Three new species of Heliamphora (Sarraceniaceae) from the Guayana Highlands of Venezuela

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Three new species of *Heliamphora (Sarraceniaceae)* from the Guayana Highlands of Venezuela

Abstract

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Heliamphora uncinata, H. ciliata and *H. huberi* are described as species new to science and illustrated. They are compared with their putative relatives, ecological notes are included and an identification list for all specimens examined is appended. The petaloid tepals of *H. uncinata* bear nectaries in the basal half of their adaxial surface and it shares this feature with *H. exappendiculata*. This is the first record of nuptial nectaries for the genus *Heliamphora*.

Resumen

Heliamphora uncinata, H. ciliata y *H. huberi* se describen como especies nuevas para la ciencia y se ilustran. Las nuevas especies se comparan con sus parientes supuestos; además se incluye información ecológica, y una lista de la identificación para todos los especímenes examinados. Los tepalos petaloides de *H. uncinata* tienen nectarios en la mitad de la base de la superficie adaxial y comparte esta característica con *H. exappendiculata*. Es el primer registro de nectarios florales para el género *Heliamphora*.

Additional key words: *Heliamphora ciliata, Heliamphora huberi, Heliamphora uncinata,* carnivorous plants, taxonomy, nuptial and extranuptial nectaries

Introduction

During taxonomic studies of the Guayana Highlands endemic genus *Heliamphora* Benth., the authors examined numerous herbarium specimens deposited in the herbaria MO, NY and VEN (abbreviations after Thiers 2008+). During this occasion some specimens were discovered that did not fit any of the currently described species, three of which are described as new species in the present article.

In February 1983, Julian A. Steyermark, Otto Huber and Victor Carreño Espinosa collected several interesting specimens of *Heliamphora* on Amurí-tepui of the Chimantá massif (Macizo del Chimantá, an extensive, cleft sandstone mountain system, consisting of several separated tepuis; for nomenclature of the highlands of the Venezuelan Guayana, see Huber 1995). The collections were deposited at MO, NY and VEN, where they were filed as *H. minor* Gleason and *H. heterodoxa* Steyerm., respectively. One of these collections was made in a *Bonnetia* tepui forest, the other in a narrow canyon where *Heliamphora* grows on vertical sandstone walls. Steyermark, in his realignment of the genus *Heliamphora,* noted that the collection of *H. minor* from Amurí-tepui differs from typical *H. minor* in pitcher shape and size (Steyermark 1984).

A closer inspection of those collections clearly revealed that the specimens represent neither *H. minor,* a species restricted to Auyán-tepui, nor *H. heterodoxa* which seems to be endemic to Ptari-tepui and its surroundings, but rather two distinct undescribed species.

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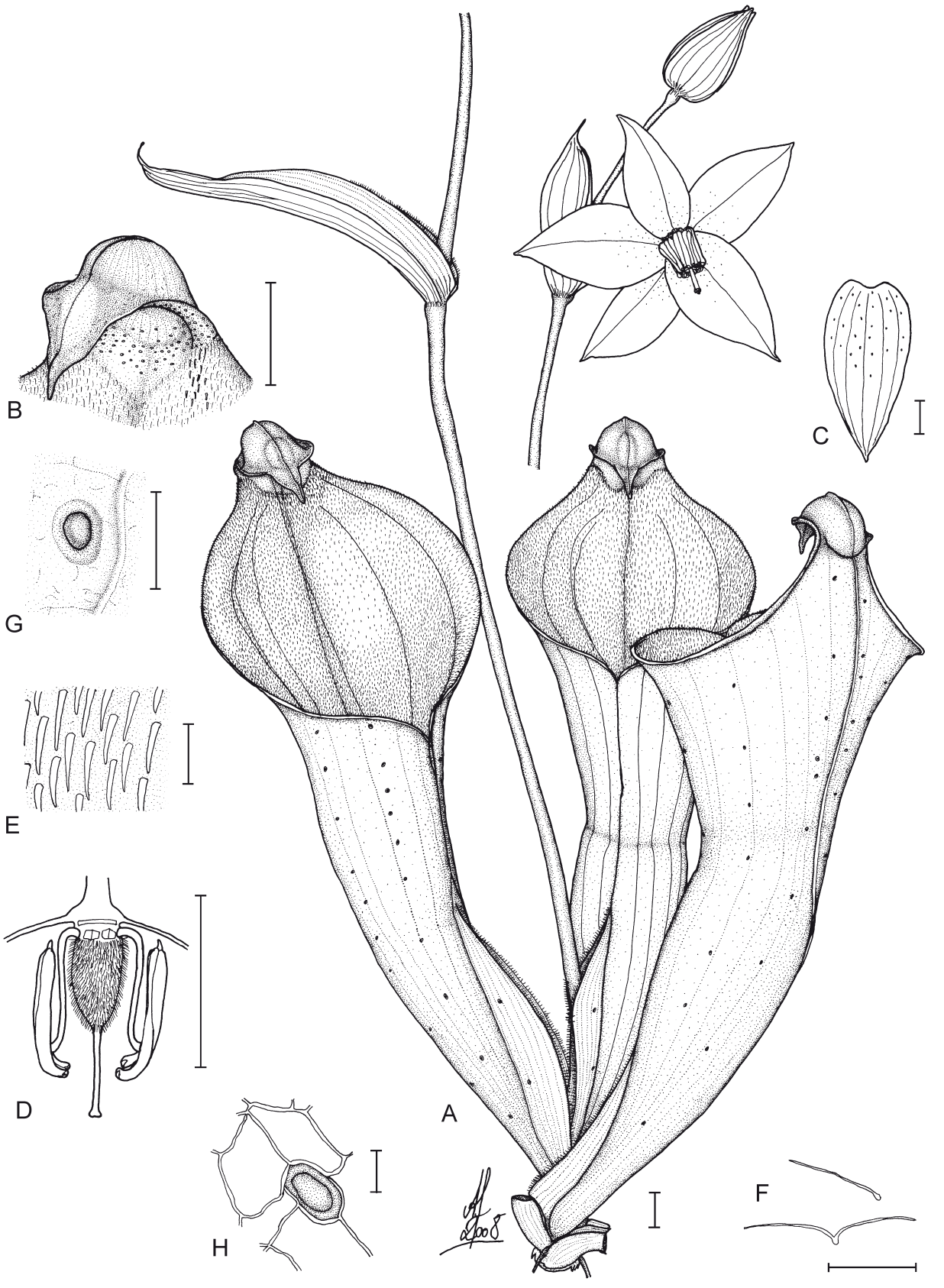

Fig. 1. *Heliamphora uncinata* – A: habit of flowering plant; B: pitcher appendage; C: perianth segment; D: diagrammatic section of flower at anthesis; E: trichomes of upper interior leaf surface; F: trichomes of exterior leaf surface; G: nectar gland of pitcher exterior surface; H: nectar gland from tepal base. – Scale bars: A–D = 10 mm, E = 0.3 mm, F, H = 0.1 mm, G = 1 mm. – Drawing by Andreas Fleischmann from *Steyermark & al. 128568*.

In December 1984, Otto Huber & al. collected specimens of a stunted *Heliamphora* that was further identified as *H. minor* and deposited in MO, NY and VEN. Interestingly, the plants were found at an altitude of only 900 m in a swampy area of the Gran Sabana approximately 50 kilometres east of Auyán-tepui. This is the lowest documented finding of any *Heliamphora* so far. *H. minor* in contrast is known as a strict highland plant occurring only on Auyán-tepui at more than 2000 m altitude. The lowland specimens revealed interesting characteristics clearly separating these from *H. minor* and from the related, recently described *H. pulchella* Wistuba & al.

These three taxa are described as new species, based exclusively on the comparative study of specimens deposited in the herbaria F, M, MO, NY and VEN.

Heliamphora uncinata Nerz, Wistuba & A. Fleischm., **sp. nov.**

Holotype: Venezuela, Estado Bolívar, Macizo del Chimantá, on wet face of shaded grotto by stream, pequenas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepui (Sector W del Acopán-tepui) [small plateaus at the northern base of upper cliffs of Amurí-tepui], aprox. 5°10'N, 62°07'W, c. 1850 m, 2.–5.2.1983, *J. A. Steyermark & al. 128568* (VEN; isotype: MO). – Fig. 1.

Heliamphora exappendiculata (Maguire & Steyerm.) Nerz & Wistuba similis sed amphora majore 25–35 cm longa cum appendice e basi latissima galeata, apice acuto uncinatoque.

Perennial herb. *Rhizomes* branching, plants forming clumps with age. *Leaves (pitchers)* tubular, elongated, ventricose in the lower $^2/_3$, infundibulate in the upper third and expanded to the mouth, 25–35 cm long, 8–10 cm wide in the upper part, greenish with red; interior pitcher surface in the upper third densely covered with coarse retrorse trichomes up to 0.3 mm in length and c. 0.1 mm distant from each other, in the middle part glabrous, in the basal part coarsely ciliate; exterior pitcher surface scarcely covered by simple or bifid, white trichomes of c. 0.1 mm length and with 4–6 rows of distinctive reddish extrafloral nectary glands of c. 0.5 mm in diameter distributed along the veins; pitcher with narrowly oval pore ("drain slit") in the ventral suture at about half of the pitcher length, hidden by the compressed alae, thus not easily visible. *Alae* 2, conspicuous at the lower third of the pitcher, c. 1 cm wide at the base, graduating into the ventral pitcher surface above, margin ciliate, with few nectary glands along the veins. *Pitcher appendage* helmet-shaped, arising from a very broad, up to 15 mm wide base, with acute hook-like triangular apex; appendage up to 15 mm high, 15 mm wide and 20 mm long including the rostrate apical tip, triangular apex to 5 mm long and 8 mm wide near the base; the nectar-secreting area and the sharply pointed triangular tip of the lid slanted towards the pitcher opening. *Inflorescence* a one-sided, 1–6-flowered raceme, scape terete, glabrous, 70–100 cm long, c. 5 mm in diameter near the base. *Pedicels* terete, glabrous, 3–5 cm long, c. 2 mm in diameter. *Bracts* subtending the flowers ovate, 4–5 cm long, lowermost bract often developed as a rudimentary pitcher up to 8 cm long. *Tepals* 4(–5), petaloid, oblong-lanceolate, 5–6 cm long, 2–2.5 cm wide, white to pinkish white at anthesis, persistent in fruit, with few circular to elliptic, reddish nectaries c. 0.1 × 0.2 mm, scattered between the veins in the basal half of the adaxial surface. *Stamens* 10(–11), filaments c. 9 mm long, anthers basifixed, poricidal, uniformly 8–9 mm long. *Ovary* 3-celled, densely pubescent, c. 5 mm long, c. 4 mm in diameter. *Styles* united to a pistil, glabrous, 5–6 mm long. *Capsule* 3-valved, 2–2.5 cm long, 1–1.5 cm in diameter, with pedicel nodding at maturity. *Seed* 3 mm long, 3 mm wide, yellowish brown, surrounded by a membranous wing with undulate margin.

Etymology. — The epithet refers to the distinctive hook-shaped pitcher appendage, which is unique in the genus *Heliamphora*.

Distribution and habitat. — Endemic to Venezuela, Estado Bolívar, Chimantá massif. *Heliamphora uncinata* is only known from a single collection at the type location, a narrow canyon on Amurí-tepui (the western sector of Acopán-tepui), where it grows mainly on the vertical sandstone cliff surface in shaded conditions in humus pockets and cracks at c. 1850 m. The only other species of *Heliamphora* known so far that preferably grows on vertical, wet sandstone walls is *H. exappendiculata* (Maguire & Steyerm.) Nerz & Wistuba.

Notes. — *Heliamphora uncinata* seems to be related to *H. exappendiculata* (see Table 1), with which it shares characters of pitcher shape, growth habit and the presence of floral and extrafloral nectaries. The striking hook-shaped pitcher appendage easily distinguishes this species from all other species of the genus. *H. heterodoxa* has a very well developed spoon-shaped appendage carrying the nectar secreting glandular area, while *H. exappendiculata* only has a rudimentary pitcher appendage or no appendage at all. In *H. exappendiculata* the nectar secreting area is embedded in the apical end of the pitcher surface.

Heliamphora uncinata and the related *H. exappendiculata* are the sole members of the genus known so far to have perianth segments with floral nectaries. These minute nectar glands (according to Vogel (1998), the few-celled nectar secreting glands of *Sarraceniaceae* are better characterized by the anatomical term "nectarioles") are scattered between the veins on the adaxial surface in the basal half of the petals (Fig. 1C). This is the first record of nuptial nectar for *Heliamphora*. So far, *Sarracenia* has been reported to be the only genus of *Sarraceniaceae*

Table 1. Comparison of *Heliamphora uncinata, H. exappendiculata, H. heterodoxa* s.str. (excluding the recently separated *H. folliculata* Wistuba & al. and *H. glabra* (Maguire) Nerz & al.), *H. folliculata* and *H. glabra*.

	H. uncinata	***H. exappendiculata***	***H. heterodoxa*** s.str.	***H. folliculata***	***H. glabra***
Pitcher dimensions [max. l × w]	35 × 10 cm	25 × 10 cm	20 × 8 cm	30 × 6 cm	45 × 8 cm
Pitcher shape	ventricose in the lower $^2/_3$, infundibulate in the upper $^1/_3$ and expanded near the mouth	ventricose in the lower part, infundibulate to broad infundibulate in the upper part	infundibulate to ventricose in the lower $^1/_3$, slightly infundibulate in the upper part, expanded near the mouth	infundibulate in the lower $^1/_3$, cylindrical in the upper part, not expanded near the mouth, ventral side compressed inwards	ventricose in the lower $^1/_3$, tubular to narrowly infundibulate in the upper $^2/_3$, expanded near the mouth
Pitcher mouth	back of the pitcher elevated into the lid	back of the pitcher often not elevated, sometimes forming a small triangular neck	back of the pitcher elevated forming the base from which the lid emerges	back of the pitcher not elevated	back of the pitcher elevated forming the base from which the lid emerges
Appendage	helmet-shaped with hook-like apex, the nectar-secreting area and the sharply pointed triangular tip of the lid slanted towards the pitcher opening	absent or rudimentary as a small tip; nectar-secreting area round to ovate, embedded in the apical end of the pitcher surface	strongly helmet-shaped, constricted at the base, sometimes spoon-shaped	slightly helmet-shaped from very broad base, sharply bent towards pitcher mouth, not constricted at the base, with hollow tubular chamber on the back of the lid	strongly helmet-shaped with knob-like outgrowth on top, constricted at the base
Appendage insertion	emerging from a very broad base	appendage included into pitcher margin	on a triangular base	emerging from a very broad base or appendage included into pitcher margin	on elongated triangular base
Indumentum of upper $^1/_3$ of pitcher interior	covered with short, coarse, retrorse trichomes up to 0.3 mm long	covered with short, coarse, retrorse trichomes c. 0.1 mm long	covered with short, coarse, retrorse trichomes up to 0.3 mm long	glabrous, only margins of mouth with trichomes up to 0.2 mm long	glabrous
Peduncle	up to 100 cm long, glabrous	up to 40 cm long, glabrous	30–70 cm, glabrous	up to 50 cm long, glabrous	up to 80 cm long, glabrous
Pedicels	3–5 cm long, glabrous	3–5 cm long, glabrous	to 8 cm long, glabrous	3–6 cm long, glabrous	5–8 cm long, glabrous
Floral nectaries	present	present	absent	absent	absent
Anthers	c. 10; 8–9 mm long	8–10; (7–)7.5(–8) mm long	(8–)10(–14); 6(–7)8 mm long	c. 10; 7–8 mm long	10–15; 6–8 mm long
Distribution	Chimantá massif: Amurí-tepui (1850 m)	Chimantá massif and Aprada massif (1000–3000 m)	Ptari-tepui (1600–2450 m) and surrounding lowlands of the Sierra de Lema to Cerro Venamo (to 1200 m)	Los Testigos massif (Aparamán range) (2135–2500 m)	Cerro El Sol (Uei-tepui) to Roraimita-tepui, eastern flank of Roraima-tepui (1200–2000 m)

with nectar producing flowers, whereas the two genera *Heliamphora* and *Darlingtonia* have been considered to have nectarless flowers (Renner 1989; Vogel 1998).

Heliamphora ciliata Wistuba, Nerz & A. Fleischm., **sp. nov.**

Holotype: Venezuela, Estado Bolívar, sabanitas alargadas en la altiplanicie al NE del Aprada-tepui, aprox. 30 km al ESE de Kamarata [small savanna patches on the upland plateau of the NE slope of Aprada-tepui, approx. 30 km ESE of Kamarata], 5°40'N, 62°05'W, 900 m, 12.12.1984, *Huber & al. 9921* (VEN; isotypes: MO, NY). – Fig. 2.

Heliamphora minor Gleason similis sed amphora extus nervo medio sparse ciliato, appendice e basi lata spatulato-dilatato, 2 × 1.5 cm, extus longe patenter piloso.

Perennial herb. *Rhizomes* branching, plants forming clumps with age. *Leaves (pitchers)* tubular, ventricose in the lower third, slightly infundibulate and expanded in the upper third, 10–20 cm long, up to 4–6 cm wide in the upper part, reddish; interior pitcher surface in the upper third densely covered with c. 0.2 mm long, fine trichomes and up to 3 mm long, retrorse trichomes, middle part glabrous, basal part coarsely ciliate; exterior pitcher surface with an indumentum of short, appressed, simple or bifid, white trichomes c. 0.1 mm long, and on the upper part of the midrib with patent, deciduous, white ciliae up to 5 mm long; pitcher without pore. *Alae* 2, 5–8 mm at the base, graduating into the ventral pitcher surface at about half of the pitcher length, margins ciliate. *Pitcher appendage* spoon-shaped, slightly narrowed at the base, up to 2 cm long and 1.5 cm wide, arising directly from a triangular neck, back of the appendage covered with a conspicuous tuft of deciduous white ciliae up to 6 mm in length. *Inflorescence* a one-sided, 1–2(–3)-flowered raceme, scape terete, pubescent in the upper third, up to 80 cm long. *Pedicels* terete, 3–5 cm long, densely pubescent with fine hairs and sparse patent, up to 2 mm long ciliae.

Table 2. Comparison of *Heliamphora ciliata, H. minor, H. pulchella* and *H. huberi.*

	H. ciliata	***H. pulchella***	***H. minor***	***H. huberi***
Pitcher dimensions [max. l × w]	15 × 5 cm	20 × 8 cm	15 × 6 cm	30 × 6 cm
Pitcher shape	pitchers ventricose in the lower $^2/_3$, slightly infundibulate and expanded in the upper $^1/_3$	pitchers slightly ventricose in the lower $^2/_3$, broadly infundibulate and expanded in the upper $^1/_3$	pitchers slightly ventricose in the lower $^2/_3$, broadly infundibulate and expanded in the upper $^1/_3$	ventricose to subtubular in the lower $^2/_3$, slightly infundibulate to elongated in the upper $^1/_3$
Pitcher mouth	back of the pitcher with pronounced triangular neck	back of the pitcher not elevated, often pitcher lobes overarching lid insertion	back of the pitcher with pronounced triangular neck	back of the pitcher slightly elevated
Appendage	lobes of the nectar spoon fused only mildly; with patent, deciduous, to 5 mm long, white hairs on back of the appendage (Fig. 2B)	distinctively helmet-shaped lobes of the nectar spoon fused extensively; appendage glabrous (Fig. 2C)	lobes of the nectar spoon fused only mildly; appendage glabrous (Fig. 2D)	helmet-shaped, strongly narrowed at the base with an upwards facing appendage on the outside near the tip
Appendage insertion	lid emerging from a broad base	mostly arising directly from the rim of the pitcher	mostly on distinct stalk formed by the midrib arising from the tip of the triangular neck	arising directly from the rim of the pitcher with short stalk
Indumentum of upper $^1/_3$ of pitcher interior	densely covered with short, fine trichomes c. 0.2 mm long and coarse, retrorse trichomes to 3 mm long (Fig. 2B)	scattered coarse bristles up to 5 mm long, surface glabrous between these bristles (Fig. 2C)	densely covered with short, coarse, retrorse trichomes up to 0.2 mm long (Fig. 2D) or glabrous.	covered with short, coarse, retrorse trichomes up to 0.3 mm long
Peduncle	to 80 cm long, pubescent	to 50 cm long, upper part pubescent	to 50 cm long, upper part pubescent or glabrous	to 80 cm long, upper part glabrous or pubescent
Pedicels	3–5 cm long, pubescent and with additional patent ciliae	to 5 cm long, pubescent	to 5 cm long, pubescent	to 5 cm long, pubescent
Anthers	10–15; 3–4 mm long	(7–)8–15; 4 mm long	15–20; (3–)3.5(–4.5) mm long	10–12; 7–8 mm long
Distribution	Gran Sabana uplands (900 m)	Chimantá massif and Aprada massif (1850–2550 m)	Auyán-tepui (1500–2300 m)	Chimantá massif and Angasima (1850–2200 m)

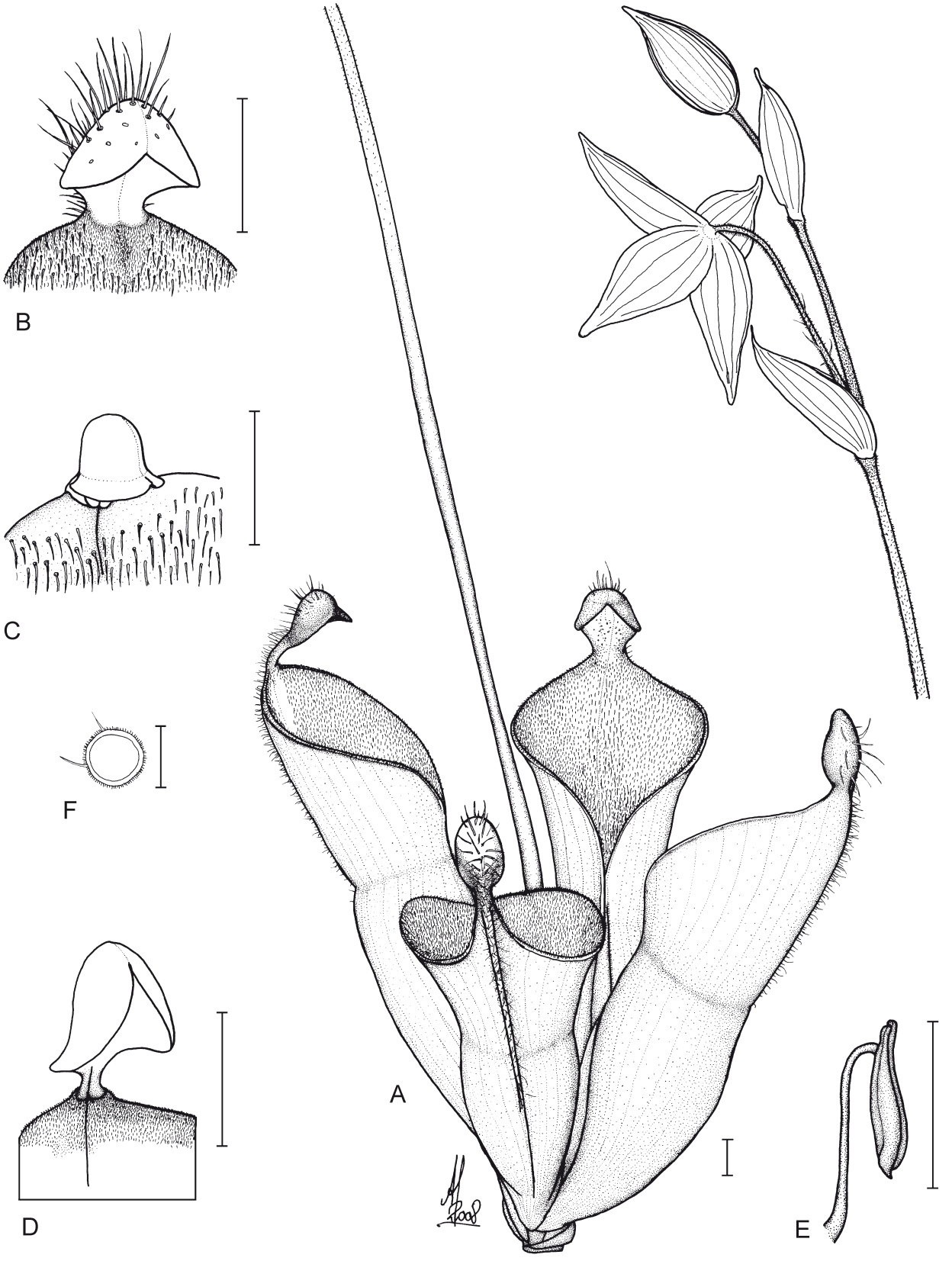

Fig. 2. A, B, E, F: *Heliamphora ciliata* – A: habit of flowering plant; B: pitcher appendage and indumentum of upper interior leaf surface E: stamen; F: diagrammatic cross section of pedicel. – C: *H. pulchella:* pitcher appendage and indumentum of upper interior leaf surface. – D: *H. minor:* pitcher appendage and indumentum of upper interior leaf surface; . – Scale bars: A–D = 10 mm, E = 4.5 mm, F = 1.5 mm. – Drawing by Andreas Fleischmann from *Huber & al. 9917 (*A, B, E, F); *Wurdack 34237* (C) and *Brewer-Carías s.n.* (D).

Bracts ovate, 4–10 cm long. *Tepals* 4, oblong-lanceolate, 4–5 cm long, 2–3 cm wide, white to pinkish white at anthesis, dark red and persisting at fruit, without nectaries on adaxial surface. *Stamens* 10–15, filaments 7 mm long, anthers basifixed, poricidal, oblong-lanceolate in outline, 3–4 mm long, 1 mm wide. *Ovary* 3-celled, pubescent. *Styles* united to a pistil, glabrous, 5–6 mm long. *Capsule* on upright pedicel (no ripe capsule available for measurements). *Seed* not seen.

Etymology. — The specific epithet refers to the tuft of ciliate, white hair on the back of the pitcher appendage and the conspicuous row of white trichomes on the back of the pitcher midrib.

Distribution and habitat. — Endemic to Venezuela, Estado Bolívar. *Heliamphora ciliata* is only known from a few swampy meadows in the Gran Sabana uplands northeast of Aprada-tepui, where the plants grow in patches together with *Stegolepis* sp. *(Rapateaceae)* in low, broad-leaved meadow vegetation (Huber & al. 2001). These swamps are located at an altitude of only 900 m. Therefore, *H. ciliata* can be considered as a submontane species, in contrast to most other members of the genus, which are endemic to the plateaus and summits of the tepuis (Berry & al. 2005; McPherson 2006). The only other species known from a similar habitat in the lowlands of the Gran Sabana is *H. heterodoxa,* of which populations occur in broad-leaved savanna in the Sierra de Lema, northeastern Bolívar state, as low as 1200 m (*Holst & al. 2173* and others).

Notes. — *Heliamphora ciliata* seems to be related to *H. minor* and *H. pulchella*. With these species it shares floral characteristics such as the size of anthers as well as the pubescent peduncle and pedicels, and capsules that are upright in fruit, as well as pitchers without a "drainage pore". It can, however, easily be distinguished by the arrangement of prominent hairs on the back of the pitcher, the tuft of deciduous, ciliate, white hairs on the pitcher appendage (which, however, can be lost or broken in some herbarium specimens), the much wider base from which the appendage emerges, and the indumentum of both, fine, c. 0.2 mm long hairs and coarse to 2 mm long trichomes in the upper third of the interior pitcher surface, as well as the pedicel with dense pubescent fine hairs and additional sparse, up to 2 mm long ciliae (see Table 2).

Additional material examined. — Venezuela: Estado Bolívar, sabanitas alargadas en la altiplanicie [small savanna patches on the upland plateau], al NE del Aprada-tepui, aprox. 30 km al ESE de Kamarata, 5°40'N, 62°05'W, 900 m, formando pequeños grupos en la sabana, frecuente. Mitad superior de las cisternas, escapo y pedicelos rojo vino, flor blanca, anteras amarillas [forming small groups in the savanna, frequent. Upper half of the pitchers, scape and pedicels wine-red, flowers white, anthers yellow], 12.12.1984, *Huber & al. 9917* (NY, VEN).

Heliamphora huberi A. Fleischm., Wistuba & Nerz, **sp. nov.**

Holotype: Venezuela, Estado Bolívar, Distrito Piar, cumbre del Angasima-("Adanta")-tepui, altiplanicie poco inclinada hacia el NE con sabana arbustiva en el sector Nor-occidental [summit of Angasima-("Adanta")-tepui, high plateau little inclined towards the northeast, with shrubby savanna in the northwestern part], aprox. 40 km al WNW de la Misión de Wonkén, 5°03'N, 62°07'W, 2100 m, 4.3.1986, *Huber 11366* (VEN; isotypes: MO, NY). – Fig. 3.

Heliamphora minor Gleason similis sed amphora elongata 20–30 cm longa ad 6 cm lata, appendice stipitata, apice breviter rostrato sursum curvato.

Perennial herb. *Rhizomes* branching, plants forming clumps with age. *Leaves (pitchers)* tubular, ventricose to subtubular in the lower $^2/_3$, slightly infundibulate to elongated in the upper third, 20–30 cm long, up to 6 cm wide in the upper part, greenish with red veins; interior pitcher surface in the upper third covered with short, retrorse trichomes up to 0.3 mm long and c. 0.1 mm distant from each other, margins of the pitcher opening with a dense rim of slightly curved, retrorse trichomes up to 1 mm long; middle part of pitcher glabrous, basal part coarsely ciliate; exterior pitcher surface scarcely covered with simple or bifid, appressed, white, c. 0.1 mm long trichomes, appearing almost glabrous; pitcher without pore. *Alae* 2, c. 1 cm wide at the base, graduating into the ventral pitcher surface just below the pitcher opening, margins ciliate. *Pitcher appendage* helmet-shaped, on a short stalk arising abruptly from the back of the pitcher, 15–20 mm high, 15–20 mm long and 10–15 mm wide, with an upwards facing beak-like appendage, 1–1.5 mm long on the outside near the tip, appendage interior with scattered, pitted nectary glands c. 0.1 mm in diameter, red. *Inflorescence* a one-sided, 1–4-flowered, raceme up to 80 cm long; scape terete, to 5 mm in diameter, glabrous in the lower part, slightly pubescent in the upper part from the lowermost bract on. *Pedicels* terete, up to 5 cm long, c. 3 mm in diameter, densely pubescent. *Bracts* oblong to ovate, lowermost bract 5–6 cm long, margins finely ciliate, upper bracts to 3 cm long, with glabrous margins. *Tepals* 4, petaloid, oblong-lanceolate, up to 5 cm long and 1.2–2 cm wide in the broadest part, white to pinkish white at anthesis, persistent in fruit, without nectaries. *Stamens* 10–12(–13), filaments c. 7 mm long, anthers basifixed, poricidal, oblong-lanceolate in outline, 7–8 mm long. *Ovary* 3-celled, pubescent, c. 5 mm long, c. 2 mm in diameter. *Styles* united to a pistil, glabrous, 4–6 mm long. *Capsule* 3-valved, 1.5–2.5 cm long, c. 1 cm in diameter, yellowish green, pedicel nodding in

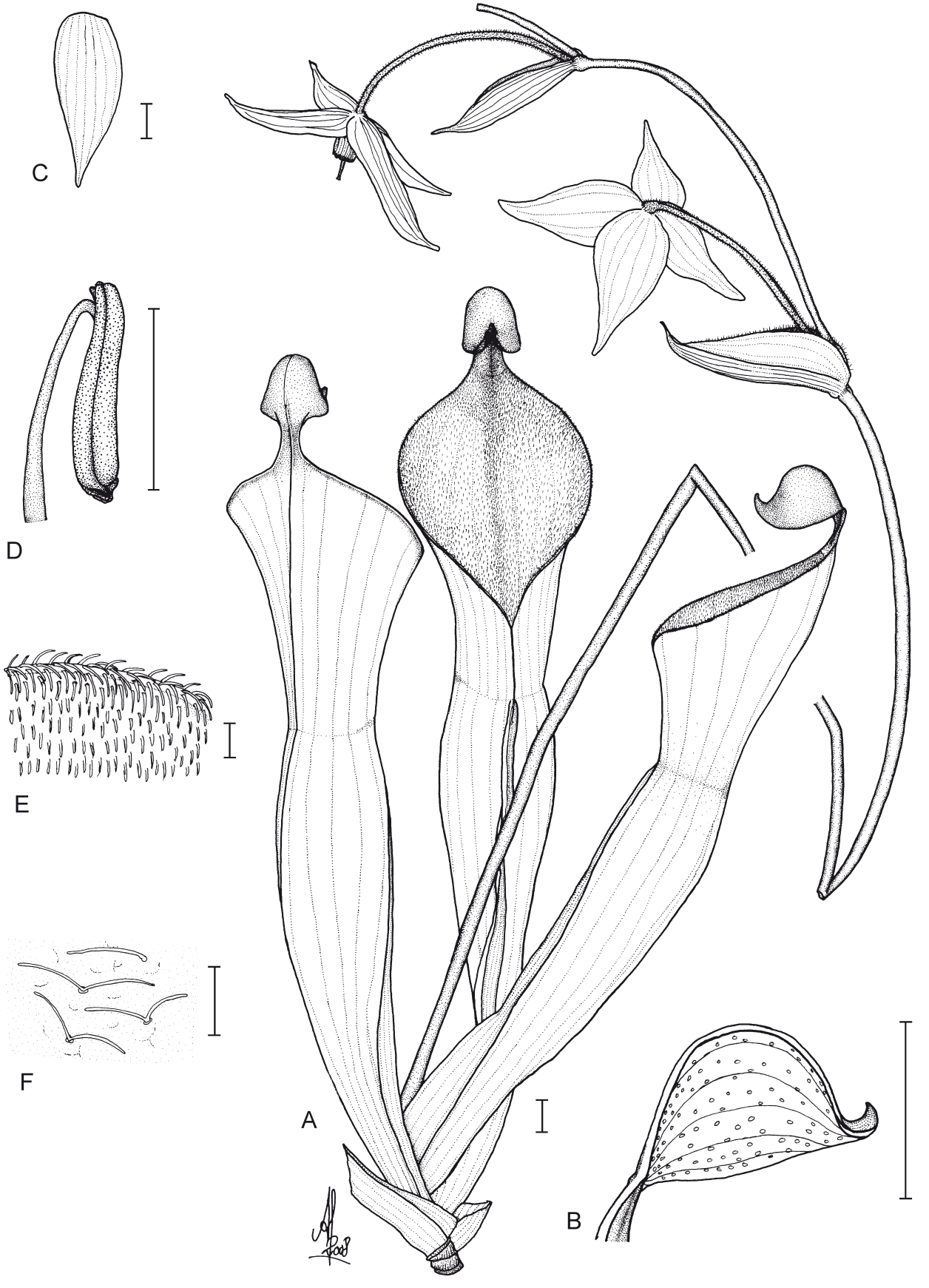

Fig. 3. *Heliamphora huberi* – A: habit of flowering plant; B: cross-section of pitcher appendage; C: perianth segment; D: stamen; E: indumentum of upper interior leaf surface near pitcher opening; F: trichomes of exterior leaf surface. – Scale bars: A–C = 10 mm, D = 5 mm, E = 1 mm, F = 0.1 mm. – Drawing by Andreas Fleischmann from *Huber 11366*.

fruit. *Seed* 3–4 mm long, 3 mm wide, yellowish brown, surrounded by a membranous wing with undulate margin.

Etymology. — This species is dedicated to Dr Otto Huber, Caracas, a well-known botanist and plant ecologist who contributed much to the knowledge of the Venezuelan Pantepui region and the flora and vegetation of the Guayana Highlands. He made the type collection of this species on Angasima-tepui during an expedition in 1986.

Distribution and habitat. – *Heliamphora huberi* is endemic to the mountain plateaus of the Chimantá massif, where it has been recorded so far from Angasima-tepui, the border of Torono- and Chimantá-tepui, Apacará-tepui, Amurí-tepui and from the summit of adjacent Acopán-tepui, growing at elevations of 1850–2200 m. The plants always grow partially shaded, but have been collected in slightly different habitats: on Angasima-tepui in highland meadows with interspersed tepui scrub, on Acopán-tepui, in wet, shady cliffs and on Amurí-tepui in tepui dwarf forest dominated by *Bonnetia* spp. *(Bonnetiaceae)*.

Notes. — *Heliamphora huberi* shares some floral characteristics with species related to *H. heterodoxa,* as it has anthers of more than 5 mm in length. However, the pedicels are densely pubescent in *H. huberi*, whereas in the remaining species related to *H. heterodoxa* they are entirely glabrous. Pubescent pedicels can be found in *H. minor, H. pulchella, H. ciliata* and *H. chimantensis* Wistuba & al. (as well as in the distinct monopodial stem-forming *H. neblinae* Maguire and *H. tatei* Gleason of the southwestern tepuis in the Venezuelan state of Amazonas). The anthers of these species are, however, shorter than 5 mm. The length of the poricidal anthers seems to be a constant character in all species of *Heliamphora,* which are all adapted to buzz-pollination (Renner 1989). Another character that *H. huberi* has in common with species related to *H. heterodoxa* are capsules that are nodding in fruit. In contrast, in the closely allied species *H. minor, H. pulchella, H. ciliata* and *H. chimantensis* the pedicel etiolates and deflexes after anthesis, so that the ripe seed capsules are held upright in fruit.

Heliamphora huberi has pitchers lacking the short elongated-oval pore ("drain slit", Lloyd 1942; "drainage hole", McPherson 2006) in the ventral suture, which is present in most *Heliamphora* species at the transition zone between the hairy upper part and the glabrous ventricose water-filled part. Pitcher leaves without a pore are so far only known from the closely related *H. minor, H. pulchella, H. chimantensis* (McPherson 2006) and *H. ciliata*.

Considering the morphology of *Heliamphora huberi,* which shares several intermediate characters between species related to *H. minor* and *H. heterodoxa,* we assume a hybrid origin of this species, most likely in the area of the Chimantá massif, presumably involving a species related to *H. heterodoxa* and *H. pulchella*.

At some locations *Heliamphora huberi* occurs sympatrically with *H. pulchella* and putative hybrids between both species can be found (e.g., Chimantá massif, Apacará-tepui: *Huber & Colella 8699* (NY, VEN); *Steyermark & al. 128269* (MO, VEN; but the duplicate at NY represents the parent species *H. pulchella*), Abacapá-tepui: *Huber & Dezzeo 8588* (MO, NY, VEN); Acopán-tepui: *Cardona 2277* (MO, the duplicate at VEN represents the parent species *H. huberi*)). The hybrids are similar to *H. huberi* in general appearance, but can readily be distinguished by the presence of scattered, long, retrorse bristles on the upper part of the interior pitcher surface. From the parent *H. pulchella* the hybrid differs in generally larger pitcher dimensions and the conspicuously stalked pitcher appendage.

Additional material examined. – Venezuela: Estado Bolívar: Macizo del Chimantá, Pequeñas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepui (Sector W del Acopán-tepui) [small plateaus at the northern base of upper cliffs of Amurí-tepui]. aprox. 5°10'N, 62°07'W, c. 1850 m, 2.–5.2.1983, *Steyermark & al. 128666* (MO, NY, VEN); Macizo del Chimantá, sector centro-norte, planicie poco disectada en la región sur-oriental del Apacará-tepui [central northern sector, little dissected plateau in the south-east region of Apacará-tepui], c. 2150 m, coll. 11.–14.3.1986, *Huber 11526* (VEN; the duplicate in NY represents the hybrid *H. huberi* × *H. pulchella;* the duplicate in MO represents *H. puchella*); Cerro Acopán [Acopán-tepui], río Caroní, en suelo cenagoso y sombredo [sic!] de la cumbre del cerro [in muddy and shaded ground of the summit of the mountain], 2200 m, Oct. 1947, *Cardona 2277* (VEN; the duplicate in MO represents a collection of the hybrid *H. huberi* × *H. pulchella*); Macizo del Chimantá, sector centro-meridional, amplio valle ubicado entre el borde nor-oriental del Torono-tepui y la sección central del Chimantá-tepui, drenando al Sur. Vegetación predominante de arbustales densos sobre diabasa y vegetación rupícola sobre terrazas rocosas de arenisca, c. 2100 m, 11.–15.2.1985, *Huber & al. 10176* (MO, VEN; the duplicate at NY represents a hybrid with *H. pulchella*).

Conclusion

Adding the three newly described species *Heliamphora uncinata, H. ciliata* and *H. huberi* to those recognised in the last treatments (Berry & al. 2005; McPherson 2006), the neotropical pitcher plant genus *Heliamphora* now comprises 18 species. Therefore, it represents the most species rich genus of the *Sarraceniaceae,* outnumbering the North American pitcher plant genus *Sarracenia* L., which includes eight species (Schnell 2002). Eleven of the currently known species of *Heliamphora* had been discovered just in the last few decades, and were described new to science in the past ten years (Nerz & Wistuba 2006; Nerz & al. 2006; Wistuba & al. 2005;

Carow & al. 2005; Nerz 2004; Wistuba & al. 2002; Wistuba & al. 2001; Nerz & Wistuba 2000). Considering the endemic distribution of the genus *Heliamphora* on the remote tepuis and slopes of the Guayana Highlands, and the inaccessibility of these regions, which are often only poorly explored, it may not be surprising if some more species will be discovered in the near future.

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Appendix: Identification list

The following specimens have been examined and annotated by the first author of this study:

Heliamphora ciliata: *Huber & al. 9917* (NY, VEN); *Huber & al. 9921* (holotype: VEN, isotypes: MO, NY).

Heliamphora exappendiculata: *Bernardi 796* (NY); *Cardona 51648* (VEN); *Huber 12091* (NY, VEN); *Steyermark & Wurdack 441* (NY, VEN); *Steyermark & Wurdack 1135* (NY, VEN); *Steyermark 74888* (NY, VEN); *Steyermark & al. 115934* (MO); *Steyermark & al. 128489* (MO, NY, VEN); *Steyermark & al. 132045* (MO); *Wurdack 34236* (NY, VEN); *Wurdack 34262* (holotype: NY; isotypes: F, NY, VEN).

Heliamphora folliculata: *Delascio 13036* (MO); *Delascio 13090* (MO, VEN); *Delascio 13137* (MO, VEN); *Holst & al. 2923* (MO, VEN); *Holst 3485* (MO, VEN); *Huber 12581* (VEN); *Liesner & al. 21105* (MO, NY, VEN); *Steyermark & al. 132007* (VEN); *Wistuba & al. Ap070101* (NY); *Wistuba & al. Mur080101* (holotype: VEN; isotype VEN).

Heliamphora glabra: *Clarke 11732* (MO); *Maguire & Maguire 40412* (holotype: NY).

Heliamphora huberi: *Cardona 2277* (VEN; the duplicate in MO represents a collection of the hybrid *H. huberi* x *H. pulchella*); *Huber & al. 10176* (MO, VEN; the duplicate in NY represents a hybrid with *H. pulchella*); *Huber 11366* (holotype: VEN, isotypes: MO, NY); *Huber 11526* (VEN; the duplicate in NY represents the hybrid *H. huberi* × *H. pulchella;* the duplicate in MO represents *H. puchella*); *Steyermark & al. 128666* (VEN (2 sheets), MO, NY).

***Heliamphora huberi* × *H. pulchella*:** *Cardona 2277* (MO; the duplicate at VEN represents *H. huberi*); *Huber & Dezzeo 8588* (MO, NY, VEN); *Huber & Colella 8699* (NY, VEN); *Huber & al. 10176* (NY; the duplicates at MO and VEN represent *H. huberi*); *Huber 11526* (NY; the duplicate in VEN represents the parent species *H. huberi*; the duplicate in MO represents *H. puchella*); *Steyermark & al. 128269* (MO, VEN; the duplicate in NY represents *H. pulchella*).

Heliamphora heterodoxa: *Davidse 4756* (MO); *Holst & al. 2173* (MO, VEN); *Holst 3587* (MO, VEN); *Hopkins & al. 9* (VEN); *Huber 9812* (MO, NY, VEN); *Huber 12509* (VEN); *Huber 12495* (VEN); *Kral 72201* (MO, VEN); *Kral & al. 81900* (NY, MO); *Maguire & Wurdack 33890* (M, NY, P, VEN); *Moore & al. 9750* (NY, VEN); *Ramirez 747* (VEN); *Ramirez 830* (VEN); *Ramirez 964* (VEN); *Ramirez & al. 4759* (VEN); *Steyermark & Nilsson 336* (NY, VEN); *Steyermark & Nilsson 337* (NY, VEN); Steyermark *& Nilsson 338* (VEN); *Steyermark & Nilsson 666* (NY, VEN); *Steyermark 59651* (F, NY); *Steyermark 59766* (holotype: F, isotype: NY); *Steyermark 59934* (F, NY, VEN); *Steyermark 60242* (F, NY); *Steyermark & Dunsterville 104240* (NY, VEN); *Steyermark & al. 115698* (VEN); *Steyermark & al. 115742* (MO, VEN); *Steyermark & Pruski 121104* (VEN).

Heliamphora minor: *Bogner 990* (M); *Brewer-Carias s.n.* (MO 2827006, NY *s.n.*, VEN 128435); *Cardona 2661* (NY, VEN); *Delascio 13762* (VEN); *Delascio 17041* (VEN); *Foldats 7008* (VEN); *Holst 3003* (MO, NY, VEN); *Huber & al. 8088* (VEN); *Luteyn & Steyermark 9590* (NY, VEN); *Oliva & Michelangeli 011* (VEN); *Prance & Huber 28244* (NY); *Schnee 1581* (MO); *Steyermark 93493* (NY, VEN); *Steyermark 93712* (NY); *Steyermark & al. 116001* (MO, VEN); *Tate 1126* (holotype: NY, isotype: NY); *Vareschi & Foldats 4835* (NY, VEN).

***Heliamphora pulchella*:** *Delascio 14661* (VEN); *Huber & Steyermark 6969* (VEN); *Huber & Steyermark 7083* (VEN); *Huber & Colella 8695* (MO, NY, VEN); *Huber & Colella 8748* (MO, NY, VEN); *Huber & al. 8870* (MO, NY, VEN); *Huber & Colella 8940* (VEN); *Huber 9279* (MO, NY, VEN); *Huber 9570* (NY, VEN); *Huber 11360* (MO, NY, VEN); *Huber 11422* (NY, VEN); *Huber 11526* (MO; the duplicate in NY represents the hybrid *H. huberi* × *H. pulchella;* the duplicate in VEN represents *H. huberi*); *Kral & al. 81913* (MO, NY); *Pruski & Huber 3569* (holotype: VEN, isotype: NY); *Steyermark & Wurdack 903* (NY, VEN); *Steyermark & Wurdack 987* (NY, VEN); *Steyermark 74904* (NY, VEN); *Steyermark 75776* (VEN, NY); *Steyermark 74904* (VEN); *Steyermark & al. 115758* (MO, VEN); *Steyermark & al. 115854* (MO, VEN); *Steyermark & al. 128068* (VEN); *Steyermark & al. 128087* (MO, NY); *Steyermark & al. 128269* (NY; the duplicates in MO and VEN represent the hybrid *H. huberi* × *H. pulchella*); *Steyermark & al. 128416* (MO); *Steyermark & al. 128417* (MO); *Steyermark & al. 128592* (MO, VEN); *Steyermark & al. 128772* (MO, NY, VEN); *Steyermark & al. 128976* (MO, NY, VEN); *Steyermark & al. 129895* (NY, VEN); *Wurdack & Steyermark 575* (NY); *Wurdack 34172* (NY, VEN); *Wurdack 34237* (NY, VEN).

Heliamphora uncinata: *Steyermark & al. 128568* (holotype: VEN, isotype: MO).