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Cataracta, a new monotypic genus segregated from *Physalis* (Solanaceae)

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Abstract

We describe a new monotypic genus *Cataracta* based on *Physalis microphysa*. From 1896 to 2016, five different authors have pointed out that removing *P. microphysa* from *Physalis* may contribute to the monophyly of the genus. Recent phylogenetic analyses showed that *P. microphysa* does not share the most recent common ancestor with *Physalis*, and its taxonomic position remained uncertain. Therefore, this taxonomic change is necessary. The diagnostic traits of *Physalis microphysa* are the fruiting calyx that loosely covers the fruit, remaining open apically, with lobes as long as, or longer than the tube, a dry berry with thin pericarp, and a dehiscent epicarp covered by a thick cuticle. In contrast, *Physalis* species with typical morphologies have an inflated and completely closed fruiting calyx at the apex that fully envelopes the fleshy berry. The anatomical evidence and molecular phylogenetic analysis with six cpDNA and three nDNA regions performed with Maximum Likelihood and Bayesian Inference confirm that *P. microphysa* can be recognized as a distinct genus from *Leucophysalis*, *Physalis* and *Quincula*. *Cataracta gen. nov*. is sister to *Chamaesaracha* and along with the closely related *Quincula* grows in arid to semi-arid environments in Mexico and North America. An artificial key to Physalidinae genera is included.

Key words: fruit anatomy, inflated calyx, *Cataracta microphysa*, phylogeny, subtribe Physalidinae

Introduction

The tribe Physalidae Miers (1849: 179) (Solanaceae Jussieu (1789:124)) contains 30 genera and is divided into three subtribes: Iochrominae Reveal (2012: 217), Physalidinae Reveal (2012: 218), and Whitaninae Reveal (2012: 220) (Olmstead *et al.* 2008). For subtribe Physalidinae, 13 genera are currently recognized (Deanna *et al.* 2019). Six of them are monotypic, including *Alkekengi* Mill. (1754: 54), *Calliphysalis* Whitson (2011: 137), *Capsicophysalis* Averett & M. Martínez (2009: 72), *Oryctes* S. Watson (1871: 274), *Quincula* Raf. (1832: 145), and *Schraderanthus* Averett (2009: 54). Six other genera in Physalidinae include two to 10 species each: *Brachistus* Miers (1849: 261), *Chamaesaracha* (A. Gray) Beth & Hook (1876: 891), *Leucophysalis* Rydb. (1896: 365), *Physaliastrum* Makino (1914: 20), *Tzeltalia* E. Estrada & M. Martínez (1998: 289), and *Witheringia* L´Hér. (1788: 19) (Hunziker 2000; Averett, 1973, 2009, 2010). The largest genus in Physalidinae is *Physalis* Linnaeus (1753: 182) with 95 species (POWO, 2022). The monophyly of some of these genera has been confirmed, but *Physalis* remains paraphyletic (Whitson & Manos, 2005; Olmstead *et al.* 2008; Särkinen *et al.* 2013; Zamora-Tavares *et al.* 2016; Deanna *et al.* 2019).

Physalis has species with high morphological variation and a complex taxonomic history. From Linnaeus (1753) to Rydberg (1896), the characters used to subdivide the genus and discriminate groups of species include habit, flower arrangement, fruiting calyx shape, and type of pubescence (Martínez 1999). Rydberg recognized three sections: *Microphysalis* Rydb. (1896: 320), *Megista* Rydb. (1896: 322), and *Euphysalis* Rydb. (1896: 319). He included seven groups of species (Martínez 1999). Menzel (1951) elevated the groups to sections in her cytotaxonomic study. She also found a high correlation between the floral parts size and habit with the number and size of the chromosomes. Martínez (1999) proposed the most recent infrageneric classification, which follows Rydberg's system but includes most of the

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Mexican species that previous works had ignored. Life form, inflorescence structure and position, flower and fruit morphology, trichome micromorphology, and ecological distribution were considered. According to Martínez (1999), *Physalis* is segregated into four subgenera: 1) *Physalis* L. (1753: 182)*,* 2) *Physalodendron* (G. Don) M. Martinez (1999: 279), 3) *Quincula* (Raf.) M. Martinez (1999: 280), and 4) *Rydbergis* Hendrych (1989: 1).

Previous phylogenetic analyses with molecular data (Whitson & Manos 2005, Zamora-Tavares *et al.* 2016; Deanna *et al.* 2019) showed that the morphologically atypical *Physalis* species do not share a common ancestor with the typical species, making *Physalis* a paraphyletic group. For example, *Physalis microphysa* A. Gray (1886: 402) groups either with *Quincula lobata* (Torr.) Raf. (1832:145) (Zamora-Tavares *et al.* 2016) or behaves as the sister species to *Leucophysalis* genus (Deanna *et al.* 2019), both phylogenetic placements with low statistical support. In contrast, the species of *Physalis* that exhibit the typical morphology (one flower per node, rotate yellow corolla, fleshy fruits, foveolate seeds and an accrescent fruiting calyx that fully envelops the fruit) belong to the subgenus *Rydbergis* and form a natural group (Whitson & Manos 2005, Zamora-Tavares *et al.* 2016). Resolving the paraphyly implicates either merging almost all the small "physaloid" genera (as *Chamaesaracha* A. Gray, *Quincula* Raf., *Margaranthus* Schltdl. (1838: 8)), as noted by Rydberg (1896), or segregating the morphological and molecular dissimilar species into new genera. The paraphyly of *Physalis* has been partially resolved through taxonomic changes like the inclusion of *Margaranthus solanaceus* Schltdl. (1838: 8) as *Physalis solanacea* (Schltdl.) Axelius (1995: 11) and by the segregation and the recognition as new genus of *Physalis alkekengi* Linnaeus (1753: 182) as *Alkekengi officinarum* Moench (1753: 183) (Whitson, 2011), and *P. carpenteri* Riddell (1853: 610) as *Calliphysalis carpenteri* (Riddell) M. Whitson (2012: 137). All three species have atypical morphologies that were used to separate them from *Physalis s.s.*: *Physalis solanacea* has a purple urceolate corolla, *Alkekengi* has white stellate corollas with clearly separated lobes, and *Calliphysalis* has several flowers per node. Additionally, *Alkekengi* and *Calliphysalis* both have idioblasts amongst the seeds in their fruits. Asa Gray described *P. microphysa* from a collection made by Pringle in Chihuahua, in northern Mexico, observing that it had a rotate corolla similar to *Quincula lobata*. In his revision of the North American species of *Physalis* and related genera, Rydberg (1896) classified *P. microphysa* in the monotypic section *Microphysalis*, because it has an open fruiting calyx at the apex, with lobes as long as or longer than the tube, a condition not found in other species in the genus. He also suggested that the removal of *P. microphysa* and *P. lobata* would make *Physalis* a natural group. However, further taxonomic changes are needed to make *Physalis* a monophyletic group.

To contribute to the monophyly of *Physalis*, we propose the recognition of *P. microphysa* as a distinct genus. We use anatomical and molecular evidence to describe the monotypic new genus *Cataracta* that comprises a single species previously known as *P. microphysa*. We compare the general morphology to distinguish *Cataracta* from *Chamaesaracha*, *Oryctes*, *Physalis* and *Quincula*, and provide a full morphological description and distribution map of the new genus.

Materials and Methods

Fruit anatomical comparison:—Three fruits of *Physalis angulata* Linnaeus (1753:183) and *P. microphysa* were fixed in FAA and stored at room temperature until processed. Whole fruits were sliced in half and the seeds were removed prior to dehydration. Samples were processed by standard paraffin protocols of Ruzin (1999) and Johansen (1940). Sections of 12 µm thick were obtained in a Leica rotary microtome and stained with safranin-fast green. The slides were mounted in resin and are stored at the Universidad de Querétaro anatomy collection. Observation and photography were made in an Axio Observer.Z1 (Zeiss) microscope. Microphotographs were obtained with Axiocam ICs5 and measured using the ZEN Zeiss software.

Taxon sampling:—We constructed the analysis at the generic level based on previous molecular phylogenies of the subtribe Physalidinae (Whitson & Manos 2005; Zamora-Tavares *et al.* 2016, Deanna *et al.* 2019). We included samples of the 13 genera recognized in the subtribe: *Alkekengi, Brachistus, Calliphysalis, Capsicophysalis, Chamaesaracha, Leucophysalis, Oryctes, Physaliastrum, Physalis, Quincula, Schraderanthus, Tzeltalia* and *Witheringia.* As outgroup we used *Iochroma* Benth (1945: 20)*, Deprea* Raf. (1838: 57), and *Capsicum* Linnaeus (1753: 188).

Molecular DNA matrix:—Sequences of six chloroplast DNA regions, *mat*K, *ndh*F, *rbc*L, *rpl*32-*trn*L, *trn*L and *ycf1*-3, and three nuclear DNA markers (ITS, LEAFY and GBSSI region between exons 8 and 10) were generated using primers and protocols described in previous studies (Whitson and Manos, 2005; Zamora-Tavares *et al.* 2016; Deanna *et al.* 2019). Most of the sequences of nDNA used in our current study were published in previous papers (Whitson & Manos, 2005; Zamora-Tavares *et al.* 2016; Deanna *et al.* 2019). Some sequences of nDNA and cpDNA regions were newly generated for *Capsicophysalis potosina* (B.L. Rob. & Greenm.) Averett & M. Martínez (2009: 72)*, Cataracta microphysa comb. nov, Chamesaracha coronopus* (Dunal) A. Gray (1876: 540), *C. rzedowskiana* Hunz. (1980:23), *Leucophysalis grandiflora* (Hook.) Rydb.(1896:336), *L. nana* (A. Gray) Averett (1971: 380), *Physaliastrum heterophyllum* (Hemsl.) Migo (1939:171), *Physalis campechiana* Linnaeus (1759:933), *P. melanocystis* (B.L. Rob.) Bitter 1924: 369), and *Quincula lobata*. Finally, most of the cpDNA were extracted from plastomes that were generated by Sandoval-Padilla *et al.* (in press; Appendix 1, Tables A1–A2).

Phylogenetic analysis:—Matrices with the DNA sequences for each of the regions were generated using Mesquite v. 3.81 (Maddison & Maddison 2023). DNA sequences were aligned using SEAVIEW v. 4 (Gouy *et al.* 2010) with the MUSCLE algorithm (Edgar 2004). Aligned sequences were analyzed to obtain the best-fitting nucleotide substitution models for each of the regions was identified using jModelTest v. 2 (Darriba 2012) based on the Akaike Information Criterion (Posada & Crandall 1998). The molecular datasets were concatenated using Mesquite v. 3.7. The phylogenetic analyses were conducted using Maximum Likelihood (ML) in RAxML v. 8 (Stamatakis 2014) and Bayesian Inference (BI) in MrBayes v. 3.2.7a (Ronquist *et al.* 2012) using the CIPRES platform (Miller *et al.* 2010). Branch support for the ML run was assessing by resampling with 1000 rapid bootstrap inferences. The BI analysis was run for 20 million generations, where trees were sampled every 1000 generations. The best tree of ML and the consensus tree of the BI were displayed in FigTree v. 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/).

Artificial key:—We built an artificial dichotomous key for the identification of the 13 genera of the subtribe Physalidinae plus the new genus. The key is based on diagnostic morphological characters, habitat preferences and geographic distribution.

Results

Anatomy:—The fleshy berries of *Physalis angulata*, a member of subgenus *Rydbergis* has two carpels. In its early stage, the exocarp has a thin one-celled uninterrupted epidermis of 11 µm thick. The mesocarp is composed of 12 to 14 parenchyma cells that are radially compressed and nucleated. This area has the vascular bundles. The endocarp, at the inner portion of the vascular bundles, consists of large parenchyma cells of 360 µm long, which lacks vascular bundles or sclerenchyma cells of 360 µm long, which lacks vascular bundles or sclerenchyma cells (Fig. 1A). In its mature stage, the exocarp of *P. angulata* is 13.5 µm thick, and the mesocarp increases its thickness formed by 14 to 15 cell layers. The endocarp also increases the number of cells to 7–8 cells. (Fig. 1B). In both early and mature stages, the fruit of *P. microphysa* has a large evident cuticle, 35 µm thick. The exocarp is one cell layer thick, and the cells are 24 µm in size. The mesocarp has 7–9 cells, which are 94.9 µm thick (Fig. 1C). In immature fruits, the mesocarp has vascular bundles, but in mature fruits the tissue disintegrates and the exocarp breaks irregularly (Fig. 1D).

Phylogeny:—The results for each separate region were incongruent, as some of the outgroup taxa were mixed with the ingroup; besides all nine topologies had poor support (Appendix 1, Figs. A1–A9, Table A3). On the other hand, with the concatenated matrix, better support values were obtained for the relationships recovered. The concatenated dataset had an aligned length of 9047 characters. With this data set, the monophyly of the subtribe Physalidinae is confirmed (Fig. 2); however, few relationships remain unclear due to low support. *Physaliastrum* is the most early divergent genus in the subtribe. Then, a clade formed by *Tzeltalia*, *Schraderanthus*, *Brachistus* and *Witheringia*, is sister to the rest of the taxa. In the next group (BS=56, PP=0.95), one clade includes *Oryctes* and *Leucophysalis* as sister of another two clades. With very low support, (BS = 12, PP=0.82) the first one contains *Calliphysalis* and *Alkekengi* as sister taxa and a sister clade formed by *Chamaesaracha rzedowskiana* Hunziker (1980: 23) and *Capsicophysalis potosina* (B.L. Rob. & Greenm.) Averett & M. Martínez (2009: 72). In the second best supported one (BS= 60, PP= 1), *Quincula* is the sister of the remaining taxa that group as follows: a clade that contains *Chamaesaracha coronopus* (Dunal) A. Gray (1876: 540), and *Cataracta gen. nov.* that shares the most common recent ancestor with the species of *Physalis* subgen. *Physalodendron* and subgen. *Rydbergis* (Fig. 2, Appendix 1, Figure A10).

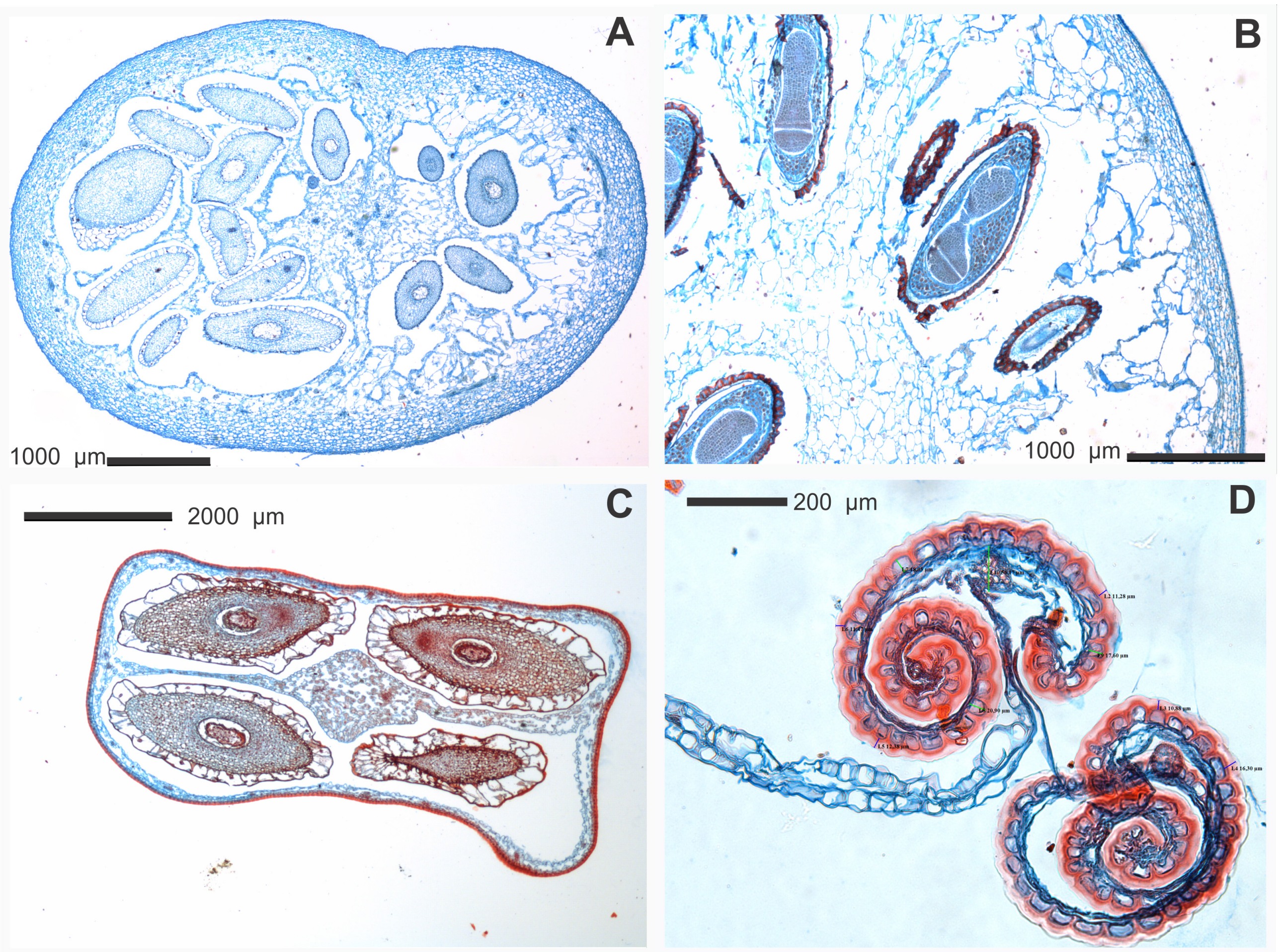

FIGURE 1. Fruit anatomical comparison of *Physalis angulata* and *Cataracta microphysa.* Cross sections of **A.** Entire fruit of *Physalis angulata* in early development stage and **B.** *Physalis angulata* in mature stage. Cross sections of fruit in mature stage **C.** Entire fruit of *Cataracta microphysa* of early development stage and **D.** *Cataracta microphysa* in mature stage (Photos of Mahinda Martínez and Alan Herrera).

Taxonomic treatment

Artificial key to the Physalidinae genera including *Cataracta gen. nov*

1. Fruiting calyx not expanded or similar in size to flowering calyx .... *Witheringia*
\- Fruiting calyx expanded 2
2. Fruiting calyx somewhat expanded, larger than the flowering calyx, but smaller than the mature fruit 3
\- Fruiting calyx highly expanded, as large as or larger than the mature fruit 5
3. Corolla purple, tubular........ *Oryctes*
\- Corolla whitish, yellow or yellow green, purple, lobed or rotate........ 4
4. Inflorescence with (3) 5–10 (15) flowers, corolla lobed, growing in wet forest in the mountains of Mexico and Central America .... *Brachistus*
\- Inflorescence with 1–2 flowers, corolla rotate, growing in the arid regions of SW USA and N Mexico .... *Chamaesaracha*
5. Fruiting calyx inflated around the fruit or reflexed 6
\- Fruiting calyx tightly covering entire berry or loosely surrounding berry, but open at the apex 12
6. Fruiting calyx with reflexed lobes 7
\- Fruiting calyx inflated, closed at the apex of the lobes 8
7. 1–2 flowers in axillary fascicles, corolla less than 3 cm wide, with or without maculations in the throat .... *Capsicophysalis*
\- 6–8 flowers in axillary fascicles, corolla 4–5 cm wide, green maculations consisting of small dots in the throat.... *Schraderanthus*
8. Flowers solitary .... *Physalis ss*
\- Flowers fasciculate 9
9. Corolla unlobed, pentagonal to round when flattened and viewed from the front........ 10

- Corolla stellate, distinctly star-shaped, lobes longer than the corolla 11

10. Corolla yellow with five dark maculations, growing in coastal plains of the SE of USA .... *Calliphysalis*

- Corolla purple, without maculations, growing in SW USA and N Mexico .... *Quincula*

11. Fruiting calyx red at maturity of the fruit, membranaceous aspect .... *Alkekengi*

- Fruiting calyx purple at maturity, papyraceous or leathery aspect .... *Physalis* sugbgen. *Physalodendron*

12. Corolla rotate, slightly lobed, fruiting calyx tightly enveloping the fruit 13

- Fruiting calyx loosely surrounding berry, open at the apex 14

13. Fruiting calyx not ribbed nor angled, without ornamentations, plants of North America .... *Leucophysalis*

- Fruiting calyx with veins obscure or thickened into angles or ribs, mostly muricate with soft emergences that appear scale-like when dry, plants of Asia .... *Physaliastrum*

14. Perennial herb, plants of N of Mexico .... *Cataracta gen. nov.*

- Shrub with soft stems, reclining, fruiting calyx always green, plants of wet forest of S Mexico and Central America .... *Tzeltalia*

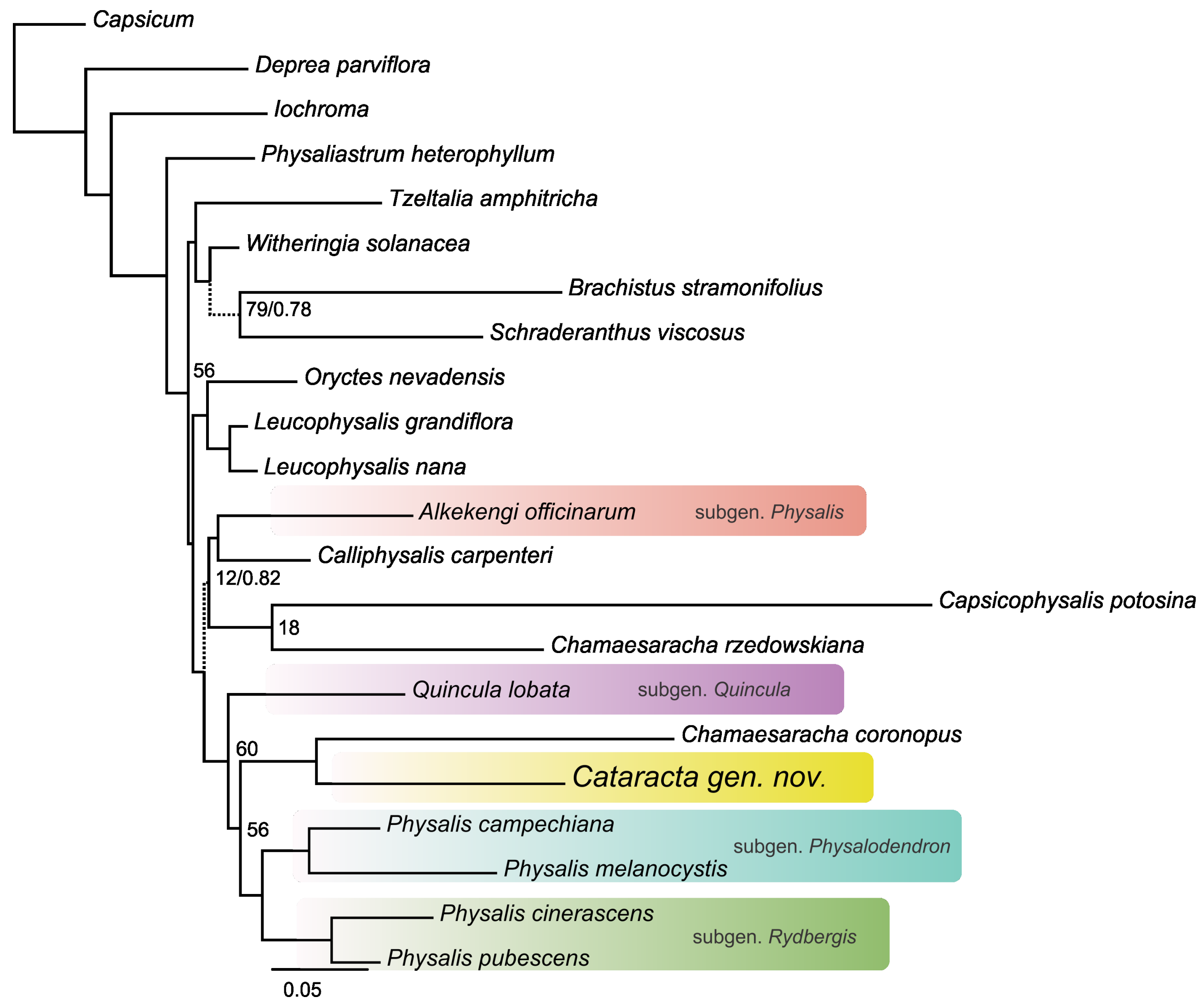

FIGURE 2. Phylogenetic relationships of Physalidinae based on Bayesian 50% majority consensus tree and Maximum likelihood with three nDNA and six cpDNA regions. The colored boxes indicate the subgeneric classification of *Physalis* proposed by Martinez (1998) and the phylogenetic position of *Cataracta gen. nov*. Dashed lines show the branches with posterior probabilities and bootstrap support less than 0.95 and 70, respectively. Numbers at the left of the nodes are posterior probabilities, and numbers to the right are bootstrap support values.

Cataracta P. Zamora-Tavares, O. Vargas & M. Martínez, *gen. nov.*

Type:—*Cataracta microphysa* (A. Gray) P. Zamora-Tavares, O. Vargas & M. Martínez.

Basionym:—*Physalis microphysa* A. Gray. Proc. Amer. Acad. Arts 21: 402. 1886.

Etymology:—The name *Cataracta* honors U.T. Waterfall, who extensively studied the genus *Physalis*.

Herbae erectae, circa 20–40 cm altae, radices perennes; foliis 12–20 mm longo et 10–23 mm lata crenato-repandis, floralibus 12 a 20 mm diameter; corolla ochroleuca maculis fusco-luteis, plano-rotata; calyce fructifero ovato tereti 9–12 mm longo et 8–12 mm lata, fructus non capsularis dehiscens, seminibus crassiusculis immarginatis favoso-rugulosis.

Erect perennial rhizomatous herb, branched from a woody base, 15 to 60 cm long, with a long and thin rhizome; the entire plant densely pubescent with simple eglandular and glandular multi-cellular trichomes of 0.2–1 mm long; leaves reniform to ovate or subhastate, 1.2–2.0 cm long and 1.0–2.3 cm wide, margin entire or sinuous with one to three teeth; leaf trichomes more or less appressed, generally shorter than stem trichomes; petiole 0.5–1.2 cm long but the most basal ones up to 6 cm long; flowers solitary on pedicels of 2 to 5 mm long; floral calyx 4–6 mm wide at the base, lobes lanceolate to slightly acuminate, lobed from the middle to a third of their length; corolla rotated with five small lobed tips, 1.2–2.0 cm in diameter, whitish yellowish with yellow to greenish maculas composed by tiny dots at the base of the lobes, anthers ovate-oblong, yellow, 1–1.5 mm long, on glabrous filaments 2–3 mm long; fruiting calyx terete, ovate-oblong to campanulate, 9–12 mm long and 8–12 mm wide, lobes acuminate, 2–4 mm long, lobes sometimes reflexed; fruit dehiscent dry berry, pericarp dry that breaks into irregular portions exposing the seeds, 5 to 7 seeds per fruit; seeds reniform with reticulate dark brown testa, 2 mm in diameter.

Comparison:—*Cataracta microphysa* is a perennial herb (Fig. 3A) with a solitary axillary flower as in *Physalis*, but the rotate whitish-colored corollas with a slight yellow or greenish tinge resembling those of *Chamaesaracha* spp. and the corolla shape resembling those of *Quincula* (Fig 3B). The fruiting calyx is terete, ovate-oblong to campanulate, inflated like in *Physalis*, but differing in being open-flaring apically and the lobes of the calyx are rolled outward (Fig 3C). The fruit is not a fleshy, non-dehiscent berry as in *Physalis*, but is a dehiscent, dry berry with a thin, dry pericarp closer to the dry fruits of *Chamaesaracha* and *Oryctes*, with the unique feature of dehiscing along irregular lines (Figs. 3D–E). The seed testa is dark brown and faveolated-rugous, while seeds of *Physalis* and *Chamaesaracha* species do not have such ornamentation (Fig 3D). A full comparison of the five morphologically closely genera is shown in Table 1 and Figure 4.

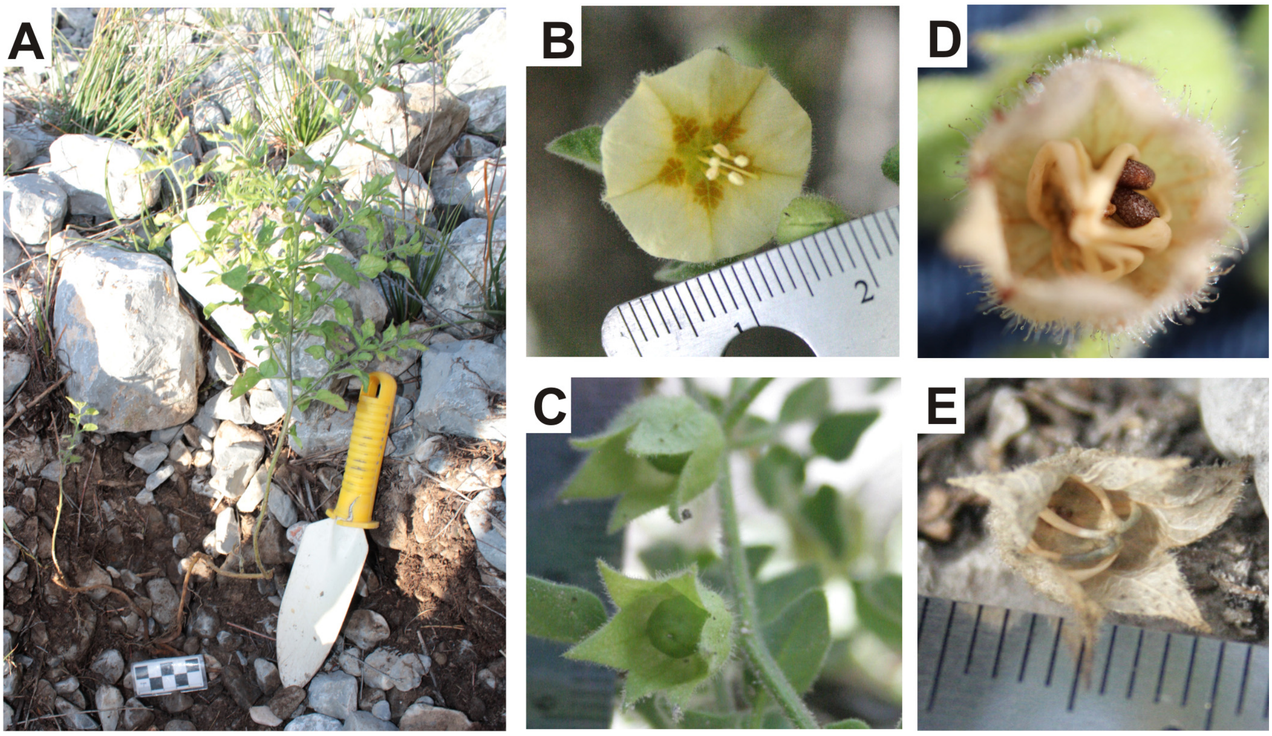

FIGURE 3. *Cataracta microphysa comb. nov*. A. Perennial herb with a rhizome of 30–40 cm long. B. One flower per axil, corolla plane rotated with a slight yellowish or greenish tinge. C. The fruiting calyx is teretish, ovate-oblong to campanulate, and open-flaring apically. D. Fruit with a thin, dry pericarp, with dark brown seeds and faveolated-rugous testa. E. The dry fruits dehiscing along irregular lines (Photos of Pilar Zamora-Tavares and Mahinda Martínez).

TABLE 1. Comparison of *Cataracta gen. nov*. and four genera with similar habitats and morphology, *Chamaesaracha*, *Oryctes*, *Physalis sensu stricto,* and *Quincula*, based on 16 morphological characters. ? = not observed by the authors.

Character/ Taxon	***Cataracta* gen. nov**	***Chamaesaracha***	***Oryctes***	***Physalis s.s.***	***Quincula***
Habit	Perennial	Perennial	Perennial	Perennial, annual	Perennial
Life form	Herbaceous	Herbaceous	Herbaceous	Herbaceous, shrubby	Herbaceous
Type of trichomes	Simple in different sizes, some glandular ones	Simple, glandular and branched	Simple, glandular and branched	Simple and branched, bifid, capitate, straight, curved, short or long	Vesicles whitish, crystalline, scale-shaped
Flowers per node	1	1	4 to 5	1 or more	1 to 5
Expansion of fruiting calyx	Inflated	Accrescent tightly covering entire berry	Accrescent adpressed to the dry fruit	Inflated	Inflated
Calyx coverage of the fruit	Full	Almost full	Almost full	Full	Full
Corolla shape	Rotate expanded	Rotate	Tubular	Campanulate, rotate, urceolate, funnelform	Rotate
Corolla main color	Whitish-yellow	Whitish-yellow	Pinkish to yellow	Whitish, yellow, purple, orange	Purple
Macula shape	Composite	Composite	Absent	Absent, solid, composite	Absent
Macula color	Greenish-yellow	Greenish-yellow	Absent	Greenish, yellowish, purple	Absent
Pubescence location inside the corolla	Base of corolla throat, behind the filaments of the stamens	Base of corolla throat, forming bearings alternating with the filaments of the stamens	Base of corolla throat	Base of corolla throat, behind and on the filaments of the stamens	Base of corolla throat, behind the filaments of the stamens
Anther color	Yellow	Yellow	Yellow	Yellow, purple, blue	Yellow
Fruit type	Non-capsular dehiscent	Berry with thin pericarp	Non- capsular dehiscent	Berry	Berry with thin pericarp
Idioblasts	Absent	Absent	Present	Absent	Absent
Seed color	Dark brown	Yellow	?	Yellow, light brown, dark brown	Yellow
Habitat	Arid and semi-arid areas of northern Mexico	Arid and semi-arid areas of northern Mexico and southern USA	Arid areas of Nevada, USA	Most types of habitats of the Americas, Caribbean and Antilles	Arid and semi-arid areas of northern Mexico and southern USA

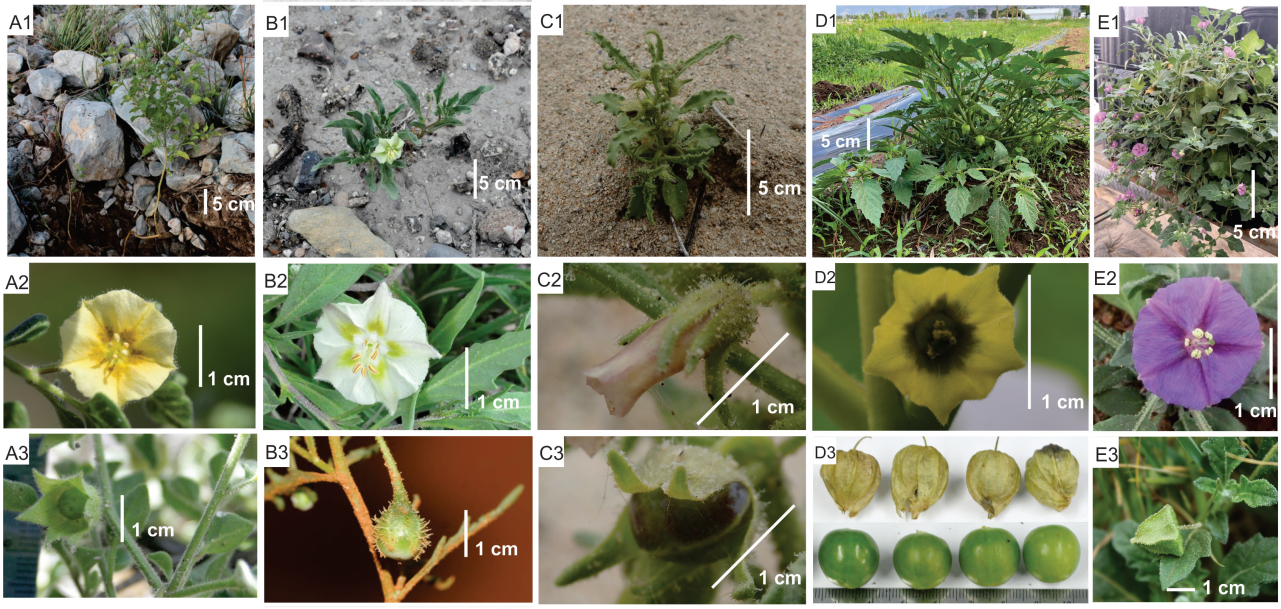

FIGURE 4. Comparisons of habit, flower and fruit traits among *Cataracta* gen. nov. (A1–A3), *Chamesaracha* (B1–B3), *Oryctes* (C1–C3), *Physalis* (D1–D3), and *Quincula* (E1–E3) (Photos of Pilar Zamora-Tavares, Mahinda Martínez and Ofelia Vargas-Ponce, B3 provided by Juan Carlos Delgado, C1–C3 by Sophie Winitsky, and E3 by Rocio Deanna).

Phenology:—This species flowers and fruits from May to October, with a peak in fruiting from September to October.

Distribution:—Endemic to Mexico; states of Chihuahua, Coahuila, Nuevo León, and Tamaulipas (Fig. 5).

Habitat:—In xerophytic scrub and in transition with pine-oak forests.

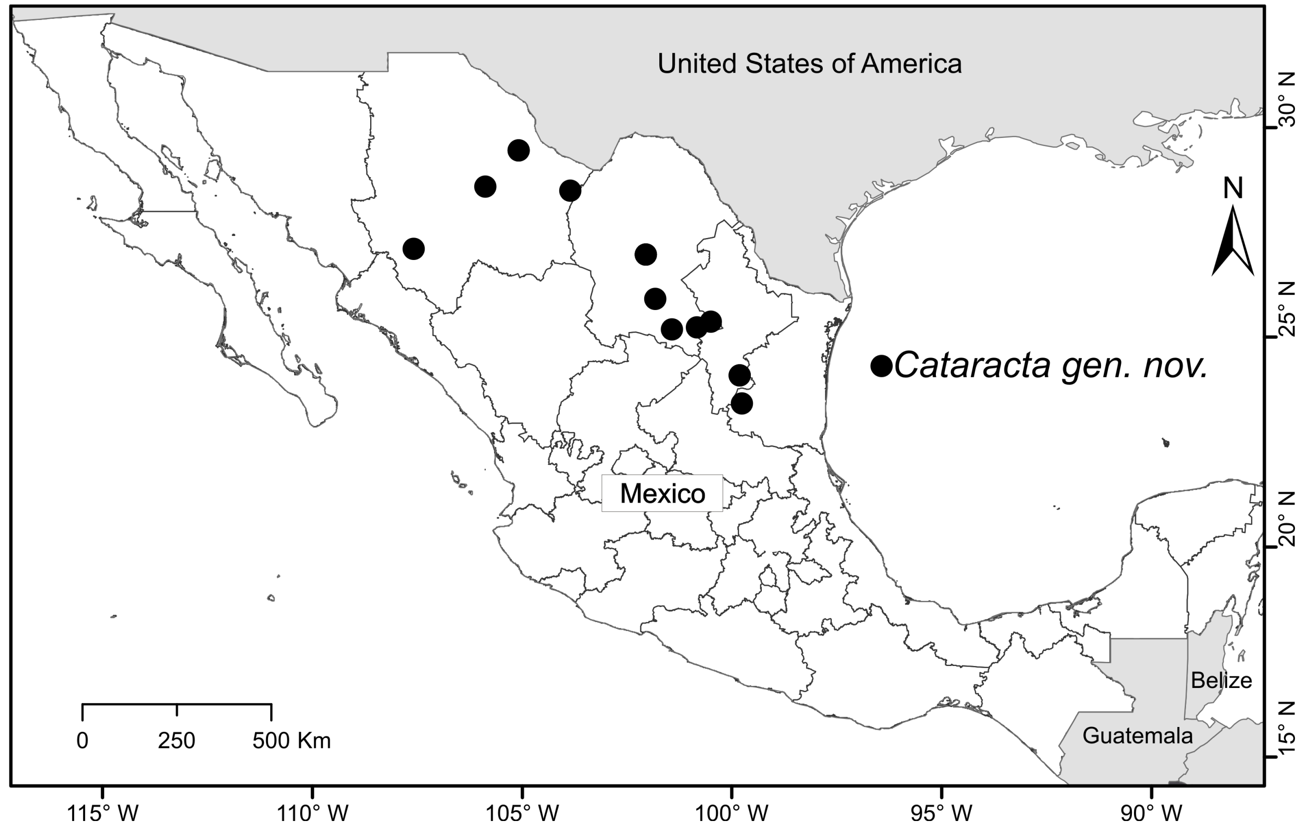

FIGURE 5. Geographic distribution of *Cataracta gen. nov.*

Representative specimens examined. MEXICO. Chihuahua: Santa Eulalia Mts*, C.G. Pringle 317* (MO, MEXU); Batopilas de Manuel Gómez Morín, E of La Bufa, on S side of Barranca de Batopilas, 3300 ft, 27–31 Oct 1973, *R. Bye 5677* (MEXU); Coyame, 16 miles SW of Coyame along Hwy 16 in narrow alluvial arroyo in Chihuahua Desert Scrub, near 29°16'N, 105°16'W, 16 Sep 1972, *J. Henrickson 7649* (ANSM, IEB, MEXU); Julimes, ca 31 (air) miles NW of Julimes in a SW facing canyon above Rancho El Recuerdo in Sierra de Carrasco (S. of Sierra de Chorreras), 4500 ft, 28°47'N, 105°09'W, 15 Sep 1973, *J. Henrickson 12940* (MEXU); Camargo, Sierra de las Pampas west of Hacienda El Berrendo, 1600–1800 m, 27°20'N, 104°43'W, 25 Aug 1972, *F. Chiang et al. 8829* (MEXU). Coahuila: Cuatro Cienegas, 22 (air) miles WNW of Cuatro Cienegas, in lower Canyon de la Hacienda of limestone Sierra de la Madera, 2–3 miles from roads end, 5200 ft, 27°03'N, 102°25'W, 26 Sep 1973, *J. Henrickson 13556* (MEXU); Cuatro Cienegas, 35 (air) km of Cuatro Cienegas, in the lower limestone Canyon de la Hacienda on northside of Sierra de la Madera, 4700 ft, 27°05'N, 102°25'W, 4 Aug 1973, *J. Henrickson 11850* (ANSM, MEXU); Cuatro Cienegas, 28 (air) miles WNW of Cuatro Cienegas, on the N slope of the Sierra de la Madera, 7.5 (air) miles W of Rancho Cerro de la Madera, at base of Cañon Desiderio, in upper Cañon Posos, 1700–1800 m, 27°19'N, 102°30'W, 13 Aug 1976, *J. Henrickson 15311* (MEXU); Tlahualilo de Zaragoza, 29 (air) miles NE of Tlahualilo on west-facing shale slope on the east side of Sierra de los Remedios, 3750 ft, 26°36'N, 103°05'W, 9 Aug 1973, *J. Henrickson 12174b* (MEXU); Ramos Arizpe, Valle de los Angeles, Sierra de la Paila, without collector data (ENCB); Arteaga, al norte del Ejido Chapultepec, Sierra La Laja, 2473 m, 25°15'24'N, 100°51'54"W, 14 Jul 2004, *F.J. Encina 116* (ANSM); Arteaga, Puerto San Lorenzo, Cerro La Campana, Sierra Hermosa, 2460 m, 2 Aug 1979, *L. Arce s.n.* (ANSM); Arteaga, Sierra de la Madera in Cañada de la Hacienda, NW of Cuatro Cienegas, 1850 m, 27°04'N, 102°25'20" W, 15 May 1992, *M.H. Mayfield 1395* (ANSM). General Cepeda, km 20 de la brecha La Paz-La Casita, 300 m al S de La Casita rumbo al Tejocote, 2092 m, 25°11'40"N, 101°26'26"W, 10 Sep 2017, *A. Castro et al.* (CIIDIR). Nuevo León: Aramberri, La Escondida-San Francisco, 1750 m, 26 Aug 1992, *G.B. Hinton et al. 22355* (ANSM, IEB, MEXU). Tamaulipas: Bustamante, 4.8 mi NW of Hwy 101 on road to Bustamante; W-facing, steep slope overlooking deep valley, 1670 m, 23°25'N, 99°40'W, 15 Jun 1987, *G. Nesom et al. 5977* (MEXU, QMEX).

Discussion

Dry dehiscent berries or non-capsular fruits have emerged independently at least three times in Solanaceae (Knapp 2002). This type of fruit appears in the clade *Hyoscyamus* Linnaeus (1753: 179)*,* in the genus *Solanum* and in Physalidinae, in the genus *Oryctes* (Knapp 2002). *Cataracta gen. nov.* represents the fourth event in the family, and the second for the Physalidinae subtribe, since *Cataracta gen. nov.* and *Oryctes* do not share a recent common ancestor. Similar to *Cataracta gen. nov*., *Chamaesaracha*, *Oryctes* and *Quincula* have a berry with thin pericarp, with or without dehiscence; therefore, anatomical studies are needed in those taxa. Moreover, *Chamaesaracha*, *Quincula* and *Cataracta gen nov.* are either monotypic or have few species and have diversified in arid zones. Bolgrem & Erickson (2005) found that the evolution of fleshy fruits is correlated with habitat changes towards places with less light and with unpredictable disturbances, where frugivores can select them. Therefore, it is probable that the dry fruits in these taxa and others in Solanaceae are an adaptation to arid or semi-arid conditions (Knapp 2002). Additionally, dry fruits are dispersed by passive processes such as gravity or runoff (Hoare & Knapp 1997; Knapp 2002). In this sense, the dehiscence of the dry fruits ensures seed dispersal.

Cataracta gen. nov. shares the most recent common ancestor with *Chamaesaracha coronopus*; these taxa grow in arid and semi-arid zones of northern Mexico and the southern USA (Hunziker 2000; Averett 2010). As mentioned before, the observation of the removal of *Physalis microphysa* from *Physalis* in order to make it a natural group has been pointed out by five other authors after Rydberg (1896) (Waterfall 1967; Martínez 1999; Hunziker 2000; Whitson & Manos 2005; Zamora Tavares *et al.* 2016). Moreover, in all previous phylogenetic estimations with molecular data, *P. microphysa* does not share the most recent common ancestor with *Physalis*, and its position changes depending on the data set. The analysis performed by Whitson & Manos (2005) with two nuclear regions shows that *P. microphysa* separates from the clade of morphologically typical *Physalis*. In another analysis which includes both morphological and molecular data, *P. microphysa* forms a clade with *Quincula lobata,* and both are the sister taxa of *Chamaesaracha* (Zamora-Tavares *et al.* 2016). The analysis of Deanna (2019) based on one cpDNA and three nDNA regions recovers *P. microphysa* as sister to *Leucophysalis*. The three previous estimations had low bootstrap support and posterior probabilities (BS = 58%, PP = < 0.95). In our study and with the current dataset (six cpDNA regions, three nDNA regions sequences, and 10 morphological characters) the phylogenetic relationships have strong support (BS=76%, PP= 1) to split *Cataracta* from the morphologically typical *Physalis* species.

Conclusion

The anatomical and molecular evidence supports the segregation of *Physalis microphysa* as the *Cataracta gen. nov.* within the Physalidinae subtribe. With this taxonomic arrangement, we are closer to a monophyletic *Physalis* genus. The systematics of the Physalidinae is still a challenge.

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