Abstract:
Background and Aims: *Brenesia* was originally proposed to accommodate an odd taxon among the Orchidaceae subtribe Pleurothallidinae. This species is characterized by its sessile leaves, secondary stems covered by inflated sheaths and, especially, by a raceme produced at the base of the secondary stem. A few more closely related taxa were discovered afterwards, but the generic name has mostly been placed under the synonymy of *Pleurothallis*. Recent DNA-based studies showed that *Brenesia* constitutes a monophyletic group within the genus *Acianthera*. We present here a review of *Acianthera* subgenus *Brenesia*, delimiting each species in the group and providing a key for their identification.

Methods: Specialized literature, specimens deposited in scientific collections, in cultivation, or available at online databases were reviewed. For each species, their known localities were georeferenced and displayed on a map of Mexico and Central America using QGIS software; also, their conservation status was assessed according to the IUCN Red List.

Key results: *Acianthera* subg. *Brenesia* includes five species distributed from central Veracruz, Mexico, to Panama. The species included in this group are *Acianthera costaricensis* from Costa Rica and Panama; *A. herrerae* from Chiapas, in Mexico, and Guatemala; *A. johnsonii* from Chiapas (Mexico) to Honduras; and *A. sotoana* from Veracruz and Oaxaca (Mexico). For each taxon, a morphological description, drawing, photo, information concerning nomenclature, distribution, habitat, phenology, and comparison with similar taxa are provided. *Acianthera rzedowskiiarum* is described as a new species from Chiapas, based on specimens previously confused with *A. johnsonii*.

Conclusions: *Acianthera* subgenus *Brenesia* has a distribution restricted to Central America. Four of its five species are native to Mexico, and one is restricted to southern Central America.

Key words: *Acianthera costaricensis*, *Acianthera herrerae*, *Acianthera johnsonii*, *Acianthera rzedowskiiarum*, *Acianthera sotoana*, Middle America.

Resumen:
Antecedentes y Objetivos: *Brenesia* fue propuesto originalmente para acomodar un extraño taxón en la subtribu Pleurothallidinae de Orchidaceae. Esta especie se caracteriza por sus hojas sésiles, tallos secundarios cubiertos por vainas infladas y, sobre todo, por un racemo producido en la base del tallo secundario. Luego se descubrieron algunos taxon similares adicionales, pero el nombre genérico por lo general fue incluído bajo la sinonimia de *Pleurothallis*. Estudios recientes basados en el ADN demostraron que *Brenesia* constituye un grupo monofilético dentro del género *Acianthera*. Aquí presentamos una revisión de las especies de *Acianthera* subgénero *Brenesia*, delimitando cada especie del grupo y proporcionando una clave para su identificación.

Métodos: Se revisó literatura especializada, ejemplares depositados en colecciones científicas, en cultivo o disponibles en bases de datos en línea. Para cada especie sus localidades conocidas fueron georreferenciadas y sobrepuestas en un mapa de México y Centroamérica usando el software QGIS; además, se evaluó su estado de conservación de acuerdo con los Criterios de la Lista Roja de la UICN.

Resultados clave: *Acianthera* subg. *Brenesia* incluye cinco especies distribuidas desde el centro de Veracruz, México, hasta Panamá. Estas especies son *Acianthera costaricensis* de Costa Rica y Panamá; *A. herrerae* de Chiapas, en México, y Guatemala; *A. johnsonii* de Chiapas (México) a Honduras y *A. sotoana* de Veracruz y Oaxaca (México). Para cada taxón se presenta una descripción morfológica, dibujo, foto, información sobre nomenclatura, distribución, hábitat, fenología y una comparación con taxones similares. *Acianthera rzedowksiarum* se describe como nueva especie basada en especímenes de Chiapas previamente confundidos con *A. johnsonii*.

Conclusiones: *Acianthera* subgénero *Brenesia* tiene una distribución restringida a América Central. Cuatro de sus cinco especies son nativas de México y una se restringe al sur de América Central.

Palabras clave: *Acianthera costaricensis*, *Acianthera herrerae*, *Acianthera johnsonii*, *Acianthera rzedowskiiarum*, *Acianthera sotoana*, América Central.
Introduction

The genus *Acianthera* Scheidw. belongs to the family Orchidaceae and comprises little more than 300 species (Karremans, 2016; Karremans and Vieira-Uribe, 2020), which grow as epiphytes, lithophytes, or rarely as terrestrials in dry to wet forest, from Mexico to Uruguay and Northern Argentina, including the Antilles (Luer, 2004). Brazil is a center of diversity for the genus; about 135 species have been reported to be native to the country (Barros et al., 2015). As currently defined, *Acianthera* is divided into four monophyletic subgenera: A. subg. *Acianthera*, A. subg. *Antilla* (Luer) Karremans, A. subg. *Brenesia* (Schltr.) Karremans, and A. subg. *Kraenzlinella* (Kuntze) Karremans (Karremans et al., 2016).

*A. johnsonii* from Costa Rica, *Pleurothallis* Luer, from Guatemala, which, in the Sierra Madre of Chiapas, the genuine *A. johnsonii* in Solano and Soto (2003) have now been determined to correspond to a different, yet undescribed species. Meanwhile, specimens of the true *A. johnsonii* have been recently collected from the Sierra Madre of Chiapas. The genuine *A. johnsonii* as well as the misidentified *Acianthera* species are described and illustrated here.

The aim of the current study was to conduct a review of *Acianthera* subgenus *Brenesia* based on specialized literature, specimens deposited in scientific collections, in cultivation, or available in online databases. For each species in the group a morphological description, drawing or photo, information concerning nomenclature, distribution, habitat, phenology, conservation status assessment and comparison with similar taxa are provided.

Materials and Methods

For each taxon nomenclatural information was acquired from type specimens and original descriptions. Historical protologues were accessible from Biodiversity Heritage Library (BHL, 2023). The type specimens were available online from the herbaria AMES, AMO, CR, MO, and US (acronyms according to Thiers, 2023). An online search for additional specimens for the group was carried out through
the Global Biodiversity Information Facility (GBIF, 2023), SEINet data portal (SEINet, 2023), and the citizen science network iNaturalista (Naturalista, 2021).

The descriptions for each species were based on cultivated specimens in the living orchid collections of the AMO Herbarium and Soconusco Botanical Garden (El Colegio de la Frontera Sur, Tapachula, Chiapas, Mexico), specialized literature (Luer, 1991, 2004, 2023; Sayers and Du Plooy, 2003; Solano and Soto, 2003; Nelson Sutherland and Ortiz-Kafati, 2007; Solano, 2010, 2015; Karremans et al., 2016), as well as on herborized specimens housed at the herbaria AMES, AMO, B, CR, ECO-TA-H, F, HEM, JBL, LAGU, MO, NY, OAX, SEL, RENZ, TEFH, US, W, and XAL (acronyms according to Thiers, 2023). Line drawings were prepared from fresh material with a drawing tube adapted to a stereomicroscope (Wild Heerbrugg Type 308700, Gais, Switzerland). Additionally, with the authors’ permission, the quality of the photographs presented here were edited with Adobe Photoshop® CS4.

For each species, information concerning nomenclature, distribution, habitat, phenology, conservation status, and representative specimens is provided here. A morphological comparison of each taxon with the other species of Acianthera subg. Brenesia was based on the specialized literature cited above. The known localities for each species were georeferenced and displayed on a map of Mexico and Central America (Fig. 1) using QGIS v. 3.32 software (QGIS, 2023). A key for the Mesoamerican subgenera of Acianthera, as well as for the species of Acianthera subg. Acianthera, was prepared. For each species the conservation status was assessed according to the IUCN Red List Criteria (IUCN, 2019).

Figure 1: Map of the known localities of Acianthera subgen. Brenesia (Schltr.) Karremans in Mexico and Middle America. Map by Raúl Rivera.
Results

Taxonomy

Middle American species of *Acianthera* belong to three of the following four subgenera according to Karremans et al. (2016). No species of *Acianthera* subg. *Antilla* are known to occur in the region.

Key for the subgenera of *Acianthera*

1a. Stems with 3-5 internodes, covered by laterally compressed, overlapping, inflated sheaths .............................................. *Acianthera* subg. *Brenesia*

1b. Stems with 2 internodes, covered by tubular, adpressed sheaths ................................................................. *Acianthera* subg. *Kraenzlinella*

2a. Habit erect; flowers star-like; lateral sepals free or united up to 1/3 of their length; petals basally auriculate .............................................. *Acianthera* subg. *Acianthera*

2b. Habit erect or pendulous; flowers bilabiate; lateral sepals totally united to each other; petals not basally auriculate .............................................. *Acianthera* subg. *Kraenzlinella*

3a. Leaf margins entire, plants occurring on the mainland throughout the Neotropics .............................................. *Acianthera* subg. *Acianthera*

3b. Leaf margins denticulate or erose, plants endemic to the Caribbean islands .................. *Acianthera* subg. *Antilla*


Rupicolous, terrestrial, or epiphytic, caespitose or short repent herb; rhizome or primary stem short, globose, with 3 internodes, roots cylindrical, flexuous, whitish; secondary stem or ramicaul erect, formed by 3-5 internodes; covered by laterally compressed, overlapping sheaths, inflated towards the apex, scarious, red spotted; leaf elliptic to oblong-elliptic, fleshy, sessile or attenuate at the base into a short conduplicate petiole; inflorescence from the apex or on the basal nodes of the secondary stem, racemose, multi-flowered; floral bracts obliquely funnel-shaped, obtuse, white or green translucent with reddish dots, overlapping; flowers tubular or subglobose, trigonous in trans-section; sepals fleshy, axially carinate, 5-7-veined, cellular-papillose or hirsute-papillose, lateral sepals fused into a concave, bifid synsepal; petals fleshy, subulate to linear-rhombic, 3-veined; lip fleshy, pandurate, unguiculate, 3-veined, lamina with a pair of submarginal calli extended along the middle part of the lip; column slender, cylindrical or semicylindrical, with a well-developed foot; stigmatic cavity and rostellum ventral; anther cap ventral, pollinia 2, ovoid, laterally compressed, yellow, with granulose caudicles; ovary trigonous, subpyramidal, articled to a cylindrical pedicel.

The five species now recognized in this subgenus can be identified with the following key.

Key to the species of *Acianthera* subg. *Brenesia*

1a. Leaf sessile; sepals scurfy or glandular-papillose .......... 2

1b. Leaf attenuate at the base into a short conduplicate petiole; sepals long hairy or glandular-papillose ......... 3

2a. Flowers sub-globose in form, whitish in background and densely dark red dotted; sepals scurfy .................. *A. johnsonii* (Ames) Pridgeon & M.W. Chase

2b. Flowers tubular in form, yellow in background with red dots; sepals glandular-papillose .............................................. *A. rzedowskii* Solano & Karremans sp. nov.

3a. Sepals mucronate; petals linear-rhombic, acuminate; lip ovate to oblanceolate, without uncinate lobes .... 4

3b. Sepals conspicuously apiculate; petals subulate-rhombic, long acuminate, with obtuse angles at the middle; lip pandurate, with uncinate lateral lobes .................. *A. herrerae* (Luer) Solano & Soto Arenas

4a. Raceme <3 cm long; leaves elliptic; lip oblanceolate; plants from Veracruz and Oaxaca (Mexico) .......................................................... *A. sotoana* Solano

4b. Raceme >5 cm long; leaves elliptic to elliptic-ovate; lip ovate; plants from Costa Rica and Panama ................. ............ *A. costaricensis* (Schltr.) Pupulin & Karremans


**Type:** COSTA RICA. (Alajuela, San Ramón), bois humides à San Pedro de San Ramon, 1200 m, IX.1921, A. M. Brenes 117 (holotype: B (destroyed), lectotype designated in Barringer (1986): AMES-28732!, isolectotype: CR-18505! (photo at AMES!).

Epiphytic or terrestrial, shortly repent herb, up to 35 cm tall; secondary stem 3-13 cm long, cylindrical, formed by 3-4 internodes; leaf 8-23 × 2-7 cm, elliptic to elliptic-ovate, acute to obtuse, attenuate and conduplicate at the base; inflorescence up to 12 cm long, only from a basal node on the secondary stem, creeping, with up to 15 flowers, arranged perpendicularly to the rachis, most open at the same time, peduncle cylindrical, 2 cm long; floral bracts 5 mm long; flowers 25 mm long, tubular, gaping; sepals and petals yellow or orange with purple dots, lip yellow with purple spots in the basal middle, column white with purple stripes, anther purple; sepals long hairy on both surfaces, the hairs dark purple, apically mucronate, lanceolate-rhombic, long acuminate petals, and ovate lip, with a pyramidal callus near the base (Fig. 3). The most similar species are *Acianthera sotoana* and *A. herrerae*, especially in their habit and coloration of the flowers. *Table 1* shows the characteristics that allow distinguishing these species.

Conservation status: Data Deficient according to the IUCN (2019) categories and criteria. For a proper assessment of its risk category it is necessary to know if the species persists in the localities reported below, estimate the size and number of populations, identify the risk factors threatening its populations and habitat, and model its distribution to estimate the extent of occurrence and area of occupancy.

Additional specimens examined: COSTA RICA. Province Alajuela, district San Ramón, Las Nubes en San Ramón, 20.XI.1932, A. M. Brenes 156 (AMES, CR); La Paz de San Ramón, 30.VII.1932, A. M. Brenes 35 (NY). Province Guanacaste, district La Cruz, P.N. Guanacaste, Estación Biológica Maritza, cima del volcán Orosí, 1300 m, 21.VIII.2007, J. F. Morales 15522 (CR-INB); loc. cit., *M. Grayum and A. Rojas...
Figure 2: Photo of the type of *Brenesia costaricensis* Schltr. in AMES. Reproduced with permission of The Orchid Herbarium of Oak Ames of Harvard University.

Figure 3: *Acianthera costaricensis* (Schltr.) Pupulin & Karremans. A. habit; B. flower; C. perianth; D. ovary, column and lip in lateral view; E. lip in ventral and lateral views; F. anther cap and pollinaria. Lankester Composite Digital Plate by Franco Pupulin, based on *D. Bogarin 11373* (JBL-sprit) from Costa Rica.
Table 1: Summary of the main differences between species of *Acianthera* subgenus *Brenesia* (Schltr.) Karremans.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>A. costaricensis</em> (Schltr.) Pupulin &amp; Karremans</th>
<th><em>A. herrerae</em> (Luer) Solano &amp; Soto Arenas</th>
<th><em>A. johnsonii</em> (Ames) Pridgeon &amp; M.W. Chase</th>
<th><em>A. rzedowskiiarum</em> Solano &amp; Karremans sp. nov.</th>
<th><em>A. sotoana</em> Solano</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf form</td>
<td>elliptic to oblong-elliptic</td>
<td>elliptic</td>
<td>elliptic, ovate, or ovate-oblong</td>
<td>elliptic to oblong-elliptic</td>
<td>elliptic</td>
</tr>
<tr>
<td>Leaf size</td>
<td>8-23 × 2-7 cm</td>
<td>10-17 × 3.5-6.5 cm</td>
<td>8-14 × 2.5-5.5 cm</td>
<td>5-7 × 2-2.5 cm</td>
<td>10-19 × 4-6 cm</td>
</tr>
<tr>
<td>Leaf base</td>
<td>attenuate and conduplicate</td>
<td>attenuate and conduplicate</td>
<td>sessile</td>
<td>sessile</td>
<td>sessile</td>
</tr>
<tr>
<td>Inflorescence origin</td>
<td>basal node on the secondary stem</td>
<td>basal node on the secondary stem</td>
<td>apex of the secondary stem, sometimes from the basal node of secondary stem</td>
<td>apex of the secondary stem, sometimes from the basal node of it</td>
<td>apex of the secondary stem, sometimes from the basal node of it</td>
</tr>
<tr>
<td>Flores per raceme</td>
<td>up to 15</td>
<td>up to 7</td>
<td>up to 9</td>
<td>up to 7</td>
<td>up to 10</td>
</tr>
<tr>
<td>Flower arrangement</td>
<td>secund, perpendicular along the rachis</td>
<td>secund, subparallel along to the rachis</td>
<td>distichous, perpendicular along the rachis</td>
<td>secund, subparallel along to the rachis</td>
<td>secund (basal raceme) or distichous (apical raceme), perpendicular along the rachis</td>
</tr>
<tr>
<td>Flower color</td>
<td>yellow or orange, purple dotted</td>
<td>yellow, purple dotted</td>
<td>white, densely red dark dotted</td>
<td>yellow, dark red dotted</td>
<td>yellow-brown to yellow-orange, densely purple dotted</td>
</tr>
<tr>
<td>Flower size (length)</td>
<td>25 mm</td>
<td>20 mm</td>
<td>12-17 mm</td>
<td>15-17 mm</td>
<td>17-21 mm</td>
</tr>
<tr>
<td>Sepal apex</td>
<td>acute to obtuse, mucronate</td>
<td>acuminulate, apiculate</td>
<td>obtuse (dorsal) or acute (lateral), shortly apiculate</td>
<td>acute, apiculate, recurved</td>
<td>subacute, mucronate</td>
</tr>
<tr>
<td>Sepal ornamentation</td>
<td>purple hairs</td>
<td>glandular-pubescent</td>
<td>glandular-papillose</td>
<td>cellular-papillose</td>
<td>glandular-pubescent</td>
</tr>
<tr>
<td>Sepal, veins</td>
<td>5</td>
<td>3-5</td>
<td>5-7</td>
<td>7</td>
<td>5-7</td>
</tr>
<tr>
<td>Petal form</td>
<td>lanceolate-rhombic, long acuminate, not angled at the middle</td>
<td>subulate-rhombic, long acuminate, prominently angled at the middle</td>
<td>obliquely oblaneolate to oblaneolate-rhombic, acute, not angled at the middle</td>
<td>linear-narrowly rhombic, acuminate, falcate, not angled at the middle</td>
<td>lanceolate-subrhombic, oblique, acuminate, not angled at the middle</td>
</tr>
<tr>
<td>Lip form</td>
<td>ovate, obtuse</td>
<td>pandurate, apiculate</td>
<td>ovate-pandurate, obtuse to rounded</td>
<td>ovate-pandurate, rounded</td>
<td>cordate-sagittate, acute</td>
</tr>
<tr>
<td>Lip, lateral lobes</td>
<td>erect, rounded</td>
<td>uncinate</td>
<td>absent</td>
<td>erect, rounded</td>
<td>erect, rounded</td>
</tr>
<tr>
<td>Lip, basal callus</td>
<td>pyramidal, erect</td>
<td>transverse lamella</td>
<td>V-like, low</td>
<td>ovate, erect</td>
<td>prominent, erect, incurved</td>
</tr>
<tr>
<td>Distribution</td>
<td>Costa Rica, Panama</td>
<td>Guatemala, Mexico (Chiapas)</td>
<td>Belize, Guatemala, El Salvador, Honduras, Mexico (Chiapas)</td>
<td>Guatemala, Mexico (Chiapas)</td>
<td>Mexico (Oaxaca, Veracruz)</td>
</tr>
</tbody>
</table>


Terrestrial, short repent herb, up to 35 cm tall; secondary stem 3-12 cm long, formed by 3-4 internodes; leaf 10-17 × 3.5-6.5 cm, elliptic, obtuse, attenuate and conduplicate at the base; inflorescence 2.5 cm long, a raceme produced only from the basal node of the secondary stem, creeping, up to 5 simultaneous flowers, peduncle 1 cm long; floral bracts 5 mm long; flowers 20 mm long, rounded semi-closed, arranged subparallel along the rachis; sepals and petals yellow with purple dots, lip yellow; sepals glandular-pubescent on the abaxial surface, ciliate, apiculate, 3-5-veined, dorsal sepal 17-19 × 5-6.5 mm, lanceolate, acuminate, lateral sepals 19-21 × 12 mm when spread out, fused along 2/3 of their length into a concave, ovobovate, deeply bifid synsepal, each one ovate-lanceolate, acuminate, slightly oblique; petals 14 × 4 mm, subulate-rhombic, long acuminate, 3-veined, ciliate at the middle, with obtuse angles at the middle; lip 7.5 × 4 mm, arching, 3-lobed, pandurate, obtuse, apiculate, verrucose on the adaxial surface, lateral lobes uncinate, antrorse, erect, lamina with low submarginal calli at the middle, and a transverse lamella near the base; with a pair of diminutive, auricled lobes at the base; column 6 mm long, 1 mm wide, arching, clinandrium denticulate at the margin, with a straight foot column, 3 mm long; stigmatic cavity obovate; rostellum laminar, convex; anther 0.8 × 0.6 mm, ovoid-spheric, pollinia 0.5 mm long; ovary 3-4 mm long, pyramidal, glandular-pubescent, articulated to a cylindrical pedicel, 3 mm long; capsule not seen.

Phenology: this species flowers from August to December.

Distribution and habitat: so far, Acianthera herrerae is only known from Chiapas in Mexico, and Guatemala (Fig. 1), where it grows as a terrestrial in wet Pinus-Quercus forests, at 2000-2100 m elevation (Luer, 1991).

Taxonomic notes: Acianthera herrerae is recognized by its large habit, the base of the leaf attenuate and conduplicate, creeping raceme produced only from the basal node of the secondary stem, yellow with purple blotched flowers, acuminate, apiculate, and glandular-pubescent sepals, and a conspicuously pandurate lip with uncinate erect lateral lobes (Figs. 4, 5). Acianthera costaricensis and A. sotoana are similar, especially in the size of the plant and the flower coloration. Table 1 shows the characteristics that allow distinguishing these species.

Conservation status: Data Deficient according to the IUCN (2019) categories and criteria. For a proper assessment it is necessary to know if the species persists in the localities reported below, estimate the size and number of populations, identify the risk factors threatening its populations and habitat, and model its distribution to estimate the extent of occurrence and area of occupancy. Acianthera herrerae is poorly known and represented in scientific collections.
Figure 4: Acianthera herrerae (Luer) Solano & Soto Arenas. A. habit; B. flower; C. perianth; D. Lip; E. Lip, column, and ovary in lateral view. Drawing by Carlyle Luer based on the holotype specimen. Reproduced with permission of the Missouri Botanical Garden.
Figure 5: Acianthera herrerae (Luer) Solano & Soto Arenas. Photograph by Ron Parsons based on a cultivated specimen collected by Moises Behar s.n. in Guatemala.

Additional specimens examined: GUATEMALA. Department Quetzaltenango, Zunil, collected by J. Herrera, M. Behar 80 (MO). Department San Marcos, barrancos 6 miles SW of town of Tajomulco, NW slopes of volcán Tajomulco, 2300-2800 m, 26.II.1940, J. A. Steyermark 36687 (F). Department Zacapa, Sierra Las Minas; Zacapa, upper slopes along rio Repollal to summit of mountain, 2100-2400 m, 12-13.I.1942, J. A. Steyermark 42505 (AMES, F).

Other specimen: MEXICO. Chiapas, región del volcán Tacaná, O. Suárez s.n. (photo from a plant cultivated at La Encantada, Oaxaca, Mexico (Suárez, 2004).


**Type:** GUATEMALA. Alta Verapaz, Chamá to Cobán, 3000 ft, 15.VIII.1920, H. Johnson 901 (holotype: AMES-74369!, isotypes: F-867639!, US-1081162!).

**Distribution and habitat:** *Acianthera johnsonii* is known to occur in Mexico (Chiapas), Belize (Sayers and Du Plooy, 2003), Guatemala, El Salvador, and Honduras (Nelson Sutherland and Ortíz-Kafati, 2007). In Mexico the species is only known from the Sierra Madre of Chiapas, on the Cerro Boquerón and in the El Triunfo Biosphere Reserve, from (914)-1200 to 2400 m elevation. The species grows as a terrestrial, rupicolous, or epiphyte, on humus carpets in *Pinus* forest, *Pinus-Quercus* forest, and secondary vegetation derived from cloud forest, often on calcareous substrate.

**Phenology:** this species flowers from May to November.

**Taxonomic notes:** specimens from the Altos of Chiapas previously determined as *A. johnsonii* (Solano and Soto, 2003) are described here as a new species. However, its presence in Mexico is confirmed with specimens collected in southeastern Chiapas (Sierra Madre of Chiapas), close to the border with Guatemala. According to Karremans and Vieira-UrIBE (2020), *A. johnsonii* is recognized by its raceme emerging from the apex or base of the secondary stem, reddish, almost globose flowers, and glandular-papillose, non-hairy sepals (Figs. 6, 7). This species is similar to *A. costaricensis* and in the past they have been considered conspecific (Ames and Correll, 1952; Hamer, 1974; Luer, 1977; Solano and Soto, 2003). However, *A. costaricensis* differs notably in several traits; *A. rzedowskiaurum* sp. nov. is similar in its habit. Table 1 shows the characteristics that allow distinguishing these species.

**Garay** (1956) considered *Brenesia costaricensis* as morphologically the same as *Pleurothallis johnsonii*, and
indicated that “Recent collections submitted by Mrs. R(uth) Oberg extend the range of the species to southern Mexico...”, note attached to the holotype sheet of *Pleurothallis johnsonii* at AMES (Fig. 8). Those specimens have not been located at AMES. However, Mrs. Oberg and Robert Dressler visited San Cristobal de las Casas and from there they went to the Ocotal lagoons (northeast Chiapas), where they collected orchids (Oberg, 1959). Oberg’s specimens probably came from Los Altos of Chiapas and corresponded to *A. rzedowskii* sp. nov., which grows in the periphery of San Cristobal de las Casas. A photo of *A. johnsonii* was published, as *Pleurothallis johnsonii*, by Behar and Tinschert (1998: p. 112).

Conservation status: Data Deficient according to the IUCN (2019) categories and criteria. For a proper assessment of its risk category it is necessary to know if the species persists in the localities reported below, estimate the size and number of populations, and model its distribution to estimate the extent of occurrence and area of occupancy. In Mexico *Acianthera johnsonii* is known from few localities and is scarcely represented in scientific collections, even though the region where it grows has been well explored floristically in recent years. The known Mexican localities are within a region where some anthropogenic factors put its biodiversity at risk: habitat loss and transformation for shifting and permanent agriculture, cattle ranching, timber extraction, transformation of the traditional coffee plantations into full-sun ones, increase in human settlements, and extraction for illicit wildlife traffic (Solano et al., 2016). A proposal to extend the Tacana Volcano Biosphere Reserve (where ecosystems above 1500 m are well-conserved in comparison with those from lower elevations), connecting it with the Cerro Boquerón...
Figure 8: Holotype of *Pleurothallis johnsonii* Ames. Reproduced with permission of The Orchid Herbarium of Oak Ames of Harvard University.
(CONANP, 2011), would increase the area protected, the variety of environments, the species that inhabit them, and the biological connectivity of their ecosystems (Solano et al., 2016).

Additional specimens examined: COSTA RICA. Cultivation, sent to the MSBG in X.1975 from C.R. by John Hall s.n. (SEL). EL SALVADOR. Department La Libertad, municipality Quezaltepeque, Boquerón, interior of San Salvador volcano, 1800 m, 3.VIII.1969, F. Hamer 73 (AMES, LAGU, SEL). GUATEMALA. Department Quetzaltenango, locality unknown, 1600 m, 20.VIII.1948, J. Renz 4826 (RENZ). HONDURAS. Department Comayagua, municipality Meambar, Agua Caliente, vagueada de los ríos Chamo y Humuya, 35 km E Iago Yojoa, 220 m, 22.XI-31.XII.1980, C. Nelson 6392 et al. (TEFH); Meambar, 610 m, 30.VII.1933, J. B. Edwards 468 (AMES); El Achote, hills above the plains of Siguatepeque, 1350 m, 8.IX.1936, T. G. Yuncker 6398 et al. (AMES, NY); Siguatepeque, km 132 on Tegucigalpa highway, 1372 m, 17.IX.1932, J. B. Edwards 247 (AMES), 248 (AMES, NY). Department Francisco Morazán, municipality Distrito Central, 45 km NO de Tegucigalpa, unión de los ríos S. Isidro y Las Moras, 1300 m, 23.VIII.1991, C. Nelson 12025 and R. Andino (TEFH); 45 km NO de Tegucigalpa, quebrada de San Isidro, 5 km N y 2 km O de Zambrano, 1300 m, 10-15.VIII.1991, C. Nelson 11797 and R. Andino (TEFH); 45 km NO de Tegucigalpa, orilla quebrada de La Protección, 3 km S y 5 km O de Zambrano, 1200 m, 12.IX.1991, C. Nelson and R. Andino 12355 (TEFH); 45 km NO de Tegucigalpa, quebrada de Las Moras, 6 km N y 2 km O de Zambrano, 1300 m, 10-15.VIII.1991, C. Nelson 11890 and R. Andino (TEFH). Department Intibucá, municipality Yamaronigua, montaña Camaco en los alrededores de Yamaronigua, 2.VII.1973, C. Bejarano 135 (TEFH). Without locality, cultivated by H. H. Morgan, X.1975, J. Nepple s.n. (SEL); without locality, donated to SEL by George Kennedy, flowered in cultivation, 5.VIII.1976, C. Luer 1042 (SEL). MEXICO. Chiapas. municipality Motozintla, Boquerón - Buenavista, camino Boquerón Buenavista a Finca Hamburgo, A. Damon s.n. (ECO-TA-H). Municipality Siltepec, La Lucha, Reserva de la Biosfera El Triunfo, 21.VII. 2005, H. Reyes-Esco-
Figure 9: *Acianthera rzedowskiiarum* Solano & Karremans. A. habit; B. inflorescence; C. perianth; D. lip, column, and ovary in lateral view; E. lip; F. column in ventral view; G. anther cap and pollinarium. Line drawing by Rodolfo Solano based on the holotype.
Figure 10: Acianthera rzedowskiiarum Solano & Karremans. A. habit; B. flower; C. perianth; D. lip, column, and ovary in lateral view; E. anther cap and pollinarium. Line drawing by Eric Hágsater based on E. W. Greenwood and J. P. Brenan 572 (AMO), from Chiapas, Mexico.

acute, channeled, lateral sepals 12.6 × 10.5 mm, fused along 2/3 of their length into an ovate, concave, deeply bifid synsepal, each one elliptic and acute when spread out, forming a chain at their bases; petals 9 × 2.1-2.2 mm, fleshy, linear-narrowly rhombic, acuminate, falcate, widened above the middle, 3-veined, with a small and auricled projection on the labellar base, ciliate above the middle; lip 5.8 × 3 mm, fleshy, arching, 3-lobed, ovate-pandurate, rounded, 3-veined, lateral lobes erect, rounded, lamina channeled between the submarginal calli along the middle part part of the lip, with an ovate erect callus near the base; column 5.5 mm long, 1.5 mm wide, with an arching, cylindrical body, clinandrium trapezoidal, entire; stigmatic cavity subquadrate, viscous at the interior, rostellum quadrato, membranous, recurved at their margins; anther 0.9 mm long and wide, semi-globose, pollinia 0.5 mm long; ovary 3.8-4 mm long, trigonous, glabrous, pedicel terete; capsule 9 mm long, 3 mm wide, ellipsoid, subtrigonous, with ribs and dehiscence lines thickened.

Etymology: the specific name honors the contributions to the knowledge of the Mexican flora during almost six decades by the matrimony of Jerzy Rzedowski and Graciela Calderón de Rzedowski (both recently deceased), affectionately known as the Rzedowski.

Phenology: this species flowers from August to October.
Distribution and habitat: so far, this species is only known from Los Altos (The Highlands) of Chiapas, Mexico. It is likely to occur in Guatemala too. *Acianthera rzedowskiiarum* grows as a rupicolous or terrestrial along road-cuts and cliffs within *Pinus-Quercus* forests, or in secondary vegetation derived from it, often on calcareous substrate, from 1700 to 2420 m elevation. The species is sympatric with other members of Pleurothallidinae recently described from Chiapas, including *Stelis zootrophionoides* Castañeda-Zárate & Ramos-Castro and *Stelis mirandae* Beutelsp. & Mor.-Mol. Interestingly, the currently known distribution of these three species seems to be restricted
to Los Altos of Chiapas (Ramos-Castro et al., 2012; García-González et al., 2015; Beutelspacher-Baigts and Moreno-Molina, 2018).

Taxonomic notes: among Acianthera subg. Brenesia this species is recognized by its small habit, creeping inflorescence produced from the stem base, semi-closed yellow flowers with reddish dots, and linear-narrowly rhombic and falcate petals (Figs. 9, 10, 11). The most similar species is A. johnsonii (Figs. 5, 6). Table 1 shows the characteristics that allow distinguishing between both taxa.

Photos of A. rzedowskiiarum were previously published. It appeared with the name A. johnsonii in Soto et al. (2007: fig. 0010) and Beutelspacher-Baigts and Moreno-Molina (2018: p. 201), and as an unnamed species in Karremans and Vieira-Urbe (2020: p. 45). Photographs published on iNaturalista (Naturalista, 2023b) show a specimen similar to A. rzedowskiiarum recorded at Quiche, Guatemala, which, unlike the specimens from Chiapas, has sepals with larger red spots.

Conservation status: Data Deficient according to the IUCN (2019) categories and criteria. For a proper assessment of its risk category it is necessary to know if the species persists in their localities reported below, estimate the size and number of populations, and model its distribution to estimate the extent of occurrence and area of occupancy. Acianthera rzedowskiiarum is known from few localities and is scarcely represented in scientific collections, it may have not been noticed by botanists working in Los Altos of Chiapas or Guatemala, even though these regions have been well-explored floristically. In Chiapas the species grows in a relatively accessible area where the forests persist as remnant fragments and are close to human settlements and the urbanized area of San Cristóbal de las Casas. Natural vegetation in this region is facing anthropogenic effects due to the expansion of urban areas, extraction of wood and firewood, opening of lands for agriculture and sheep grazing, and extraction of plants for commercial and/or ritual purposes (García-González et al., 2015; Jiménez-López et al., 2019). Nonetheless, in this region remnant forests are within small ecological reserves where the species can grow. There is no knowledge of the populations of the species and its habitat in Guatemala.


TYPE. MEXICO. Oaxaca, municipio Totontepec Villa de Morelos, Cañón del Río Toro, sobre el banco del río, 1800 m, colectado IX.1977, prensado 23.VII.1983, O. Suárez sub E. Hágsater 5536 (holotype: AMO!, isotype: AMO!).

Rupicolous or occasionally epiphytic herb, up to 36.5 cm tall; roots 1.2-2 mm diameter; secondary formed by 4-5 internodes, 4-17.5 cm long, 1.6-3.5 mm diameter, covered by scarious sheaths; leaves 10-19 × 4-6 cm, elliptic, obtuse, recurved at the apex, sessile; inflorescence 5-6.5 cm long, up to 10 simultaneous flowers, generally from the basal node of the secondary stem and creeping, sometimes from the apex of the secondary stem and reclined on the adaxial surface of the leaf, peduncle 1-3 cm long, 2 mm diameter, with 2 (basal peduncle) or 5 (apical peduncle) obliquely infundibuliform bracts, obtuse, overlapping,
6-7.7 mm long, the apical peduncle covered at the base by a scarious spathaceous bract; floral bracts 7.9-8.7 mm long; flowers 17-21 mm long, tubular, semi-close, yellowish-brown to yellowish orange, densely purple dotted on both surfaces, petal yellowish-brown with purple dots, lip orange with purple dots, column and anther purple; sepals glandular-pubescent on both surface, hairs dark red, ciliate, apically mucronate, 5-7-veined, dorsal sepal 17-18.5 × 5 mm, lanceolate to oblong-lanceolate, subacute, lateral sepals 18.4-21.5 × 10-13.4 mm, fused along 2/3 of their length into an oblong-lanceolate, concave, deeply bifid synsepals; petals 11.2-12.3 × 2 mm, lanceolate-subhombic, oblique, acuminate, 3-veined, ciliate along the upper 2/3; lip 5.5 × 2.1 mm when spread out, arching, 3-lobed, conduplicate, cordate-sagittate, acute, lateral lobes erect, rounded, lamina channeled between the submarginal calli, with a prominent, incurved, reddish callus near the base; column 5 mm long, 1 mm wide, slightly arching, with an incurved foot column, clinandrium 3-dentate; stigmatic cavity obovate, rostellum laminar, convex; anther 1 × 0.8 mm, ovoid-spheric, pollinia 0.6 mm long; ovary pyramidal, glandular pubescent, articulated to a cylindrical pedicel; capsule not seen.

Phenology: this species flowers between June and December. The fruits begin to develop in October; between December and March they ripe and release the seeds.

Distribution and habitat: endemic to Mexico. The species is known from the southern Sierra Madre Oriental and the Sierra Los Tuxtlas, Veracruz, and Northern Mountains of Oaxaca (Fig. 1). The populations are located between 1125 and 1800 m elevation, in areas with cloud forest where permanent streams are commonly present. The specimens grow on rocks on top of a layer of moss or organic matter, but sometimes they become epiphytes.

Taxonomic notes: the species was previously reported from Chiapas by Solano (2015) based on a sterile specimen (Damon s.n., ECO-TA-H). In the meantime, it flowered and was confirmed to correspond to A. johnsonii instead. Therefore, at this time A. sotoana is exclusively known to occur in northern Oaxaca and central and southern Veracruz. A photo of A. sotoana was included by Flores-Palacios and Valencia-Díaz (2007), under the name Pleurothallis cf. herrerae, from a specimen traded in a market of the city of Xalapa, Veracruz. Acianthera sotoana (Figs. 12, 13) is very similar to A. costaricensis and it has been suggested that both could be conspecific (Karremans and Vieira-Uribe, 2020). Acianthera sotoana can be distinguished from A. costaricensis according to the traits that are compared between both taxa in Table 1.

Conservation status: Data Deficient according to the IUCN (2019) categories and criteria. For a proper assessment of its risk category it is necessary to know if the species persists in its localities reported below, estimate the size and number of populations, and model its distribution to estimate the extent of occurrence and area of occupancy. Localities of this species are in or close to protected natural areas: Pico de Orizaba-Cofre de Perote National Park (Veracruz), Los Tuxtlas Biosphere Reserve (Veracruz) and Santa María Huitepec Communal Reserve (Oaxaca), where there is still favorable habitat for the species. However, outside these protected areas (especially in Veracruz) the habitat has been severely transformed for shifting and permanent agriculture, cattle ranching, transformation of the traditional coffee plantations into full-sun ones and increase in human settlements. An additional risk factor could be the occasional extraction of specimens for illicit trade, as was reported by Flores-Palacios and Valencia-Díaz (2007).

Figure 12: *Acianthera sotoana* Solano. A. habit; B. inflorescence; C. flower with detail of the dark red hairs on the sepals abaxial surface and glandules on the ovary; D. perianth; E. lip, column, and ovary in lateral view; F. petal with detail of the marginal hairs; G. lip in natural form; H. lip spread out; I. column upper part; J. anther cap and pollinarium. Line drawing by Rodolfo Solano, based on the holotype.
Discussion

In this study we adhere to Karremans (2016) in recognizing Brenesia as part of Acianthera, rather than as a distinct genus, as treated by Luer (2023) in volume VII of Flora Mesoamericana. Luer’s treatment of Brenesia encompassed three species: B. costaricensis, B. herrerae, and B. johnsonii. In Flora Mesoamericana, A. costaricensis and A. herrerae were regarded as endemic to Costa Rica and Guatemala, respectively. Meanwhile, A. johnsonii was considered as a variable species distributed from Oaxaca and Chiapas (Mexico) to Panama; this delimitation included what is now recognized as A. sotoana and A. rzedowskiarum. Furthermore, in Flora Mesoamericana the reports of A. johnsonii in Costa Rica and Panama were based on specimens determined under that name at AMES (Brenes 156, Allen 3575, respectively), which we now reassigned to A. costaricensis. Luer passed away in 2019 and the editors of this Flora did not update his treatment for Brenesia (as
well as other Pleurothallidiane groups prepared by the author).

The five species recognized here in *Acianthera* subg. *Brenesia* extend from central Veracruz and northern Oaxaca (Mexico) to Panama. *Acianthera costaricensis* represents the southernmost species, *A. sotoana* the northernmost one and restricted to Mexico, and *A. johnsonii* as the most widely distributed taxon. The former Mexican specimens initially labeled as *A. johnsonii*, from the Altos of Chiapas, were inaccurately determined; they, in fact, correspond to the species described here as *A. rzedowskiarum*, which had been classified under *A. johnsonii* in previous checklists of Mexican Orchidaceae (Soto et al., 2007; Beutelspacher-Baigts and Moreno-Molina, 2018). Nonetheless, we confirm the presence of *A. johnsonii* in southeastern Chiapas.

*Acianthera* subg. *Brenesia* exhibits a close relationship with *Acianthera* subgenera *Antilla* and *Kraenzlinella*, which form a well-supported monophyletic group occupying the basal branch within *Acianthera* (Karremans et al., 2016). This highlights the importance of Mesoamerican and Antillean regions in the evolutionary history and diversification of a genus that currently presents a higher richness in Brazil, where slightly under half of the 300 *Acianthera* species have been documented (Barros et al., 2015). This context makes it interesting for future studies that facilitate estimations of the origin time and the geological events related to the diversification of the genus’ basal lineage.

All species within *Acianthera* subg. *Brenesia* were categorized here as Data Deficient, as our knowledge is primarily limited to the number of localities for each species; however, many of them were recorded from specimens collected over 50 years ago in El Salvador, Guatemala, and Honduras, regions we have not visited. We believe that for a thorough assessment and assignment of risk categories, the following steps are imperative: i) validation of each species’ continued presence where recorded; ii) estimation of population number, size, and long-term viability for each taxon; iii) identification of risk factors threatening each species and its habitat; and iv) modelling the distribution of each species to estimate its extent of occurrence and area of occupancy. So, assigning Data Deficient category to each taxon under- scores the need for more information and acknowledges the possibility that forthcoming research might be required to determine the extinction risk of these species.

**Author contributions**

RS designed the study. RS and AK consulted scientific collections, contributed to the acquisition of data, elaborated the species descriptions, and drafted the manuscript. RS assessed the conservation status of the species using the IUCN criteria. RS addressed the manuscript corrections.

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**Literature cited**


