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RAFAEL COSTA SILVA

SISTEMÁTICA DE *LYCIANTHES* (DUNAL) HASSL. (SOLANACEAE) NO BRASIL

Recife
2018

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To my wife, Fernanda Formiga.

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ABSTRACT

With about 200 species, *Lycianthes* (Dunal) Hassler is one of the most representative genera of the Solanaceae family. The most complete treatment for the genus was done by Georg Bitter in 1919, who proposed an infrageneric classification system for *Lycianthes*, which included detailed descriptions of 134 species, however, it does not present illustrations or a key for identification of the treated species. For more than a century the species of *Lycianthes* were included in *Solanum*, due to the great morphological similarity of their flowers, evidenced mainly by the stellate corolla and the poricide anthers. On the other hand, the presence of appendages at the calyx evidences the great affinity of *Lycianthes* with *Capsicum*. Recent phylogenetic studies, including molecular studies have supported the position of *Lycianthes* in the Capsiceae tribe, reinforcing its phylogenetic affinity with *Capsicum*. In Brazil, the informations for *Lycianthes* are scarce, with the first records made in Flora Brasiliensis, where only two species were described as part of *Solanum*. Currently, the list of species of Flora do Brasil presents only one list with nine species of the genus. The present work was developed with the objective of carrying out a taxonomic study of *Lycianthes* for Brazil. For this, morphological, nomenclature and classic taxonomic studies were performed, complemented by anatomical studies. As a results, we present the taxonomic treatment of 12 species and a key to the separation of the *Lycianthes* species found in Brazil, including the description of a new species, a new combination, five synonymies, 14 lectopifications. In addition to the taxonomic treatment, a study of the leaf anatomy is presented, where the importance of these anatomical characters as a subsidy to the taxonomy of *Lycianthes* is evaluated. These results are organized in four manuscripts, of these, two manuscripts of taxonomy and nomenclature were already published in two specialized journals in 2018, and two other are being finalized to be submitted for publication in specialized journals: one presents a taxonomic review of *Lycianthes* species for Brazil, and the other brings the leaf anatomical data as support to the taxonomy of *Lycianthes*. This thesis represents an important contribution to the taxonomy of *Lycianthes* and fills a large gap of information about the taxonomy of the genus and constitutes the most complete treatment for the *Lycianthes* species of Brazil.

Keywords: Capsiceae. *Lycianthes* subg. *Polymeris*. Sect. *Eupolymeris*. Leaf anatomy. Taxonomy of *Lycianthes*.

RESUMO

Com cerca de 200 espécies, *Lycianthes* (Dunal) Hassler é um dos gêneros mais representativos da família Solanaceae. O tratamento mais completo para o gênero foi realizado por Georg Bitter, em 1919, que propôs um sistema de classificação infragenérico para *Lycianthes*, no qual incluiu descrições detalhadas de 134 espécies, entretanto, não apresenta ilustrações nem uma chave para identificação das espécies tratadas. Durante mais de um século as espécies de *Lycianthes* estavam incluídas em *Solanum*, devido à grande semelhança morfológica de suas flores, evidenciadas, principalmente, pelas corolas estreladas com as anteras poricidas. Por outro lado, a presença de apêndices no cálice evidencia a grande afinidade de *Lycianthes* com *Capsicum*. Os estudos filogenéticos recentes, incluindo moleculares têm apoiado a posição de *Lycianthes* na tribo *Capsiceae*, reforçando sua afinidade filogenética com *Capsicum*. No Brasil, as informações para *Lycianthes* são escassas, com os primeiros registros feitos na Flora Brasiliensis, onde apenas duas espécies são descritas como parte de *Solanum*. Atualmente, a lista de espécies da Flora do Brasil apresenta apenas uma lista com nove espécies do gênero. O presente trabalho foi desenvolvido com o objetivo de realizar um estudo taxonômico de *Lycianthes* para o Brasil. Para tanto, foram realizados estudos morfológicos, nomenclaturais e de taxonomia clássica, complementados por estudos anatômicos. Como resultados apresenta-se o tratamento taxonômico de 12 espécies, incluindo a descrição de uma nova espécie, uma nova combinação, cinco sinonímias, 14 lectotipificações, além de uma chave para a separação das espécies de *Lycianthes* encontradas no Brasil. Além do tratamento taxonômico, apresenta-se um estudo da anatomia foliar, onde são avaliadas a importância desses caracteres anatômicos como subsídio à taxonomia de *Lycianthes*. Esses resultados têm sido organizados em quatro manuscritos, que estão sendo submetidos a publicação em periódicos especializados: o primeiro apresenta lectotipificações e sinonimizações; o segundo trata de atualizações no gênero, que inclui a proposição de uma nova espécie de *Lycianthes* para o Brasil, com novas sinonimizações e uma nova combinação; e o terceiro apresenta uma revisão taxonômica de *Lycianthes* para o Brasil, onde apresenta-se um tratamento taxonômico completo, com descrições das espécies, informações sobre a distribuição e notas taxonômicas, além de ilustrações e uma chave para identificação das espécies. O quarto traz os dados anatômicos foliares e comentários sobre sua utilidade na taxonomia do grupo. O presente trabalho representa uma importante contribuição

à taxonomia de *Lycianthes* e preenche uma grande lacuna de informações sobre sua taxonomia, constituindo o mais completo tratamento para o gênero no Brasil.

Palavras-chave: Capsiceae. *Lycianthes* subg. *Polymeris*. Sect. *Eupolymeris*. Anatomia foliar.

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1 INTRODUCTION

One of the most basic questions in biology concerns the number of living organisms on Earth. Although this questioning has been done for centuries, we do not know within an order of magnitude how many species there are on Earth. Current estimates of species diversity approximate about 8.7 million species (MORA ET AL., 2011). However, despite this wide range of estimates, there are only about 6,000 taxonomists working to classify all organisms on Earth (WILSON, 2004).

The diversity of Spermatophyta, a relatively well-studied group when compared to other taxa, has traditionally been estimated around 250,000 species (MABBERLEY, 1997). More recent accounts, particularly those using abundant online species lists and databases, have increased this number to about 350,000 (PATON et al., 2008) or up to 400,000 (GOVAERTS, 2001). To begin to understand the biology of life on Earth, scientists must continue to collect, identify, and describe these organisms, in addition to making their classifications accessible to others. A current wave of global biodiversity study comes at a time of great technological advances that give the ability to place taxonomic work in a phylogenetic context. The phylogenetic perspective can be used to assess character evolution, helping scientists to understand adaptive processes and diversification.

Solanaceae is one of the largest and most complex families of Angiosperms, with widespread distribution in all continents and around 2,500 species and 100 genera, according to Olmstead et al. (2008), with *Solanum* being the richest and most widely distributed. It is a group of great economic importance, with food, medicinal and ornamental species, among which stand out *Solanum*, *Brugmansia*, *Brunfelsia*, *Capsicum*, *Datura* and *Nicotiana* genera, among others.

The family includes species used in human food, sources of drugs of pharmacological interest and also toxic ones. Among the species widely cultivated as food, we highlight the potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.), eggplant (*Solanum melongena* L.) and pepper (*Capsicum* spp), among others. As a source of pharmacologically active drugs, we highlight *Atropa belladonna* L., *Hyoscyamus niger* L., *Mandragora officinarum* L., *Brugmansia* spp. and *Datura* spp., with tropic alkaloids that act on the central nervous system. Besides the pharmacological importance, Solanaceae have species with narcotic and hallucinogenic properties like *Nicotiana tabacum* L. and some species of *Brunfelsia*, *Brugmansia* and *Datura*, among others, that have been used in magic rituals and superstitions, from the oldest civilizations (RODDICK , 1991).

Traditional classifications have recognized two subfamilies, Cestroideae and Solanoideae (D'ARCY, 1979, 1991; HUNZIKER, 1979, 2001; OLMSTEAD, PALMER 1992). However, Hunziker (2001) proposed a treatment based on different taxonomic evidence, using from morphological characters to phytochemicals, where Solanaceae is divided into six subfamilies and 21 tribes.

The intergeneric similarity observed in the family, also constitutes an important aspect in the taxonomy of other genera of Solanaceae. The fragile circumscription, inherent to close intergeneric relations, results in innumerable misconceptions such as the *Lycianthes* species, which for a long time were considered as part of *Solanum*. A relevant aspect, especially from the conservation point of view, is related to the small representation of some species in herbaria, indicating that they are poor collected, probably because they occur in restricted environments or in places of difficult access or, because they are in possible extinction due to the destruction of their habitats. Cases like this can be exemplified by the genera *Dyssochroma*, *Solandra* and *Lycianthes*, focus of this work, based on the data of Stehmann et al, (2013) for the list of Brazil.

1.1 THE GENUS *LYCIANTHES*

Lycianthes comprises about 200 species, predominantly Neotropical, only 25 species occur in Asia, Indo-Malaysia and Australia. Species of *Lycianthes* are characterized as herbs, perennial shrubs, or lianas, stellate corolla with calyx presenting 5 to 10 appendix, usually referred as teeth, similar to those observed in some species of *Capsicum*, characteristics only observed in Solanaceae in the genus *Capsicum* and *Lycianthes*, according to (D'ARCY, 1986). On the other hand, in *Lycianthes* the anthers are poricide like those of *Solanum*.

1.1.1 Taxonomic history of *Lycianthes*

The genus *Lycianthes* was formally proposed by Hassler (1917). However, prior to this treatment, the species currently belonging to *Lycianthes* were included in *Solanum*. The first researcher to work with these species as a distinct group was Dunal (1813, 1816), who monographed the genus *Solanum*. In this work the author included in the group *Polymeris*, section *Inermia*, without a defined hierarchical position, 61 species that currently belong to *Lycianthes*, based on the presence of appendages in the calyx and the morphology of the axillary peduncles, characteristic of *Lycianthes* (KNNAP, 1983).

The *Polymeris* group was elevated to section status by Walpers (1844), who proposed two more sections to the genus: *Lycioides* and *Holochlaina*. Subsequently, Dunal (1852) combined the three sections of Walpers (1844) in the subsection which he named *Lycianthes*, consisting of two series, *Meiomeris* and *Polymeris*, and four subseries, *Pseudolycianthes*, *Eulycianthes*, *Gonianthes*, and *Lobanthes*.

Hassler (1917) proposed the genus *Lycianthes* transferring three species of subsection *Eulycianthes* (*L. lycioides*, *L. dombeyi* and *L. candicans*), raising it to the generic level. Hassler (1917), when performing an anatomical study of these species, observed the presence of stone cells in the endocarp of the fruit, characteristic used as differential evidence to the proposition of the genus.

Bitter (1919) expanded the circumscription of *Lycianthes*, including 134 species of subsection *Lycianthes* sensu Dunal, and for the first time suggested a greater morphological affinity between *Lycianthes* and *Capsicum* based on the morphology of the calyx. In his monograph, the most complete work for the genus so far, Bitter (1919) established a infrageneric classification system, dividing *Lycianthes* into four subgenera (*Eulycianthes*, *Polymeris*, *Cypellocalyx* and *Syngenesia*) subdivided in 11 sections and 13 series. Since then, about 80 new species have been proposed to the genus, totaling about 200 species.

Two names for the concept of *Lycianthes* predate this name in literature. Rafinesque published the name *Otilix* in 1828, based on *Solanum lycioides*, but this new genus remained in obscurity and was not used by later authors. In 1888, Baillon proposed the genus *Parascopolia* based on a collection by Thiebaud (*P. acapulcensis*) from Acapulco, Mexico. It is unclear why Baillon proposed this genus since, as pointed out by Bitter, Dunal clearly took into consideration similar specimens in his subsection *Lycianthes*. In his description of *Parascopolia*, Baillon noticed the 8-10 teeth in the calyx, a character that clearly indicates that this taxon belonged to *Lycianthes*, but described the anthers as rimose. Bitter (1919) states that *P. acapulcensis* should probably be transferred to *Lycianthes*, but wasn't able to see its type in Paris. Unable to solve this situation by checking the dehiscence of the anthers, he postponed *Lycianthes* synonymization with *Parascopolia*. After seeing a photograph of *P. acapulcensis*, D'Arcy proposed its inclusion in *Lycianthes* and the conservation of the name *Lycianthes* over *Parascopolia* and *Otilix*. This proposition was approved in 1973 (McVaugh, 1973).

Some authors (MORTON, 1944, 1976; HUNZIKER, 1979; SYMON 1985,1987) continued to consider *Lycianthes* as part of *Solanum* despite Bitter's monograph. However, D'Arcy (1986) and Barboza and Hunziker (1992) corroborate the importance of the anatomy

and morphology of the calyx in *Lycianthes*. In addition, molecular analysis performed with Solanaceae have corroborated Bitter's hypothesis that *Capsicum* and not *Solanum* is the closest related group to *Lycianthes* (OLMSTEAD, PALMER, 1992; SÄRKINEN ET AL., 2013).

Informations on *Lycianthes* are sporadic and rare, found mostly in floristic surveys (STANDLEY, 1928; STANDLEY, MORTON, 1938; D'ARCY, 1973; GENTRY, STANDLEY, 1974; NEE, 1986; BARBOZA, HUNZIKER, 1992; ZHI-Yun ET AL. 1994). Only the series *Meizonodontae* (DEAN, 2004), *Microlobae* (DEAN, 2007) and *Radicantes* (REYES, 2015), all subordinate to *Lycianthes* subg. *Polymeris* sect. *Perennans*, were taxonomically reviewed, which highlights the need for additional studies for the group.

Table 1- Infrageneric divisions of *Lycianthes* sensu Bitter (1919)

Subgenus	Section	Series	N ° species
<i>Eulycianthes</i>			2 spp
<i>Polymeris</i>	<i>Eupolymeris</i>	Series Pliochondrae	8 spp
		Series Oligochondrae	18 spp
		Series Virgata	13 spp
		Series Glanduliferae	3 spp
		Series Tricolores	2 spp
		Series Caribaccolae	9 spp
	<i>Kittoides</i>	-	1 spp
	<i>Perennans</i>	2 series	9 spp
	<i>Asaropsis</i>	-	2 spp
	<i>Simplicipila</i>	3 series	30 spp
	<i>Asiomelanesia</i>	2 series	13 spp
<i>Synantheroides</i>	-	6 spp	
<i>Cypellocalyx</i>	-	1 series	17 spp
<i>Syngensis</i>	-	-	1 spp
Insertae sedis	-	-	ca. 80 spp

1.1.2 Phylogenetic context of *Lycianthes*

According to the molecular studies of Olmstead et al. (1999), *Lycianthes* is paraphyletic and has *Capsicum* as a sister group, genus with which it has great affinity. However, the study was based on a sampling limited to only five species of *Lycianthes* and two species of *Capsicum*. In a more recent phylogenetic study for Solanaceae, Olmstead et al. (2008), found once again that paraphyletism of *Lycianthes*, with a moderately supported clade (79% bootstrap) formed by species of *Lycianthes* section *Eupolymeris*, section *Asiomelanesia* and *Capsicum*. In this work, the Tribe Capsiceae is formed by *Capsicum* and *Lycianthes* and the authors comment on the possibility of unifying both genera, since the monophyly of *Lycianthes* is only possible when it is grouped with *Capsicum*. Thus, some species of

Lycianthes would have to be transferred to *Capsicum* based on the priority rule. Another possibility suggested by Olmstead et al. (1999) would be splitting *Lycianthes* into at least two more genera.

Särkinen et al. (2013), when performing the most complete phylogeny for Solanaceae so far, found once again, a well supported clade corresponding to tribe Capsiceae, where *Capsicum* is clearly monophyletic and *Lycianthes* is divided into two main clades. In this late study 36 species of *Lycianthes* were included and 25 of *Capsicum*.

1.1.3 Uses of *Lycianthes*

Lycianthes species are difficult to collect due to the reasons mentioned in previous topics. However, a few species are widely spread and have economical importance since they can be cultivated as food and a few species had their biological activities, phytochemistry and pharmacology attributes investigated.

Fruits of *Lycianthes asarifolia* are reported to be edible due to their sweet taste (ROJAS; D'ARCY, 1997). *Lycianthes moziniana* is used in Mexico for domestic consumption, small-scale commercialization and ceremonial offerings of the Day of the Dead festivals (WILLIAM, 1993).

Lycianthes synanthera is commonly consumed in the diet of rural communities of Guatemala and is regarded as a potential nutrient and energy deficiencies reducer (SALAZAR ET AL., 2006). The amount of protein, carbohydrate and crude fiber found in *L. synanthera* leaves is greater than other commonly consumed edible leaves (PICCINELLI ET AL., 2005). It also possess antibacterial, antifungal, and cytotoxic activities (NIÑO ET AL. 2006).

Lycianthes rantonnetii is the only one reported as ornamental (ROJAS; D'ARCY, 1997; ACOSTA ET AL., 2005), even though *L. asarifolia* is commonly grown in gardens (pers. obs.).

Methanolic extracts of *Lycianthes radiata* were shown to have anti-oxidant properties (MOSQUERO ET AL., 2009). Dichloromethane extracts of *L. acutifolia* is reported to have weak to moderate antimycotic activity, according to NIÑO et al. (2003).

1.1.4 *Lycianthes* in Brazil

Information about *Lycianthes* in Brazil is very scarce, as well as its representation in the national herbaria. In the most comprehensive treatment for Solanaceae, by Sendtner

(1852), only two species which currently belong to *Lycianthes*, are included in the family as part of the genus *Solanum*: *Solanum glandulosum* Ruiz & Pav. (= *Lycianthes glandulosa* (Ruiz & Pav) Bitter and *Solanum violaefolium* Schott (= *Lycianthes asarifolia* (Kunth & Bouché) Bitter).

More recently, Stehmann, et al. (2010) presented a list of 17 names related to the species of the genus, with accepted names, synonyms and the degree of endemism of *Lycianthes*, with 10 accepted species: *L. amatitlanensis* (J.M.Coult. & Donn.Sm.) Bitter *L. asarifolia* (Kunth & Bouché) Bitter, *L. coffeifolia* Bitter, *L. glandulosa* (Ruiz & Pav.) Bitter, *L. inaequilatera* (Rusby) Bitter, *L. leptocaulis* (Rusby) Rusby, *L. pauciflora* (Vahl) Bitter, *L. rantonnei* (Carrière) Bitter, *L. repens* (Spreng.) Bitter, *L. stenoloba* (Van Heurck & Müll.Arg.) Bitter. The greatest richness and diversity of the genus for the country is recorded in the northern region, with seven species, followed by the southeast region, with four species.

All species mentioned above are subordinate to *Lycianthes* subg. *Polymeris* that is the largest one and is characterized by herbaceous perennial or shrub habit, fruits with stony cells and numerous seeds, without sclerenchyma cells. It is the most diversified, with about 110 species, subordinated to the sections *Eupolymeris*, *Kittoides*, *Perennens*, *Asaropsis*, *Simplicipila*, *Asiomelanesia*, *Synantheroides*, based mainly on the presence of stony cells, stamen size and flowering time (diurnal or nocturnal).

The representativeness of *Lycianthes* in herbaria is relatively low when compared with other genera of the family Solanaceae. For Brazilian herbariums, there are about 68,000 *Solanum* records, while *Lycianthes* is represented by only about 841 exsicates.

One of the reasons for the low representativeness of collections of *Lycianthes* might be the fact that many species have flowers that close during the day, making them inconspicuous (NEE, 1982). According to Dean (2004) they occur only in small populations, which may also be one reason for this genus to be so poorly sampled. The few collections in herbaria, together with the difficulty related to the access and understanding of Bitter's monograph, written in German, may have contributed to the lack of attention given to the genus *Lycianthes*.

The current information for *Lycianthes*, as a whole, is not very representative. Relevant data that enable correct identification and delimitation of its species are scarce, as well as morphological and molecular data. The use of additional tools to classical taxonomic and morpho-anatomical studies, such as anatomy, ultrastructure, phytochemistry and molecular studies are necessary, since these data are lacking for *Lycianthes*.

This set of facts mentioned above produces collections with a considerable number of misidentified specimens in the herbariums, which associated with the existence of some

species with complex and dubious delimitation has made the taxonomic understanding of *Lycianthes* a difficult task. Possibly, the lack of understanding of the morphological variations in the same taxon may have led to the formation of several taxonomic complexes, for example *L. asarifolia* / *L. repens* and *L. amatitlanensis* / *L. acutifolia* / *L. inaequilatera* / *L. radiata* and *L. pauciflora* / *L. cearaensis* / *L. glandulosa* whose circumscriptions are not precise.

The genus has been reported as a paraphyletic group, suggesting its division into two groups. A study of the molecular phylogeny of *Lycianthes* that includes the largest number possible of species and includes in the external group the type species of the genus *Capsicum*, can contribute to the delimitation of species whose circumscription is uncertain or dubious, as well as to clarify the position of *Lycianthes* in relation to *Capsicum*.

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2 TAXONOMIC TREATMENT

This chapter consists of three manuscripts. The first establishes nomenclatural notes with lectotipifications and new synonyms. The second one is an update in the genus *Lycianthes* with the description of a new species for Brazil, synonyms and a new combination. The last one consists in a taxonomic treatment of the Brazilian species of *Lycianthes*, with taxonomic descriptions of 12 species, complemented by discussion on their taxonomy, habitat and phenology, a key of identification, illustrations and the geographic distribution.

2.1 MANUSCRIPT 1- LECTOTYPIFICATIONS OF SIX TAXA IN *LYCIANTHES*
(SOLANACEAE)

RAFAEL COSTA-SILVA¹ & MARIA DE FÁTIMA AGRA^{1,2}

LECTOTYPIFICATIONS OF SIX TAXA IN *LYCIANTHES* (SOLANACEAE)RAFAEL COSTA-SILVA¹ & MARIA DE FÁTIMA AGRA^{1,2}

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Abstract

Lycianthes comprises about 200 species, distributed mostly in the Neotropics but with 30 species in the Old World. It is a taxonomically complex group, and for more than a century its species were treated as part of *Solanum*. Together with *Capsicum* it constitutes the tribe *Capsiceae*. In this work six new lectotypes are designated for the following taxa of *Lycianthes*: *L. acutangula* (Griseb.) Bitter ssp. *compressibaccata* (Bitter) Bitter, *L. cearaensis* Bitter, *L. coffeifolium* Bitter, *L. longidentata* Bitter, *L. ulei* Bitter, and *Solanum asarifolium* Kunth & Bouché. *Lycianthes cearaensis* is shown to be distinct from *L. pauciflora* (Vahl) Bitter and *Lycianthes amatilanensis* (Coult. & Donn. Sm.) Bitter to be distinct from *Lycianthes inaequilatera* (Rusby) Bitter.

Keywords

Brazil, Capsiceae, lectotype, *Solanum*, Solanoideae, South America

Introduction

Lycianthes Hassler (1917) comprises about 200 species with a nearly cosmopolitan distribution, and, together with *Capsicum* L. (1753), constitutes the tribe Capsiceae D'Arcy (1996), according to Olmstead et al. (1999) and Särkinen et al. (2013). For more than a century, species belonging to *Lycianthes* were included in *Solanum*. The genus *Lycianthes* was formally proposed by Hassler (1917), based on the presence of stone cells in the fruits, axillary inflorescences, calyx appendages (sometimes called teeth) that emerge below the truncated calyx edges, subrotate to rotate (stellate) corollas, and poricidal anthers.

The circumscription of *Lycianthes* was expanded by Bitter (1919) to include 132 species, 52 varieties, and one form. Of these, 84 names were new combinations of taxa previously included in *Solanum* subsect. *Lycianthes* Dunal (1852), and 48 were proposed as new species. In his work, Bitter (1919) for the first time suggested the morphological affinity of *Lycianthes* with *Capsicum* based on the calyx morphology. Bitter's work on *Lycianthes* is still the most comprehensive treatment for the genus, although about 80 new species have since been proposed (D'ARCY 1973; GENTRY, STANDLEY, 1973; BARBOSA, HUZINKER, 1992; ROJAS, D'ARCY, 1997; DEAN, 1994, 1998, 2014; OROZCO ET AL. 2008).

Of the 202 new taxa proposed by Bitter (1919), about 70 had their type specimens deposited at the Berlin Herbarium (B). Most of these, however, are not there now as the Berlin Herbarium was largely destroyed in 1943 during the Second World War, a great loss to science, as thousands of type specimens were destroyed (MERRILL, 1943; HIEPKO, 1987). Although a few specimens of the Solanaceae survived, only one specimen of *Lycianthes*, the type of *Lycianthes hypomalaca* Bitter (1919), is accounted for in the current Berlin Herbarium database.

The Neotropical region was a field of interest for the Berlin Herbarium, which consequently housed numerous types from the Neotropical region (GRIMÉ; PLOWMAN 1986). Among these collections, those by the German botanist Ernst Ule stand out. These were incorporated into the Berlin Herbarium (B) in 1915 (HIEPKO, 1987), and used by Bitter (1919) in his treatment of *Lycianthes*. Several new species were based on Ule's collections including, *L. cearaensis*, *L. coffeifolium*, *L. longidentata*, *L. ulei* and *Solanum compressibaccatum*, *inter alia*.

Another important private collection was that of G.S. Kunth, which was incorporated in the Berlin Herbarium in the 1830s when he became deputy director of the Botanical Garden

(Hiepko, 1987). From this collection came the material analyzed by him for the description of *Solanum asarifolium*, which was cultivated in the Botanical Garden of Berlin (Ind. Sem. Hort. Berol, 10. 1845) from seeds sent by E. Otto from Caracas. In our revision of the genus *Lycianthes* for the Flora of Brazil, specimens were compared with type collections and images available online from the following herbaria (the acronyms follow THIERS, 2017), ALCB, AWH, BM, BR, BREM, C, E, EAN, F, G, GH, HBG, HUEFS, IAN, INPA, IPA, JPB, K, L, M, MG, MO, NY, P, R, RB, S, U, UFP, US, and W.

We have chosen lectotypes for the species whose types were lost in the Berlin Herbarium, according to Article 9.2 of the International Code of Nomenclature for algae, fungi and plants (ICN, MCNEILL ET AL., 2012). We have given priority to isotypes and collections cited by Bitter (1919), many of which were annotated by him and have his own signature. All material indicated as lectotype and isolectotype conform to the protologues, and the photographs taken by MacBride, whose negatives are deposited at the Herbarium of Field Museum of Natural History (F) and available in the Field Museum botany collection database.

In the type citation, the word “photo” refers to phototype or a printed image deposited in a herbarium, available online in the herbaria databases or in sites such as JSTOR Plants. Barcode numbers are given after the acronyms. If the barcode isn’t available, the acronym is followed by the accession number. When the typified name is not an accepted name, the accepted name is given immediately after the type designation.

1. *Lycianthes ceareaensis* Bitter, Abh. Naturwiss. Vereine Bremen 24: 346. 1919.

Type:—BRAZIL. Ceará: Serra de Maranguape, 600 m, Oct 1910, *E. Ule 9103* (Holotype B†, photo of holotype F-2564]; lectotype: NY00138709!, designated here; isolectotypes: K000585757!, L0003587!; US00027870!).

Notes. The holotype of *Lycianthes ceareaensis* was deposited in B (Bitter 1919), but destroyed during World War II. We have located four specimens of *E. Ule 9103*, which have handwritten notes made by Bitter, and are designating here the most complete and well-preserved specimen (NY 138709) as the lectotype for *L. ceareaensis*.

Lycianthes ceareaensis was treated in the Flora of Brasil (2017) as a synonym of *L. pauciflora* (Vahl) Bitter (1919: 341). However, after analyzing the types and herbarium material of these two taxa, we confirm that they are distinct, and can be distinguished by leaf morphology, indumentum, calyx appendages, and ovary format. *Lycianthes ceareaensis* has elliptic to narrowly elliptic leaves, tomentose indumentum on the abaxial leaf surface, a cupuliform calyx with curved appendages in fruit, and an ovoid ovary. *Lycianthes pauciflora*

differs in the ovate to ovate-elliptic leaves, lax indumentum, pateliform calyx with reflexed appendages in fruit, and a globose ovary.

2. *Solanum compressibaccatum* Bitter, Repert. Spec. Nov. Regni Veg. 12: 456. 1913.

Type:—PERU. Dept. Loreto: Cerro de Ponasa, 1200 m, Feb 1903, *E. Ule 6800* (Holotype B†, photo of holotype F-2560!; lectotype HBG511426!, designated here; isolectotypes: CORD 00004168!, G! [without barcode], K000585774!, L0403129!).

Accepted name. *Lycianthes leptocaulis* (Rusby) Rusby (1926).

≡ *Brachistus leptocaulis* Rusby (1899: 26). Type:— Bolivia, Dept. La Paz, Prov. Larecaja, Guanay, 2000 ft, Maio 1886, *H. Rusby 2657* (NY138557!)

Notes. *Solanum compressibaccatum* was described by Bitter (1913: 456) based on *E. Ule 6800*, a plant with a climbing habit from Amazonian Peru. Subsequently, Bitter (1919: 358) transferred it to *Lycianthes* as *Lycianthes acutangula* (Griseb.) Bitter ssp. *compressibaccata* (Bitter) Bitter. The holotype deposited at B was destroyed during World War II, and here we are designating the isotype deposited at HBG as the lectotype. This specimen was identified by Bitter himself, and is in good condition with flowers, fruits and leaves.

The specimen of *Ule 6800* at HBG is annotated as an isotype of *Lycianthes stenoloba* (Van Heurck & Muell. Arg.) Bitter (1919). However, this designation is incorrect since the type material of *Lycianthes stenoloba* is *R. Spruce 4210* which was deposited in the Van Heurck Herbarium, now incorporated in the herbarium of the Botanic Garden Meise (BR). The basionym of this species is *Solanum stenlobum* Van Heurck & Muell. Arg. (in VAN HEURCK, 1870) collected at Tarapoto, Peru.

3. *Lycianthes coffeifolia* Bitter, Abh. Naturwiss. Vereine Bremen 24: 432. 1919.

Type:—BRAZIL. Amazonas: Acregebiet, Monte Mo, Nov 1911, *E. Ule 9737* (Holotype B†, photo of holotype F-2566!); lectotype US00027875!, designated here; isolectotypes: G00446591! [two sheets], K000585765!, L2881751!.

= *Solanum coffeifolium* (Bitter) C. V. Morton (1944:64).

Notes. *Lycianthes coffeifolia* was placed by Bitter in section *Simplicipila* Bitter. The holotype was *E. Ule 9737*, deposited at the Berlin herbarium (B) and evidently destroyed. The isotypes in G, K, L and US are all in good condition. Those in G and US are well preserved with developed leaves, floral buds, flowers and fruits, while those at K and L only have

vegetative shoots with fruits. We choose as lectotype the isotype at US (US-00027875), which is clearly annotated by Bitter. The duplicates at G, K and L are designated as isolectotypes.

4. *Lycianthes longidentata* Bitter, Abh. Naturwiss. Vereine Bremen 24: 356. 1919.

Type:—BRAZIL. Amazonas: Rio Acre, Estella, Seringal São Francisco, Mar 1911, *E. Ule* 9733 (Holotype B†, photo of holotype F-2582!; lectotype NY00138711!, designated here; isolectotypes: K000585776!, L2881557!, MG14567!, S042937!, U0113835!, US00027888!).

Accepted name. *Lycianthes leptocaulis* (Rusby) Rusby (1926: 210).

≡ *Brachistus leptocaulis* Rusby (1899: 199).

= *Solanum longidentatum* (Bitter) C. V. Morton (1944: 64).

Notes. *Lycianthes longidentata* was described by Bitter in *Lycianthes* sect. *Eupolymeris* Bitter (1919) based on the calyx having 10 appendages in two unequal series, which reach up to 1 cm in length, and stamens with unequal filament lengths. Bitter cited the holotype at Berlin (B), which was destroyed in 1943. The isotype deposited at New York (NY138711) is chosen as lectotype as it is in good condition with flowers and fruits. It bears the label "Ex. Mus. Bot, Berol".

5. *Lycianthes ulei* Bitter, Abh. Naturwiss. Vereine Bremen 24: 437. 1919.

Type:—BRAZIL. Amazonas: Rio Acre, Seringal São Francisco, Apr 1911, *E. Ule* 9764 (Holotype B†, photo of holotype F-2592!; lectotype NY-00138719! designated here; isolectotypes G! [without herbarium number], K000585766!, L2881358!, MG14596!, U0113836!, US00027900!).

Accepted name. *Lycianthes amatitlanensis* (Coult. & Donn. Sm.) Bitter (1919).

Notes. The holotype was deposited in B but was destroyed in 1943. We are designating the specimen at New York (NY) as lectotype. This is in good condition and is the only duplicate that has the annotation "Ex. Mus. Bot. Berol".

Martinez et al. (2002) and Jorgensen et al. (2014) consider *Lycianthes amatitlanensis* to be a synonym of *Lycianthes inaequilatera* (Rusby) Bitter (1919: 439). However, examination of the types of these taxa clearly indicates them to be different species. *Lycianthes amatitlanensis* can be recognized for having erect branches, shiny leaves, and conspicuous calyx appendages (2.0-3.0 mm long), which are linear and pilose at anthesis. On the other

hand, *Lycianthes inaequilatera* has zig zag branches, dull leaves, inconspicuous calyx appendages, less than 1 mm long, which are glabrescent at anthesis. We consider *Lycianthes amatilanensis* is a distinct taxon and not synonymous with *L. inaequilatera*, thus corroborating the previous observations of Rojas and Darcy (1997) and Bohs (2015).

6. *Solanum asarifolium* Kunth & Bouché, Ind. Sem. Hort. Berol. 10. 1845.

Type:—A plant cultivated in Berlin in 1842 from seeds from Venezuela, Caracas, *E. Otto s.n.* (Holotype: B†, photo of holotype F-2562!; lectotype: P00430541!, designated here).

Accepted name. *Lycianthes asarifolia* (Kunth & Bouché) Bitter (1919:423).

Notes. The unnumbered collection of *E. Otto* at the Muséum National d'Histoire Naturelle of Paris (P-430541) donated by the Herbarium of Berlin in 1855 is designated as lectotype. The lectotype is in good condition, showing a plant with roots, two well-developed leaves, and one flower. It corresponds to the protologue of *Solanum asarifolium* Kunth & Bouché and is the only collection of Otto we have located.

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2.2 MANUSCRIPT 2 - UPDATES IN *LYCIANTHES* (SOLANACEAE): A NEW SPECIES
FROM BRAZIL, NOTES ON TAXONOMY, AND A KEY TO IDENTIFICATION OF
BRAZILIAN SPECIES

UPDATES IN *LYCIANTHES* (SOLANACEAE): A NEW SPECIES FROM BRAZIL,
NOTES ON TAXONOMY, AND A KEY TO IDENTIFICATION OF BRAZILIAN
SPECIES

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Abstract

During the review work for the genus *Lycianthes*, as part of the taxonomic treatment for Brazilian Flora, a new species, *Lycianthes bitteri* Costa-Silva & Agra, was recognized for the State of Bahia, which is described and illustrated here. It is member of *Lycianthes* subg. *Polymeris*, and is related to *L. pauciflora* (Vahl) Bitter and *L. cearaensis* Bitter, from which it differs by its petiole depressed adaxially, calyx with linear and explanate appendices in two series, ovary somewhat conical, and indument with a mix of dendritic and stellate trichomes. Comments on its distribution, status of conservation, and its affinities with other *Lycianthes* are discussed. In addition, a new combination, five new synonyms, and a lectotypification are proposed, and a key to identify the Brazilian *Lycianthes* species is presented.

Introduction

Lycianthes (Dunal) Hassler has about 207 species, according to Solanaceae Source (2017), with tropical distribution occurring mainly in the Neotropical region, and also in the Old World where about 30 species occur in Asia and Australia (DEAN, 2004), with its center of diversity in the new world, from Mexico to Argentina (DEAN, 2004; DEAN ET AL. 2017).

For more than a century, *Lycianthes* species were positioned as part of the genus *Solanum*, from which they were segregated and formally proposed as a new genus by Hassler (1917), mainly based on the presence of stone cells in the endocarp of the fruits, characteristic used as differential evidence to the proposition of the genus. In his monograph for *Lycianthes*, Bitter (1919) divided the genus into four subgenera, seven sections and 15 series and was the first to suggest the affinity between *Lycianthes* and *Capsicum*, a genus with which it shares some morphological characteristics such as the calyx with truncated lobes, from which five to ten appendices may emerge, usually referred to as teeth, that according to D'Arcy (1986) are expansions of the vascular bundles of the calyx.

Molecular studies (OLMSTEAD; PALMER, 1992; BOHS; OLMSTEAD, 1997; OLMSTEAD ET AL. 2008; SÄRKINEN ET AL., 2013) have supported *Lycianthes* as sister groups *Capsicum* constituting the tribe Capsiceae, as suggested previously by Bitter (1919), and have also strengthened the segregation of *Lycianthes* from *Solanum*, genus with which it shares some characters like the corolla's morphology, and the poricidal anthers.

According to the Flora do Brasil 2020 (under construction, 2017), there is an estimation of the occurrence of nine species in Brazil, with greater diversity in the northern region of the country, with six species. The distribution of these species comprises a range of phytogeographical domains, such as the Amazon, Cerrado, Atlantic Rainforest and Pantanal, composing phytophysionomies of campinarana forest, highland floodplain forests, semideciduous seasonal forest and ombrophilous forest.

While preparing a taxonomic review for *Lycianthes*, as part of the treatment for Brazilian Flora, a new species, *Lycianthes bitteri* Costa-Silva & Agra, was recognized for the State of Bahia, based on its distinctive morphological characters that placed it as a member of *Lycianthes* sect. *Eupolymeris* Bitter (1919), which is the largest group of *Lycianthes* subg. *Polymeris*, with about 60 Neotropical species, characterized by the calyx with 10 unequal appendices, linear to subulate, unequal stamens, and not connivent anthers. *Lycianthes bitteri* is related to *L. pauciflora* (Vahl) Bitter and *L. cearaensis* Bitter, from which it differs by its petiole depressed adaxially, calyx with linear and explanate appendices in two series, ovary somewhat conical, and indument with dendritic and stellate trichomes. The new species is

described and illustrated here, and comments on its distribution, status of conservation, and its affinities with other *Lycianthes* are discussed. In addition, a new combination, five new synonyms, a lectotypification are proposed, and also a key to identify the Brazilian *Lycianthes* species is presented.

Materials and methods

Field observations and examination of live plants on the field, and herbaria specimens to obtain morphological and ecological data and, also were compared with type collections and images available online from the herbaria: ALCB, AWH, BM, BR, BREM, C, CEPEC, E, EAN, F, G, GH, HBG, HUEFS, IAN, INPA, IPA, JPB, K, L, M, MA, MG, MO, NY, P, R, RB, S, U, UFP, US, and W, the acronyms according Thiers (2017), Figure 1 was prepared from digital photographs of fresh fertile plant material (flowered and fructified), as well as from rehydrated samples from herbarium specimens. All studied specimens are cited in the text.

***Lycianthes bitteri* Costa-Silva & Agra, sp. nov. (Fig. 1-3)**

This species is related to *L. pauciflora* (Vahl) Bitter and *L. cearaensis* Bitter, from which differs by its more dense indument with stellate stalked and dendritic trichomes, petiole depressed adaxially, calyx with longer linear and explanate appendices in two series in fructified calyx, as well as by having the ovary somewhat conical.

Type:—BRAZIL. Bahia: Município de Amargosa, Serra do Timbó, estrada para Barata Azul, 13°06'19"S, 39° 40' 32" W, 800 m, 02 Dec 2009 (fl, fr), *Agra et al.* 7185 (holotype: JPB; isotypes: NY!; RB!; UFP).

Etymology

The specific epithet honors Georg Bitter, a botanist from Germany who studied *Lycianthes*, and elaborated the most complete taxonomic treatment for the genus, in recognition of his important botanical work, especially with this interesting and challenging genus of Solanaceae.

Description

Shrubs scandent, 1.0—2.0 m tall, branched, perennial; branches and stems terete, ferruginous to Brown, striate to rugose, indument stellate-puberulous, yellowish to ferruginous, trichomes stellate, sessile and short stalked, 3—6 lateral rays, many-celled, uniseriate, and dendritic trichomes with branched lateral rays, hyaline, *Sympodial* units difoliate, anisophyllous, and unifoliate in proximal branches. *Leaves* alternate, simple; petiole short, 0.6—1.5 x 0.1—0.2 cm, slightly grooved, tomentose, ferruginous, stellate and dendritic trichomes similar to those of branches; blades chartaceous, 5.5—13.0 x 3.0—6.5 cm, weakly discolored, ovate and angusto-ovate in distal leaves, and ovate or elliptic in the proximal, somewhat glossy on the adaxial surface, 6—10 veins, impressed on the adaxial surface, prominent on abaxial surface, sparse pilose on the adaxial surface, stellate trichomes on the blade, and on the midrib, stellate-velutinous to stellate-tomentose on abaxial surface, trichomes stellate, stalked (stalk 2—3 celled), and dendritic trichomes on the abaxial midrib; acute to acuminate at the apex, margin entire to slightly sinuate, base cuneate, rounded, and somewhat subcordate; *Inflorescence* indeterminate fascicle, axillary, sessile, 1—3-flowers, opposite to the leaf; pedicel slender in flower, enlarged in fruit, 0.8—1.5 cm long, erect at maturity, terete, stellate-tomentose, trichomes stellate-stalked, yellowish to ferruginous. *Flowers* perfect, pentamerous, monoclinous; calyx cupuliform, campanulate, truncate at the apex, 6.0—7.0 x 8.0—9.0 mm, 10-appendages, unequal, in two series, emerging at 1.3 to 1.5 mm below the apex, the largest 3.0—6.5 mm long, the smallest 2.0—5.8 mm long, stellate-tomentose, trichomes similar to those of the pedicel; corolla campanulate, white, 1.8—2.0 cm diam., lobes elliptic, 1.5—1.7 x 0.3—0.4 cm, pilose on the outer surface, interpetalar tissue, glabrous, well-developed, 0.3—0.4 cm; stamens 5, unequal (1 + 4): one largest, 4.5—5.0 mm long, 4 smaller ones with short filaments 1.9—2.2 cm long, anthers yellow, attenuate from the base to the apex, the largest 6.0—6.2 mm long, the smaller 5.8—6.0 mm long, sub-sagittate to slightly asymmetric at the base, 1.5—2.0 mm wide, pores extrorse; ovary conical, glabrous, 2.0—2.1 x 1.5—1.7 mm; style glabrous 1.0—1.1 cm length, straight, slightly curved to the apex, stigma oblong-clavate, 1.0—1.5 mm long, minutely papillose, bright green. *Fruit* globose, upright, 1.5—2.0 cm in diameter, glabrous, orange when ripe, green to yellow-green when young, drying brownish, surrounded by the persistent, somewhat accrescent calyx, the epicarp leathery, the calyx appendages linear, explanate, unequal, in two series, the smallest 0.5—0.7 cm long, the largest 0.8—1.0 cm long, stellate-tomentose. *Seeds* up to 20, ovoid to sub-reniform, compressed, seed coat slightly wavy, reticulated, beige to light brown, 2.7—3.4 mm in diameter.

Distribution, habitat and ecology

Lycianthes bitteri is an endemic species to the State of Bahia Brazil (Figure 3) that occurs in disjunct areas. It was collected in forest edges, and in secondary forests, however, few collections of this species can be found in herbaria.

Samples of *L. bitteri* were collected at different altitudes, from 40 m to 900 m above sea level. In Serra do Timbó, a mountain range characterized by rugged relief, covered mainly by semi-deciduous tropical forests and reaching elevations between 800 and 900m. According to Ab'Sáber (1977), Serra do Timbó is a transitional area between the Caatinga, Cerrado and the Atlantic Forest. The humid tropical climate prevails in the Serra do Timbó, but the region is surrounded by sub-humid and semi-arid climates.

The other locality is Serra Bonita that has a unique habitat with important altitudinal gradients of native Atlantic Forest, varying from 300 to 1,080 m of elevations (AMORIM ET AL. 2009). It is located in the Camacan basin, and is characterized by the hot and humid climate, type Af (KÖPPEN, 1936), with absence of dry season. Clear variations of humidity and temperature are found in its vegetation, which alternates from an evergreen forest to semi-deciduous humid forest, elements from lower elevations to mountain forest (RPPN SERRA BONITA, 2016).

Flowering and fruiting samples were collected from December to June.

Conservation Status

Due to insufficient data on population size and species abundance, *L. bitteri* should be classified as "Data deficient" (DD), according to the IUCN criteria.

Additional Specimens Examined (paratypes)

Brazil. Bahia: Mun. Amargosa, Fazenda Mucuri, Riacho do Meio, área de estudos do Projeto Timbó/ Centro Sapucaia 13°10'20'' S 39°9'34'' W 25 jan 2007, *Cardoso 1602* (HUEFS); Mun Arataca: RPPN Caminho das Pedras, em trilha de acesso ao Peito-de-moça, 15°10'25''S 39°20'30'', 15 jun 2006, *Amorim 6062* (CEPEC, NY); Mun. Camacan, RPPN: Serra Bonita, 10 km W de Camacan na estrada para Jacarecí, 6km SW na estrada para RPPN e Torre de transmissão. Trilha de acesso a RPPN. 15°23'35''S 39°33'53''W, 850 m, 25 mar 2007, *Amorim 6958* (CEPEC, NY).

Similar species

The set of morphological characters showed by *Lycianthes bitteri*, such as scandent shrub, ferruginous indument, and stellate trichomes place this species belonging to the *Lycianthes* subg. *Polymeris* sect. *Eupolymeris* ser. *Oligochondrae* Bitter (1919). Due to its characteristics, in some herbaria the specimens were identified as *L. pauciflora* (Vahl) Bitter (1919), name commonly associated with specimens that exhibit these characteristics and occur from French Guiana to the Southeast region of Brazil and the Brazilian Amazon.

They can be differentiated by several characters, like an adaxially depressed petiole, and inflorescences opposite to the leaves in *L. bitterii*, while in *L. pauciflora* the petiole is cylindrical, and the inflorescences are in the same direction as the leaves; the tomentose calyx with linear and longer appendices in flower, which are explanate and bi-seriate in fruit in *L. bitteri*, differing from *L. pauciflora* with shorter, glabrous to glabrescent, and reflexed appendices (in flower and in fruit); the ovary is conical in *L. bitterii* and it is rounded in *L. pauciflora*. The velutinous to tomentose indument of *L. bitteri* is denser and persistent even after the process of herborization, whereas in *L. pauciflora* it is glabrescent.

Lycianthes bitterii also shares some morphological characters with *L. cearaensis* Bitter (1919), an endemic species to the Northeast region of Brazil (Alagoas, Ceará, Paraíba and Pernambuco). It can be differentiated from *L. cearaensis* by the latter's canaliculate petiole, calyx with linear and uniseriate appendices rounded at the apex, and also by a tomentose indument on the branches, petioles and pedicels with stalked stellate trichomes, which are different from that observed in *L. bitteri*. In addition, dendritic trichomes with bifurcate lateral rays are observed only in *L. bitteri*, and do not occur in *L. cearaensis* and in *L. pauciflora*. A list of differential morphological characters for these three species can be found in Table 1.

Notes on Taxonomy

1. *Lycianthes compressibaccata* (Bitter) Costa-Silva & Agra *comb. nov.*

Basionym: *Solanum compressibaccatum* Bitter (1913 p. 456). *Syn. Nov.*

Type: PERU. Depto. Loreto: Cerro de Ponasa, 1200 m, Feb 1903, *E. Ule 6800* (B† =F photo 2560!; lectotype: HBG, barcode 511426 [photo!]; isolectotypes: CORD 4168 photo!, G! K 585774 [photo!]; MG 6634!). Designated by Costa-Silva and Agra (in press).

Based on the same type: *Lycianthes acutangula* (Griseb.) Bitter ssp. *compressibaccata* (Bitter) Bitter (1919 p. 358). *Syn. Nov.*

Taxonomic synonym: *Lycianthes leptocaulis* (Rusby) Rusby (1926 p. 210).

Type: Bolivia, Depto. La Paz, Prov. Larecaja, Guanay, 2000 ft, Maio 1886, *H. Rusby 2657* (Holotype: NY 138557!). *Syn. Nov.*

Notes

Solanum compressibaccatum was proposed by Bitter (1913) and, according to the description in the protologue, it is a climbing plant, with geminate lanceolate leaves, acuminate at the apex, calyx with unequal linear appendages, white corollas infundibuliform, five unequal stamens and globose berries. Bitter (1919) transferred it to *Lycianthes* and described it as *L. acutangula* subsp. *compressibaccata*. *Lycianthes acutangula* (Griseb.) Bitter was proposed having as basionym *Solanum acutangulum* Griseb., which, according to Article 32.1 and 38 of the Melbourne Code (MCNEILL ET AL., 2012) constitutes a *nomen nudum*, since its protologue presents neither a description or diagnosis nor makes any reference to an ancient taxon, therefore, not validly published.

The analysis of the collection of *Ule 6800*, that corresponds to the type specimens of *S. compressibaccatum* and *Lycianthes acutangula* ssp. *compressibaccata*, showed leaves narrow-elliptic, acute or acuminate at the apex, rotate corollas, unequal stamens and globose berries that constitutes a set of characters similar to those also observed in the types specimens of *L. leptocaulis* (Rusby 2657). These evidences clearly showed that they are a single species, thus we propose the synonymization of *L. leptocaulis* under *L. compressibaccatum*.

Hocke et al. (2009) and Rojas, D'Arcy (1997) considered *Lycianthes acutangula* ssp. *compressibaccata* as a synonym of *L. stenoloba* (Van Heurck & Müll. Arg.) Bitter, however, we do not agree with this proposal. The analysis of types clearly revealed them to be two distinct species, whose morphological characters of the leaves and flowers are distinctive to separate these taxa. The white funnel shaped corolla with an interpetal tissue in *S. compressibaccatum* is completely different of *L. stenoloba*, which presents the corolla rotate, clearly lobed without interpetalar tissue.

2. Taxonomic Synonym: *Solanum sylvicola* Brandege. (1917 p. 373). Syn. Nov.

Type: MEXICO, Edo. Chiapas: Finca Irlanda, Jun 1914, C. Purpus 7315 (Holotype: UC! 173378; isotype M! 01811815).

Accepted Name: *Lycianthes amatitlanensis* (J. M. Coult. & Donn. Smith 1904: 420) Bitter (1919 p. 441).

Type: Sintipos: GUATEMALA. Departamento Amatitlán: Barranca de Eminencia, 1200 m, Feb 1892, J. Donnell Smith 1457 (B† = F! 267179 barcode V0073065F; lectotype US 1324447 barcode 27445! designated here; isolectotypes: GH! 77435!; K n.v.); syntypes:

Departamento Alta Verapaz: Cubilquitz, 350 m, Jul 1901, *H. von Tuerckheim* 7753 (M!, NY! 138966, US! 398323 barcode 01014252, US! 1324445 barcode 01269193); Departamento Alta Verapaz: Cubilquitz, 350 m, Feb 1903, *H. von Tuerckheim* 8488 (F! 185826 barcode V0073066F, M! 171813, NY! 138963, NY! 1388964, US! 576619 barcode 01014253, US! 1324446 barcode 01269192).

Notes

Solanum sylvicola is a taxon proposed by Townshend S. Brandege (1917), based on a plant collected in Mexico, which has shrub habit, geminate anisophyllous leaves with asymmetric blades, calyx with conspicuous appendages, about 4.0 mm long, and corolla with lanceolate lobes. However, an analysis of the types of *Solanum sylvicola* (deposited at M) and *Lycianthes amatitlanensis* (F, M, NY and US) revealed them to belong to a single taxon. The indument of *Solanum sylvicola* was described by Brandege (1917) as setose-hirsute, but the analysis of its isotype showed that it is not different from that observed in *L. amatitlanensis*, which is described as strigose, characterized by the presence of simple, pluricellular, and uniseriate trichomes. Moreover, the vegetative and reproductive characters do not show morphological differences that support their position as different species.

In addition, the isotype of *S. sylvicola* deposited at M herbarium has a handwritten label made by Bitter identifying it as *L. amatitlanensis*, but Bitter (1919) didn't propose a formal synonymization for this name. Thus, the found evidence lead us to propose the synonymization of *S. sylvicola* under the accepted name *L. amatitlanensis*, based on the absence of differential taxonomic characters revealed by the analysis of its types.

3. Taxonomic Synonym: *Lycianthes poeppigii* Bitter (1919 p. 345). *Syn. nov.*

Type: PERU. Dept. Loreto: Prov. Alto Amazonas, ["Maynas"], próximo a Yurimaguas, Abr., *E. Poeppig* 2406 (Holotype: W 0003089 [photo!]; isotype P! barcode P00430724).

Accepted name: *Lycianthes glandulosa* (Ruiz & Pavón, 1799 p. 35) Bitter (1919 p. 348).

Type: PERU. Departamento Junín: Prov. Chanchamayo, Vitoc, *H. Ruiz & J. Pavón s.n.* (Lectotype: MA 747073 [photo!]; isolectotype: F 843590 fragment- [photo!]) designed by Knapp (2008).

Notes

Lycianthes poeppigii was proposed by Bitter (1919) based on a collection made by Eduard Friederich Poeppig, in the Province of Maynas, Peru, which is described as a scandent shrub,

with false-geminated leaves on the apical branches, stellate trichomes, calyx pateliform-cupulate at the fruit with 10 unequal appendages, and rotate corolla. On the notes of its protologue, Bitter (1919) noticed the similarity with *L. glandulosa*, and also commentend that the distinguishing characters between them would be the indument composed of considerably larger stalked stellate trichomes, the glabrous blade on the adaxial surface, and the unequal stamens with the fifth filament and anthers slightly larger in *L. poeppigi*.

The analysis of the types of *Lycianthes poeppigi* (isotype at P herbarium and photo of the holotype at W), as well as the types of *L. glandulosa* (lectotype at MA and the isotype at F) showed no distinctive characters that allow us to consider them as different species. It should be noted that the area of occurrence of the type of *L. poeppigi* corresponds to the same area of occurrence of *L. glandulosa*.

The characteristics pointed out by Bitter as taxonomically diagnostic to *L. poeppigi* correspond to the characters easily influenced by environmental variables, such as indument, and also the size of the anthers of *L. poeppigi* that is in the range of variance of *L. glandulosa*. They are only a reflection of the phenotypic plasticity, and do not support the proposition of *L. poeppigi* to be a distinct species of *L. glandulosa*. Moreover, other characters are common to these specimens, such as the presence of stellate trichomes, blade leaf elliptic, oblong-elliptic to oval-elliptic, calyx campanulate with ten, linear and unequal appendages, and constitute a set of features wich clearly evidence that they belong to only one taxon, reasons why we propose this synonymization.

Key to identification of *Lycianthes* in Brazil

1. Prostrate herbs, radicanat at the nodes; sympodial units plurifoliate; leaves cordate or sagitate at the base; pedicel curved at the apex 2
 - Subshrubs and erect or scandent shrubs; sympodial units unifoliate or difoliate geminate. Leaves rounded, attenuate, subcordate, cuneate, and oblique at the base; pedicel erect, upright or pending..... 3
 2. Solitary leaves, ovate or deltoid; corolla white; calyx accrescent to the 1/4 basal on the fruit..... *L. asarifolia*
 - Geminate leaves, reniform or orbicular; corolla lilac to purple; calyx accrescent above the 1/2 of the fruit..... *L. repens*
 3. Subshrubs and erect shrubs..... 4
 - Scandent shrubs or lianas..... 7

4. Calyx appendages of equal sizes (teeth), arranged in one series; equal stamen; corolla white..... 5
 – Calyx appendages of unequal sizes (teeth), arranged in two series; unequal stamens; corolla purple..... *L. rantonnetii*
5. Geminate and anisophyllous leaves, with asymmetric blades; calyx appendages linear, erect, not curved on the flower and fruit; berries globose..... 6
 – Solitary leaves with symmetric blades; calyx appendages curved at the flower and fruit; berries oblong..... *L. coffeifolia*
6. Calyx appendages conspicuous at the flower, 2.0-3.0 mm long; shiny leaves..... *L. amatitlanensis*
 – Calyx appendages inconspicuous at the flower, less than 1 mm de long; dull Leaves..... *L. inaequilatera*
7. Entire plant with simple trichomes..... 8
 – Entire plant with stellate and/or dendritic trichomes..... 9
8. Leaves with elliptic or oblong-elliptic blades; acute or acuminate at the Apex. Rotate corolla; Calyx with linear appendages (teeth), green on flower and fruit; unequal stamens (1+4).....*L. compressibaccata*
 – Leaves with obovate blades, cuspidate at the apex. Calyx with subulate appendages (teeth), green on flower and purple, with enlarged base, attenuating to the apex on the fruit; stellate corolla; Equal stamen..... *L. stenoloba*
9. Sympodial units unifoliate 10
 – Sympodial units difoliate geminate 11
10. Calyx lobes truncated on the flower; unequal appendages in more than two series, 4--5 mm long, emerging from the ¼ apical of the calyx*L. glandulosa*
 – Calyx lobes slightly cuspidate on the flower, unequal appendages in two series, 6--9 mm long, emerging from the 2/3 basal of the calyx *L. pauciflora*
11. Blade leaves cuneate or attenuate at the base; indument with stellate-stalked and dendritic trichomes on the leaf blades; calyx pateliform with linear appendages (teeth), explanate at the fruit, 0.5-1.0 cm long, ovary conical..... *L. bitteri*
 – Blade leaves rounded or oblique at the base; indument with stellate trichomes, without dendritic trichomes; calyx cupuliform, with narrow-obovate appendages (teeth), curved at the fruit, 3.0-4.0 mm long; ovary ovoid..... *L. cearaensis*

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Table 1. Main distinctive characters between *Lycianthes bitteri* Costa-Silva & Agra, *Lycianthes ceareaensis* Bitter and *Lycianthes pauciflora* (Vahl) Bitter.

State of characters	<i>Lycianthes bitteri</i>	<i>Lycianthes ceareaensis</i>	<i>Lycianthes pauciflora</i>
Dendritic trichomes	Present	Absent	Absent
Shape of leaf blade	Ovate to oval-elliptical	Elliptical-lanceolate to oval-lanceolate	Ovate
Petiole shape	Depressed adaxially	Canaliculate	Cilindrical
Size of flower pedicel	1.4—1.7 cm	0,5—1.0 cm	1.0—1. 3 cm
Appex of the calyx appendices in flower	Rounded	Truncate	Obtuse
Size of the appendices of frutified calyx	0.5—1.0 cm	0.3—0.4 cm	0.1—0.2 cm
Appendices of the frutified calyx	Explanate	Slightly arched	Strongly reflexed
Shape of ovary	Conical	Ovoid	Globose

Fig. 1. *Lycianthes bitteri* Costa-Silva et Agra. A and C. Flowering and fruiting branch; B. Detail of stellate trichomes; D. Detail of the flower; E. Detail of the androecium F. Frutified branch. From Agra *et al.* 7185.

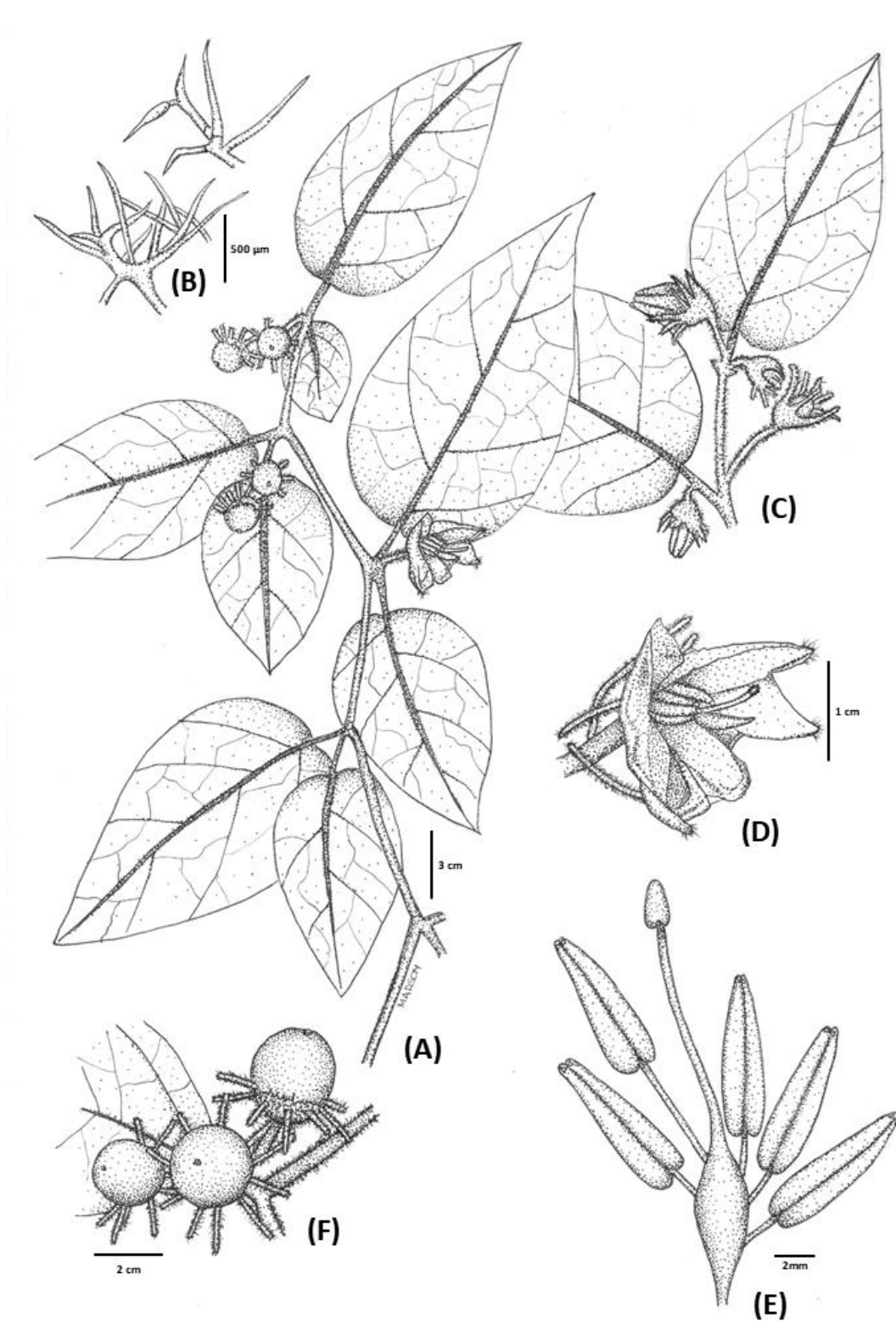


Fig. 2. *Lycianthes bitteri* Costa-Silva et Agra. A-B. Detail of androecium in flower with exerted pores of the anthers; B. Isolated flower; C. Terminal branch with fruits; D. Fruits with fruitful calyces with explanate appendices; E. Bud flower; F. Isolated seed (A-C, photo by M.F. Agra; and D, photo by Domingos Cardoso).

From Agra et al. 7185.

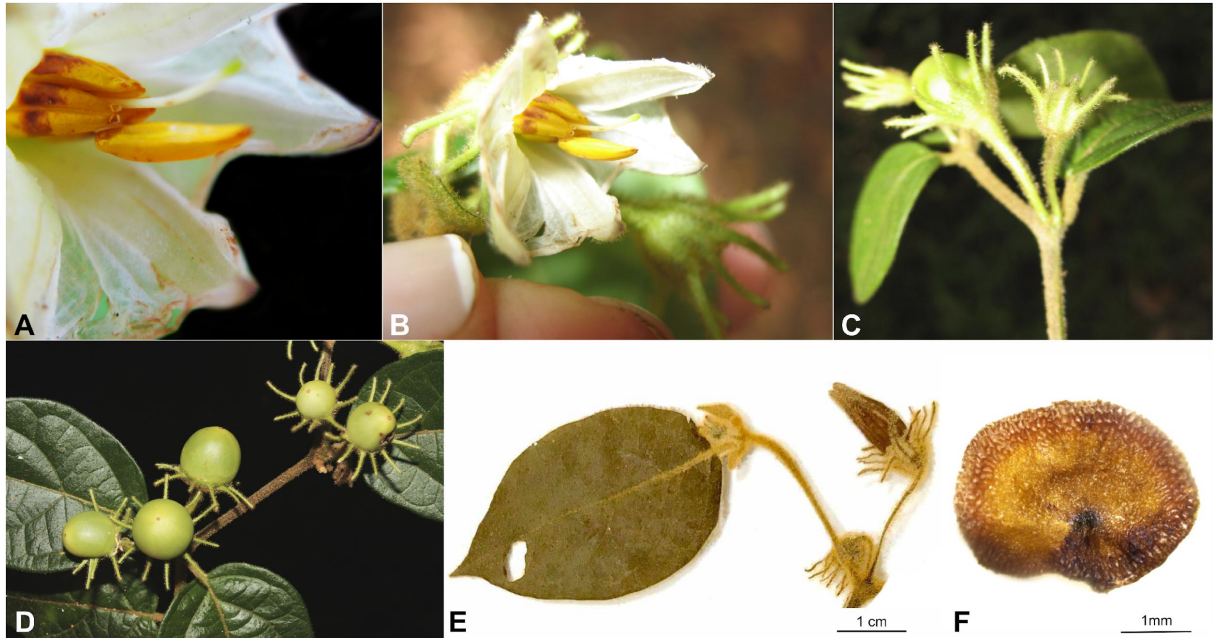
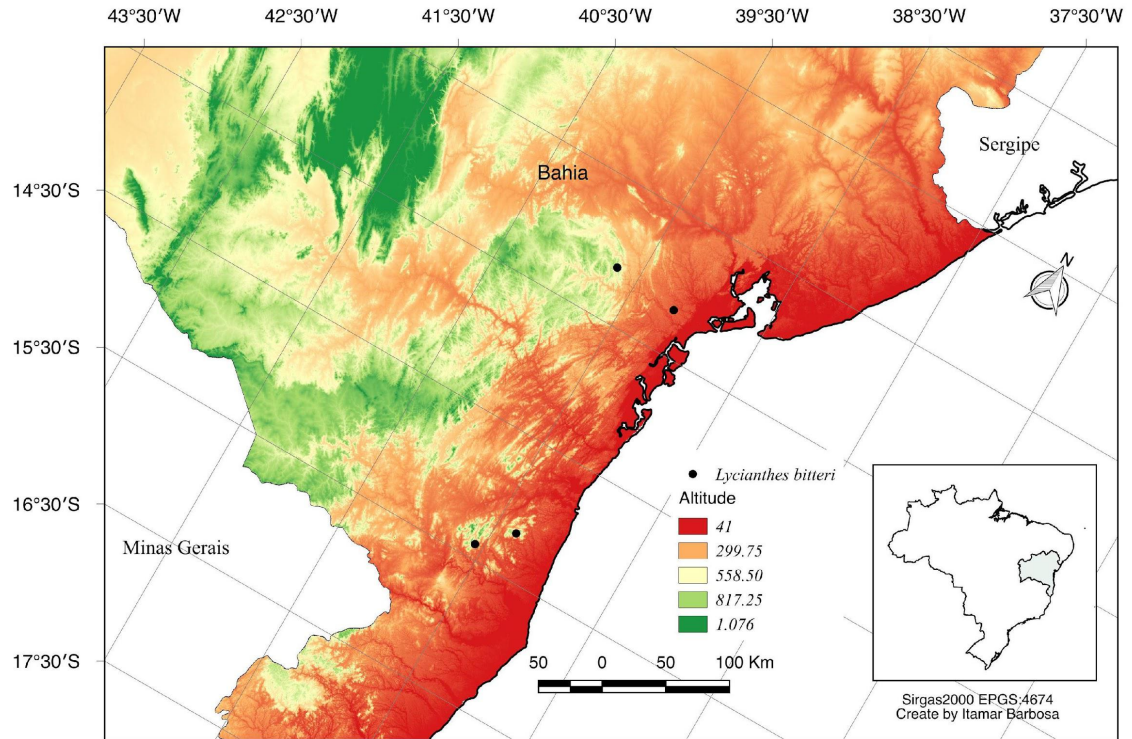


Fig. 3. Map of distribution of *Lycianthes bitteri* Costa-Silva & Agra in the State of Bahia, Brazil.



2.3 MANUSCRIPT 3 - TAXONOMIC REVISION OF *LYCIANTHES* (SOLANACEAE) OF
BRAZIL

To be submitted to Phytotaxa

TAXONOMIC REVISION OF *LYCIANTHES* (DUNAL) HASSLER (SOLANACEAE) OF BRAZIL

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Abstract

With about 200 species, *Lycianthes* (Dunal) Hassler is one of the most representative genera of the Solanaceae family. Despite the relative diversity, the genus lacked modern treatments, and its full revision was made by Georg Bitter in 1919. In addition, it is considered a genus of difficult taxonomy. Due to the small number of diagnostic characters and the great similarity with *Solanum*, a genus in which its species were long included, *Lycianthes* accumulated some nomenclature and systematic problems in its history, mainly the synonymy. In Brazil, the information for the genus were relatively scarce and in order to fill the gap of information about this genus we are presenting descriptions, taxonomic and distribution notes, illustrations, and a key for identification of the 12 species that occur in Brazil, along with six lectotypifications.

Keywords: Brazil, *Capsiceae*, *Solanum*, *Neotropics*

Introduction

Lycianthes comprises about 200 species, predominantly Neotropical, only about 25 species occur in Asia, Indo-Malaysia and Australia. Species of *Lycianthes* are characterized as shrub, perennial herbs or lianas, stellate to rotate corolla, calyx with five to 10 appendages, usually known as teeth, characteristics only observed in *Capsicum* and *Lycianthes*, according to D'Arcy (1986). On the other hand, in *Lycianthes* the anthers are poricide like those of *Solanum*.

The genus *Lycianthes* was formally proposed by Hassler (1917). However, prior to this treatment, the species currently belonging to *Lycianthes* were included in *Solanum*. The first researcher to work with these species as a distinct group was Dunal (1813, 1816), who monographed the genus *Solanum*. In this work the author included 61 species that currently belong to *Lycianthes* in the group *Polymeris*, section *Inermia*, without a defined hierarchical position, based on the presence of appendices in the calyx and the morphology of the axillary peduncles, characteristic of *Lycianthes* (Knapp, 1983).

The *Polymeris* group was elevated to section status by Walpers (1844), who proposed two more sections to *Solanum*: *Lycioides* and *Holochlaina*. Subsequently, Dunal (1852) merged the three sections of Walpers (1844) in the subsection which he named *Lycianthes*, consisting of two series, *Meiomeris* and *Polymeris*, and four subsections, *Pseudolycianhtes*, *Eulycianthes*, *Gonianthes*, and *Lobanthes*.

Hassler (1917) proposed the genus *Lycianthes* with the transfer of three species of *Solanum* subser. *Eulycianthes*: *L. lycioides*, *L. dombeyi* and *L. candicans*, raising it to the generic level. This proposal was based on the anatomical studies of these species performed by Hassler & Bitter (1917), who observed the presence of stone cells in the endocarp of the fruit, a characteristic that was used as differential evidence to the proposition of the genus.

The *Lycianthes* circumscription was expanded by Bitter (1919), that included 134 species of *Solanum* subsect. *Lycianthes* Dunal and, for the first time, suggested a greater affinity of *Lycianthes* with *Capsicum* over *Solanum*, based on the morphology of the calyx. The author also proposed four subgenera- *Eulycianhtes*, *Polymeris*, *Cypellocalyx* and *Syngensis*, 11 sections and 13 series for *Lycianthes*, and it is still the most complete work for the genus. Since then, about 80 new species have been proposed for *Lycianthes*, which currently has a total of about 200 species.

Even after Bitter's (1919) treatment, some authors such as Morton (1944, 1976), Hunziker (1979), and Symon (1985, 1987) still considered *Lycianthes* as part of *Solanum*. However, other works such as D'Arcy (1986) and Barboza and Hunziker (1992), which emphasize the importance of the anatomy and morphology of the calyx of *Lycianthes*, recognized it as a distinct taxon of *Solanum*. In addition, the more recent molecular analyzes in Solanaceae by Olmstead & Palmer (1992), Olmstead et al., (2008), and Särkinen (2013) have corroborated with Bitter's (1919) suggestion that *Capsicum* and not *Solanum* is the closest group to *Lycianthes*.

***Lycianthes* in Brazil**

In Brazil, the information for *Lycianthes* is very scarce, as well as its representation in the national herbaria. In the most comprehensive treatment for Solanaceae by Sendtner (1846), only two species, currently belonging to *Lycianthes*, are included: *Solanum glandulosum* Ruiz & Pavon (1799: 167), currently *Lycianthes glandulosa* (Ruiz & Pav.) Bitter (1919: 348), and *Solanum violaefolium* Schott (1827: 603), whose accepted name is *Lycianthes asarifolia* (Kunth & Bouché) Bitter (1919: 423).

Others informations for *Lycianthes* in Brazil were registered by Carvalho (1997), Rodal (2005), Soares (2006), Soares et al. (2008), and Udulutsch et al. (2010), but it is not very representative and even non-existent for some regions, focusing mainly on listing of species and floristic surveys.

More recently, Stehmann et al. (2010) presented a list of 17 names related to *Lycianthes*, including ten accepted names, seven synonyms, and the degree of endemism of species. The authors also recorded the greatest richness of the genus for the northern region of Brazil, where seven species are found, followed by the southeast region, with four species.

The present work aims to provide a taxonomic treatment to *Lycianthes* in Brazil, in order to fill the gap of information about its taxonomy, contributing to the knowledge of this important and almost unknown genus in Brazil, as well as to the systematics of Solanaceae.

Material & Methods

The circumscription of the species treated here was based on the evaluation of herbarium specimens and field observations, when possible, and are supported by morphological evidence. More than 700 specimens were examined, whose morphological data were analyzed measured and 51 type specimens of the following herbariums, listed

according to Thiers et al. (2017): A, AWH, BM, BR, C, CEPEC, E, EAN, F, G, GH, IAN, INPA, JPB, K, L, M, MA, MG, MO, NY, P, PEUFR, RB, UFP, US, UT and W.

The identification of the species was performed through morphological analysis of the differential characters of the habit, leaves, inflorescences, flowers (calyx, corolla, androecium and gynoecium), fruits and seeds, when available, supported by the specialized bibliography (SEITHE, 1846; DUNAL, 1852, BITTER, 1913, 1919; MORTON, 1944; BARBOZA; HUNZINKER, 1992; ROJAS; D'ARCY, 1997; BOHS, 2015). The species concept used in this taxonomic treatment is the morphological concept of Cronquist (1978), based on the measures of herbarium specimens mentioned above. For the delimitation of the species the characters that are generally more preserved were emphasized, such as the indument, leaf morphology, flowers, fruits and seeds.

The terminology of leaf, flower and fruit morphology followed Stearn (1983) and Harris & Harris (2001), and the indument and trichomes followed Seithe (1979) and Harris & Harris (2001). The author's names follow Brumitt and Powell (1992).

Taxonomic treatment

Lycianthes (Dunal, in Candolle 1852: 29) Hassler (1917: 180). Type:—*Lycianthes lycioides* L.(1917: 181). Type:— *Solanum lycioides* L.(1767: 46). Lectotypified by Knapp and Jarvis (1991: 342)

= *Otilix* Rafinesque, (1830: 87). Type:—*Solanum lycioides* L. (1767: 46)

= *Parascopolia* Baillon (1888: 338). Type:— *Parascopolia acapulcensis* Baillon (1888: 339.)

= *Solanum* subsect. *Lycianthes* Dunal (in Candolle 1852: 29). Type:— *Solanum lycioides* L

= *Solanum* sect. *Lycianthes* (Dunal) Wettstein, (in Engler & Prantl 1891: 22).

= *Solanum* subg. *Lycianthes* (Dunal) Bitter, Bot. Jahrb. Syst. 54: 424 in obs., 442 in footnote. 1917. Type:— based on *Solanum* subsect. *Lycianthes* Dunal.

Herbs rhizomatous, **shrubs** or **lianas**, branche teretes, erect or in zigzag, striate, glabrous to pubescent with simple multicellular trichomes adpressed or setose, stalked or sessile stellate, branched, bifurcated and glandular capitate trichomes, hyaline to rusty. **Sympodial units** unifoliate or difoliate geminate. **Leaves** simple, solitary or geminate; blade symmetrical or asymmetrical, chartaceous, cordiform, ovate, elliptic to oblong-elliptic, base sagitate, cordate, cuneate, or rounded, margins entire, apex acute, acuminate, rounded or obtuse; petioles terete, slightly rugose; glabrous or pilose. **Inflorescences** solitary or fasciculate, axillary, opposite or adjacent to the leaves. **Flowers** perfect, pentamerous, monoclinal, opening one at a time.

Calyx cupuliform, campanulate or patelliform, truncate at the apex, 10-appendages emerging at $\frac{1}{2}$ – $\frac{1}{4}$ below the margin, glabrous or pilose, reflexed, curved or explanate. **Corolla** white, lilac to purple, rotate, stellate, campanulate, interpetalar tissue entire or partially splitted, glabrous or puberulent. **Androecium** with five stamens, filaments straight of equal or unequal length, four shorter and one longer, glabrous, anthers yellow, elliptic, lanceolate, or oblong, attenuate to the apex, dehiscence poricide, pores terminal, extrorse, rounded, elliptic, pores of the longer stamens dehiscing toward the style or upwards, pores of shorter stamens dehiscing toward or away from the style. **Gynoecium** with ovary globose, conical, and ovoid, glabrous; style glabrous, exceeding or at the same size of the anthers, slightly curved at the apex, straight; stigma oblong-clavate, clavate, bilobed, minutely papillose, bright green. **Fruit** a berry, globose, ovoid, elliptic, lacking sclerotic granules, green when immature, and red, orange, or yellow at maturity; pedicel enlarged, upright and terete to subterete, green to ferruginous, glabrous, pubescent, or with stellate indument, trichomes simple (glandular and eglandular), branched and stellate. Seeds numerous, discoid, slightly reniform, elliptic, compressed, surface rust-colored, yellowish, beige, finely pitted to reticulate.

Key to identification of *Lycianthes* in Brazil

1. Prostrate herbs, radicanat at the nodes; sympodial units plurifoliate; leaves cordate or sagitate at the base; pedicel curved at the apex 2
 - Subshrubs and erect or scandent shrubs; sympodial units unifoliate or difoliate geminate. Leaves rounded, attenuate, subcordate, cuneate, and oblique at the base; pedicel erect, upright or pending..... 3
 2. Solitary leaves, ovate or deltoid; corolla white; calyx accrescent to the $\frac{1}{4}$ basal on the fruit (Bahia, Mato Grosso do Sul, Minas Gerais, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Rondônia, Santa Catarina, São Paulo) **2. *L. asarifolia***
 - Geminate leaves, reniform or orbicular; corolla lilac to purple; calyx accrescent above the $\frac{1}{2}$ of the fruit (Bahia, Paraná)..... **11. *L. repens***
 3. Subshrubs and erect shrubs..... 4
 - Scandent shrubs or lianas..... 7
 4. Calyx appendages of equal sizes (teeth), arranged in one series; equal stamen; corolla white..... 5
 - Calyx appendages of unequal sizes (teeth), arranged in two series; unequal stamens; corolla purple (Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro)..... **10. *L. rantonnetii***

5. Geminate and anisophyllous leaves, with asymmetric blades; calyx appendages linear, erect, not curved on the flower and fruit; berries globose..... 6
- Solitary leaves with symmetric blades; calyx appendages curved at the flower and fruit; berries oblong (Acre) **5. *L. coffeifolia***
6. Calyx appendages conspicuous at the flower, 2.0-3.0 mm long; shiny leaves (Acre).....**1. *L. amatitlanensis***
- Calyx appendages inconspicuous at the flower, less than 1 mm de long; dull. Leaves (Acre)..... **8. *L. inaequilatera***
7. Entire plant with simple trichomes..... 8
- Entire plant with stellate and/or dendritic trichomes..... 9
8. Leaves with elliptic or oblong-elliptic blades; acute or acuminate at the Apex. Rotaceous corolla; Calyx with linear appendages (teeth), green on flower and fruit; unequal stamens (1+4) (Acre, Rondônia)**6. *L. compressibacata***
- Leaves with obovate blades, cuspidate at the apex. Calyx with subulate appendages (teeth), green on flower and purple, with enlarged base, attenuating to the apex on the fruit; stellate corolla; Equal stamen (Acre, Amapá).....**12. *L. stenoloba***
9. Sympodial units unifoliate 10
- Sympodial units difoliate geminate 11
10. Calyx lobes truncated on the flower; unequal appendages in more than two series, 4--5 mm long, emerging from the $\frac{1}{4}$ apical of the calyx (Acre, Amapá, Amazonas, Maranhão, Mato Grosso do Sul, Pará, Paraná, Rondônia)**7. *L. glandulosa***
- Calyx lobes slightly cuspidate on the flower, unequal appendages in two series, 6--9 mm long, emerging from the $\frac{2}{3}$ basal of the calyx (Acre, Amapá, Amazonas, Bahia, Mato Grosso, Minas Gerais, Pará, Paraná, Rondônia, Roraima)**9. *L. pauciflora***
11. Blade leaves cuneate or attenuate at the base; indument with stellate-stalked and dendritic trichomes on the leaf blades; calyx pateliform with linear appendages (teeth), explanate at the fruit, 0.5-1.0 cm long, ovary conic (Bahia).....**3. *L. bitteri***
- Blade leaves rounded or oblique at the base; indument with stellate trichomes, without dendritic trichomes; calyx cupuliform, with narrow-obovate appendages (teeth), curved at the fruit, 3.0-4.0 mm long; ovary ovoid (Alagoas, Ceará, Paraíba, Pernambuco).....**4. *L. cearaensis***

1. *Lycianthes amatitlanensis* (J.M.Coulter & Donnell-Smith. 1904: 420) Bitter (1919: 441).

≡ *Solanum amatitlanense* J.M.Coult. & Donn. Sm. (1904: 420)

Type: GUATEMALA. Departamento Amatitlán: Barranca de Eminencia, 1200 m, Feb 1892, *J. Donnell Smith 1457* (lectotype US 1324447 barcode 27445! designated here; isolectotypes: F! barcode V0073065F; GH! 77435!; K n.v.); syntypes: Departamento Alta Verapaz: Cubilquütz, 350 m, Jul 1901, *H. von Tuerckheim 7753* (M!, NY! 138966, US! 398323 barcode 01014252, US! 1324445 barcode 01269193); Departamento Alta Verapaz: Cubilquütz, 350 m, Feb 1903, *H. von Tuerckheim 8488* (F! 185826 barcode V0073066F, M! 171813, NY! 138963, NY! 1388964, US! 576619 barcode 01014253, US! 1324446 barcode 01269192).

= *Solanum sylvicola* Brandege (1917: 373). Type:—MEXICO, Edo. Chiapas: Finca Irlanda, Jun 1914, *C. Purpus 7315* (Holotype: UC! 173378; isotype M! 01811815). Synonymized by Costa-Silva & Agra (2018 in press)

= *Lycianthes ulei* Bitter (1919: 437). Type:—BRAZIL. Amazonas: Rio Acre, Seringal São Francisco, Abr 1911, *E. Ule 9764* (Holotype B†, =F photo 2592!; Lectotype: NY barcode 138719 [photo!]; isolectotypes G!, K 585766 [photo!], L 2881358 [photo!], MG! 14596, U 49194 [photo!], US 1615234 [photo 27900!]). Synonymized by D'Arcy (1973) and lectotyped by Costa-Silva & Agra (2018b)

= *Lycianthes ulei* Bitter ssp. *dolichodonta* Bitter (1919: 438). ECUADOR. Provincia Guayas: Balao, Feb 1892, *H. Eggers 14409* (Holotype: M 0171814!; isotype: US 1324959!). Synonymized by D'Arcy (1973).

Subshrub, erect, 1.0—2.0 m tall, perennial, unbranched. **Stem** terete, green at the apex (young parts) and brown at the base (mature parts), indument strigose, trichomes simple, multicellular, uniseriate, 3—6 celled. **Sympodial units** difoliolate geminate, anisophyllous. **Leaves** geminate, unequal, indument strigose, similar to the branches; lamina membranaceous, concolor, margins entire, ciliate, the largest 14.0—18.5 x 3.5—6.5 cm, anguste-elliptic, apex acute or acuminate, base cuneate or oblique, slightly decurrent on the petiole, glossy on the adaxial surface, 24—26 secondary veins, pressed on the adaxial surface, and prominent on the abaxial surface; petiole short, 0.8—1.5 cm long. on the greater leaves, strigose with trichomes similar to those of the stems; the smaller lamina, 2.0—3.0 x 1.0—1.7 cm, sessile, elliptical, apex acute, base assymmetric, 4—8 secondary veins; indument strigose,

trichomes simple, glandular and eglandular, 3—8-celled, uniseriate, adpressed, more dense on the veins. **Inflorescence** in fascicles, 2—4-flowers; pedicel thin in flower, 0.7—2.2 cm long, enlarged in fruit, 2.0—3.3 cm long., erect in flower and fruit, indument strigose, trichomes similar to those in the stems. **Flowers** perfect, pentamerous, monoclinous. **Calyx** cupuliform, truncate at the apex, 1.5—2.0 x 2.8—3.0 mm, 10- appendages, linear, emerging from the edge of the calyx tube, sometimes slightly unequal, 0.2—0.3 cm. **Corolla** white, rotata, 0.6—0.9 cm diam, lobes lanceolate-elliptic; 5-stamens, equal, filaments 0.14—0.15 cm long, anthers 0.3—0.4 mm long, attenuate to the apex; ovary subglobose, glabrous, 1.0—1.5 mm long, style 0.5—0.6 cm long, stigma capitate. **Berry** globose, red, 0.6—0.8 cm diam.; calyx in fruit with accrescent appendages, erect, 0.4—0.5 cm long; pedicel 0.8—1.4 cm long. **Seeds** not seen.

Discussion: — *Lycianthes amatitlanensis* is characterized by the presence of glossy and large leaves, dense and strigose pubescence with simple, multicellular, uniseriate and long trichomes. The calyx appendages are linear and pilose, conspicuous, and enlarged in fruit. The Brazilian collections of this species are usually mixed with those of *L. inaequilatera* (Rusby) Bitter (1919: 439), a species that has been confused and misidentified. These two species share the habit as subshrub, and the asymmetric geminate anisophyllous leaves, characters that correspond to the delimitation of *Lycianthes* sect. *Simplicipila* serie *Strigulosae*, according to Bitter (1919: 433).

Martinez et al. (2002) and Jorgensen et al. (2014) consider *Lycianthes amatitlanensis* to be a synonym of *Lycianthes inaequilatera* (Rusby) Bitter (1919: 439). The examination of the types of these taxa clearly indicates them to be different species. *Lycianthes amatitlanensis* can be recognized for having erect branches, shiny leaves, and conspicuous calyx appendages (2.0—3.0 mm long), which are linear and pilose at anthesis. Differently, *Lycianthes inaequilatera* has zigzag branches, dull leaves, inconspicuous calyx appendages, less than 1 mm long, which are glabrescent at anthesis. In light of these evidences, we consider that *Lycianthes amatitlanensis* is a distinct taxon and not synonymous with *L. inaequilatera*, corroborating with the previous observations of Rojas and Darcy (1997) and Bohs (2015). For illustrations, check Rojas and D'Arcy (1997).

Phenology:— Flowered material was observed from August to February, and with fruits were recorded from specimens collected between February to July.

Distribution and Habitat: — Occurs from Mexico to Bolivia and Brazil. In Brazil it was recorded only to the State of Acre (Fig. 2), where it is found in moist areas, near rivers or in edges of Forest, and roadsides, cloud forests of primary vegetation.

Specimens examined:— BRAZIL. Acre: Sena Madureira, 15 oct 1978, *Lima 238* (INPA); Sem local, s.d. Ule 9764 (K). COLOMBIA: Antioquia: Municipio de Tarazá, 9 nov 1987, *Callejas et al. 5478* (F). BOLIVIA. Depto. De Santa Cruz: Sara, 20 feb 1916, *Steinbach 2898* (G). ECUADOR. Provincia Pichinca: reserva Florística ecológica “Rio Guajalito”, 31 aug 1985, *Vlastimil 586* (G). Los Rios: Río Palenque, 22 feb 1976, *Gentry 10125* (F); 12 nov 1979, *Schupp 41* (F). Napo: Estacion del INIAP, 16 may 1986, *Baker 7001* (MG); Puerto Misahualli, 18-30 may 1985, *Palacios 00443* (F). GUATEMALA. Departamento Amatitlan: Barranca de Emnienca, s.d., *Smith 1457* (K); Departamento Chimaternalgo, 20 set 1942, *Steyrmark 52098*(G). PANAMA. Cocle: Cerro Pilon, 16 mar 1973, *Liesner 733* (F). Comarca de San Blas, 10 aug 1984, *Nevers 3658, 3865* (G); Darien: Parque Nacional del Darien, 13 oct 1987, *Hammel 16172* (MG). PERU. Amazonas: Quebrada Huampami, 3 apr 1973, *Ancuash 148* (F); 6 jun 1973, *Kayap 878* (F). Huánuco: Panchieta; Codo de Pozuzo, 21 oct 1982, *Foster 9361* (G, F). Madre de Díos: Manu, Parque Nacional de Manu, 20 aug 1973, *Foster 2704* (F). San Martín: Shapaja, 8 sep 1977, *Schunke 9812* (F). VENEZUELA. Sucre: Peninsula de Paria, 7 aug 1966, *Steyrmark 96125* (F).

2. *Lycianthes asarifolia* (Kunth & Bouché, 1845:10) Bitter (1919: 423).

≡ *Solanum asarifolium* Kunth & Bouché (1845:10). Type: Cultivated in Berlin, 1842, seeds from Venezuela, D.F., Caracas, *E. Otto s.n.* (B†, =F photo 2562!); Lectotype: P P00430541!. Lectotipified by Costa-Silva (2018).

=*Solanum violifolium* Schott var. *asarifolium* (Kunth & Bouché 1845:10) Hassl (1918:221). Synonymized by Barboza and Hunziker (1992)

= *Solanum chodatianum* Huber (1906:602). Type: Peru, Depto; Loreto, Prov. Ucayali, Río Ucayali, Contamana, 15 Nov 1898, *J. Huber 1336* (MG! 1336, =F foto 45292!; isotype: F 602865! Barcode V0073230F). Synonymized by Bitter (1919)

= *Solanum violifolium* Schott var. *asarifolium* (Kunth & Bouché) Hassl. fma. *decadontum* Hassl.(1918: 221). Syntypes: Paraguai, Río Pilcomayo, 12 Feb 1888–1890, *T. Morong 920* (G

n.v., NY 172243!, 172244!); *T. Rojas 6205 (n.v.)*. Synonymized by Barboza and Hunziker (1992).

=*Solanum violifolium* Schott var. *majus* Dunal fma. *chacoense* Hassl. (1918:20). Type: Paraguay, Chaco, Río Pilcomayo, Jul 1906, *T. Rojas 275* (Holotype G!; isotypes: K! 000585761, K! 000585762). Synonymized by Barboza and Hunziker (1992).

= *Solanum violifolium* Schott var. *majus* Dunal (1852:164). Type: Bolivia, Depto. Santa Cruz, Santa Cruz de la Sierra, *A. d'Orbigny 619* (Holótipo: BR! 8290410; isótipos: P! 384862, P! 384863). Synonymized by Barboza and Hunziker

= *Solanum violifolium* Schott fma. *lilaciniflorum* Hassl., Trab. Mus. Farm. Fac. Cienc. Med. Buenos Aires 21: 106. 1909. Type: Paraguay, Río Pilcomayo, *T. Rojas 605* (Holotype: G?; isotype: K! barcode K000585759, K000585760, SI *n.v.*).

Herb creeping, stoloniferous; branche terete, green, striate to rugose, indument puberulent on the internodes, trichomes simple, eglandular, multicellular, unisseriate. **Sympodial units** plurifoliate. **Leaves** solitary, pedicel 2.0-13 cm long, canaliculate, puberulous to glabrous, simple multicelular unisseriate trichomes; lamina chartaceous, 4.0—6.5 x 2.5—6.0 cm, weakly discolor, glabrous, ovate to deltoid, glossy on the abaxial surface, 7—10 secondary veins, impressed on the adaxial surface, prominent on abaxial surface, acuminate or obtuse at the apex, margins entire, base cordiform or sagitate. **Inflorescences** sessile, 1—flowered, indument puberulent, trichomes similar to those on the branches. **Flowers** solitary, perfect, pentamerous, monoclinal; pedicel 4.8—8.0 cm long, curved at the apex, glabrescent to puberulent, trichomes simple. **Calyx** campanulate, 2.5—4.0 cm long., 10-appendages, inconspicuous, evident on the dry plant. **Corolla** rotate, white, 0.6—1.1 x 1.2—2.2 cm, lobes elliptic, 0.6—1.2 x 0.3—0.6 cm, interpetalar tissue well-developed, glabrous. **Androecium** with 5-stamens, equal, filament 1.3—1.5 mm long, glabrous, anthers oblong, 2.5—3.5 mm long. **Gynoecium** with ovary conical to subglobose, glabrous, 1.5—2.0 mm diam., style, glabrous, 5.0—6.0 mm long, stigma clavate, bilobed, green, 1.0—1.5 mm. **Berry** globose, orange, 1.4—1.7 cm diam., calyx accrescent on ¼ basal; pedicel terete, 6.0—12.3 cm **Seeds** not seen.

Discussion:— *Lycianthes asarifolia* and *L. repens* share many morphological characters, however, they present significant differences, which we can highlight based on the analyze of the collections under this name (*Hatschbach 61463* and *Smith et al., 1487*), which are deposited at the herbaria M and P.

According to Bitter (1919: 426), *Lycianthes asarifolia* is distinguished from *L. repens* by its solitary and larger leaves, longer pedicel, and glabrescent indument, while *L. repens* has geminate and unequal leaves, shorter pedicel, and pubescent indument.

In addition, the unnumbered collection of *E. Otto* at the Muséum National d'Histoire Naturelle of Paris (P-430541) donated by the Herbarium of Berlin in 1855 was designated as lectotype by Costa-Silva & Agra (2018). The lectotype is in good condition, showing a plant with roots, two well-developed leaves, and one flower, which corresponds to the protologue of *Solanum asarifolium* Kunth & Bouché and is the only collection of Otto we have located.

Although some authors (Flora of Brazil, 2020) consider them a single species, a taxonomic definition was possible after an analysis of the nomenclatural type of *L. asarifolia* at P Herbarium, and also by the analysis of many samples of *L. repens*, that had its type specimen destroyed by fire at the Berlin Herbarium. Since we have been able to analyze many samples of these species that showed distinctive characters, which appears in both: the original description of the basionym *Boldoa repens* Spreng. (1825: 179) and in Bitter's description, we decided to treat them as distinct taxonomic entities. For illustrations, check Barboza & Hunzinker (1992) and Rojas and D'Arcy (1997).

Distribution, habitat and ecology:— *Lycianthes asarifolia* presents a wide range of distribution, occurring from Venezuela to Paraguay and the Brazilian Amazon (Fig. 2), appears again in the northeast of Argentina and South of Brazil, also can be found in the northeast region as an invasive species or cultivated as ornamental. It occurs in disturbed areas, along roads or on forest edges.

Phenology:— Flowered specimens were observed through the year, and frutified specimens were registered from May to December.

Ethnobotany:— The fruits of *L. asarifolia* are reported to be edible, and to have a sweet taste (William 1993) and (Scarpa 2009). It is known as “motojobobo” (Michel 104), “motobobo” (Williams 668) in Bolivia, and as “ajcillo” (Rodriguez 74) in Venezuela.

Specimens Examined: — BRAZIL. Bahia: Ilhéus, s.d., Jesus 661 (CEPEC), Área do Centro de Pesquisas do Cacau, 16 apr 1991, Santos 457 (CEPEC); Itabuna, 27 sep 1982, Santos 3805 (CEPEC). Mato Grosso do Sul: Corumbá, Porto Morrinho, 20 jun 2006, Barbosa 1580 (RB). Paraíba: Areia, 24 jul 1987, sin col. 9 (EAN). Minas Gerais: Carangola, jun 1988, Leoni 389

(RB), 24 jan 2009, *Lima 31* (RB). Paraná: Londrina, 27 oct 1986, *Perri s.n* (RB). Pernambuco: Recife, 8 nov 2011, *Amorim 1228* (UFP); 09 set 1970, *Clemencia s.n.* (UFP); 15 feb 2012, Sampaio 60 (UFP, JPB). Rio de Janeiro: Niterói, 23 nov 2002, *Barros 1727* (RB); Niteroi, Reserva ecológica Darcy Ribeiro, 03 apr 2005, *Coqueiro 121* (RB), 29 jul 2005, *Coqueiro 140* (RB); Rio de Janeiro, 25 apr 2012, *Bandeira 101* (RB). Rondônia: Costa Marques, 30 mar 1987, *Nee 34583* (INPA, NY). Santa Catarina: Blumenau, 24 feb 2012, *Funes 386* (FURB). São Paulo: Campinas, 15 mar 1950, *Dedecca s.n.* (UFP); Piracicaba, 4 nov 2011, *Souza 36005* (ESA).

Additional specimens: ARGENTINA. Orán: Aguaray, Las Lagunas, feb 1940, *Schreiter 11193* (F). Santa Barbara: Jujuy, Vinalito, 7 jul 1937, *Cabrera 4072* (F). Tucumán: San Miguel de Tucumán, 8 mar 1983, *Bohs 2112* (F). BOLIVIA. Chuquisaca: Tomina, Monteagudo, 8 mar 1981, *Beck 6374* (F). La Paz: Nor Yungas, Caranavica, 18 sep 1981, *Beck 4818* (F). Santa Cruz: Andrés Ibañez, 8 feb 1988, *Williams 668* (F); Cordillera, 8 jan 1982, *Michel 104* (F); Santa Cruz, 09 dec 1993, *Toledo & Chuvé 283* (F). PARAGUAY: Pilcomayo River, 1888-890, *Morong 920* (F). PERU. Madre de Dios: Manu, Rio Manu, Quebrada Romero, 30 act 1987, *Sobrevila 2055* (F, US). Puerto Maldonado, 9 apr 1954, *Rauti-Hitsch s.n.* (F); 21 apr 1977, *Gentry 19620* (F). VENEZUELA. Miranda: Caracas, 31 dec 1944, *Steyemark 60971* (F); 2 aug 1979, *Nee 17146* (F). Zamora: Santa Maria, 1 sep 1974, *Rodriguez 74* (F).

3. *Lycianthes bitteri* Costa-Silva & Agra (2018b:2)

Type:—BRAZIL. Bahia: Município de Amargosa, Serra do Timbó, estrada para Barata Azul, 13°06'19"S, 39° 40' 32" W, 800 m, 02 Dec 2009 (fl, fr), *Agra et al. 7185* (holotype: JPB!; isotypes: NY!; RB!; UFP).

Shrubs scandent, 1.0—2.0 m tall, branched, perennial; branches and stems terete, ferruginous to brown, striate to rugose, indument stellate-puberulous, yellowish to ferruginous, trichomes stellate, sessile and short stalked, 3—6 lateral rays, many-celled, uniseriate, and dendritic trichomes with branched lateral rays, hyaline, **Symphodial units** difoliate, anisophyllous, and unifoliate in proximal branches. **Leaves** alternate, simple; petiole short, 0.6—1.5 x 0.1—0.2 cm, slightly grooved, tomentose, ferruginous, stellate and dendritic trichomes similar to those of branches; lamina chartaceous, 5.5—13.0 x 3.0—6.5 cm, weakly discolored, ovate

and angusto-ovate in distal leaves, and ovate or elliptic in the proximal, somewhat glossy on the adaxial surface, 6—10 veins, impressed on the adaxial surface, prominent on the abaxial surface, sparse stellate on the adaxial surface and midrib, stellate trichomes stalked, abaxial surface stellate-velutinous to stellate-tomentose, trichomes stellate-stalked (stalk 2—3-celled), and midrib with dendritic trichomes, apex acute to acuminate, margin entire to slightly sinuate, base cuneate, rounded, and somewhat subcordate. **Inflorescence** indeterminate, fascicle axillary, sessile, 1—3-flowers, opposite to the leaf; pedicel slender in flower, 0,8-1,5 cm long, enlarged in fruit, pendulous, erect at maturity, terete, stellate-tomentose, yellowish to ferruginous, trichomes stellate-stalked. **Flowers** perfect, pentamerous, monoclinous; calyx cupuliform, campanulate, truncate at the apex, 6.0—7.0 x 8.0—9.0 mm, 10-appendages, unequal, in two series, emerging from 1.3—1.5 mm below at the apex, the largest 3.0—6.5 mm long, the smallest 2.0—5.8 mm long, stellate-tomentose, trichomes similar to those of the pedicel; corolla campanulate, white, 1.8—2.0 cm diam., lobes elliptic, 1.5—1.7 x 0.3—0.4 cm, puberulous on the outer surface, trichomes stellate, interpetalar tissue glabrous, well-developed, 0.3—0.4 cm; stamens 5, unequal (1 + 4): one largest, 4.5—5.0 mm long, 4 smaller ones with short filaments 1.9—2.2 cm long, anthers yellow, attenuate from the base to the apex, the largest 6.0—6.2 mm long, the smaller 5.8—6.0 mm long, sub-sagitate to slightly asymmetric at the base, 1.5—2.0 mm wide, pores extrorse; ovary conical, glabrous, 2.0—2.1 x 1.5—1.7 mm; style glabrous 1.0—1.1 cm length, straight, slightly curved to the apex, stigma oblong-clavate, 1.0—1.5 mm long, minutely papillose, bright green. **Fruit** globose, 1.5—2.0 cm in diameter, glabrous, orange when ripe, green to yellow-green when young, drying brownish, surrounded by the persistent, somewhat accrescent calyx, the epicarp leathery, the calyx appendages linear, explanate, unequal, in two series, the smallest 0.5—0.7 cm long, the largest 0.8—1.0 cm long, stellate-tomentose; pedicel upright, enlarged, 1.5—2.3 cm long, brownish, trichomes similar to those on the branches. **Seeds** up to 20, ovoid to sub-reniform, compressed, 2.7—3.4 mm in diameter, seed coat slightly waved, reticulated, beige to light brown.

Discussion:— The set of morphological characters showed by *Lycianthes bitteri*, such as scandent shrub, ferruginous indument, and stellate trichomes place this species belonging to the *Lycianthes* subg. *Polymeris* sect. *Eupolymeris* ser. *Oligochondrae* Bitter (1919). Due to its characteristics, in some herbaria the specimens were identified as *L. pauciflora* (Vahl) Bitter (1919), name commonly associated with specimens that exhibit these characteristics and occur from French Guiana to the Southeast region of Brazil and the Brazilian Amazon.

They can be differentiated by several characters, like an adaxially depressed petiole, and inflorescences opposite to the leaves in *L. bitterii*, while in *L. pauciflora* the petiole is cylindrical, and the inflorescences are in the same direction as the leaves; the tomentose calyx with linear and longer appendices in flower, which are explanate and two series in fruit in *L. bitterii*, differing from *L. pauciflora* with shorter, glabrous to glabrescent, and reflexed appendices (in flower and in fruit); the ovary is conical in *L. bitterii* and it is rounded in *L. pauciflora*. The velutinous to tomentose indument of *L. bitterii* is denser and persistent even after the process of herborization, whereas in *L. pauciflora* it is glabrescent.

Lycianthes bitterii also shares some morphological characters with *L. cearaensis* Bitter (1919), an endemic species to the Northeast region of Brazil (Alagoas, Ceará, Paraíba and Pernambuco). It can be differentiated from *L. cearaensis* by the latter's canaliculate petiole, calyx with linear and uniseriate appendices rounded at the apex, and also by a tomentose indument on the branches, petioles and pedicels with stalked stellate trichomes, which are different from that observed in *L. bitterii*. In addition, dendritic trichomes with bifurcate lateral rays are observed only in *L. bitterii*, and do not occur in *L. cearaensis* and in *L. pauciflora*.

Distribution, habitat and ecology:— *Lycianthes bitterii* is an endemic species to the State of Bahia Brazil that occurs in disjunct areas (Fig. 2). It was collected in forest edges, and in secondary forests, however, few collections of this species can be found in herbaria.

Samples of *L. bitterii* were collected at different altitudes, from 40 m to 900 m above sea level. In Serra do Timbó, a mountain range characterized by rugged relief, covered mainly by semi-deciduous tropical forests and reaching elevations between 800 and 900m. According to Ab'Sáber (1977), Serra do Timbó is a transitional area between the Caatinga, Cerrado and the Atlantic Forest. The humid tropical climate prevails in the Serra do Timbó, but the region is surrounded by sub-humid and semi-arid climates.

The other locality is Serra Bonita that has a unique habitat with important altitudinal gradients of native Atlantic Forest, varying from 300 to 1,080 m of elevations (Amorim et al. 2009). It is located in the Camacan basin, and is characterized by the hot and humid climate, type Af (Köppen 1936), with absence of dry season. Clear variations of humidity and temperature are found in its vegetation, which alternates from an evergreen forest to Semi-deciduous humid forest, elements from lower elevations to mountain forest (RPPN SERRA BONITA 2016).

Phenology:— Flowering and fruiting samples were collected from December to June.

Ethnobotany:— Unknown.

Specimens Examined— BRAZIL. Bahia: Mun. Amargosa, Fazenda Mucuri, Riacho do Meio, área de estudos do Projeto Timbó/ Centro Sapucaia 13°10'20'' S 39°9'34'' W 25 jan 2007, *Cardoso 1602* (HUEFS); Mun Arataca: RPPN Caminho das Pedras, em trilha de acesso ao Peito-de-moça, 15°10'25''S 39°20'30'', 15 jun 2006, *Amorim 6062* (CEPEC, NY); Mun. Camacan, RPPN: Serra Bonita, 10 km W de Camacan na estrada para Jacarecí, 6km SW na estrada para RPPN e Torre de transmissão. Trilha de acesso a RPPN. 15°23'35''S 39°33'53''W, 850 m, 25 mar 2007, *Amorim 6958* (CEPEC, NY).

4. *Lycianthes cearaensis* Bitter (1919: 346). Type:—BRAZIL. Ceará: Serra de Maranguape, 600 m, Oct 1910, *E. Ule 9103* (Holotype B† F foto 2564!; lectotype: NY 138709 [photo!]; isoelectotypes: K 585757 [photo!] 16153675, L 602560, barcode 3587 [photo!]; US 16153675 [photo 27870!]. Lectotype designated by Costa-Silva and Agra (2018).

Shrub scandent, 2.0—5.0 m tall, branched, perennial; branches and stems terete, brown, striate to rugose, indument stellate-puberulous, yellowish to ferruginous, trichomes stellate, sessile and short stalked, 3—6 lateral rays. **Symphodial** units unifoliolate. **Leaves** simple; petiole, 0.5—1.5 cm long, slightly grooved, tomentose, yellowish to ferruginous, trichomes stellate similar to those of branches; lamina chartaceous, 6.0—10 x 2.5—6.5 cm, weakly discolored, elliptic to anguste-elliptic, adaxial surface somewhat glossy, glabrescent, stellate trichomes on the midrib, abaxial surface scabrous, trichomes stellate, short stalked; 8—10 veins, impressed on the adaxial surface, prominent on abaxial surface, acute to acuminate at the apex, margin sinuate, base cuneate and somewhat oblique. **Inflorescence** indeterminate, fascicle axillary, sessile, 1—2—flowers. **Flowers** perfect, pentamerous, monoclinal; pedicel, pendent, 0.5—1.0 cm long, terete, stellate-tomentose, trichomes stellate-stalked, yellowish. **Calyx** cupuliform-campanulate, truncate at the apex, 3.5—5.0 x 5.0—6.0 mm, 10-appendages emerging at 1.2—1.3 mm below at the apex, unequal, in two series, linear, curved at the apex the largest 1.5—2.0 mm, the smallest 1.0—1.5 mm long, stellate-puberulent, trichomes similar to those of the pedicel. **Corolla** rotate, white, 1.0—2.0 cm diam., lobes lanceolate-elliptic, 0.6—1.0 x 0.2—0.4 cm, glabrous, interpetalar tissue well-developed. **Androecium** stamens 5, unequal (1 + 4): one largest, 4 smaller ones; 1-filament longer, 5.6—6.0 mm, 4-

filaments shorter, 1.5—2.0 mm long, anthers yellow, attenuate from the base to the apex, 5.7—6.0 mm long, sub-sagitate at the base, 1.5—2.0 mm wide; **Gynoecium** with ovary ovoid, glabrous, 2.0—2.5 x 1.4—1.6 mm; style glabrous 1.4—1.8 cm long, straight, stigma oblong-clavate, 1.0—1.2 mm long, minutely papillose, bright green. **Fruit** a berry globose, pendent, 1.0—2.0 cm in diameter, glabrous, green to yellow-green when young, red when ripe, drying brownish, the epicarp leathery, the calyx appendages slight curved at the apex, unequal, in two series, 3.0—6.0 mm long, stellate-puberulent; pedicel erect at maturity, glabrescent, trichomes stellate. *Seeds* up to 20, sub-reniform, compressed, 2.6—2.8 mm diam, reticulate, beige to ferruginous.

Discussion: — *Lycianthes ceareaensis* is a species proposed by Bitter based on a collection of Ule made in Serra de Maranguape, in the state of Ceará. This species can be recognized by habit as scandent shrub, with leaves described by Bitter as false geminates (the leaves can be geminate on more distal new branches), indument tomentose, composed of stellate trichomes, elliptic or oblong-elliptic leaves, calyx with 10 oblong-obovate unequal appendages, corolla white and unequal stamens.

Lycianthes ceareaensis shows great morphological affinity with *L. pauciflora* and, recognizing this affinity, Bitter (1919) positioned these two species in *Lycianthes* series *Oligocondrae*. However, *L. ceareaensis* was considered as a synonym of *L. pauciflora* in the List of species of the Flora of Brazil by Stehmann et al. (2015).

In the Brazilian herbaria, the collections of *L. ceareaensis* and *L. pauciflora* are mostly mixed, and misidentified, although *L. ceareaensis* can be distinguished from *L. pauciflora* by its denser tomentose indument, calyx fructiferous cupuliform with curved appendages, and ovary ovoid, while *L. pauciflora* presents loose indument, calyx fructiferous pateliform with reflexed appendages, and ovary globose. These characters can be visualized on Fig.4.

Distribuição e Habitat:— *Lycianthes ceareaensis* is an endemic species of Brazilian flora that presents records of occurrence for the Atlantic Forest region on the north of the São Francisco River, with preference for well preserved environments with high humidity rates. They can be found in ombrophilous forests and in forests located in semi-arid highlands and plateaus, locally called Brejos de Altitude, in the state of Ceará, Paraíba, Pernambuco and Alagoas (Fig. 4), which due to the characteristics of their relief have milder temperatures and higher humidity.

Phenology:— Flower and fruits were observed from July to April.

Ethnobotany:— There is no record of popular uses for *L. cearaensis*.

Specimens Examined:— BRAZIL. Alagoas: Ibatiguara, 11 dec 2001, *Oliveira 700* (UFP); 18 mar 2009, *Oliveira 852* (PEUFR, UFP); Murici, 16 mar 2002, *Carvalho 7097* (NY), 18 nov 2003, *Falcão 70* (UFP); Pedra Talhada, 05 dec 1994, *Cervil et al 7264* (G); Quebrangulo, ReBio da Pedra Talhada, 24 jan 2012, *Sampaio 53* (UFP, JPB), *Amorim 1394* (NY, UFP); 04 sept 2012, *Sampaio 94* (UFP); 09 dec 2014, *Nusbaumer 4546* (UFP). Ceará: Guaramiranga, 08 jan 1994, *Oliveira s.n.* (EAC); s.d., *Oliveira e Moura 372* (JPB); Maranguape, Trilha da Pirapora, 27 sept 2014, *Sampaio 107* (EAC); Pacatuba, Sítio Boqueirão, Serra da Aratanha, 25 mar 2000, Souza 415 (EAC); Serra de Maranguape, 22 jan 955, *Andrade-Lima 2315* (IPA); 06 jan 1992, *Félix 4669* (EAN). Paraíba: Areia, Mata do Pau-ferro, 28 nov 1980, *130* (EAN); 07 mar 2012, *Sampaio 67* (UFP, JPB); 13 apr 2005, *Agra 6476* (JPB); 17 oct 1988, *Félix 1410* (EAN). Pernambuco: Bonito, 15 mar 1995, *Henrique et al. 07* (UFP), *Andrade 25* (NY), 09 feb 1996, *Tschá 542* (PEUFR), 06 mar 1996, *Pimentel 75* (PEUFR); Caruaru, Brejo dos Cavalos, 01 dec 1994, *Travassos 258* (NY); 16 may 1996, *Tschá 777* (PEUFR), 2 jan 1972, *Barbosa s.n.* (UFP); Escada, 21 jul 1967, *Lira 29* (UFP), 07 mar 1968, *Lira 194* (IPA); Jaqueira, 29 jan 2013, *Amorim 1744* (JPB, NY, UFP); Lagoa dos Gatos, 22 nov 2011, *Amorim 1254* (JPB, UFP); Lagoa do Ouro, 09 dec 2014, *Nusbaumer 4546* (NY); São Vicente Férrer, 27 may 1998, *Ferraz 315* (PEUFR); 31 jul 1998, *Ferraz 358, 366* (PEUFR); Tamandaré, 29 feb 2000, *Oliveira 570* (PEUFR).

5. *Lycianthes coffeifolia* Bitter (1919: 432). Holotype:— BRASIL. Amazonas: Acregebiet, Monte Mo, Nov 1911, *E. Ule 9737* (Holotype: B†, =F photo 2566!); lectotype: US 1615264 [photo 27875!]; isolectotypes: G! [2 exsicatae]; L 602560 [photo 2881751!], K 585765 [photo!]). Lectotype, designated by Costa-Silva & Agra (2018).

Shrubs, erect, 0.5—1.0 m tall, branched, perennial. Branches brown, estriate, rugose, glabrescent, trichomes simple, multicellular, uniseriate, yellowish, hyaline. **Sympodial units** usually unifoliate, or difoliate, false-geminate in superior branches. **Leaves** simple; petiole short 0.3—0.5 cm long, striate, glabrous; lamina chartaceous, 6.0—17.2 x 1.9—5.5, concolor, elliptical, oblong-elliptic, obovate, dull, glabrous in both surfaces, 10—15—veins, impressed on the adaxial and prominent on the abaxial surface, apex acuminate or acute, margins

slightly wavy, base cuneate, puberulent on the midrib, trichomes simple, eglandular, multicellular, unisseriate. **Inflorescences** 3—5 flowers; pedicel pending on flower, 2.0—6.0 mm long, glabrescent, trichome simple, eglandular, similar to the petiole. **Flowers** perfect, pentamerous, monoclinal. **Calyx** cupuliform, tube 1.4—1.5 cm long, 10-appendages in one series, 2.0—2.3 mm long., lanceolate, attenuating toward de apex, glabrous, emerging on the edge of the tube. **Corola** white, stellate, 1.2—1.5 cm diam., lanceolate lobes, acute, 6—6.3 mm, glabrous, interpetalar tissue conecting the petals on the basal $\frac{1}{2}$; estamens 5, equal, filaments 8-10 mm long, anthers oblong, connate, 3.6—3.7 mm long.; ovary ovoid to conical, 1.87x1.2 mm, glabrous; style 3.8—4.0 mm long, erect, stigma clavate, bright green, glandular. **Fruit** a berry, long-ellipsoid, 1.5—1.8 cm diam., epicarp glabrous, red; pedicel erect on fruit, pilose, trichomes; calyx frutiferous accrescent, 10-appendages, subulate, recurved, 0.0—0.0 mm long. **Seeds** not seen.

Discussion: — *Lycianthes coffeifolia* was positioned by Bitter in *Lycianthes* sect. *Simplicipila* (1919: 426), a group of species that is characterized by their equal stamens, trichomes simple, eglandular, multicellular. This species can be easily recognized by their elliptic-obovate leaves, pedicel pendent in flower and erect in fruit, calyx patelifome with 10 appendages short, recurved, and by its red and alonged berry. This set of character can be observed on Fig. 1. The representation of *L. coffeifolia* in the Brazilian herbaria is very low, probably because its distribution in Brazil is restricted to the State of Acre, and only nine specimens were found until the end of this work.

Distribution and Habitat:— In Brazil, *L. coffeifolia* is restricted to the State of Acre (Fig.4), occurring in areas near rivers, and gallery forests, with preference for humid soils. It may also occur occasionally in disturbed areas at the edge of the forest, in wetlands. The collection sites for the material examined correspond to the area of Acre state municipalities, which overlap the area of Chandless State Park, located in the Purus river basin (SEMA 2010). A large variety of phytophysiognomies can be observed in this region, with predominance of more open canopy typologies (open deciduous forest with bamboo and / or palm). There is the occurrence of pioneer formations, in different stages of succession due to the dynamics of the Chandless River, of Open Ombrophylous Forest in Flood Terraces, Dense Ombrophylous Forest, Deciduous Forest (sometimes dominated by bamboo, sometimes by palm) and, to a lesser extent, the occurrence of vegetation on lakes of fluvial origin, permanently flooded (SEMA 2010).

Phenology:— Flowers and fruits were observed from May to November.

Ethnobotany:— *Lycianthes coffeifolia* is popularly known as 'mane-kabia-bata' by the indigenous Kaxinawá ethnic group, where the plant is used to treat snakebite (*Ehringhaus et al.*, 401). It is known as “Ajisillo” (*Shcunke 4576*) and “Quintillo Sacha” (*Schunke 6511*) in Peru

Specimens Examined: BRAZIL. Acre. Cruzeiro do Sul, s.d., D. C. *Daly 7638, 10907* (NY); s.d., D. J. M. *Maas 12867* (NY); Marechal Traumaturgo, 01 may 2001, *Daly 10807* (NY); Manoel Urbano- Parque Estadual Chandless, 26 nov 2010, *H. Medeiros 753* (RB); Santa Rosa dos Purús, s.d., *M Silveira 1461* (NY); Sena Madureira, 04 oct 1968, *Prance 7819* (INPA, NY); Tarauca, s.d., *Eringhaus 401* (NY), s.d., *C. Figueiredo 856* (NY).

Additional specimens: PERU. Huanuco: Huamalies, 2 nov 1938, *Stork 9565* (F). Junin: Puerto Bermudez, 14-17 jul 1929, *Killip 26635* (F). Loreto: Lower Rio Huallaga, oct-nov 1929, *Williams 5270* (F). San Martín: Fundo Correviento, 28 may 1964, *Schunke 6511* (F); Mariscal Caceres, Tocache Nuevo, 17 dec 1970, *Schunke 4576* (F); 8 jun 1970, *Schunke 4040* (F);

6. *Lycianthes compressibaccata* (Bitter) Costa-Silva & Agra comb. nov.

≡ *Solanum compressibaccatum* Bitter (1913 p. 456). *Syn. Nov.*

Type: PERU. Depto. Loreto: Cerro de Ponasa, 1200 m, Feb 1903, *E. Ule 6800* (B† =F photo 2560!; lectotype: HBG, barcode 511426 [photo!]; isolectotypes: CORD 4168 photo!, G! K 585774 [photo!]; MG 6634!). Designated by Costa-Silva and Agra (2018, in press).

= *Lycianthes leptocaulis* (Rusby) Rusby (1926: 210). *Syn. Nov.*

≡ *Brachistus leptocaulis* Rusby (1899:199). Type:— Bolivia, Depto. La Paz, Prov. Larecaja, Guanay, 2000 ft, Maio 1886, *H. Rusby 2657* (NY 138557!)

= *Brachistus actinocalyx* H.J.P.Winkler. (1909: 245). Type: — Bolivia, Depto. La Paz, Prov. Larecaja, Mapiri, Charopampa, 570 m, Nov 1907, *O. Buchtien 1432* (Isotypes NY 7510!, NY 7511!, US barcode 1175858!). Synonymized by Nee (2014).

= *Brachistus virgatus* H.J.P. Winkler (1909: 245). Type: — Bolivia, Depto. La Paz, Prov. Larecaja, San Carlos bei Mapiri, 750 m, Aug 1907, *O. Buchtien 1433* (Holotype: BRA. *n.v.* isotype: US 00027414 barcode 1133333!). Synonymized by Nee (2014).

= *Lycianthes actinocalyx* (H.J.P. Winkl.) Bitter (1919: 338). Based on *Brachistus actinocalyx* H.J.P. Winkl. Synonymized by Nee (2014).

= *Lycianthes acutangula* (Griseb.) Bitter ssp. *compressibaccata* (Bitter) Bitter (1919:358)

= *Lycianthes buchtienii* Bitter (1919: 337). Based on *Brachistus virgatus* H.J.P.Winkl. (1909:245). non *Lycianthes virgata* (Lam.) Bitter.

= *Lycianthes longidentata* Bitter (1919: 356). Type:—BRAZIL. Amazonas: Rio Acre, Estella, Seringal São Francisco, Mar 1911, *E. Ule* 9733 Holotype: B† =F photo 2582!; lectotype: NY 138711 [photo!]; isoelectotypes: K 585776 [photo!], L 2881557 [photo!], MG 273740! S 04-2937 [Photo!], U 113835 [photo!], US 1615237 [photo 27888!]. Synonymized by Nee (2014), and lectotype designed by Costa-Silva and Agra (2018).

=*Solanum actinocalyx* (H.J.P. Winkler) Hunz. (1969: 167). Synonymized by Nee (2014)

Liana branched,, perennial, 2.0—4.0 m high; branches branched, terete, glabrous, striate lengthwise. **Sympodial units** unifoliate. **Leaves** solitary, simple, petiole slightly grooved, short, 0.5—1.0 cm long, indument puberulent, trichomes simple, multicellular, uniseriate lamina membranaceous to chartaceous, 3.7—8.3 x 1.8—3.0 cm, concolor, elliptic to oblong-elliptic, adaxial and abaxial surface, glabrescent, trichomes simple, eglandular, multicellular, uniseriate on the midrib and secondary veins, sparse on the lamina, 6—8 veins, impressed on the adaxial surface, prominent on abaxial surface, apex acute or acuminate, margins slightly sinuate, base cuneate or oblique. **Inflorescence** indeterminate, fascicle axillary, sessile, 2—3—flowers. **Flowers** perfect, pentamerous, monoclinal, pedicel terete, 2.5—3.0 cm long, glabrescent, slender on the proximal portion, slightly enlarged near the calyx. **Calyx** campanulate, 2.6—2.8 x 1.0—1.5 cm, truncate, 10—appendages, emerging at 0.5—0.7 mm from the calyx apex, unequal in two series, the smaller ones 0.4—0.5 mm long, the bigger one 6.0—6.5 mm long, puberulent trichomes diminute, simple, multicellular, 2—4 celled, uniseriate. **Corolla** lilac to white, rotate, 1.6—3.0 cm diam., lobes oblong-elliptic, 1.5—0.7 cm long, puberulent at the apex, interpetalar tissue well-developed, glabrous, 0.6—0.7 cm wide. **Androecium** with 5 stamens, unequal, filaments unequal (1+4), one largest, 2.0—2.5 mm long, 4 smaller 0.6—0.8 mm long, anthers yellow, oblong, 3.2—3.9 mm long. **Gynoecium** with ovary ovoid, glabrous 0.8—1.2 mm diam., style glabrous, 5.0—5.2 mm long, stigma white, clavate, 0.5—1.0 mm long. **Fruit** a berry subglobose, 0.7—0.8 cm diam.; pedicel 2.0—2.5 cm long, slightly expanded from the 1/3 basal until the calyx; calyx accrescent, appendages enlarged, 0.8—2.0 cm long, explanate, somewhat arched or bent on herbarium samples. **Seeds** not seen.

Discussion:— *Solanum compressibaccatum* was proposed by Bitter (1913) and, according to the description in the protologue, it is a climbing plant, with geminate lanceolate leaves,

acuminate at the apex, calyx with unequal linear appendages, white corollas infundibuliform, five unequal stamens and globose berries. Bitter (1919) transferred it to *Lycianthes* and described it as *L. acutangula* subsp. *compressibaccata*. *Lycianthes acutangula* (Griseb.) Bitter was proposed having as basionym *Solanum acutangulum* Griseb., which, according to Article 32.1 and 38 of the Melbourne Code (MCNEILL ET AL., 2012) constitutes a nomen nudum, since it was not validly published, it was published without a description or diagnosis or a reference to an ancient taxon.

L. compressibaccata can be easily recognized by the showy corolla that varies between white to lilac, and by the appendages of the calyx that are considerably elongated. Samples from Peru and Bolivia can be confused with *Lycianthes acutangula*, which is a species with great morphological affinity, but it can be differentiated by the ovate leaves, more oblong corolla lobes, and interpetal tissue parted, giving a stellate appearance to the corolla, and to the ovoid fruit.

The analysis of the collection of *Ule 6800*, that corresponds to the type specimens of *S. compressibaccatum* and *Lycianthes acutangula* ssp. *compressibaccata*, showed leaves narrow-elliptic, acute or acuminate at the apex, rotaceous corollas, unequal stamens and globose berries that constitutes a set of characters similar to those also observed in the types specimens of *L. leptocaulis* (Rusby 2657). These evidences clearly showed that they are a single species, thus we propose the synonymization of *L. leptocaulis* under *L. compressibaccatum*.

Collections of *Lycianthes compressibaccata* and *L. stenoloba* are often mixed in Brazilian herbaria, probably because these two species have a very remarkable feature of elongated appendages, which are very similar in the dry material, and they are often used to attribute to one of these names. *L. compressibaccata* can be distinguished by its elliptic leaves, acute or acuminate at the apex, corolla somewhat campanulate with an interpetal tissue, and green appendages on the fruit calyx, while *L. stenoloba* has obovate leaves with a cuspidate apex, corolla rotata, and purple appendages on the fruit calyx.

Hocke et al. (2009) considered *Lycianthes acutangula* ssp. *compressibaccata* as a synonym of *L. stenoloba* (Van Heurck & Müll. Arg.) Bitter, however, we do not agree with this proposal. The analysis of types clearly revealed them to be two distinct species, whose morphological characters of the leaves and flowers are distinctive to separate these taxa, the white, somewhat campanulate corolla with an interpetal tissue in *S. compressibaccatum* is completely different of *L. stenoloba*, which presents the corolla rotata, clearly lobed without interpetalar tissue.

Phenology:— Flowers and fruits were observed from October to May.

Distribution and Habitat:— The distribution of *Lycianthes leptoculis* is concentrated in the Amazon region of Brazil, Bolivia and Peru (Fig. 6), usually found in areas of open vegetation. In Brazil, it is a common species in the states of Rondônia and Acre and can be found on forest edges, living in dry land or clay soils and anthropic environments, such as farms, pastures and in areas disturbed by mining activities.

Specimens Examined:— BRAZIL. Acre: Acrelândia, 6 oct 2003, *Acevedo-Rodriguez*, 13733 (RB), 09-15 nov 2006, *Obermuller* 94 (RB); Assis Brasil, 18 dec 2016, *Costa* 1041 (RB); Capichaba, *Acevedo-Rdgz* 13623 (RB); Rio Branco, Estrada Rio Branco- Brasileia, 03 oct 1980, *Lowrie* 363 (MG); Sena Madureira, Fazenda Nova Olinda, 21 oct 1993, *Silveira* 589 (INPA); Xapuri, 14 nov 2009, *Medeiros* 266 (RB); 02 nov 2011, *Medeiros* 861 (RB). Rondônia: Ariquemes, 10 may 1982, *Teixeira* 259 (MG); 11 may 1982, *Teixeira* 358 (RB); 25 apr 1987, *Nee* 35039 (INPA); Campo Novo, 25 apr 1987, *Nee* 35039 (RB); Costa Marques, 10 nov 1996, *Lobato* 1252 (MG); Massangana, Mineração Taboca, 10 oct 1979, *Zarucehi* 2661 (INPA, MG, RB); Mineração Campo Novo, 22 apr 1987, *Nee* 34966 (INPA); 14 oct 1979, *Vieira* 447 (INPA, MG); Mineração Taboca, 09 oct 1979, *Vieira* 334 (INPA, RB); Porto Velho, Estrada Porto Velho- Cuiabá, 12 feb 1983, *Teixeira* 1444 (MG); 25 oct 1997, *Lobato* 2219 (MG); São Lourenço, 27 nov 1968, *Prance* 8924 (INPA). PERU: Depto. Huánuco: Maquipaza, Schunke 1077 (G);

7. *Lycianthes glandulosa* (Ruiz & Pavón, 1799: 35) Bitter (1919: 348).

Type:— *Solanum glandulosum* Ruiz & Pavón. PERU. Departamento Junín: Prov. Chanchamayo, Vitoc, *H. Ruiz & J. Pavón s.n.* (lectotype: MA 747073 [photo!]; isolectotype F 843590 fragment- [photo!]). Lectotipified by Knapp (2008).

=*Solanum vitocense* Dunal (1852: 176). Type:— PERU, Departamento Junín: Prov. Chanchamayo, Vitoc, *J. Pavón* 39 (Holotype: G! barcode: 357865). Synonymized by Bitter (1919)

=*Solanum pseudolycoioides* Chodat & Hassler. (1903: 84), as “*pseudolyccoides*”. Type:— PARAGUAY. Sierra de Maracayú, Arroyo Mocoy, Oct. *E. Hassler* 4912 (Holotype: G! barcode G00229596; isotypes: BM 00074098 [photo!]; K 585756 [photo!], MO! 503606; NY! 172142; P! barcode 368685, 1902-0002874). Synonymized by Nee (2014).

=*Lycianthes hypomalaca* Bitter (1919: 344). Type:—BRASIL. Amazonas: Acregebiet, Estella, Seringal Auristella, Abr 1911, *E. Ule 9734* (Holotype: B 100248778 [photo!] isotypes G!, MG 14568!, US 1615226!, barcode 00027884). Synonymized by Nee (2014).

=*Lycianthes poeppigii* Bitter (1919: 345). Type:— PERU. Departamento. Loreto: Prov. Alto Amazonas, ["Maynas"], próximo a Yurimaguas, Abr., *E. Poeppig 2406* (Holotype: W *n.v.*; isotype P! barcode P00430724). *Sin. nov.*

=*Lycianthes pseudolycioides* (Chodat & Hassl.) Bitter (1919: 352). Type:— *Solanum pseudolycioides* Chodat & Hassl.

=*Solanum hypomalacum* (Bitter) C.V.Morton (1944.: 64). Type: based on *Lycianthes hypomalaca* Bitter.

= *Lycianthes australe* (C.V.Morton (1944: 62) Hunz. & Barboza (1992: 29). Type:— *Solanum australe* C.V.Morton, based on *Solanum pseudolycioides* Chodat & Hassl.

=*Solanum poeppigii* (Bitter) C.V.Morton (1944: 66). Type: **based on** *Lycianthes poeppigii* Bitter.

Shrub scandent, 2.0—6.0 m tall. Stem and branches teretes, ferruginous, indument stellate-pubescent, trichomes branched and stellate, short stalked, 3—5 lateral rays. **Sympodial units** unifoliate. **Leaves** alternate, false geminate in the upper branches; petiole 0.4—1.0 cm compr., terete, indument tomentose, similar to the branches; lamina cartaceous, 3.6—8.7 x 1.9—4.6 cm, discolour, ovate, oval-elliptic, anguste-ovate, dull, apex acute; margin entire to slightly crenate; surface adaxial surface with indument pubescent?, tomentose on the ribs, trichomes stellate, short stalked, 4—5 lateral rays, abaxial surface pubescent to tomentose, more compact than upper surface; trichomes branched and stellate similar to those of the adaxial surface; 8—10 lateral veins, impressed on the adaxial surface, slightly prominent on the abaxial surface. **Inflorescences** axilar, fascicles sessiles, 3—8 flowers; pedicel terete, pendent, 0.3—1.2 cm long, tomentoso-ferruginous, trichomes stellate similar to the branches. **Flowers** monoclinal, pentamers. **Calyx** cupuliform, 0.4 cm diam., tube 2.0—3.3 cm long, 10-appendages, unequal, rounded at the apex, emerging from the ¼ of the calyx apex, arranged in three series, a smaller series 2.0—2.4 mm long, one intermediate 3.0—3.7 mm long, and one longer, 5.0—8.0 mm long, glabrescent to pubescent, trichomes similar to the pedicel. **Corolla** campanulate, white, 2.0—2.5 cm diam., lobes lanceolate to elliptic-lanceolate, 1.0—1.3 cm long, puberulous externally, interpetal tissue glabrous, 5.6—6.0 mm,

linking the petals 1.5 mm below to the petalar apex. **Androceum** pentamerous, stamens unequal (1+4): one with the filament longer, 5.2—6.0 mm long; four shorter, 1.0—1.3 mm; anthers 5.7—6.0 mm long, attenuated to the apex, sagitate at the base. **Gineceum** with ovary subglobose, glabrous, 1.0—1.4 mm diam.; style 10.0 mm; stigma, somewhat bilobed, glandular, about 1.0 x 0.5 mm diam., dark green. **Fruit** globose, orange at maturity, 0.8—1.0 cm diam., calyx persistent and accrescent, 1.5—1.7 cm diam., appendages perpendicular to the fruit, apex slightly curved, 0.4—0.5 cm long; pedicel erect, terete, glabrescent trichomes stellate sessile. **Seeds** not seen.

Discussion:— *Lycianthes glandulosa* is characterized by the scandent habit, with false-geminated leaves on the apical branches, stellate trichomes, short stalks or sessile, inflorescences with 3—8 flowers, calyx pateliform-cupulate at the fruit with 10 unequal appendages, and rotate corolla. However, some collections of this species have been confused with *L. pauciflora* in some Brazilian herbaria, mainly due to the sympatric distribution in the Amazon region of Brazil. Thus, because they are both climbing plants with stellate trichomes, and have other similar characters, they are usually erroneously identified in the herbaria. However, *Lycianthes glandulosa* clearly differentiates from *L. pauciflora*, because it has broader leaves, more congested inflorescences, and the shortest and widest calyx appendages, besides being unequal, in more than two series, not reflections.

Distribution and habitat: — *Lycianthes glandulosa* occurs on forest edges, may inhabit dry land capoeiras or clay soils, disturbing environments and in secondary forests.

Phenology:— Flowered plants were observed from april to november, and frutified plants in May and December.

Ethnobotany:— There is no record of popular uses for *L. glandulosa* in Brazil. In Bolivia it is known by the indigenous name as “bimitsëxëjoni”.

Specimens Examined: BRAZIL. Acre: Brasiléia, Basin of Rio Acre, tribuary of Rio Purus, Colônia Santo Antônio, 21 oct 1997, *Daly 9674* (NY); Mâncio Lima, 8 nov 1991, *Cid Ferreira 10619* (NY); Porto Acre, 22 jun 1994, *Oliveira 274* (MO), Rio Branco, 5 jun 1991, *Daly 6850* (MO); 23 oct 1980, *Cid Ferreira 3020* (NY, RB); Tarauacá, 26 jun 2006, *Silveira 4076* (RB). Amapá: Mazagão, 19 set 1985, *Pires 631* (NY); Porto Terezinha, 20 nov 1954,

Cowan 38465 (NY). Amazonas: Embira, jun 1933, *Krukoff 4874* (MO); Humaitá, 14 sep-11 oct 1934, *Krukoff 6364* (MO). Maranhão: Vila Rondon, 09 aug 1976, Pinheiro 46 (IAN). Mato Grosso do Sul: Chapada dos Guimarães, 23 feb 1997, *Nave et al. 1176* (RB); Porto Murtinho, 14 nov 2002, *Hatschbach 74208* (NY). Pará: Ananideua, 21 nov 1957, Silva 469 (IAN); Parà: Rodovia Belém- Brasília km 90, 21 set 1959, *Kuhlman 266* (SP). Paraná: Lobato, 18 jul 1962, *Gomes e Matos 1189* (RB); Londrina, Mata do Godoy, *Favoretto s.n.* (RB), Fazenda Santa Helena, 04 sep 1986, *Paro 14* (RB), 15 may 1986, *Pizzaia 65* (RB); 20 jun 1985, *Rodas 10* (RB); Medianeira, 23 feb 1971, *Hatschbach 26482* (F); Parque Nacional do Iguazu, 12 may 1949, *Duarte 1758* (F); São Pedro do Ivaí, 15 oct 2003, *Ribas 5616* (RB), 19 dec 2003, *Ribas 5272* (RB). Rondônia: Chapada dos Parecis, 02 nov 1979, *Vieira 865* (INPA, MO); Vilhena, 02 nov 1979, *Vieira 865* (MO,NY).

Additional specimens: ARGENTINA. Misiones: Iguazu, Parque Nacional Iguazpu, 16 dec 1991, *Vanni 2885* (F). BOLÍVIA. Beni: Vaca Diez, 1 dec 1983, *Boom 4059* (F). Pando: Abuna, Rio Madeira, 19 nov 1968, Prance 8638 (F). Santa Cruz: Sercado, 29 aug 1925, *Steinbach 7194* (F). PARAGUAY. Alto Paraná: Estancia Rio bonito, 26 dec 1994, *Zardini 41758* (RB); Reserva Biológica, cerca del rio Itabó, 16 oct 1996, *Schinini 31473* (F). PERU. Huanuco: Divisoria, 14 sep 1946, *Woytkowski 34530* (F). Junin: between Puert Bermudez and Cahuapanas, 28—19 jul 1929, Killip 26709 (F). Loreto: Coronel Portillo, Iparia, 16 sep 1968, *Schunke 2785* (F); Gamitanacocha, 6 feb 1935, *Schunke 178* (F); Maynas, 20 jul 1968, *McDaniel 10718* (F), 20 oct 1976, *Revilla 1558* (F); Santa Rosa, 11 nov 1929, *Williams 4956* (F). San Martin: Chazutu, Rio Huallaga, mar 1935, *Klug 3991* (F).

8. *Lycianthes inaequilatera* (Rusby 1896:90) Bitter (1919:439)

≡ *Bassovia inaequilatera* Rusby (1896: 90). Type: — Bolívia, Depto. La Paz, Prov. Larecaja, entre Tipuani e Guanay, Dez 1892, *M. Bang 1708* (Lectotype: NY! 00138545, designated here; isolectotypes: NY! barcode 00138544; NY! barcode 00138546; A 76919 [photo!], BM 815915 [photo!], E 190709 [photo!], F 77804!, GH 77688 [photo!], M! barcode 0171840, MICH 1109881 [photo!], MO! 2495247, PH 30426 [photo!], US! barcode 1175833, W 1893-0005612 [photo!]).

= *Brachistus inaequilaterus* (Rusby 1896: 60) Rusby (1907: 470) Type: based on *Bassovia inaequilatera* Rusby.

= *Bassovia fendleri* Rusby (1899: 197). Type: — Bolivia, Depto. La Paz, Yungas, 6000 ft, 1885, *H. Rusby 770* (Lectotype: NY 138541!, designated here; isolectotypes: NY 138542! US 1416211!). Synonymized by Nee et al. (2014).

= *Brachistus fendleri* (Rusby) Rusby (1907: 210) Bull. New York Bot. Gard. 4: 470. 1907.
Based on *Bassovia fendleri* Rusby.

= *Lycianthes fendleri* (Rusby) Rusby, Bull. Torrey Bot. Club. 53: 210. 1926.

= *Brachistus subfalcatus* Rusby (1912:117) Type:— Bolivia, Depto. La Paz, Prov. Iturrealde, San Buenaventura, 1400 ft, 14 Nov 1901, R. S. Williams 660 (Holotype: NY! barcode 138563; isotype US! barcode 1175846). Synonymized by Nee et al. (2014).

= *Lycianthes subfalcata* (Rusby) Rusby (1927: 349).

Subshrub, erect, 1.0—2.0 m tall, perennial; branches flexuous, terete, in zigzag, green, striate, indument strigose, glabrescent in older branches; trichomes simple, eglandular, multicellular, unisseriate. **Sympodial units** difoliate, geminate, anisophyllous. **Leaves** geminate, simple; petiole terete, short, 0.5—0.8 cm long, indument strigose, trichomes similar to those of the branches; lamina entire, membranaceous to chartaceous, discolor, unbright, indument strigose, trichomes simples, multicellular, uniseriate, similar to those of the petiole, denser on the midrib, the main veins impressed on the adaxial surface, prominent on abaxial surface, the longer 16.5—20 x 4—6.5 cm, elliptic, anguste-elliptic to large-elliptic, 16—24 veins, the smaller 2.3—3.6 x 1.3—1.6 cm, ovate, 8—12 veins, acuminate at the apex, margin ciliate, base strongly oblique or obtuse, slightly decurrent to the petiole. **Inflorescences** indeterminate, fascicle axillary, sessile, 1—4-flowers. **Flowers** perfect, pentamerous, monoclinal; pedicel terete, erect, 2.0—3.0 cm long, indument strigose, trichomes similar to those of petiole. **Calyx** campanulate, 2.3—2.5 X 2.0—2.1 mm, indument and trichomes similar to those of petiole, 10-appendages, subulate, emerging from the calyx apex, sometimes inconspicuous, slightly unequal, 2.0—4.0 mm long. **Corolla** rotate, white, 0.8—0.9 x 0.9—1.0 cm, lobes lanceolate, 3.0—5.0 mm long, pubescent on the outter surface, trichomes simple eglandular. **Androecium** 5 stamens, equal, filaments 3.0—3.5 mm long; anthers yellow, anguste-elliptic, slightly attenuated to the apex, 2.5—3.0 mm long. **Gynoecium** with ovary ovoid, 1.0—1.1 x 0.5—0.6 mm; style glabrous, 6—6.5 mm long, stigma capitate, 0.8—1.0 mm long. **Fruit** a berry, red at maturity, subglobose, 0.4—1.0 cm in diameter, glabrous; pedicel erect, 0.6—1.5 cm long, slightly enlarged, pilose, trichomes simples, eglandular; calyx appendages erect, 2.0—3.0 mm long, slightly unequal, glabrous. **Seeds** not seen.

Discussion:— *Lycianthes inaequilatera* is characterized by its subshrub habit, with indument with simple trichomes, leaves geminate and anisophyllous, with asymmetric blades, calyx

with short appendages, sometimes inconspicuous in flower. This species was originally proposed by Rusby (1896) as belonging to the genus *Bassovia* and later transferred to *Lycianthes* by Bitter (1919).

The name *Bassovia fendleri* (Rusby) was given by Rusby (1899) to a shrub collected in Bolivia with simple trichomes and asymmetric leaves, which was later transferred to *Lycianthes* by Rusby (1926).

The other name given by Rusby (1912) was *Brachistus subfalcatius* for a plant also collected in Bolivia, which presents a shrub habit, indument strigose of simple trichomes. However when proposing *B. subfalcatius* as a new species, Rusby (1912) did not have access to flowered material and he described only the material with fruit, without reporting any features of the calyx appendages, later Rusby (1927) also proposed the transference of this name to *Lycianthes*. Both names, *B. fendleri* and *B. subfalcatius*, were listed by Nee (2014) as synonymous of *L. inaequilatera* in the Catalog of Vascular Plants of Bolivia. After analyzing the types of *B. fendleri* and *B. subfalcatius* deposited at NY and US herbaria, we agree with Nee (2014), since the types of both showed characters diagnostic to *L. inaequilatera*, such as the geminate leaves, with asymmetric blades, strigose indument of simple and adpressed trichomes, and also the calyx with short subulate appendages.

Lycianthes inaequilatera is morphologically similar to *L. amatitlanensis* with which it is often confused, but can be differentiated since *L. inaequilatera* has more branches in strongly zigzag, the calyx appendages are inconspicuous to diminute and glabrescent, and dull leaves. Differently from *L. amatitlanensis* that has erect branches, leaves glossy, longer and evident calyx appendages with pubescent indument.

Some authors like Brako & Zarucchi (1993) consider *L. amatitlanensis* as a synonym of *L. inaequilatera*, but when we analyzed Brazilian specimens, we could observe similar characters that were mentioned by Rojas and D'Arcy (1997) as a differentials for these two species and, therefore, also consider them as distinct taxa. For illustrations check Rojas and D'Arcy (1997).

Phenology:— Flowering and fruiting samples were collected from October to March.

Distribution and Habitat:— *L. inaequilatera* is a neotropical species with distribution exclusively in South America. Samples of this species were collected in Bolivia, Brazil Colombia and Venezuela.

In Brazil, this species is rare and was registered only for the State of Acre (Fig. 6), in the areas around the Purus River and its tributaries. It is common in wetlands near rivers, forest on steep slopes and in lowland or dry land forests, in poorly drained soils, usually prefers shaded areas, but may also occur in open canopy areas with still shaded understorey. It can also occur in edges of disturbed areas.

Examined Specimens:— BRASIL. Acre: Brasileia, Basin of Rio Purus, upper Rio Acre, Colônia Santo Antônio, 29 Mar 1998, *Daly 9875* (NY); Marechal Taumaturgo, Reserva extrativista do Alto Juruá, Rio Juruá, right Bank, 6 Apr 1993, *Daly 7802* (NY); Manoel Urbano, Rio Purus, Seringal Terra Nova, Colocação Terra Nova, 23 nov 1996, *Daly 9111* (NY); Santa Rosa, Rio/Igarapé Santa Rosa, tributary of Rio Purus, 15 mar 2002, *Daly 11374* (MO, NY) Sena Madureira, Basin of Rio Purus, Rio Macauã, Colocação Apuí, 29 mar 1994, *Daly 8070* (MO, NY), Rio Macauã, Colocação Cala Boca, 29 mar 1994, *Lima 505* (NY), Basin of Rio Purus, Rio Iaco, right bank, nova Olinda, 25 oct 1993, *Daly 7919* (NY).

Additional specimens: — PERU. Madre de Dios: Manu, PARque Nacional Manu, 8 oct 196, *Foster 11688* (F). San Martín: Mariscal Cáceres, Tocache Nuevo, 14 dec 1981, *Plowman 11390* (F). San Martín, 23 sep 1986, *Knapp 8376* (MO). VENEZUELA. Sucre: Peninsula de Paria, 17 oct 1984, *Knapp 6766* (F).

9. *Lycianthes pauciflora* (Vahl) Bitter (1919: 341).

≡ *Solanum pauciflorum* Vahl (1796:20). Type:— Martinique, *sine col.*, s.n. (Holotype: C 10019191!).

= *Solanum geminatum* Vahl (1796: 21). Type: — French Guiana, Cayenne, *J. von Rohr s.n.* (Holotype: C LNR-6059 *n.v.*; Isotypes: BM 601927-S [photo!]).

= *Solanum speciosum* Dunal (1813:179). Syntypes: West Indies, based on Burm. Plant Amer. p. 242, tab. 245, fig. 5; Plum. cat. p. 4; Tourn. Inst. 150. Synonymized by Bitter (1919).

= *Solanum sylvaticum* Dunal (1816:24). Type: Venezuela, Edo. Sucre, Cumaná, 1799–1880, *A. Humboldt & A. Bonpland s.n.* (Holotype: P!). Synonymized by Hokche (2008).

= *Lycianthes speciosa* (Dunal) Lourteig (1987:442).

= *Solanum guianense* Dunal (1852:166). Type:— French Guiana, Caiena, *J. Aublet s.n.* (Holotype: GDC 00145624!; Isotype: P 385034!)

= *Solanum neglectum* Bert. ex Dunal, in A. DC., Prodr. 13(1): 170. 1852. Pro syn. *S. sylvaticum* HBK. Cited: Colombia Prov. Santa Martha, *C. Bertero s.n.* (GDC!).

- = *Brachistus hispidus* Rusby (1899: 198). Type: — Bolivia, Depto. La Paz, Prov. Iturralde, Guanay, May 1886, 2000 ft, H. *Rusby 2524* (Holotype NY 138556!) Synonymized by Nee (2014)
- = *Solanum japurense* Dunal (1852: 174). Type:— Brazil, Est. Amazonas, Rio Negro, Japurá, C. *Martius s.n.* (M!). Synonymized by Rojas & D’Arcy (1997)
- = *Lycianthes guianensis* (Dunal) Bitter (1919: 347). Type:— *Solanum guianense* Dunal
- = *Lycianthes japurensis* (Dunal) Bitter (1919: 350). Type:— *Solanum japurense* Dunal
- = *Lycianthes pearcei* Bitter (1919: 355). Type: — Bolivia, Corico [likely Depto. La Paz, Prov. Nor Yungas, Coroico], 700–900 m, Jan 1866, R. *Pearce s.n.* (Holotype: BM 815942 [photo!]). Synonymized by Nee (2014).
- = *Lycianthes geminata* (Vahl) Bitter (1919: 392). Type:— *Solanum geminatum* Vahl.
- = *Lycianthes hispida* (Rusby) Rusby (1926: 210). Type:— *Brachistus hispidus* Rusby
- = *Lycianthes tomentella* Rusby (1926: 211). Type:— Bolivia, Depto. La Paz, Yungas, M. Bang 630 (Holotype NY 138718! ex Col. Coll. or NY 138717! ex Coll. Pharm.; isotypes E 190708 [photo!], GH 77122 [photo!], PH 16315 [photo!], US 1324774 barcode 27897 [photo!], US 98923 barcode 1102013 [photo!]).
- = *Lycianthes pyrifolia* Rusby (1919: 212). Type: Bolivia, Depto. Cochabamba, near Cochabamba, Espíritu Santo, 750 m, Jun 1909, O. *Buchtien 2816* (Holotype NY 138713!) Synonymized by Nee (2014).
- = *Solanum caucaense* (Bitter) C.V.Morton var. *glabrescens* C.V.Morton, Contrib. U.S. Natl. Herb. 29: 58. 1944. Type: Colombia, Depto. Chocó, Tutunendo, 80 m, 19–20 May 1931, W. *Archer 2132* (Holotype US 1519156!). Synonymized by Hokche (2008).
- = *Solanum luxurians* C.V.Morton (1944: 66). Type:— *Lycianthes pearcei* Bitter.
- = *Lycianthes dominicana* C.V.Morton & Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1057. 1938. Type: — Costa Rica, Santo Domingo de Vara Blanca, 2200 m, Feb 1937, M. *Valerio 1550* (Holotype: F 258219 [photo!]). Synonymized by Bohs (2015).

Shrubs scandent, 1.0–5.0 m tall, branched, perennial; branches and stems terete, brown, striate, indument stellate-puberulous, yellowish to ferruginous, trichomes stellate, sessile and short stalked, 3–6 lateral rays, many-celled, and trichomes simples, eglandular, multicellular, uniseriate, hyaline. **Sympodial units** unifoliate. **Leaves** simples; petiole short, 1.0–2.5 cm long, terete, pubescent to tomentose, ferruginous, trichomes stellate similar to those of branches; lamina chartaceous, 5.0–12.0 x 3.5–5.0 cm, weakly discolor, ovate to large-

elliptic, adaxial surface somewhat glossy, sparse-stellate, trichomes stellate mainly on the midrib, abaxial surface stellate-velutinous to stellate-tomentose, trichomes stellate, stalked, stalk 2—3 celled; 8—12 secondary veins, impressed on the adaxial surface, prominent on abaxial surface; apex acute, acuminate or obtuse, margin entire, base cuneate, rounded. **Inflorescence** indeterminate, fascicle, axillary, sessile, 2—5—flowered. **Flowers** perfect, pentamerous, monoclinal; pedicel, 1.0—2.5 cm long, erect at maturity, terete, stellate-pubescent to tomentose, trichomes stellate-stalked, yellowish to ferruginous. **Calyx** campanulate, sinuate at the apex, tube 4.0—4.8 mm long, 10-appendages emerging at the basal 2/3 of the calyx, about 1.4 to 1.6 mm below the apex, slightly unequal, 1.5—1.7 mm long, glabrescent, trichomes similar to those of the pedicel; **Corolla** rotate, white, 1.3—3.5 cm diam., lobes lanceolate, 1.2—1.3 cm, pilose on the outer surface, well-developed glabrous interpetalar tissue, 0.9—1.0 cm. **Androecium** 5-stamens, unequal (1 + 4): one largest, filaments 5.8—6.0 mm long, 4 smaller ones with short filaments 1.0—1.2 mm long, anthers yellow, attenuate from the base to the apex, 5.0—5.3 mm long, sagitate to sub-sagitate at the base, pores extrorse. **Gynoecium** ovary globose, glabrous, 2.2—2.5 mm diam.; style glabrous 1.0—1.1 cm length, straight, slightly curved to the apex, stigma slightly bilobed, 0.7—1.0 mm long, bright green. **Fruit** globose, upright, 1.5–2.5 cm in diameter, glabrous, red when ripe, green to yellow-green when young, drying brownish; calyx accrescent and detached from the fruit, calyx appendages reflexed, slightly unequal, 0.4—1.0 cm long, stellate-pubescent; *Seeds* numerous, 2.6—3.6 x 2.8—3.3 mm, obovoid, compressed, testa reticulate, beige.

Discussion: — *Lycianthes pauciflora* has a wide range of distribution and its vegetative characters usually vary according to the environment, generating different morphotypes and causing diverse misidentifications in Brazilian herbaria. In this work, all specimens resembling the type of *Solanum pauciflorum* (*sin. col.*, *s.n.*-C 10019191) are combined: lianas, corolla white, calyx with 10 slightly unequal appendages, glabrous or pubescent, tending to expand and become reflexed in the fruit.

Lycianthes pauciflora was described in literature three times, besides the description of its protologue and the protologue of *Solanum pauciflorum*. D'Arcy (1973) described this species for the Flora of Panama under the name *L. guianensis*, highlighting the glabrous leaves and calyx, and the unequal stamens. Rojas & D'Arcy (1997) emphasize the observed pubescence variation, being dense and rusty in fruitful branches, with the appendages of the calyx becoming reflexed or not in the fruit, and the edge of the calyx tube reflexed or plicate,

in the specimens collected in Venezuela . Although this same general pattern is observed in Brazilian specimens, the calyx appendages represented in illustrations of Rojas & D'Arcy (1997) do not correspond to those presented by *L. pauciflora* in Brazil. Bohs (2015) emphasizes the stellate and multiangulated trichomes, unequal stamens, globose fruits to ellipsoids which also corresponds to the characteristics observed in the Brazilian specimens.

Distribution and Habitat:— Species with wide distribution, occurring from Guatemala to Argentina (Fig. 6). In Brazil it occurs in the Amazon, Atlantic Forest and there are records for the Pantanal, in Mato Grosso do Sul state. There are no records of occurrence for the driest regions of Brazil such as the Cerrado and the Caatinga, being a species that prefers humid environments. In the northeast region, it was found in forests of altitude, occurring at elevations of 800 to 1050 m in Bahia State.

Phenology:— Flowering samples were collected from may to December, fruiting samples from July to February.

Ethnobotany: — Popularly known as “Joá” in Amapa state (*Pires 631*)

Specimens Examined:— BRAZIL. **Acre:** Aldeota, between Porangaba and Papagaio, Rio Juruá-Mirim, 18 may 1973, *Mass P13100* (INPA); Cruzeiro do Sul, Vicinity of Serra da Moa, *Prance 12381* (INPA); Rio Branco, estrada para Sena Madureira km 40, 23 oct 1980, *Cid 3020* (INPA). **Amapá:** Clevelandia, 2 aug 1960, *Westra 47301* (NY); Macapá, 3 jan 1985, *Daly 4036* (NY); Mazagão, Morros do Felipe, 10 oct 1987, *Beck 33* (INPA, MG, NY), 19 sep 1985, *Pires-O'Brien 631* (NY); Serra do navio, 01 nov 1954, *Cowan 38101* (NY); 20 nov 1954, *Cowan 38465* (NY). **Amazonas:** Lago do castanho-Mirim, 27 jun 1973, *Albuquerque 904* (INPA); Tabatinga, El Marco, north of Leticia-Tabatinga, 24 jul 1973, *Prance 16856* (INPA); Tefé, 17 jul 1991, *Tavares 405* (RB, INPA). **Bahia:** Itacaré, 29 jan 1977, *Harley 18366* (RB); Esplanada, algodão, 12°10'S 37°58'0"W, *Popovkin 1448* (HUEFS); Igrapiúna, Assentamento Mirante, próximo a comunidade de Pedra Branca, 22 may 2007, *Nunes 1793* (HUEFS); Ilhéus, 12 feb 2014, *Amorim 8458* (CEPEC, NY, RB); Santa Terezinha, Serra da Jibóia, 12°51'17''S 39°28'30''W, 5 jun 1999, *França et al. 2976*; 31 mar 2001, *Silva 523* (HUEFS); 12°50'S 39°28'W, 14 apr 2001, *Ribeiro-Filho 191* (HUEFS); Ubaitaba 24 nov 2010, *Daneu 463* (CEPEC, RB); Uruçuca, Parque Estadual Serra do Conduru, 21 apr 2000, *Jardim 2961* (CEPEC); Wenceslau Guimarães, 15 may 1992, *Thomas 9330* (CEPEC, NY, RB). **Mato Grosso:** Aripuanã, 19 jan 1977, *Gomes 503* (INPA). **Minas Gerais:** Marliéria, Parque Estadual do Rio Doce, 06 dec 1996, *Lombardi 1505* (BHCB). **Pará:** Belém, 18 dec

1942, *Archer 8001* (NY); Oriximiná, 4 jun 1980, *Martinelli 6778* (NY); Paragominas, Itinga do Pará, Fazenda Caboré, 01 dec 1979, *Maciel 400* (INPA); Parque Indígena do Tumucumaque, 25 feb 1970, *Cavalcante 2516* (NY); Serra dos Carajás, 8-12 de 1981, *Daly 1964* (INPA); Tapajós, sep 1931, *Krukoff 1182* (NY). **Paraná:** Londrina, 23 jan 2013, *Kassner-Filho 6* (FURB), Fazenda Santa Helena, 15 may 1986, *Pizzaia 65* (RB). **Rondônia:** Vilhena, 02 nov 1979, *Vieira 865* (RB). **Roraima:** Waimari-Atoari Indian Reserve, 16 nov 1977, *Steward 15* (INPA).

Additional specimens: VENEZUELA. Bolívar: sin. loc., 5-8 feb 1961, *Steyermark 89040* (RB)

10. *Lycianthes rantonnetii* (Carrière) Bitter (1919: 332).

≡ *Solanum rantonnetii* Carrière (1859:135) Type— Cultivated at France, Dept. Var, Hyères, by *Rantonnet s.n.*, the seeds from Argentina, prob. Prov. Buenos Aires, Río de la Plata. [Annotation: as "Rantonnei"] (Lectotype: P! P05107112).

= *Solanum corniculatum* Hiern, (187778: 45). Type: —Brazil, *A. Glaziou 1078* (Holotype: C *n.v.*; isotype BR barcode BR0000005522347 [photo!]). Synonymized by Bitter (1919).

= *Solanum muticum* N.E.Br. (1894: 6). Type:— Cultivated in Uruguay, Depto. Montevideo, Montevideo, originally from Paraguay, *Gibert 56* (Lectotype: K barcode K000585755 [photo!], **designated here**; syntype: *Gibert 641 n.v.*). Synonymized by Bitter (1919).

= *Solanum urbanum* Morong (1893:177). Type:— Paraguay, Asunción, *T. Morong 147* (Lectotype: NY 172225! **Designated here**, isolectotypes: MO 2495263!; PH *n.v.*, US 1324871!, WIS *n.v.*); Syntypes: Asunción, *T. Morong 708* (MO *n.v.*, NY 172226!).

Shrubs scandent, 1.0—2.0 m alt., branched, perennial; branches terete, glabrescent, trichomes glandular, branched, bifurcate. **Symphodial units** plurifoliate. **Leaves** solitaires; petiole 1.2—3.0 cm long, slightly grooved, pubescent, trichomes similar to those of the branches; lamina chartaceous, ovate to anguste-ovate, 3.0—9.0 x 1.3—4.6 cm, discolor, adaxial surface sparsely pilose, trichomes simples, eglandular, brached, bifurcate, abaxial surface pilose, trichomes similiar to those of the adaxial surface, compact on the veins, base cuneate, oblique or acute, margin entire to slightly sinuate, apex acute. **Inflorescence** indeterminate, fascicle axillary, 4—6 flowered. Flowers perfect, pentamerous, monoclinal; pedicel terete, 1.8—3.0 cm long, pubescent, trichomes similar to those of the branches. **Calyx** campanulate, 3.0—4.0 cm long, pubescent, trichomes branched, bifurcate, 10—appendages, linear, emerging from the edge of the calyx tube, unequal, in two series, the largest ones 3.0—4.0 mm long, the shorter 2.0—2.5 mm long, green. **Corolla** rotate, purple to deeple blue,

2.0—2.5 cm diam., lobes lanceolate, interpetal tissue plicate. **Androecium** with 5-stamens, unequal filaments, (2+3), 2—largest, 1.3—0.3 cm long, 3—shorter, 0.2—0.3 cm long; anthers yellow, oblong, 0.3—0.4 cm long. **Gynoecium** with ovary ovoid, glabrous, 1.8—2.0 mm; style terete, glabrous, 1.4—1.6 mm; stigma capitate, slightly bilobed, 0.45—0.5 mm long. **Fruit** a berry, globose, 0.8—1.0 cm diam., yellow to orange, pedicel enlarged, calyx accrescent, pateliform, glabrous. **Seeds** not seen.

Discussion: —*Lycianthes rantonnetii* can be easily distinguished among Brazilian specimens of *Lycianthes* by its branched and bifurcate trichomes, the corolla large rotata, up to 2.5 cm diam., purple to deep blue evidencing the five unequal (3+2) yellow anthers, and by the orange fruit. It is close related to *L. fasciculata*, a species from Bolivia, Paraguay and Argentina, that differs from *L. rantonnetii* by having white corolla, shorter anthers and bilabiate stigma (BARBOZA; HUNZINKER, 1992).

Lycianthes rantonnetii was proposed by Carrière (1859) based on material cultivated at the P, from seeds that came from Argentina near the River La Plata area. Later, Lescuyer (1859) described this species using the spelling *L. rantonnetti*, but didn't explained the reasons for changing the orthography. This misspelling was also adopted by Bitter (1919), when transferring this name to *Lycianthes*. Barbosa & Hunzinker (1992), treating the genus for Argentina, describe this species using the spelling of Carrière (1859). However, according to International Code of Nomenclature of algae, fungi and plants, Art 60.7, ex. 17, the name is correctly cited as *L. rantonnetii*.

On the prologue of this species, no specimen was cited as holotype. The specimen at P (P05107112) is an specimen that was collected at the gardens of P, in the same year of the publication of *L. rantonnetii* and, thus, we are designating it as lectotype for this name, following the article 9.11 of the International Code of nomenclature for algae, fungi and plants.

Solanum muticum is a name proposed by Brown (1894) based on material cultivated in Uruguay and originally from Paraguay. The author cited two collections in the prologue of *S. muticum*, *Gibert 56*, deposited at K, and *Gibert 641*, which, although we have searched heavily, we could not locate it. The collection of *Gibert 65*, deposited at K is very well preserved, with many flower and fruit, which led us to choose it as lectotype of *Solanum muticum*.

The name of *Solanum urbanum* was proposed by Morong (1893) based on material from Paraguay, he cited two specimens collected in Assuncion by *Morong 147* and *708*. We

analyzed specimens of these collection deposited at MO, NY, PH and US, and we chose to designate as lectotype of *S. urbanum* the specimen of *Morong 174*, deposited at NY (172225), which is a well preserved type material, with many flowers.

Phenology: — Flowers and fruits were observed from January to October.

Ethnobotany:— *L. rantonnetii* is a species with potencial economic importance, once it is commonly used as ornamental due its showy inflorescences with purple corollas.

Distribution and Habitat: — *Lycianthes rantonnetii* occurs in Paraguay, Argentina and South and Southeast of Brazil. There are also registers of occurrence in the Mato Grosso do Sul state. It can be found in disturbed areas, forest edges, roadsides, calcareous or humid soils.

Specimens Examined: BRAZIL. Mato Grosso Do Sul: Bonito, 15 nov 2002, *Hatschbach 10765* (BHCB). Minas Gerais: Brejo do Amparo, 10 nov 1989, *Ratter 6408* (RB); Januária on road to serra das Araras, 19 apr 1973, *Anderson 9186* (RB); sem local, 1 jan 1816, *Saint-Hilaire s.n.* (P). Paraná: Foz do Iguaçu, Rio Ocu, s.d., *Hatschbach 23160* (RB,F); Londrina, 02 oct 1986, *Perri s.n.* (RB), 08 mar 2004, *Lovato 494* (HUEF); Medianeira, Missal, 09 feb 1969, *Hatschbach 21102* (RB); Parque nacional do Iguaçu, 12 may 1949, *Duarte 1758* (RB), 20 feb 1960, *Pereira 5387* (F, RB); 14 may 1949, *Duarte 1817* (RB); 20 feb 1960, *E. Pereira 5387* (RB). Rio de Janeiro: Rio de Janeiro, Arboreto do Jardim botânico, 05 may 1997, *Freitas 002* (RB); Gaya, Mafra, 26 nov 1989, *Carvalho s.n.* (RB).

Additional specimens: ARGENTINA: Candelaria: Misiones, 20 jan 1993, *Schinini 27592* (F). Capital: Corrientes, 6 mar 1992, *Krapovickas 44061* (F). PARAGUAY. Guairá: Villarica, *Jogersen 3670* (F); Misiones: Yacyreta, 7 dec 2002, *Zardini 59429* (RB).

11. *Lycianthes repens* (Spreng.) Bitter (1919: 425).

≡ *Boldoa repens* Spreng. (1824: 179). Type: Brazil [between Rio de Janeiro and Bahia], *F. Sellow [1545]* (B†)

= *Solanum violifolium* Schott, in Sprengel (1827: 403) as “violae-folium”. Type: Brazil, H. Schott *s.n.* (Holotype :W! “5407”).

Herb creeping, stoloniferous; branches terete, green, indument pilose, trichomes simples multicellular, eglandular. **Sympodial units** plurifoliate, geminate. Leaves geminate,

anisophyllous, petiole 1.5—4.0 cm long, pubescent, simple multicelular uniseriate trichomes; lamina chartaceous, 0.8—3.0 x 1.5—4.0 cm, weakly discolor, reniform, orbicular, rounded to obtuse at the apex, margins entire, base cordate, adaxial surface pubescent, trichomes similar to those on the petioles, adaxial surface pubescent trichomes simple eglandular, 6—10 secondary veins, impressed on the adaxial surface, prominent on abaxial surface, **Inflorescences** sessile, 1—flowered. Flower solitary, perfect, pentamerous, monoclinal; pedicel pubescent, 2.0—3.8 cm long., curved at the apex; **Calyx** campanulate, 2.0—3.2 cm long., with 10 conspicuous appendages, in two series, 1.0—2.0 mm long, glabrous??. **Corolla** campanulate, lilac to purple, 0.8—1.1 cm diam, lobes elliptic, interpetalar tissue well-developed, glabrous. **Androecium** with 5 stamens, filament equal, 0.8—1.0 mm long, glabrous, anthers oblong, 2.0—3.0 mm long; **Gynoecium** with ovary conic, 1.0— 1.5 mm diam., glabrous; style glabrous, 3.0—5.0 mm long; stigma capitate . **Fruit** a berry, glabrous, 1.0—1.2 cm diam., calyx accrescent at the median portion; appendages. **Seeds** not seen.

Discussion:— Sendtner (1846), in his treatment for the Flora Brasiliensis, described *Solanum violifolium* with geminate , purple corolla, and the calyx accrescent to the half of the fruit, and also about the indument pilose of plant, a set of characters also observed and included in the description of this species by Bitter (1919), when transferring it to *Lycianthes*.

Bitter (1919) proposed a new combination for the name *Boldoa repens* and referred *Solanum violifolium* Schott as its synonym. Unfortunately, the protologue of *Solanum violifolium* Sprengel (1827: 403) could not be found, and thus we could not locate and analyze its type. However, we had access to the material examined and cited by Bitter (1919): *Pohl 5407* (F), *Warming s.n.* (NY), *Dúsen 3216, 11315* (F), and also to the collection of *Sellow s.n.* (W) that was identified and has a handwritten annotation by Bitter. All this specimens present the characteristics cited as differential for *L. repens*. We also analyzed material from M, HUEFS, and SPF, with pubescence and an accrescent calyx.

In addition, *L. repens* has been synonymized with *L. asarifolia* (Kunth & Bouché) Bitter, whose distinguishing characters are clear and distinctive, and are already described in detail in this work, in the treatment of *L. asarifolia*.

Distribution, habitat and ecology:— It is an unusual species, endemic to Brazil, that occurs from Bahia to Paraná in preserved areas of Atlantic Forest (Fig. 8).

Phenology:— Flower and fruit were observed from December to February

Ethnobotany:— Unknown.

Specimens Examined —: BRAZIL. Bahia: Itacaré, feb 1920, *Riedel s.n.* (NY). Minas Gerais: Cerro Azul, Cabeceiras do Ribeirão do Tigre, 7 dec 1994, *Hatscbach 61463* (HUEFS, M); Lagoa Santa, s.d., *Warming s.n.* (NY); Matozinhos, 2 dec 2006, *Ceccantini 3027* (SPF); “provincia Minarum”, sin. Loc., *Martius s.n.* (MO). Paraná: Prudentópolis, 06 feb 1911, *Dusén 11315* (F). *sine locci, s.d. Pohl 5407* (F).

12. *Lycianthes stenoloba* (Van Heurck & Muell. Arg.) Bitter (1919: 358).

≡*Solanum stenolobum* Van Heurck & Muell. Arg., in Van Heurck (1870: 69). Type: — Peru, Depto. San Martín, Prov. San Martín, Tarapoto, 1855–1856, *R. Spruce 4210* (Lectotype GDC!, **designated here**; isoelectotypes BR 522204 [photo!], E barcode E00205022 [photo!], K barcode K000201929 [photo], K000201930 [photo!]!, NY! 172186)

=*Bassovia stenoloba* (Van Heurck & Muell. Arg.) Britton ex Rusby, (1895: 232). Based on *Solanum stenolobum* Van Heurck & Muell. Arg.

Shrub scandent, 2.0—4.0 m height, branched, perennial; branches terete, green, glabrous to puberulent, trichomes simple, eglandular, multicelular, uniseriate. **Symphodial units** difoliate geminate, anisophyllous, unifoliate on proximal branches. **Leaves** simple; petiole short, 0.4—1.0 cm long, slightly grooved, puberulent, trichomes similar to those on the branches; lamina chartaceous, obovate, the largest ones 7.5—14.0 x 3.4—5.5 cm, the smaller 3.0—7.5 x 2.5—3.5 cm, discolour, adaxial and abaxial surfaces sparse pilose, trichomes simples, multicellular, setose, concentrated on the main veins; base cuneate, margins entire, apex cuspidate or acuminate; 10—16 veins, impressed on the adaxial surface, prominent on abaxial surface. **Inflorescences** indeterminate, fascicle axillary, sessile, 1—6 flowers. **Flowers** perfect, pentamerous, monoclinal; pedicel erect, terete, 1.5—3.0 cm long, glabrous. **Calyx** campanulate, 0.5—0.8 cm long, glabrous, 10-appendages, unequal, in two series, the largest ones 0.4—0.5 cm compr., the shorter 0.2—0.35 cm long, Green. **Corolla** stellate, white, 1.0—1.5 X 1.0—2.5 cm, lobes anguste-elliptic, 0.5—0.8 x 0.5—1.0, glabrous; **Androecium** with 5-stamens, equal; filaments 1.0—2.0 cm long; anthers yellow, attenuate from the base to the apex, 0.4—0.6 cm long; **Gynoecium** with ovary ovoid to conical, glabrous, 0.18—0.2 x 1.4—1.54 mm, style glabrous, 1.0—1.2 cm long; stigma capitate, about 1.0 mm diam., slightly bilobed. **Fruit** a berry, ovoid, Orange at maturity, calyx cupulate, appendages purple, unequal, the smaller 0.5—1.0 cm long, the largest 0.9—2.0 cm long, with broadened base,

attenuating to the apex, somewhat linear, glabrous; pedicel 2.3— 2.7 cm long, glabrous. **Seeds** not seen.

Discussion:— *L. stenoloba* can be easily identified through the corolla with parted lobes conferring its stellate aspect, the morphology of the calyx with linear appendages, which extend during development, reaching up to 2 cm, and acquire purple color, and by ovoid fruit (F.

Rojas & D'Arcy (1997) listed the names *L. acutangula* Bitter, *L. acutangula* subsp *compressibaccata* and *L. longidentata* as synonyms of *L. stenoloba*. However, after analysis of their types, we conclude that these are different species. In the present work, we agree with the synonymization performed by Nee (2014) that proposes *L. longidentata* as a synonym for *L. leptocaulis*.

The corolla in these three species is somewhat campanulate that have a well-developed interpetal membrane that give to corolla a round appearance, the calyx appendages of the fruit are green and linear, besides the fruits being globose berries, and the branches are pilose, so they are distinct species, and they can not be considered as synonyms with *L. stenoloba*.

When van Heurck proposed *Solanum stenolobum*, he cited two specimens of the same collection (*Spruce 4210*), one at BR and the other at G-DC, however, he didn't specified a holotype. Thus, we propose the exsicata deposited at G-DC as a lectotype since it is the most preserved specimen and presents well developed leaves, buds, flowers and fruit.

Heurck (1870) proposed *Solanum stenolobum* as a new species, and he mentioned two specimens of the same collection (*Spruce 4210*), one deposited at BR and the other at G-DC, however, he didn't specified a holotype, which clearly evidences the need to designate a lectotype. Thus, after analysis of the material at G-DC and also BR we found that the specimen of G-DC, besides being quoted in the protologue, it is in excellent condition, and also has flower buds, flowers and fruits, unlike the BR specimen that has only a few flowers. In view of the above, we designate here the specimen of G-DC as the lectotype of *L. stenoloba*.

Phenology:— Flowers and fruits were observed from October to February.

Distribution and Habitat:— *L. stenoloba* occurs in wetlands in the riverbeds of Peru, Venezuela and Brazil, where the records of its occurrence are only for the States of Acre and Amapá, Brazilian Amazonia (Fig. 8).

Specimens Examined:— BRAZIL. Acre: Bujari, Bacia do Rio Purus, 27 dec 2015, *D. S. Costa et al.* 704 (RB); Jordão, 05 feb 2009, *Michelangeli et al.* 1286 (RB); Porvir, 15 nov 1923, *Kuhlmann* 822 (RB); Rio Branco, 10 oct 1980, *Lowrie et al.* 465 (RB); Santa Rosa, Rio Chambuiacu, 13 mar 2002, *Daly* 11313 (NY). Amapá: Mazagão, Morro do Felipe, 01 oct 1986, *Pires* 1398 (INPA).

Additional specimens: PERU. Depto Loreto: Tarapoto, Dec 1902, *Ule* 6873, 6751 (G

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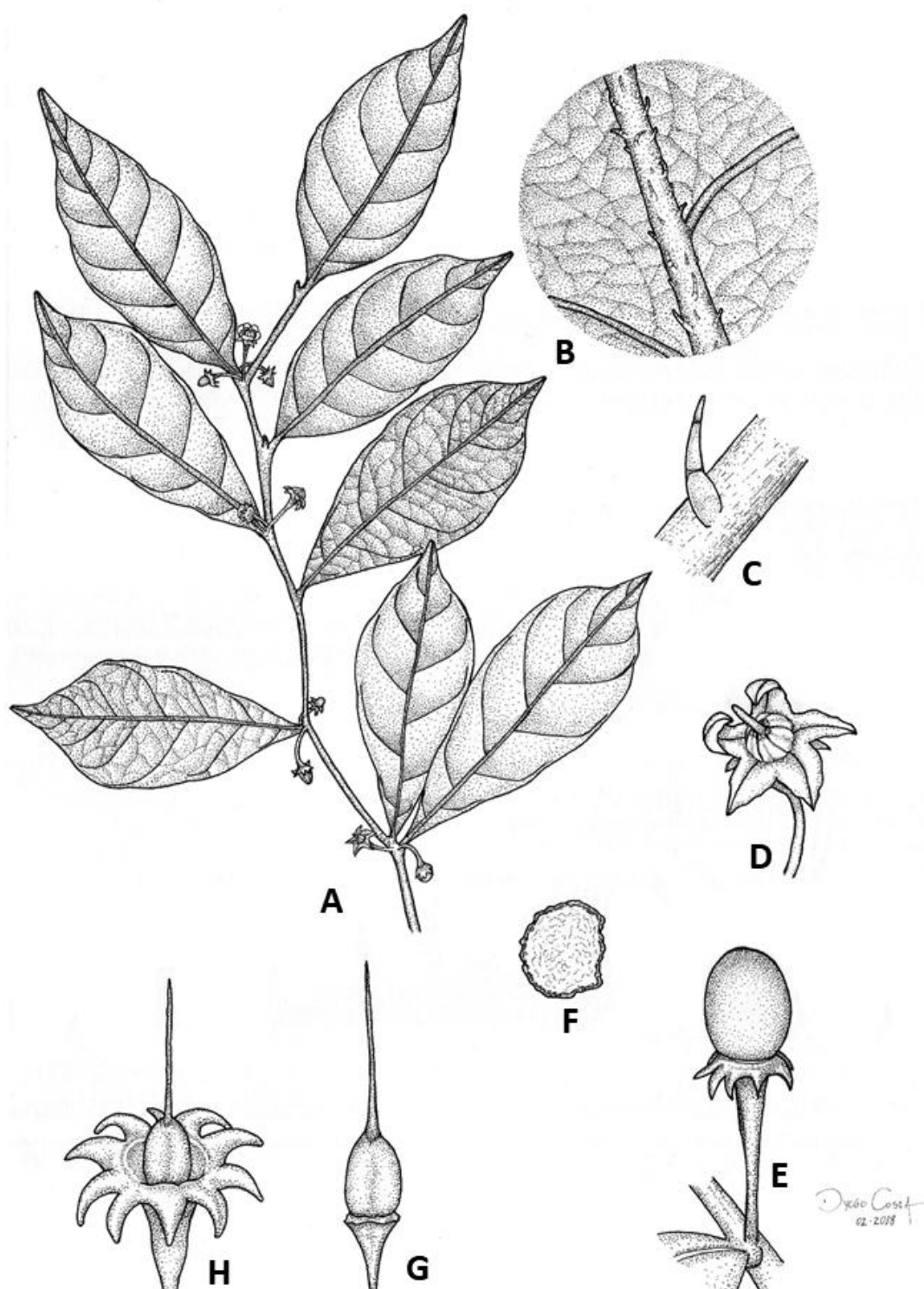


Figura 1. *Lycianthes coffeifolia* Bitter: **A.** Flowering and Fruiting branch. **B.** Details of the indument on the main vein of the blade. **C.** Detail of simple eglandular trichome. **D.** Detail of the flower. **E.** Detail of fruit. **F.** Detail of seed. **G.** Detail of the gynoecium. **H.** Detail of calyx and gynoecium.

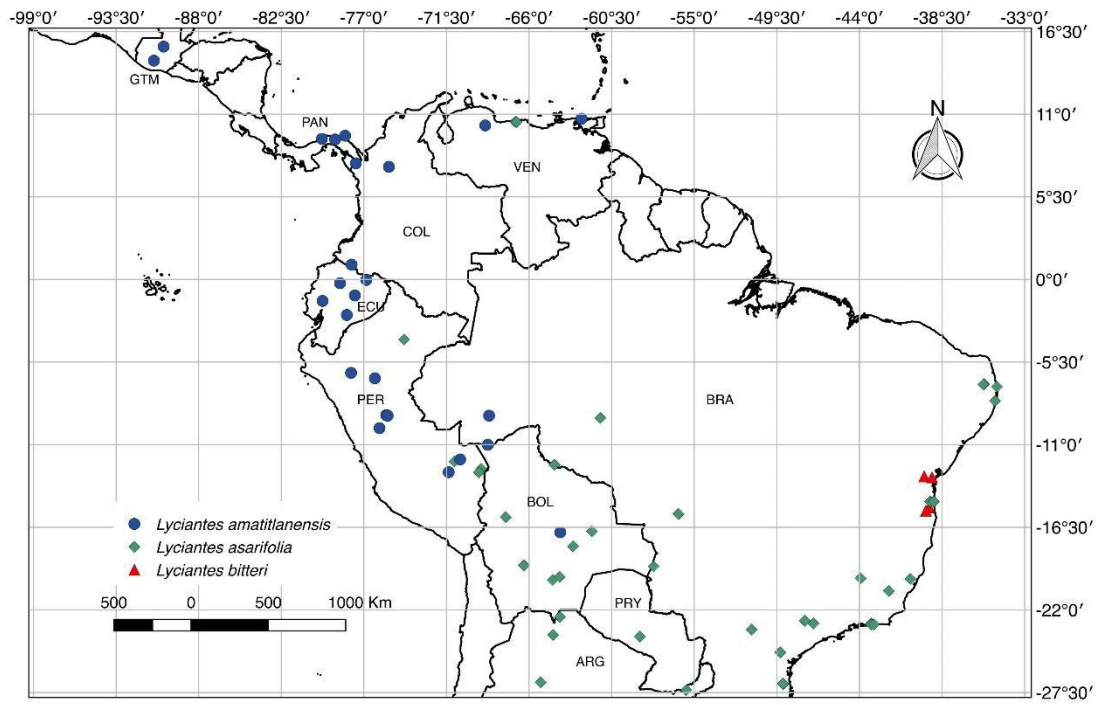


Figure 2. Distribution of *Lycianthes amatitlanensis*, *L. asarifolia* and *L. bitteri*.

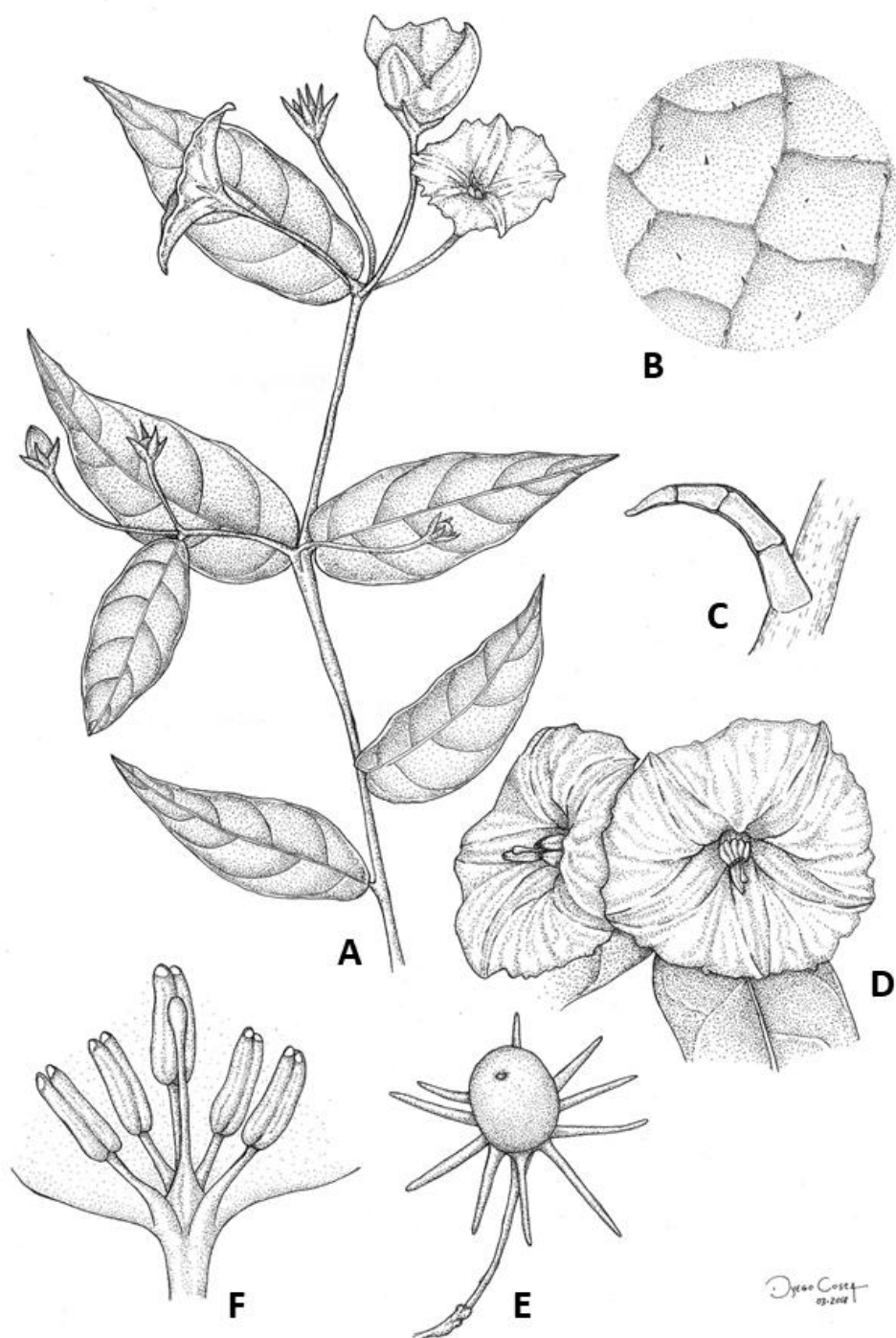


Figure 3. *Lycianthes compressibaccata* (Bitter) Costa-Silva & Agra. **A.** Flowering branch. **B.** Indument. **C.** Simple eglandular trichome. **D.** Flower. **E.** Fruit. **F.** Androecium and Gynoecium.

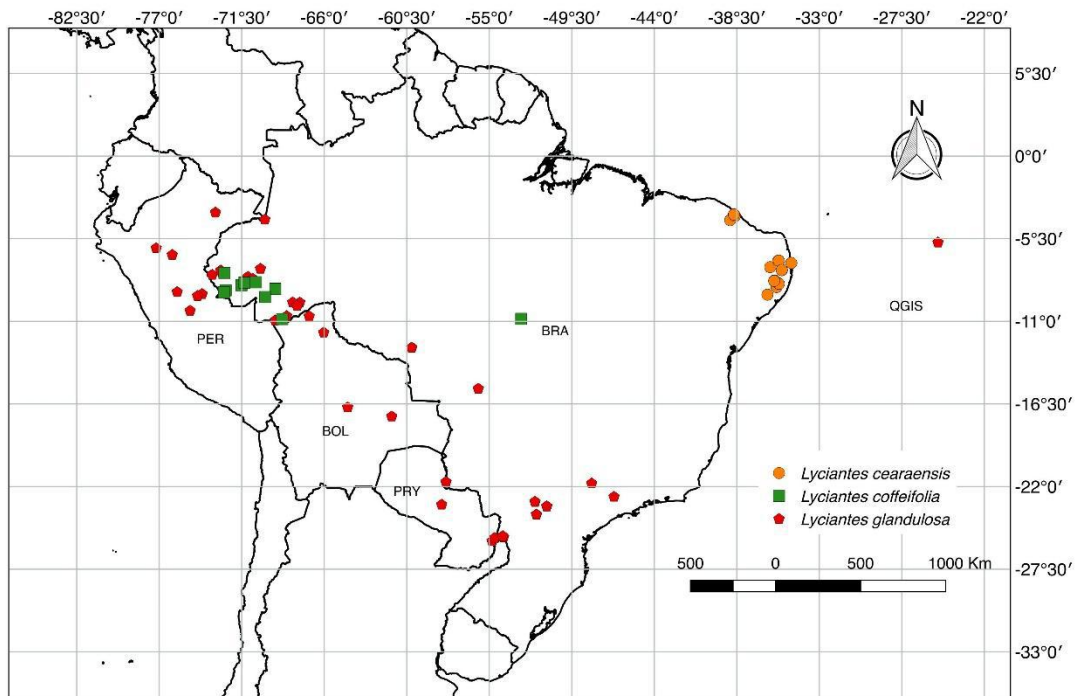


Figure 4. Distribution of *Lycianthes cearaensis*, *L. coffeifolia* and *L. glandulosa*.

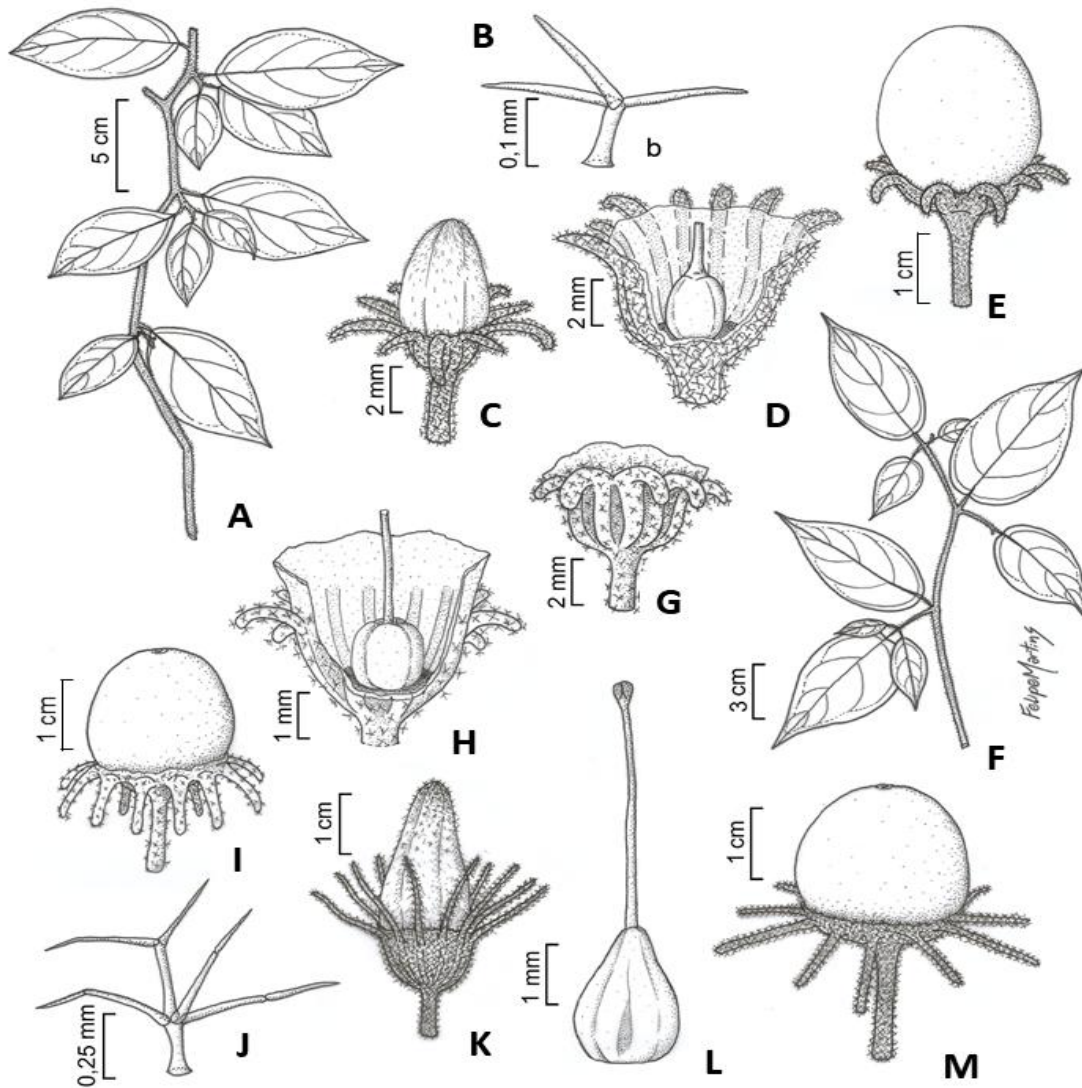


Figure 5. A-E. *Lycianthes ceareaensis* Bitter: A. branch and leaves; B. Stellate trichome; C. Flower bud; D. Calyx and detail of the ovary; E. Fruit. F-I. *Lycianthes pauciflora* (Vahl) Bitter: F. Branch and leaves; G. Calyx; H. Calyx and detail of the ovary; I. Fruit. J-M. *Lycianthes bitteri* Costa-Silva & Agra: J. Dendritic trichome. K. Flower bud. L. Gynoecium. M. Fruit.

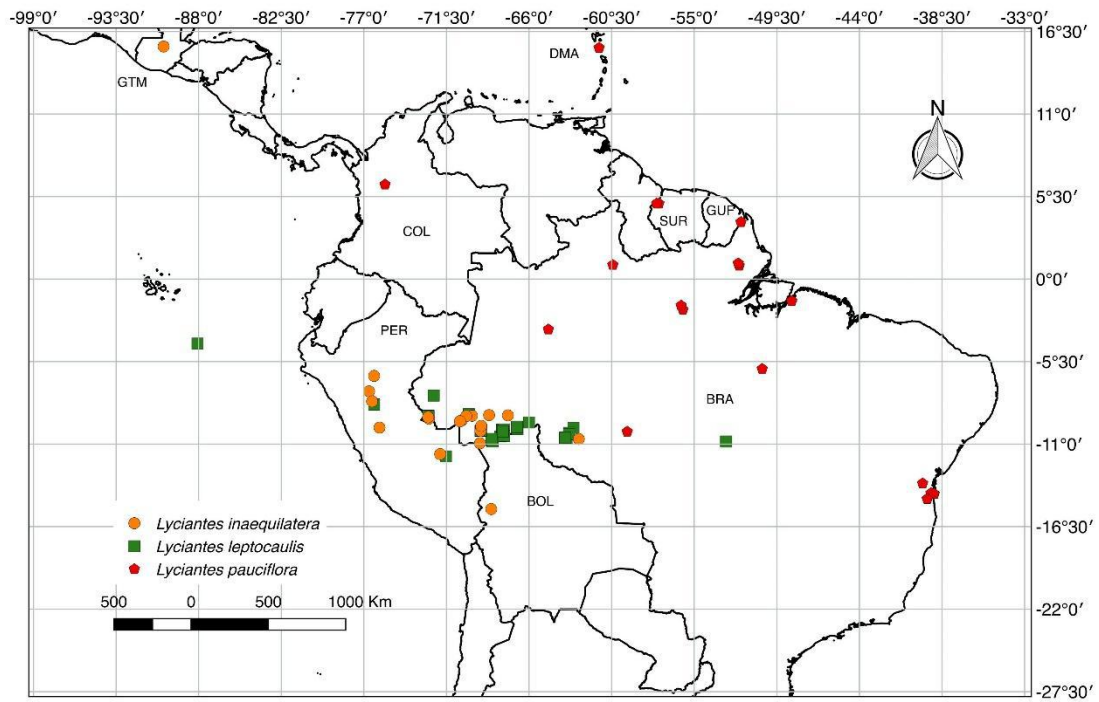


Figure 6. Distribution of *Lycianthes inaequilatera*, *L. compressibaccata* and *L. pauciflora*.

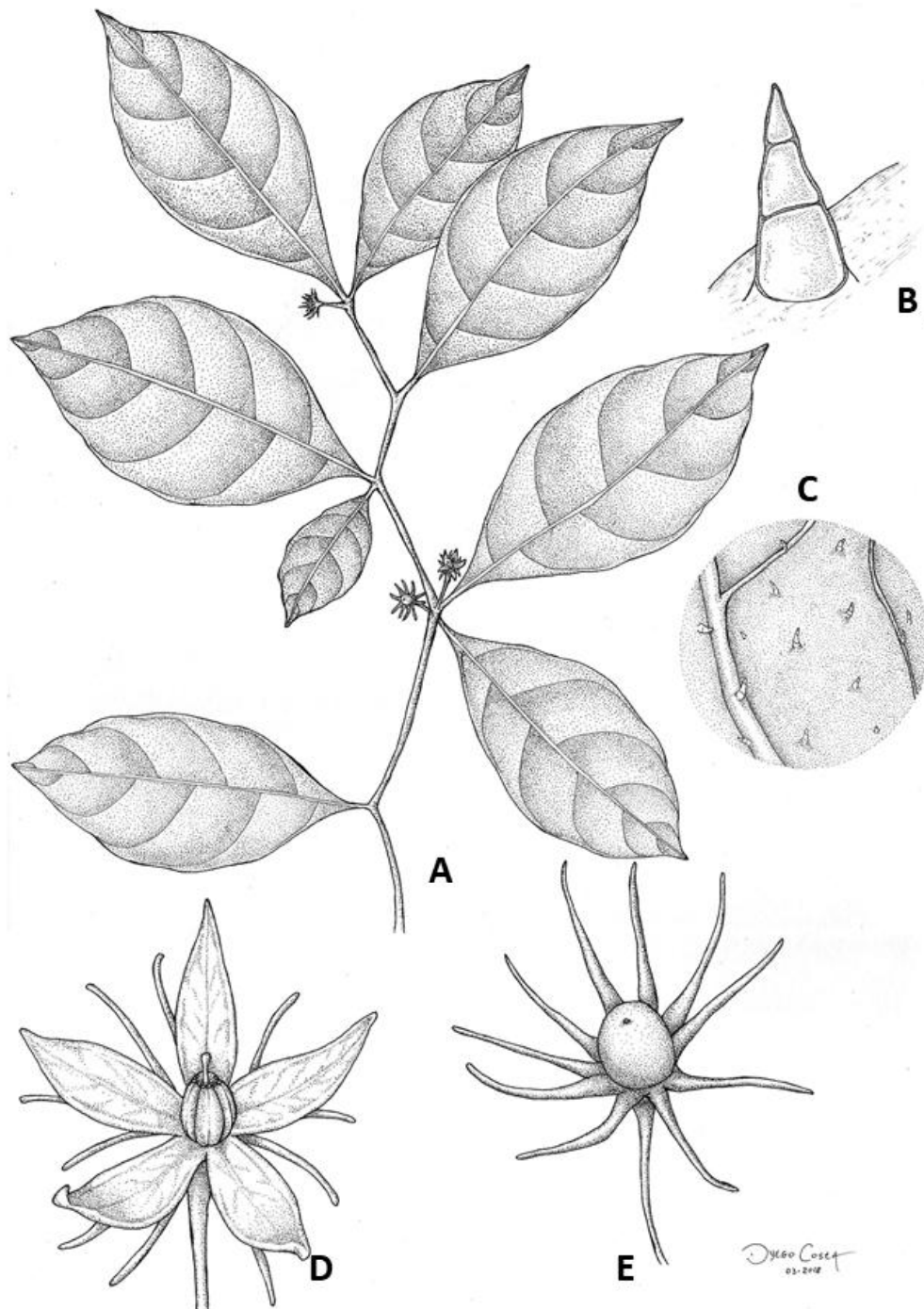


Figure 7. *Lycianthes stenoloba* (van Heurck & Arg. Müll.) Bitter. **A.** Flowering branch; **B.** Simple eglandular trichome. **C.** Indument. **D.** Flower. **E.** Fruit.

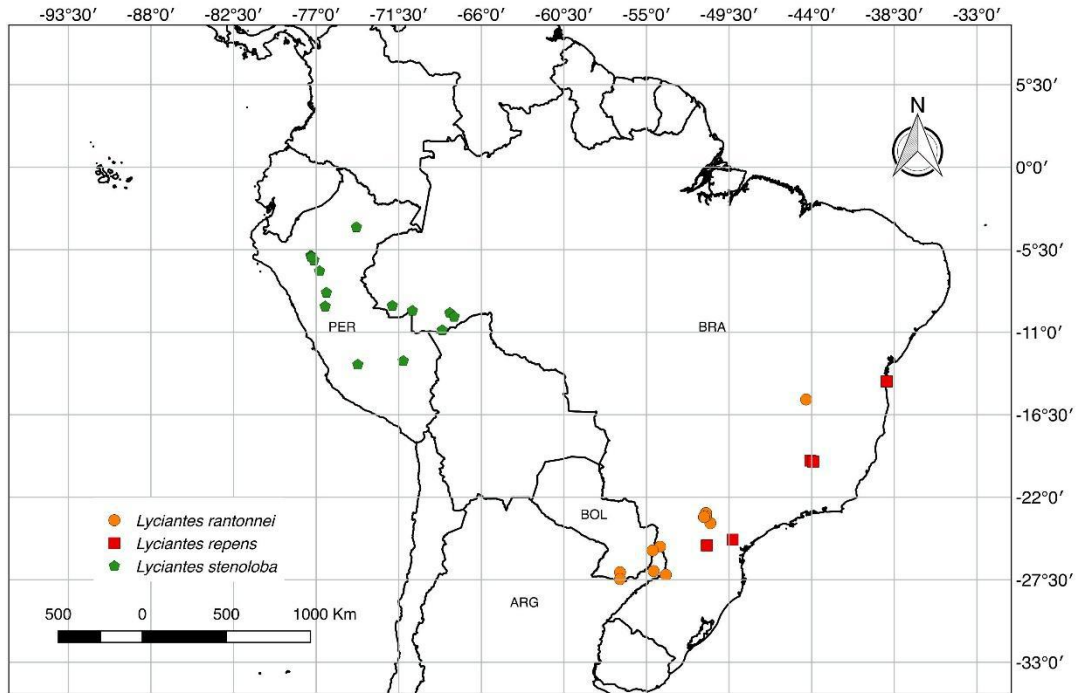


Figure 8. Distribution of *Lycianthes rantonnetii*, *L. repens* and *L. stenoloba*.

3 ANATOMICAL STUDY

Leaf anatomical characters have been used in Solanaceae as an additional tool for the classification of infrageneric taxa. Micromorphology data of the epidermis and the petiole have also been used to make systematic inferences in the genera *Solanum* and *Capsicum*. The objective of this chapter is to investigate the importance of these characters as an aid of the infrageneric classification of *Lycianthes*.

3.1 MANUSCRIPT 4 - ANATOMY OF LEAF EPIDERMIS AND PETIOLE OF 27
SPECIES OF *LYCIANTHES* SUBG. *POLYMERIS* BITTER (SOLANACEAE) AS A
SUPPORT TO ITS TAXONOMY

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ANATOMY OF LEAF EPIDERMIS AND PETIOLE OF 27 SPECIES OF *LYCIANTHES*
SUBG. *POLYMERIS* BITTER (SOLANACEAE) AS A SUPPORT TO ITS TAXONOMY

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Abstract

Lycianthes comprises about 200 species, predominantly Neotropical. *Lycianthes* subg. *Polymeris* is the infrageneric taxa that stands out most and is characterized by herbaceous or shrub habit, perennial, fruits with stone cells and numerous seeds, without sclerenchymatic cells. In the present study, we present an analysis of the anatomical characters of the leaf epidermis and petioles of 27 species of the subgenus *Polymeris*, with the goal of evaluating the importance of its anatomy as an additional support to the taxonomy and the infrageneric classification of *Lycianthes*. The results show that the shape of the anticlinal walls, stomata distribution patterns, the presence of epicuticular waxes and papillae on the epidermis, as well as the anatomy of the petiole (contour and vascular bundles) constitute a set of distinctive characters for the studied species. In addition, the anatomy of the epidermis and petioles of *Lycianthes* subg. *Polymeris* can be used as an additional tool to its taxonomy and systematics, not only to differentiate species but also on the delimitation of the infrageneric taxa at the levels of sections and series.

Introduction

Lycianthes comprises about 200 species, predominantly Neotropical, approximately 30 species occur in the Old World (DEAN, 2004). It is a genus whose species are characterized as perennial herbs or shrubs and lianas, with rotate to campanulate corolla, poricide anthers and calyx with 5 to 10 appendages, similar to some species of *Capsicum* (D'ARCY, 1986).

Lycianthes has been placed in the tribe Capsiceae along with *Capsicum*, according to the most recent molecular phylogenies (OLMSTEAD ET AL., 2008; SÄRKINEN ET AL., 2013). However, unlike *Capsicum*, where the delimitation of taxonomic groups has been aided by cytogenetic (MOSCONE 1990; SCALDAFERRO ET AL., 2013), molecular (GARCÍA ET AL., 2016) and anatomical studies (COSA, 2014; GARCÍA ET AL., 2016; PALCHETTI ET AL., 2014), the infraespecific relations within the genus *Lycianthes* have been little or not studied.

The the most complete treatment for *Lycianthes* is carried out by Bitter (1919), in which 134 species are described and subordinated to an infrageneric classification system. Bitter (1919) divided the genus into four subgenera, seven sections and 15 series. *Lycianthes* subg. *Polymeris* is the infrageneric taxa that stands out since is the most diversified, characterized by herbaceous or shrub habit, perennial, fruits with stone cells and numerous seeds, without sclerenchyma cells.

Lycianthes subg. *Polymeris* has about 110 species subordinated to seven sections: *Eupolymeris*, *Kittoides*, *Perennens*, *Asaropsis*, *Simplicipila*, *Asiomelanesia*, *Synantheroides* proposed by Bitter (1919) based on the presence of stone cells, size of the stamens and anthesis time (day or night).

These infrageneric divisions in *Lycianthes* rely on relatively few characteristics such as the anatomy of the fruit, the morphology of indument and anthers, the presence/absence of appendages in the calyx, and their geographical distribution. They are groupings of species

with little morphological cohesion, e.g. the series *Oligochondrae*, *Virgatae* and *Caribaccolae*, that include many species of neotropical lianas with ferruginous indument and stellate trichomes.

A few of these infrageneric taxa proposed by Bitter (1919) present good morphological definition, among which the following stand out: (1) *Lycianthes* series *Meizonodontae*, with perennial herbs, with tuberous roots and uniflorous inflorescences (DEAN 2004); 2) the series *Strigulosae*, shrubs with asymmetric leaves and simple trichomes; 3) series *Tricolores*, shrubs with variegated corollas, with three green spots at the point of insertion of stamens and unequal stamens (DEAN 2017); 4) the section *Asaropsis*, composed of rhizomatous herbs with chordate leaves.

Leaf anatomy characters such as vascularization, morphology of epidermal cells, stomata, trichomes, cuticles and epicuticular waxes have been shown to be of great importance, as they are additional tool for taxonomic studies in different groups of Angiosperms, such as Asteraceae (SZYMURA; WOLSKI, 2011), Fagaceae (ZHOU; XIA, 2012), Dracaena (DENK et al., 2014) and Ericaceae (WANG ET AL., 2015).

Anatomical studies using micromorphological and structural characters of the leaf epidermis have been performed in different groups of Solanaceae, aiming to understand and support infrageneric classification like those made for *Solanum* (ROJAS; MESA, 1991; GRANADA-CHACON; ROJAS, 2004; ARAÚJO ET AL, 2010; NURIT-SILVA; AGRA, 2011; NURIT-SILVA ET AL., 2012; SAMPAIO ET AL., 2014), for *Brunfelsia* (ARAÚJO, 2016) and also for *Capsicum* (DIAS ET AL, 2011; PALCHETTI ET AL. , 2014).

In addition to the epidermal features, the petiole anatomy is also an important source of additional information, with considerable diagnostic value, according to Solereder (1908) and Metcalfe & Chalk (1979). Recent studies have proved the taxonomic value of the

comparative anatomy of petioles in angiosperms, such as those of Novikoff & Mitka (2015), Graciano-Ribeiro et al. (2016), Talip et al. (2017), and Song and Hong (2018).

Although studies of the leaf anatomy epidermis have been performed in *Solanum*, *Brunfelsia* and *Capsicum*, and have presented relevant results for their taxonomy, these studies are non-existent for *Lycianthes*. In addition, studies with a focus on the anatomy of the leaf petiole, whose characters have been shown to be importance to the taxonomy of several taxonomic groups, have not yet been made for Solanaceae.

In the present study, we present an analysis of the anatomical characters of the epidermis and leaf petioles of 27 species of *Lycianthes* subg. *Polymeris*, representatives of four sections (*Eupolymeris*, *Asaropsis*, *Simplicipila* and *Synantheroides*), with the objective of evaluating the importance of these anatomical characters and providing additional support to the taxonomy and to the infrageneric classification of *Lycianthes*,

Material e Methods

The samples used in this study come from specimens of the following herbaria: EAN, G, JPB, P, UFP and UT. Epidermis and petioles of 27 species of *Lycianthes* subg. *Polymeris*, representatives of four sections: *Eupolymeris* (12 species), *Asaropsis* (1 species), *Simplicipila* (10 species) *Synantheroides* (4 species) were analyzed. A list of the investigated species organized according to Bitter's (1919) infrageneric classification can be seen in Table 1, details of the specimens analyzed are described in Table 2.

Analysis of the micromorphology of the leaf epidermis

Three leaves from the third and fifth nodes of 3 individuals were used for each species, from which fragments of the medial portions of the midrib, the border, the region between the

ribs and the petiole were extracted for cross and paradermic sections. Subsequently, the sections were clarified with sodium hypochlorite (2%), neutralized with acetic acid (0.1%), washed in distilled water, stained with a mixture of safranin and astra blue, mounted between lamina and coverslip with glycerol (50%), the blades were sealed with colorless enamel.

To check the constancy of the epidermal structures, at least five slides were assembled from different parts of a single leaf for each species. The observations and imaging were performed in a photomicroscope (Leica DM750, Switzerland) with Qwin system coupled to a video camera (Leica ICC50 DH) for image capture. The classification of stomata and trichomes was based on Wilkinson (1979), that of epicuticular waxes followed Barthlot (1981).

Results

The anatomical features observed in the present study regarding the anatomy of the leaf epidermis (Table 3) were: the shape of the anticlinal walls on both sides of the leaf blade, stomata distribution pattern, stomata type, trichome type and presence of other appendix such as papillae or waxes. Regarding the petiole (Table 1), we analyzed the outline of the petiole, the arrangement and number of vascular bundles, as well as the presence of trichomes. To simplify the organization of results and avoid long descriptions, the structures were divided into easily identifiable types, illustrated by photographs as shown below:

Shape of anticlinal walls

The anticlinal walls of epidermis cells may have three patterns in *Lycianthes*: straight, curved and sinuous anticlinal walls. These patterns may vary between different species and also between leafs of the same species. The sinuous pattern on the abaxial surface was predominant and observed in 27 species (Figures 1-6): *L. acutifolia* (Fig. 1-B), *L.*

amatitlanensis (Fig. 1-D), *L. bitteri* (Fig. 1-H), *L. ceareaensis* (Fig. 2-B). *L. coffeifolia* (Fig. 2-D), *L. compressibaccata* (Fig. 2-F), *L. fasciculata* (Fig. 2-H), *L. ferruginea* (Fig. 3-B), *L. furcatistellata* (Fig. 3-D), *L. glandulosa* (Fig. 3-F), *L. heteroclita* (Fig. 3-H), *L. pilifera*, *L. inaequilatera* (Fig. 6-D), *L. lasiophylla*, *L. lenta*, *L. medusocalyx* (Fig. 4-B), *L. multiflora* (Fig. 4-D), *L. nitida* (Fig. 4-F), *L. pauciflora* (Fig. 4-H), *L. pilifera*, *L. quichensis* (Fig. 5-B), *L. radiata* (Fig. 5-D), *L. sancataeclarae* (Fig. 5-F), *L. stenoloba* (Fig. 6-F), *L. stephanocalyx* (Fig. 5-H), *L. synanthera* (Fig. 6-B) e *L. tricolor*. Only *L. asarifolia* (Fig. 1-A, B) has straight to curve anticlinal walls on both surfaces.

The patterns observed in the adaxial surface vary among the different groups of species. Sinuous anticlinal walls were observed in 12 species: *L. acutifolia* (Fig. 1-A), *L. amatitlanensis* (Fig. 1-C), *L. bitteri* (Fig. 1-G), *L. fasciculata* (Fig. 2-G), *L. glandulosa* (Fig. 3-E), *L. lenta*, *L. multiflora* (Fig. 4-C), *L. pilifera*, *L. quichensis* (Fig. 5-A), *L. santaeclarae* (Fig. 5-E), *L. stephanocalyx* (Fig. 5-G) and *L. tricolor*. Curve anticlinal wall were observed on the adaxial surface of five species: *L. furcatistellata* (Fig. 3-C), *L. heteroclita* (Fig. 3-G), *L. nitida* (Fig. 4-E), *L. radiata* (Fig. 5-C) and *L. synanthera* (Fig. 6-A). Straight walls were observed in: *L. coffeifolia* (Fig. 2-C), *L. compressibaccata* (Fig. 2-E), *L. lasiophylla*, *L. medusocalyx* (Fig. 4-A), *L. pauciflora* (Fig. 4-G). Variations of these patterns were observed in *L. asarifolia*, (Fig. 1-E), *L. ceareaensis* (Fig. 2-A) e *L. ferruginea* (Fig. 3-A) with straight to curve anticlinal walls, and in *L. inaequilatera* with curve to sinuous walls.

Stomatic complex

Regarding the distribution of stomata, the leaf blades of *Lycianthes* species can be hypostomatic or amphistomatic. Hypostomatic leaves were observed in 17 species: *Lycianthes bitteri*, *L. ferruginea*, *L. furcatistellata*, *L. heteroclita*, *L. multiflora*, *L. nitida*, *L. pauciflora*, *L. stenoloba*, *L. stephanocalyx*, *L. tricolor*, *L. ceareaensis*, as well as in all the

studied species of *Lycianthes* serie *Strigulosae*. Amphistomatic leaves were observed in 10 species: *L. asarifolia*, *L. cearaensis*, *L. compressibaccata*, *L. fasciculata*, *L. glandulosa*, *L. lenta*, *L. sanctaeclarae* e *L. synanthera*, and also on in the analyzed species of *Lycianthes* serie *Piliferae*, except *L. stephanocalyx*. Some species were considered amphihypostomatic, taking into consideration the occurrence of at least one stomata per field, at the objective lens of 40x, as observed in three species: *L. coffeifolia*, *L. compressibaccata* e *L. lenta*.

Regarding the types of stomata, *Lycianthes* presented two basic types: anisocytic and anomocytic. In plants whose leaves have amphistomatic distribution, the predominant stomata on the adaxial surface is anisocytic, but anomocytic stomata were also observed, but in a smaller quantity, on the adaxial surface of two species: *L. fasciculata* and *L. asarifolia*. On the abaxial surface, anisocytic and anomocytic occur simultaneously in 21 species, about 78% of the studied species, only 15% (*L. amatitlanensis*, *L. asarifolia*, *L. nitida* and *L. stephanocalyx*) presented only anisocytic stomata on the abaxial surface.

Trichomes, papillae and waxes

Indument varies from glabrescent to tomentose, presenting variations between those two types, and in *L. stenoloba* is completely papillose on the adaxial surface, making it difficult to see the shape of anticlinal walls. Papillae can also occur in *L. heteroclita*, *L. compressibaccata* e *L. synanthera*. Seven types trichomes were observed: glandular (Type 1, Fig. 7 D-E), simple multicellular uniseriate (Type 2, Fig. 7 F-L), simple setose trichomes (Type 3, Fig. 7 M-O); sessile (type 4, Fig. 7 P-Q) or stalked (Type 5, Fig. 7 R-V) stellate trichomes; branched or bifurcate (Type 6, Fig. 7 W, X, Z) e dendritic (Type 7, Fig. 7 Y).

The glandular trichomes observed in *Lycianthes* are stalked, the stalks composed of a single cell, with globular and multicellular glands, usually 4- 6 cells (Fig. 7-D), except *L.*

ferruginea (Fig. 7-E) which presents glands with more than 10 cells. These trichomes were observed in all analyzed species.

The simple trichomes in *Lycianthes* are exclusively multicellular and the number of cells varied from two to seven cells. This type of trichome varied according to the general pattern and could be subdivided into other types: 1. Simple multicellular trichomes with cuticle granules, observed on *L. amatitlanensis* (Fig.7 F-G), *L. fasciculata* (Fig. 7. H), *L. radiata*, and *L. stephanocalyx* (Fig. 7. I); 2. Simple multicellular trichomes without granules, on *L. compressibaccata* (Fig. 7. J-K), *L. medusocalyx* (Fig. 4 A) and *L. quichenses* (Fig. 7. L). The last also occurs on *L. inaequilatera*, but present a widening in the base of the cells as differential (Fig. 6. C). Simple setose trichomes were characteristic for five species: *L. coffeifolia* (Fig. 7 M), *L. heteroclita* (Fig. 7. N), *L. stenoloba* (Fig. 6 E; 7 O) and *L. synanthera*.

Stellate trichomes can be sessile or stalked, with three to eight lateral rays without cuticle granules. Sessile stellate trichomes are present on *L. furcatistellata* (Fig. 7. P) and *L. multiflora* (Fig. 7.Q), and stalked stellate trichomes are present on six species: *L. ferruginea* (Fig. 7. T), *L. pauciflora* (Fig. 7. V), *L. glandulosa* (Fig. 7. U), *L. lenta*, *L. cearaensis* (Fig. 7. R) and *L. bitteri* (Fig. 7. S).

Branched multicellular trichomes were observed on *L. fasciculata* (Fig. 7. W) and *L. sanctaeclarae* (Fig. 7. X). Dendritic trichomes were found on *L. bitteri* (Fig. 7. Y) and stalked bifurcate trichomes were exclusive to *L. sanctaeclarae* (Fig. 7. Z).

Outline of the petiole

Regarding the outline of the petiole in the middle portion, four patterns were observed: rounded to semi-circular (Type 1); biconvex with projection towards to the adaxial surface (Type 2); Plane-convex (Type 3), when the adaxial surface is flat and winged (Type 4).

The petiole outline is rounded in *L. asarifolia* (Fig. 8 C), *L. bitteri* (Fig. 8 D) e *L. ceareaensis* (Fig. 8 E). Biconvex outlines with projections toward the adaxial surface were observed in 14 species: *L. acutifolia* (Fig. 8 A), *L. coffeifolia* (Fig. 8 F), *L. compressibaccata* (Fig. 8 G), *L. ferruginea* (Fig. 8 I), *L. furcatistellata* (Fig. 8 J), *L. glandulosa* (Fig. 8 K), *L. heteroclita* (Fig. 8 L), *L. lasiophylla* (Fig. 8 N), *L. pauciflora* (Fig. 8 R), *L. pilifera* (Fig. 8 S), *L. stephanocalyx* (Fig. 8 X) e *L. tricolor* (Fig. 8 Z). Petioles with plane-convex outline are presente in: *L. amatitlanensis* (Fig. 8 B), *L. inaequilatera* (Fig. 8 M), *L. lenta* (Fig. 8 O), *L. nítida* (Fig. 8 Q), *L. radiata* (Fig. 8 U) and *L. sanctaeclarae* (Fig. 8 V).

Arrangement of vascular bundles in the medial portion of the petioles

Taking into account the arrangement of the central vascular bundles, the petioles of the analyzed *Lycianthes* species present two main patterns in their medial portion: arc-shaped and V-shaped, when the central vascularization is formed by two central bundles arranged diagonally and the basal part of the bundles suggest and acute angle. The V-shape was observed only in *L. asarifolia* (Fig. 8 C), all of the other species have arc-shaped bundles.

Number of vascular bundles in the medial portion of the petioles

Regarding the number of vascular bundles, the central bundles and accessories were considered separately. Thus, *Lycianthes* petioles can have two central vascular bundles, as observed in *L. asarifolia*, *L. coffeifolia*, *L. heteroclita*, *L. inaequilatera*, *L. lasiophylla*, *L. multiflora*, *L. pilifera*, *L. quichensis*, *L. stenoloba* e *L. stephanocalyx*, or only a single central vascular bundle, observed in the other species, about 63% of the total.

Lycianthes species may have two to four accessory vascular bundles. The presence of two accessory bundles was observed in 25 species (92.26% of the total). Only two species, *L.*

nitida and *L. radiata* present four accessory bundles, corresponding to only about 7.74% of the total.

Discussion

The analysis of the epidermis showed that the sinuous pattern of the anticlinal walls on the abaxial face observed in the analyzed species is common to Solanaceae species, as already reported to *Solanum* (ARAÚJO ET AL. 2010; NURIT-SILVA; AGRA, 2011; NURIT-SILVA ET AL. 2012; SAMPAIO ET AL, 2014), *Brunfelsia* (ARAÚJO, 2016) e *Capsicum* (PALCHETTI ET AL., 2014). The epidermal cell walls on the adaxial surface ranged from straight to sinuous, and the distribution of these characters in the *Lycianthes* species does not coincide with any of the classical infrageneric divisions proposed by Bitter (1919). Although the straight wall pattern is a characteristic commonly observed in plants of xeric environments, the same was observed in *L. coffeifolia*, *L. compressibaccata*, *L. lasiophylla*, *L. medusocalyx* and *L. pauciflora* species found in the Amazonian biome.

In general, the pattern of sinuosity in cell walls is quite variable and its use in taxonomy should be done with caution (STACE, 1965), since it is strongly influenced by environmental factors (WATSON, 1942) which makes it a character with little taxonomic value also for other genera of the family, as in *Capsicum* (PALCHETTI ET AL, 2014).

In Solanaceae, stomata can occur on both surfaces or are restricted to the abaxial surface (METCALFE; CHALK, 1950); both cases are observed in *Lycianthes* species, but the hypostomatic pattern predominates among the species. All species of *Lycianthes* serie *Strigulosae* are hypostomatic, but with the exception of this group, the stomatal distribution pattern can not be used to delimit specific groups

The types of stomata observed in *Lycianthes* species, anisocytic and anomocytic, are common to the Solanaceae family, even on a single leaf blade as observed in *Solanum*

(METCALFE; CHALK 1950; AHMAD 1964; ROJAS; RODRÍGUEZ, 1991; COSA ET AL. 1998; NURIT-SILVA ET AL. 2007, 2012; NURIT-SILVA; AGRA 2011) e *Capsicum* (PALCHETTI ET AL. 2014).

Papillae can be considered scleromorphic structures that arise on surfaces that are under intense exposure to light and serve as a strategy to reduce the amount of radiation that reaches the mesophyll (JOORDAN ET AL 2008, JORDAN ET AL 2005). *Lycianthes heteroclita* and *L. synanthera* are morphologically similar species and may occur in areas of intense light such as road sides and riverbanks (BOHS, 2015), as well as *L. leptocaulis* and *L. stenoloba*, suggesting that the occurrence of papillae is related to an adaptive response of the plant since the emergence of photoprotective structures is more related to the vegetation structure than to the environmental parameters (JOORDAN ET AL., 1998).

According to Metcalfe and Chalk (1950), different types of trichomes occur in Solanaceae and characteristics related to trichomes and indument can be used to identify different taxa. Studies for the genus *Solanum* have demonstrated the taxonomic importance of the distribution and typology of the trichomes in the different infrageneric levels, where some of them have diagnostic value, useful in the establishment of affinities and distinctive patterns for sections or species (SEITHE, 1962, 1979; ROE, 1972; NURIT-SILVA et al. 2012).

Trichomes are structures commonly used for systematic purposes as they are easily observable, and their distribution and variations in the constitution of the indument may provide useful characteristics for the delimitation of taxonomic groups. This may be commonly observed in Solanaceae, which, according to Metcalfe & Chalk (1950), present a great diversity of trichomes. Some studies that use characteristics of indument and trichomes to delimit infrageneric groups were carried out among Solanaceae genera, especially in *Solanum*, that has a classification based only on trichome types (SEITHE 1979). Although this system was little accepted, trichomes continued to be successfully used in the delimitation

of *Solanum* infrageneric taxa such as the section *Geminata* (ROJAS, 2007), *Crinitum* (ARAÚJO, 2010), *Polytrichum* (NURIT-SILVA; AGRA, 2011), *Torva* (NURIT-SILVA ET AL., 2012) and *Brevantherum* (SAMPAIO ET AL., 2014).

In *Lycianthes*, trichomes are used by Bitter (1919) to delimit a few infrageneric taxa, such as the section *Simplicipila*, which present species with simple trichomes. Among the infrageneric divisions analyzed in this work, the section *Simplicipila* is the one that presents greater uniformity as to the typology of trichomes, with multicellular simple trichomes. In addition the series that are subordinate to this section can be differentiated as to the types of simple trichome.

The species of series *Piliferae* have setose erect trichomes and the series *Strigulosae* have simple adpress trichomes. Among the series of the section *Eupolymeris*, the series *Caribaccolae* and *Virgata* present indument formed by stellate trichomes; and the series *Oligochondrae* can be divided into two groups of species: those with stellate trichomes (*L. bitteri*, *L. cearaensis*, *L. ferruginea*, *L. glandulosa*, *L. pauciflora*), and with setose trichomes (*L. compressibaccata*, *L. stenoloba*). The only species of the series *Tricolores*, *L. tricolor*, analyzed in this study presents the pattern referred to in this series (DEAN, 2017) with simple trichomes.

Hare (1944) emphasized caution when using petiole characteristics in taxonomic inferences, since vascular characteristics of the petiole evolved primarily in response to mechanical needs, assuming the shape that best supports the vertical curvature resulting from leaf weight, as well as lateral stress due to the action of the wind. Thus, this character is mainly adaptive and functional and for this reason have little taxonomic significance if there isn't constancy of this character in a given taxon. In this context, the arch or V-shaped vascular system observed in *Lycianthes* species may have only functional value.

Taxonomic implications

The identification and delimitation of some taxa could be done infrageneric and interspecific level with the support of the micromorphological characters of the epidermis and the petiole, even when they presented slight variations.

Lycianthes sect. *Eupolymeris*

The morphoanatomic data of *Lycianthes* sect. *Eupolymeris* analyzed in this work do not contribute to the delimitation of the section itself, but it brings us interesting data regarding the delimitation of some species.

Lycianthes pauciflora is a liana, with ferruginous indument, stellate trichomes and White rotate corolla, that occurs in the neotropical region, from the Caribbean region to Argentina (ROJAS; D'ARCY, 1997; COSTA-SILVA; AGRA, 2018), and probably is the most attributed name to species that have such characteristics. According to Costa-Silva & Agra (2018), *L. bitteri* and *L. cearaensis*, species from the Northeast region of Brazil, are morphologically similar to *L. pauciflora*, which led to errors in the identifications of these species. The petiole of *L. pauciflora* has a biconvex outline, with projections facing the adaxial surface, differing from *L. bitteri* and *L. cearaensis*, that have a semicircular outline. Petiole measurements also differ among the three species (see Table 3), with *L. pauciflora* being the species with the smallest proportions.

Lycianthes pauciflora is also morphologically similar to *L. glandulosa* and their distribution overlaps in the Amazon and Southeastern Brazil. We can differentiate these two taxons by the sinuous anticlinal walls on the adaxial surface, amphistomatic leaves and petiole with two central vascular bundles in *L. glandulosa*, while *L. pauciflora* has straight anticlinal walls, hypostomatic leaves and petiole with only one vascular bundle.

Lycianthes compressibaccata was considered a synonym of *L. stenoloba* by Rojas & D'arcy (1997), however, Costa-Silva & Agra (2018) point to diagnostic characters that separate these two taxa. Such information is also corroborated by the fully papillose epidermis on the adaxial surface and the winged petiole of *L. stenoloba*, differing from *L. compressibaccata* whose cells have straight anticlinal walls on the adaxial surface, sparse papillae and biconvex with projections outline of the petiole.

Lycianthes sect. *Simplicipila*

‘This section was proposed by Bitter (1919), taking into account the shrub habit, the equal stamens and the presence of simple trichomes. It was divided into two series: *Piliferae* and *Strigulosae*. Morphoanatomical data can be used to differentiate the *Piliferae* series, which presents amphistomatic leaves and petioles with two central vascular bundles as the predominant pattern, from the series *Strigulosae*, that presents hypostomatic leaves with petioles with a single vascular bundle as the predominant pattern.

Lycianthes sect. *Synantheroides*

This section proposed by Bitter (1919) is composed of epiphytic plants and according to Bohs (2015), *L. heteroclita*, *L. nitida* and *L. sanctaeclarae* are usually confused with *L. synanthera*. The characters presented in this study can also help to delimit these species. *Lycianthes sanctaeclarae* is the only one presenting sinuous anticlinal walls on the adaxial surface, while the others have curved walls. *Lycianthes synanthera* is the only species of this section that presents winged petiole, differing from *L. nitida* and *L. sanctaeclarae* that present plane-convex petioles and from *L. heteroclita* that presents biconvex petiole with projections facing the adaxial surface. Only *L. heteroclita* presents two central vascular bundles on the petiole and only *L. nitida* presents four accessory vascular bundles. Petiole measurements are also a differential between the four species (see Table 3).

Conclusions

The combination of the characters of the micromorphology of the leaf epidermis and petiole is an important source of information for the delimitation of the 12 species of *Lycianthes*. The results suggest that the shape of the anticlinal walls, the pattern of stomata distribution, epicuticular waxes, and papillae of the epidermis, as well as the anatomy of the petiole (outline and vascular bundles) constitute a set of distinctive characters of taxonomic value, which can be used as an additional tool to the taxonomy of *Lycianthes*, not only in the differentiation between species but also in the delimitation of infrageneric taxa, at section and series levels.

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Table 1. Species of the *Lycianthes* subg. *Polymeris* analyzed in this study, organized on the infrageneric classification proposed by Bitter (1919).

Subgenus	Sections	Series	Species	
<i>Polymeris</i>	<i>Eupolymeris</i>	Series Oligochondrae	<i>L. compressibaccata</i> (Bitter) Costa-Silva & Agra	
			<i>L. ferruginea</i> Bitter	
			<i>L. glandulosa</i> (Ruiz & Pav.) Bitter	
			<i>L. cearaensis</i> Bitter	
			<i>L. pauciflora</i> (Vahl.) Bitter	
			<i>L. stenoloba</i> (van Heurck & Müll. Arg.) Bitter	
			<i>L. bitteri</i> Costa-Silva & Agra	
		Series Pliochondrae	<i>L. fasciculata</i> (Rusby) Bitter	
		Series Virgata	<i>L. lenta</i> (Cav.) Bitter	
			<i>L. multiflora</i> Bitter	
		Series Tricolores	<i>L. tricolor</i> (Sessé & Moc. ex Dunal) Bitter	
		Series Caribaccolae	<i>L. furcatistellata</i> Bitter	
		<i>Asaropsis</i>	-	<i>L. asarifolia</i> (Kunth & Bouché) Bitter
		<i>Simplicipila</i>	Series Piliferae	<i>L. coffeifolia</i> Bitter
<i>L. pilifera</i> (Benth.) Bitter				
<i>L. quichensis</i> (Coult & Donn. Sm.) Bitter				
<i>L. stephanocalyx</i> (Brandegge) Bitter				
Series Strigulosae	<i>L. acutifolia</i> (Ruiz & Pav.) Bitter			
	<i>L. amatitlanensis</i> (Coult & Donn. Sm.) Bitter			
	<i>L. inaequilatera</i> (Rusby) Bitter			
	<i>L. lasiophyla</i> (Hub. & Bonpl. Ex Dunal) Bitter			
	<i>L. medusocalyx</i> (Bitter) Bitter			
	<i>L. radiata</i> (Sendtn.) Bitter			
<i>Synantheroides</i>	-		<i>L. heteroclita</i> (Sendtn.) Bitter	
			<i>L. synanthera</i> (Sendtn.) Bitter	
			<i>L. nitida</i> Bitter	
		<i>L. sanctaeclarae</i> (Greenman) D'Arcy		

Table 2. Specimens used in the analysis of the morphoanatomy of the epidermis and petiole

Species	Vouchers
<i>L. acutifolia</i> (Ruiz & Pav.) Bitter	Venezuela: <i>Pittier 10057</i> (G); <i>Pittier9378</i> (G), <i>Humbert 26105</i> (G)
<i>L. amatitlanensis</i> (Coult & Donn. Sm.) Bitter	Costa Rica: <i>Bohs 2552</i> . Panama: <i>Nevers 3864</i> (G), <i>Vlatismil 586</i> (G)
<i>L. asarifolia</i> (Kunth & Bouché) Bitter	Brazil: <i>Santos 4571</i> , <i>Costa-Silva 91</i> (UFP). Paraguay: <i>Bohs 3214</i> (UT)
<i>L. bitteri</i> Costa-Silva & Agra	Brazil: <i>Agra 7185</i> , <i>7191</i> (JPB)
<i>L. cearaensis</i> Bitter	Brazil: <i>Agra 6476</i> (JPB), <i>Oliveria 372</i> (JPB), <i>Silva 523</i> (JPB), <i>Sampaio 94</i> (UFP)
<i>L. coffeifolia</i> Bitter	Brazil: <i>Medeiros 753</i> (RB), <i>Ule 9737</i> (G)
<i>L. compressibaccata</i> (Bitter) <i>Costa-Silva & A.</i>	Brazil: <i>Medeiros 681</i> (RB). Peru: <i>Schunke 1077</i> (G), <i>Ule 6800</i> (G)
<i>L. fasciculata</i> (Rusby) Bitter	Argentina: <i>Bohs 3051</i> (UT), <i>Nee & Bohs 50750</i> (UT)
<i>L. ferruginea</i> Bitter	Venezuela: <i>Fendler 991</i> (G), <i>Bohn 5433</i> (G)
<i>L. furcatistellata</i> Bitter	Costa Rica: <i>Bohs 3105</i> (UT)
<i>L. glandulosa</i> (Ruiz & Pav.) Bitter	Brazil: <i>Ule 9734</i> (G), <i>Giacomin 2926</i> (RB), <i>Ribas 5616</i> (RB), <i>Torke 2023</i> (RB). Peru: <i>Shuncke 1893</i>
<i>L. heteroclita</i> (Sendtn.) Bitter	Costa Rica: <i>Mora 1593</i> (JPB), <i>Soto 678</i> (JPB). Mexico: <i>Bohs 3496</i>
<i>L. inaequilatera</i> (Rusby) Bitter	Ecuador: <i>Vlatismil 2295</i> (JPB)
<i>L. lasiophylla</i> (Hub. & Bonpl. Ex Dunal) Bitter	Bonpland 433 (P)
<i>L. lenta</i> (Cav.) Bitter	Mexico: <i>Bohs 3920</i> (UT)
<i>L. medusocalyx</i> (Bitter) Bitter	Ecuador: <i>Neill 7005</i> (G)
<i>L. multiflora</i> Bitter	Costa Rica: <i>Aguillar 6278</i> (JPB), <i>BOhs 2569</i> (UT), <i>Chaves 1463</i> (JPB)
<i>L. nitida</i> Bitter	Costa Rica: <i>Soto 608</i> (JPB)
<i>L. pauciflora</i> (Vahl.) Bitter	Brazil: <i>Thomas 9330</i> (JPB). Dominica: <i>sin col.</i> (RB). Paraguay: <i>Stutz 1340</i> (G).
<i>L. pilifera</i> (Benth.) Bitter	Cultivated: <i>Bohs 2525</i> (UT)
<i>L. quichensis</i> (Coult & Donn. Sm.) Bitter	Guatemala: <i>Tuerckheim 11</i> (G)
<i>L. radiata</i> (Sendtn.) Bitter	Colombia: <i>Hartweg 1293</i> (G). Ecuador: <i>Vlatismil 1256</i> (G)
<i>L. sanctaclarae</i> (Greenman) D'Arcy	Costa Rica: <i>Bohs 2395</i> (UT)
<i>L. stenoloba</i> (van Heurck & Müll. Arg.) Bitter	Brazil: <i>Michelangeli 1286</i> (RB), <i>Ule 6571</i> (G)
<i>L. stephanocalyx</i> (Brandege) Bitter	Mexico: <i>Dean 2562</i> (UT)
<i>L. synanthera</i> (Sendtn.) Bitter	Costa Rica: <i>Bohs 2376</i> (UT)
<i>L. tricolor</i> (Sessé & Moc. ex Dunal) Bitter	Cultivated: <i>Bohs 3163</i> (UT)

Table 3. Micromorphological characters of the epidermis of 27 species of *Lycianthes* subg. *Polymeris*. Abbreviations: **amphi**: amphistomatic leaves; **amphihypo**: amphihypostomatic leaves; **aniso**: anisocytic stomata; **anomo**: anomocytic stomata; **cur**: curve anticlinal walls; **hypo**: hypostomatic leaves; **str**: straight anticlinal walls; **sin**: sinuous anticlinal walls; **1**: glandular trichomes; **2**: simple multicellulare uniseriate trichomes; **3**: Setose trichomes; **4**: Sessile stellate trichomes; **5**: Stalked stellate trichomes; **6**: Branched or bifurcate trichomes; **7**: dendritic trichomes.

	Anticlinal walls		Stomata type	Stomata distribution	Trichome types	Othes structures
	Adaxial surface	Abaxial surface				
<i>L. acutifolia</i> (Ruiz & Pav.) Bitter	Sin	Sin	Aniso, anomo	Hypo	1,2	-
<i>L. amatitlanensis</i> (Coult & Donn. Sm.) Bitter	Sin	Sin	Aniso	Hypo	1,2	-
<i>L. asarifolia</i> (Kunth & Bouché) Bitter	Str-curv	Str-cur	Aniso, anomo	Amphi	1,2	-
<i>L. bitteri</i> Costa-Silva & Agra	Sin	Sin	Aniso, anomo	Hypo	1,5,7	-
<i>L. cearaensis</i> Bitter	Str-cur	Sin	Aniso, anomo	Amphi	1,5	-
<i>L. coffeifolia</i> Bitter	Str	Sin	Aniso, anomo	Amphihypo	1,3	Waxes
<i>L. compressibaccata</i> (Bitter) Costa-Silva & A.	Str	Sin	Aniso, anomo	Amphihypo	1,2	Papillae
<i>L. fasciculata</i> (Rusby) Bitter	Str	Sin	Aniso, anomo	Amphi	1,2,6	-
<i>L. ferruginea</i> Bitter	Str-cur	Sin	Aniso, anomo	Hypo	1,5	-
<i>L. furcatistellata</i> Bitter	Cur	Sin	Aniso, anomo	Hypo	1,5	-
<i>L. glandulosa</i> (Ruiz & Pav.) Bitter	Sin	Sin	Aniso, anomo	Amphi	1,4,5	-
<i>L. heteroclita</i> (Sendtn.) Bitter	Cur	Sin	Aniso, anomo	Hypo	1,3	Papillae
<i>L. inaequilatera</i> (Rusby) Bitter	Cur-sin	Sin	Anomo	Hypo	1,2	-
<i>L. lasiophyla</i> (Hub. & Bonpl. Ex Dunal) Bitter	Str	Sin	-	Hypo	1,2	-
<i>L. lenta</i> (Cav.) Bitter	Sin	Sin	Aniso	Amphihypo	1,5	-
<i>L. medusocalyx</i> (Bitter) Bitter	Str	Sin	Aniso, anomo	Hypo	1,2	-
<i>L. multiflora</i> Bitter	Sin	Sin	Aniso, anomo	Hypo	1,5	-
<i>L. nitida</i> Bitter	Cur	Sin	Aniso	Hypo	1	-
<i>L. pauciflora</i> (Vahl.) Bitter	Str	Sin	Aniso, anomo	Hypo	1,5	-
<i>L. pilifera</i> (Benth.) Bitter	Sin	Sin	Aniso, anomo	Amphi	1,2,3	-
<i>L. quichensis</i> (Coult & Donn. Sm.) Bitter	Sin	Sin	Aniso, anomo	Amphi	1,2	-
<i>L. radiata</i> (Sendtn.) Bitter	Cur	Sin	Aniso, anomo	Hypo	1,2	-
<i>L. sanctaeclarae</i> (Greenman) D'Arcy	Sin	Sin	Aniso, anomo	Hypo	1,6	-
<i>L. stenoloba</i> (van Heurck & Müll. Arg.) Bitter	-	Sin	Anomo	Hypo	1,3	Papillae
<i>L. stephanocalyx</i> (Brandegee) Bitter	Sin	Sin	Aniso	Hypo	1,2	-
<i>L. synanthera</i> (Sendtn.) Bitter	Cur	Sin	Aniso, anomo	Amphi	1,3	Papillae
<i>L. tricolor</i> (Sessé & Moc. ex Dunal) Bitter	Sin	Sin	Aniso, anomo	Hypo	1,2	-

Tabela 4. Characters of the median region of the petiole of 27 species of *Lycianthes* subg. *Polymeris*.

	Outline of the petiole (Type)	Shape of the central bundle	Number of central vascular bundles	Number of accessory vasculares bundles	Length of petiole (cross section)	Width of petiole (cross section)	Width of the vascular bundle
<i>L. acutifolia</i> (Ruiz & Pav.) Bitter	2	Arc	1	2	0,865-0,924	0,820-0,869	0,294-0,317
<i>L. amatitlanensis</i> (Coult & Donn. Sm.) Bitter	3	Arc	1	2	1,109-1,154	1,465-1,486	0,487-0,505
<i>L. asarifolia</i> (Kunth & Bouché) Bitter	1	V	2	2	2,110-2,457	2,057-2,272	0,606-0,679
<i>L. bitteri</i> Costa-Silva & Agra	1	Arc	1	2	1,600-1,629	1,971-2,137	0,869-0,886
<i>L. ceareaensis</i> Bitter	1	Arc	1	2	1,496-1,513	1,764-1,864	0,680-0,709
<i>L. coffeifolia</i> Bitter	2	Arc	2	2	1,225-1,553	1,504-1,523	0,692-0,780
<i>L. compressibaccata</i> (Bitter) Costa-Silva & Agra	2	Arc	1	2	1,187-1,197	1,218-1,289	0,501-0,572
<i>L. fasciculata</i> (Rusby) Bitter	4	Arc	1	2	0,839-0,891	0,924-0,982	0,468-0,497
<i>L. ferruginea</i> Bitter	2	Arc	1	2	1,611-1,677	1,647-1,674	0,813-0,833
<i>L. furcatistellata</i> Bitter	2	Arc	1	2	1,426-1,442	1,856-1,902	0,838-0,859
<i>L. glandulosa</i> (Ruiz & Pav.) Bitter	2	Arc	1	2	1,415-1,754	1,660-1,941	0,655-1,058
<i>L. heteroclita</i> (Sendtn.) Bitter	2	Arc	2	2	1,669-1,718	1,880-1,912	0,934-0,960
<i>L. inaequilatera</i> (Rusby) Bitter	3	Arc	2	2	1,389-1,479	1,484-1,644	0,526-0,538
<i>L. lasiophyla</i> (Hub. & Bonpl. Ex Dunal) Bitter	2	Arc	2	2	1,133-1,280	1,247-1,422	0,520-0,619
<i>L. lenta</i> (Cav.) Bitter	3	Arc	1	2	1,576-1,616	1,880-1,882	1,010-1,012
<i>L. multiflora</i> Bitter	3?	Arc	2	2	1,090-1,113	1,368-1,523	0,648-0,667
<i>L. nitida</i> Bitter	3	Arc	1	4	1,240-1,446	1,971-2,254	0,980-1,032
<i>L. pauciflora</i> (Vahl.) Bitter	2	Arc	1	2	1,189-1,201	1,408-1,420	0,580-0,587
<i>L. pilifera</i> (Benth.) Bitter	2	Arc	2	2	1,271-1,289	1,477-1,492	0,629-0,654
<i>L. quichensis</i> (Coult & Donn. Sm.) Bitter	4	Arc	2	2	0,910-1,198	1,069-1,345	0,554-0,769
<i>L. radiata</i> (Sendtn.) Bitter	3	Arc	1	4	1,338-1,368	1,324-1,374	0,540-0,631
<i>L. sanctaeclarae</i> (Greenman) D'Arcy	3	Arc	1	2	1,574-1,681	2,149-2,263	0,737-1,046
<i>L. stenoloba</i> (van Heurck & Müll. Arg.) Bitter	4	Arc	2	2	1,064-1,262	2,179-2,197	0,770-0,866
<i>L. stephanocalyx</i> (Brandeggee) Bitter	2	Arc	2	2	1,544-1,564	1,541-1,660	0,657-0,676
<i>L. synanthera</i> (Sendtn.) Bitter	4	Arc	1	2	1,148-1,125	1,313-1,250	0,649-0,677
<i>L. tricolor</i> (Sessé & Moc. ex Dunal) Bitter	2	Arc	1	2	1,215-1,220	0,990-0,994	0,425-0,479

Figure 1- Leaf epidermis in front view. A-B. Hypostomatic leaf of *L. acutifolia*: A. Adaxial surface; B. Abaxial surface with anisocytic and anomocytic stomata. C-D. Hypostomatic leaves of *L. amatitlanensis*: C. Adaxial surface; D. Abaxial surface with anisocytic stomata. E-F. Amphistomatic leaf of *L. asarifolia*: E. Adaxial surface; F. Abaxial surface with anisocytic stomata. G-H. Hypostomatic leaf of *L. bitteri*: G. Adaxial surface; H. Abaxial surface with anisocytic and anomocytic stomata. Legend, **ani**: anisocytic stomata; **ano**: anomocytic stomata, **tri**: Trichome.

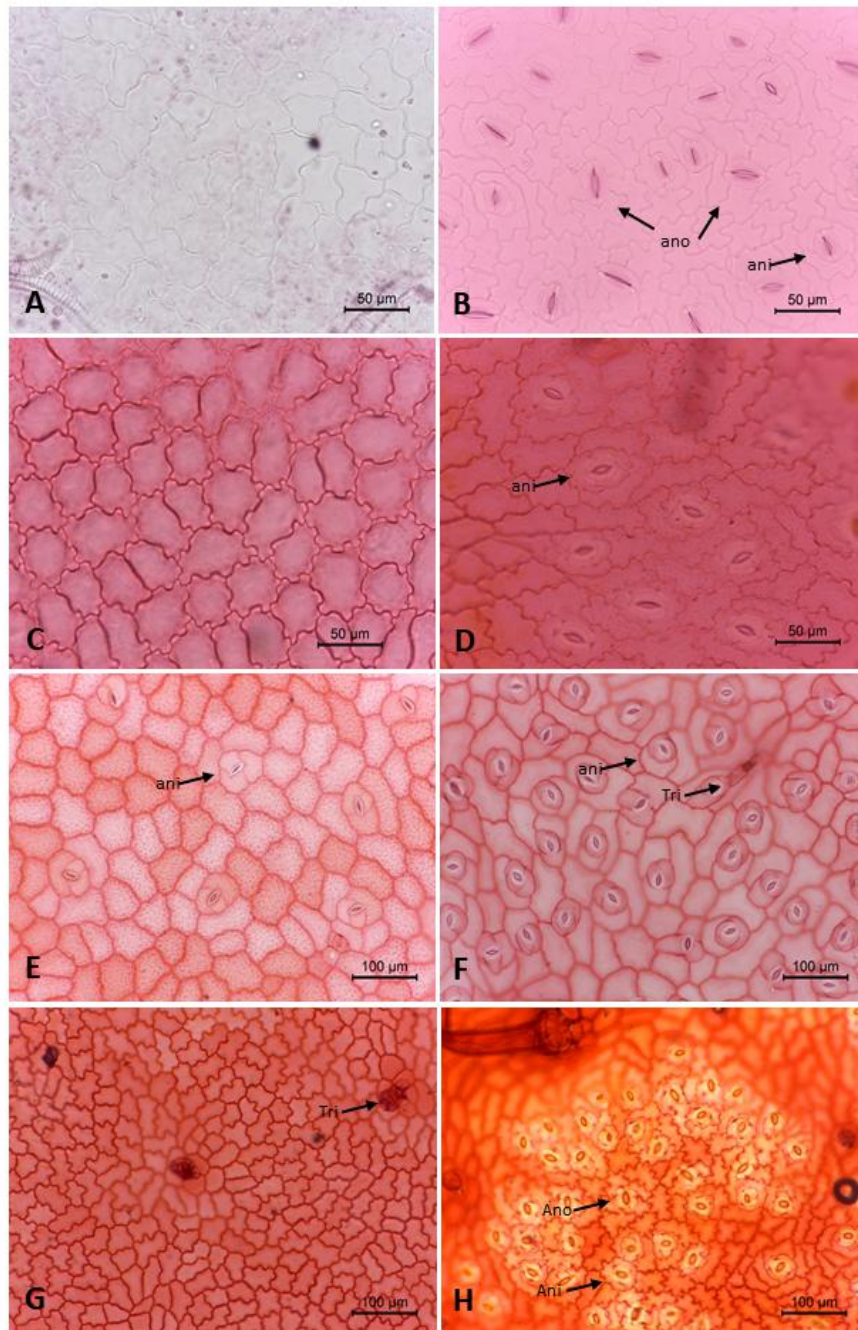


Figure 2- Leaf epidermis in front view. A-B. Hypostomatic leaf of *L. cearaensis*: A. Adaxial surface with stellate trichomes and glandular trichomes; B. Abaxial surface with anisocytic and anomocytic stomata and stellate trichomes. C-D. Amphihypostomatic leaf of *L. coffeifolia*: C. Adaxial surface with anisocytic stomata; D. Abaxial surface with anisocytic stomata. E-F. Amphihypostomatic leaf of *L. compressibaccata*: E. Adaxial surface with anisocytic and anomocytic stomata; F. Abaxial surface with anisocytic and anomocytic stomata. G-H. Amphistomatic leaf of *L. fasciculata*: G. Adaxial surface with anisocytic and anomocytic stomata; H. Abaxial surface with anisocytic and anomocytic stomata. Legend, **ani**: anisocytic stomata; **ano**: anomocytic stomata..

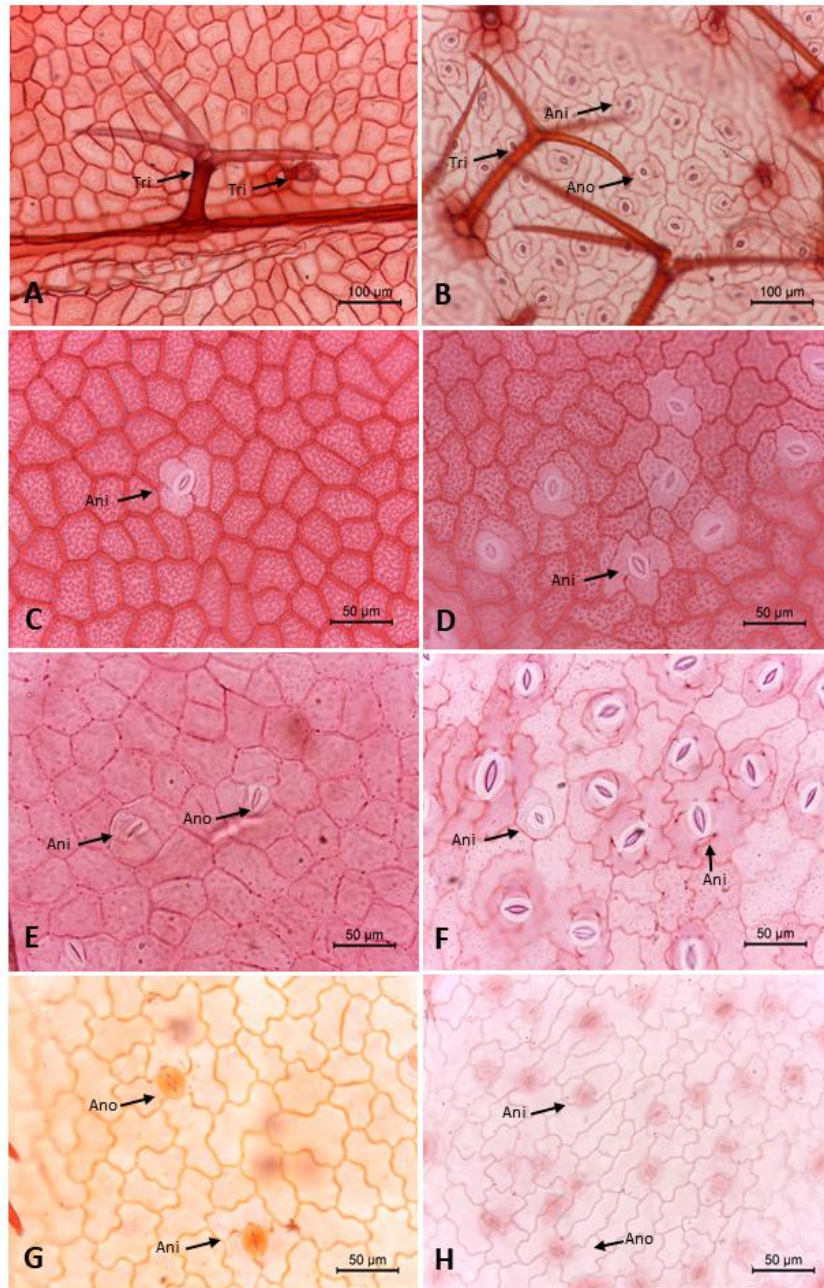


Figura 3-Leaf epidermis in front view. A-B. Hypoestomatic leaf of *L. ferruginea*: A. Adaxial surface; B. Abaxial surface with anisocytic and anomocytic stomata. C-D. Hypoestomatic leaf of *L. furcatistellata*: C. Adaxial surface; D. Abaxial surface with anisocytic and anomocytic stomata. E-F. Amphistomatic leaf of *L. glandulosa*: E. Adaxial surface with anisocytic and anomocytic stomata; F. Adaxial surface with anisocytic and anomocytic stomata. G-H. Amphistomatic leaf of *L. heteroclita*: E. Adaxial surface with anisocytic, anomocytic stomata and papilla; F. Abaxial surface with anisocytic and anomocytic stomata; pediculated glandular trichoma. Legend, **ani**: anisocytic stomata; **ano**: anomocytic stomata; **tri**: trichome; **pap**: papilla.

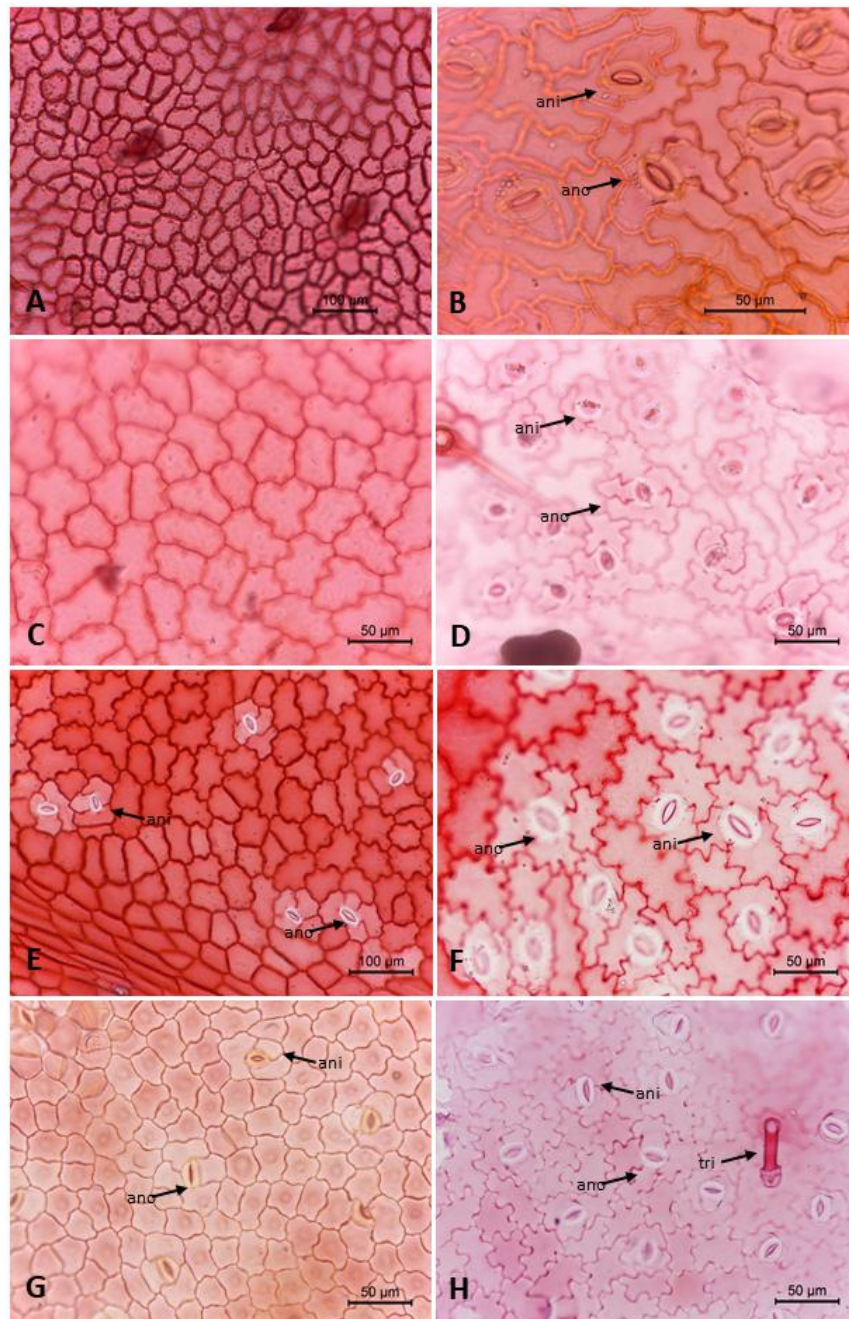


Figure 4. Leaf epidermis in front view. A-B. Hypostomatic leaf of *L. medusocalyx*: A. Adaxial surface, showing simple trichoma; B. Abaxial surface with anisocytic and anomocytic stomata; pedicled glandular trichoma. C-D. Hypoestomatic leaf of *L. multiflora*: C. Adaxial surface; D. Abaxial surface with anisocytic and anomocytic stomata. E-F. Amphistomatic leaf of *L. nitida*: E. Adaxial surface; F. Abaxial surface with anisocytic and anomocytic stomata. G-H. *L. pauciflora*: G. Adaxial surface; H. Abaxial surface with anisocytic and anomocytic stomata. Legend, **ani**: anisocytic stomata; **ano**: anomocytic stomata.

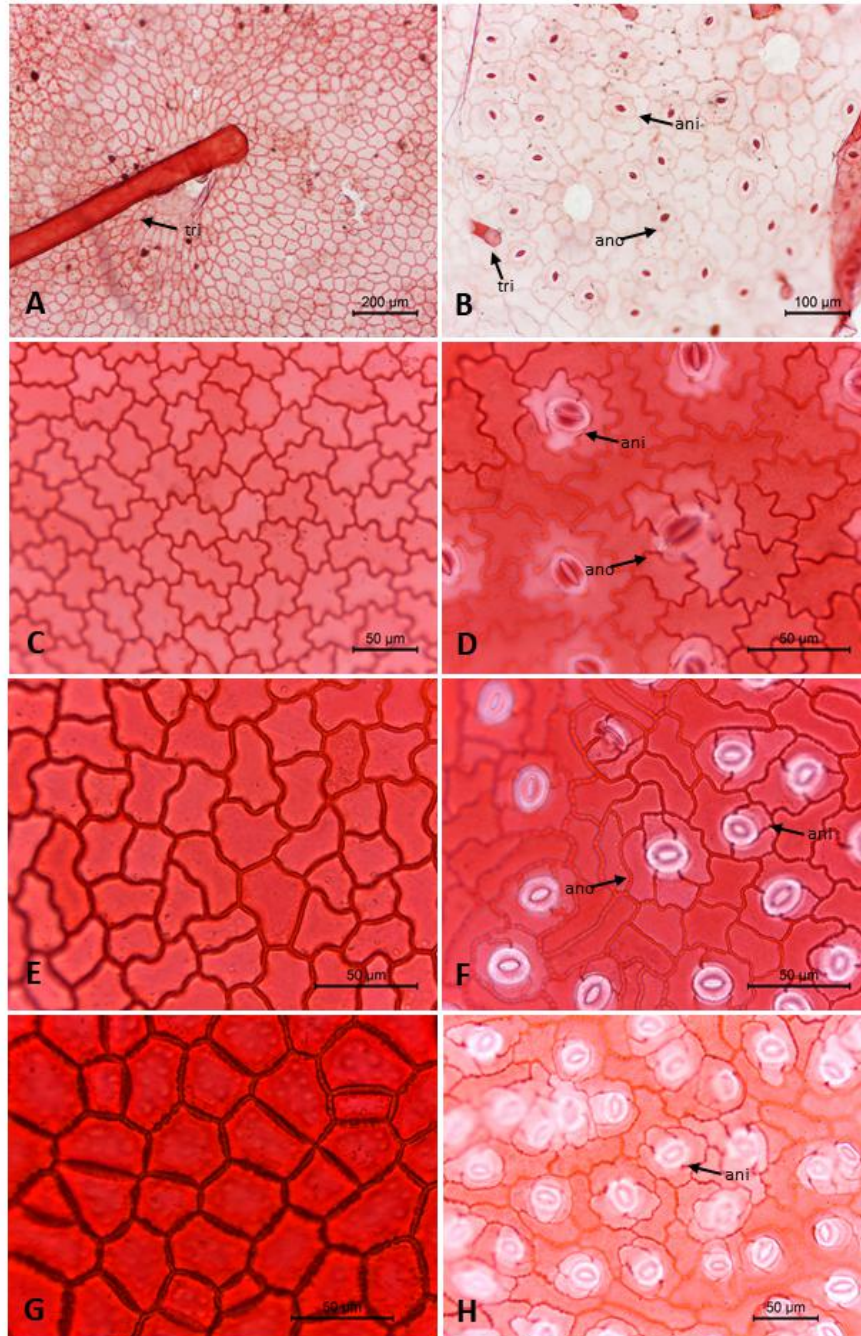


Figura 5- Leaf epidermis in front view. A-B. Amphistomatic leaf of *L. quichensis*: A. Adaxial surface with anisocytic stomata; B. Abaxial face with anisocytic and anomocytic stomata; pediculated glandular tricoma. C-D. Hypostomatic leaf of *L. radiata*: C. Adaxial surface; D. Abaxial surface with anisocytic and anomocytic stomata. E-F. *L. sancataeclarae* amphistomatic leaf: E. Adaxial surface; F. Abaxial face with anisocytic and anomocytic stomata. G-H. Hypostomatic leaf of *L. stephanocalyx*: G. Adaxial surface; H. Abaxial surface with anisocytic stomata. Legend, **ani**: anisocytic stomata; **ano**: anomocytic stomata.

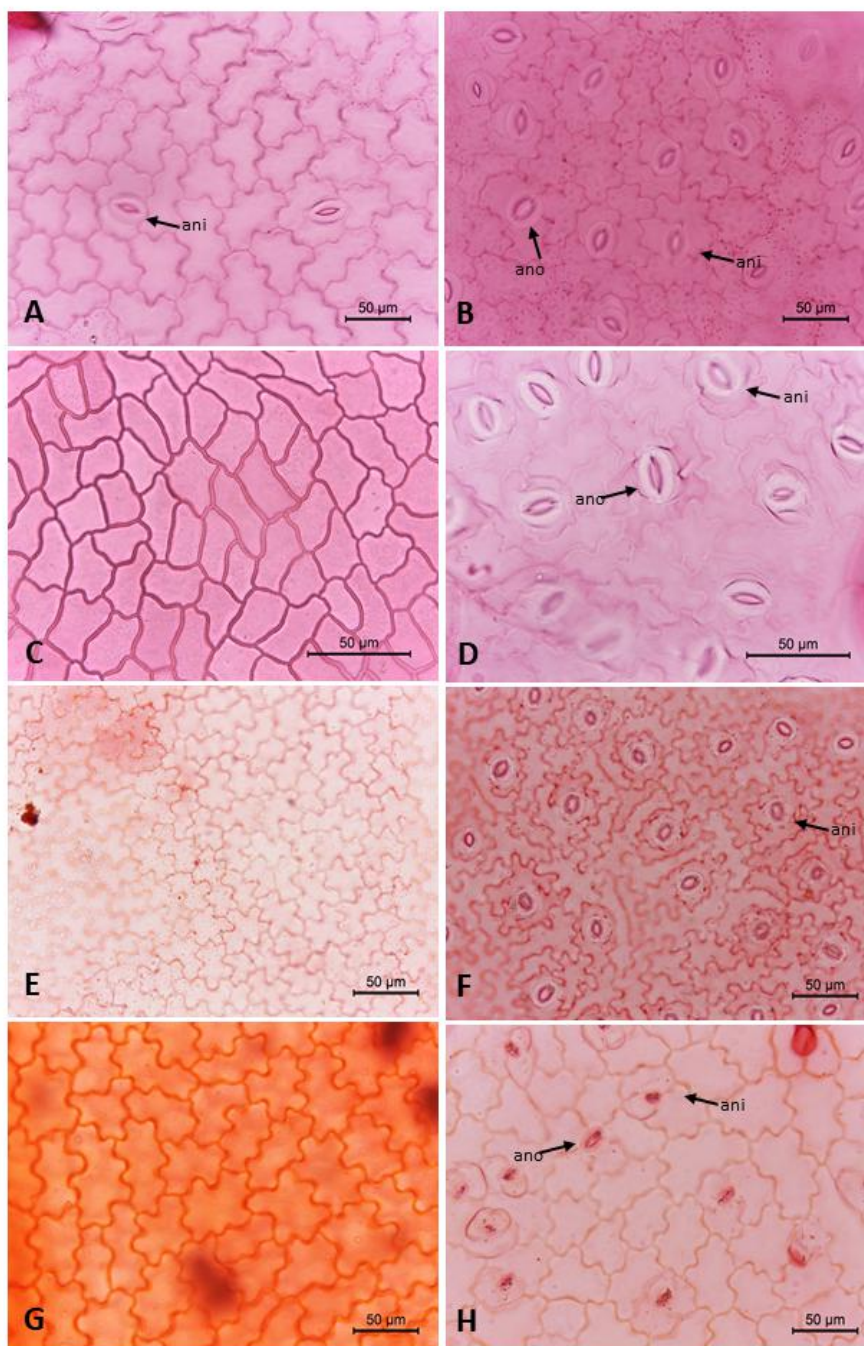


Figure 6-Leaf epidermis in front view. A-B. *L. synanthera* amphistomatic leaf: A. Adaxial surface with anisocytic stomata; B. Abaxial surface with anisocytic and anomocytic stomata. C-D. Hypostomatic leaf of *L. inaequilatera*: C. Adaxial surface with simple trichomes; D. Abaxial surface with anomocytic stomata. E-F: Hypostomatic leaf of *L. stenoloba*: E- Adaxial papillose surface; F. Abaxial surface with anomocytic stoma. Legend, **ani**: anisocytic stomata; **ano**: anomocytic stomata; **tris**: simple trichome; **trist**: setose trichome.

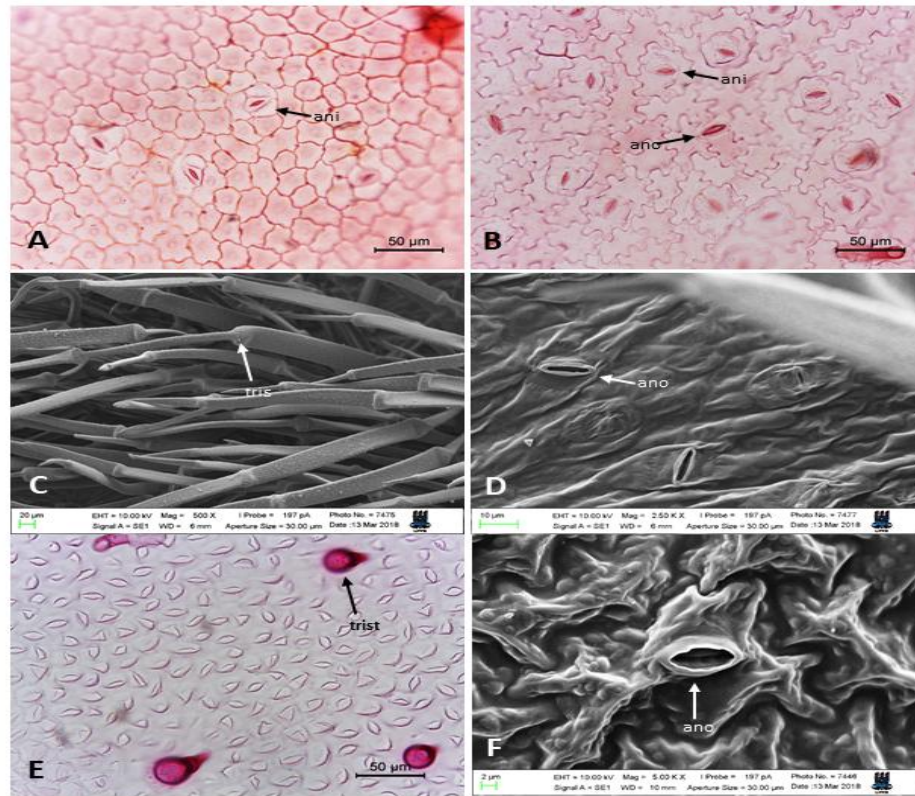


Figure 7. Papillae and types of trichome. **A-C.** Papillae on the adaxial surface **A.** *L. compressibaccata*; **B.** *L. heteroclita*; **C.** *L. syanthera*. **D-E.** Glandular pediculated trichomes: **D.** *L. asarifolia*; **E.** *L. ferruginea*. **F-L.** Simple multicellular uniseriate trichomes: **F.** *L. amatitlanensis*; **G.** Detail evidencing epicuticular wax granules on the surface of the trichome. **H.** *L. fasciculata*; **I.** *L. stephanocalyx*; **J-K.** *L. compressibaccata*; **L.** *L. quichensis*. **M-O.** Setose trichomes: **M.** *L. coffeifolia*; **N.** *L. heteroclita*; **O.** *L. stenoloba*; **P-Q.** Sessile stellate trichomes: **P.** *L. furcatistellata*; **Q.** *L. multiflora*. **R-V.** Pediculate stellate trichomes: **R.** *L. cearaensis*; **S.** *L. bitteri*; **T.** *L. ferruginea*; **U.** *L. glandulosa*; **V.** *L. pauciflora*. **W-X.** Branched trichomes: **W.** *L. fasciculata*; **X.** *L. sanctaeclarae*. **Y.** Dendritic trichomes in *L. bitteri*. **Z.** Bifurcate trichomes in *L. sanctaeclarae*. **AA.** Crystal-type epicuticular wax granules in *L. coffeifolia*.

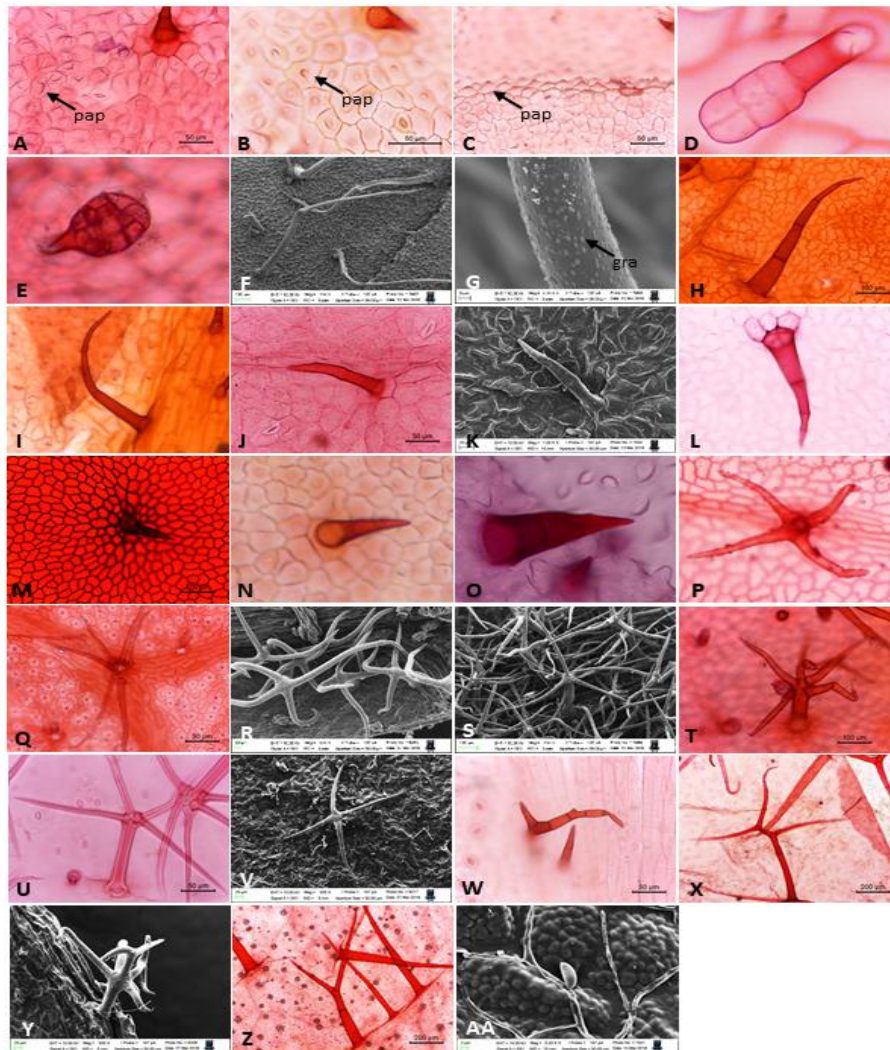
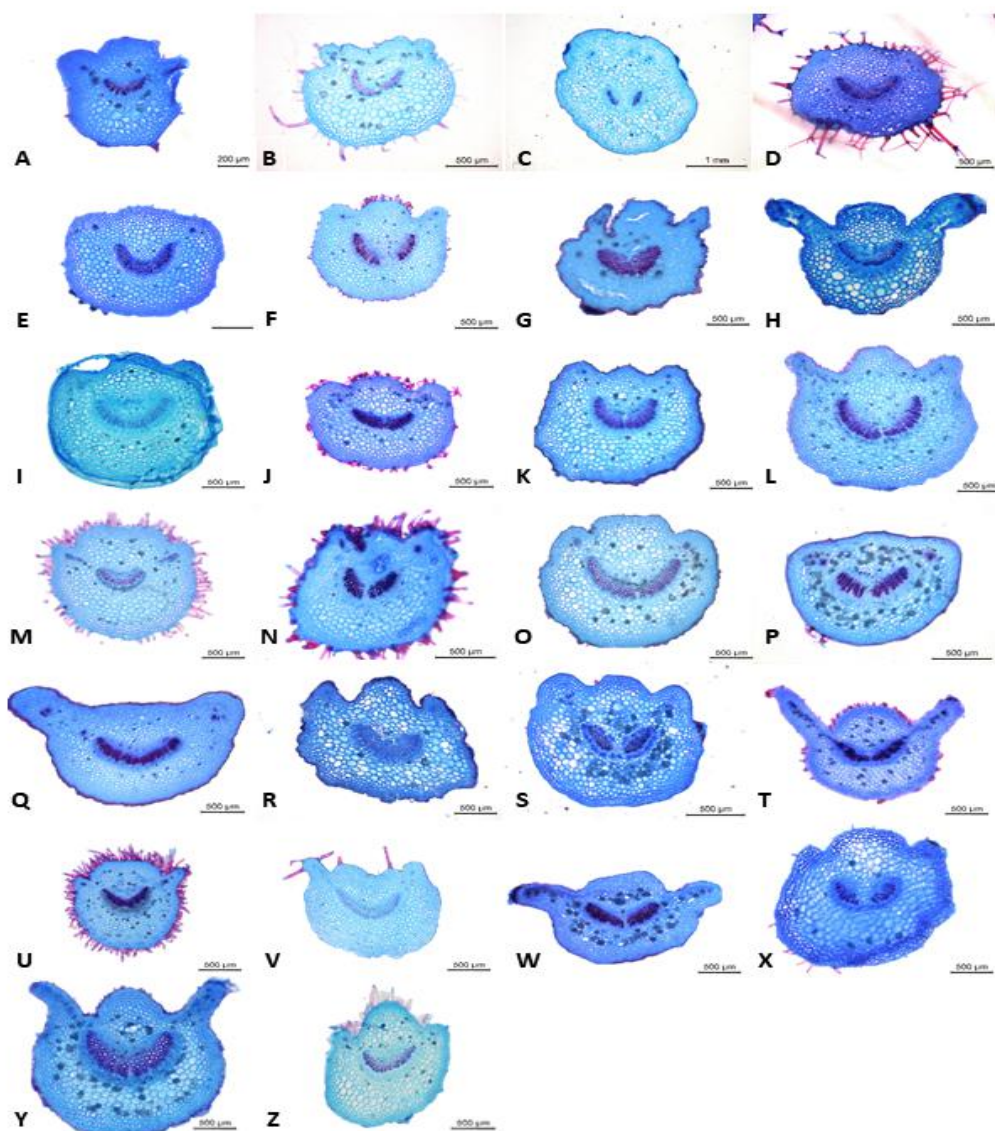


Figure 8. Outline of petioles of analysed species of *Lycianthes* subg. *Polymeris*. **A.** *L. acutifolia*; **B.** *L. amatitlanensis*; **C.** *L. asarifolia*; **D.** *L. bitteri*. **E.** *L. ceareaensis* Bitter; **F.** *L. coffeifolia*; **G.** *L. compressibaccata*; **H.** *L. fasciculata*; **I.** *L. ferruginea*; **J.** *L. furcatistellata*; **K.** *L. glandulosa*; **L.** *L. heteróclita*; **M.** *L. inaequilatera*; **N.** *L. lasiophylla*; **O.** *L. lenta*; **P.** *L. multiflora*; **Q.** *L. nitida*; **R.** *L. pauciflora*; **S.** *L. pilifera*; **T.** *L. quichensis*; **U.** *L. radiata*; **V.** *L. sanctaeclarae*; **W.** *L. stenoloba*; **X.** *L. stephanocalyx*; **Y.** *L. synanthera*; **Z.** *L. tricolor*..



4 FINAL CONSIDERATIONS

With the conclusion of this study, the knowledge of *Lycianthes* for Brazil has advanced in several aspects.

Although the number of species represented for Brazil did not have an expressive increase, the delimitation of some species is more precise, as in the case of the *L. pauciflora/L.cearaensis/L. bitteri* group and *L. asarifolia/L. repens* group. Thus, with the proposition of a new species, a new combination, 14 lectotypifications and five new synonyms, 12 species of *Lycianthes* are recognized for Brazil.

The analyzed leaf morphoanatomical data are useful to solve taxonomic issues, helping to delimit some infrageneric taxa, especially in the series levels and interspecific issues.

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APÊNDICE A – ARTIGO PUBLICADO NA PHYTOTAXA

Artigo “Lectotypifications of six taxa in *Lycianthes* (Solanaceae)” publicado no periódico Phytotaxa. DOI: <https://doi.org/10.11646/phytotaxa.348.4.6>



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Lectotypifications of six taxa in *Lycianthes* (Solanaceae)

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Lycianthes comprises about 200 species, distributed mostly in the Neotropics but with 30 species in the Old World. It is a taxonomically complex group, and for more than a century its species were treated as part of *Solanum*. Together with *Capsicum* it constitutes the tribe Capsiceae. In this work six new lectotypes are designated for the following taxa of *Lycianthes*: *L. acutangula* (Griseb.) Bitter ssp. *compressibaccata* (Bitter) Bitter, *L. ceareaensis* Bitter, *L. coffeifolium* Bitter, *L. longidentata* Bitter, *L. ullei* Bitter, and *Solanum asarifolium* Kunth & Bouché. *Lycianthes ceareaensis* is shown to be distinct from *L. pauciflora* (Vahl) Bitter and *Lycianthes amatilanensis* (Coul. & Donn. Sm.) Bitter to be distinct from *Lycianthes inaequilatera* (Rusby) Bitter.

Keywords: Brazil, Capsiceae, lectotype, *Solanum*, Solanoideae, South America

Introduction

Lycianthes Hassler (1917: 180) comprises about 200 species with a nearly cosmopolitan distribution, and, together with *Capsicum* L. (1753:185), constitutes the tribe Capsiceae D'Arcy (1996: 273), according to Olmstead *et al.* (1999) and Särkinen *et al.* (2013). For more than a century, species belonging to *Lycianthes* were included in *Solanum*. The genus *Lycianthes* was formally proposed by Hassler (1917: 180), based on the presence of stone cells in the fruits, axillary inflorescences, calyx appendages (sometimes called teeth) that emerge below the truncated calyx edges, subtrotate to rotate (stellate) corollas, and poricidal anthers.

The circumscription of *Lycianthes* was expanded by Bitter (1919) to include 132 species, 52 varieties, and one form. Of these, 84 names were new combinations of taxa previously included in *Solanum* subsect. *Lycianthes* Dunal (1852: 156), and 48 were proposed as new species. In his work, Bitter (1919) for the first time suggested the morphological affinity of *Lycianthes* with *Capsicum* based on the calyx morphology. Bitter's work on *Lycianthes* is still the most comprehensive treatment for the genus, although about 80 new species have since been proposed (D'Arcy 1973; Gentry & Standley, 1973; Barbosa & Huzinker, 1992; Rojas & D'Arcy, 1997; Dean, 1994, 1998, 2014; Orozco *et al.* 2008).

Of the 202 new taxa proposed by Bitter (1919), about 70 had their type specimens deposited at the Berlin Herbarium (B). Most of these, however, are not there now as the Berlin Herbarium was largely destroyed in 1943 during the Second World War, a great loss to science, as thousands of type specimens were destroyed (Merrill, 1943; Tiepko, 1987). Although a few specimens of the Solanaceae survived, only one specimen of *Lycianthes*, the type of *Lycianthes hypomalaca* Bitter (1919: 344), is accounted for in the current Berlin Herbarium database.

The Neotropical region was a field of interest for the Berlin Herbarium, which consequently housed numerous types from the Neotropical region (Grimé & Plowman 1986: 932). Among these collections, those by the German botanist Ernst Ule stand out. These were incorporated into the Berlin Herbarium (B) in 1915 (Tiepko, 1987), and used by Bitter (1919) in his treatment of *Lycianthes*. Several new species were based on Ule's collections including, *L. ceareaensis*, *L. coffeifolium*, *L. longidentata*, *L. ullei* and *Solanum compressibaccatum*, *inter alia*.

Another important private collection was that of G.S. Knuth, which was incorporated in the Berlin Herbarium in the 1830s when he became deputy director of the Botanical Garden (Tiepko, 1987). From this collection came the material analyzed by him for the description of *Solanum asarifolium*, which was cultivated in the Botanical Garden of Berlin (Ind. Sem. Hort. Berol. 10, 1845) from seeds sent by E. Otto from Caracas. In our revision of the genus *Lycianthes* for the Flora of Brazil, specimens were compared with type collections and images available online from the following herbaria (the acronyms follow Thiers, 2017), ALCB, AWH, BM, BR, BREM, C, E, EAN, F, G, GH, HBG, HUJES, IAN, INPA, IPA, JPB, K, L, M, MG, MO, NY, P, R, RB, S, U, UJFP, US, and W.

We have chosen lectotypes for the species whose types were lost in the Berlin Herbarium, according to Article 9.2 of the International Code of Nomenclature for algae, fungi and plants (ICN, McNeill *et al.*, 2012). We have given priority to isotypes and collections cited by Bitter (1919), many of which were annotated by him and have his own signature. All material indicated as lectotype and isolectotype conform to the protologues, and the photographs taken by MacBride, whose negatives are deposited at the Herbarium of Field Museum of Natural History (F) and available in the Field Museum botany collection database.

In the type citation, the word “photo” refers to phototype or a printed image deposited in a herbarium, available online in the herbaria databases or in sites such as JSTOR Plants. Barcode numbers are given after the acronyms. If the barcode isn’t available, the acronym is followed by the accession number. When the typified name is not an accepted name, the accepted name is given immediately after the type designation.

1. *Lycianthes cearaensis* Bitter, Abh. Naturwiss. Vereine Bremen 24: 346. 1919

Type:—BRAZIL. Ceará: Serra de Maranguape, 600 m, Oct 1910, *E. Ule 9103* (Holotype B†, photo of holotype F-2564); lectotype: NY00138709!, designated here; isolectotypes: K000585757!, L0003587!, US00027870!.

Notes. The holotype of *Lycianthes cearaensis* was deposited in B (Bitter 1919), but destroyed during World War II. We have located four specimens of *E. Ule 9103*, which have handwritten notes made by Bitter, and are designating here the most complete and well-preserved specimen (NY 138709) as the lectotype for *L. cearaensis*.

Lycianthes cearaensis was treated in the Flora of Brasil (2017) as a synonym of *L. pauciflora* (Vahl) Bitter (1919: 341). However, after analyzing the types and herbarium material of these two taxa, we confirm that they are distinct, and can be distinguished by leaf morphology, indumentum, calyx appendages, and ovary format. *Lycianthes cearaensis* has elliptic to narrowly elliptic leaves, tomentose indumentum on the abaxial leaf surface, a cupuliform calyx with curved appendages in fruit, and an ovoid ovary. *Lycianthes pauciflora* differs in the ovate to ovate-elliptic leaves, lax indumentum, pateliform calyx with reflexed appendages in fruit, and a globose ovary.

2. *Solanum compressibaccatum* Bitter, Repert. Spec. Nov. Regni Veg. 12: 456. 1913

Type:—PERU. Dept. Loreto: Cerro de Ponasa, 1200 m, Feb 1903, *E. Ule 6800* (Holotype B†, photo of holotype F-2560!; lectotype HBG511426!, designated here; isolectotypes: CORD 00004168!, G! [without barcode], K000585774!, L0403129!).

Accepted name. *Lycianthes leptocaulis* (Rusby) Rusby (1926: 210).

≡ *Brachistus leptocaulis* Rusby (1899: 26). Type:— Bolivia, Dept. La Paz, Prov. Larecaja, Guanay, 2000 ft, Maio 1886, *H. Rusby 2657* (NY138557!)

Notes. *Solanum compressibaccatum* was described by Bitter (1913: 456) based on *E. Ule 6800*, a plant with a climbing habit from Amazonian Peru. Subsequently, Bitter (1919: 358) transferred it to *Lycianthes* as *Lycianthes acutangula* (Griseb.) Bitter ssp. *compressibaccata* (Bitter) Bitter. The holotype deposited at B was destroyed during World War II, and here we are designating the isotype deposited at HBG as the lectotype. This specimen was identified by Bitter himself, and is in good condition with flowers, fruits and leaves.

The specimen of *Ule 6800* at HBG is annotated as an isotype of *Lycianthes stenoloba* (Van Heurck & Muell. Arg.) Bitter (1919: 358). However, this designation is incorrect since the type material of *Lycianthes stenoloba* is *R. Spruce 4210* which was deposited in the Van Heurck Herbarium, now incorporated in the herbarium of the Botanic Garden Meise (BR). The basionym of this species is *Solanum stenolobum* Van Heurck & Muell. Arg. (in Van Heurck, 1870: 69) collected at Tarapoto, Peru.

3. *Lycianthes coffeifolia* Bitter, Abh. Naturwiss. Vereine Bremen 24: 432. 1919

Type:—BRAZIL. Amazonas: Acre-gebiet, Monte Mo, Nov 1911, *E. Ule 9737* (Holotype B†, photo of holotype F-2566!); lectotype US00027875!, designated here; isolectotypes: G00446591! [two sheets], K000585765!, L2881751!.

= *Solanum coffeifolium* (Bitter) C. V. Morton (1944:64).

Notes. *Lycianthes coffeifolia* was placed by Bitter in section *Simplicipila* Bitter. The holotype was *E. Ule 9737*, deposited at the Berlin herbarium (B) and evidently destroyed. The isotypes in G, K, L and US are all in good condition. Those in G and US are well preserved with developed leaves, floral buds, flowers and fruits, while those at K and L only have vegetative shoots with fruits. We choose as lectotype the isotype at US (US-00027875), which is clearly annotated by Bitter. The duplicates at G, K and L are designated as isolectotypes.

4. *Lycianthes longidentata* Bitter, Abh. Naturwiss. Vereine Bremen 24: 356. 1919

Type:—BRAZIL. Amazonas: Rio Acre, Estella, Seringal São Francisco, Mar 1911, *E. Ule* 9733 (Holotype B†, photo of holotype F-2582!; lectotype NY00138711!, designated here; isoelectotypes: K000585776!, L2881557!, MG14567!, S042937!, U0113835!, US00027888!).

Accepted name. *Lycianthes leptocaulis* (Rusby) Rusby (1926: 210).

≡ *Brachistus leptocaulis* Rusby (1899: 199).

= *Solanum longidentatum* (Bitter) C. V. Morton (1944: 64).

Notes. *Lycianthes longidentata* was described by Bitter in *Lycianthes* sect. *Eupolymeris* Bitter (1919: 331) based on the calyx having 10 appendages in two unequal series, which reach up to 1 cm in length, and stamens with unequal filament lengths. Bitter cited the holotype at Berlin (B), which was destroyed in 1943. The isotype deposited at New York (NY138711) is chosen as lectotype as it is in good condition with flowers and fruits. It bears the label “Ex. Mus. Bot. Berol”.

5. *Lycianthes ulei* Bitter, Abh. Naturwiss. Vereine Bremen 24: 437. 1919

Type:—BRAZIL. Amazonas: Rio Acre, Seringal São Francisco, Apr 1911, *E. Ule* 9764 (Holotype B†, photo of holotype F-2592!; lectotype NY-00138719! designated here; isoelectotypes G! [without herbarium number], K000585766!, L2881358!, MG14596!, U0113836!, US00027900!).

Accepted name. *Lycianthes amatitlanensis* (Coul. & Donn. Sm.) Bitter (1919:441).

Notes. The holotype was deposited in B but was destroyed in 1943. We are designating the specimen at New York (NY) as lectotype. This is in good condition and is the only duplicate that has the annotation “Ex. Mus. Bot. Berol”.

Martinez *et al.* (2002) and Jorgensen *et al.* (2014) consider *Lycianthes amatitlanensis* to be a synonym of *Lycianthes inaequilatera* (Rusby) Bitter (1919: 439). However, examination of the types of these taxa clearly indicates them to be different species. *Lycianthes amatitlanensis* can be recognized for having erect branches, shiny leaves, and conspicuous calyx appendages (2.0-3.0 mm long), which are linear and pilose at anthesis. On the other hand, *Lycianthes inaequilatera* has zig zag branches, dull leaves, inconspicuous calyx appendages, less than 1 mm long, which are glabrescent at anthesis. We consider *Lycianthes amatitlanensis* is a distinct taxon and not synonymous with *L. inaequilatera*, thus corroborating the previous observations of Rojas and Darcy (1997) and Bohs (2015).

6. *Solanum asarifolium* Kunth & Bouché, Ind. Sem. Hort. Berol. 10. 1845

Type:—A plant cultivated in Berlin in 1842 from seeds from Venezuela, Caracas, *E. Otto* s.n. (Holotype: B†, photo of holotype F-2562!; lectotype: P00430541!, designated here).

Accepted name. *Lycianthes asarifolia* (Kunth & Bouché) Bitter (1919:423).

Notes. The unnumbered collection of *E. Otto* at the Muséum National d’Histoire Naturelle of Paris (P-430541) donated by the Herbarium of Berlin in 1855 is designated as lectotype. The lectotype is in good condition, showing a plant with roots, two well-developed leaves, and one flower. It corresponds to the protologue of *Solanum asarifolium* Kunth & Bouché and is the only collection of Otto we have located.

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APENDICE B – ARTIGO PUBLICADO NA NORDIC JOURNAL OF BOTANY

Artigo “Updates in *Lycianthes* (Solanaceae): a new species from Brazil, notes on taxonomy, and a key to identification of Brazilian species” publicado no periódico Nordic Journal of Botany. DOI: 10.1111/njb.01949

NORDIC JOURNAL OF BOTANY

Research

Updates on *Lycianthes* (Solanaceae): a new species from Brazil, notes on taxonomy, and a key to identification of Brazilian species

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During studies of the genus *Lycianthes* as part of a taxonomic treatment for the Brazilian flora, a new species, *Lycianthes bitteri* Costa-Silva & Agra, was recognized from Bahia State, which is described and illustrated here. It is member of *Lycianthes* subg. *Polymeris* and related to *L. pauciflora* (Vahl) Bitter and *L. cearaensis* Bitter, from which it differs by having petioles depressed adaxially, calyx with linear appendices in two series, radiate and widely spreading, ovary somewhat conical, and indument composed of a mix of dendritic and stellate trichomes. Information about its distribution, conservation status, and affinities with other *Lycianthes* species are discussed. Additionally, four new synonyms and a lectotypification are proposed, and a key to all Brazilian *Lycianthes* species is presented.

Keywords: *Lycianthes bitteri*, Capsicaceae, *Solanum*

Introduction

According to the Solanaceae Source (2017), *Lycianthes* (Dunal) Hassler comprises approximately 207 species with distributions mainly in the neotropics, from Mexico to Argentina, but also in the Old World, with approximately 30 species occurring in Asia and Australia (Dean 2004, Dean et al. 2017).

Lycianthes was considered a part of the genus *Solanum* for more than a century. They were segregated, however, and formally proposed as a new genus by Hassler (1917), based mainly on anatomical studies that revealed the presence of stone cells in the fruit endocarp – a characteristic thought to differentiate the two genera. In his monograph of *Lycianthes*, Bitter (1919) divided the genus into four subgenera, seven sections, and 15 series. He was the first to suggest an affinity between *Lycianthes* and *Capsicum* due to similarities between their calyx morphologies (with five to ten appendages, or teeth, often emerging below the truncate margin). The anatomical studies of D’Arcy (1986) established those teeth as extensions of the calyx vascular bundles.



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Molecular studies (Olmstead and Palmer 1997, Bohs and Olmstead 1997, Olmstead et al. 2008, Särkinen et al. 2013) have supported *Lycianthes* and *Capsicum* as sister groups constituting the tribe Capsiceae, as had been suggested by Bitter (1919). Those studies also highlighted the remoteness of *Lycianthes* from *Solanum*, in spite of their shared characters, e.g. poricidal anthers and lack of nectar.

According to the 'Flora do Brasil 2020' (in preparation), an estimated nine species of *Lycianthes* occur in Brazil, with the greatest diversity in the northern region of the country (with six species). The distributions of those species fall within a wide range of phytogeographical domains, such as the Amazon, Cerrado, Atlantic Rainforest and Pantanal, composing phytophysiognomies of *campinarana* forests, highland floodplain forests, semideciduous seasonal forests, and ombrophilous forests (Forzza et al. 2010).

While preparing a taxonomic review of *Lycianthes* as part of a treatment for the Brazilian flora, a new species, *Lycianthes bitteri* Costa-Silva & Agra, was recognized from Bahia State. Its distinctive morphological characters place it as a member of *Lycianthes* sect. *Eupolymeris* Bitter (1919), the largest section of *Lycianthes* subg. *Polymeris* with approximately 60 neotropical species. The section *Eupolymeris* is characterized by having a calyx with 10 unequal appendices, linear to subulate, and unequal stamens. The new species is described and illustrated here, with comments on its distribution, conservation status, and affinities with other *Lycianthes*. Additionally, five new synonyms and a lectotypification are proposed, and a key to all the Brazilian *Lycianthes* species is presented.

Material and methods

The studies here were based on observations of live plants in the field, of herbarium specimens for morphological and ecological data, and of type collections and images available online from the A, ALCB, AWH, BM, BR, BREM, C, CEPEC, E, EAN, F, G, GH, HBG, HUEFS, IAN, INPA, IPA, JPB, K, L, M, MA, MG, MO, NY, P, R, RB, S, U, UFP, US, and W herbaria. Figure 1 was prepared from digital photographs of fresh fertile plant material (flowers and fruits), as well as from rehydrated herbarium specimens. All specimens studied are cited in the text.

Lycianthes bitteri Costa-Silva & Agra sp. nov. (Fig. 1–3)

A species related to *L. pauciflora* (Vahl) Bitter and *L. cearaensis* Bitter, from which it differs by having a denser indument with stalked stellate and dendritic trichomes, petioles depressed adaxially, calyx with longer linear radiate and widely spreading appendices in two series in the fruiting calyx, and somewhat conical ovary.

Type: Brazil. Bahia: Municipality of Amargosa, Serra do Timbó, road to Barata Azul, 13°06'19"S, 39°40'32"W, 800 m a.s.l., 2 Dec 2009 (fl, fr), Agra et al. 7185 (holotype: JPB!, isotypes: NY!, RB!, UFP!).

Etymology

The specific epithet honors Georg Bitter, a German botanist who studied *Lycianthes*, and published the most complete taxonomic treatment for the genus, in recognition of his important botanical work, especially with this interesting and challenging genus of Solanaceae.

Description

Scandent shrub, 1.0–2.0 m tall, branched, perennial; branches and stems terete, ferruginous to brown, striate to rugose; indument stellate-puberulous, yellowish to ferruginous, with stellate trichomes sessile and short stalked with 3–6 lateral rays, and hyaline dendritic trichomes with branched lateral rays. Sympodial units difoliate, anisophyllous. Leaves alternate, simple; petiole short, 0.6–1.5 × 0.1–0.2 cm, depressed adaxially, tomentose, ferruginous, with stellate and dendritic trichomes similar to those of branches; blades chartaceous, 5.5–13.0 × 3.0–6.5 cm, weakly discolored, ovate to oval-elliptical, somewhat glossy on the adaxial surface, with 4–5 pairs of veins, impressed on the adaxial surface, prominent on abaxial surface, acute to acuminate at apex, with entire to slightly sinuate margin, at base cuneate, rounded, and subcordate, sparsely pilose on the adaxial surface with stellate trichomes on the blade and midrib, stellate-velutinous to stellate-tomentose on the abaxial surface; the trichomes stellate, stalked (stalk 2–3-celled), with dendritic trichomes on the abaxial midrib. Inflorescence an axillary, sessile fascicle of 1–3-flowers; pedicels slender in flower, 0.8–1.5 cm long, elongated in fruit, erect at maturity, terete, stellate-tomentose, with trichomes stalked, yellowish to ferruginous. Flowers perfect, pentamerous; calyx campanulate, truncate at apex, 6.0–7.0 × 8.0–9.0 mm, with 10 unequal appendages in two series emerging at 1.3–1.5 mm below the apex, the largest 3.0–6.5 mm long, the smallest 2.0–5.8 mm long, stellate-tomentose, with trichomes similar to those of the pedicels; corolla campanulate, white, 1.8–2.0 cm in diameter, its lobes elliptic, 1.5–1.7 × 0.3–0.4 cm, pilose on the outer surface, with interpetalar tissue glabrous and well-developed, 0.3–0.4 cm wide. Stamens 5, unequal (1+4): one with a larger filament, 4.5–5.0 mm long, 4 smaller ones with shorter filaments, 1.9–2.2 cm long; anthers yellow, attenuate from base to apex, the largest 6.0–6.2 mm long, the smaller 5.8–6.0 mm long, sub-sagittate to slightly asymmetric at base, 1.5–2.0 mm wide; anther pores extrorse. Ovary conical, glabrous, 2.0–2.1 × 1.5–1.7 mm; style glabrous 1.0–1.1 cm long, straight, slightly curved at apex; stigma oblong-clavate, 1.0–1.5 mm long, minutely papillose, bright green. Fruit globose, held upright, 1.5–2.0 cm in diameter, glabrous, orange when ripe, green to yellow-green when young, drying brownish, surrounded by the persistent, somewhat accrescent calyx; epicarp leathery; calyx appendages linear, widely spreading, unequal, in two series, the smallest 0.5–0.7 cm long, the largest 0.8–1.0 cm long, stellate-tomentose. Seeds up to 20, ovoid to subreniform, compressed; seed coat slightly wavy, reticulated, beige to light brown, 2.7–3.4 mm in diameter.

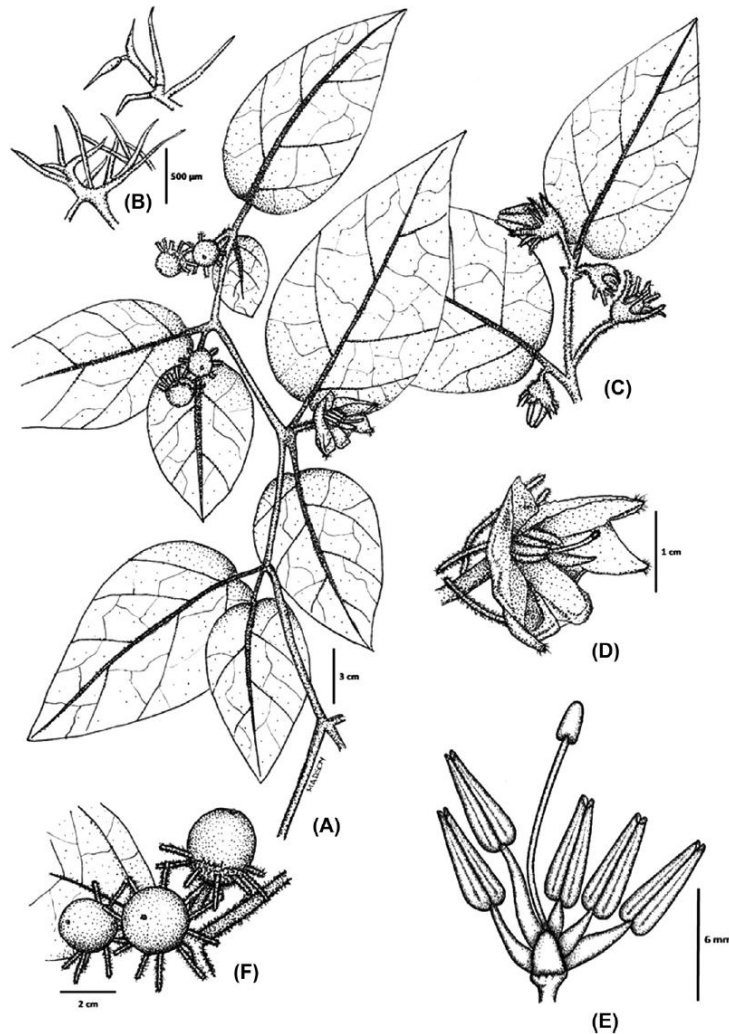


Figure 1. *Lycianthes bitteri* sp. nov. (A), (C) Flowering and fruiting branch, (B) detail of dendritic trichomes, (D) detail of the flower, (E) detail of the androecium and gynoecium, (F) fruiting branch. From Agra et al. 7185.

Distribution, habitat and ecology

Lycianthes bitteri is endemic to Bahia State, Brazil (Fig. 3). It has been collected along forest edges and in secondary forests from 40–900 m a.s.l. Few collections of this species are found in herbaria.

Lycianthes bitteri has been collected from two areas in Bahia, Serra do Timbó and Serra Bonita. The Serra do Timbó is a rugged mountain range covered mainly by semi-deciduous tropical forests, and reaching elevations between 800–900 m a.s.l. According to Ab'Saber (1977), Serra do Timbó is a transition area between the Caatinga, Cerrado and Atlantic Forest

phytophysiognomies. Most of the range has a humid tropical climate, although the region is surrounded by sub-humid and semi-arid areas.

The other locality where *L. bitteri* is found is Serra Bonita, which offers a unique habitat with altitudinal gradients of native Atlantic Forest ranging from 300 to 1080 m a.s.l. (Amorim et al. 2009). It is located in the Camacan basin and is characterized by a hot and humid climate (type Af; Köppen 1936) with the absence of a dry season. Flowering and fruiting samples were collected from December to June.

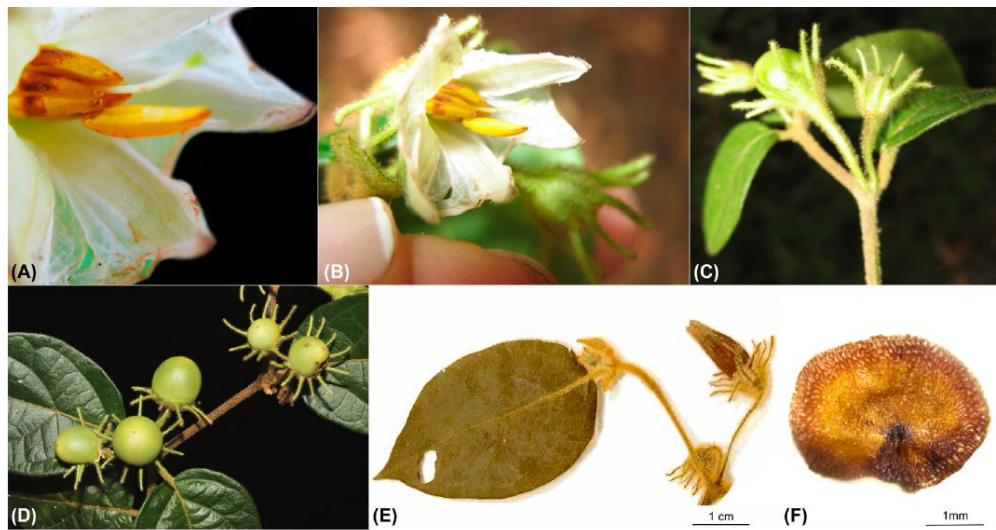


Figure 2. *Lycianthes bitteri* sp. nov. (A)–(B) detail of androecium in flower, showing unequal stamens with anther pores, (B) isolated flower (C) terminal branch with fruits, (D) fruits with calyxes with widely spreading appendages, (E) branch with flower bud, (F) seed. (A)–(C) photo by M. F. Agra, (D) photo by Domingos Cardoso. From Agra et al. 7185.

Conservation status

Due to insufficient data on population sizes and species abundances, *L. bitteri* should be classified as 'Data deficient' (DD), according to IUCN (2017) criteria.

Similar species

The morphological characters of *Lycianthes bitteri*, such as its scandent habit, ferruginous indument, and stellate trichomes place this species in *Lycianthes* subg. *Polymeris* sect. *Eupolymeris*.

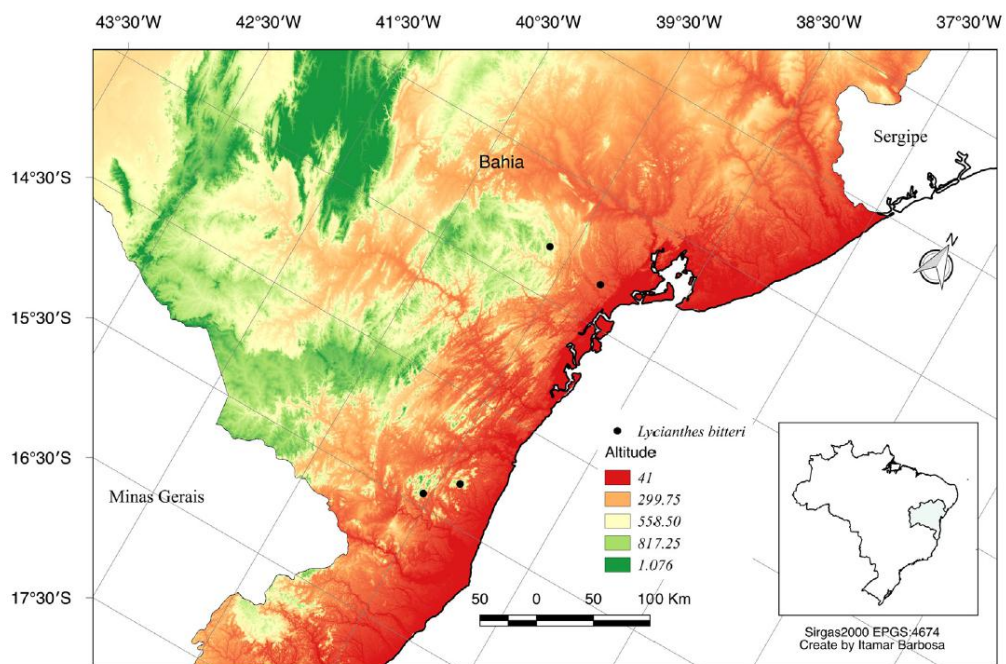


Figure 3. Map of the distribution of *Lycianthes bitteri* sp. nov. in Bahia State, Brazil.

ser. *Oligochondrae* Bitter (1919), which is characterized by an erect or scandent shrub habit, a rotate, campanulate to infundibuliform corolla, with unequal filaments, and non-connivent anthers. Some herbarium specimens of *L. bitteri* have previously been identified as *L. pauciflora* (Vahl) Bitter (1919), a name commonly associated with specimens that exhibit those characteristics and which occur from French Guiana and the Brazilian Amazon to the southeastern region of Brazil.

Lycianthes bitteri is most similar to *L. pauciflora* and *L. ceareaensis*, but can be distinguished from them by the presence of dendritic trichomes with bifurcate lateral rays. Dendritic trichomes do not occur on *L. ceareaensis* or *L. pauciflora*. Additionally, *L. bitteri* can be distinguished from *L. pauciflora* by its adaxially depressed petiole, and inflorescences held in the opposite direction of the leaves in the former, whereas in *L. pauciflora* the petiole is cylindrical, and the inflorescences are held in the same direction as the leaves. *Lycianthes bitteri* has a tomentose calyx with linear and longer appendices in the flowers, which are radiate and widely spreading, in two series, in the fruit, emerging near the edge of the calyx, whereas *L. pauciflora* has glabrous to glabrescent, shorter, and reflexed appendages, emerging below the apical 1/4 of the flower and fruit. The ovary is conical in *L. bitterii* and globose in *L. pauciflora*. The velutinous to tomentose indument of *L. bitteri* is dense and persistent even after drying, whereas *L. pauciflora* is glabrescent.

Lycianthes bitterii also shares some morphological characters with *L. ceareaensis* Bitter (1919), a species endemic to northeastern Brazil (the states of Alagoas, Ceará, Paraíba, and Pernambuco). It can be differentiated from *L. ceareaensis* by the latter having a canaliculate petiole, calyx with linear and uniseriate appendices, rounded at the apex, and by a tomentose indument on the branches, petioles and pedicels with only stalked stellate trichomes – differing from *L. bitteri*, which has the petiole depressed adaxially, calyx with linear unequal appendices in two series, and the indument on the branches, petioles and pedicels with dendritic trichomes. The characteristics of those three species can be found in Table 1.

Additional specimens examined (paratypes)

Brazil. Bahia: Municipality of Amargosa, Fazenda Mucuri, Riacho do Meio, study area of the Timbó Project/ Sapucaia Center 13°10'20"S, 39°9'34"W, 25 Jan 2007, Cardoso 1602 (HUEFS); Municipality of Arataca, Private Reserve

of Natural Patrimony (RPPN) Caminho das Pedras, at access trail to Peito-de-Moça, 15°10'25"S, 39°20'30"W, 15 Jun 2006, Amorim 6062 (CEPEC, NY); Municipality of Camacan, Private Reserve of Natural Patrimony (RPPN) Serra Bonita, 10 km west from Camacan at road to Jacareci, 6 km southwest, on road to RPPN and Transmission Tower, access trail to RPPN, 15°23'35"S, 39°33'53"W, 850 m a.s.l., 25 Mar 2007, Amorim 6958 (CEPEC, NY).

Notes on taxonomy

Taxonomic synonym: *Solanum compressibaccatum* Bitter (1913, p. 456) syn. nov.

Type: Peru. Department of Loreto: Cerro de Ponasa, 1200 m a.s.l., Feb 1903, E. Ule 6800 (B† =F photo 2560!, lectotype: HBG, barcode 511426 [photo!], isocotypes: CORD 4168 photo!, G! K 585774 [photo!]; MG 6634!). Designated by Costa-Silva and Agra (2018).

Based on the same type: *Lycianthes acutangula* (Griseb.) Bitter (nom. nud.) ssp. *compressibaccata* (Bitter) Bitter (1919 p. 358), comb. inval.

Accepted name: *Lycianthes leptocaulis* (Rusby) Rusby (1926, p. 210).

Type: Bolivia, Department of La Paz, Province Larecaja, Guanay, 2000 ft, May 1886, H. Rusby 2657 (holotype: NY 138557!).

Notes

Solanum compressibaccatum was proposed by Bitter (1913) and, according to the description in the protologue, it is a climbing plant, with geminate lanceolate leaves, acuminate at the apex, calyx with unequal linear appendages, white infundibuliform corollas, five unequal stamens, and globose berries. Bitter (1919) transferred it to *Lycianthes* as *L. acutangula* subsp. *compressibaccata*. The taxon *Lycianthes acutangula* (Griseb.) Bitter was proposed having as the basionym *Solanum acutangulum* Griseb., which, according to Article 32.1 and 38 of the Melbourne Code (McNeill et al. 2012) constitutes a nomen nudum, since its protologue presents neither a description or diagnosis, nor makes any reference to a previously described taxon, and was therefore not validly published.

Table 1. Main distinctive characters of *Lycianthes bitteri* sp. nov., *L. ceareaensis* and *L. pauciflora*.

State of characters	<i>L. bitteri</i>	<i>L. ceareaensis</i>	<i>L. pauciflora</i>
Dendritic trichomes	Present	Absent	Absent
Shape of leaf blade	Ovate to oval-elliptical	Elliptical-lanceolate to oval-lanceolate	Ovate
Petiole shape	Depressed adaxially	Canaliculate	Cylindrical
Length of flower pedicel (cm)	1.4–1.7	0.5–1.0	1.0–1.3
Apex of the calyx appendices in flower	Rounded	Truncate	Obtuse
Length of the appendices of frutified calyx (cm)	0.5–1.0	0.3–0.4	0.1–0.2
Position of appendages in frutified calyx	Radiate and widely spreading	Slightly arched	Strongly reflexed
Shape of ovary	Conical	Ovoid	Globose

The analysis of the collection Ule 6800, which corresponds to the type specimens of *S. compressibaccatum* and *Lycianthes acutangula* ssp. *compressibaccata*, showed leaves narrow-elliptic, acute or acuminate at the apex, rotate corollas, unequal stamens, and globose berries, which constitute a set of characters similar to those also observed in the types specimens of *L. leptocaulis* (Rusby 2657). Those features clearly indicated that they are a single species, and we therefore propose the synonymization of *L. compressibaccatum* under *L. leptocaulis*.

Hocke et al. (2008) and Rojas and D'Arcy (1997) considered *Lycianthes acutangula* ssp. *compressibaccata* as a synonym of *L. stenoloba* (Van Heurck & Müll. Arg.) Bitter; we do not, however, agree with that proposal. The analysis of the types of both taxa clearly revealed them as different species based on the morphologies of their leaves and flowers. The white funnel-shaped corolla with interpetal tissue of *S. compressibaccatum* is completely different from that of *L. stenoloba*, which has a rotate corolla, without interpetalar tissue.

Taxonomic synonym: *Solanum sylvicola* Brandegees (1917, p. 373) **syn. nov.**

Type: Mexico, State of Chiapas: Finca Irlanda, Jun 1914, C. Purpus 7315 (holotype: UC! 173378, isotype: M! 01811815).

Accepted name: *Lycianthes amatitlanensis* (J. M. Coult. & Donn. in Smith 1904, p. 420) Bitter (1919, p. 441).

Type: Guatemala. Department of Amatitlán: Barranca de Eminencia, 1200 m a.s.l., Feb 1892, J. Donnell Smith 1457 (B† = F! 267179 barcode V0073065F; lectotype: US 1324447 barcode 27445! designated here; isoelectotypes: GH! 77435!; K n.v.). Syntypes: Department of Alta Verapaz: Cubilquitz, 350 m a.s.l., Jul 1901, H. von Tuerckheim 7753 (M!, NY! 138966, US! 398323 barcode 01014252, US! 1324445 barcode 01269193); Department of Alta Verapaz: Cubilquitz, 350 m a.s.l., Feb 1903, H. von Tuerckheim 8488 (F! 185826 barcode V0073066F, M! 171813, NY! 138963, NY! 1388964, US! 576619 barcode 01014253, US! 1324446 barcode 01269192).

Notes

Solanum sylvicola was proposed by Townshend S. Brandegees (1917) based on a plant collected in Mexico with a shrubby habit, geminate anisophyllous leaves with asymmetric blades, calyx with conspicuous appendages approximately 4.0 mm long, and corolla with lanceolate lobes. Analyses of the types of *Solanum sylvicola* (deposited at M) and *Lycianthes amatitlanensis* (GH, F, M, NY, UC and US), however, revealed them to belong to a single taxon. The indument of *Solanum sylvicola* was described by Brandegees (1917) as setose-hirsute, but the analysis of its isotype showed it not to be different from the indument observed in *L. amatitlanensis*, which is described as

strigose, with the presence of simple, multi-cellular and uniseriate trichomes.

Additionally, the isotype of *S. sylvicola*, deposited at M, has a handwritten label by Bitter identifying it as *L. amatitlanensis*, although Bitter (1919) did not propose a formal synonymization for that name, leading us to propose the synonymy of *S. sylvicola* under the accepted name *L. amatitlanensis*, based on the absence of differential taxonomic characters revealed by analyses of their types.

Taxonomic synonym: *Lycianthes poeppigii* Bitter (1919, p. 345) **syn. nov.**

Type: Peru. Department of Loreto: Province Alto Amazonas, ["Maynas"], next to Yurimaguas, Apr. E. Poeppig 2406 (holotype: W 0003089 [photo!]; isotype: P! barcode P00430724).

Accepted name: *Lycianthes glandulosa* (Ruiz and Pavón 1799, p. 35) Bitter (1919, p. 348).

Type: Peru. Department of Junín: Province Chanchamayo, H. Ruiz and J. Pavón s.n. (lectotype: MA 747073 [photo!]; isoelectotype: F 843590 fragment- [photo!]), designated by Knapp (2008).

Notes

Lycianthes poeppigii was proposed by Bitter (1919) based on a collection made by Eduard Friederich Poeppig, in the Province of Maynas, Peru. It was described as a scandent shrub, with false-geminate leaves on the apical branches, stellate trichomes, calyx patelliform-cupulate at the fruit with 10 unequal appendages, and a rotate corolla. In the protologue, Bitter (1919) noted its similarity to *L. glandulosa*, and also commented that the distinguishing characters between them were the indument composed of considerably larger stalked stellate trichomes, the blade being glabrous on the adaxial surface, and unequal stamens, with the fifth filament and anthers being slightly larger in *L. poeppigii*.

The analysis of the type collections of *Lycianthes poeppigii* (isotype at P and photograph of the holotype at W), as well as the types of *L. glandulosa* (lectotype at MA and the isotype at F) showed no distinctive characters that would allow us to consider them different species. The characteristics pointed out by Bitter as taxonomically diagnostic of *L. poeppigii* are characters easily influenced by environmental conditions, such as the indument and the size of the anthers of *L. poeppigii* – which are within the range of variation of *L. glandulosa*. Those characters only reflect phenotypic plasticity and do not support the distinctness of *L. poeppigii* from *L. glandulosa*. Additionally, other characters seen in the type specimens (such as the presence of stellate trichomes, leaf blade elliptic, oblong-elliptic to oval-elliptic, calyx campanulate with ten linear and unequal appendages) clearly indicate that they belong to one and the same taxon.

Key to identification of *Lycianthes* in Brazil:

1. Prostrate herbs, rooting at the nodes; sympodial units plurifoliate; leaves cordate or sagittate at base; pedicels curved at apex 2
– Erect or scandent shrubs or lianas; sympodial units unifoliate or difoliate, geminate; leaves rounded, attenuate, subcordate, cuneate, or oblique at base; pedicels erect, upright or completely pendent 3
2. Leaves solitary, ovate or deltoid; corolla white; fruiting calyx accrescent and covering the basal 1/4 basal of the fruit *L. asarifolia*
– Leaves geminate, reniform or orbicular; corolla lilac to purple; fruiting calyx accrescent, covering the basal 1/2 of the fruit *L. repens*
3. Subshrubs or shrubs erect 4
– Scandent shrubs or lianas 7
4. Stamens equal; corolla white 5
– Stamens somewhat unequal; corolla purple to blue *L. rantonnetii*
5. Leaves geminate, anisophyllous, with asymmetric blades; calyx appendages linear, erect, not reflexed in flower and fruit; berries globose 6
– Leaves solitary with symmetric blades; calyx appendages subulate, reflexed in flower and fruit; berries oblong *L. coffeifolia*
6. Calyx appendages conspicuous in flower, 2.0–3.0 mm long; leaves shiny *L. amatitlanensis*
– Calyx appendages inconspicuous in flower, less than 1 mm long; leaves dull *L. inaequilatera*
7. Entire plant with simple trichomes 8
– Entire plant with stellate and/or dendritic trichomes 9
8. Leaf blades elliptic or oblong-elliptic, acute or acuminate at apex; corolla rotate; calyx appendages (teeth) linear, green in flower and fruit; stamens unequal (1+4) *L. compressibaccata*
– Leaf blades obovate, cuspidate at apex; corolla stellate; calyx appendages (teeth) subulate, green in flower with enlarged base, attenuating to the apex, purple in fruit; stamens equal *L. stenoloba*
9. Entire plant glabrescent, stellate-glandular trichomes sparse 10
– Entire plant pubescent, with stellate and dendritic trichomes 11
10. Edge of calyx truncate in the flower, with unequal appendages in more than two series, 4–5 mm long, emerging from the apical 1/4 of the calyx *L. glandulosa*
– Edge of calyx slightly cuspidate in flower, with unequal appendages in two series, 6–9 mm long, emerging from the basal 2/3 of the calyx *L. pauciflora*
11. Leaf blades cuneate or attenuate at base; indument with stalked-stellate and dendritic trichomes; ovary conical; calyx with linear appendages (teeth), radiate and widely spreading in fruit, 0.5–1.0 cm long *L. bitteri*

– Leaf blades rounded or oblique at the base; indument with only stalked-stellate trichomes (dendritic trichomes absent); ovary ovoid; calyx with narrow-obovate appendages (teeth), curved at apex in fruit, 3.0–4.0 mm long *L. ceareaensis*

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