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A new species of *Ombrophytum* (Balanophoraceae) from Chile, with notes on subterranean organs and vegetative reproduction in the family

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Abstract

The Chilean desert specimens of *Ombrophytum* (Balanophoraceae) reported in the literature as *O. subterraneum* (Asplund) Hansen differ structurally in several respects from that species, which was described from moist tropical forest in Bolivia. Therefore the Chilean specimens are treated as a narrowly endemic, separate species, *Ombrophytum chilensis* Kuijt & Delprete, on the basis of the type specimen and published photographs. Discussions on morphology, distribution and conservation status are provided for this species. Critical comments on the underground organs and reproduction in Neotropical Balanophoraceae are also presented.

Key Words: *Corynaea*, *Helosis*, *Langsdorffia*, *Thonningia*, parasitic plants, underground structures

Introduction

The holoparasitic family Balanophoraceae in the New World consists of 7 genera and about 19 species (Hansen 1980; Cardoso & Braga 2015; Cardoso *et al.* 2011; Delprete 2004, 2014 [20 species, including the new species here described]). In most cases, species of this family are rare and often very local in occurrence. The brittle, succulent nature of plants has further limited available study material, and comparisons between species have consequently often proven difficult or inconclusive. Hansen (1980) reported four species in the genus *Ombrophytum* Poeppig ex Endlicher (Endlicher 1836: 32), occurring in a great diversity of western South American habitats, including moist tropical forests in Bolivia, the arid Galapagos Islands, and the Atacama Desert of northern Chile. A fifth species of *Ombrophytum*, from French Guiana, was added by Delprete (2014), and a sixth species, from Colombia, awaits description by Guzmán Guzmán (in press). The Chilean plants of this genus have been reported as *O. subterraneum* (Asplund 1928: 274) B. Hansen (1980: 62) by Mauseth & Montenegro (1992) and Mauseth *et al.* (1992). Close scrutiny, however, has shown that significant structural differences exist from that species, and the Chilean plants are here described as a new species. Therefore, with the new species to be published by Guzmán Guzmán (in press), *Ombrophytum* is here recognized as a genus of seven species.

Ombrophytum chilensis Kuijt & Delprete, *sp. nov.*

Type:—CHILE. Antofagasta: [Pukará de] Lasana [ca. 22°17'S, 68°38'W; Lasana is in the canyon of the Río Loa, about 10 km N of Chiu Chiu], 6 July 1969 (fl, fr), *H.C. Martin 486* (holotype: SI! [Sheet A]; isotype: SI! [Sheet B]). [SI specimens have no barcode or accession number] (Figs. 1–3).

Diagnosis:—*Ombrophytum chilensis* differs from the other species of the genus in the translucent scales on the young peduncle (Fig. 3), while the other species apparently have naked peduncles, except for *O. subterraneum* having some scattered scales. Equally distinctive are the large, mostly tridentate fertile bracts (i.e., subtending inflorescence branches) that intergrade with the scales below (i.e., on the peduncle), while in other species of the genus they have

a truncate-obconical stalk and a hemi-ellipsoid head in *O. guayanensis* Delprete (2014: 264, figs. 1D, F)), or they are clavate in *O. violaceum* B. Hansen (1977: 231; Hansen 1980: 58), or with a filiform stalk and distally obtriangular in *O. microlepis* B. Hansen (1980: 60, figs. 24F, G), or with a flat stalk and a “subulate to bifurcate or irregularly incised dent protruding upward from its lower part” (Hansen 1980: 64) in *O. subterraneum*.

Fleshy parasitic plants at least partially subterranean at initial stages; the succulent inflorescences originating endogenously from an irregularly shaped tuber with a fairly smooth surface. Volva basally sheathing, smooth, irregularly split laterally, mostly bifid, brownish, continuous with the tuber surface, covering about half or more of the peduncle. Peduncle at least 2–3 cm thick, white, the exposed portion bearing numerous, spirally inserted, whitish, translucent scales that have a flat limb terminating distally into one to three acute tips, the middle one largest. Inflorescence to 30 cm long, to 8 cm wide (fide Mauseth *et al.* 1992: 409 [Mauseth & Montenegro (1992: 456) wrote that the inflorescence is up to 80 cm tall, but we believe that is a typographical error]), branched portion globose to broadly ovoid, round to somewhat tapered at apex. Scales grading into tridentate fertile bracts above, each of the latter subtending an inflorescence branch; scales and floriferous bracts apparently caducous. Male inflorescence branches not seen. Female inflorescence branches about 100 or more per inflorescence, each about 2 cm long and 1 cm thick, terminating in a flat, more or less lobed pelta that extends somewhat downwards; with at least 60–70 per inflorescence branch; flowers closely packed below the pelta. Female flowers consisting of a globular ovary ca. 1.5 mm in diameter, red when fresh. Styles 2, emerging from a slight apical depression of the ovary, short, whitish, topped by a capitate stigma. Perianth lacking. Fruit a one-seeded structure essentially unchanged from the ovary but slightly larger, red; styles deciduous.

Observations:—No male flowers are visible in the splendid photograph (Fig. 3) taken by J.D. Mauseth (and published in Murata 1997), leading to the possibility that *O. chilensis* is dioecious. Mauseth *et al.* (1992) excavated at least 30 plants, many of them in anthesis, but male flowers are not mentioned. Hansen (1980: 64) described *O. subterraneum sensu* Hansen (including *O. chilensis*), as bisexual plants or only with female inflorescences, while the other species in the genus are monoecious (Hansen 1980, Delprete 2014). In the description of *O. subterraneum* (including the Chilean specimens), Hansen (1980) described male and female branches, while in the discussion he (Hansen 1980: 66) wrote that “The variation [in *O. subterraneum sensu* Hansen] is mostly found in in the shape and colour of the inflorescences and in the distribution of the sexes, some individuals being entirely female, others bisexual, even within the same population (Galapagos). These characters have proven to be most unreliable for taxonomic purposes in other genera of Balanophoraceae also, e.g., within *Balanophora* [J.R. Forster & J.G.A. Forster (1775: 50)] (Hansen 1972).” However, as the definition of *O. subterraneum sensu* Hansen includes the Chilean plants, *O. subterraneum* should be re-delimited, excluding the Chilean plants. Also, it is possible that the entirely female individuals that Hansen examined are those from Chile; however, this remains to be confirmed. In all the other species of the genus, the lower inflorescence branches are female, the upper ones male. Male flowers in *Ombrophytum* (presumably including *O. chilensis*) consist of nothing but two stamens with short filaments and elongate, biloculate anthers dehiscing longitudinally (See Asplund 1928: figs. 3a–b; Delprete 2014: figs. 1d–e). As in the female flowers, there is no evidence of a perianth.

As mentioned above, *O. chilensis* is thought to be dioecious, while the other species of the genus are monoecious. The Galapagos plants are perhaps sometimes bisexual and possibly apomictic (Hansen 1980: 67), but reliable evidence for the latter condition is lacking.

Additional specimen studied:—CHILE. Antofagasta: Calama, March 1946, A. Pfister *s.n.* (S). The current renovation of the Botany Building at S has denied us the possibility to inspect this specimen. However, the excellent photographs of it present in the data base there (<http://herbarium.nrm.se/>) leave no doubt that it represents *O. chilensis*. In fact, it possibly derives from the same locality as the type. This collection thus represents the second known herbarium specimen of this species.

Distribution and Ecology:—At this time it appears that the above cited Antofagasta site represents the only Chilean one, not just for the genus, but for Balanophoraceae generally. Ecologically, the present species is unusual in existing in one of the most arid regions worldwide, while other species of the genus are mostly found in moist tropical forests, with the possible exception of the Galapagos population that has previously been assigned to *O. subterraneum*.

Phenology:—Mauseth *et al.* (1992) reported that the plants he collected near the town of Chiu Chiu were in flower and fruit in May and August; and the type specimens, also with flowers and fruits, were collected in July. The Region of Antofagasta has a desert climate, without any considerable precipitation throughout the year. The period May–August corresponds with the cooler winter season.

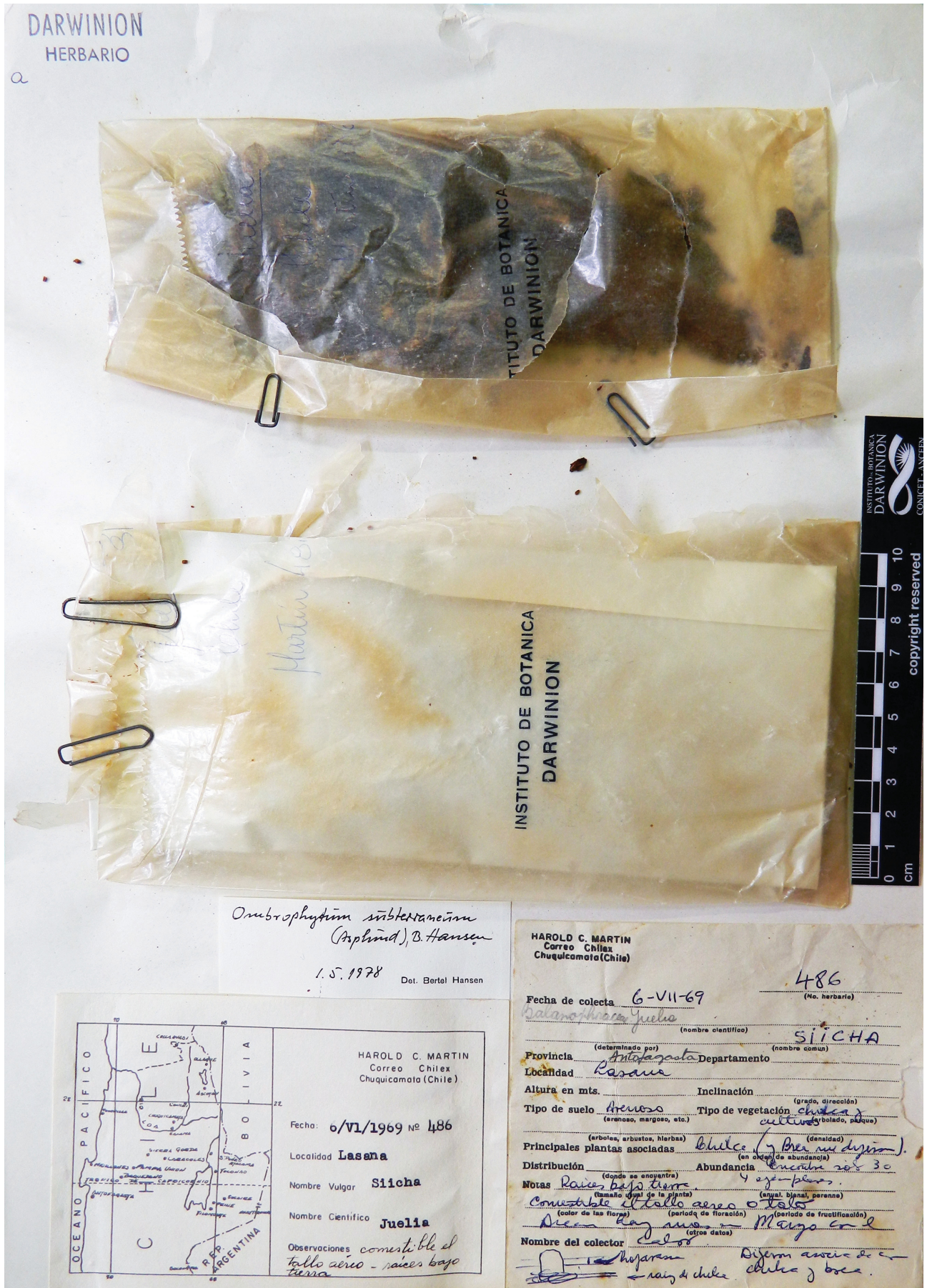


FIGURE 1. Holotype of *Ombrophytum chilensis*, Martin 468 (SI [Sheet A]). Courtesy M. Belgrano.

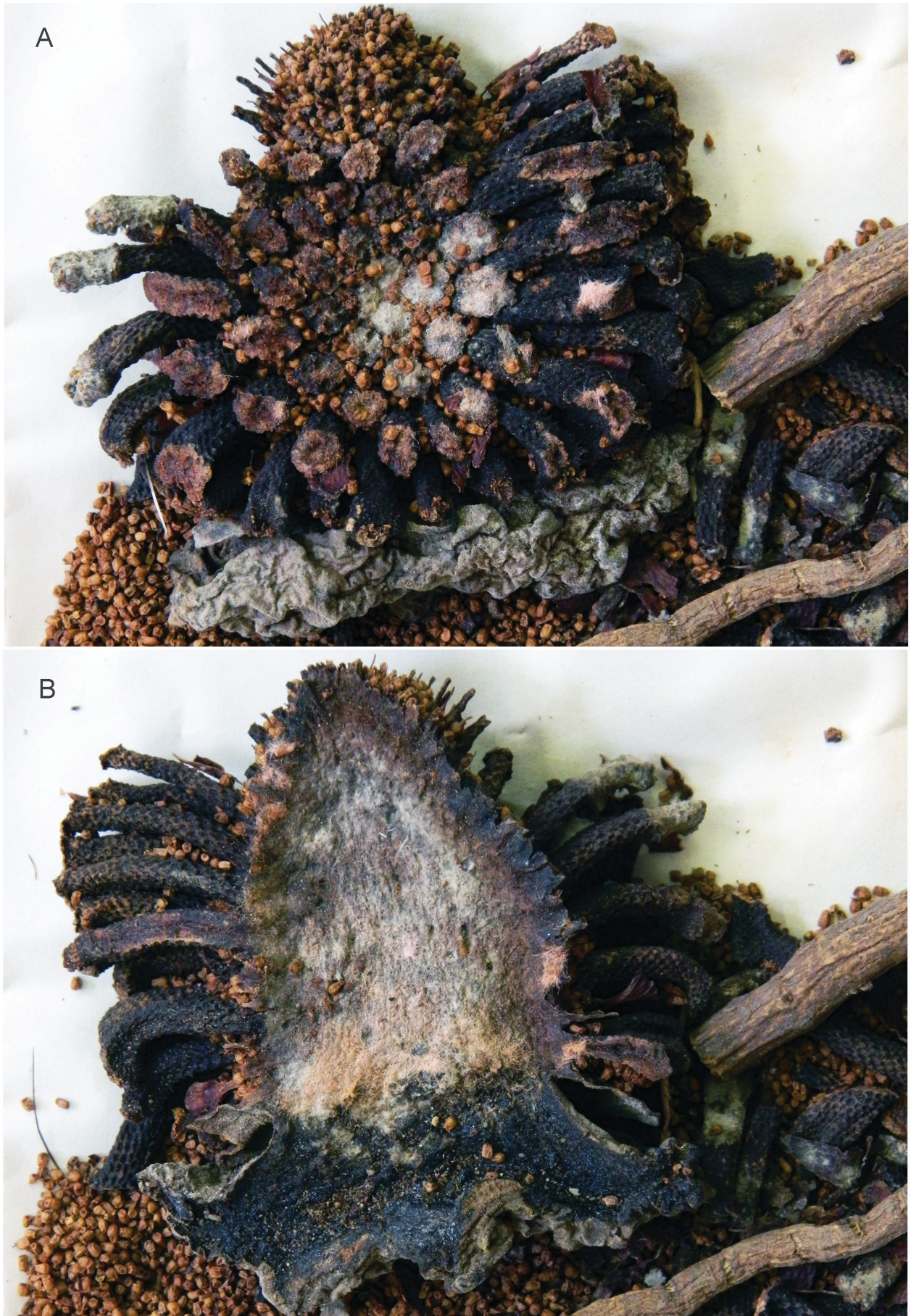


FIGURE 2. *Ombrophytum chilensis*, details from holotype specimen (*Martin 468* (SI [Sheet A])). **A**, Specimen from upper envelope (see Fig. 1), view from external side; **B**, Same specimen, view from dissected side. Courtesy M. Belgrano.



FIGURE 3. Inflorescences of *Ombrophytum chilensis*, from Murata (1997). Photograph by J.D. Mauseth (near Chiu Chiu, Chile), reproduced with permission.

Vernacular name:—Siicha (*H.C. Martin 486*).

Suggested conservation status:—**Endangered (EN)**. This species is known by two gatherings of herbarium specimens in the Province of Antofagasta. The label of the specimens from Calama, collected in 1946 (*A. Pfister s.n.*), does not report the number of individuals present at the time of collection. The label of the type specimen, from nearby Pukará de Lasana [ca. 22°17'S, 68°38'W; ca. 10 km N of Chiu Chiu] collected in 1969 (*H.C. Martin 486*), reports a population of 20–30 individuals at the time of collection.

Two additional collections of this species have been reported (as “*O. subterraneum*”) by Mauseth *et al.* (1992) from “the town of Chiuchiu, on highway 21, about 24 km east of Calama. In August 1987, twenty plants infecting cultivated alfalfa were collected, and in May 1991, ten plants infecting *Tessaria absinthioides* DC. (Asteraceae) were collected. At both times, the plants were alive, healthy, and many were flowering.” Mauseth and Montenegro (1992) stated that “A voucher specimen (JMD 1987-506) was deposited at TEX”; however, no voucher specimen is present in that herbarium (G. Yatskievych, pers. comm.).

The fleshy inflorescence peduncle of *Ombrophytum* is edible. Sleumer (1954) reported that it has a sweetish taste and was much collected and consumed by the local inhabitants near the Bolivian type locality of *O. subterraneum*. The base of the *O. chilensis* inflorescence is also prized as a delicacy near its type locality (Mauseth *et al.* 1992); a similar statement appears on the label of its type specimen. Almost 50 years ago, Pizarro (1971) already listed this species (as “*O. subterraneum*”) among the Chilean plants in risk of extinction, due to the intense extraction activities of this edible plant.

We estimate that the extent of occurrence (EEO) between the towns Calama and Lasana (ca. 43 km by road from each other) is approximately 200 km². Also, the limited data available report populations of 20–30 individuals of this species. Therefore, taking into account the small EEO, the relatively small populations, the intense extraction in its natural environment, and the IUCN (2012, 2019) recommendations, we suggest to place *O. chilensis* in the Endangered (EN) category.

Notes on pollination:—The specific epithet of the most common species in the genus has probably given rise to the assumption that flowering, or even fruiting, takes place underground. There is little doubt that the formation of the inflorescence and flowers take place below ground. However, whether the female flowers are receptive to pollen while still below ground is debatable. Guzmán Guzmán (in press) has observed the activity of a beetle (Belidae: Oxycorina) on the exposed inflorescences of his new species, from Colombia, and such insects may also effect pollination in *O. chilensis*. It should be noted that in those species with separate male and female inflorescence branches, the male portion is always at the distal portion of the inflorescence, and thus sheds pollen above ground. Pollination activity in the genus is in need of careful observations.

Borchsenius and Olesen (1990) observed the pollination of *Lophophytum mirabile* Schott & Endlicher (1832: 1, tab. 1), a taxon closely related to *Ombrophytum*. They observed 25 individuals growing in seasonally flooded forest (várzea) near the Río Napo, Amazonian Ecuador. The species is monoecious, with female branches below ground and male branches above ground. Five Coleoptera spp. and one Meliponinae sp. were observed on the flowering plant. The beetles were a Chrysomelidae sp., two Nitidulidae spp., a Staphylinidae sp., and a Curculionidae sp. The Chrysomelidae and Nitidulidae spp. “landed on the ground close to the plant or directly on their male part. After landing they disappeared between the bracts down to the female part. Chrysomelidae and Nitidulidae caught on the female part all carried a pure load of *Lophophytum* pollen. Thus they may act as pollinators.” (Borchsenius and Olesen 1990: 502–502, figs. 1–2). It is possible that the monoecious species of *Ombrophytum* share a similar pollination pattern.

Hosts and distribution:—Host specificity in the genus is low (Hansen 2015), a number of dicotyledonous families having been recorded. Mauseth *et al.* (1992) mentioned *Tessaria absinthioides* (Hooker & Arnott 1832: 57) A.P. de Candolle (1836: 457) [= *Pluchea absinthioides* (Hooker & Arnott) H. Robinson (1973: 284); Asteraceae] and even cultivated *Medicago sativa* Linnaeus (1753: 778; Leguminosae) as hosts of *O. chilensis*.

It is interesting to observe that species of *Ombrophytum* appear to occur in very limited, rare populations. These may be visualized as metapopulations maintaining themselves precariously in consequence of limited dispersal mechanisms (see Barkman *et al.* 2017, on Rafflesiaceae). Such limitations, in turn, would imply significant longevity of seeds, and even the need for proximity of host roots (or other organs) that would stimulate germination, as is well known for some unrelated parasitic angiosperms (Kuijt 1969; Heide-Jørgensen 2008). It is perhaps possible to speculate about a syndrome consisting of (1) the production of extremely large numbers of very small seeds or fruits (at least 7,000 per inflorescence in *Ombrophytum chilensis*, and 270,000 per flower in *Rafflesia* spp. (Barkman *et al.* 2017); (2) their much extended viability; (3) their need to be stimulated by host exudates in order to germinate; and (4) their lack of specialized dispersal mechanisms resulting in (5) the species tendency to form distinct metapopulations—a syndrome that may have evolved independently in the most highly derived holoparasitic plant families.

Galapagos Islands collection of *Ombrophytum*

The reported features of the Galapagos collection (C, which we were not able to inspect) by *Adersen* (1976) indicate that it is similar to *O. chilensis* (See Hansen 1980, fig. 28). The Galapagos plants also bear a conspicuous terminal protrusion on the upward-pointing limb of its bracts. However, the comparable portion in *O. chilensis* is not subulate, but flat, rather broadly triangular, translucent, and usually flanked by two smaller dents. More importantly, the Galapagos material mostly has its inflorescences divided into distal male and proximal female parts, while no male flowers have yet been identified anywhere in *O. chilensis*, even on its distal portions. The inflorescence peduncle of Galapagos plants is smooth, about 4 cm long in Hansen's illustration, but 2–4 cm long and occupied by translucent, apparently caducous, scales in *O. chilensis*. The former plants have fertile inflorescence portions about twice as long as broad, but that portion in *O. chilensis* is much broader and shorter, and may be described as globose at early stage and ovoid when fully expanded. As mentioned earlier, Galapagos plants have been erroneously identified as *O. subterraneum*; their sex distribution and other features differ significantly from that species.

Notes on underground structures in Neotropical Balanophoraceae

It is not surprising that underground structures in the family have not been adequately studied. In all cases, they develop on the host root a massive, tuberous, often multi-lobed organ from which one or more inflorescences emerge. The surface features of these organs vary greatly, some being coarsely verrucose, others being essentially smooth (See the various illustrations in Eichler 1869, Hansen 1980 & 2015, Hooker 1856). In *Balanophora* (a Paleotropical genus), it has been shown that surface characteristics may be of importance in delimiting species (Kuijt & Dong 1992).

In some Neotropical genera, however, we find additional developments that require attention. The most detailed exposition of these underground structures was presented by Hooker (1856) and Eichler (1869); many of these illustrations are reproduced in Hansen (1980, 2015) and elsewhere. While remembering the difficulties in excavating Balanophoraceae and their hosts, it appears that non-tuberous structures are found only in *Helosis* L.C.M. Richard (1822: 432), *Corynaea* J.D. Hooker (1856: 31, 54), *Ombrophytum*, and *Langsdorffia* Martius (1818: 179). At least some of these structures seem to bear new plants where contacting host roots, but caution is required before reaching such conclusion. The non-committal term “runner” is appropriate when their morphological nature is not established or convincing.

Corynaea tubers produce slender roots (Kuijt & Bruns 1987) that emerge from the tuber. They do not appear to branch, and lack both root hairs and root caps. Their surface is studded with small clusters of light-colored cells which also are seen on the tuber itself. Endodermis and pericycle are lacking, and there is very little vascular tissue, which is arranged in two slender bundles separated by parenchyma cells. It has not been determined whether the roots are endogenous or exogenous. No new haustorial contacts were reported on the roots. While these organs may certainly be called roots, they thus have anomalous structural features.

Ombrophytum chilensis produces slender root-like structures endogenously from the bottom side of the tuber (Mauseth *et al.* 1992, fig. 2); a small volva is present at the base. They lack a root cap, having a shoot-like tunica-corporis apical organization, and may reach 20 cm in length and 2–3 mm in thickness. Anatomically, they show a stem-like organization with a mixture of only vessel elements and phloem with parenchyma in the center (or only parenchyma), and 4 or 5 collateral bundles. The authors believe that “runners could initiate infections where they contacted host roots ...; one runner being only 6 cm long had initiated 5 small tubers”. As mentioned before, we do not know if such small tubers might not represent new individuals derived from germinating seeds, which are produced in great quantity. The runners occasionally branch. The tubers of the Guzmán Guzmán species (in press) are said to develop runners that eventually will bear new inflorescences; this report also invites more detailed documentation.

Hooker (1856) in plate 15 (as *Helosis mexicana* Liebmann (1847: 181), reproduced in Hansen 2015, fig. 77) illustrated the excavated runner system of *Helosis cayanensis* (Swartz 1788: 12) Sprengel (1826: 765); perhaps only the stout runners generate new inflorescences. A few minute tubers are present on host roots, clearly representing new individuals. It is obvious that the stout, branching runners of *H. cayanensis* not only generate inflorescences but also often have young tubers attached to them (Hansen 1980, fig. 15A, reproduced from Eichler 1869). However, as mentioned, there is no way of ascertaining whether or not these young tubers are the products of germinating seeds, because host roots are seen to be connected to them in each case. The same is true for plate 5 in Eichler (1869, depicting another group of tubers of the same species). The correct interpretation of a tangled mass of infected host roots is a difficult and laborious matter.

The underground structure of *Langsdorffia hypogaea* Martius (1818: 179, tab. 5), as depicted in plate 1 of Eichler (1869), presents us with another, related interpretational dilemma. In this figure, the parasitic organ is an elongated tuber from which numerous leafless, non-articulated, runners emerge, each terminating in at least one inflorescence.

The surfaces of these runners, their ramifications, and the main tuber form a smooth continuum, suggesting that the runners are not endogenous. In *Helosis*, we find a small, distinct volva partway up each inflorescence peduncle (Hansen 2015, fig. 77); in *Langsdorffia* (Eichler 1869, pl. 2, fig. 12), an inconspicuous volva exists immediately below the terminal inflorescence, the runner below it being leafless. Inexplicably, the terminal inflorescence of *Langsdorffia* may sometimes be supported by an elongate structure that bears numerous leafy scales (Hansen 1980, fig. 29F).

The elongated structures of *Corynaea*, *Helosis*, *Langsdorffia* and *Ombrophytum* thus seem to fall into two quite different categories, quite aside from any reproductive potential. In *Ombrophytum*, we clearly see endogenous, thin structures that surely may be referred to as roots, while the issue is not clear in *Corynaea*. The observed anatomical anomalies are paralleled in roots of some other parasitic plants, as in the epicortical roots of some mistletoes (Kuijt 1969). In contrast, in *Langsdorffia* and *Helosis* the runners are apparently not endogenous, in the former bearing terminal inflorescences and sometimes leaf scales below the small volva; it thus appears likely that they represent modified stems even where leafless. None of the genera outside the Neotropics appear to develop either type of subterranean organs, with the sole exception of the South African *Thonningia sanguinea* Vahl (1810: 125, tab. 6), described by Mangenot (1947) as “capturing” host roots by small parasitic roots.

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