was investigated. Nectar amount and its concentration were measured and sugar amount calculated. The obtained data were plotted in a ternary graph and compared to observed pollinators. Four differing pollination syndromes were classified based on nectar production and known pollinators. With increasing flower size, nectar and sugar amount increases too, and sugar concentration of the nectar is decreasing. As a consequence main pollinators are changing, corresponding to the postulated groups, from mainly short-tongued bees to long-tongued bees, to hummingbirds and finally to rodents and finches. It can be postulated that within Loasaceae subfam. Loasoideae shifts from bee- to hummingbird-pollination took place at least four times.

A complex reward partitioning in *Nasa macrothyrsa* was explored in chapter 9. Thigmonastic as well as triggered stamen movement were investigated. Numbers of moved stamen were counted for both treatments per time interval. Using the same time interval, nectar replenishment was measured repeatedly. Triggered stamen movement shows increased anther resp. pollen presentation compared to thigmonastic stamen movement, whereas nectar production is a continuous process. Frequent pollinator visits therefore increase the amount of pollen presented in natural habitats. Offering always little portions of reward, increases the probability of pollinator visits and ensures that with pollen dusted pollinators move on to other flowers. This pollinator behaviour will increase outcrossing and the potential fitness of the *N. macrothyrsa* population.

In chapters 7 and 9 it is shown that Loasoideae taxa are isolated through pollinator preferences. In chapter 10 isolating mechanisms were tested similarly for Andean *Mimulus* species. Five Chilean *Mimulus* species were investigated for nectar production, flower size and crossability, using the same methods as described before. Additionally, floral UV-patterns of

the taxa were compared. Nectar production is differing among the tested species and pollinator observations underline that preferences in nectar, flower size, flower colour and UV-patterns do exist. Fully developed fruits and seeds show that postmating isolating mechanisms fail and that the species are kept isolated by premating isolating mechanisms.

There is proof that within *Caiophora* and *Mimulus* postmating isolating mechanisms are not fully developed. In the Andes only few hybrids of both genera have been observed, most of them due to human impact. Pollinator preferences show, that in nature the species are kept apart through premating isolating mechanisms.

Zusammenfassung

Die Gattung *Caiophora* gehört zu den Loasaceae subfam. Loasoideae. Die Arten sind überwiegend in den Hochlagen der Anden verbreitet. Ihr Verbreitungsgebiet reicht von Zentralchile/Argentinien bis nach Südecuador und von 2500 bis 5000 m ü. M. Es gibt circa 50 Arten, einige von ihnen sind endemisch in kleinen Gebieten.

In Kapitel 2 wird eine vorläufige Phylogenie aller Gattungen und Abstammungslinien der Loasaceae subfam. Loasoideae vorgestellt. In die Analyse des trnl(UAA) Introns wurden alle Gattungen und infragenerischen Einheiten mit einbezogen. Die erhaltene Phylogenie wird als Grundlage verwendet, um auf ein hypothetisches Verwandtschaftsverhältnis innerhalb der Loasaceae subfam. Loasoideae zu schließen. Die möglichen morphologischen Apomorphien wurden in einem Kladogramm den entsprechenden Positionen zugeordnet. Die nächsten Verwandten von *Caiophora* sind Taxa aus dem so genannten “Südandinen *Loasa*” Verwandtschaftskreis. Neben *Caiophora* umfasst die Abstammungslinie die Gattungen *Blumenbachia*, *Loasa* s.str. und *Scyphanthus*. Ihr enges Verwandtschaftsverhältnis wird durch mehrere morphologische Merkmale bestätigt. Ihre geographische Verbreitung überlappt im mediterranen Chile. Es wird vermutet, dass die “Südandine *Loasa*” Klade im mediterranen bzw. gemäßigten Südamerika entstanden ist und *Caiophora* mit der Hebung der Anden nach Norden migrierte und dort radiierte.

Kapitel 3 ist die erste Revision der chilenischen *Caiophora* Arten. *Caiophora deserticola* Weigend & Mark.Ackermann wird hier als für die Wissenschaft neue Art beschrieben und einige Namen werden in die Synonymie verwiesen. Die Arbeit umfasst für alle chilenischen Arten einen Artenschlüssel, vollständige morphologische Beschreibungen, Bemerkungen zur Ökologie, Chromosomenzahlen und Abbildungen.

Kapitel 4 und 5 umfassen Checklisten für alle Loasaceae Gattungen und Arten des südlichen Südamerikas. Basierend auf revidiertem Herbarbelegen and analysierter Literatur, werden Synonyme, Standortangaben, Höhenverbreitung, Vorkommen in den einzelnen Ländern und Departments für alle untersuchten Arten angegeben. In Kapitel 4 werden sieben Gattungen und 67 Arten für Argentinien, Südbrasilien, Chile, Paraguay und Uruguay anerkannt, 48 davon sind im Gebiet endemisch und eine Art ist eingeschleppt. In Kapitel 5 werden fünf Gattungen und 27 Arten für Bolivien angegeben, vier davon endemisch.

Die Morphologie der Samenoberflächen und die Samenanatomie wurden für alle Gattungen des „Südandinen *Loasa*“ Verwandtschaftskreises in Kapitel 6 untersucht. Es wurden Vertreter von *Scyphanthus*, von nahezu allen Sektionen der Gattungen *Blumenbachia* und *Loasa*, sowie aus allen informalen *Caiophora* Artengruppen analysiert. Rasterelektronen- und Lichtmikroskopie wurden für die Analyse der Morphologie und Anatomie verwendet.

Samenmerkmale wurden zur Stützung der Verwandtschaftsverhältnisse innerhalb und zwischen den einzelnen Abstammungslinien verglichen. Ausbreitungsmechanismen, sowie Samenmorphologie und –gewicht werden diskutiert und in einem Kladogramm dargestellt.

Sieben *Caiophora* Arten wurden in Kapitel 7 auf postzygotische Isolationsmechanismen hin untersucht. Die einzelnen Arten wurden in 37 Kombinationen kreuzbestäubt. Blüten von Arten aus der gleichen, aber auch zwischen verschiedenen Artgruppen wurden dazu handbestäubt. Die sich entwickelten Früchte wurden gezählt, die Samen gewogen, danach ausgesät und anhand der sich entwickelten Sämlinge die Keimraten ermittelt. Als Maß der Fitness wurde der Kreuzbarkeitsindex kalkuliert. Keimraten und Kreuzbarkeitsindeces zeigen, dass die F1-Nachkommen lebensfähig sind und die meisten der Kombinationen eine höhere Fitness (Kreuzbarkeitsindex >1) als ihre Eltern aufweisen. Der hohe Frucht- und Samenansatz, sowie die Keimraten der Hybridnachkommen zeigen, dass postzygotische Isolationsmechanismen in *Caiophora* nicht entwickelt sind.

Arten der Loasaceae unterscheiden sich in ihrer Blütenmorphologie. Die untersuchten Gattungen und Arten unterscheiden sich in Blütengröße, -form und -farbe, sowie in ihrer Funktionalität. Die große Vielfalt an morphologischen Unterschieden bezüglich der Blüten, beobachteter Bestäuber (Hymenoptera, Diptera, Lepidoptera, Trochilidae und Mammalia) und wenige dokumentierte Hybriden deuten darauf hin, dass Taxa der Unterfamilie Loasoideae ökologisch durch Bestäuberpräferenzen isoliert sind.

Die Nektarproduktion von Loasaceae-Blüten aus sieben Gattungen und 31 Arten wurden in Kapitel 8 untersucht. Dazu wurde die Nektarmenge und deren Konzentration gemessen und die Zuckermenge errechnet. Die erhaltenen Daten wurden in einem Dreiecksdiagramm dargestellt und mit den beobachteten Bestäubern verglichen. Vier unterschiedliche Bestäubungssyndrome können, basierend auf Nektarproduktion und bekannten Bestäubern, unterschieden werden. Mit zunehmender Blütengröße nimmt auch die Nektar- und Zuckermenge zu, wohingegen die Zuckerkonzentration des Nektars abnimmt. Damit einhergehend kommt es zu einem Wechsel der Hauptbestäuber entsprechend der postulierten Gruppen von Kurzzungen-Bienen, zu Langzungen-Bienen, zu Kolibris und letztendlich zu Säugern und Finken. Es wird gezeigt, dass es innerhalb der Loasaceae subfam. Loasoideae mindestens viermal zu einer Entstehung der Kolibribestäubung kam, die aus Bienenbestäubung hervorgegangen ist.

Eine komplexe Aufteilung der Belohnung (Nahrung) wurde an *Nasa macrothyrsa* Blüten in Kapitel 9 untersucht. Dazu wurden thigmonastische sowie ausgelöste Staubblattbewegung erforscht. Die Anzahl der in das Zentrum gewanderten Staubblätter wurde für beide Behandlungen pro Zeitintervall gezählt. In den gleichen Zeitintervallen wurde die Nektarnachproduktion ermittelt. Die ausgelöste Staubblattbewegung weist, verglichen mit der thigmonastischen, ein erhöhtes Staubblatt- bzw. Pollenangebot auf, wohingegen die Nektarnachproduktion ein kontinuierlicher Prozess ist. Häufige Bestäuberbesucher lösen daher in der Natur ein erhöhtes Angebot an Pollen aus. Das ständige Angebot von kleinen Nahrungsportionen erhöht die Wahrscheinlichkeit wiederkehrender Bestäuberbesuche und stellt sicher, dass die mit Pollen bepackten Bestäuber zu anderen Blüten weiterziehen. Dieses Bestäuberverhalten erhöht die Wahrscheinlichkeit der Fremdbestäubung und die potentielle Fitness der *N. macrothyrsa* Population.

In Kapitel 7 und 9 wurde gezeigt, dass Loasaceae Taxa durch Bestäuberpräferenzen isoliert sind. In Kapitel 10 werden Isolationsmechanismen gleichermaßen für andine *Mimulus* Arten getestet. Fünf chilenische *Mimulus* Arten wurden auf ihre Nektarproduktion, Blütengröße und Kreuzbarkeit untersucht, unter Verwendung der bereits beschrieben Methoden. Zusätzlich wurden die UV-Muster der Blüten der einzelnen Arten verglichen. Die Nektarproduktion unterscheidet sich zwischen den untersuchten Arten und Bestäuberbeobachtungen zeigen, dass Präferenzen in Nektar, Blütengröße, -farbe und UV-Mustern existieren. Normal entwickelte Früchte und Samen bestätigen, dass postzygotische Isolationsmechanismen fehlen und die Arten durch präzygotische Isolationsmechanismen isoliert sind.

Es wurde bewiesen, dass innerhalb von *Caiophora* und *Mimulus* postzygotische Isolationsmechanismen nicht voll entwickelt sind. In den Anden wurden bisher nur wenige Hybriden der jeweiligen Gattungen gefunden, die meisten sind auf den Einfluss des Menschen zurückzuführen. Bestäuberpräferenzen zeigen, dass die Arten am natürlichen Standort durch präzygotische Isolationsmechanismen isoliert werden.

Contribution to Chapters

Chapter 2: Weigend M, Gottschling M, Hoot S, Ackermann M. 2004. A preliminary phylogeny of Loasaceae subfam. Loasoideae (Angiospermae: Cornales) based on trnL(UAA) sequence data, with consequences for systematics and historical biogeography. Organisms Diversity & Evolution 4: 73-90.

Own contribution: I performed parts of the investigation (SEM, LM) and wrote the corresponding parts of materials and methods and discussion.

Chapter 3: Ackermann M, Weigend M. 2007. Notes on the genus *Caiophora* (Loasoideae, Loasaceae) in Chile and neighbouring countries. Darwiniana (San Isidro) 45: 45-67.

Own contribution: Revision of literature and herbarium specimens, writing of the manuscript (together with M. Weigend).

Chapter 4: Weigend M, Grau J, Ackermann M. 2008. Loasaceae. In: Zuloaga FO, Morrone O, Belgrano MJ eds. Catalogue of the Vascular Plants of the Southern Cone (Argentina, Southern Brazil, Chile, Paraguay, and Uruguay). St. Louis, Mo., U.S.A., Missouri Botanical Garden Press.

Own contribution: Revision of literature and herbarium specimens (*Caiophora*), writing of the manuscript (together with M. Weigend).

Chapter 5: Weigend M, Ackermann M. forthc. Loasaceae. In: Jörgensen PM ed. The Catalogue of the Vascular Plants of Bolivia. St. Louis, Missouri Botanical Garden Press.

Own contribution: Revision of literature and herbarium specimens (*Caiophora*), writing of the manuscript (together with M. Weigend).

Chapter 6: Weigend M, Gröger A, Ackermann M. 2005. The seeds of Loasaceae subfam. Loasoideae (Cornales) II: Seed morphology of “South Andean Loasas” (*Loasa*, *Caiophora*, *Scyphanthus* and *Blumenbachia*). Flora 200: 569-591.

Own contribution: I performed parts of the investigation (SEM, LM) and wrote the corresponding parts of materials and methods and discussion.

Chapter 7: Ackermann M, Achatz M, Weigend M. 2008. Hybridization and crossability in *Caiophora* (Loasaceae subfam. Loasoideae): Are interfertile species and inbred populations results of a recent radiation? American Journal of Botany 95: 1109-1121.

Own contribution: Participation in study design (together with M. Weigend), experimental work (together with M. Achatz), revision of literature, performance of analysis and writing of manuscript.

Chapter 8: Ackermann M, Weigend M. 2006. Nectar, floral morphology and pollination syndrome in Loasaceae subfam. Loasoideae (Cornales). Annals of Botany 98: 503-514.

Own contribution: Study design (together with M. Weigend), experimental work, data analysis and writing of manuscript.

Chapter 9: Weigend M, Ackermann M, Henning T. 2010. Reloading the revolver - male fitness as a simple explanation for complex reward partitioning in *Nasa macrothyrsa* (Loasaceae, Cornales). Biological Journal of the Linnean Society 100: 124-131.

Own contributions: Performed part of the experiment (nectar production), writing of corresponding parts of material and methods, results and discussion.

Chapter 10: Ackermann M, Karabascheva G, Martinez-Harms J. Weigend M. (in prep.) Chilean *Mimulus* (Phrymaceae) – premating isolating mechanisms and floral ecology of flashy coloured Monkey flowers.

Own contributions: Study design (together with M. Weigend), experimental work (together with G. Karabascheva and J. Martinez-Harms), data analysis and writing of manuscript. (Chapter included with permission of the co-authors).

Curriculum Vitae

For reasons of data protection, the curriculum vitae is not included in the online version

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten

Publication List

Ackermann M, Weigend M. (in prep.) A revision of *Caiophora* (*Caiophora pterosperma*-group, Loasaceae) from Peru

Ackermann M, Karabascheva G, Martinez-Harms J, Weigend M. (in prep.) Chilean *Mimulus* (Phrymaceae) – premating isolating mechanisms and floral ecology of flashy coloured Monkey flowers.

Mittelbach M, Ackermann M, Hilger HH, Weigend M. (in prep.) Generalist flowers and the evolution of floral traits in an taxonomic and ecological context: A study on floral ecology of Boraginaceae.

Henning T, Ackermann M, Weigend M. (in prep.) Complex, but not cheap - floral rewards and floral behaviour in thigmonastic Loasaceae.

Müller-Doblies U, Ackermann M, Weigend M, Müller-Doblies D. (subm. 03.11.2010) De Liliifloris Notulae 9. The only hitherto known *Spiloxene* species (Hypoxidaceae) from Namibia is a new species, *Spiloxene etesionamibensis*, and a new *Spiloxene* species from Namaqualand (Northern Cape), *S. namaquana*. Feddes Repertorium.

Ackermann M. Pollination and reproductive system. In. Weigend M, Selvi F, Thomas DC, Hilger HH. (submitted 10.03.2010) Boraginaceae. In: Kadereit J. ed, The Families and Genera of the Vascular Plants X.

Weigend M, Ackermann M. (In press) Loasaceae. In: Jörgensen PM. Checklist of the Flora of Bolivia. Missouri Botanical Gardens Monographs.

Weigend M, Ackermann M, Henning T. (2010) Reloading the revolver – male fitness as a simple explanation for complex reward partitioning in *Nasa macrothyrsa* (Loasaceae, Cornales). Biological Journal of the Linnean Society 100 (1): 124-131.

Weigend M, Ackermann M, Grau J. (2008) Loasaceae. In: Zuloaga FO, Morrone O, Belgrano M. eds. Catalogue of the Vascular Plants of the Southern Cone (Argentina, Southern Brazil, Chile, Paraguay, and Uruguay). Monographs in Systematic Botany from the Missouri Botanical Garden 107: 2413-2424.

Ackermann M, Achatz M, Weigend M. (2008) Hybridization and crossability in *Caiophora* (Loasaceae subfam. Loasoideae): Are interfertile species and inbred populations results of a recent radiation? American Journal of Botany 95: 1109-1121.

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Mittelbach M, Ackermann M, Hilger HH, Weigend M. (2011) Buzz for pollen - buzz for nectar? Floral rewards in Boraginaceae. Abstract and talk. BioSystematics Berlin.

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Appendix

Appendix A. (Seed morphology of „South Andean Loasas")

Voucher specimens and herbaria where they are deposited, for abbreviations for infrageneric entities see Fig. 6.1 (codes: sem = scanning electron microscopy, tem = transission electron microscopy, lm = light microscopy; herbarium acronyms from Index Herbariorum; abbreviations for infrageneric groups: BlBl – *Blumenbachia* section *Blumenbachia*, BlGr – *Blumenbachia* section *Gripidea*, BlAn – *Blumenbachia* section *Angulatae*, LoDe – *Loasa* ser. *Deserticolae*, LoFl – *Loasa* ser. *Floribundae*, LoLo – *Loasa* ser. *Loasa*, LoMc – *Loasa* ser. *Macrospermae*, LoAc – *Loasa* ser. *Acaules*, LoMc – *Loasa* ser. *Volubiles*, LoPi – *Loasa* ser. *Pinnatae*, CaAr – *Caiophora arechavaletae* group, CaCh – *Caiophora chuquitensis* group, CaCi – *Caiophora cirsiifolia* group, CaLa – *Caiophora lateritia* group, CaCl – *Caiophora clavata* group, CaCa – *Caiophora carduifolia* group, CaNi – *Caiophora nivalis* group, CaCr – *Caiophora coronata* group, CaPt – *Caiophora pterosperma* group, CaCo – *Caiophora contorta* group).

Blumenbachia eichleri Urb. – BlGr – (sem) Schlindwein, 610 (TUEB);

Blumenbachia espigneira Gay – BlAn – (sem) Weigend et al., 6816 (BRCO, BSB, M, NY);

Blumenbachia exalata Weigend – BlGr – (sem) Camargo, 61809 (M); (sem) Sehnem, 3886 (B, M);

Blumenbachia hieronymii Urb. – BlBl – (lm, sem) Weigend, s.n. (KW_124, Bot. Garden München, M);

Blumenbachia insignis Schrad. – BlBl – (sem) Fabris, 2691 (M);

Blumenbachia latifolia Camb. – BlBl – (sem) Schlindwein, 495 (TUEB); (sem) Reineck & Czermack 9 (F);

Blumenbachia prietea Gay – BlAn – (lm) Weigend et al., 6879, (sem) Weigend et al., 6823 (BRCO, BSB, M, NY);

Blumenbachia silvestris Poepp. – BlAn – (sem) Bayer, 795 (M), (lm, sem) Weigend et al., 6999 (BRCO, BSB, M, NY), (sem) Weigend et al., s.n. (BSB);

Caiophora andina Urb. & Gilg – CaCh – (sem) Kraus, s.n. (M);

Caiophora arechavaletae (Urb.) Urb. & Gilg – CaAr – (sem) Schlindwein, 397 (TUEB);

Caiophora buraeavii Urb. & Gilg – CaLa – (sem) Kraus, s.n. (M);

Caiophora canarinoides (Lenne´ & C.Koch) Urb. & Gilg – CaLa – (sem) Ackermann, 375 (BSB, HUSA, M, USM);

Caiophora carduifolia K.Presl – CaCa – (sem) Weigend et al., 2000/326; (lm) Weigend et al., 5415 (BSB, HUT, M, USM);

Caiophora cernua (Griseb.) Urb. & Gilg – CaCl – (sem) Sleumer 37 (B);

Caiophora cirsiifolia K.Presl – CaCi – (sem) Weigend & Foerther, 97/797 (M, USM); (sem, tem) Weigend et al., 97/465 (M, USM); (sem) Weigend et al., 97/314 (M, USM); (sem) Weigend et al., 97/464 (M, USM); (lm) Dostert, 98/156 (M, USM);

Caiophora contorta (Desr.) K.Presl – CaCo – (sem) Weigend et al., 97/323 (M, USM);

Caiophora coronata (Arn.) Hook. & Arn. – CaCr – (sem) Ackermann, 123 (BSB, Herb. Ackermann);

Caiophora grandiflora (G.Don) Weigend & Mark.Ackermann – CaCo – (sem) Weigend & Dostert 97/31 (M, USM);

Caiophora madrequisa Killip – CaLa – (lm) M. & K. Weigend, 2000/240 (HUT, M, NY, USM); (sem) Ackermann, 356 (BSB, HUSA, M, USM), (sem) M. & K. Weigend, 2000/101 (M, NY, USM), (sem) M. & K. Weigend, 2000/301 (M, NY, USM);

Caiophora pentlandii (Graham) Loudon – CaCr – (sem) Weigend & Förther, 97/783 (M, USM);

Caiophora cf. *pterosperma* (Ruiz & Pav. ex G.Don) Urb. & Gilg – CaPt – (sem) Weigend et al., 5118 (BSB, HUT, M, USM); (lm) Weigend et al., 5484 (BSB, HUT, M, USM);

Caiophora pterosperma (Ruiz & Pav. ex G.Don) Urb. & Gilg – CaPt – (sem) Weigend & Dostert 97/29 (F, M, USM);

Caiophora pulchella Urb. & Gilg – CaNi – (sem) Cuezo & Barkley, s.n. anno, 1950 (W);

Caiophora scarlatina Urb. & Gilg – CaCh – (sem) M. & K. Weigend, 2000/108 (HUT, M, NY, USM);

Caiophora superba Phil. – CaCh – (sem) Weigend & Förther, 97/802 (F, M, USM);

Loasa acanthifolia Desr. – LoLo – (lm, sem) Weigend et al., 6924 (BRCO, BSB, M, NY);

Loasa acerifolia Domb. – LoMc – (sem) Weigend et al., 6848 (BRCO, BSB, M, NY);

Loasa artemisiifolia Poepp. – LoPi – (sem) Grau, 3055 (M);

Loasa asterias Dusen – LoPi – (sem, lm) Weigend, 6991 (BRCO, BSB, M);

Loasa bergii Hieron. – LoPi – (sem) Weigend et al., 6899 (BRCO, BSB, M);

Loasa elongata Phil. – LoDe – (sem) Rechinger & Rechinger, 63390 (M); (sem) Ackermann, 514 (BSB, CONC, M, SGO);

Loasa filicifolia Poepp. – LoPi – (sem) Weigend et al., 6933 (BRCO, M, NY);

Loasa floribunda Hook. & Arn. – LoFl – (sem) Montero, 296 (M);

Loasa gayana Urb. & Gilg – LoVo – (lm, sem) Weigend et al., 7057 (BSB, M);

Loasa heterophylla Hook. & Arn. – LoMc – (sem) Jiles, 6448 (M);

Loasa lateritia Gill. – LoAc – (sem) Grau, 3076 (M);

Loasa martinii Phil. – LoVo – (sem) Montero, 7905 (M);

Loasa micrantha Poepp. – LoVo – (sem) Po¨ ppig, s.n. (M);

Loasa nana Phil. – LoPi – (sem) Weigend et al., 7080 (BSB, M);

Loasa nitida Desr. – LoMc – (sem, tem) Weigend et al., 7346 (BSB, M); (sem, tem) Weigend et al., 2000/901 (BSB, HUT, M, USM);

Loasa pallida Gill. – LoFl – (sem) Bayer, 655 (M);

Loasa paradoxa Urb. & Gilg – LoPi – (sem) Sparre & Constance, 10897 (UC);

Loasa poeppigiana Urb. & Gilg – LoPi – (sem) Ricardi & Marticorena, 5099/1483 (CONC);

Loasa sigmoidea Urb. & Gilg – LoPi – (sem) – Marticorena & Matthei, 1039 (CONC);

Loasa urmenetae Phil. – LoDe – (sem) King, s.n. (SGO);

Loasa volubilis Domb. – LoPi – (sem) Gay, s.n. anno, 1839 (P);

Scyphanthus elegans D.Don – (sem) Grandjot, s.n. March, 1933 (M);

Scyphanthus stenocarpus Urb. – (sem) Buchtien, 361 (M); (sem) Aravena, 33318 (UC);

Appendix B (Hybridization and crossability in *Caiophora*)

Vouchers for accessions used for experimental crosses and for putative hybrids and corresponding parental taxa observed in the field (+ C = herbarium sheets from cultivated plants deposited in BSB; abbreviation after plant names author indicate department of origin in Peru).

C. andina Urb. & Gilg (AR): Peru, Depto. Arequipa, Prov. Arequipa, Distr. Chiguate, near the tunnel of Simbral, 4300 m a.s.l., S16° 22′ 48.4″ W071° 18′ 17.9″, 05.12.2006, M. Ackermann, E. Gonzales L. & F. Sinca C. 641+ C (BSB, HUSA, USM).

C. andina Urb. & Gilg (AY): Peru, Depto. Ayacucho, Prov. Huanta, road from Quinua to Tambo, 4300 m a.s.l., S12° 59′ W074° 05′, 19.02.2000, M. & K. Weigend 2000/374 (HUSA, M, NY, USM).

C. andina Urb. & Gilg × *C. cirsiifolia* C.Presl (AR): Peru, Depto. Arequipa, Prov. Arequipa, Distr. Chiguate, above the tunnel of Simbral, 4250 m a.s.l., S16° 22′ 48.4″ W071° 18′ 17.9″, 05.12.2006, M. Ackermann, E. Gonzales L. & F. Sinca C. 643 (BSB, HUSA, USM).

C. andina Urb. & Gilg × *C. cirsiifolia* C.Presl (AY): Peru, Depto. Ayacucho, Prov. La Mar, road from Quinua to Tambo, at Laguna Toctococha, 4040 m a.s.l., S12° 58′ W074° 05′, 19.02.2000, M. & K. Weigend 2000/376 (HUSA, M, NY, USM).

C. canarinoides (Lenne & C.Koch) Urb. & Gilg (PU): Peru, Depto. Puno, Prov. Sandia, road from Cuyocuyo to Sandia, 3350 m a.s.l., S14° 26′ 38″ W069° 31′ 50″, 25.09.2002, M. Ackermann 375 + C (BSB, BSB, F, HUSA, M, NY, USM).

C. carduifolia C.Presl (AP): Peru, Depto. Apurimac, Prov. Andahuaylas, road from Abancay to Andahuaylas, km 86, 3700 m a.s.l., S13° 41′ W073° 08′, 16.02.2000, M. & K. Weigend 2000/326 + C (HUSA, M, NY, USM).

C. carduifolia C.Presl (CU): Peru, Depto. Cuzco, Prov. Calca, road from Calca to Lares, 3700 m a.s.l., S13° 15′ W071° 54′, 06.02.2000, M. & K. Weigend 2000/178 (HUSA, M, NY, USM).

C. carduifolia C.Presl x *C. chuquitensis* (Meyen) Urb. & Gilg (CU): Peru, Depto. Cuzco, Prov. Calca, road from Calca to Amparaes, shortly after turn to Amparaes, 4300 m a.s.l., S13° 12′ W071° 54′, 06.02.2000, M. & K. Weigend 2000/184 (HUSA, M, NY, USM).

C. chuquitensis (Meyen) Urb. & Gilg (CU1): Peru, Depto. Cuzco, Prov. Calca, road from Calca to Lares, after Rancal, 4000 m a.s.l., S13° 10′ 26″ W071° 57′ 55″, 11.09.2002, M. Ackermann, N. Salinas & D. Kollehn 274 + C (BSB, HUSA, M).

C. chuquitensis (Meyen) Urb. & Gilg (CU2): Peru, Depto. Cuzco, Prov. Calca, road from Calca to Amparaes, shortly after turn to Amparaes, 4300 m a.s.l., S13° 12′ W071° 54′, 06.02.2000, M. & K. Weigend 2000/185 (HUSA, M, NY, USM).

C. cirsiifolia C.Presl (AN): Peru, Depto. Ancash, Prov. Huaraz, Rio Grande/ Rio Chaccan, toward Pariacoto, 2999 m a.s.l., 18L0200571 UTM8942645, 16.05.2003, M. Weigend, T. Henning & O. Mohr 7697 + C (BSB, USM).

C. cirsiifolia C.Presl (AR): Peru, Depto. Arequipa, Prov. Arequipa, Distr. Chiguata, near the tunnel Simbral, 4300 m a.s.l., S16° 22′ 48.4″ W071° 18′ 17.9″, 05.12.2006, M. Ackermann, E. Gonzales L. & F. Sinca C. 642 (BSB).

C. cirsiifolia C.Presl (AY): Peru, Depto. Ayacucho, Prov. La Mar, road from Quinua to Tambo, at Laguna Toctococha, 4040 m a.s.l., S12° 58′ W074° 05′, 19.02.2000, M. & K. Weigend 2000/377 (HUSA, M, NY, USM).

C. cirsiifolia C.Presl (CA1): Peru, Depto. Cajamarca, Prov. Santa Cruz, La Florida, above Monteseco, 1200–1500 m a.s.l., 05.05.2003, M. Weigend, T. Henning & O. Mohr 7559 + C (BSB, USM).

C. cirsiifolia C.Presl (CA2): Peru, Depto. Cajamarca, Prov. Hualgayoc, 3600 m a.s.l., S06° 48′ 35.5″ W078° 57′ 03.7″, 02.05.2003, M. Weigend, T. Henning & O. Mohr 7510 + C (BSB, USM).

C. cirsiifolia C.Presl (TA): Peru, Depto. Tacna, Prov. Tarata, 16 km above Candarave on Mazo Cruz road (196 km W of Ilave), 3680 m a.s.l., 09.10.1997, Weigend & H. Förther 97/797 (M, USM).

C. cirsiifolia C.Presl × *C. deserticola* Weigend & Mark.Ackermann (TA): Peru, Depto. Tacna, Prov. Tarata, 16 km above Candarave on Mazo Cruz road (196 km W of Ilave), 3680 m a.s.l., 09.10.1997, Weigend & H. Förther 97/796 (M, USM).

C. deserticola Weigend & Mark.Ackermann (MO): Peru, Depto. Moquegua, Prov. General Sanchez Cerro, between Puquina and Omate, last roadbends before the descent to Omate, near Charijon, ca. 3000 m a.s.l., 21.05.2003, M. Weigend, T. Henning & O. Mohr 7761 + C (BSB, HUSA, USM).

C. deserticola Weigend & Mark.Ackermann (TA): Peru, Depto. Tacna, Prov. Tarata, 16 km above Candarave on Mazo Cruz road (196 km W of Ilave), 3680 m a.s.l., 09.10.1997, Weigend & H. Förther 97/795 (M, USM).

C. madrequisa Killip (PU): Peru, Depto. Puno, Prov. Paucartambo, road from Paucartambo to Tres Cruces, Parque Nacional Manu, 3050 m a.s.l., S13° 10′ 50″ W071° 36′ 37″, 18.09.2002, M. Ackermann 356 + C (BSB, HUSA, M, NY, USM).

C. pentlandii (Paxton) G.Don ex Loudon (PU): Peru, Depto. Puno, Prov. Melgar, road from Sicuani to Nunoa, ca. 3 km before Nunoa, 4000 m a.s.l., S14° 31′ 07″ W70° 37′ 31″, 20.09.2002, M. Ackermann 360 + C (BSB, F, HUSA, M, NY, USM).

Appendix C (Pollination syndrome in Loasoideae)

Voucher data (multiple accessions of species are differentiated by Arabic numeral in brackets in list and throughout the text):

Aosa rupestris (Hook.) Weigend—cultivated from seeds collected in Bahía, Brazil by S. Vogel, Vienna, M. Weigend 7138 (B, M, BM).

Blumenbachia hieronymi Urb.—cultivated plants from Botanical Garden Berlin-Dahlem, 27. September 2004, M. Ackermann 601 (BSB).

Blumenbachia insignis Schrad.—cultivated plants from Botanical Garden Berlin-Dahlem, 27. September 2004, M. Weigend 7475 (BSB).

Caiophora canarinoides (Lenné & C.Koch) Urb. & Gilg—Peru, Depto. Puno, Prov. Sandia, road from Cuyocuyo passing Banos de Cuyocuyo, old Inca trail, 14°28´S, 69°32´W, 3550 m, 25. September 2002, M. Ackermann 395 (BSB, HUSA, M, USM).

Caiophora carduifolia C.Presl (1)—Peru, Depto. Apurimac, Prov. Andahuaylas. road from Abancay to Andahuaylas, km 86, 13°41´S, 73°08´W, 3700 m, 16. February 2000, M. & K. Weigend 2000/326 (HUSA, NY).

Caiophora carduifolia C.Presl (2)—Peru, Depto. Cuzco, Prov. Paucartambo, SE from Cuzco, from Saylla to Paucartambo, village of Huancarani, 13°30´S, 71°38´W, 3880 m, 17. September 2002, M. Ackermann & N. Salinas, 333 (BSB, HUSA, M, USM).

Caiophora carduifolia C.Presl (3)—Peru, Depto. Cuzco, Prov. Calca, road from Calca to Lares, after Rancal, 13°12´S, 71°56´W, 4310 m, 11. September 2002, M. Ackermann et al. 554 (BSB, HUSA, M).

Caiophora carduifolia C.Presl (4)—Peru, Depto. Cuzco, Prov. Urubamba, road from Urubamba to Quillabamba, between Ollantaytambo and Abra Malaga, S13°12´S, 72°17´W, approx. 3500 m, 12. September 2002, M. Ackermann & D. Kollehn 288 (BSB, F, HUSA, M, NY, USM).

Caiophora carduifolia C.Presl (5)—Peru, Depto. Cuzco, Prov. Cuzco, SE from Cuzco, from Saylla on small road to the ruins of Tipon, 13°34´S, 71°47´W, 3440 m, 17. September 2002, M. Ackermann & N. Salinas 329 (BSB, HUSA, M).

Caiophora carduifolia C.Presl (6)—Peru, Depto. Cuzco, Prov. Cuzco, road from San Jeronimo to Huacoto (small street to the east), fields near Huacoto, 13°30´S, 71°51´W, 4130 m, 13. September 2002, M. Ackermann & N. Salinas 296 (BSB, HUSA, M, USM, NY, F).

Caiophora cf. *madrequisa* Killip—Peru, Depto. Puno, Prov. Paucartambo, road from Paucartambo to Tres Cruces, Parque Nacional Manu, 13°10´S, 71°36´W, 3050 m, 18.

September 2002, M. Ackermann 356 (BSB, HUSA, M, NY, USM).

Caiophora cf. *superba* Phil.—Peru, Depto. Moquegua, Prov. General Sanchez Cerro, between Puwuina and Omate, last road bends before the descent to Omate, near Charijon, approx. 3000 m, 21. May 2003, M. Weigend et al. 7761 (BSB).

Caiophora chuquitensis (Meyen) Urb. & Gilg (1)—Peru, Depto. Cuzco, Prov. Calca, road from Calca to Lares, after Rancal, 13°10´S, 71°57´W, 4000 m, 11. September 2002, M. Ackermann et al. 274 (BSB, HUSA, M).

Caiophora cirsiifolia C.Presl (1)—Peru, Depto. Arequipa, Prov. Arequipa, environment of Chiquata, east from Arequipa, 16°24´S, 71°22´W, 3100 m, 1. October 2002, M. Ackermann et al. 420 (BSB, F, HUSA, M, NY, USM).

Caiophora cirsiifolia C.Presl (2)—Peru, Depto. Lima, Prov. Yauyos,Road from Yauyos to Jauja, after Tomas, 12°17´S, 75°48´W, approx. 2300 m, 7. October 2002, M. Weigend et al. 7260 (BSB, HUSA, M, NY, USM).

Caiophora cirsiifolia C.Presl (3)—Peru, Depto. Cajamarca, Prov. Santa Cruz, La Florida, above Monteseco, 1200—1500 m, 5. May 2003, M. Weigend et al. 7559 (BSB).

Caiophora cirsiifolia C.Presl (4)—Peru, Depto. Ancash, Prov. Huarez, Rio Grande/ Rio Chaccan, towards Pariacoto, 18L 0200571 UTM8942645, 2999 m, 16. May 2003, M. Weigend et al. 7697 (BSB, USM).

Caiophora grandiflora (G.Don) Weigend & Mark.Ackermann (1)—Peru, Depto. Cajamarca, Prov. San Miguel, road San Miguel to Tongad (Sta. Rosa—Hualgayoc), 6°46´S, 78°38´W, 3986 m, 2. May 2003, M. Weigend et al. 7509 (BSB, USM).

Caiophora grandiflora (G.Don) Weigend & Mark.Ackermann (2)—Peru, Depto. Cajamarca, Prov. Hualgayoc, 6°48´S, 78°57´W, 3600 m, 2. May 2003, M. Weigend et al. 7510 (BSB, USM).

Caiophora lateritia Benth.—cultivated plants from Botanical Garden Berlin Dahlem, 1. August 2004, M. Ackermann 603 (BSB).

Caiophora nivalis Lillo—Argentina, Prov. Mendoza, Vallecitos. 2826 m, 32°58´S, 69°21´W, 8.–18. January 2003, A. A. Cocucci et al. 2219 (CORD).

Caiophora pentlandii (Paxton) G.Don ex Loudon (1)—Peru, Depto. Puno, Prov. Melgar, road from Sicuani to Nunoa, approx. 3 km before Nunoa, 14°31´S, 70°37´W, 4000 m, 20. September 2002, M. Ackermann 360 (BSB, F, HUSA, M, NY, USM).

Caiophora pentlandii (Paxton) G.Don ex Loudon (2)—Peru, Depto. Puno, Prov. Puno, road from Puno to Juliaca, Ruins of Sillustani, 15°43´S, 70°09´W, 3880 m, 23. September 2002, M. Ackermann 366 (BSB, F, HUSA, M, NY, USM).

Loasa acanthifolia Desr. var. *albomaculata* Gunckel—Argentina, Prov. Neuquen, Depto. Aluminé, road N of Lago Quillén towards Lago Hui Hui, 39°22´S, 71°14´W, 1050 m, 17.

January 2002, M. Weigend et al. 6925 (BRCO, BSB, M).

Loasa gayana Urb. & Gilg—Chile, X. Región, Los Lagos, road entre Lagos and Osorno, 25 km E of Osorno, approx. 2 km N of road, entrance to Fundo Los Pellines, 40°35´S, 72°50´W, 132 m, 3. February 2002, M. Weigend et al. 7057 (B, M, NY).

Loasa sclareifolia Juss.- Chile, VIII Region del BioBio, Prov. de Nuble, east of San Fabian de Alico, orig. collection J. Grau, July 2005, M. Weigend 8183 (BSB, M).

Nasa dillonii Weigend—Peru, Depto. Cajamarca, Prov. Santa Cruz: La Florida, above Monteseco, 1200—1500 m, 5. May 2003, M. Weigend et al. 7556 (B, USM).

Nasa dyeri (Urb. & Gilg) Weigend ssp. *australis* Dostert & Weigend—Peru, Depto. Amazonas, Prov. Bagua, trail from La Peca to El Arenal, just above El Arenal, 1200 m, April 1998, N. Dostert 98/80 (M, USM).

Nasa macrothyrsa (Urb. & Gilg) Weigend—Peru, Depto Cajamarca, Prov. San Miguel, one of the last road bends before San Miguel, 7°00´S, 78°51´W, 2517 m, 30. April 2003, M. Weigend et al. 7471 (BSB, HUT, USM).

Nasa moroensis Weigend—Peru, Depto. Ancash, Prov. Huaylas, Rio Grande/Río Chacchan, 2143 m, 16. May 2003, M. Weigend et al. 7694 (BSB, HUT, M, USM).

Nasa olmosiana (J.F.Macbr.) Weigend—Depto. Cajamarca, Prov. Santa Cruz, road from Monte Seco to Espinal, close to turn off to La Florida, 600–800 m. 7. March 1998 to 9. May 1998, Nicolas Dostert 98/163-C (BSB, M).

Nasa picta (Hook.f.) Weigend—Peru. Depto. Cajamarca. Prov. Chota, Huambos, 93 km from Chota on road Huambos, Llama Chiclayo, 2300 m. 14. May 1998, M. Weigend & N. Dostert 98/158 (B, USM).

Nasa poissoniana (Urb. & Gilg) Weigend—Peru, Depto. La Libertad, Prov. Pataz, road Buldibuyo to Tayabamba, 8°07´S, 77°23´W, 3163 m, 24. April 2004, M. Weigend & Ch. Schwarzer 8007 (B, USM).

Nasa triphylla (Juss.) Weigend ssp. *flavipes* Weigend & Dostert—Peru, Depto. Piura, Prov. Huancabamba, due west of town, 1700—1900 m, May 1998, M. Weigend & N. Dostert 98/203 (M, USM).

Nasa triphylla (Juss.) Weigend ssp. *triphylla*—cultivated plants from Botanical Garden Berlin Dahlem, 1. August2004, M. Ackermann 602 (BSB).

Nasa triphylla (Juss.) Weigend ssp. nov. ined.—Peru, Depto. La Libertad, Prov. Sanchez Carrion, road Huamachuco to Chagual-Pataz, after Chugay and between Molino Viejo and Aricapampa, 7°48´S, 77°41´W, 2389 m, 20. April 2004, M. Weigend & Ch. Schwarzer 7913 (B, USM).

Nasa urens (Jaq.) Weigend—Peru, Depto. Lima, Prov. Yauyos, road from Quilmana to Panamericana, km 122 on Panamericana, Lomas de Quilmana, 12°57´S, 76°26´W, approx. 320 m, 8. October 2002, M. Weigend et al. 7327 (BSB, HUSA, M, NY, USM).

Nasa vargasii (Macbr.) Weigend—Peru, Depto. Huánuco. Prov. Ambo. Road from Huánuco to Cerro de Pasco, km 27,3 km from Ambo. 2300 m. 10°11´S, 76°10´W, 3. April 2001, Weigend et al. 5463 (B, HUT, M, USM).

Presliophytum arequipensis Weigend—Peru, Depto. Moquegua, Moquegua on road to Torata, 1855 m, 13. October 1997, M. Weigend and H. Förther 97/848 (M, USM).

Presliophytum heucheraefolium (Killip) Weigend—Peru, Depto. Ancash, Prov. Huaylas, Rio Grande/Rio Chacchan, 18L 0181840 UTM 8941740, 16. May 2003, M. Weigend et al. 7691 (BSB, USM).

Presliophytum incanum (Graham) Weigend—Peru, Depto. Lima, Prov. Huarochiri, Matucana, 2400 m, M. Weigend and N. Dostert 97/12 (M, USM).

Xylopodia klaprothioides Weigend—Peru, Depto. Cajamarca, Prov. Contumaza, road Contumaza to Chilete, first road bend after highest point of pass. 2900 m. April 1997, M. Weigend et al. 97/450 (M, USM).