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Physalis and physaloids: A recent and complex evolutionary history



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ABSTRACT

The complex evolutionary history of the subtribe Physalinae is reflected in the poor resolution of the relationships of *Physalis* and the physaloid genera. We hypothesize that this low resolution is caused by recent evolutionary history in a complex geographic setting. The aims of this study were twofold: (1) To determine the phylogenetic relationships of the current genera recognized in Physalinae in order to identify monophyletic groups and resolve the physaloid grade; and (2) to determine the probable causes of the recent divergence in Physalinae. We conducted phylogenetic analyses with maximum likelihood (ML) and Bayesian inference with 50 Physalinae species and 19 others as outgroups, using morphological and molecular data from five plastid and two nuclear regions. A relaxed molecular clock was obtained from the ML topology and ancestral area reconstruction was conducted using the DEC model. The genera *Chamaesaracha*, *Leucophysalis*, and *Physalis* subgenus *Rydbergis* were recovered as monophyletic. Three clades, *Alkekengi–Calliphysalis*, *Schraderanthus–Tzeltalia*, and *Witheringia–Brachistus*, also received good support. However, even with morphological data and that of the DNA of seven regions, the tree was not completely resolved and many clades remained unsupported. Physalinae diverged at the end of the Miocene (~9.22 Mya) with one trend indicating that the greatest diversification within the subtribe occurred during the last 5 My. The Neotropical region presented the highest probability (45%) of being the ancestral area of Physalinae followed by the Mexican Transition Zone (35%). During the Pliocene and Pleistocene, the geographical areas where species were found experienced significant geological and climatic changes, giving rise to rapid and relatively recent diversification events in Physalinae. Thus, recent origin, high diversification, and morphological complexity have contributed, at least with the currently available methods, to the inability to completely disentangle the phylogenetic relationships of Physalinae.

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1. Introduction

Stable classification schemes are important for understanding the natural history of biological groups. There are many methodological approaches available at present, employing diverse evidence sources (Borsch et al., 2015); nevertheless, this has

proved to be a very difficult task in groups of recent origin, high diversification, and morphological complexity that lead to a problematic taxonomic history (Carstens and Knowles, 2007; Flores-Rentería et al., 2013). This occurs with the subtribe Physalinae (Miers) Hunz. (Solanaceae), which exhibits apparent similarity in flower and fruit morphology, hampering clear discrimination among its genera. Four (Hunziker, 2001) to nine genera (Olmstead et al., 2008; Whitson and Manos, 2005), with 104–108 species, are recognized in the subtribe. Two emblematic problems are the taxonomic placement of *Margaranthus* Axelius and *Quincula* (Torr.) Raf., which have been recognized either as independent genera (Axelius, 1996; Whitson and Manos, 2005) or as part of *Physalis* L. (Martínez, 1999). In our analysis, we follow the nomenclature of Martínez and refer to these taxa as *P. lobata* and *P. solanaceous*. As presently circumscribed, Physalinae includes

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12 genera: *Alkekengi* Mill., *Brachistus* Miers, *Calliphysalis* Whitson, *Capsicophysalis* (Bitter) Averett & M. Martínez, *Chamaesaracha* A. Gray ex Franch. & Sav, *Leucophysalis* Rydb., *Oryctes* S. Watson, *Physaliastrum* Makino, *Physalis* L., *Schraderanthus* Averett, *Tzeltalia* E. Estrada & M. Martínez, and *Witheringia* Miers.

Phylogenetic analyses have shown that the subtribe Physalinae is a monophyletic group (Whitson and Manos, 2005; Olmstead et al., 2008; Li et al., 2013). Furthermore, Whitson and Manos (2005) recovered *Chamaesaracha*, *Physalis* subgenus *Rydbergis*, and *Witheringia* as monophyletic groups; however, many genera proved to be polyphyletic or paraphyletic, or their relationships remained unsolved. For instance, *Leucophysalis* would be monophyletic if *L. viscosa* Hunz. is excluded (Whitson and Manos, 2005), while *Physalis*, which includes the subgenera *Physalis*, *Physalodendron*, *Quincula*, and *Rydbergis* (Martínez, 1999), is paraphyletic. The basis for this hypothesis, obtained from the analysis of two nuclear and two chloroplast regions (Olmstead et al., 2008; Whitson and Manos, 2005), is that *P. campechiana* L., *P. lobata* Torr., *P. melanocystis* (B.L. Rob.) Bitter, and *P. microphysa* A. Gray, do not group within *Physalis* and form the physaloid grade together with the genera *Alkekengi*, *Calliphysalis*, *Chamaesaracha*, *Leucophysalis*, and *Oryctes* (Olmstead et al., 2008; Whitson and Manos, 2005). These genera only present fruiting calyx expansion to a limited degree, while in *Physalis* this expansion is complete. In turn, *P. campechiana*, *P. lobata*, *P. melanocystis*, and *P. microphysa* have atypical morphological characteristics in *Physalis*, such as shrubby habit, lobed fascicled flowers, or a purple corolla, among others. Typical *Physalis* species belonging to the subgenus *Rydbergis sensu* Martínez (1999) are herbaceous and possess solitary flowers, a yellow corolla, and an accrescent and inflated fruiting calyx.

Several studies have focused on resolving the circumscription and natural relationships of *Physalis* and the physaloids (Axelius, 1996; Martínez, 1999; Whitson and Manos, 2005). Based on morphological features, Rydberg (1896) suggested that the exclusion of atypical species of *Physalis* (i.e., *P. lobata*, *P. microphysa*) would create a natural group of this genus. Rydberg also noted that the genera related to *Physalis* are *Chamaesaracha*, *Leucophysalis*, and *Oryctes*. Cladistic analyses of morphological and molecular data have included *Margaranthus* within *Physalis* (Axelius, 1996; Whitson and Manos, 2005). Similarly, based on morphological characteristics, *P. amphitrica* (Bitter) Standl. & Steyerl. and *P. calidaria* Standl. & Steyerl. are segregated as the genus *Tzeltalia* (Estrada and Martínez, 1998). In order to partially correct the paraphyly of *Physalis*, Whitson (2011, 2012) segregated *P. alkekengi* L. and *P. carpenteri* Riddell ex Rydb. into the genera *Alkekengi* and *Calliphysalis*, respectively. This segregation was based on molecular evidence and the distinctive morphological characteristics of those species (Whitson and Manos, 2005). However, to continue this restructuring of the subtribe Physalinae, it is necessary to re-analyze its phylogenetic relationships by increasing the quantity of available molecular data and including *Capsicophysalis* and *Physaliastrum*. The molecular evidence suggests that the latter forms part of the subtribe Physalinae (Li et al., 2013). Also, the tropical species of *Chamaesaracha* are difficult to treat. Hunziker (2001) recognized three species *Chamaesaracha cernua*, *C. potosina* and *C. rzedowskiana* in the section *Capsicophysalis*. Meanwhile Averett and Martínez (2009) lumping *C. cernua* Hunz. and *C. potosina* Rob. & Greenm. in the monotypic genus *Capsicophysalis* as *Capsicophysalis potosina* (Rob. & Greenm.) Averett & Martínez. It is also necessary to analyze the relationship of *C. rzedowskiana* Hunz. with the physaloids and to reconsider the taxonomic placement of this species.

Knowledge regarding the date and geographical area of diversification of organisms helps to determine the probable causes of intricate evolutionary histories (Morrone, 2007). When Särkinen et al. (2013) dated Solanaceae, they indirectly inferred that

Physalinae diverged approximately 8–11 Mya. This suggests that the poor resolution of the phylogenetic relationships within the subtribe found by Whitson and Manos (2005) could be the result of a rapid and complex evolutionary history. For groups with recent divergence or accelerated diversification, resolution of the phylogenetic tree is often difficult to achieve, as is the case with *Inga* Mill. (Richardson et al., 2001), *Solanum* L. (Särkinen et al., 2013), *Ixora* L. (Tosh et al., 2013), and *Meehania* Britton (Deng et al., 2015). So that, establishing a temporary framework for the evolutionary history of Physalinae could contribute to the understanding of the processes that shaped it and comprehend their disjunct geographical distribution.

Physalinae is primarily distributed in the Americas, with two disjunct genera in Asia and Europe. *Calliphysalis*, *Chamaesaracha*, *Leucophysalis*, and *Oryctes* are distributed in North America. *Capsicophysalis*, *Schraderanthus*, *Tzeltalia*, and *Witheringia* are found in Mexico, Central America, and South America. *Alkekengi* and *Physaliastrum* are mostly located in China, Japan, and Vietnam. *Physalis* is the most diverse genus of the subtribe; it is distributed naturally in the United States, Mexico, Central America, South America, and the West Indies, with a few introduced species in the tropics of the Old World (Martínez, 1998). The current geographic distribution of the subtribe reflects its wide range of ecological requirements, occurring as it does in 209 (Zamora-Tavares, unpublished results) of the 825 terrestrial ecoregions recognized by Olson et al. (2001). Nevertheless, estimation of the ancestral distribution areas is required in order to understand the processes that contribute to its diversification. This approach provides evidence for the reconstruction of scenarios in which the evolutionary histories of groups of organisms unfolded (Meseguer et al., 2015). Phylogenetic hypotheses are used in the context of historical biogeography for these estimations in order to explain common distribution patterns among species, including the reconstruction of ancestral geographic ranges in the branches of the tree of life (Ree and Sanmartín, 2009). Our hypothesis therefore considers it likely that the current distribution of Physalinae is the result of recent geological events, as well as the dispersal ability of the subtribe (Zamora-Tavares et al., unpublished data). Our objectives are therefore: (1) To determine the phylogenetic relationships of the current genera recognized in Physalinae in order to identify monophyletic groups and resolve the physaloid grade; and (2) determine the probable causes of recent divergence in Physalinae.

2. Materials and methods

2.1. Taxon sampling

The ingroup comprised 50 taxa belonging to the subtribe Physalinae. The 12 recognized genera of the subtribe were sampled. All of the monotypic genera (*Alkekengi*, *Calliphysalis*, *Capsicophysalis*, *Oryctes*, and *Schraderanthus*) were represented, along with one species each of *Brachistus*, *Physaliastrum*, and *Tzeltalia*, the two species of *Leucophysalis*, two of *Witheringia*, four of *Chamaesaracha* (50% of total taxa), and 33 species of *Physalis* (nearly 40% of the total). The *Physalis* species were selected in order to get representatives the four subgenera *sensu* Martínez (1999), including those species of the physaloid grade. Also, all sections included in the subgenus *Rydbergis* were represented by at least one species. The outgroup was formed by taxa closely related to the subtribe, such as the genera *Iochnoma* Benth., *Vassobia* Rusby, *Larnax* Miers, and *Withania* Pauquy, along with 16 taxa representing the majority of the Solanaceae tribes (Olmstead et al., 2008) and three other species, *Montinia caryophyllacea* Thunb. (Montiniaceae), *Convolvulus arvensis* L., and *Ipomoea batatas* (L.)

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