Heliamphora electrum (Sarraceniaceae), an enigmatic species of marsh pitcher plant from the Sierra de Lema of Venezuela

Michal R. Golos • School of Biological Sciences • University of Bristol • 24 Tyndall Avenue • Bristol BS8 1TQ • UK • michal.golos@bristol.ac.uk
Joachim Nerz • Jägerstraße 50 • 71032 Böblingen • Germany • joachim.nerz@onlinehome.de
François Sockhom Mey • 9 rue René Lothon • 27110 Epégard • France • meyfr@yahoo.fr
Andreas Wistuba • Friedhofweg 4 • 88437 Maselheim • Germany • andreas@wistuba.com

Keywords: Cerro Uei, Cerro Venamo, Guiana Highlands, new species, Sarraceniaceae, taxonomy, tepui, toponymy
Date Received: 10 November 2023
https://doi.org/10.55360/cpn531.mg102

Abstract: A new species of marsh pitcher plant, *Heliamphora electrum*, is described from the Sierra de Lema in Venezuela. It is distinguished most clearly from its closest congeners by the presence of bimorphic retentive hairs on the inner surface of the pitcher and in certain aspects of nectar spoon morphology. Known with certainty only from three localities, including Cerro Venamo and neighbouring Cerro Uei, and expected to be highly localised where it does occur, *H. electrum* is provisionally assessed as Endangered against the IUCN Red List criteria, with a proviso that the species' range may prove to be significantly wider than is currently appreciated.

Due to the confused toponymy of the Cerro Venamo region, the exact provenance of the original herbarium material of *Heliamphora electrum* – collected in the early 1960s by Julian Steyermark and colleagues – has been the subject of considerable debate. Drawing on a comprehensive review of historical documentary material, including maps, photographs, herbarium specimens, unpublished field notes, and contemporaneous literature, we clarify the original collecting localities of this species and thereby resolve a long-standing puzzle in *Heliamphora* phytogeography.

Introduction

Heliamphora (Sarraceniaceae) is a Neotropical genus of pitcher plants endemic to the Guiana Shield of northern South America. They are found on the summit plateaus and cliffs of the imposing table mountains of the region (known as 'tepuis') as well as in the surrounding uplands, predominantly in Venezuela but also extending into adjoining regions of Brazil and Guyana.

The most recent monograph of McPherson *et al.* (2011) recognised 23 species of *Heliamphora*, with several more included as incompletely diagnosed taxa. Little taxonomic work has been done on the genus since, with the notable exception of the description of *H. minor* var. *pilosa* by Fleischmann & Grande Allende (2012), and the clarification of the status of *H. heterodoxa*, which was originally established on the basis of hybrid material now understood to be *H. collina* × *H. purpurascens* (Wrazidlo 2019; Wrazidlo & Fleischmann 2019). The formal description of *H. electrum* herein brings the total number of recognised *Heliamphora* species to 24.

First collection from Cerro Uei: The earliest herbarium material known to us that is referrable to *Heliamphora electrum* was collected on 19 April 1960 by American botanist Julian Alfred Steyermark (1909–1988), the preeminent plant collector of the Venezuelan Guayana (see Davidse 1989; Huber 1995b:77), and Sven Adolf Natanael Nilsson (1929–2007), assistant in systematic botany (later docent) at Sweden's Uppsala University. The collections were undertaken as part of a joint expedition to the Sierra de Lema and Gran Sabana – both in southeastern Venezuela – between 13 April and 4 May 1960, by the Botanical Institute of Venezuela's Ministry of Agriculture and Livestock (Instituto Botánico, Ministerio de Agricultura y Cría) and the Institute of Systematic Botany at Uppsala University (Steyermark 1960; Steyermark & Nilsson 1962:59).

In total, 845 specimen numbers (not counting duplicates) were collected during the expedition (Steyermark 1960; Steyermark & Nilsson 1962:59; cf. Lasser 1971:17). These were the first botanical collections from the region (Brewer-Carías 1987:49), the results of which were published over the following years in the journal of the Venezuelan Society of Natural Sciences, yielding numerous botanical novelties (Steyermark & Nilsson 1962, 1963; Steyermark 1966a; see also Foldats 1961; Harling 1963). Separately, Nilsson published on aquatic fungi found during this expedition in the journal of the Swedish Botanical Society (Nilsson 1962), which later also carried a general account of his explorations in Venezuela (Nilsson 1964).

The specimens of *Heliamphora electrum* span three numbers and at least seven sheets (*Steyermark & Nilsson 336*, *337* & *338*, NY!×2, UPS!, US!, VEN!×3). Their collection locality is recorded as *ca.* 1100–1340 m on 'Uei-tepui', a rather obscure mountain near the frontier with Guyana. Steyermark initially used 'Uei-tepui' and 'Cerro Uei' interchangeably, both on herbarium labels and in the literature (Steyermark 1964b:212, 257, 1967:209, 254, 311, 339), before apparently settling on the latter name (Steyermark 1979:210, 1982:207). We have followed his example, as this avoids confusion with other mesas known as 'Uei-tepui' (see "Toponymy of Cerro Uei").

Several days after encountering *Heliamphora electrum*, Steyermark and Nilsson collected the earliest known herbarium specimens of *H. heterodoxa* from the Gran Sabana (and the first that match the widely accepted concept of this species sensu Wrazidlo & Fleischmann 2019; see "Materials and methods") (*Steyermark & Nilsson 666*, NY!, RSA!, UPS!, US!, VEN!). Nilsson (1964:220) alludes to the discovery of both of these species when he writes: "one of these *Heliamphora* species was also found both on a small plateau mountain and in a lower savanna area" (translated from Swedish). Nilsson goes on to make explicit mention of *H. electrum* on Cerro Uei: "On the plateau mountain Uei-tepui at km 125, *Heliamphora* and *Brocchinia* [Bromeliaceae] also occur, and a large number of endemic species were collected on its summit." (Nilsson 1964:222; translated from Swedish).

Second collection from Cerro Venamo: Though Steyermark and Nilsson had already reached Cerro Venamo during their 1960 expedition (when they botanised its northwestern slopes; Nilsson 1962; Steyermark & Nilsson 1962:61), it would not be until three years later that *Heliamphora electrum* was collected from there for the first (and apparently only) time. On this occasion, Steyermark travelled with the orchidologist husband-and-wife team of Galfrid Clement Keyworth "Stalky" Dunsterville (1905–1988) and Ellinor Freeman "Nora" Dunsterville (1904–2004) (see Pridgeon 1989; Romero-González 1989; Webb 1990). Together, they made 884 botanical collections (not counting duplicates) between 24 December 1963 and 15 January 1964, the vast majority on and around Cerro Venamo (Steyermark 1964a), including numerous taxonomic novelties (Robinson 1965; Taylor 1989; Dauphin & Ilkiu-Borges 2002; Romero-González *et al.* 2015).

Material of *Heliamphora electrum*, consisting of at least four sheets, was collected on 31 December from the southwestern part of Cerro Venamo at 1395–1400 m (Fig. 1; *Steyermark, Dunsterville & Dunsterville 92477*, K!, NY!, US!, VEN!). It is designated here as the type material of the species.

Steyermark botanised the region on several other occasions. This included an expedition of 5–11 March 1962 with Venezuelan botanist Leandro Aristeguieta (1923–2012), during which the pair collected 105 specimen numbers and once again reached the summit of Cerro Uei (Steyermark & Nilsson 1962:59; Steyermark 1964b:257–258), as well as a return trip with the Dunstervilles in December 1970 that included explorations of Cerro Uei's lower slopes. However, judging by the lack of preserved specimens, it appears that no *Heliamphora* were encountered on these occasions.

Discovery of a third population: Steyermark did not record coordinates for his early collections in the Sierra de Lema, leading to some uncertainty over his precise collecting localities (see "Collection localities of *Heliamphora electrum*"). A number of concerted efforts were made in the early-to-mid-2000s to relocate Steyermark's original *Heliamphora* populations from this region. However, helicopter surveys of the eastern part of the Sierra de Lema, close to the border with Guyana, did not reveal any evidence of habitat suitable for *Heliamphora* among the densely forested terrain (J. Nerz, pers. observ.).

A third population of *Heliamphora electrum* was eventually discovered on 11 February 2006, on an undetermined mesa some distance west of Cerros Uei and Venamo and lying roughly between Ptari-tepui and the settlement of Luepa, by a team comprising Joachim Nerz, Andreas Wistuba, and Urs Zimmermann. The exact coordinates of this site were not recorded and remain uncertain, but its elevation was estimated at roughly 1600 m; a population of *H. heterodoxa* was found at a slightly lower elevation nearby (see "Distribution and ecology").

Taxonomic treatment of *Heliamphora* from the Cerro Venamo region: Steyermark initially recorded the material from Cerro Venamo as an indeterminate *Heliamphora*, later identifying it as *H.* aff. *nutans* (Fig. 2).[1] Subsequently, labels affixed by botanists to Steyermark's specimens from Cerros Uei and Venamo have invariably assigned them to *H. heterodoxa* (see "Additional specimens examined"). Correspondingly, the few mentions in the literature of *Heliamphora* from the region follow this identification. For example, Cerro Venamo is given as a locality of *H. heterodoxa* in the treatment of the genus for *Flora of the Venezuelan Guayana* (Berry *et al.* 2005:141). Similarly, in a 2009 taxonomic paper describing three new species of *Heliamphora*, the range of *H. heterodoxa* is said to extend to Cerro Venamo at up to 1200 m elevation, and material from Cerro Uei (*Steyermark & Nilsson 336*, *337* & *338*) is explicitly assigned to that species (Fleischmann *et al.* 2009:276, 283; see also Fleischmann 2012).

While the important taxonomic works of Maguire (1978) and Steyermark (1984) do not discuss the presence of *Heliamphora* in the Cerro Venamo region, they both assign to *H. heterodoxa* var. *heterodoxa* specimens of *H. electrum* from Cerro Uei (*Steyermark & Nilsson 336* & *337* in Maguire 1978:53 and *Steyermark & Nilsson 338* in Steyermark 1984:307). No mention at all is made of Cerros Uei and Venamo in the subsequent popular treatments by Baumgartl (1993) and McPherson (2006).

Heliamphora electrum has circulated in the horticultural trade for some years under the informal names *H. collina* "Venamo top" and *H.* sp. Venamo.

[1] At the time, a conservative approach to *Heliamphora* taxonomy predominated, and many of the major tepuis remained unexplored. As such, only six species were recognised in the genus (see Steyermark 1951:241–242).

Figure 1: Holotype of *Heliamphora electrum* (*Steyermark, Dunsterville & Dunsterville 92477*), deposited at the herbarium of the Royal Botanic Gardens, Kew. The bimorphic retentive hairs are clearly discernible in this specimen; note also the long, creeping stem. The strongly infundibular form of the pitchers likely reflects the shady habitat at the collection site. Photograph by M.R. Golos.

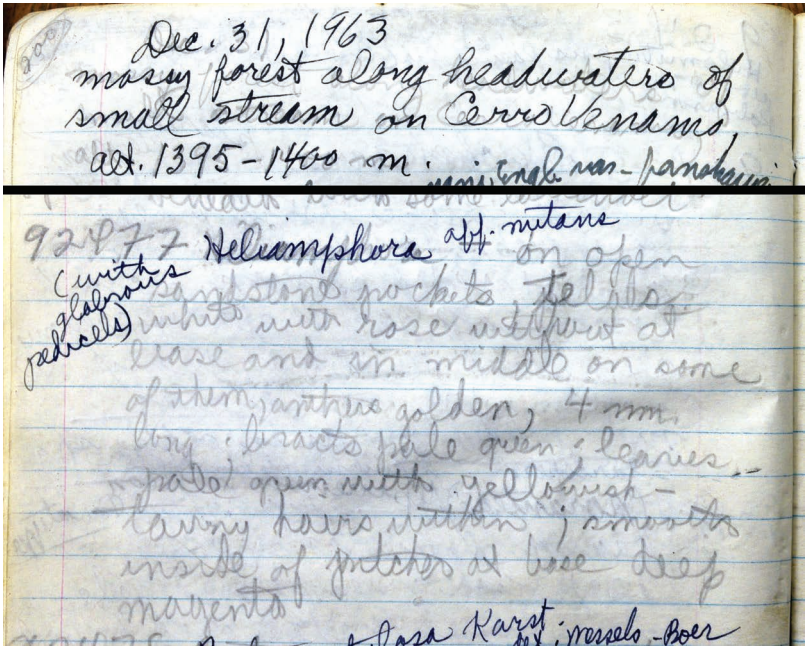


Figure 2: Excerpts from Steyermark's collections notebook for 1963–1964 (Steyermark 1964a), showing his original notes for the type collection number *Steyermark, Dunsterville & Dunsterville 92477*, including the collecting locality (top). It can be seen that he originally identified it only as an indeterminate *Heliamphora* and later appended "aff. *nutans*", this determination apparently based on its "glabrous pedicels". Photographs by M.R. Golos.

Geographical setting and toponymy

Sierra de Lema and Troncal 10: The Sierra de Lema[2] is a mountainous upland region that constitutes the northern limit of the Gran Sabana and forms the drainage divide between the basins of the Río Caroní to the south and the Río Cuyuní to the north (Fig. 3A; Schubert & Huber 1990:11; Huber 1995a:37; Brewer-Carías 2007, 2012). It is generally regarded as stretching between Cerro Venamo, on the border with Guyana, westwards towards the northern foothills of the Ptari massif and the Los Testigos chain of tepuis, a span of some 70–80 km (Matallana 1937:16, 61; Huber *et al.* 2001:17, 37; Brewer-Carías 2012:74), though by some definitions it continues to Auyán-tepui (Huber 1995a:37) or, when considering the entirety of the Caroní–Cuyuní drainage divide, all the way to a point near the confluence of the Río Caroní with the Río Paragua, a length of more than 200 km (Aguerrevere *et al.* 1939:532; Brewer-Carías 2011:2, 2012:74–76).

[2] Sometimes written as 'Serranía de Lema' or translated as 'Lema Range' (Schubert & Huber 1990:60–63) or 'Lema Mountains' (Pérez 2018a, b). The etymology is uncertain but may derive from a mining concession of the late 19th century owned by an individual or company named 'Lehman' (Charles Brewer-Carías, pers. comm.; see Brewer-Carías 2011). The range is known as 'Pürema' by the native Pemón (Antonio Hitcher, pers. comm.).

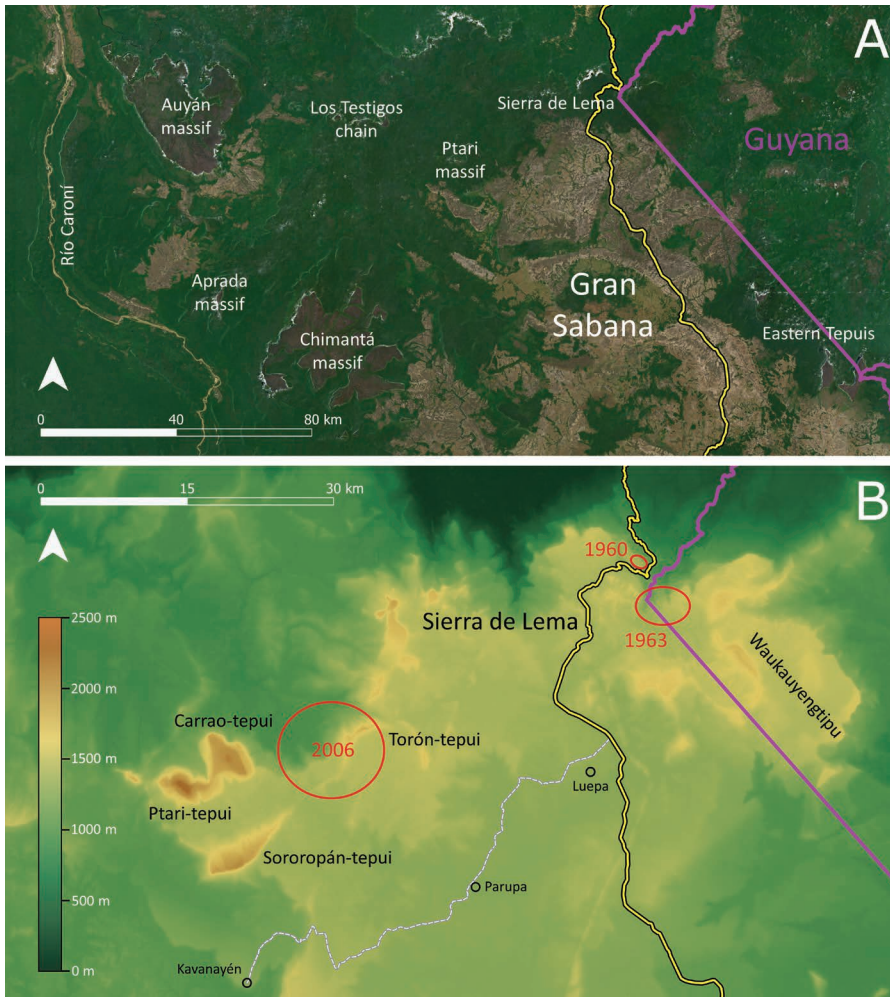


Figure 3: (A) Satellite overview of the Gran Sabana, Sierra de Lema, and adjacent areas, showing the locations of several well-known tepui complexes, the western course of the Río Caroní, and the variable degree of vegetation coverage across the region. The modern route of Troncal 10 is indicated by a yellow and black line; though essentially the same, it differs very slightly from that of the original dirt road used by Steyermark, Nilsson, and the Dunstervilles. The international borders between Venezuela, Guyana, and Brazil are indicated on the right, including the full extent of the straight-line section of the Schomburgk Line. (B) Terrain elevation map of the Sierra de Lema and northern Gran Sabana, showing Waukauyengtipu and the constituent tepuis of the Ptari massif. The discovery dates and approximate localities of the three recorded *Heliamphora electrum* populations are indicated in red, the size of each ellipse reflecting the respective level of uncertainty. The largely unpaved road to Kavanayén is indicated with a dashed line. Maps prepared by M.R. Golos.

The Sierra de Lema consists primarily of Precambrian sandstones of the Roraima Group, which form flat-topped mesas of intermediate elevation (generally *ca.* 1000–1600 m). These are interspersed with more rounded summits formed from Mesozoic diabase intrusions (Steyermark 1979:210; Huber 1995a:37). Unlike the much drier Gran Sabana to the south, the Sierra de Lema is almost entirely forested (Fig. 3A), does not generally host human settlements, and remains very little explored.

The region was largely inaccessible to outsiders prior to the creation of a north–south road beginning in the 1950s (Huber *et al.* 2001:11). At the time of Steyermark's collections in the early 1960s, this was little more than a dirt path and stretched for just over half of its intended length, the final 58 km being traversable only by cars equipped with a winch and 4-wheel drive (see Steyermark & Nilsson 1962:59; Dunsterville 1979; Dunsterville & Dunsterville 1988:161–163). Today it is a modern, paved, two-lane highway known as Troncal 10 (Trunk Road 10) and remains the only major road in the region (Fig. 3A). Now, as in Steyermark's time, points of interest along this route are referenced by their distance, in kilometres, measured southwards from the small town of El Dorado (06°43'N 61°38'W) along the road's winding path through the lowlands of the Río Cuyuní basin and thence the uplands of the Sierra de Lema and Gran Sabana (see Marrero 1995, 1997; Huber *et al.* 2001).

The toponymy of the Sierra de Lema, like that of much of the Pantepui region, remains greatly confused (Vila 1960:59; Huber *et al.* 2001:124; Wrazidlo *et al.* 2022). Unfortunately, the two names used by Steyermark to refer to the collection localities of *Heliamphora electrum* – 'Cerro Venamo' and 'Cerro Uei' – both have convoluted histories, leading to much debate about the species' provenance.

Toponymy of Cerro Venamo: The name 'Cerro Venamo'[3] is commonly associated with the Guyana–Venezuela border area, and specifically the northern terminus of the straight-line section of the 'Schomburgk Line' (or 'Venamo Line'; Maguire 1970:86) that runs northwestwards from the international tripoint on the summit plateau of Roraima-tepui (Fig. 3A; Marrero 1991:13, 93; Gazsó 1995:25, 191; Huber & Berry 1995; Anderson 2003:879). However, this northern terminus does not obviously correspond to any particular mountain, being defined instead by the supposed westernmost source of the eponymous Río Venamo (determined in 1905 to lie at 05°56'55.4"N 61°23'24.7"W[4]; see "The Geographer" 1963:2, 5).

A rather small mesa centred on 05°58.7'N 61°23.9'W (*ca.* 1400 m high) is the only clearly delimited, tepui-like mountain in the immediate vicinity of this point. A number of recent sources identify this mesa as the 'Cerro Venamo' botanised by Steyermark in the 1960s (Dauphin & Ilkiu-Borges 2002; Wrazidlo *et al.* 2022). In contrast, some maps apply this name to the irregular and roughly circular mountain complex centred on 05°56.6'N 61°24.7'W (*ca.* 1600 m high), directly SSW of the aforementioned mesa (Pérez 2018a, b). A still different localisation was provided by Rice (2018) who – citing data collected by Lee Braithwaite – placed Cerro Venamo in a far more southerly position (05.49°N 61.14°W), close to the foothills of the Ilú–Tramen massif. The stated height of Cerro Venamo has also varied widely between sources, with 1563 m (e.g., Matallana 1937:68, map; Vila 1960:377) and 1890 m (e.g., MTDGS 1964; Marrero 1997:37; Dauphin & Ilkiu-Borges 2002)

[3] Rarely written as 'Cerro del Venamo' and sometimes translated as 'Mount Venamo' or 'Venamo Hill'. Its Pemón name is occasionally transcribed as 'Wenamuk' or 'Venamuk' (Marrero 1996, 1997:37).

[4] Judging by satellite imagery, these coordinates appear to be inaccurate, whether considering the Río Venamo proper or its major local tributary, the Río El Danto (lit. 'The Tapir' in Venezuelan Spanish; see "Collection localities of *Heliamphora electrum*") (M. Golos, pers. observ.).

being two oft-repeated figures, though Steyermark himself gave an estimate of *ca.* 1600–1650 m (Steyermark 1979:210, 1982:207; Huber 1995a:37).[5]

Waukauyengtipu (lit. 'mountain of the place of the butterfly' in Pemón; Kelloff *et al.* 2011:44), a geographically distinct forested escarpment (*ca.* 1600 m high) southeast of the aforementioned tepui-like mesa and lying predominantly in Guyana (Fig. 3B; Wrazidlo *et al.* 2022), has at times been equated with Cerro Venamo (e.g., Rice 2018; Rull *et al.* 2019a:19; Rull & Vegas-Vilarrúbia 2020:375). It was the small Venezuelan portion of Waukauyengtipu that was designated as 'Cerro Venamo Natural Monument' in 1990 (see "Conservation status"). Waukauyengtipu has been the target of two botanical expeditions to date – in 1997 and 2019 (Czechowicz 2022). Both expeditions found *Heliamphora* growing on its upper reaches (for photos see Clarke 2008; Wrazidlo 2021). Specimens of this taxon collected during the first trip (*Clarke 5832*, K!, L!, NY!, US!) were initially identified as *H. nutans* (Kelloff *et al.* 2011:46, 167), a determination likely made by default, that species being the only *Heliamphora* recognised from Guyana at the time (David Clarke, pers. comm.). In actuality, these plants appear to represent a variant of *H. heterodoxa* (Wrazidlo 2021) and remain the only confirmed population of this species from Guyana.

Cerro Venamo derives its name from that of the Río Venamo (known as the 'Wenamu River' in Guyana), of which it is ostensibly the source (Vila 1960:377). For this reason, it is sometimes called 'Wenamu Head' in Guyana (Stainforth 1966). The river, in turn, is named for *wenamuk* ('rations' in Pemón), apparently in an allusion to the historical practice of fisherman who, travelling from afar, would bring plentiful rations so they could continue fishing on the river for extended periods (Agard *et al.* 2019:187). Though little has been written about Cerro Venamo, it – *sensu lato* – has notably been the target of a number of detailed studies of bryophytes (Robinson 1965; Désamoré *et al.* 2010; Riina *et al.* 2019:133) and scorpions (González-Sponga 1972, 1978, 1981; Rojas-Runjaic & De Sousa 2007; Ochoa & Rojas-Runjaic 2019), though it is not always clear which particular mountain was sampled.

Toponymy of Cerro Uei: Cerro Uei[6] is an altogether more obscure mountain. The name makes an early appearance in the works of Capuchin missionary Baltasar de Matallana (1906–1966), who was one of the earliest foreigners to explore the region and in 1937 produced the first detailed map of the wider Gran Sabana (Matallana 1937; see Brewer-Carías 2012). Matallana wrote that what the locals called 'Uei-tepui' was the easternmost of four major promontories of the Sierra de Lema visible when approaching from the north, and that its name (*uei* being the Pemón word for 'sun') derives from its easterly, sunrise-facing position (Matallana 1948). He described the mountain as an "immense bastion" ("*inmenso baluarte*") that the missionaries called 'La Torre' (lit. 'The Tower') on account of its shape (Matallana 1948). Moving westwards, the other three promontories were said to be Cerros Manakauarái, Kurek, and Muná (Matallana 1937:13–14, 1948).[7] The likeliest candidate for Matallana's Uei-tepui would seem to be the *ca.* 1600 m high plateau centred on 06º00.0'N 61º27.2'W, though this name is today applied to the small, sharply pointed peak at 05°59.3'N 61°29.5'W (Fig. 4; *ca.* 1000 m high; Charles Brewer-Carías, pers. comm.).

[5] Due to its confused toponymy, this entire region of intermediate-elevation mesas appears as 'Cerro Venamo Area' on some maps (Pérez 2018a, b). The pioneering Capuchin missionary Baltasar de Matallana regarded Cerro Venamo as forming part of a larger range that he called 'Sierra del Venamo' (Matallana 1937:61, map); variant names include 'Serranía Venamo' (Weidmann 1986:159) and 'Venamo Range' (Schubert & Huber 1990:12).

[6] Also written as 'Uei-tepui'; variant transcriptions include 'Wei' and 'Uey'.

[7] The etymologies of the Pemón names 'Manakauarái', 'Kurek', and 'Muná' are, respectively, 'vagina', a type of tree known locally as *kurek*, and 'termite' (Matallana 1937:75–76; Charles Brewer-Carías, pers. comm.).

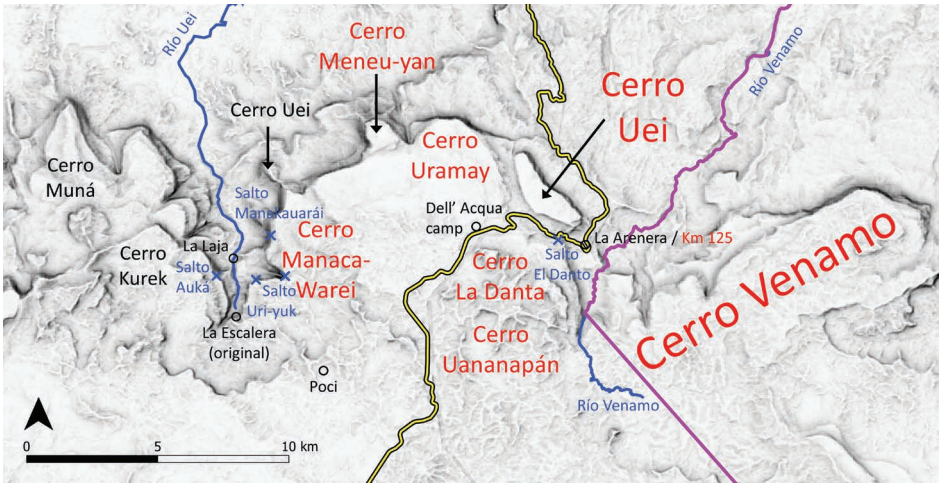


Figure 4: Topographic relief map of the eastern Sierra de Lema, showing in red our understanding of Steyermark's application of local toponyms (the localisations of his Cerros La Danta, Uei, and Venamo being the most confident and those of Cerros Meneu-yan and Uramay the least). Major rivers and waterfalls are indicated in blue. Other localities discussed in the text are shown in black. The locations of Cerros Kurek and Muná have been inferred from the descriptions appearing in Matallana (1937, 1948) and should be regarded as conjectural. The location of Poci is based on Bohn *et al.* (2020:S-6–7). The remaining localities are sourced from Marrero (1997), Huber *et al.* (2001), Brewer-Carías (2012), and personal communications with the last author. Map prepared by M.R. Golos.

Confusingly, the eponymous Río Uei[8], a tributary of the Río Cuyuní, has its source some distance to the south of the aforementioned 'Cerros Uei' (see Lasso *et al.* 2009:28, 42, 129–130). Specifically, it arises near a site called 'Poci' (Vila 1960:377), thence emerging between Cerros Kurek and Manakauarái[9], above a pair of adjacent sites known as 'La Laja' (lit. 'The Slab') and 'La Escalera' (lit. 'The Ladder' or 'The Staircase'; Fig. 4), both of these latter names having their origins in early explorations of the region by missionaries in the 1930s (see Huber *et al.* 2001:127–128; Brewer-Carías 2012). This can lead to further confusion, as the toponym 'La Escalera' was later transposed – and is now more commonly applied – to the stretch of Troncal 10 that steeply ascends the Sierra de Lema some 10–15 km to the east (see Schubert & Huber 1990:62; Huber *et al.* 2001:43; Sanoja 2009; Brewer-Carías 2012:76–80).[10]

[8] Often spelled 'Uey' (Lasso *et al.* 2009) and sometimes erroneously transcribed as 'Buey' after the Spanish word for 'ox' (Charles Brewer-Carías, pers. comm.); the variant 'Huey' is also occasionally seen (e.g., Machado-Allison *et al.* 2000). The river has also appeared on maps under the name 'Lema' (Pérez 2018a, b).

[9] The extensive valley formed by the Río Uei features four major waterfalls, of which three have recorded Pemón names: 'Auká' in the west, 'Manakauarái' in the northeast, and 'Uri-yuk' in the southeast (Fig. 4), meaning, respectively, 'radiance' or 'splendour', 'vagina', and most likely 'place covered by sedges' (Charles Brewer-Carías, pers. comm.; see Oliva-Esteve 2000:44–45 4 figs.; Brewer-Carías 2012:73–80 figs. 1–2, 11, 14).

[10] The mesas roughly spanning the gap between the original and new 'La Escaleras' appear on some maps as the 'La Escalera Mountains' (Pérez 2018a, b). The original La Escalera consisted of a ladder of sticks and vines that made possible the scaling of a cerro known as 'Arakansak' (lit. 'closed' in Pemón; see Matallana 1937:14).

The Cerro Uei of the Sierra de Lema should not be confused with other regional (and generally more prominent) mesas that are commonly or occasionally known by the name 'Uei-tepui', of which there are at least four: Serra do Sol (*ca.* 2150 m; 05°01'N 60°37'W; the southernmost member of the Eastern Tepuis chain, on the Brazil–Venezuela border, known in Venezuela as 'Cerro El Sol'); Cerro El Sol (*ca.* 1750 m; 06°06.8'N 62°33.0'W; a satellite peak off the northern flank of Auyán-tepui); Wei-Assipu-tepui (*ca.* 2400 m; 05°13.2'N 60°42.3'W; a minor tepui lying just northeast of Roraima-tepui, also known as 'Roraimita' or 'Little Roraima'); and Wei-tepui (*ca.* 1650 m; 05°16.7'N 61°46.0'W; a small forested ridge located east of the Chimantá massif, also known as 'La Aguja', lit. 'The Needle'; Office of Geography 1961:236; Brewer-Carías 2012:77 fig. 9; Antonio Hitcher, pers. comm.).[11]

Mountains botanised by Steyermark and colleagues: There has been much debate as to the precise localities visited by Steyermark in the Sierra de Lema, particularly the mountain he called Cerro Venamo. The original account of his explorations (Steyermark & Nilsson 1962) offers probably the clearest exposition of the relevant topography. Since this paper is difficult to source and many of the mesas mentioned are highly obscure, with names that have very seldom (if ever) appeared in the literature since, we have reproduced below selected parts to aid understanding of the original collecting localities:

> "To the inhabitants of the region, the prominent cerro towering northwest of the old road camp at kilometer 125 is known as Uei-tepui. Immediately to the east and southeast are the ramifications of the large sandstone mountain of Cerro Venamo, part of which lies in Venezuela. […]
>
> To the west of Uei-tepui and occupying the headwaters of the Rio Cuyuni and Rio Chicanán is a large undulating mesa known on the maps as Sierra de Lema and consisting of a number of escarpments and promontories, given individual names by the inhabitants of the region. Viewed from east to west, the various cerros or promontories which presented themselves were named by the Indians of the region as follows: Uei-tepui, Uramay-tepui, Meneu-yan-tepui, Manaca-Warei-tepui, and La Escalera. These promontories lie between Cerro Venamo and the main part of the Sierra de Lema, and are drained by the Rio Uei and Rio Cuyuni proper." (Steyermark & Nilsson 1962:61)

The "old road camp" that is used as a point of reference is stated to be at Km 125 along what is now Troncal 10. By modern reckoning, this would place it around 05°57.6'N 61°25.5'W, very close to the former main camp for workers of the construction firm Dell' Acqua (Fig. 4), which paved and carried out major improvements to the road in 1985–1989 (see Huber *et al.* 2001:42). Crucially, however, the official starting point for progressive distances along Troncal 10 was changed some years after Steyermark's initial collections, reducing them by *ca.* 7–8 km (Dunsterville & Dunsterville 1978b:442, 1988:152, 220; Dunsterville 1981:18). As such, Km 125 – an important reference point for numerous botanical collections – became Km 117 (Dunsterville & Dunsterville 1978b:442, 1988:152).

This would place Steyermark's road camp at approximately 05°57.8'N 61°23.0'W, in the vicinity of La Arenera (lit. 'The Sand Pit') at Km 117.9 (Fig. 4), a radio antenna communications station

[11] This shared toponymy has in the past led to confusion between Cerro Uei and Serra do Sol (see e.g., Duno de Stefano *et al.* 2002:129, Duno de Stefano 2013:176, and Graham 2019:167, who all give coordinates for Serra do Sol when citing herbarium material from Cerro Uei and its surroundings collected by Steyermark and Nilsson).

and park ranger outpost occupying a site cleared for early road construction in 1965–1970 and later used as a quarry during paving in 1985–1989 (see Marrero 1997:38; Huber *et al.* 2001:41). From here, it is clear that the "prominent" and "towering" mesa lying to the northwest that Steyermark called 'Uei-tepui' is that centred on 05°58.7'N 61°23.9'W (Fig.4; *ca.* 1400 m in elevation). And from this it follows that Steyermark's Cerro Venamo, which he described as an expansive mountain straddling the Guyanese-Venezuelan border whose slopes were located immediately to the east and southeast, must be that indicated in Fig. 4 (*ca.* 1650 m in elevation). The heights of these two mesas, as gleaned from digital terrain model data, are broadly congruent with the elevations later given by Steyermark of 1300 m for Cerro Uei and 1650 m for Cerro Venamo (Steyermark 1979:210, 1982:207).

It should be noted that Steyermark & Nilsson (1962) used the toponym 'La Escalera' in its original sense, hence its stated westerly position relative to Cerro Uei and close proximity to 'Manaca-Warei-tepui' (Fig. 4) – clearly a variant transcription of Matallana's 'Manakauarái' (see "Toponymy of Cerro Uei"). The remaining two mountains mentioned by the authors – 'Meneu-yan' and 'Uramay' (Fig. 4; the former perhaps meaning 'ink container'; cf. *menu-yen* in Armellada & Olza 1999:252) – are very obscure and may represent highly localised toponyms with no extant currency (Charles Brewer-Carías, pers. comm.).[12]

Galfrid and Ellinor Dunsterville, who accompanied Steyermark on his 1963–1964 expedition, wrote widely about their orchid-hunting trips across Venezuela. They consistently described the form of the 'Cerro Venamo' they jointly botanised in terms congruent with the mountain identified as such here, emphasising its "less vertical-sided" appearance (Dunsterville 1966:59) and regarding it as "not very impressive" (Dunsterville & Dunsterville 1982:710, 1988:255). Their most detailed description appeared in the third volume of *Venezuelan Orchids Illustrated*:

> "[Cerro Venamo] is long and fairly wide, with a gently undulating top culminating at about 6000 ft [1830 m; *sic*!]. It lies on the border of British Guiana. Its base is covered with dense rain forest which becomes progressively more dwarf (and more dense) as altitude increases. The top bears lighter scrubby forest, tall scrubs and grass with some patches of taller forest. The flanks are very rich indeed in orchids, in common with the adjoining region known as "Km. 125 south of El Dorado"." (Dunsterville & Garay 1965:33)

In a later account, Galfrid Dunsterville adjusted the estimated elevation of Cerro Venamo to the more accurate 5500 ft (*ca.* 1680 m), adding: "it has a number of cliffs and bluffs, but does not have the dramatic cliff-walls and bare top of the typical "tepui" type of table mountain" (Dunsterville 1970:190). Elsewhere, the couple wrote of "a small elevation called Cerro Wei that faces the much larger Cerro Venamo whose base is only a mile [1.6 km] away" (Dunsterville & Dunsterville 1978b:442, 1988:152), in general agreement with our identifications of these two mountains.

[12] In the near vicinity, Steyermark and Nilsson also distinguished – and botanised – Cerro La Danta (lit. 'The Tapir' in Venezuelan Spanish) and Cerro Uananapán (rarely 'Wananapán'; lit. 'Casupal', or 'place of the *casupo*', a name given to a number of species of Heliconiaceae and Marantaceae with large, superficially banana-like leaves that are traditionally used for wrapping food and other items; Charles Brewer-Carías, pers. comm.; Matallana 1937:80). Based on information recorded in Steyermark (1960), these two names appear to have been used to denote, respectively, the northern and southern extents of a single mountain complex south of Steyermark's Cerro Uei (Fig. 4). Steyermark regarded Cerro Uananapán as the highest element of the eastern Sierra de Lema at *ca.* 1700 m (Steyermark 1979:210, 1982:207), in broad agreement with earlier authors who gave even greater elevations of 1763–1800 m (see Matallana 1937:14, 68, map; Vila 1960:377), though these appear to be significant overestimates, at least when considering the area explored by Steyermark and Nilsson.

Our localisation of Steyermark's Cerro Venamo is also notably in line with maps appearing in the works of both Steyermark and the Dunstervilles, which consistently show Cerro Venamo as lying *east* of Troncal 10 (Dunsterville & Garay 1966, 1972, 1976; Dunsterville & Dunsterville 1973, 1988; Steyermark 1976:map no. 6) – not west as does Steyermark's Cerro Uei.

The mesa identified here as Steyermark's Cerro Venamo lies almost entirely within Guyana, with only its westernmost projections extending into Venezuela. Some years later, Steyermark explicitly listed Cerro Venamo as a Guyanese element of the sandstone tepui formations (Steyermark 1986b:317). Similarly, the Dunstervilles described Cerro Venamo as lying "entirely inside Guyana" (Dunsterville & Dunsterville 1978b:442, 1988:152). This discrepancy can be explained by the fact that detailed maps of the region were not available to them during the expedition; this, combined with the lack of physical boundary markers, meant that "even the pinning down of an international boundary [was] vague" (Dunsterville 1970:190).[13]

Our identification of Steyermark's Cerro Venamo is notably at odds with previous literature. Dauphin & Ilkiu-Borges (2002) determined the location of Steyermark's Cerro Venamo to be 05°59'N 61°23'W (i.e., what we identify as his Cerro Uei), the elevation of which they gave as 1890 m. Though Wrazidlo *et al.* (2022) correctly pointed out that the stated elevation is much too high for the mesa at these approximate coordinates, they agreed with Dauphin and Ilkiu-Borges that it was indeed the 'Cerro Venamo' visited by Steyermark in 1963–1964 and estimated for it a revised maximum elevation of *ca.* 1420 m based on digital terrain model data – significantly lower than that given by Steyermark for his Cerro Venamo. Similarly, our identification differs from the region indicated – very approximately – on the maps of McPherson *et al.* (2011:243, foldout), which is shown to lie some distance northwest of the northern terminus of the straight-line section of the 'Schomburgk Line'. However, our interpretation appears to be in line with the maps shown in Brewer-Carías (2012:77) and descriptions in other works (e.g., Weidmann 1986:167).

Collection localities of *Heliamphora electrum*: Cerro Uei and particularly Cerro Venamo are substantial mountains, having summit areas of 2.8 km^2 and *ca.* 50 km^2, respectively (M. Golos, pers. observ.). It would therefore be useful to identify the precise localities from which the existing herbarium specimens of *Heliamphora electrum* were collected.

Steyermark's collections notebook covering the first expedition to Cerro Uei (Steyermark 1960), though helpful in understanding the overall route taken by him and Nilsson, does not appear to provide clues on specific localities beyond those already found on the relevant herbarium labels. Nilsson gave a talk about his botanical explorations of Venezuela at the Botanical Society of Stockholm (Botaniska Sällskapet i Stockholm) on 20 March 1964, during which he presented numerous colour photographs (Anon. 1965:253). If still extant, these photographs might shed light on the precise route taken by Steyermark and Nilsson. However, Nilsson's archives were apparently not donated to Uppsala University Library (Anna Fredriksson, pers. comm.) and, despite much effort, it has not been possible to trace them.

From the available evidence, it is only possible to state that *Heliamphora electrum* was collected from Cerro Uei's heavily vegetated summit plateau, somewhere between the southeastern escarpment and the summit, and apparently also from the summit area itself (Fig. 3B; see "Additional specimens examined"). More generally, it is clear that Steyermark and Nilsson mainly explored the area around what was then known as Km 125 (where they collected *H. electrum*), though they

[13] During Steyermark's 1963–1964 expedition, the Dunstervilles relied on "a small map showing the boundary splitting [Cerro Venamo] in half", leaving them "to hope that anything we found on the western side would be legitimately Venezuelan" (Dunsterville 1970:190).

briefly ventured as far south as Km 150 (as was) near the settlement of Luepa (where they collected *H. heterodoxa*), at which point contiguous forest gave way to savanna (Steyermark 1960; Steyermark & Nilsson 1962:60; Nilsson 1964:221).

Considerably more can be said about the collecting localities of the 1963–1964 expedition. There, the route taken by Steyermark and the Dunstervilles can be gleaned – with substantial granularity – from the former's collections notebook (Steyermark 1964a) supplemented by the latter's published expedition reports and related writings (esp. Dunsterville & Garay 1965; Dunsterville 1970:189–190; Dunsterville & Dunsterville 1978a:312–314, 1988:144–146).[14] From these, it is clear they followed watercourses to ascend the westernmost slopes of Cerro Venamo, very close to the Guyana–Venezuela border.

The trio appear to have made three camps during their ascent of Cerro Venamo. The first was the 'Río Venamo Camp' at *ca.* 1000 m, at the side of what Steyermark (1964a) described as the "right-hand (west) fork" (looking upstream) of the Río Venamo, and which the Dunstervilles called a "tributary of Río Venamo" (Dunsterville & Garay 1965:292) and "the small stream of the Río Venamo itself" (Dunsterville & Dunsterville 1982:710, 1988:255). Presumably, this refers to the Río El Danto, a tributary of the Río Venamo well known for its series of picturesque waterfalls – collectively known as Salto El Danto – at Km 119.7 (Fig. 4; 05°57'51"N 61°23'29"W; see Duellman 1997:7–8 fig. 6; Marrero 1997:38; Huber *et al.* 2001:41 fig.). What Steyermark (1964a) referred to as the "left-hand (east) fork" of the Río Venamo must have been the Río Venamo proper (which would more accurately be called the *south* fork; the junction between the two is at 05°57'03"N 61°22'43"W). A 'Second Camp' was established at *ca.* 1400 m, halfway between the first camp and what Steyermark (1964a) described as the summit (1575 m high) of the southwestern portion of Cerro Venamo, and a 'Last Camp' was made near the aforementioned summit (see Dunsterville & Garay 1965:124, 176, 204).

The collection locality of *Heliamphora electrum* is recorded as "mossy forest along headwaters of small stream on Cerro Venamo" (Fig. 2; Steyermark 1964a). Notably, this stream is not described as a 'fork' of the Río Venamo – a nomenclature used consistently up to that point – suggesting that it was a smaller watercourse. The sequence of collecting localities recorded by Steyermark (1964a) directly preceding and following this site would seem to point to the minor tributary that flows into the Río Venamo at 05°57'01"N 61°22'42"W as the likeliest candidate.[15] Moving upstream along this tributary (in a southeasterly direction) would soon lead to an extensive area of dwarfed vegetation – clearly visible in satellite imagery – on Cerro Venamo's somewhat uneven summit plateau. This patch of dwarfed vegetation extends southwards for several kilometres to 05°55'24"N 61°21'34"W and agrees with the elevation of *ca.* 1400 m recorded at the type locality of *H. electrum*. Moreover, assuming physiognomic constancy over the intervening years[16], this area would appear to be a good match for the relevant habitat described in Steyermark (1964a). As such, it

[14] The papers of Galfrid Dunsterville, who kept detailed notes for each of his expeditions, would likely be another important source, but these were apparently destroyed in a fire at a Venezuelan storage facility, with no copies known to exist (Gustavo Romero, pers. comm.). Though the Dunstervilles published several photographs from their 1963–1964 expedition to Cerro Venamo (see Dunsterville & Garay 1966:57–58; Dunsterville & Dunsterville 1982, 1988:iv, 254–256), these do not appear to reveal much about the precise localities they botanised.

[15] Judging by digital terrain model data, this tributary additionally offers the lowest-gradient route of ascent of Cerro Venamo's summit area (M. Golos, pers. observ.).

[16] This seems likely; the same area of dwarfed vegetation is already clearly discernible in Landsat imagery from the mid-1980s (a particularly clear image is available for 5 April 1987 – product identifier L1: LT05_L1TP_233056_19870405_20201014_02_T1; see USGS 2023).

seems plausible – even probable – that the type material of *H. electrum* was collected within Guyanese rather than Venezuelan territory (Fig. 3B).

Materials and methods

The description of *Heliamphora electrum* is based on field observations carried out in the Sierra de Lema in February 2006 by J. Nerz and A. Wistuba, as well as examinations of the type specimens and other representative herbarium materials (see "Additional specimens examined") and live cultivated plants of verified provenance (from the vicinity of Ptari-tepui). Small-scale structures such as glands and hairs were examined with a 30× hand lens and under a light microscope.

While preparing the manuscript, the authors reviewed all relevant *Heliamphora* material deposited at K, L, MO, P, TNS, and VEN herbaria (acronyms follow Thiers 2023). Additionally, online scans were consulted of material at B, BRIT, F, GH, IAN, MICH, NY, RSA, TEX, UPS, US, and WIS. Steyermark's collections notebook for 1963–1964 (Steyermark 1964a), held at the archives of the Missouri Botanical Garden (MBG) and including annotations and corrections by later authors, was also consulted, as were photographs of his 1960 notebook (Steyermark 1960), also deposited at MBG.

For scanning electron microscopy (SEM), samples taken from cultivated material were fixed in 4% glutaraldehyde in 0.1 M phosphate buffer, dehydrated via an ethanol dilution series (*ca.* 1–3 hr in each of 25, 50, and 75% ethanol, overnight in 100% ethanol), critical-point dried (Leica CPD300), and sputter coated (Quorum Q150R ES) with 10 nm of gold–palladium. Samples were imaged under a Zeiss Evo 15 SEM at an accelerating voltage of 20 kV, working distance of 8.5–9.5 mm, and with a 100 pA probe.

The species concept of *Heliamphora heterodoxa* used herein follows that of Wrazidlo & Fleischmann (2019); that is, it corresponds to the familiar taxon found in the uplands of the Gran Sabana and Sierra de Lema but does not encompass plants from the cliffs of Ptari-tepui (the species' type locality), which are instead understood to originate from a hybrid swarm involving *H. collina* and *H. purpurascens*. Wrazidlo & Fleischmann (2019) proposed a replacement type from the Gran Sabana (*Steyermark, Dunsterville & Dunsterville 104240*, NY!, S n.v., US!, VEN n.v.) to conserve the name *H. heterodoxa* in line with the general understanding of this taxon in both the recent botanical literature and within the horticultural community. However, two votes on the proposal by the Nomenclature Committee for Vascular Plants narrowly failed to gain consensus to recommend its acceptance (Applequist 2023:909) and the status of this taxon therefore remains formally unresolved.

Maps were created with QGIS 3.28 Firenze (QGIS 2022) using the MapTiler v4.7.0 plugin (specifically the OpenStreetMap, Satellite, and Terrain vector basemaps; MapTiler 2023; OpenStreetMap contributors 2023) and the Relief Visualization Toolbox v0.9.6 plugin (specifically the Archaeological (VAT) preset for steep terrain; Kokalj *et al.* 2023). EarthExplorer was consulted extensively for high-resolution satellite imagery, including Esri World Imagery and historical Landsat datasets (USGS 2023). The international border between Guyana and Venezuela followed and shown herein is that established by the 1899 Paris Arbitral Award and widely recognised internationally (see Anderson 2003:879) but rejected by the Venezuelan government, which instead recognises the western two-thirds of Guyana as part of its own territory, which it calls 'Guayana Esequiba' (often appearing on Venezuelan maps as 'Zona en Reclamación').

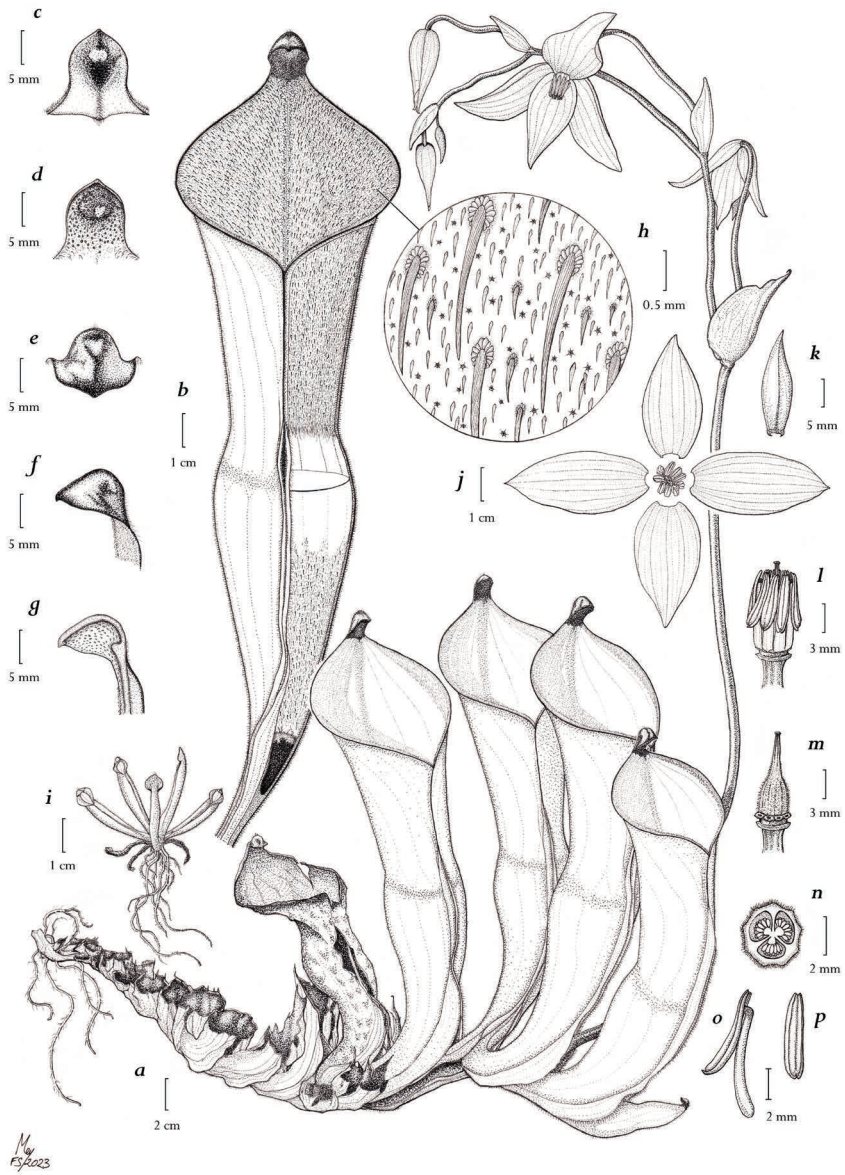


Figure 5: *Heliamphora electrum* Golos, Nerz, Mey & Wistuba. (a) Mature flowering plant with creeping stem. (b) Pitcher showing detail of exterior (left) and interior (right), including distribution of retentive hairs and internal water level. (c–f) Detail of nectar spoon in dorsal (c), ventral (d), superior (e), and lateral (f) views. (g) Nectar spoon in lateral section, showing shallow nectar chamber and glands thereof. (h) Detail of retentive hairs of central portion of inner trapping surface. (i) Juvenile plant. (j) Exploded view of perianth and central reproductive organs. (k) Bract. (l) Pistil surrounded by stamens (following removal of tepals). (m) Pistil (following removal of stamens). (n) Ovary in transverse section. (o) Stamen. (p) Anther. Illustration by F.S. Mey.

Heliamphora electrum Golos, Nerz, Mey & Wistuba, *spec. nov.* (Figs. 5–9)
Type: VENEZUELA: Estado Bolívar, Cerro Venamo (parte Sur-Oeste [southwestern part]), [c]erca de los Límites con la Guayana Inglesa [near the border with British Guyana], bosque muscoso a lo largo de las cabeceras de una pequeña quebrada arriba de la ladera escarpada de arenisca [mossy forest along the headwaters of a small stream above the steep sandstone slope], 1395–1400 m, 31 December 1963, *Steyermark, Dunsterville & Dunsterville 92477* (**holotype** K! [s.n.]; **isotypes** NY! [#02710934], US! [#01017942/2583962], VEN! [#85143]) [long creeping stem with 3–5 mature pitchers and inflorescence (K, NY, US), or same but lacking substantial stem (VEN); label reads: "In open sandstone pockets; rare and local; tepals white with rose[,] without at base and in the middle of some of them; anthers golden, 4 mm long; bracts pale green; leaves pale green with yellowish-tawny hairs within; smooth inside of pitcher at base deep magenta"; identified as indeterminate *Heliamphora* initially, as *H.* aff. *nutans* on account of "glabrous pedicels" by J.A. Steyermark, 1964 (NY, VEN), as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and as *H. heterodoxa* by both J.A. Steyermark, 1978 (VEN), and by A. Fleischmann, March 2009 (NY)].
– *H. heterodoxa* var. *heterodoxa* auct. non Steyerm.: sensu Maguire (1978:53–54, figs. 45E–H [=*H. chimantensis*], 46A–B [=*H. heterodoxa*] & 47E–H [=*H. heterodoxa*]), quae pro parte = *H. chimantensis*, *H. electrum*, *H. heterodoxa*, ?*H. collina* & ? *H. collina* × *H. purpurascens*
– *H. heterodoxa* var. *heterodoxa* auct. non Steyerm. (1951:239): sensu Steyermark (1984:303, 305, 307, 311), quae pro parte = *H. chimantensis*, *H. electrum*, *H. glabra*, *H. heterodoxa* & ? *H. collina* × *H. purpurascens*
– *H. heterodoxa* auct. non Steyerm.: sensu Fleischmann *et al.* (2009:283), quae pro parte = *H. electrum*, *H. heterodoxa*, *H. purpurascens*, ?*H. collina* & ? *H. collina* × *H. purpurascens*

Figure 6: *Heliamphora electrum* growing among *Stegolepis* plants. The characteristic bimorphic retentive hairs are clearly visible on the inner pitcher wall. Photograph by J. Nerz.

Diagnosis: Differs from *Heliamphora collina* Wistuba, Nerz, S.McPherson & A.Fleischm. in having (differences in parentheses) pitchers with uniformly bimorphic retentive hairs in upper portion of interior, large golden and minute white, the former emerging from conspicuous protuberances (vs. monomorphic in upper portion, only lengthening towards water line, minute, white, without distinct protuberances), and nectar spoon arising from a short stalk, with a short apical tip and shallow nectar chamber (vs. nectar spoon arising directly from the pitcher neck or from a very short stalk, laterally appressed at rear, without apical tip, and with a well-developed nectar chamber).
Description: Herbaceous perennial. *Rhizomes* conspicuous, branching, plants forming dense clumps over time and developing creeping stem to at least *ca.* 30 cm long. *Pitchers* tubular, elongated, basal third to half infundibular, slightly ventricose, contracting at waterline to form a dainty waist, gradually widening again towards the mouth, up to 20–25(–40) cm tall, up to 5.5 cm wide in the upper part, interior and exterior yellowish-green suffused orange to red when growing under moderate light, burgundy throughout under intense light, major veins and particularly midrib often noticeably darker than rest, especially in developing pitchers; two discrete lengths of retentive hairs evenly distributed throughout interior surface down to the drainage slit, the more numerous shorter hairs *ca.* 0.2 mm long and white, the longer 1–2 mm long and white upon opening, turning golden with age, each emanating from conspicuous, often dark red protuberance; larger hairs diminishing in size towards margins and below nectar spoon but otherwise consistent across vast majority of exposed interior surface; retentive hairs ending in abrupt but irregular line directly below nectar spoon; exterior pitcher surface sometimes bearing conspicuous extrafloral

Figure 7: A clump of *Heliamphora electrum* growing at the base of a large *Stegolepis* plant. Note the generally light colouration of the pitchers. Some of the more shaded traps near the rear have taken on a wide-mouthed, infundibular form similar to that of the holotype. Photograph by J. Nerz.

nectaries either side of the midrib, surface scarcely covered by bifid white trichomes *ca.* 0.2 mm long when growing under moderate light, significantly more developed under intense light with developing pitchers puberulous; pitcher opening dipping markedly at front; narrowly oval pore or drainage slit, 1.5 mm long, 1–1.5 mm wide, hidden in the ventral suture of the compressed alae at about half of the pitcher length. *Alae* 2, conspicuous, *ca.* 1 cm wide at the base, graduating into the ventral pitcher surface at between half and 2/3 of the pitcher length, margins bearing 1 mm long cilia. *Nectar spoon* helmet-shaped, arising from a broad, up to 1 cm wide base forming a short stalk and variably bent forward; 0.9–1 cm long and 0.8–1 cm wide including a short apical tip *ca.* 0.5 mm long; orange to burgundy; rear of the nectar spoon very sparsely covered with *ca.* 0.2 mm trichomes at the base near the midrib when growing under moderate light, sometimes conspicuously hairy under intense light; abaxial surface of nectar spoon with numerous round nectar glands 0.05–0.1 mm in diameter, shallow nectar chamber *ca.* 1 mm deep. *Inflorescence* a one-sided 3–7-flowered raceme, *ca.* 43–82 cm long, scape terete, glabrous, *ca.* 5 mm in diameter near the base. *Pedicels* terete, glabrous, 1.5–9.5 cm long. *Bracts* subtending the flowers, ovate with an acute sometimes recurved apex, lowermost bract much larger, developed as a very rudimentary pitcher with small alae and a minute filiform hood instead of a round pitcher mouth with a nectar spoon, *ca.* 3.8–6 cm long, rarely a fully developed pitcher (cf. *Steyermark & Nilsson 338*, VEN!), subsequent bracts 1.2–3.5 cm long. *Tepals* 4(–5), petaloid, ovate-lanceolate, inner narrower than outer and with a less acute apex, first and largest flower with tepals 3–5.5 cm long, 1–2.7 cm wide, white to rose-white at anthesis, becoming pale green and persisting to fruiting, without nectaries on adaxial surface. *Stamens* 8–9, filaments 7–8 mm long, anthers 4–8 mm long, 1.5 mm wide, basifixed, poricidal, oblong-lanceolate in outline. *Ovary* 3-celled, densely pubescent, 4.5–5 mm long, 3 mm in diameter. *Style* glabrous, up to 6 mm long. *Capsule* and s*eeds* not documented in detail.

Etymology: The specific epithet *electrum*, used here as a noun in apposition, is the Latin name for the naturally occurring alloy of gold and silver; the word is used in the same sense in English. It here alludes to the distinctive combination of yellow macro-hairs and white micro-hairs that form the lustrous indumentum of the inner trapping surface of the pitchers.

Phenology: Little is known of the phenology of this species. Herbarium specimens that include floral material were collected in the months of April and December, and fruiting plants with ripe seeds were found during field observations in February 2006 (J. Nerz & A. Wistuba, pers. observ.).

Distribution and ecology: *Heliamphora electrum* is thus far known only from the upper reaches of three mesas in the Sierra de Lema of Bolívar state, Venezuela: Cerro Uei and neighbouring Cerro Venamo, both close to the Guyanese-Venezuelan border (where the species was collected in 1960 and 1963, respectively), and an undetermined third mountain some distance west, in the general vicinity of Ptari-tepui (where it was observed in 2006; Fig. 10).[17] Given the very close proximity of the first two sites to Guyanese territory, it is likely that this species also occurs in that country, not least on the central and eastern parts of Steyermark's Cerro Venamo, which lie entirely within Guyana. *Heliamphora electrum* has a confirmed elevational range of *ca.* 1100–1400 m, though it might occur as high as *ca.* 1600 m based on the estimated elevation of the undetermined westernmost locality.

[17] As such, it is the second-northernmost known *Heliamphora* species after *H. minor* on the Auyán massif (specifically Auyántepui and its northern satellite mesa Cerro La Luna; McPherson *et al.* 2011:305).

Figure 8: *Heliamphora electrum* growing alongside *Orectanthe sceptrum*. This clump shows well-developed nectar spoons. A juvenile pitcher is visible at bottom-right. Photograph by A. Wistuba.

Figure 9: A richly pigmented specimen of *Heliamphora electrum*, showing the morphological plasticity of these plants. Note the almost complete absence of a nectar spoon in the pitchers on the right and left as compared to the well-developed appendage of the central pitcher, as well as differences in retentive hair development. A sympatric heather (*Ledothamnus* sp.) is visible just above the pitchers. Photograph by A. Wistuba.

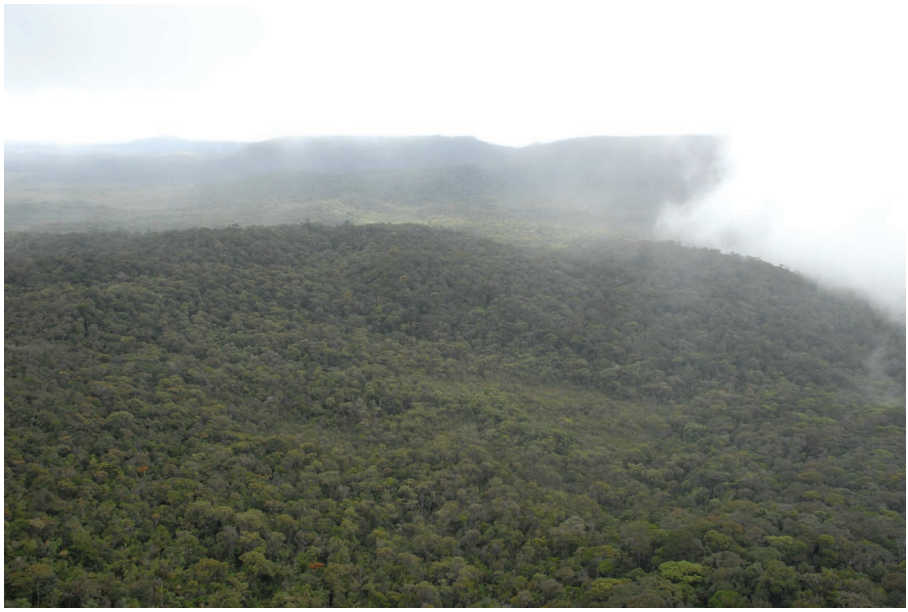


Figure 10: Aerial view of the undulating and predominantly forested landscape of the Sierra de Lema in the vicinity of the *Heliamphora electrum* site discovered in 2006. Photograph by J. Nerz.

According to the original herbarium labels, the type material of *Heliamphora electrum* was collected from the southwestern part of Cerro Venamo, from "mossy forest along the headwaters of a small stream above the steep sandstone slope" (translated from the original Spanish) at 1395–1400 m. The plants were described as "rare and local" and were found in "open sandstone pockets" (Fig. 1). The specimens from Cerro Uei were collected from "exposed places" in dwarf forest on the mountain's upper reaches, at *ca.* 1100–1340 m, where they grew with *Brocchinia* (Steyermark 1960; Nilsson 1964:222; see "Additional specimens examined").

Steyermark's collections notebook from his 1963–1964 expedition to the Sierra de Lema (Steyermark 1964a) provides insight into the flora occurring sympatrically and in the vicinity of the *Heliamphora electrum* population found on Cerro Venamo. Vascular plants listed as collected on the same day and from the same locality as the type material include the bladderwort *Utricularia jamesoniana* (Lentibulariaceae), as well the following taxa (grouped by family): *Bactris ptariana* (Arecaceae); *Chorisepalum acuminatum* and *C. carnosum* (Gentianaceae); *Clusia* sect. *Euclusia* sp. and *Moronobea jenmanii* var. *fanshawei* (both Clusiaceae); *Couma rigida* (Apocynaceae); *Dacryodes steyermarkii* (Burseraceae); *Epidendrum vespa* (=*Prosthechea vespa*), *E.* sp., *Lepanthopsis* sp., *Octomeria* aff. *filifolia*, *O.* aff. *minor*, and *O.* sp. (all Orchidaceae); *Eugenia kaieteurensis* and *Myrcia bolivarensis* (both Myrtaceae); *Philodendron englereanum* (Araceae); *Phoradendron crassifolium* (Santalaceae); *Pradosia beardii* (Sapotaceae); *Sarcopera tepuiensis* (Marcgraviaceae); *Sloanea crassifolia* (Elaeocarpaceae); *Sphaeropteris macrosora* var. *macrosora* (Cyatheaceae); *Tillandsia stenoglossa* (Bromeliaceae); and various unidentified ferns. Non-vascular flora collected concurrently include the liverwort *Herbertus juniperoideus* (Herbertaceae) and the lichens *Herpothallon sanguineum* (Arthoniaceae), *Parmelia* sp. (Parmeliaceae), *Sticta* sp. (Peltigeraceae), and *Tomasellia*

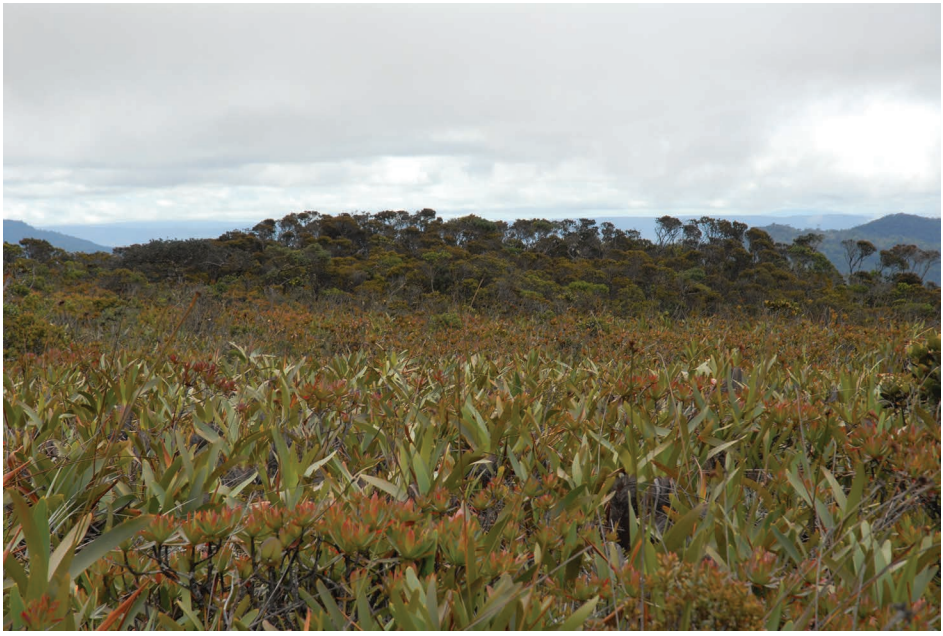


Figure 11: The clearing in which *Heliamphora electrum* was discovered in 2006. Some areas have more woody elements consisting of dense *Bonnetia* stands. The undulating profile of the Sierra de Lema can be seen in the distance. Photograph by J. Nerz.

sparsella (Mycoporaceae), in addition to numerous indeterminate taxa from both groups (Steyermark 1964a).

The *Heliamphora electrum* population discovered in February 2006 was found in an isolated patch of open marshland (roughly estimated at 500 × 500 m; Fig. 11) surrounded by a large area of contiguous forest, and lying approximately between Ptari-tepui and the settlement of Luepa in the vicinity of a crescent-shaped elevation (up to *ca.* 1800 m high) sometimes referred to as 'Muna-' and/or 'Torón-tepui' (Fig. 3B; MTDGS 1964; Marrero 1996, 1997:91; Pérez 2018a, b). The habitat was dominated by *Stegolepis* (Rapateaceae), with *Brocchinia reducta* and *Bonnetia* sp. (Bonnetiaceae) also being common (Fig. 12); other characteristic Pantepui taxa such as *Ledothamnus* sp. (Ericaceae) and *Orectanthe sceptrum* (Xyridaceae) were also in evidence (Figs. 8–9). The size of this *H. electrum* population is uncertain, but it may have comprised several hundred individuals. Precise elevation readings were not taken, but the site was slightly higher than comparable nearby open patches and is estimated to have been at *ca.* 1600 m. A typical variant of *H. heterodoxa* was found in a similar (though larger) clearing at a lower elevation of *ca.* 1300–1400 m in the vicinity of the same mesa, slightly southeast of the *H. electrum* colony, where it grew with *Drosera* cf. *roraimae* (Droseraceae) (Figs. 13–14).[18] No obvious hybrids were found in either population.

Natural hybrids: No natural hybrids involving *Heliamphora electrum* have been recorded with certainty, though the close proximity of some *H. heterodoxa* populations makes it possible that the

[18] Interestingly, there exists herbarium material of typical *Heliamphora heterodoxa* from an even more northerly site within the Sierra de Lema, collected at *ca.* 1650 m elevation (see *Huber 12495,* K!; *Kral 81881*, BRIT n.v., GH!, MICH!, NY!, US!).

two species occasionally interbreed. A herbarium specimen from Cerro Uei with atypical nectar spoon morphology and uniformly short retentive hairs in the upper part of the pitcher (*Steyermark & Nilsson 336*, NY!) might conceivably represent such a cross.

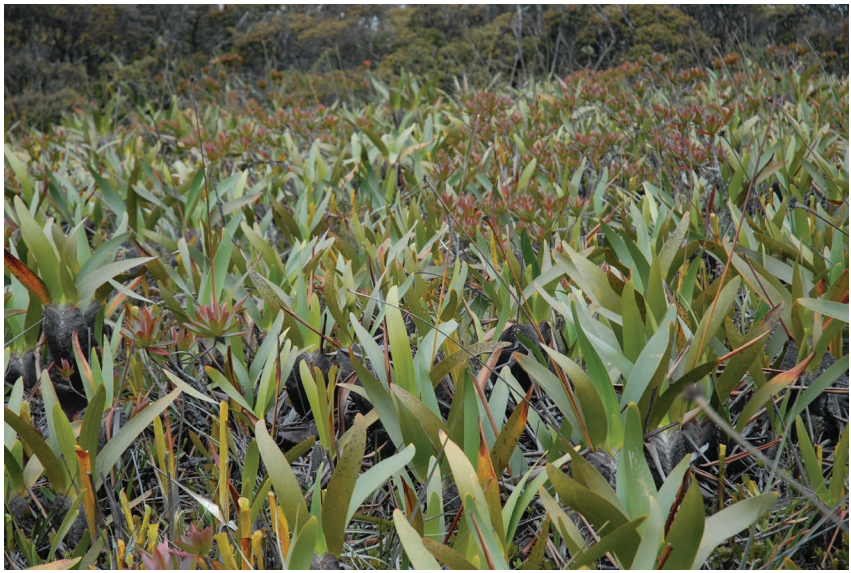


Figure 12: Natural habitat of *Heliamphora electrum*: a marshland forest clearing dominated by *Stegolepis* as well as *Bonnetia* and *Brocchinia reducta*. Photograph by J. Nerz.

Figure 13: *Heliamphora heterodoxa* found near the base of the mesa hosting *H. electrum*. Photograph by J. Nerz.

Conservation status: *Heliamphora electrum* is known with certainty from only three localities within the Sierra de Lema and the status of two of these populations has not been verified since the early 1960s. Though its natural range is likely to be considerably more extensive than currently appreciated, its distribution is probably highly fragmented and localised given its apparent confinement to forest clearings, which are few in number and limited in total extent across the otherwise entirely forested terrain of the Sierra de Lema (see "Ecological context"). On one of the three occasions that this species has been encountered in the wild, it was described as "rare and local" (*Steyermark, Dunsterville & Dunsterville 92477*, K!, NY!, US!, VEN!). Its hypothesised scarcity is further supported by the fact that the 2006 discovery of a third population followed numerous failed attempts to relocate this taxon.

The Sierra de Lema remains almost entirely pristine and *Heliamphora electrum* is unlikely to be threatened by human encroachment in the foreseeable future. However, as with many Pantepui endemics, it is likely to be negatively impacted by climate change over the coming decades, due to its limited opportunity to migrate upwards in response to warming (see Rull *et al.* 2019b).

Virtually the entirety of the Sierra de Lema falls within the bounds of Canaima National Park, which since its 1975 expansion has encompassed both the western population of *Heliamphora electrum* discovered in 2006 and Steyermark's Cerro Uei, though Steyermark's Cerro Venamo falls just outside its limits (see Lazo *et al.* 2004). A mountain referred to as 'Cerro Venamo' has since 1990 been designated as a Venezuelan Natural Monument on account of its rich cloud forest biodiversity and is therefore nominally also afforded a certain level of protection (Huber 1995d:200; Bevilacqua *et al.* 2019:390). However, this protected area does not correspond to the mountain

Figure 14: Dwarfed plants of *Heliamphora heterodoxa* growing in a more exposed location at the same site; note the darker pitcher colouration and more compact growth. Photograph by A. Wistuba.

botanised by Steyermark. Instead, it comprises only the southwesternmost escarpments of Waukauyengtipu, being enscribed by a triangle with vertices at 05º45'N 61º17'W and the points on the straight-line section of the 'Schomburgk Line' directly north and east of these coordinates (see Zambrano *et al.* 2004). This area consists largely of savanna and gallery forest associated with the headwaters of the Río Uchii (see Wrazidlo 2021; Wrazidlo *et al.* 2022) and is therefore unlikely to harbour *H. electrum*.

The population of *Heliamphora electrum* recorded from Steyermark's Cerro Venamo is likely to extend into Guyana, and the type material may indeed originate from there (see "Collection localities of *Heliamphora electrum*"). The relevant Guyanese territory lacks formal protected status but is divided between two land titles issued in 1991 to the indigenous communities of Kaikan and Paruima (see Agard *et al.* 2019).

Given all of the above, and based on observations of *Heliamphora electrum* made *in situ* together with information gleaned from voucher specimens, we tentatively assess the species as Endangered (EN) against the IUCN 3.1 Red List criteria (IUCN 2012). Specifically, it satisfies criteria EN B1ab(ii,iii,v)+2ab(ii,iii,v), i.e., the species has an extent of occurrence (EOO) of <5000 km^2, an area of occupancy (AOO) of <500 km^2, and is known from no more than five locations, with projected declines in area of occupancy, quality of habitat, and number of mature individuals.

Additional specimens examined:

***Heliamphora electrum*—**VENEZUELA: Uei-tepui [Cerro Uei] summit (NY, VEN) or between southeastern slope and summit (US), between Luepa and Cerro Venamo [*sic*], exposed places, dwarfed forest, elevation variously given as 1100–1300 m (US), 1220 m (UPS), and 1340 m (NY, VEN), 19 April 1960, *Steyermark & Nilsson 336* (NY! [#02710924], UPS! [#V-062206], US! [#01017937/2486460], VEN! [#46485]) [mature pitchers with inflorescence and stem fragment (all sheets); label reads: "Outer tepals 4.5–5.5 cm long, 2.2–2.8 cm wide; inner tepals 5–6 cm long, 1.8–2.2 cm wide, white suffused with pink"; identified as *H. heterodoxa* initially, as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and as *H. heterodoxa* by A. Fleischmann, March 2009 (NY); NY specimen has uniformly short retentive hairs in the upper part of the pitcher and a more elaborated nectar spoon morphology with a pronounced central concavity]; Uei-tepui [Cerro Uei] summit, between Luepa and Cerro Venamo [*sic*], dwarfed forest, 1340 m, 19 April 1960, *Steyermark & Nilsson 337* (NY! [#02710932], VEN! [#46484]) [two separate pitchers (one dissected), separate inflorescence (NY), clump of mature pitchers with two inflorescences and substantial creeping stem (VEN); label reads: "smaller extreme encountered [...]. Inner tepals 3.5–3.9 cm long, 1.6–1.8 cm wide; outer tepals 3.8 cm long, 1.6 cm [wide]"; identified as *H. heterodoxa* initially, as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and as *H. heterodoxa* by A. Fleischmann, March 2009 (NY)]; Uei-tepui [Cerro Uei] summit, between Luepa and Cerro Venamo [*sic*], dwarfed forest, 1340 m, 19 April 1960, *Steyermark & Nilsson 338* (VEN! [#46487]) [etiolated rosette of mature pitchers with long inflorescence bearing well-developed bract pitcher; label reads: "Note scape with one leaf attached 3/4 way up"; identified as *H. heterodoxa* initially].

***Heliamphora collina*—**VENEZUELA: altiplanicie ubicada al Sur del Terekeyuren-tepui [high plateau located south of Tereke-yurén-tepui], aprox. 40 km al NE de la Misión de Kamarata [approx. 40 km NE of the Kamarata Mission], vegetación predominante herbáceo-fruticosa y arbustiva [predominantly herbaceous-fruticose and shrubby vegetation], 05°51'N 62°03'W, 1780 m, 15 January 1986, *Huber & Gorzula 11147* (NY! [#02710906], VEN! [#284439]) [stem with mature pitcher(s), inflorescence, and substantial stem with roots (both sheets); label reads: "Formando pequeños grupos en la sombra de arbustos, no muy frecuente. Cisternas y opérculo

verde. Flores blancas con estambres amarillos." (Forming small groups in the shade of shrubs, not very frequent. Pitcher and nectar spoons green. White flowers with yellow stamens.); identified as *H. heterodoxa* by J.A. Steyermark, 1986, and as *H. collina* by A. Fleischmann, March 2009 (NY); paratype]; Camarcaibarai-tepui [=Kamarkawarai-tepui], southwest facing shoulder [see Steyermark 1986a], scrubby wet savanna, 05°52'N 62°01'W, 1800 m, 22 May 1986, *Steyermark, Liesner & Holst 132007* (L! ex U [#U.1733185/006992], MO! [#MO-1551313/3335924], NY! [#02710907], US! [#00692699/3205724], VEN! [#240832]) [mature pitchers with inflorescence, with or without substantial stem (all sheets); label reads: "Common"; identified as *H. heterodoxa* by J.A. Steyermark, 1986, and as *H. collina* by A. Fleischmann, March 2009 (NY); paratype]; Camarcaibarai-tepui [=Kamarkawarai-tepui], southwest facing shoulder [see Steyermark 1986a], 05°52'N 62°01'W, 1800–1825 m, 22–24 May 1986, *Steyermark, Liesner & Holst 132045* (MO n.v. [#MO-1551316/3384073], NY! [#02710908], VEN! [#248354]) [stem with mature pitcher(s), inflorescence, and substantial stem with roots (NY, VEN); label reads: "Pitchers elongated with small nectar appendage. In shaded depression of forest of *Bonnetia roraimae* of recumbent stems of trees and shrubs."; identified as *H. heterodoxa* var. *exappendiculata* by J.A. Steyermark, 1986, and as *H. collina* by A. Fleischmann, March 2009 (NY); paratype]; Murisipan-tepui, savanna-covered southern projection [see Steyermark 1986a], 05°51'N 62°02'W, 1700 m, 26 May 1986, *Steyermark, Liesner & Holst 132114* (**holotype** VEN! [#243155]; **isotypes** BRIT n.v. ex VDB [#420925], MO n.v. [#MO-1551309/3335925], NY! [#02684234]) [clump of dwarfed mature pitchers with inflorescences (NY, VEN); label reads: "common in savanna"; identified as *H. heterodoxa* by J.A. Steyermark, 1986, and as *H. collina* by A. Fleischmann, March 2009 (NY)].

Heliamphora heterodoxa (sensu Wrazidlo & Fleischmann 2019)—GUYANA: Waukauyengtipu, 20 km W [of] Paruima, wet savanna with *Xyris* & *Brocchinia*, 05°49'58"N 61°14'05"W, 1430 m, 18 July 1997, *Clarke 5832* (K! [s.n.], L! ex U [#U.1733182/0080530], NY! [#02710930], US! [#00723770/3426064]) [clump of mature pitchers with inflorescence (all sheets); label reads: "Insectivorous herb; stems & bracts red, sepals white with pink tinges, stamens yellow, carpels green"; identified as *H. nutans* by D. Clarke, 1997, and by Kelloff *et al.* (2011:167), and as *H. heterodoxa* by A. Fleischmann, March 2009 (NY)]. VENEZUELA: [Gran Sabana], northeast of Luepa, vicinity of camp 150 at Km 150 in valley of savanna of Río Uarama below Uarama-tepui, depressed open area of wet savanna, 1220 m, 25 April 1960, *Steyermark & Nilsson 666* (NY! [#02710933], RSA! [#RSA0270707/190614], UPS! [#V-062382], US! [#01017938/2486461], VEN! [#46486]) [mature pitchers with inflorescences and partial stem with roots (all sheets); label reads: "Tepals white, the inner ones with pale pink, the outer deep rose-purple without"; floral material in envelope attached to VEN annotated by J.A. Steyermark, 1983: "estambres 8" (8 stamens); identified as *H. heterodoxa* by J.A. Steyermark, 1960, as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and as *H. heterodoxa* by A. Fleischmann, March 2009 (NY)]; Gran Sabana, en el drenaje de las cabeceras del Río Aponguao [in the drainage of the headwaters of the Río Aponguao], cerca del Km 145 al sur de El Dorado [near Km 145 south of El Dorado], altiplanicie del suelo arenoso [high plateau of sandy soil], sabana pantanosa con *Heliamphora heterodoxa* y *Cottendorfia* [swampy savanna with *Heliamphora heterodoxa* and *Cottendorfia*], 1350–1400 m, 22 December 1970, *Steyermark, Dunsterville & Dunsterville 104240* (**proposed holotype of *H. heterodoxa*** [see Wrazidlo & Fleischmann 2019] VEN n.v.; **proposed isotypes** NY! [#02710929], S n.v. [#S-PL-12817], US! [#01017946/2621844]) [mature pitchers with inflorescence and stem with roots (NY, US); label reads "common" and gives "cono-ya-dá" as local Arekuna (Pemón) name for plant; pollen figured in Maguire (1978:44 fig. 46A–B, 45 fig. 47E–H)

where “excessively large” grains noted (see pp. 41, 51 table II); identified as *H. heterodoxa* by J.A. Steyermark, as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and as *H. heterodoxa* by A. Fleischmann, March 2009 (NY)]; Gran Sabana, Km 137 along El Dorado – S[anta] Elena [de Uairén] road, open savanna, 1420 m, 16 November 1978, *Luteyn, Lebrón-Luteyn & Steyermark 6277* (NY! [#02710927]) [mature pitchers with inflorescences; label reads: “Clump-forming herb. Tepals white suffused with pink at base. Common locally.”; identified as *H. heterodoxis* (*sic*) by J.A. Steyermark, 1978 and confirmed as *H. heterodoxa* by A. Fleischmann, March 2009]; Gran Sabana, between Ciudadela and junction of road to Kavanayén at Km 146, swampy savanna on same side of road as Ciudadela, 1250 m, 18 January 1980, *Steyermark & Pruski 121104* (VEN! [#134824]) [mature pitchers with inflorescence and substantial stem with roots; label reads: “frequent in swamp”; floral material in envelope annotated by J.A. Steyermark: “estambres 9” (9 stamens); identified as *H. heterodoxa* initially]; [Gran Sabana], Km 135 of road El Dorado – S[anta] Elena de Uairén, wet savanna, 1400 m, 22 November 1980, *Maas & Steyermark 5367* (K! [s.n.], L! ex U [#U.1733186]) [mature pitchers with inflorescence and partial stem with roots (both sheets); label reads: “Pitcher plant with green leaves, lid (operculum) purple, rhachis purple-red, flowers white to pinkish white”; identified as *H. heterodoxa* by J.A. Steyermark, 1980]; Gran Sabana, alrededores del Río Aponguao [around the Río Aponguao], cruce con la carretera El Dorado – Sta. Elena [junction with the El Dorado – Santa Elena de Uairén road], cerca de la Ciudadela y debajo del Cerro donde se encuentra El Fuerte Mariano Montilla [near the Ciudadela and under the hill where the ‘Mariano Montilla’ fort is located], sitio muy húmedo; sabana abierta [very humid site; open savanna], 1250 m, 18 November 1981, *Burandt Jr., Casadiego, Díaz, Campins & Decker V1055* (MO! [#MO-1551295/3503609], UCOB n.v.) [clumps of mature pitchers with inflorescences; label reads: “Planta rizomatosa; hojas tubulares, rojas en el ápice con un apéndice color rojo con forma de gorro; perianto de 2 series 2 más 3, ó 3 series de 2 más 2 grandes, y 3 pequeñas. Las 2 hojas perianticas de serie inferior colour blanco con un poco de tinte rosado, las series interiores aún más blancas; filamentos color verde claro; anteras amarillas; escapo, ramificaciones de la infl. y yemas color rojo.” (Rhizomatous plant; leaves tubular, red at apex with a red cap-shaped appendage; perianth of 2 series 2 plus 3, or 3 series of 2 plus 2 large, and 3 small. The 2 lower series perianth leaves white with a little pink tinge, the inner series even whiter; filaments light green; anthers yellow; scape, branches of inflorescence and buds red.); identified as *H. heterodoxa* by J.A. Steyermark, 1987]; [Gran Sabana], east side of road to Santa Elena [de Uairén], 146 km S of El Dorado, near Cuidadela, no elevation data, 3 July 1982, *Hopkins, Fish & Barreira 9* (NY! [#02710935], VEN! [#179423]) [mature pitchers with stem and inflorescence (both sheets); label reads: “In large clumps in marshy vegetation, common but no seedlings seen. Buds pink, open flowers pink and white, becoming yellowy-green. Voucher for collections of mosquitoes.”; identified as *H. heterodoxa* initially and confirmed by A. Fleischmann, March 2009 (NY)]; Gran Sabana, Via Kavanayén [road to Kavanayén], entre el campamento Parupa y Kavanayén [between Parupa camp and Kavanayén], aproximadamente a 55 km E del Fuerte Luepa [around 55 km E of Fort Luepa], ‘El Jardin’ ([Pemón name:] Guamu-pe = Loma de Guamu [Guamu Hill]) [local area so called for its abundance of flowers throughout the year; see López & Ramírez, 1998:16], vegetación achaparrada [stunted vegetation], no elevation data, 23 February 1983, *Ramírez 747* (VEN! [#198951]), no elevation data, 24 June 1983, *Ramírez 830* (VEN! [#198950]), 1350 m, 5 October 1984, *Ramírez 964* (NY! [#02710928], VEN! [#262648]) [mature pitchers with inflorescence (all sheets); labels read: “Monocotiledonea con flores blancas y tonalidades rosadas, hojas en forma de sifón, crece en lugares pantanosas.” (Monocotyledonous with white flowers and pinkish tones, siphon-shaped leaves, grows in marshy places.; *747*), “Planta herbácea, hasta de

aproximadamente 1 mt. de alto, incluyendo la inflorescencia, flores blanco-amarillento, con tonalidades rosadas y fragantes. Crece en lugares pantanosos." (Herbaceous plant, up to about 1 m tall including inflorescence, yellowish-white flowers, with pinkish, fragrant shades. Grows in marshy places.; *830*), "Hierba hasta 1 mt de alto, hojas en forma de sifón verdes con ápices morado-rojo, inflorescencias rojas, flores rosadas, estambres amarillos" (Herb up to 1 m tall, siphon-shaped green leaves with purple-red apices, red inflorescences, pink flowers, yellow stamens; *964*); identified as *H. heterodoxa* by J.A. Steyermark (see also López & Ramírez 1998:31) and confirmed by A. Fleischmann, March 2009 (NY)]; Gran Sabana, *ca.* 2 km N of military base at Luepa, *ca.* 1200 m, 20 December 1984, *Kral 72201* (BRIT! ex NLU [#NLU0293552/381467], BRIT n.v. ex VDB [5 sheets: #420920–420924], MO n.v. [#MO-1551312/3408011], NCU n.v. [#00044971], US! [#00692703/3073936], WIS! [#0408300]) [mature pitchers with inflorescence(s) (all sheets); label reads: "Locally abundant in sandy peaty seep areas among sandstone boulders; petals white to rose" (WIS); identified as *H. heterodoxa* by R. Kral]; [Gran Sabana], carretera El Dorado–Sta. Elena [El Dorado – Santa Elena de Uairén road], aprox. 100 km al S de El Dorado en línea directa [approx. 100 km S of El Dorado in a direct line], 1 km al N del Puente Tarota [1 km N of the Tarota Bridge], sabana pantonosa con muchos arbustos [swampy savannah with many shrubs], 05°40'N 61°30'W, 1300 m, 3 April 1985, *Holst, Steyermark & Manara 2173* (MO n.v. [#MO-1551304/3275601], VEN! [#228836]) [mature pitchers with inflorescence (VEN); label reads: "Perenne; formando colonias. Apendice da la hoja rojo obscuro; flores blancas con rosado." (Perennial; forming colonies. Leaf appendage dark red; flowers white with pink.); identified as *H. heterodoxa* by J.A. Steyermark & B. Holst, 1985]; Sierra de Lema, *ca.* 70 km NNE of Kavanayén [*sic*!; *ca.* 45 km based on coordinates provided], pequeña altiplanicie inclinada hacia el SW [small plateau inclined towards the SW], 05°57'N 61°34'W, *ca.* 1650 m, 30 January 1988, *Huber 12495* (K! [s.n.]) [mature pitchers with inflorescence; label reads: "Formando colonias en el herbazal, común. Escapo y brácteas florales rojo vino, cáliz rosado, corola blanca. Cisternas con la mitad inferior rojo vino oscuro." (Forming colonies in the grassland, common. Wine red flower scape and bracts, pink calyx, white corolla. Pitchers with the lower half dark wine red.); identified as *H. heterodoxa* by O. Huber, April 1989]; [Gran Sabana], 12 km antes de Kavanayén [12 km before Kavanayén], 1290 m, 7 April 1988, *Marcano, Sastre, Sastre & Hernandez 1032* (P! [#P06807513/PL05370836], VEN n.v.) [mature pitcher with inflorescence and partial stem with roots; label reads: "Planta terrestre, insectívora, creciendo en lugar acuoso-arenoso, tallos rojizo carmesí, flores verde claro y blanco. Sabana higrófila mesotérmica, arbustiva" (Terrestrial plant, insectivorous, growing in watery-sandy place, stems reddish crimson, flowers light green and white. Mesothermic, shrubby, hygrophilous savanna); identified as *H. heterodoxa* by V. Marcano, 1988]; Sierra de Lema, *ca.* 50 km NE of Kavanayén, high wet SE-inclined plain, broadleaf meadow on small meseta, 05°37'N 61°34'W [presumably 05°57'N was meant; cf. *Huber 12495*], 1650 m, 22 January 1993, *Kral 81881* (BRIT n.v. ex VDB [2 sheets: #420917 & 420918], GH! [#01678360], MICH! [#1660485], MO n.v. [#MO-1983921/04600997], NY! [#02710926], US! [#00692700/3288673]) [mature pitchers and inflorescences with (GH) or without (MICH, NY, US) substantial stem with roots; label reads: "Tepals pale rose within, cherry red outside"; identified as *H. heterodoxa* by R. Kral and confirmed by A. Fleischmann, March 2009 (NY)]; Gran Sabana, carretera Fuerte Luepa – Kanavayen [*sic*; Fort Luepa – Kavanayén road], 'El Jardin' [see *Ramírez 747*], no elevation data, 16 January 1994, *Ramírez, Hokche, Raimundez, Briceño & Pérez 4759* (VEN! [#295833]) [mature pitchers with inflorescences and substantial stem with roots; label reads: "Planta herbácea de aprox. 1 mt de alto, flores con perianto de color rosado con tonalidades blancas, frutos verde amarillento con tonalidades rosadas cuando inmaduros." (Herbaceous

plant about 1 m tall, flowers with pink perianth with white tones, fruits yellowish-green with pink tones when unripe.); identified as *H. heterodoxa* by N. Ramírez, 1994].

***Heliamphora ionasi*—**VENEZUELA: saddle between North Peak [Tramen-tepui] and Central Plateau [Ilú-tepui], cumbre [summit] slopes, 2400 m, 15 March 1952, *Maguire [& Boyan] 33418* (**holotype** NY! [#00069768]; **isotypes** B! [#B100248110], F! [#V0044823F/1775673], K! [#K000471790], NY! [#00069769], US! [#00100624/2701417], VEN n.v.) [mature pitcher with stem and inflorescence (holo- NY), mature pitcher and dissociated floral parts (B), dissected mature pitcher (F), mature pitcher (K, iso- NY), mature pitcher(s) with inflorescence (US); label reads: "Leaves reddish, perianth white turning red, forming huge rosettes or in curtains, occasional"; pollen figured in Maguire (1978:44 fig. 46C–H, 46 fig. 48A–C) where measurements thereof provided (see p. 51 table II); invariably identified as *H. ionasi*; name spelled '*ionesi*' by B. Maguire on original labels (NY sheets)]; from plant cultivated at Royal Botanic Gardens, Kew, said to originate from British Guiana [*sic*!; must be Venezuela based on stated locality], Ilutipu [Ilú-tepui], 22 mls. [miles] N.W. Mt. Roraima, no elevation data, 16 January 1962, *Thompson s.n.* (K! [#K000560001]) [mature pitcher and separate inflorescences; label reads: "Stems dark red/brown; bracts light green to yellow/beige; anthers deep orange; films. [filaments] and style dark brown; pitcher outer surface light green at base through pink to light brown at top. Keel light brown. Inner surface darker brown/red, pink at base. From A.D. Thompson, Georgetown, B.G. [British Guiana]"; identified as *H. nutans* initially]; Ilu Tepuy [Ilú-tepui], no elevation data, 29 December 1998, *Shibata 11207* (TNS! ex Nippon Dental College [#TNS01236806]) [etiolated mature pitchers; identified as *H. nutans* initially]; Ill Tepui [Ilú-tepui], no elevation data, 29 December 1998, *Shibata 12709* (TNS! ex Nippon Dental College [#TNS01239462]) [mature pitchers; identified as *H. ionasi* initially].

? *Heliamphora collina* × *Heliamphora purpurascens* and other indeterminate material from Ptari-tepui and its surroundings (see Wrazidlo & Fleischmann 2019)**—**VENEZUELA: Ptari-tepui, in swamp on open level portion of plateau on southeast-facing slopes [see Steyermark, 1966b:50], 1600 m, 1 November 1944, *Steyermark 59651* (F! [2 sheets: #V0307876F/1205784 & #V0307877F/1205785], NY! [#03835901]) [mature pitchers with inflorescence and stem with roots (both F sheets), very substantial (*ca.* 27 cm) stem in case of #V0307877F, or same but lacking inflorescence (NY); label reads: "Common; flowers uncommon"; identified as *H. heterodoxa* initially and as *H. purpurascens* by A. Fleischmann, 2009 (NY); paratype of *H. heterodoxa*]; Ptari-tepui, *Bonnetia roraimae* forest on southwest-facing shoulder [see Steyermark 1966b:65–70], matted on mossy exposed top of big boulder, 2000–2200 m, 2 November 1944, *Steyermark 59766* (**holotype of *H. heterodoxa*** F! [2 sheets: #F0044820F/1205786 & #F0044821F/1205787]; **isotypes** NY! [#00387772], US! [#00100621/1932082], VEN! [#25348]) [mature pitchers with inflorescences, separate dissected pitcher (F sheet #F0044820F), mature pitchers with inflorescence(s) (F sheet #F0044821F, NY, VEN), separate mature pitcher and inflorescence (US); labels read: "flowers faintly fragrant, arising near base of plant; 2 outer sepals rose-pink at base, otherwise greenish-white; a midline of pink or rose on outer sepals; 2 inner sepals white within; rachis win red as is scape; leaf pale green with suffusion" and "of wine purple-red either one color massed or in splotches; leaf tip with incurved purple-red appendage" (latter description accompanied by sketch); labelled initially as "*Heliamphora heterodoxa* Steyermark, n. sp." and confirmed as type of *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and by J. Pruski, June 1987 (NY), and of *H. heterodoxa* by A. Fleischmann, 2009 (NY); as pointed out by Wrazidlo & Fleischmann 2019, holotype sheet #F0044820F and the isotypes at NY and VEN are morphologically closer to *H. collina*, whereas holotype sheet #F0044821F and the isotype at US are closer to *H. purpurascens*]; Ptari-tepui, along

base of east-facing high sandstone bluffs [see Steyermark 1966b:71–75], in mats of *Sphagnum oxyphyllum* [per Steyermark 1951:240], 2410–2450 m, 7 November 1944, *Steyermark 59934* (F! [2 sheets: #V0307878F/1205781 & #V0307881F/1205782], GH! [#01678358], NY! [#03835902], US! [#01017948/1933642], VEN! [#25386]) [clump of large (>30 cm) mature pitchers with (NY) or without inflorescence (F sheet #V0307878F), dissected mature pitcher and separate, floriferous (≤6 large flowers per scape) inflorescences (F sheet #V0307881F), etiolated mature pitcher with separate inflorescence (GH), etiolated mature pitchers with stem and inflorescence (US, VEN); labels of NY and #V0307878F (based on original annotation on VEN) reads: "Moist base of bluffs. This collection more luxuriant with larger more elongated leaves, with longer hairs within, and longer [pedicels] with larger and more numerous flowers; flower stalks arising from base; scape dark red as are pedicels; ovary pubescent, pale green; outer sepals pale green to suffused with rose in age" and "paler green in age; leaves with red apex, margin and keel; lower part of leaves purplish-red, upper part pale green, inner surface pale green within, but dark brown-purple within in cup part at base; flowering scapes ascending; outer sepals rose without, pink within; inner sepals whitish-pink both sides. Often seen, as this specimen, growing with *Sphagnum*." (latter description accompanied by sketch with annotation: "tip of leaf not as enlarged nor incurved as in other type, but is smaller and points upward"); identified as *H. heterodoxa* initially, as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), as *H. purpurascens* by A. Fleischmann, 2009 (NY), and as *H. collina* by Wrazidlo & Fleischmann, 2019; some pitchers of NY notably bear longer retentive hairs; paratype of *H. heterodoxa*]; mesa between Ptari-tepui and Sororopán-tepui, vicinity of 'Misia Kathy Camp' [see Steyermark, 1966b:49–54, 55 fig. 7, 61 fig. 8, 63 fig. 9], 1615 m, 15–17 November 1944, *Steyermark 60242* (F! [#1205783], NY! [#02710936]) [mature pitchers with inflorescences and substantial stem with roots (F), separate inflorescences (NY); label reads: "Common in swamp with *Stegolepis*, *Xyris*, *Eriocaulon*, *Abolboda*, and bromeliads"; pencil annotation reads: "anthers 5.5–7 mm long" (F); noted by Steyermark (1951:240) as having "pedicels slightly puberulous on one side and glabrous on the other"; identified as *H. heterodoxa* initially, as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and as *H. heterodoxa* by A. Fleischmann, March 2009 (NY); paratype of *H. heterodoxa*]; Ptari-tepui, northwest slope, open boggy place savannas, 1800 m, 17 December 1952, *Maguire & Wurdack 33890* (IAN! [#96053], K! [s.n.], NY! [#02710925], P! [#P04556111/PL03865137], US! [#01017945/2253273], VEN! [#41068]) [mature pitchers with inflorescence(s) (all sheets); label reads: "Perianth white, slightly rose-flushed, stamens yellow, leaf veins reddish, abundant"; identified as *H. heterodora* (*sic*) initially and confirmed as such by A. Culham, 1996 (P), as *H. heterodoxa* var. *heterodoxa* by B. Maguire, 1973 (NY), and as *H. heterodoxa* by A. Fleischmann, March 2009 (NY)]; Ptari-tepui, slopes and rocks in vicinity of 'Cave Rock' camp below southern face of mountain [see Steyermark 1966b:35 fig. 4, 55 fig. 7, 56–62], *Bonnetia* forest and exposed rock directly upward from camp, 1600–2000 m, 14–19 August 1970, *Moore Jr., Ambrose, Dietz IV & Pfister 9750* (MICH! [#1660486], NY! [#02710931], US! [#01017940/2751657], VEN! [#100352]) [mature pitchers with inflorescence(s) and stem fragment(s) (all sheets); label reads: "On top of exposed rock and in open areas at base of rock. Plants at top smaller than those at base. Flowers pink; stamens yellow. Pitchers margined with red and red at base."; floral material in envelope attached to VEN annotated by J.A. Steyermark, 1983: "estambres 8" (8 stamens); identified as *H. heterodoxa* initially and confirmed by A. Fleischmann, March 2009 (NY)]; Ptari-tepui cumbre [summit; see Brewer-Carías 1987:112–135, 234–235], al norte de la Misión de Santa Teresita de Kavanayén [north of Kavanayén], 05°45'N 61°45'W, 2360–2420 m, 23 February 1978, *Steyermark, Espinosa, Diarmid & Brewer-Carías 115698* (MO! [2 sheets: #MO-1551296/2777077 & #MO-1551297/2777078], VEN! [#126505]) & *115742* (F! [#1878875], L! ex U [#U.1733191/387970],

MO n.v. [#MO-1551301/2777075], TEX! ex LL [#00500838], VEN! [#126518]) [mature pitchers only (F, L, MO sheet #2777077), inflorescence only (MO sheet #2777078), mature pitchers with inflorescence (TEX, both VEN sheets); label of *115698* reads: "In large colony with more elongated pitchers; flowers larger and on taller stems than seen elsewhere. In moist depressions in *Bonnetia roraimae* grove"; label of *115742* reads: "rocky open plateau"; identified as *H. heterodoxa* var. *heterodoxa* initially; TEX and VEN sheet #126505 represent typical *H. purpurascens*, L approximates a typical *H. heterodoxa*, and F, MO sheet #2777077 and VEN sheet #126518 are somewhat intermediate].

Notes on specimens examined: It would have been our preference to designate as the holotype of *Heliamphora electrum* the sheet of *Steyermark, Dunsterville & Dunsterville 92477* held at VEN, in the plant's country of origin. Unfortunately, given the current economic and sociopolitical situation in Venezuela, collections at VEN are at grave risk of damage or destruction, and many may already have been lost (see Núñez-Farfán *et al.* 2017; Torres 2019). As such, we have selected as the holotype the duplicate at K (Fig. 1), which is the best preserved of the specimens seen by us.

Discussion

Taxonomic affinities: In gross morphology, *Heliamphora electrum* most closely resembles *H. collina* and *H. heterodoxa*, from which it differs clearly in the bimorphic retentive hairs (long golden and short white; Fig. 15) that densely cover the entire upper half of the pitcher interior. The only other *Heliamphora* taxa with comparable arrangements of retentive hairs in two discrete size classes in mature plants are *H. ciliata*, *H. minor* var. *pilosa*, and some forms of *H. pulchella*. Though McPherson *et al.* (2011:94) state that this is also true of *H. ionasi*, in fully adult pitchers of that species retentive hair size follows a clear gradient, gradually increasing in size from lip to interior, and hairs of different lengths are not evenly interspersed throughout the entire upper half of the pitcher interior as they are in *H. electrum*.[19]

Though the function of the bimorphic hairs is unknown, it might be supposed that this trait is an adaptation to more effectively capture prey of different sizes (see McPherson *et al.* 2011:94–95), likely via an aquaplaning mechanism as previously demonstrated in *Heliamphora nutans* (see Bauer *et al.* 2013). As with all *Heliamphora*, under low-light conditions these hairs may be only partly expressed or not at all, which can lead to difficulty in identifying individuals to species level.

The large hairs of *Heliamphora electrum* emanate from conspicuous protuberances, reminiscent of those found in *H. ionasi* (Figs. 16–17). These macro-hairs, when mature, have a distinctive golden sheen under natural light (described as "yellowish-tawny" on the herbarium label of the type; Fig. 1). Conversely, the vast majority of *Heliamphora* species bear only retentive hairs that evenly reflect light across the visible spectrum and consequently appear white, the only other known exceptions being species from the northern part of the Eastern Tepuis chain, specifically *H. arenicola*, *H. elongata*, *H. ionasi*, and *H. nutans* (Golos 2020), and also *H. hispida* from the distant Cerro de la Neblina. These four species from the Eastern Tepuis notably appear to form a monophyletic clade (Liu & Smith 2021). The function of these divergent reflectance profiles, if any, is unknown.

[19] However, in some plants of *Heliamphora ionasi*, the marginal regions of the inner surface – particularly those directly below the nectar spoon – may include minute hairs *ca.* 50 µm long scattered among the much larger main hairs that gradually lengthen as one moves down the pitcher tube (M. Golos, pers. observ.; see Front Cover).

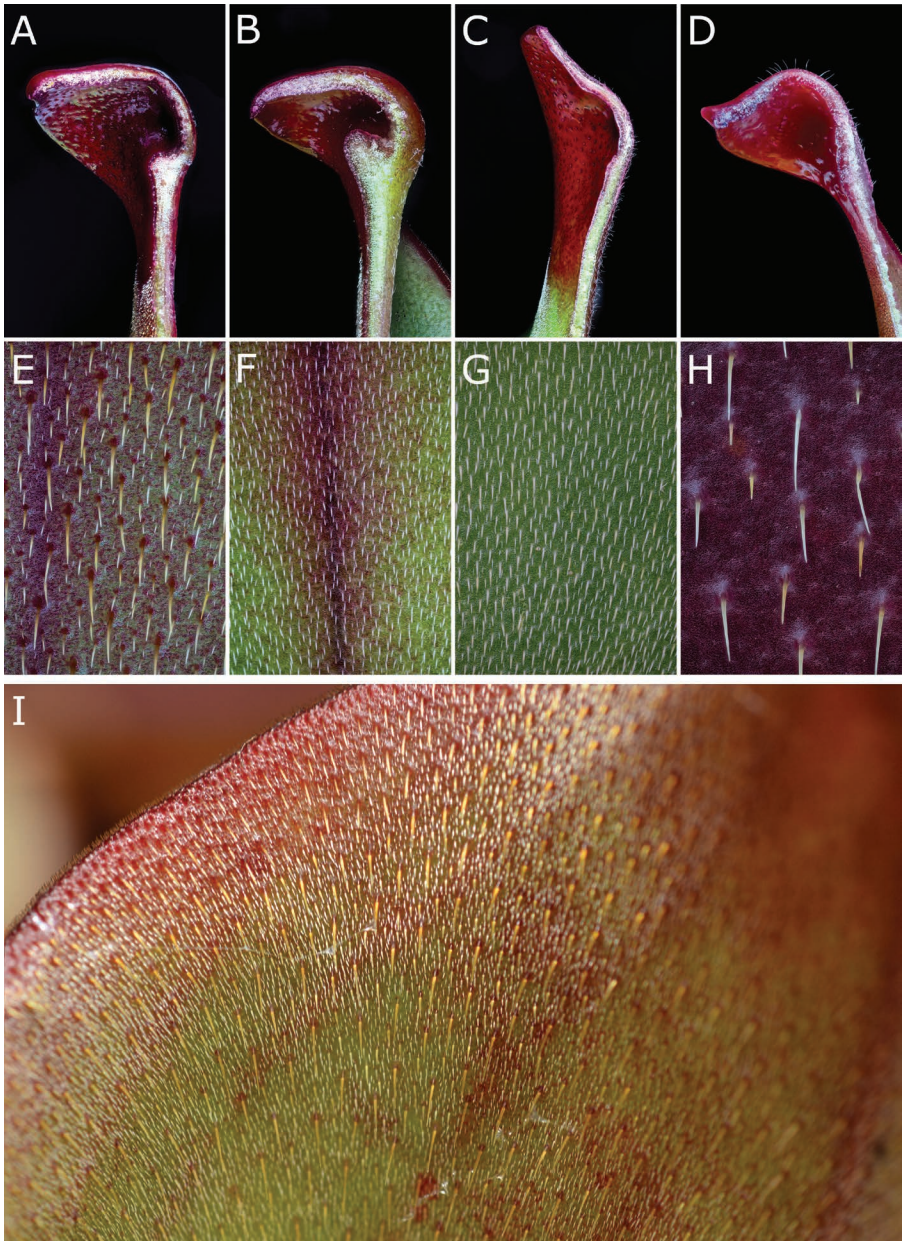


Figure 15: Comparison of nectar spoons in lateral section (A–D) and retentive hairs (E–H; to scale) of *Heliamphora electrum* (A, E) and the closely allied *H. collina* (Los Testigos foothills; B, F), *H. heterodoxa* (Luepa; C, G), and *H. ionasi* (Ilú–Tramen valley; D, H). The white micro-hairs of *H. electrum* may be more densely distributed as shown in I. Photographs A–H by A. Wistuba and I by M.R. Golos.

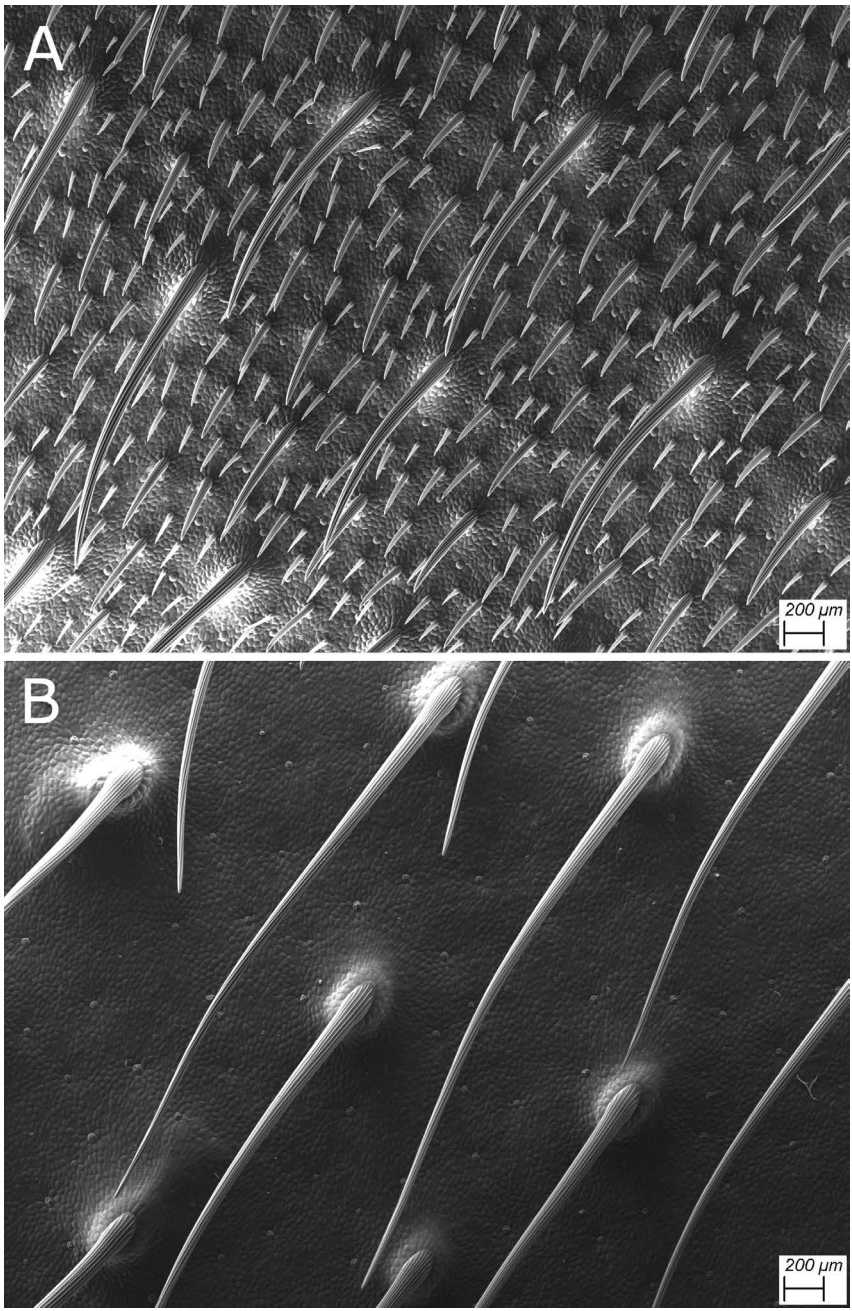


Figure 16: Electron micrographs of the retentive hairs of mature *Heliamphora electrum* (A) and *H. ionasi* (B) pitchers, from the central region of the trapping surface, viewed at the same magnification. Note *H. electrum* has hairs of two different lengths. Small glands are evenly dispersed among the hairs. Brighter areas at the base of the hairs are artefacts resulting from localised electron charging. SEMs by M.R. Golos.

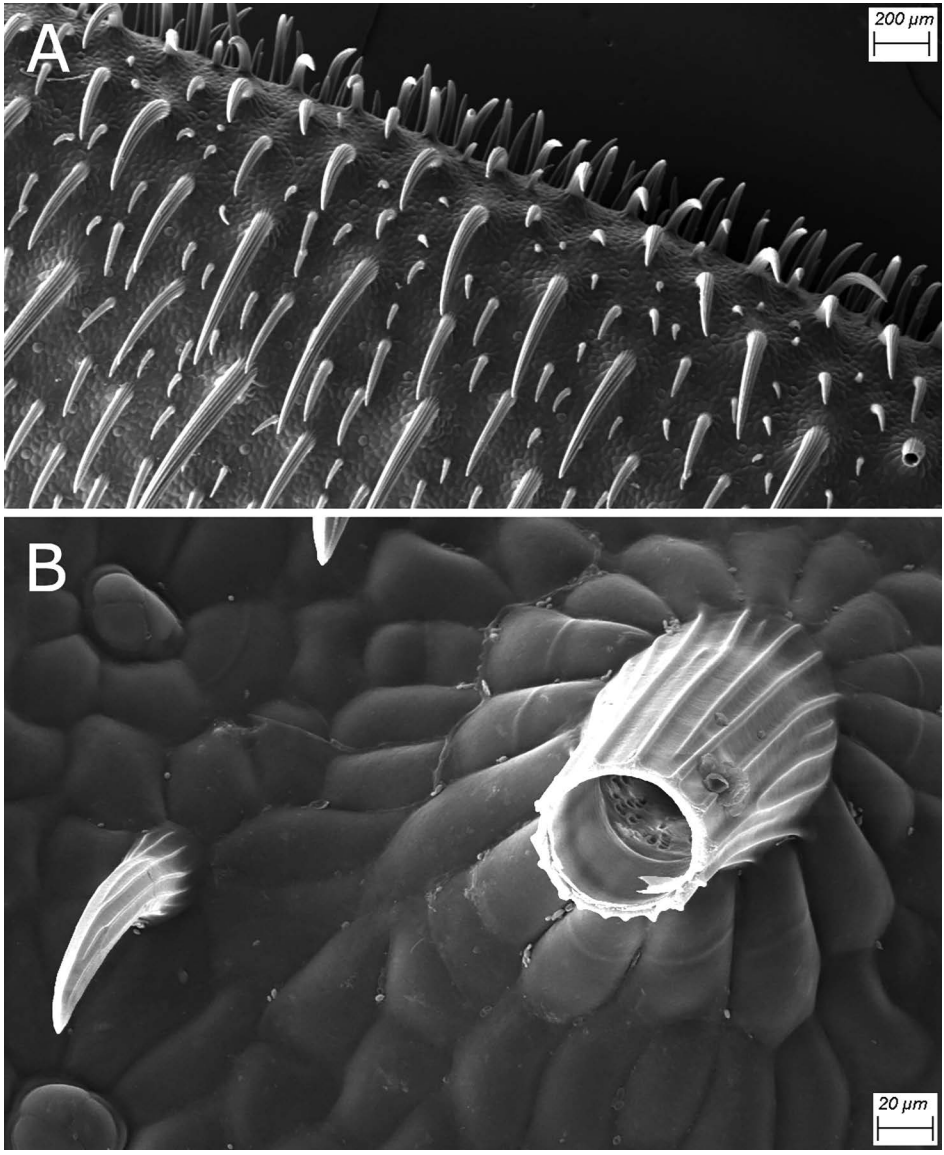


Figure 17: Electron micrographs showing *Heliamphora electrum* hairs near the outer margin of the retentive surface. Note that the macro-hairs are considerably shorter in this region and therefore less clearly differentiated from the micro-hairs. The broken trichome visible in the bottom-right of A is shown at significantly higher magnification in B. Note the 16 concentric epidermal cells making up the protuberance at the base of the broken macro-hair; this structure is lacking from the adjacent micro-hair. SEMs by M.R. Golos.

Heliamphora electrum can also be distinguished from its closest congeners by other aspects of vegetative and floral morphology (see Table 1). Notably, the nectar spoon of this species is significantly more developed than that of *H. collina*, though this difference may be masked in pitchers growing in shade, this also leading them to assume an infundibular, wide-mouthed form[20], further blurring the lines with *H. collina*. When grown under plentiful light, however, *H. electrum* more closely resembles *H. heterodoxa*, having a rhomboid mouth and a larger, more elongated nectar spoon (Fig. 18), though one that is still not as well-developed as in *H. heterodoxa* and that has a shallower nectar chamber than in *H. collina* (Fig. 15).

Table 1. A comparison of *Heliamphora electrum* and some of its putative closest relatives: *H. collina*, *H. heterodoxa*, and *H. ionasi*. Morphological characters are based on extensive field observations throughout Venezuela, supplemented by examinations of relevant type and other herbarium materials.

	H. electrum	***H. collina***	***H. heterodoxa***	***H. ionasi***
Geographical range	Sierra de Lema (Cerro Uei, Cerro Venamo, undetermined mesa east of Ptari-tepui)	Foothills of Los Testigos tepuis (Aparamán, Kamarkawarai, Murisipán, Tereke-yurén), foothills and possibly upper reaches of Ptari-tepui	Gran Sabana, Sierra de Lema, Waukauyengtipu	Ilú–Tramen massif (mostly known from main valley and slopes, rare on summit), Karaurín-tepui (M. Golos, pers. observ.)
Elevational range (m)	1100–1400 (–?1600)	1700–1825 (–?2400)	1200–1650	1800–2600
Pitcher shape	Basal third to half infundibular, with slight medial constriction, gradually widening again towards the mouth	Basal third to two-fifths infundibular, medial constriction very faint if present, more or less cylindrical or slightly infundibular towards mouth	Basal third to two-fifths infundibular, with faint medial constriction, more or less cylindrical above, widening again at the mouth	Arising from infundibular, near-horizontal basal portion, with pronounced medial constriction, broadly infundibular towards mouth
Pitcher size	Medium (usually *ca.* 20–25 cm tall)	Medium (≤25 cm tall)	Medium (≤25 cm tall)	Large (≤40–50 cm tall)

[20] This can be seen in the holotype, which was apparently collected from mossy forest and whose pitchers were said to be "pale green" (Fig. 1), and also in some *in situ* photographs (e.g., Fig. 7).

Table 1. Continued.

	H. electrum	*H. collina*	*H. heterodoxa*	*H. ionasi*
Nectar spoon shape	Helmet-shaped, arising from a short stalk, with a short apical tip, shallow nectar chamber	Helmet-shaped, laterally appressed at rear, arising directly from the pitcher neck or from a very short stalk, without apical tip, well-developed nectar chamber	Helmet-shaped with slight protuberance at front and variable bulge at top (rarely entirely flattened), margins flattened or slightly upturned, on strap-shaped stalk, lacking nectar chamber	Spoon-shaped in younger plants to partly flattened in larger plants, on short, narrow stalk, short apical tip, spherical nectar chamber towards the tip resulting in a bulge-like swelling on the adaxial surface
Nectar spoon size	Small	Small	Large	Small to large
Retentive hairs	Uniformly bimorphic in upper portion, lengthening towards water line; large golden and minute white	Of uniform length in upper portion, only lengthening towards water line; minute, white	Of uniform length in upper portion, only lengthening towards water line; minute, white	Of uniform length in given area, lengthening markedly from margin (minute) to interior (very long; ≤11 mm); white to golden
Pitcher body colour under moderate light	Yellowish-green or greenish, suffused orange to red	Yellowish-green, interior sometimes suffused pinkish-red	Yellowish-green throughout, rarely suffused red	Pinkish-orange with red veins, interior often pinkish-red with yellow and orange blotches
Inflorescence	≤82 cm long with up to 7 flowers, glabrous; pedicels ≤9.5 cm long, glabrous; ≤9 stamens; anthers oblong-lanceolate, 4–8 mm long and 1.5 mm wide	≤50 cm long with up to 4 flowers, glabrous; pedicels ≤7 cm long, glabrous; *ca.* 10 stamens; anthers oblong-lanceolate, *ca.* 6 mm long and 1.5 mm wide	≤60 cm long with up to 8 flowers, glabrous or very pubescent; pedicels ≤8 cm long; ≤15 stamens; anthers oblong, *ca.* 5 mm long and 1.5 mm wide	≤100 cm long with up to 10 flowers, glabrous to shortly but densely pubescent; pedicels ≤12 cm long; ≤15 stamens; anthers oblong-lanceolate, *ca.* 3.5 mm long

Figure 18: Cultivated plants of *Heliamphora electrum* grown under moderately strong, full-spectrum LED lights, demonstrating the potential for significant nectar spoon development and vibrant pigmentation in this species when provided plentiful illumination. Shown are younger (top) and older growth stages of the same plant, grown under *ca.* 10,000 lux and *ca.* 6000–7000 lux, respectively. Photographs by Maciej Stelmach.

Heliamphora electrum is much easier to distinguish from *H. ionasi*, from which it differs most obviously in the general shape of its pitchers, those of the latter species generally having a broad, round opening (versus much smaller and often rhomboid), a pronounced medial constriction (versus only a slight narrowing), and emerging near-horizontally and thereby being more widely spaced. The pitchers of *H. ionasi* are also significantly larger – reaching *ca.* 50 cm, they are likely to be the largest in the genus by volume, though not by height (Nerz 2014; Golos 2019). The nectar spoon of *H. ionasi* is also usually larger than that of *H. electrum* (both proportionally and in absolute terms) and has a pronounced basal constriction that is lacking in that species.

Heliamphora electrum is unlikely to be of recent hybrid origin as no putative parent species with long or at least comparably developed retentive hairs has been documented from the Sierra de Lema, the nearest recorded population of *H. ionasi* being more than 60 km distant (in the Eastern Tepuis; see Fig. 3A). Based on both morphological and geographical proximity, *H. electrum* is likely to fall into the 'E2a' clade of Liu & Smith (2021, 2023), which includes *H. collina*, *H. heterodoxa*, *H. purpurascens*, *H. sarracenioides*, and the as yet undescribed *H.* sp. 'Akopán Tepui' and *H.* sp. 'Angasima Tepui' (see McPherson *et al.* 2011:456–465), though this would need to be confirmed through genetic sequencing.

Ecological context: *Heliamphora electrum* appears to be restricted to forest clearings in the Sierra de Lema. Such clearings cover only a very small fraction of the total area of this largely forested region and, of the small number that do exist, not all host *Heliamphora* (Fig. 19), some apparently being too dry to support members of this genus (J. Nerz, pers. observ.). The species is therefore likely to have a patchy and highly localised distribution. The closely related *H. heterodoxa*, by

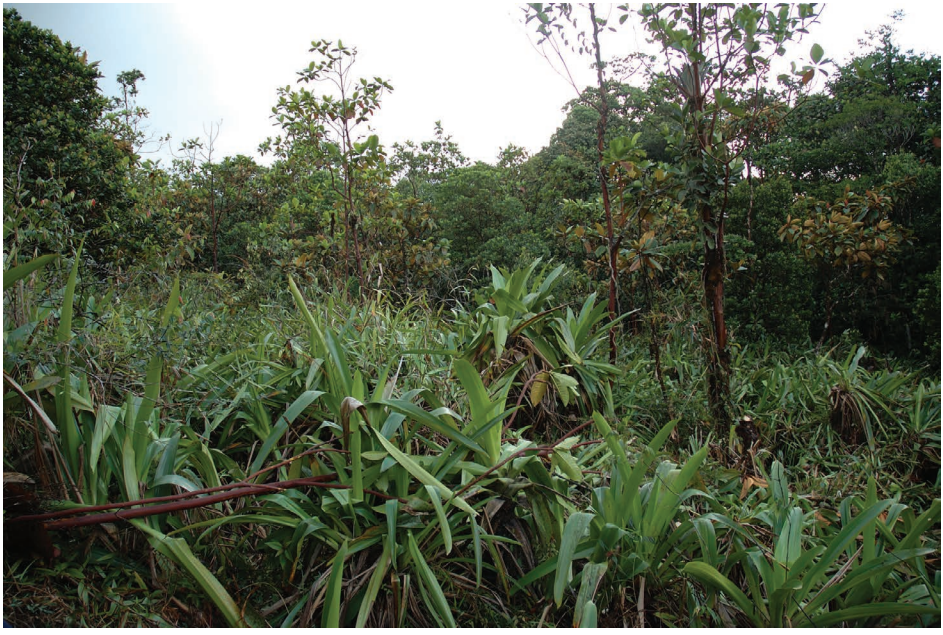


Figure 19: The only forest clearing found during an aerial survey of the eastern Sierra de Lema carried out in 2005. An intensive search of the area failed to locate any *Heliamphora*. Photograph by J. Nerz.

contrast, appears to be something of a generalist, capable of thriving in both the Sierra de Lema and the much drier Gran Sabana to the south.

Cerro Venamo and the wider Sierra de Lema are characterised by dense, submontane to montane, ombrophilous evergreen forests up to *ca.* 1600 m elevation, which continue to the slopes of the Ptari massif and the Los Testigos chain (Fig. 20; Huber 1995c:117–119; Huber & Rull 2019:152). Though contiguous with adjacent forested regions of the Pantepui biogeographic region, the eastern Sierra de Lema harbours a highly distinctive floral assemblage. Steyermark – who was probably unsurpassed in his familiarity with the vast flora of the Venezuelan Guayana, having made 27,939 collections in the region (Huber 1995b:77) and described more than a thousand taxa (Taylor 1989) – considered the phytogeography of the wider Cerro Venamo region (those areas drained by the Río Venamo and tributaries of the upper Río Cuyuní) so particular that he distinguished it as a separate plant refuge unto itself, which he referred to simply as 'Venamo' (Steyermark 1979:205, 210) and later as the 'Venamo–Cuyuni refuge' (Steyermark 1982:207).

Under Steyermark's classification, this Venamo refuge forms one of four top-level divisions of the much larger Pantepui, together with: the Gran Sabana uplands to the south; the lowland edaphic savannas and igneous *laja* outcrops of Amazonas state in the far west; and the summits and talus slopes of the tepuis themselves (see Steyermark 1979:188 fig. 1, 205, 1982:184 fig. 13.2, 200; Prance 1982:616 fig. 10). Compared to western parts of Pantepui, the forests of the Cerro Venamo region are more humid, possess a greater abundance of epiphytes, and are characterised by a sparse, shrubby-herbaceous understorey (Steyermark 1979:210; Weidmann 1986:52–54 3 figs., 167; Huber 1995c:119).

These differences may be explained by local meteorological factors. The eastern Sierra de Lema, including Cerro Venamo, forms a substantial natural barrier to northeasterly trade winds. Due to

Figure 20: Aerial view of the eastern Sierra de Lema, looking eastwards towards Guyana. Photograph by J. Nerz.

orographic precipitation, this area experiences the highest levels of rainfall of any part of the wider Gran Sabana region, reaching or even exceeding 4000 mm annually, resulting in a rain shadow of *ca.* 2500 mm annual rainfall to the south, centred on the settlements of Luepa and Parupa (Huber *et al.* 2001:22; see Fig. 3B). When they are not experiencing rain, the upper reaches of this range are often shrouded in thick fog, which has led to the development of a rich cloud forest (Schubert & Huber 1990:62).

The vast majority of the Sierra de Lema remains completely unexplored – as much a *terra incognita* now as it was in Steyermark's time (see Steyermark 1961:293–295). It is likely that *Heliamphora electrum* has a wider distribution encompassing the little-botanised or entirely unbotanised intermediate-elevation mesas stretching between Ptari-tepui and Steyermark's Cerro Uei, many of which fall within its known elevational range and may potentially offer suitable habitat based on available satellite imagery. The species is also likely to occur across the border in Guyana, which harbours contiguous and similarly unexplored upland vegetation. Clearly, further field work will be needed to confirm the extent of this species' range and to assess the status of the already recorded populations. To this end, having more precise knowledge of the original collecting localities opens the possibility of relocating the type population.

Acknowledgements: This paper is dedicated to our late friend Andy Smith (see Back Cover), well known in the carnivorous plant community as an expert cultivator, talented illustrator, and passionate explorer of many a botanical paradise, not least the Gran Sabana and its tepuis (Smith 2010). Andy successfully grew *Heliamphora electrum* for many years and was an early proponent of its recognition as a distinct species. It was through him that many enthusiasts received their plants of *H. electrum*.

The first author would like to sincerely thank a number of individuals without whom this paper would certainly not have been possible: Charles Brewer-Carías for sharing his immense knowledge of the geography, history, and toponymy of the Sierra de Lema; Antonio Hitcher for elucidating the etymology of various regional toponyms; David Clarke for sharing his knowledge and photographs of *Heliamphora heterodoxa* on Waukauyengtipu; Stewart McPherson for fruitful discussions on wild *Heliamphora* and particularly the appearance of young *H. ionasi* in habitat; Michael Schach, Manfred Speckmaier, and Mateusz Wrazidlo for information on their explorations of, respectively, the eastern Sierra de Lema, the Cerro Venamo–La Escalera region, and Waukauyengtipu; Anneleen Léger for facilitating access to the Library and Archives of the Royal Botanic Gardens, Kew; Andrew Colligan for the same at the Missouri Botanical Garden Archives and for kindly digitising Steyermark (1960); Anna Fredriksson at Uppsala University Library, Olof Byström at the university's Office for Information Provision, Registry and University Archives, Urban Lindberg at the university's Communications Division, Berit Schütz at Stiftelsen Upplandsmuseet, and Maria van der Wie at Svenska Botaniska Föreningen, for helping source information on botanist Sven Nilsson; Danielle Castronovo of Harvard Botany Libraries and Gustavo Romero of the Oakes Ames Orchid Herbarium for providing valuable information on Galfrid and Ellinor Dunsterville's surviving archival materials; Fernando Rojas-Runjaic for help sourcing scorpion literature; Chetan Bhatt, Mike Page, and Jesús Quintero for their friendship and company during field trips to Venezuela; and Emilio Pérez for his guidance and invaluable help with logistics and supplies. Sincere gratitude is extended to the staff of Missouri Botanical Garden, particularly Lauren Boyle, Mary McNamara, and James Solomon, for going above and beyond to facilitate the first author's three-day research visit in January 2020, including organising in-house accommodation.

For facilitating access to herbarium materials, we thank Martin Cheek (K), Roxali Bijmoer and Nicolien Sol (L), Lauren Boyle and James Solomon (MO), Sovanmoly Hul and Corinne Sarthou (P), and Atsushi Ebihara (TNS). We are also indebted to Thomas Carow for providing photographs of *Heliamphora* specimens deposited at VEN and to Mats Hjertson for the same at UPS. Andreas Fleischmann is gratefully acknowledged for fruitful discussions on various aspects of *Heliamphora* biology and Fernando Rivadavia for help identifying the *Drosera* found growing sympatrically with *H. heterodoxa* at the site discovered in 2006. Special thanks are extended to Maciej Stelmach for allowing us to use his photographs of cultivated *H. electrum* and for sharing details of their growing conditions, including estimates of illuminance. Finally, Urs Zimmermann is thanked for his companionship and assistance on the 2006 expedition that led to the rediscovery of *H. electrum*.

References

Agard, O., Atkinson, S., Benjamin, P., Cornelius, S., Daniels, W., Hastings, K., James, R., Joseph, G., Joseph, S., Larson, R., Garrell, M.M., Peters, C., Richmond, T., Robinson, K., Thomas, D., Thompson, N., and Walker, N. 2019. Our Land, Our Life: A participatory assessment of the land tenure situation of indigenous peoples in Guyana. Report for Region 7. Amerindian Peoples Association, Georgetown; Forest Peoples Programme, Moreton-in-Marsh; Rainforest Foundation US, New York. https://rainforestfoundation.org/wp-content/uploads/APA_LTA_R7.pdf

Aguerrevere, S.E., López, V.M., Delgado, C., and Freeman, C.A. 1939. Exploración de la Gran Sabana. [Exploration of the Gran Sabana.] Revista de Fomento 3(19): 501–542, 632–729 + 5 maps. [Reproduced in: (1) Revista de Hidrocarburos y Minas no. 8: 57–212, no. 9: 147–207 & no. 10: 273–356. (2) Exploración de la Guayana. Interalúmina, Caracas. pp. 78–162.] (in Spanish)

Anderson, E.W. 2003. International Boundaries: A Geopolitical Atlas. Routledge, New York. https://books.google.com/books?id=E7-menNPxREC

Anon. 1965. Sammankomster år 1964. [Meetings in 1964.] Svensk Botanisk Tidskrift 59(2): 249–256. (in Swedish). http://www.diva-portal.org/smash/get/diva2:1202273/FULLTEXT01.pdf

Applequist, W.L. 2023. Report of the Nomenclature Committee for Vascular Plants: 74. Taxon 72(4): 908–922. https://doi.org/10.1002/tax.12993

Armellada, C. de, and Olza, J. 1999. Gramática de la Lengua Pemón (Morfosintaxis). [Grammar of the Pemón Language (Morphosyntax)]. Universidad Católica Andrés Bello, Caracas. (in Spanish) https://books.google.com/books?id=Stsajs2WYjUC

Bauer, U., Scharmann, M., Skepper, J., and Federle, W. 2013. 'Insect aquaplaning' on a superhydrophilic hairy surface: how *Heliamphora nutans* Benth. pitcher plants capture prey. Proceedings of the Royal Society B: Biological Sciences 280(1753): article no. 20122569 [6 pp.]. https://doi.org/10.1098/rspb.2012.2569

Baumgartl, W. 1993. The genus *Heliamphora*. Carnivorous Plant Newsletter 22(4): 86–92. https://doi.org/10.55360/cpn224.wb805

Berry, P.E., Riina, R., and Steyermark, J.A. 2005. Sarraceniaceae. In: Berry, P.E., Yatskievych, K., and Holst, B.K. (eds.) Flora of the Venezuelan Guayana. Volume 9: Rutaceae–Zygophyllaceae. Missouri Botanical Garden Press, St. Louis. pp. 138–144.

Bevilacqua, M., Señaris, C., and Huber, O. 2019. Conservation of Pantepui: between complex emergency and climate change. In: Rull, V., Vegas-Vilarrúbia, T., Huber, O., and Señaris, C. (eds.) Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands. Academic Press, London. pp. 389–402. https://doi.org/10.1016/B978-0-12-815591-2.00016-1

Bohn, A., Matos, F.B., and Labiak, P.H. 2020. Taxonomy, distribution and conservation status of the fern genus *Cyclodium* (Dryopteridaceae). Willdenowia 50(2): 279–304. https://doi.org/10.3372/wi.50.50213 (electronic supplement, pp. S-1–15: https://bioone.org/journals/supplementalcontent/10.3372//wi.50.50213/wi.50.50213_Appendices.pdf)

Brewer-Carías, C. 1987. The Lost World of Venezuela and its Vegetation. Cromotip, Caracas. [Originally published in Spanish as: La Vegetación del Mundo Perdido (1978).]

Brewer-Carías, C. 2007. La Sierra de Lema. Fundación Wonken, Caracas. (in Spanish)

Brewer-Carías, C. 2011. Algo de historia de la exploración de la región. [Some history of exploration in the region.] [pp. 2–3] In: Barrio-Amorós, C.L., Brewer-Carías, C., and Fuentes-Ramos, O. Aproximación preliminar a la herpetocenosis de un bosque pluvial en la sección occidental de la Sierra de Lema, Guayana Venezolana / Preliminar aproach [*sic*] to the herpetocenosis of a rain forest in the western section of the Sierra de Lema, Venezuelan Guayana. Revista de Ecología Latinoamericana 16(1): 1–46. (in Spanish)

Brewer-Carías, C. 2012. La Sierra de Lema: una bisagra de vida. [The Sierra de Lema: a hinge of life.] Río Verde 7: 73–86. (in Spanish)

Clarke, H.D. 2008. Trip 15: Paruima – Waukauyengtipu – Konuktipu – Warimatipu. July 02, 1997 – July 27, 1997. Collections 5165–6174. National Museum of Natural History, Washington, D.C. https://web.archive.org/web/20130823061339/http://botany.si.edu/bdg/trip_desc.cfm?lastname=Clarke&trip_num=15 (expedition gallery: https://web.archive.org/web/20130823061351/http://botany.si.edu/bdg/gallery_coll.cfm?lastname=Clarke)

Czechowicz, K. 2022. Silesian scientist's expedition reveal [*sic*] errors in the maps of South America. Science in Poland, 7 March 2022. https://scienceinpoland.pl/en/news/news%2C91501%2Csilesian-scientists-expedition-reveal-errors-maps-south-america.html

Dauphin, G., and Ilkiu-Borges, A.L. 2002. Hepaticae of Cerro Venamo, Venezuela, collected by J. Steyermark. Tropical Bryology 22(1): 115–123. https://doi.org/10.11646/bde.22.1.9

Davidse, G. 1989. Julian Alfred Steyermark. Taxon 38(1): 160–163. https://www.jstor.org/stable/1220929

Désamoré, A., Vanderpoorten, A., Laenen, B., Gradstein, S.R., and Kok, P.J.R. 2010. Biogeography of the Lost World (Pantepui region, northeastern South America): insights from bryophytes. Phytotaxa 9: 254–265. https://doi.org/10.11646/phytotaxa.9.1.14

Duellman, W.E. 1997. Amphibians of La Escalera region, southeastern Venezuela: taxonomy, ecology, and biogeography. Scientific Papers: Natural History Museum, The University of Kansas no. 2: 1–52. https://www.biodiversitylibrary.org/page/16090601

Duno de Stefano, R. 2013. La familia Icacinaceae Miers en Venezuela / The Icacinaceae Miers family in Venezuela. Acta Botánica Venezuelica 35(2): 123–202. (in Spanish)

Duno de Stefano, R., Pérez-Hernández, R., and Vallejo, P. 2002 ['2000']. Distribución de la familia Icacinaceae en Venezuela y notas sobre su estado de conservación / Distribution of the family Icacinaceae in Venezuela and notes on state of its conservation. Memoria de la Fundación La Salle de Ciencias Naturales 60(154): 117–137. (in Spanish)

Dunsterville, G.C.K. 1966. The Venezuelan Guayana and its orchids. In: De Garmo, L.R. (ed.) Proceedings of the Fifth World Orchid Conference. Fifth World Orchid Conference Inc., Long Beach. pp. 53–67.

Dunsterville, G.C.K. 1970. *Phragmipedium klotzscheanum* (Rchb.f. ex Schomb.) Rolfe. The Orchid Digest 34(6): 188–190. [Reproduced without images in: The Orchid Review 78(928): 292–294.]

Dunsterville, G.C.K. 1979. *Cattleya jenmanii* – late to the party, early to leave? American Orchid Society Bulletin 48(6): 593–597.

Dunsterville, G.C.K. 1981. *Brassia bidens* from "Dumpleen Camp". American Orchid Society Bulletin 50(1): 17–20.

Dunsterville, G.C.K., and Dunsterville, E. 1973. Hunting *Houlletia lansbergii* in Venezuela. The Orchid Digest 37(1): 30–34.

Dunsterville, G.C.K., and Dunsterville, E. 1978a. *Octomeria steyermarkii*. American Orchid Society Bulletin 47(4): 312–314.

Dunsterville, G.C.K., and Dunsterville, E. 1978b. Some Venezuelan "monospecific" genera – II. American Orchid Society Bulletin 47(5): 438–442.

Dunsterville, G.C.K., and Dunsterville, E. 1982. Hunting *Phragmipedium klotzscheanum* – an agony in eight fits. American Orchid Society Bulletin 51(7): 709–712.

Dunsterville, G.C.K., and Dunsterville, E. 1988. Orchid Hunting in the Lost World (and elsewhere in Venezuela). American Orchid Society, West Palm Beach. [Book collating the authors' articles published in the American Orchid Society Bulletin.]

Dunsterville, G.C.K., and Garay, L.A. 1965, 1966, 1972 & 1976. Venezuelan Orchids Illustrated, vols. 3–6. Andre Deutsch, London.

Fleischmann, A. 2012. *Heliamphora purpurascens* Wistuba, A.Fleischm., Nerz & S. McPherson, sp. nov. AIPC Magazine special issue no. 4: 16. [Originally published in Italian in: AIPC Magazine no. 25: 16.] https://www.aipcnet.it/wp-content/uploads/2020/12/New_species_2011.pdf

Fleischmann, A., and Grande Allende, J.R. 2012 ['2011']. Taxonomía de *Heliamphora minor* Gleason (Sarraceniaceae) del Auyán-tepui, incluyendo una nueva variedad / Taxonomy of *Heliamphora minor* Gleason (Sarraceniaceae) from Auyán-tepui, including a new variety. Acta Botánica Venezuelica 34(1): 1–11. (in Spanish) https://www.jstor.org/stable/44512559

Fleischmann, A., Wistuba, A., and Nerz, J. 2009. Three new species of *Heliamphora* (Sarraceniaceae) from the Guayana Highlands of Venezuela. Willdenowia 39(2): 273–283. https://doi.org/10.3372/wi.39.39206

Foldats, E. 1961. Contribución a la orquideoflora de Venezuela III. [Contribution to the orchid flora of Venezuela III.] Boletín de la Sociedad Venezolana de Ciencias Naturales 22(100): 253–276. (in Spanish)

Gazsó, G. 1995. La Gran Sabana. Aurora, Caracas. (in Spanish with English translation by F. Jacome)

Golos, M.R. 2019. The upper limits of pitcher size in *Heliamphora* (Sarraceniaceae). Planta Carnivora 40(1): 12–18.

Golos, M.R. 2020. First observations of UV-induced fluorescence in *Heliamphora* (Sarraceniaceae) and other tepui flora. Carnivorous Plant Newsletter 49(4): e1–31. https://doi.org/10.55360/cpn494.mg117

González-Sponga, M.A. 1972. *Ananteris venezuelensis* (Scorpionida: Buthidae): nueva especie de la Guayana de Venezuela. [*Ananteris venezuelensis* (Scorpionida: Buthidae): new species from the Venezuelan Guayana.] Memoria de la Sociedad de Ciencias Naturales La Salle 32(93): 205–214. (in Spanish)

González-Sponga, M.A. 1978. Escorpiofauna de la Región Oriental del Estado Bolívar, en Venezuela. [Scorpiofauna of the Eastern Region of Bolívar State, Venezuela.] CONICIT, Caracas. (in Spanish)

González-Sponga, M.A. 1981. Seis nuevas especies del género *Tityus* en Venezuela (Scorpionida: Buthidae). [Six new species of the genus *Tityus* in Venezuela (Scorpionida: Buthidae).] Monografías Científicas Augusto Pi Suñer 12: 1–87. (in Spanish)

Graham, S.A. 2019. A revision of *Cuphea* section *Amazoniana* s. s. (Lythraceae). Systematic Botany 44(1): 146–183. https://doi.org/10.1600/036364419X697994

Harling, G. 1963. Notes on Venezuelan Cyclanthaceae. Boletín de la Sociedad Venezolana de Ciencias Naturales 25(106): 59–69.

Huber, O. 1995a. Geographical and physical features. In: Berry, P.E., Holst, B.K., and Yatskievych, K. (eds.) Flora of the Venezuelan Guayana. Volume 1: Introduction. Missouri Botanical Garden Press, St. Louis. pp. 1–61.

Huber, O. 1995b. History of botanical exploration. In: Berry, P.E., Holst, B.K., and Yatskievych, K. (eds.) Flora of the Venezuelan Guayana. Volume 1: Introduction. Missouri Botanical Garden Press, St. Louis. pp. 63–95.

Huber, O. 1995c. Vegetation. In: Berry, P.E., Holst, B.K., and Yatskievych, K. (eds.) Flora of the Venezuelan Guayana. Volume 1: Introduction. Missouri Botanical Garden Press, St. Louis. pp. 97–160.

Huber, O. 1995d. Conservation of the Venezuelan Guayana. In: Berry, P.E., Holst, B.K., and Yatskievych, K. (eds.) Flora of the Venezuelan Guayana. Volume 1: Introduction. Missouri Botanical Garden Press, St. Louis. pp. 193–218.

Huber, O., and Berry, P.E. 1995. Venezuelan Guayana – Topographical map. [1:2,000,000; 80 × 62 cm] CVG Electrificación del Caroní, Caracas; Missouri Botanical Garden, St. Louis.

Huber, O., and Rull, V. 2019. Plant communities. In: Rull, V., Vegas-Vilarrúbia, T., Huber, O., and Señaris, C. (eds.) Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands. Academic Press, London. pp. 149–164. https://doi.org/10.1016/B978-0-12-815591-2.00007-0

Huber, O., Febres, G., and Arnal, H. (eds.) 2001. Ecological Guide to the Gran Sabana. Trunk Road 10: Piedra de la Virgen – Santa Elena de Uairén. Ecograph, Caracas. [Originally published in Spanish as: Guía Ecológica de la Gran Sabana. Troncal 10: Piedra de la Virgen – Santa Elena de Uairén (2000).]

IUCN. 2012. IUCN Red List Categories and Criteria Version 3.1, 2nd ed. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK. https://www.iucnredlist.org/resources/categories-and-criteria

Kelloff, C.L., Alexander, S.N., Funk, V.A., and Clarke, H.D. 2011. Smithsonian Plant Collections, Guyana: 1995–2004, H. David Clarke. Smithsonian Institution Scholarly Press, Washington, D.C. https://doi.org/10.5479/si.0081024X.97.1

Kokalj, Ž., Zakšek, K., Oštir, K., Pehani, P., Cotar, K., and Somrak, M. 2023. Relief Visualization Toolbox. ZRC SAZU, Ljubljana. https://rvt-py.readthedocs.io

Lasser, T. 1971. Breve reseña historica de la botanica en Venezuela. [Brief historical review of botany in Venezuela.] Acta Botánica Venezuelica 6(1–4): 9–24. (in Spanish) https://www.jstor.org/stable/41740577

Lasso, C.A., Señaris, J.C., Rial, A., and Flores, A.L. (eds.) 2009. Evaluación Rápida de la Biodiversidad de los Ecosistemas Acuáticos de la Cuenca Alta del Río Cuyuní, Guayana Venezolana. [Rapid Biodiversity Assessment of the Aquatic Ecosystems of the Upper Cuyuní River Basin, Venezuelan Guayana.] Conservation International, Arlington. (in Spanish with English summaries) https://doi.org/10.1896/978-1-934151-36-5

Lazo, R., Zambrano, S., and Kalinhoff, C. 2004. Parque Nacional Canaima. In: Rodríguez, J.P., Lazo, R., Solórzano, L.A., and Rojas-Suárez, F. (eds.) Cartografía Digital Básica de las Áreas Naturales Protegidas de Venezuela: Parques Nacionales, Monumentos Naturales, Refugios de Fauna, Reservas de Fauna y Reservas de Biósfera. Instituto Venezolano de Investigaciones Científicas, Caracas. (in Spanish) [Published on CD-ROM and online.] https://web.archive.org/web/20051228104858/http://ecosig.ivic.ve/pn03.htm

Liu, S., and Smith, S.D. 2021. Phylogeny and biogeography of South American marsh pitcher plant genus *Heliamphora* (Sarraceniaceae) endemic to the Guiana Highlands. Molecular Phylogenetics and Evolution 154: article no. 106961 [8 pp.]. https://doi.org/10.1016/j.ympev.2020.106961

Liu, S., and Smith, S.D. 2023. Replicated radiations in the South American marsh pitcher plants (*Heliamphora*) lead to convergent carnivorous trap morphologies. American Journal of Botany 110(10): article no. e16230 [12 pp.]. https://doi.org/10.1002/ajb2.16230

López, M., and Ramírez, N. 1998. Síndromes de dispersión de diásporas de una comunidad arbustiva de la Guayana Venezolana / Dispersal syndromes of diaspores in a shrubland community of the Venezuelan Guayana. Ecotropicos 11(1): 15–32. (in Spanish)

Machado-Allison, A., Chernoff, B., Royero-León, R., Mago-Leccia, F., Velázquez, J., Lasso, C., López-Rojas, H., Bonilla-Rivero, A., Provenzano, F., and Silvera, C. 2000. Ictiofauna de la cuenca del Río Cuyuní en Venezuela. [Ichthyofauna of the Cuyuní River basin in Venezuela.] Interciencia 25(1): 13–21. (in Spanish) https://www.redalyc.org/articulo.oa?id=33904303

Maguire, B. 1970. On the flora of the Guayana Highland. Biotropica 2(2): 85–100. https://doi.org/10.2307/2989766

Maguire, B. 1978. Sarraceniaceae. [pp. 36–62] In: Maguire, B. [& "collaborators": Windisch, P.G., Rizzini, C.T., Howard, R.A., Meijer, W., Kubitzki, K., Steyermark, J.A., Luteyn, J.L., Huang, Y., Pires, J.M., and Gentry, A.H.] The botany of the Guayana Highland—part X. Memoirs of the New York Botanical Garden 29: 1–288.

MapTiler. 2023. MapTiler: Maps for developers. MapTiler AG, Zug. https://www.maptiler.com

Marrero, R.A. 1991. La Gran Sabana: Guía Turística. [The Gran Sabana: Tourist Guide.] Caracas. (in Spanish)

Marrero, R.A. 1995. La Gran Sabana. Manual del Viajero: Ruta Terrestre. [The Gran Sabana. Traveller's Handbook: Land Route.] Presa Peyrán, Caracas. (in Spanish)

Marrero, R.A. 1996. La Gran Sabana: Mapa Municipio Gran Sabana y Parque Nacional Canaima. [The Gran Sabana: Map of Gran Sabana Municipality and Canaima National Park.] [1:500,000 scale] Precotur, Caracas. (in Spanish)

Marrero, R.A. 1997. Guía de la Gran Sabana. [Guide to the Gran Sabana.] Oscar Todtmann, Caracas. (in Spanish with English translation by U. Balli & E. Kline)

Matallana, B. de 1937. "La Gran Sabana". Tres años de misión en los confines de Guayana. ["The Gran Sabana". Three years of missionary work in the confines of Guayana.] Boletín de la Sociedad Venezolana de Ciencias Naturales 4(29): 10–82 + attached foldout map ["Croquis de la Gran Sabana" = Sketch of the Gran Sabana; 1:500,000 scale]. (in Spanish)

Matallana, B. de 1948. La Sierra de Lema [pp. 86–87] In: Luz en la Selva: viajes y excursiones de un misionero por las selvas tropicales de Guayana (Venezuela). [Light in the Jungle: travels and excursions of a missionary in the rainforests of Guayana (Venezuela).] Pro Fide, Madrid. (in Spanish) [Section appears on p. 105 in 3rd ed. from 1960.]

McPherson, S.R. 2006. Pitcher Plants of the Americas. The McDonald & Woodward Publishing Company, Blacksburg.

McPherson, S.R., Wistuba, A., Fleischmann, A., and Nerz, J. 2011. Sarraceniaceae of South America. Redfern Natural History Productions, Poole.

Michelangeli, F.A. 2002. La Gran Sabana. Armitano, Caracas. (in Spanish)

MTDGS. 1964. Mir 1:500.000 – B-20-4 (B-20-G). [1:500,000; *ca.* 50 × 60 cm] Military Topographic Directorate of the General Staff, Moscow. (in Russian) https://www.landkartenarchiv.de/mir500.php?q=b-20-4

Nerz, J. 2014. Die Jagd nach *Heliamphora ionasi*, früher und heute. [The hunt for *Heliamphora ionasi*, past and present.] Das Taublatt no. 79: 46–65. (in German)

Nilsson, S. 1962. Some aquatic Hyphomycetes from South America. Svensk Botanisk Tidskrift 56(2): 351–361. http://www.diva-portal.org/smash/get/diva2:1202260/FULLTEXT01.pdf

Nilsson, S. 1964. Venezuela – ett land med en rik och säregen flora. [Venezuela – a country with a rich and distinctive flora.] Svensk Botanisk Tidskrift 58(1): 209–224. (in Swedish) http://www.diva-portal.org/smash/get/diva2:1202268/FULLTEXT01.pdf

Núñez-Farfán, J., Simonetti, J.A., and Roja, T.M. 2017. Venezuela's botanic heritage in jeopardy. Nature 549(7670): 31. https://doi.org/10.1038/549031b

Ochoa, J.A., and Rojas-Runjaic, F.J.M. 2019. Scorpions. In: Rull, V., Vegas-Vilarrúbia, T., Huber, O., and Señaris, C. (eds.) Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands. Academic Press, London. pp. 223–246. https://doi.org/10.1016/B978-0-12-815591-2.00010-0

Office of Geography. 1961. Venezuela: Official Standard Names Approved by the United States Board on Geographic Names. Department of the Interior, Washington, D.C. https://books.google.com/books?id=Ee3IsIgE3n0C

Oliva-Esteve, F. 2000. Bromeliads. Armitano, Caracas.

OpenStreetMap contributors. 2023. OpenStreetMap. OpenStreetMap Foundation, Cambridge. https://www.openstreetmap.org

Pérez, E. 2018a. A0-1: Topographic map of Canaima National Park and its surroundings. [1:500,000 scale; 1120 × 841 mm] Tepuiexpeditions.com.

Pérez, E. 2018b. A0-3: 3D render map of tepuis of Canaima National Park. [3D render image; 1120 × 840 mm] Tepuiexpeditions.com.

Prance, G.T. 1982. A review of the phytogeographic evidences for Pleistocene climate changes in the Neotropics. Annals of the Missouri Botanical Garden 69(3): 594–624. https://www.biodiversitylibrary.org/page/27281729

Pridgeon, A.M. 1989. G. C. K. Dunsterville, 1905–1988. American Orchid Society Bulletin 58(2): 150–152.

QGIS. 2022. QGIS: A Free and Open Source Geographic Information System. QGIS Association. https://qgis.org

Rice, B. 2018. *Heliamphora*: the various ranges and tepuis. The Carnivorous Plant FAQ v. 12. https://www.sarracenia.com/faq/faq5365.html

Riina, R., Berry, P.E., Huber, O., and Michelangeli, F.A. 2019. Vascular plants and bryophytes. In: Rull, V., Vegas-Vilarrúbia, T., Huber, O., and Señaris, C. (eds.) Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands. Academic Press, London. pp. 121–147. https://doi.org/10.1016/B978-0-12-815591-2.00006-9

Robinson, H. 1965. Venezuelan bryophytes collected by Julian A. Steyermark. Acta Botánica Venezuelica 1(1): 73–83. https://www.jstor.org/stable/41740407

Rojas-Runjaic, F.J.M., and De Sousa, L. 2007. Catálogo de los escorpiones de Venezuela (Arachnida: Scorpiones). [Catalog of the scorpions of Venezuela (Arachnida: Scorpiones).] Boletín de la Sociedad Entomológica Aragonesa no. 40: 281–307. (in Spanish)

Romero-González, G.A. 1989. G. C. K. Dunsterville, 1905–1988: an appreciation. Journal of the Arnold Arboretum 70(3): 439–441. https://www.jstor.org/stable/43782592

Romero-González, G.A., Fernández-Concha, G.C., Gerlach, G., and Cetzal-lx, W. 2015. Novelties in the orchid flora of Venezuela VIII. Subtribe Eriopsidinae. *Eriopsis*. Harvard Papers in Botany 20(2): 101–143. https://doi.org/10.3100/hpib.v20iss2.2015.n2

Rull, V., and Vegas-Vilarrúbia, T. 2020. The Pantepui "Lost World": towards a biogeographical, ecological and evolutionary synthesis of a pristine Neotropical sky-island archipelago. In: Rull, V., and Carnaval, A.C. (eds.) Neotropical Diversification: Patterns and Processes. Springer, Cham. pp. 369–413. https://doi.org/10.1007/978-3-030-31167-4_15

Rull, V., Huber, O., Vegas-Vilarrúbia, T., and Señaris, C. 2019a. Definition and characterization of the Pantepui biogeographical province. In: Rull, V., Vegas-Vilarrúbia, T., Huber, O., and Señaris, C. (eds.) Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands. Academic Press, London. pp. 3–32. https://doi.org/10.1016/B978-0-12-815591-2.00001-X

Rull, V., Nogué, S., Safont, E., and Vegas-Vilarrúbia, T. 2019b. Pantepui and global warming. In: Rull, V., Vegas-Vilarrúbia, T., Huber, O., and Señaris, C. (eds.) Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands. Academic Press, London. pp. 403–417. https://doi.org/10.1016/B978-0-12-815591-2.00017-3

Sanoja, E. 2009. Lista dendrológica de los bosques montanos de La Escalera, Sierra de Lema, Estado Bolívar, Venezuela / Dendrological list of montane forests of La Escalera, Sierra de Lema, Bolivar State, Venezuela. Acta Botánica Venezuelica 32(1): 79–111. (in Spanish) http://ve.scielo.org/scielo.php?script=sci_arttext&pid=S0084-59062009000100003

Schubert, C., and Huber, O. 1990. The Gran Sabana: Panorama of a Region. Lagoven, Caracas. [Originally published in Spanish as: La Gran Sabana: Panorámica de una Región (1989).]

Smith, A. 2010. A tour of the Venezuelan Gran Sabana and some of its tepuis. AIPC Magazine special issue no. 2: 4–95. [Published in Italian in an abbreviated form in: AIPC Magazine no. 18: 4–63.] https://www.aipcnet.it/wp-content/uploads/2020/12/AIPC_Special_Issue_2.pdf

Stainforth, R.M. 1966. Occurrence of pollen and spores in the Roraima Formation of Venezuela and British Guiana. Nature 210(5033): 292–294. https://doi.org/10.1038/210292a0

Steyermark, J.A. 1951. Sarraceniaceae. [pp. 239–242] In: Steyermark, J.A. [& "collaborators": Bartram, E.B., Morton, C.V., Swallen, J.R., McClure, F.A., Core, E.L., Gilly, C.L., Moldenke, H.N., Maguire, B., Smith, L.B., Schweinfurth, C., Yuncker, T.G., Cuatrecasas, J., and Killip, E.P.] Botanical exploration in Venezuela – I. Fieldiana: Botany 28(1): 1–242. https://www.biodiversitylibrary.org/page/2455368

Steyermark, J.A. 1960. Venezuela 1960: Steyermark–Nilsson 1–845 and [Steyermark] 86181–86188. Unpublished collections notebook held at the archives of the Missouri Botanical Garden, St. Louis.

Steyermark, J.A. 1961. Venezuela – the botanical paradise. Boletín de la Sociedad Venezolana de Ciencias Naturales 22(100): 291–297.

Steyermark, J.A. 1964a. Steyermark 1963–1964: [specimen nos.] 92166–93181. Unpublished collections notebook held at the archives of the Missouri Botanical Garden, St. Louis.

Steyermark, J.A. 1964b. Rubiaceae. [pp. 186–278] In: Maguire, B., and Wurdack, J.J. [& "collaborators": McClure, F.A., Smith, L.B., Yuncker, T.G., Allen, C.K., Kopp, L., and Steyermark, J.A.] The botany of the Guayana Highland—part V. Memoirs of the New York Botanical Garden 10(5): 1–278. https://www.biodiversitylibrary.org/page/44053087

Steyermark, J.A. [& "collaborators": Moldenke, H.N., Sandwith, N.Y., and Wurdack, J.J.] 1966a. Botanical novelties in the region of Sierra de Lema, Estado Bolívar, Venezuela – III. Boletín de la Sociedad Venezolana de Ciencias Naturales 26(110): 411–452.

Steyermark, J.A. 1966b. Flora de Ptari-tepui. [Flora of Ptari-tepui.] [pp. 30–104] In: Steyermark, J.A. Contribuciones a la flora de Venezuela: parte 5. [Contributions to the flora of Venezuela: part 5.] Acta Botánica Venezuelica 1(3–4): 9–256. (in Spanish) https://www.jstor.org/stable/44648566

Steyermark, J.A. [with sections by: Drouet, F., Fulford, M., Robinson, H., Lellinger, D.D., Morton, C.V., Gray, N., Swallen, J., Moore Jr., H.A., Harling, G., Bunting, G., Smith, L.B., Moldenke, H.N., Maguire, B., Schweinfurth, C., Cuatrecasas, J., Howard, R., Allen, C.K., Bernardi, L., Irwin, H., Edwin, G., Jablonski, E., Smith Jr., C.E., de Roon, A.C., McVaugh, R., Wurdack, J.J., Sleumer, H., Agostini, G., Taylor, P., Sandwith, N.Y., and Aristeguieta, L.] 1967. Flora del Auyan-tepui. [Flora of Auyán-tepui.] Acta Botánica Venezuelica 2(5–8): 5–370. (in Spanish) https://www.jstor.org/stable/41740412

Steyermark, J.A. 1976. Anexo III: Areas de bosques húmedos de Venezuela que requieren protección. [Annex III: Areas of rainforest in Venezuela requiring protection.] In: Hamilton, L.S., Steyermark, J.A., Veillon, J.P., and Mondolfi, E. Conservación de los Bosques Húmedos de Venezuela. [Conservation of Venezuela's Rainforests.] Sierra Club – Consejo de Bienestar Rural, Caracas. pp. 83–95 + separate foldout map ["Map no. 6: proposed biological reserves"; 1:2,000,000 scale]. (in Spanish)

Steyermark, J.A. 1979. Plant refuge and dispersal centres in Venezuela: their relict and endemic element. In: Larsen, K., and Holm-Nielsen, L.B. (eds.) Tropical Botany: Proceedings of a Symposium held at the University of Aarhus on 10–12 August 1978, organized on the occasion of the 50th anniversary of this university. Academic Press, London. pp. 185–221.

Steyermark, J.A. 1982. Relationships of some Venezuelan forest refuges with lowland tropical floras. In: Prance, G.T. (ed.) Biological Diversification in the Tropics: Proceedings of the Fifth International Symposium of the Association for Tropical Biology, held at Macuto Beach, Caracas, Venezuela, February 8–13, 1979. Columbia University Press, New York. pp. 182–220.

Steyermark, J.A. 1984. Sarraceniaceae: realignment of the genus *Heliamphora*. [pp. 302–312] In: Steyermark, J.A. Flora of the Venezuelan Guayana—I. Annals of the Missouri Botanical Garden 71(1): 297–340. https://www.biodiversitylibrary.org/page/16166604

Steyermark, J.A. 1986a. Expedition to the Lost World. Missouri Botanical Garden Bulletin 74(7): 5–7. https://www.biodiversitylibrary.org/page/7470156

Steyermark, J.A. 1986b. Speciation and endemism in the flora of the Venezuelan tepuis. In: Vuilleumier, F., and Monasterio, M. (eds.) High Altitude Tropical Biogeography. Oxford University Press, Oxford. pp. 317–373.

Steyermark, J.A., and Nilsson, S. [& "collaborators": Smith, L.B., Foldats, E., Yuncker, T.G., Smith Jr., C.E., Wurdack, J.J., and Morton, C.V.] 1962. Botanical novelties in the region of Sierra de Lema, Estado Bolívar – I. Boletín de la Sociedad Venezolana de Ciencias Naturales 23(101): 59–83.

Steyermark, J.A., and Nilsson, S. [& "collaborators": Bunting, G.S., and Sandwith, N.Y.] 1963. Botanical novelties in the region of Sierra de Lema, Estado Bolívar – 2. Boletín de la Sociedad Venezolana de Ciencias Naturales 25(106): 42–49.

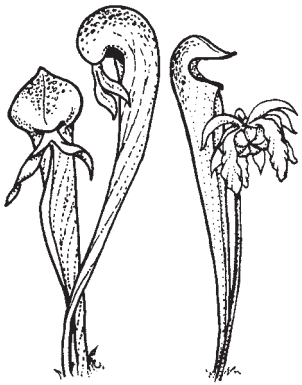
Taylor, M.S. 1989. Plant taxa described by Julian A. Steyermark. Annals of the Missouri Botanical Garden 76(3): 652–780. https://www.biodiversitylibrary.org/page/27999927

"The Geographer". 1963. International Boundary Study No. 21: March 14, 1963. British Guiana–Venezuela Boundary. Department of State, Washington, D.C. https://books.google.com/books?id=rcHGZDHNoG0C

Thiers, B.M. 2023. Index Herbariorum. A global directory of public herbaria and associated staff. [continuously updated] The New York Botanical Garden, New York. http://sweetgum.nybg.org/science/ih

Torres, J.G. 2019. Venezuelan crisis: caring for priceless botanical treasures in a failed state. Mongabay, 31 July 2019. https://news.mongabay.com/2019/07/venezuelan-crisis-caring-for-priceless-botanical-treasures-in-a-failed-state/

USGS. 2023. EarthExplorer. United States Geological Survey, Reston. https://earthexplorer.usgs.gov
Vila, P. 1960. Geografía de Venezuela, vol. 1: El territorio nacional y su ambiente físico. [Geography of Venezuela, vol. 1: The national territory and its physical environment.] Dirección de Cultura y Bellas Artes, Caracas. (in Spanish)
Webb, G.H. 1990. Obituary: Mr. G.C.K. Dunsterville. The Kipling Journal 64(253): 37–38. https://www.kiplingsociety.co.uk/wp-content/uploads/pdf/KJ253.pdf
Weidmann, K. [text mainly by Vila, M.P., and Huber, O.] 1986. La 'Gran Sabana'. Oscar Todtmann, Caracas. (in Spanish)
Wrazidlo, M. 2019. Quest for the origin of *Heliamphora heterodoxa*. Report of May 2018 expedition to Venezuela with carnivorous flora occurrences in the base areas of Ptari-tepui. Carnivorous Plant Newsletter 48(4):183–187. https://doi.org/10.55360/cpn484.mw500
Wrazidlo, M. 2021. Waukauyengtipu and Uchii River Uplands Expedition 2019 – report with photographic observations of carnivorous flora of the Paruima territory in the Cuyuni-Mazaruni Region of Guyana. Carnivorous Plant Newsletter 50(3): 141–152. https://doi.org/10.55360/cpn503.mw783
Wrazidlo, M., and Fleischmann, A. 2019. Proposal to conserve the name *Heliamphora heterodoxa* (Sarraceniaceae) with a conserved type. Taxon 68(4): 871–872. https://doi.org/10.1002/tax.12110
Wrazidlo, M., McPherson, S.R., and Clarke, H.D. 2022. Notes on misconceptions in the application of geographical names of the tepuis on the borderlands of Guyana and Venezuela and a clarification of the location of Waukauyengtipu and Cerro Venamo. Miscellanea Geographica 26(2): 75–79. https://doi.org/10.2478/mgrsd-2020-0073
Zambrano, S., Armas, M., Lazo, R., and Kalinhoff, C. 2004. Monumento Natural Tepuyes (Cerro Venamo). In: Rodríguez, J.P., Lazo, R., Solórzano, L.A., and Rojas-Suárez, F. (eds.)Cartografía Digital Básica de las Áreas Naturales Protegidas de Venezuela: Parques Nacionales, Monumentos Naturales, Refugios de Fauna, Reservas de Fauna y Reservas de Biósfera. Instituto Venezolano de Investigaciones Científicas, Caracas. (in Spanish) [Published on CD-ROM and online.] https://web.archive.org/web/20051228104828/http://ecosig.ivic.ve/mn18e.htm



CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society
www.carnivorousplants.org

Volume 53, Number 1
March 2024

Front Cover: Retentive hairs of *Heliamphora ionasi*. Though in this species bimorphic hairs are restricted to the region immediately below the rim, in the newly described *Heliamphora electrum* they cover the entire trapping surface. SEM by M.R. Golos. Article on page 4.

Back Cover: Andy Smith holding a potted *Heliamphora electrum*. Pencil and watercolour portrait by François Sockhom Mey. Article on page 4.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

All correspondence regarding dues, address changes and missing issues should be sent to the Membership Coordinator. Do not send such correspondence to the editors. Checks for subscriptions should be made to the International Carnivorous Plant Society in US funds. A one-year membership that includes a printed copy of CPN is US$40. For additional membership options, see https://icps.clubexpress.com/.

Date of effective publication of the December 2023 issue of Carnivorous Plant Newsletter: November 2, 2023.

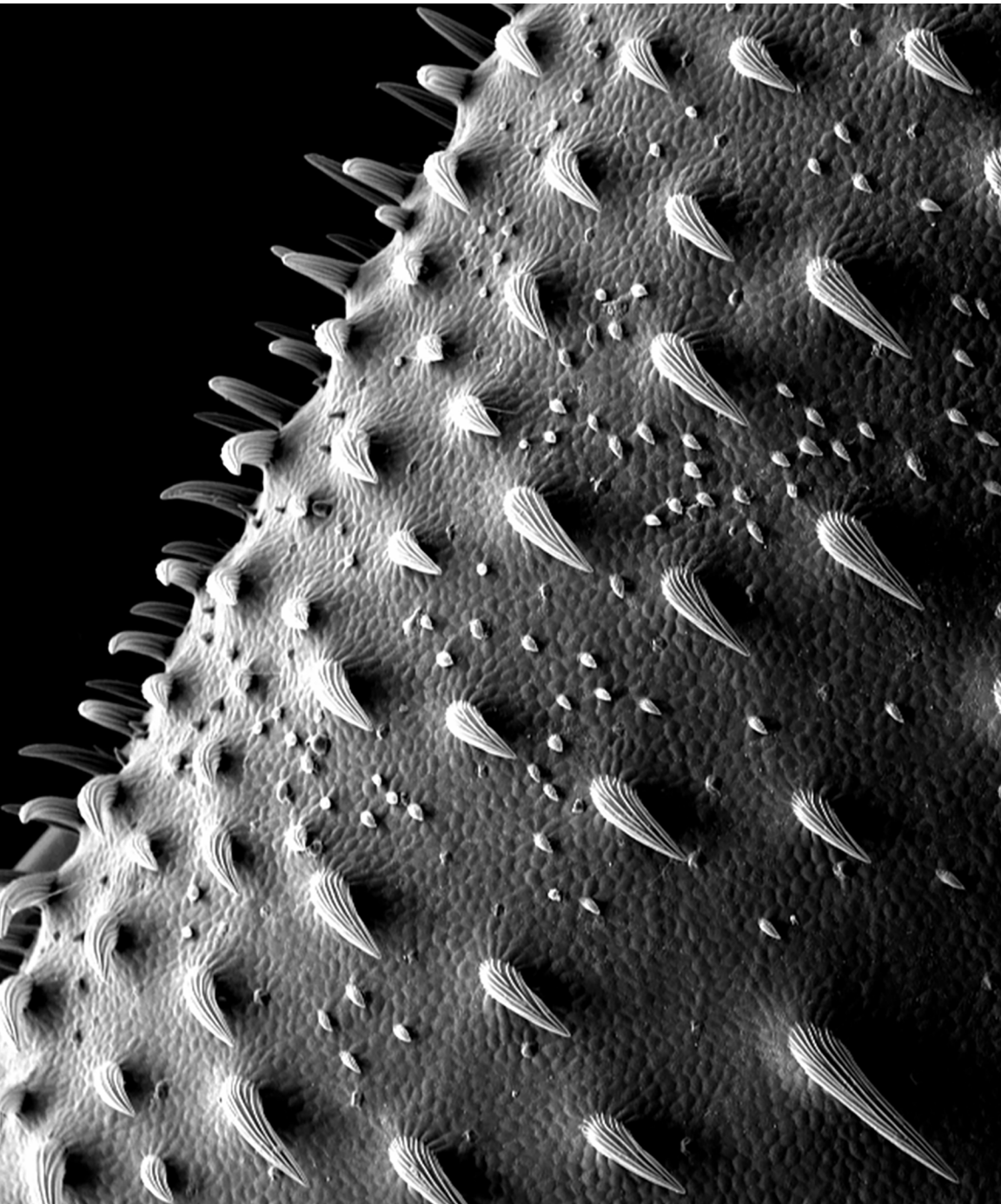
The ICPS is the International Cultivar Registration Authority (ICRA) for the names of cultivated carnivorous plants according to the International Code of Nomenclature for Cultivated Plants. Send relevant correspondence to the ICPS, Inc.

Carnivorous Plant Newsletter is published quarterly in March, June, September, and December by the ICPS, Inc., 2121 N. California Blvd., Suite 290, Walnut Creek, CA 94596, USA. Periodicals postage paid at Walnut Creek, CA and additional mailing offices. Postmaster: Send address changes to ICPS, Inc., 2121 N. California Blvd., Suite 290, Walnut Creek, CA 94596, USA. Printed by Sheridan, 810 E. 10th Street, Lawrence, KS 66044. Logo and masthead art: Paul Milauskas.
 ISSN #0190-9215

CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

Volume 53, No. 1 March 2024



"I have been growing this plant for many years, and I suspect many plants in collections may have originated from me. Unfortunately, I can't remember who I obtained the plant from in the first place. One thing for sure is it isn't H. heterodoxa. For me, the most distinctive feature of the plants are the two differing lengths of hairs on the inside of the pitcher wall... quite reflective and unique, with a distinctive pattern."
Andy Smith, July 2020