

Reassessing *Mexocarpus*: Molecular and Morphological Evidence from Mesoamerican *Palicourea* (Rubiaceae)

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INTRODUCTION & AIM

The Rubiaceae, commonly known as the coffee family, with over 14,000 species distributed across approximately 580 genera, is one of the most diverse families among angiosperms (Razafimandimbison & Rydin 2024). Morphological and molecular studies indicate that many species classified in Psychotria belong to other genera, such as *Eumachia*, *Carapichea*, *Notopleura* or *Palicourea* (Andersson 2001 Razafimandimbison et al. 2014, Taylor 2001, 2005, Taylor & Gereau 2013, Taylor et al. 2017). An example of this is the genus *Mexocarpus* segregated by Borhidi et al. (2015) to accommodate *Palicourea tetragona*. Originally described as *Cephaelis tetragona*, it was later transferred to *Palicourea* (Taylor et al. 2010), until Borhidi et al. (2015) decided that there was morphological evidence to place it in the new monotypic genus *Mexocarpus*. It is distributed in southern Mexico and Guatemala. It was segregated based on the morphology of the pyrenes, which present three lobes in a concave-triangular cross-section, with an emerging central crest and slightly thin, irregularly crenulated lateral edges (Borhidi et al. 2015). However, Berger (2018) rejected this segregation based on the argument that the pyrene morphology is not sufficient to recognize a new genus, since all other morphological traits coincide with the nocturnally flowering group in *Palicourea* circumscribed by Taylor et al. (2010). Nevertheless, other authors accept *Mexocarpus* until new evidence is given (Torres-Montúfar & Torres-Díaz 2022). To resolve this taxonomic conflict, the aim of this study is to test the position of *Mexocarpus* through molecular phylogenetic analysis and to provide a detailed morphological comparison with related species, supporting our taxonomic decision. Additionally, we present a comprehensive taxonomic description of *Mexocarpus*, with particular emphasis on the morphology of the pyrene.

METHOD

We conducted phylogenetic analyses using two nuclear markers (ETS and ITS) and one plastid marker (trnL-F) to test the phylogenetical position of *Mexocarpus tetragona*. Morphological data for *Mexocarpus tetragonus* and morphologically related species were predominantly obtained from original descriptions and type specimens, complemented by personal observations, from the field and from specimens from the following herbaria: FESC, MEXU, MO and IZTA (acronyms following Thiers cont. updated), and high-resolution images of specimens available online (from the collections of F, MO, and US). In addition, publications with descriptive data were used as a source of morphological information (Taylor 1997a, 1997b, 2012, Taylor et al. 2010).

RESULTS & DISCUSSION

The tribe Psychotrieae was retrieved as monophyletic with strong support (1.00 PP, 100 BS, 99 JK), however, the tribe Palicoureeae was found to be paraphyletic since Psychotrieae emerged inside it, more specifically, forming a polytomy with the floating taxon *Rudgea lorentensis* and a clade formed by formed by *Eumachia* and allied genera (1.00 PP, 93 BS, 89 JK) classified in Palicoureeae. The other clade of Palicoureeae is formed by *Mexocarpus* and *Palicourea* species (1.00 PP, 100 BS, 100 JK), in which the three samples of *Mexocarpus tetragonus* included in our study form a clade (1.00 PP, 100 BS, 80 JK) which is nested in an unresolved clade within *P. faxlucens* and *Palicourea tomentosa* (0.88 PP, 89 BS, 85 JK)

A general overview of pyrene morphology in cross-section shows differences in the quantity and size of the ridges, which affects the shape of the mature fruit. Of the species studied morphologically five types of pyrenes are described: the 1- to 4-ridged pyrenes with the well-developed crests and thus tetragonal dry mature fruits as *M. tetragonus*, *P. domingensis*, *Palicourea quadrilateralis*

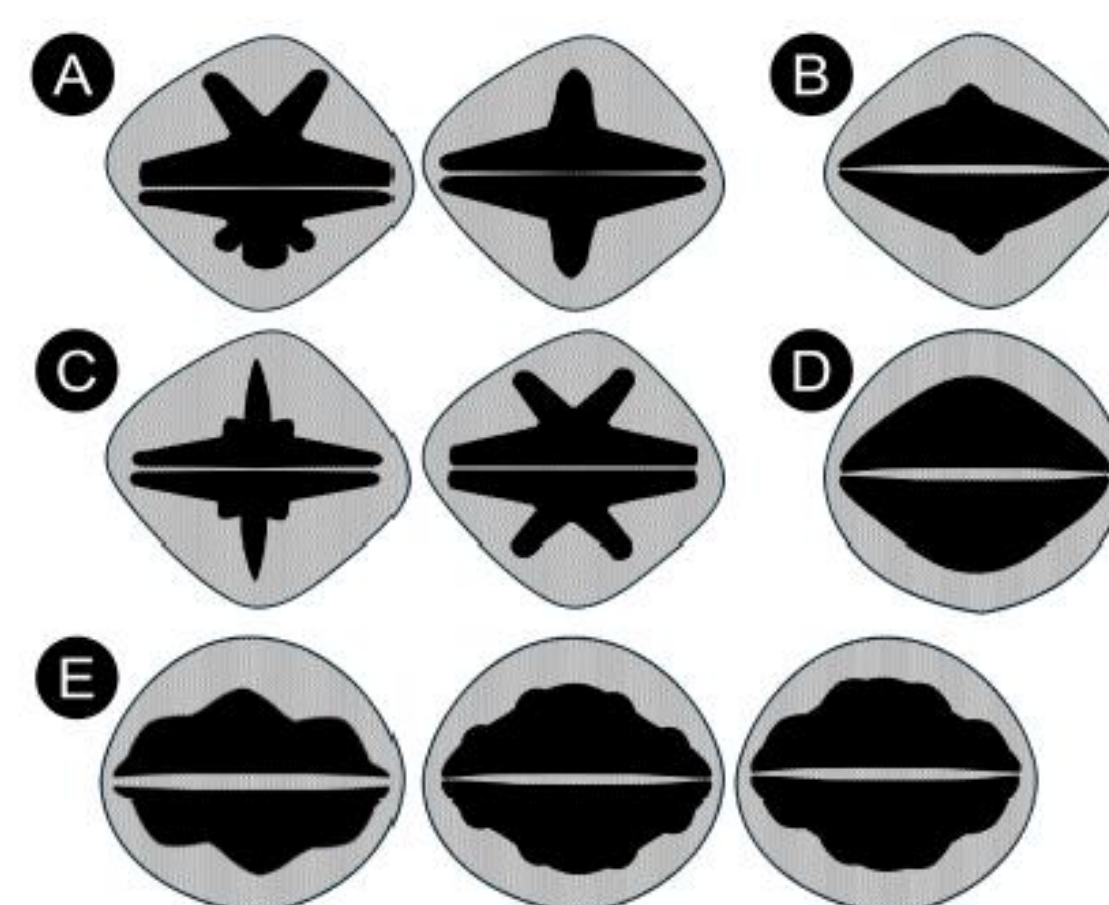
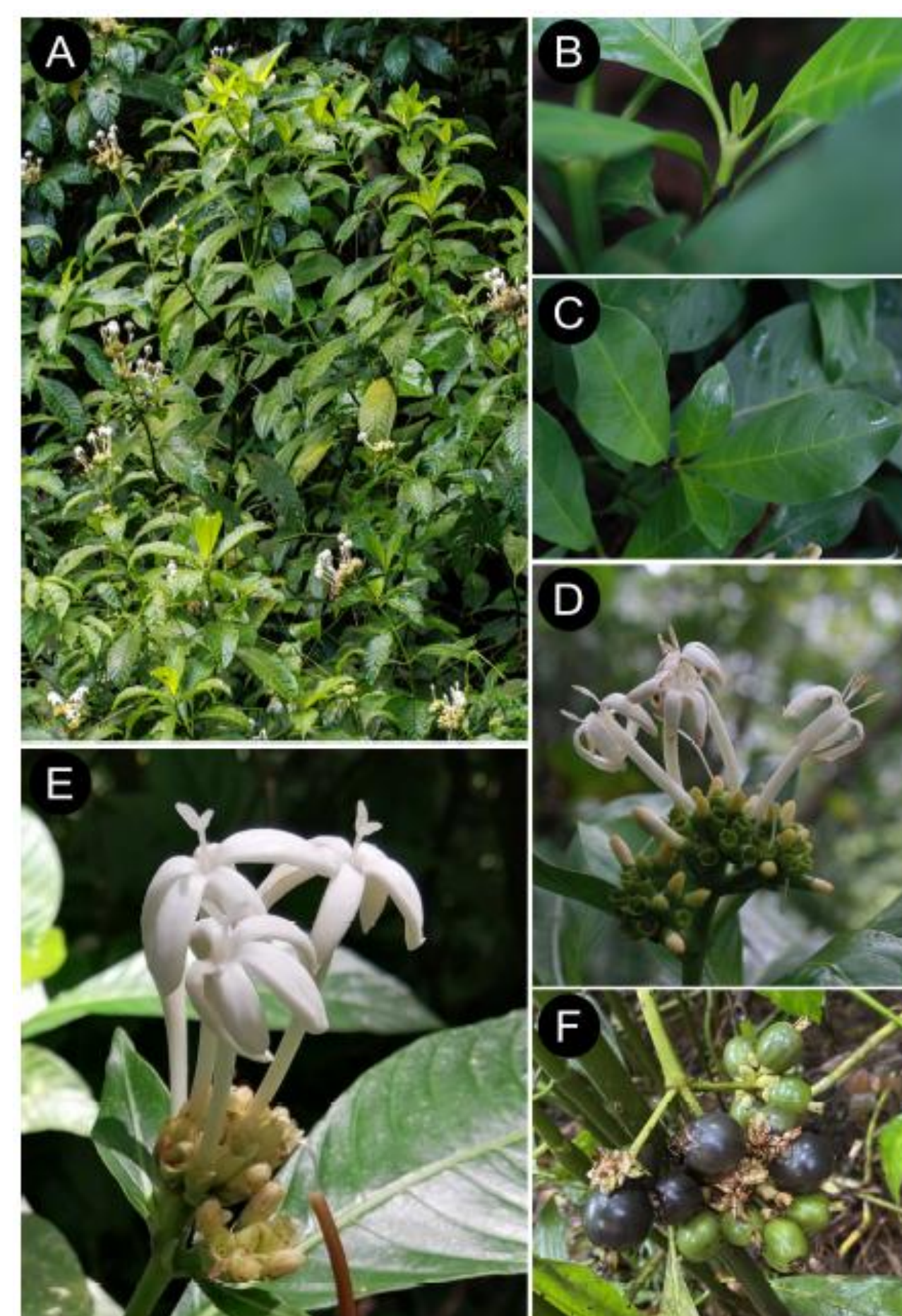


FIGURE 2. Diagrams of pyrenes of morphologically similar species. A–C: Quadrangular fruits. D–E: Spheroidal fruits. A, B: 1–4-ridged pyrenes with the well-developed crests of *Mexocarpus tetragonus* (based on A. Torres-Montúfar 808 and K. Velasco 4041 from MEXU). B: 1–small ridged pyrenes of *Palicourea semarumii* (based on Borhidi et al. 2015). C: 3–to 4-ridged pyrenes with the well-developed crests of *Palicourea domingensis* and *Palicourea quadrilateralis* (based on E. Contreras 7709 from MEXU and from Borhidi et al. 2015 and protologues). D: Not ridged pyrene surface of *Palicourea faxlucens* (based on Torres-Montúfar 663 from MEXU). E: 3–to 5–small rounded ridged pyrenes of *Palicourea deflexa*, *Palicourea elata* and *Palicourea holimensis* (based on G. Salazar 8610 from MEXU and from protologues). Schemes drawn by Eduardo Lazcano-Flores.

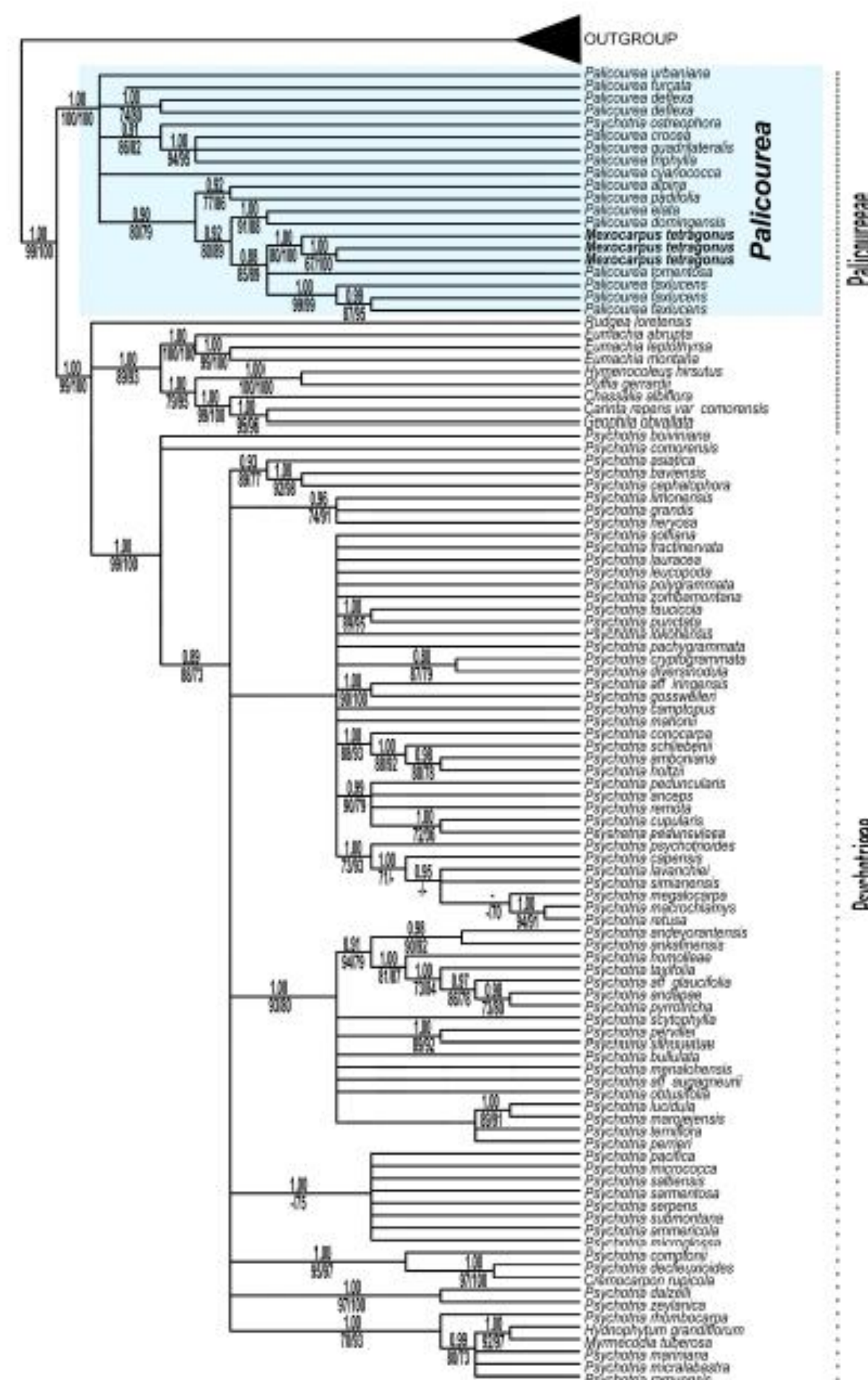


FIGURE 1. Consensus of well-supported clades present in trees inferred by all three inference methods based on combined sequence data set of plastid trnL-F, nuclear ETS and ITS. Numbers above branches correspond to Bayesian posterior probabilities and those below branches to parsimony Jackknife percentages (left) and Likelihood Bootstrap percentages (right).

Taxon	Inflorescence	Corolla color	Corolla length (cm)	Anthesis	Fruit color	Fruit form	Pyrene surface
<i>Mexocarpus tetragonus</i>	Panicles	White	2–4.5	Nocturnal	Purple-Black	Angulate	1–3 prominent acute ridges
<i>Palicourea crocea</i>	Panicles-cimose	Red, pink	0.5–0.9	Diurnal	Blue-Black	Sphaeroidal	3–5 rounded ridges
<i>Palicourea cyanococca</i>	Panicles	White, yellow, green-ochraceous	0.2–0.4	Diurnal	Blue	Sphaeroidal	4–5 rounded ridges
<i>Palicourea deflexa</i>	Panicles	White	0.2–0.4	Diurnal	Black-purple	Sphaeroidal	3–5 slightly rounded ridges
<i>Palicourea domingensis</i>	Panicles to corymbosae	White	1–2.5	Nocturnal	Black	Angulate	4–5 acute ridges
<i>Palicourea elata</i>	Capitate	White	1–1.6		Blue-Black	Sphaeroidal	3–4 slightly rounded ridges
<i>Palicourea faxlucens</i>	Capitate	White	2.5–3.5	Nocturnal	Blue	Sphaeroidal	Not ridged
<i>Palicourea hazenii</i>	Subcapitate	White	ca. 1.2		Blue	Sphaeroidal	3–4 slightly rounded ridges
<i>Palicourea holimensis</i>	Panicles	Yellow	1.1–1.2	Diurnal	Dark purple	Sphaeroidal	3–4 prominent rounded ridges
<i>Palicourea megalantha</i>	Panicles-cimose	White	2–5.3	Nocturnal	Black	Sphaeroidal	3–4 slightly rounded ridges
<i>Palicourea quadrilateralis</i>	Cymose	Purple, Blue	1.1–1.3	Diurnal	Dark	Angulate	3–4 acute ridges
<i>Palicourea semarumii</i>	Panicles	Purple, Blue	1.2–1.5	Diurnal	Blue	Angulate	1–3 prominent acute ridges

Our integrative taxonomic study provided support the synonymization of *Mexocarpus* under *Palicourea*. However, the taxonomic complexity of the group indicates the need for further systematic revisions using multiple sources of evidence, particularly in pyrene morphology and its systematic value.