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RESEARCH IN CONTEXT

Diversity, phylogeny and evolution of the rapidly evolving genus *Psidium* L. (Myrtaceae, Myrteae)

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• **Background and Aims** *Psidium* is the fourthth largest genus of Myrtaceae in the Neotropics. *Psidium guajava* is widely cultivated in the tropics for its edible fruit. It is commercially under threat due to the disease guava decline. *Psidium cattleyanum* is one of the 100 most invasive organisms in the world. Knowledge of the phylogenetic relationships within *Psidium* is poor. We aim to provide a review of the biology, morphology and ecology of *Psidium*, a phylogenetic tree, an infrageneric classification and a list of species.
• **Methods** Morphological and geographic data were obtained by studying *Psidium* in herbaria and in the field between 1988 and 2020. Forty-six herbaria were visited personally. A database of approx. 6000 specimens was constructed, and the literature was reviewed. Thirty species (about a third of the species in the genus) were sampled for molecular phylogenetic inference. Two chloroplast (*psb*A–*trn*H and *ndh*F) and two nuclear (external transcribed spacer and internal transcribed spacer) regions were targeted. Phylogenetic trees were constructed using maximum likelihood (ML; RaxML) and Bayesian inference (BI; MrBayes).
• **Key Results** *Psidium* is a monophyletic genus with four major clades recognized as sections. Section *Psidium* (ten species), to which *P. guajava* belongs, is sister to the rest of the genus; it is widespread across the Neotropics. Section *Obversifolia* (six species; restricted to the Brazilian Atlantic Forest), which includes *P. cattleyanum*, is sister to the innermost clade composed of sister sections *Apertiflora* (31 species; widespread but most diverse in the Brazilian Atlantic Forest) + *Mitranthes* (26 species; widespread in dry forests and probably diverse in the Caribbean). Characters associated with diversification within *Psidium* are discussed.
• **Conclusions** Research on pre-foliation, colleters, leaf anatomy, leaf physiology, staminal development, placentation and germination associated with the anatomy of the opercular plug is desirable. Studies are biased towards sections *Psidium* and *Obversifolia*, with other sections poorly known.

Key words: Amphistomatic leaves, animal dispersal, apomixis, guava, Neotropical flora, idioblasts, invasive species, polyploidy, stone cells, tropical fruit.

INTRODUCTION

Psidium L. (Myrtaceae) is a large, economically important genus including *Psidium guajava* L., the widely cultivated guava, and *P. cattleyanum* Sabine, one of the worst invasive alien organisms in the world (Global Invasive Species Database, 2013 – a list that includes plants, animals and micro-organisms). *Psidium* is the fourth most species-rich genus of Myrtaceae in

the Neotropics (Govaerts *et al.*, 2021) and new species are still being described. Since the beginning of the 21st century, 15 new species have been described, re-established or transferred to *Psidium* (Landrum and Sobral, 2006; Landrum and Funch, 2008; Soares-Silva and Proença, 2008; Proença *et al.*, 2010, 2017, 2020; Landrum and Parra, 2014; Landrum and Proença, 2015; Tuler *et al.*, 2016, 2017b, 2019b, 2020a, b). There are currently 113 accepted names in *Psidium* in The Plant List

(http://www.theplantlist.org), although species described since 2014 are not listed; if they were included, The Plant List would show 122 accepted names. The World Checklist of Selected Plant Families (https://wcsp.science.kew.org/) that is continuously updated records 92 accepted species. It was suggested based on BAMM analysis that *Psidium* might be undergoing recent, rapid diversification in comparison with other large genera of Myrtaceae whose rates of diversification were slowing down (Vasconcelos *et al.*, 2017b); this study compared a wide spectrum of Myrteae genera (only four genera were absent).

Species of the genus *Psidium* were amongst the earliest Neotropical plants to be known and introduced into Europe along with potatoes and tobacco (Menéndez de Luarca, 1999). The first report of the guava was published in 1555 by Spanish Captain and historian Gonzalo Fernandez Oviedo y Valdés who recorded it from Hispaniola and Central America (de los Rios, 1854). The guava was also accurately described and illustrated by Clusius (1601) in his *Rariorum Plantarum Historiae* based on leaves and immature fruits of 'Guayava' specimens he had obtained from Seville (Menéndez de Luarca, 1999). Other early records were by Georg Marcgrave between 1637 and 1642 (Marcgrave and Piso, 1648) and William Dampier from 1699 (Harris *et al.*, 2017), who respectively recorded '*araças*' and '*arissahs*' (*Psidium guineense* Sw. and probably *P. oligospermum* Mart. ex DC.) from Pernambuco and Bahia in north-eastern Brazil.

Psidium guajava L. is the type species of the genus, and its present-day, widespread range has certainly been expanded by humans since pre-Colombian times (Newsom and Wing, 2004; Clement *et al.*, 2010). The guava is believed to have been domesticated by approx. 4000 BP (uncalibrated radiocarbon date; Solis *et al.*, 2001) although its exact centre of origin is uncertain (Landrum, 2017); Central America, Mexico, northern South America and north-eastern Brazil have been suggested (Nakasone and Paull, 1998; Pereira *et al.*, 2003; Clement *et al.*, 2010). Guavas were apparently introduced into the Philippines through the Acapulco–Manila galleon route during the 16th century (Merril, 1954), from whence they spread to China. This originated an early misconception that the guava was Asian; Linnaeus (1753) described it as native to India.

Psidium has been included (with a few species) in phylogenetic studies of the family Myrtaceae and tribe Myrteae (Lucas *et al.*, 2007; Vasconcelos *et al.*, 2017b) and in studies focusing on the placement of particular species (Tuler *et al.*, 2019b) or regional floras (Flickinger *et al.*, 2020), but no phylogenetic study focused on the genus has been published until now. The economic and ecological significance of *Psidium* as well as its recent taxonomic growth through the description of additional species in the 21st century makes understanding its phylogenetic relationships highly desirable. Berg (1857) recognized six sections in *Psidium* but these have been largely ignored except by some authors' attempts to detect affinities between species. Recent publications have recognized sections in large Myrtaceous genera based on phylogeny, e.g. 11 sections within *Eugenia* (>1000 species; Mazine *et al.*, 2018) and nine in *Myrcia* (774 species; Lucas *et al.*, 2018). Identifying natural, infra-generic sections within *Psidium* is necessary for effective management of the economically important and invasive species.

MATERIALS AND METHODS

Geographic distribution, morphology and ecology

A morphological overview of the genus was obtained by study of specimens of this genus in the herbarium and in the field since 1988. The following herbaria were personally consulted by C.E.B.P. or A.C.T. between 1988 and 2020: ALCB, ASE, ASU, BHCB, BM, BOTU, CAP, CEN, CGE, CEPEC, CVRD, FHO, FLOR, HAS, HB, HRCB, HUEMG, IAN, ICN, IPA, JBSD, K, MBM, MBML, MG, MO, NX, NY, OXF, P, PEUFR, R, RB, SAMES, SP, SPF, TEPB, UB, UEC, UEFS, UFG, USZ, VIES and W; additional material was obtained on loan from BR, C, INPA and G. A database of approx. 6000 specimens was generated, and species were morphologically characterized from this material and from the literature (Berg, 1857; Proença *et al.*, 2013; Landrum, 2017; Tuler *et al.*, 2017a; Stadnik *et al.*, 2018 and references therein). Geographic distribution was obtained from this database and from the TDWG areas in the World Checklist of Myrtaceae (Govaerts *et al.*, 2008). Leaf venation patterns follow the terminology of Hickey (1973) as applied to Myrtaceae by Cardoso and Sajo (2006).

Phylogeny

Thirty species (45 specimens), about a third of the species in the genus, were sampled for molecular phylogenetic inference; samples were obtained from Brazil, Costa Rica and the Dominican Republic (see Supplementary data Tables S1–S3). Sampling was non-random and concentrated on three groups: (1) economically important species valued for human fruit consumption; (2) invasive species that threaten the biodiversity of fragile ecosystems; and (3) taxonomically problematic species that form species complexes, i.e. the *Psidium grandifolium* complex (Landrum, 2005) and the *Psidium salutare* complex (Landrum, 2003).

Total DNA was extracted using the cetyltrimethylammonium bromide (CTAB) protocol (Doyle and Doyle, 1987) or the DNeasy kit (Qiagen) in the Laboratório de Biologia Vegetal, Universidade de Brasília or Jodrell Laboratory, Royal Botanic Garden Kew. Two chloroplast (*psb*A–*trn*H and *ndh*F) and two nuclear [external transcribed spacer (ETS) and internal transcribed spacer (ITS) 1 + 5.8S + ITS2] regions were targeted for each accession. Amplification was carried out on a Gene Amp 9700 (Applied Biosystems, CA, USA) thermal cycler under the following conditions: *psb*A–*trn*H (Hamilton, 1999), 4 min at 94 °C; 30 cycles of 1 min at 94 °C, 1 min at 48 °C, 2 min and 30 s at 72 °C; *ndh*F (Biffin *et al.*, 2006), 4 min at 94 °C; 30 cycles of 1 min at 94 °C, 1 min at 55 °C; ETS (Wright *et al.*, 2001; Lucas *et al.*, 2007), 4 min at 94 °C; 30 cycles of 1 min at 94 °C, 1 min at 50 °C, 1 min at 72 °C; and ITS (ITS1 + 5.8S + ITS2; Sun *et al.*, 1994), 2 min at 94 °C, 30 cycles of 1 min at 94 °C, 1 min at 52 °C, 1 min at 72 °C; annealing temperatures were lowered to a minimum value of 48 °C and cycles increased from 30 up to 36 in order to optimize amplification; the standard stabilizing phase was 7 min at 72 °C. PCR products were purified using the QIAquick PCR Purification Kit (Qiagen). Sequencing reactions were conducted using the Taq DyeDeoxy™ Terminator Cycle Sequencing Kit (Applied Biosystems). Sequences

were produced on an ABI 3730 Genetic Analyzer (Applied Biosystems). Complementary strands were sequenced, and consensus sequences obtained using Geneious™ version 10. Sequences were aligned using the MUSCLE plug-in implemented in Geneious™ 10 (Edgar, 2004) with default values, and visually inspected and corrected for alignment mismatches. The *psb*A–*trn*H inversion flanked by inverted repeats identified by Flickinger *et al.* (2020) in *Eugenia* was not found in the dataset; all sequences had the common configuration so no corrections were necessary.

Phylogenetic analyses were run in two separate datasets based on the number of molecular regions successfully sequenced for each specimen. First, we analysed a dataset comprising 30 species and 45 specimens in the ingroup and one specimen each of three species in the outgroup. This included specimens where two, three or four molecular regions could be sequenced; ten single-region species were not included. This inclusive analysis was performed so that more specimens could be included in the phylogenetic tree, even if this was at the cost of reducing the support of some relationships due to the gaps in the matrix. Next, we removed all accessions that were not complete for the four molecular regions in the matrix, leaving only those that could be sequenced for all markers (15 species and 20 accessions in the ingroup; two outgroups). This more restrictive analysis was important to evaluate the support of the main clades in a scenario where the molecular matrix is complete, albeit with fewer samples.

Phylogenetic trees were constructed based on maximum likelihood (ML) using RaxML (default parameters) and Bayesian inference (BI) using MrBayes on the CIPRES (Miller *et al.*, 2011) gateway. ML and BI are phylogenetic inference methods that have become common in the field since the computational advances of the late 20th century allowed calculations based on large datasets. Briefly, ML utilizes sequence data to search for trees that maximize the likelihood of a particular evolutionary history given a molecular substitution model (Huelsenbeck and Crandall, 1997). BI expands the ML assumptions to incorporate prior probabilities and accounts for uncertainty in estimations by using a Markov chain Monte Carlo (MCMC) algorithm to search for a posterior distribution of trees with high probabilities. The way in which trees are summarized differs between each method. Whereas most ML software uses bootstrap (BS) values to indicate support (Felsenstein, 1981), BI usually synthesizes the posterior probability (PP) distributions on the trees by calculating a maximum clade credibility tree (Huelsenbeck *et al.*, 2001). Consequently, metrics used to measure support of relationships are also different, varying from 0 to 100 in ML (with BS values > 70 generally considered high support; Hillis and Bull, 1993) and from 0 to 1 in BI (with values of PP > 0.95 generally considered high support; Huelsenbeck *et al.*, 2001). *Metrosideros stipularis* Hook.f. was set as the outgroup in the inclusive analysis and *Calycolpus goetheanus* (Mart. ex DC.) O.Berg in the restricted analysis, based on their placement in the family (Vasconcelos *et al.*, 2017*b*). For the BI analysis, substitution models were tested using JmodelTest (Posada, 2008) and the models that best fit the individual regions were implemented; these were GTR + G (ETS and ITS1 + 5.8S + ITS2 and *psb*A–*trn*H) and GTR + I + G (*ndh*F). Four MCMC runs of 10 million generations sampling every 1000 were performed and convergence was confirmed in Tracer [effective sample size (ESS) > 200, 0.25 burn-in].

Subgeneric classification

As recommended by the International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code), our first criterion when selecting the type species was that it fit the characteristics described in the original diagnosis of the section (Berg, 1857); all lectotypes fulfilled this criterion. Our second criterion was that the selected species was both sampled in our phylogeny and included by Berg within its section either in *Flora Brasiliensis* (Berg, 1857) or, failing this, in the *Revisio Myrtacearum Americae* (Berg, 1854) where the same characters of the sections were used as keys to groups. Thus, our third criterion was to rule out the misclassified species, and judiciously select as lectotype a species that emerged within the clade that corresponded to the section with high support in the phylogeny.

The section that includes the type species (*Psidium guajava*) was called by Berg (1857) section *Costata*; this must be substituted for the autonym *Psidium* section *Psidium*, according to Article 22 of the International Code (Shenzhen Code) of Nomenclature for Algae, Fungi, and Plants (Turland *et al.*, 2018).

RESULTS AND DISCUSSION

Geographic distribution

Psidium is naturally Neotropical in distribution, occurring from 30°N (State of Sonora, Mexico) to 38°S (Province of Buenos Aires, Argentina), including the West Indies as well as two Archipelagos in the Pacific, the Galápagos and Revillagigedo Islands (Rotman, 1976; Landrum, 2017; this study). Inspection of our database per country suggests that three apparent centres of species diversity exist: (1) West Indies, particularly Cuba and Hispaniola; (2) Central and Southern Brazil and Paraguay; and (3) Northern South America (Peru, Venezuela and the Guianas). These three areas present a wide range of natural habitats, and the large number of species of *Psidium* present seems to have been due to their successful colonization. Cuba appears to have the highest co-occurrence of species (22 species; Govaerts *et al.* 2008; this study). A detailed biogeographic study of *Psidium* will be presented elsewhere.

We recognize 92 species as definitely belonging to *Psidium* L.; 25 names in *Psidium* were considered uncertain for various reasons (see Supplementary data Table S1). The geographic distribution of the genus is characterized by a few wide-ranging species, many regional species and a few narrow endemics. Only two species, *Psidium sartorianum* (O.Berg) Nied. and *P. guineense* Sw., can be considered naturally wide-ranging, occurring almost throughout the whole area of distribution of the genus. *Psidium guajava* and *P. cattleyanum* are also widely distributed, but this is at least partially due to the action of man, and the fact that they are very invasive species (Richardson and Rejmánek, 2013).

Vegetative ecology

The most common life form is that of a shrub or small tree, but *Psidium* species can occur as small, recurrent sub-shrubs with well-developed lignotubers (hemixyles that resprout after fire

or a prolonged dry season), such as *Psidium salutare* Sprengel (Landrum, 2017), to large trees such as *Psidium myrtoides* O.Berg (Tuler *et al.*, 2017a). In fire-prone fields and savannas, *Psidium* species are small to large shrubs or treelets. In maritime and semi-desertic scrubs or woodlands, such as *Caatingas*, *Restingas* and *Pinares*, they are small to large trees. In densely forested regions, such as the Amazon and in gallery forests, several species are adapted to a riparian habit. Field notes on specimens of *Psidium* collected in the Amazon (e.g. *P. densicomum* Mart. ex DC. and *P. riparium* Mart. Ex DC.) frequently allude to a riparian habitat. Poeppig, collecting *P. densicomum* Mart. ex DC. on the Amazon River, noted that it grew exclusively along rivers and formed large aquatic populations which resembled *Rhizophora mangle* L. mangroves, with many fasciculate, red, adventitious roots and decumbent branches (Berg, 1857). Studies of this species (under the synonym *P. ovatifolium* O.Berg) in a flooded forest on the Mapire River, Venezuela (Fernandez *et al.*, 1999), showed that flooding probably does not cause water stress in that species and that submerged leaves maintained photosynthetic and leaf conductance rates similar to those observed in aerial leaves. Riparian species are not restricted to the Amazon, they also occur in Cuba (*P. orbifolium* Urban), Paraguay and south-western Brazil (*P. striatulum* Mart. ex DC.).

Psidium species are thus edaphically very variable, with species that grow on sandy soil, limestone soil, limestone soil with rocky outcrops, mesotrophic soil and water-logged soil (Fernandez *et al.*, 1999; Proença *et al.*, 2013; Landrum and Cornejo, 2016). Myrtaceae are strongly ectomycorrhizal, a rare form of symbiosis estimated to occur in 2 % of land plants (Brundrett and Tedersoo, 2018) and in up to 10 % of tracheophytes, although it can be dominant in certain environmental conditions (Wang and Qiu, 2006). *In vitro* inoculation of *Psidium cattleyanum* confirmed that it is ectomycorrhizal (Freire *et al.*, 2018), while experiments with artificial inoculation of *P. guajava* plantlets have found that species to be highly mycotrophic, with a mycorrhizal dependency index (RDMI) of 103 % (Estrada-Luna *et al.*, 2002); this index compares the dry weight of mycorrhizal plantlets with that of non-mycorrhizal plantlets.

Leaf venation and anatomy

Leaves in *Psidium* are highly variable in size, shape, morphology, venation and anatomy; if all these parameters are considered, perhaps more so than in any other genus of Tribe Myrteae. Colleters have been sometimes observed in the leaf axils (Landrum, 2017; Tuler *et al.*, 2021). Leaves vary in size from 0.4 cm in diameter in *P. nannophyllum* Liogier (1973) to 19 cm long in *P. oblongatum* O.Berg (Tuler *et al.*, 2017a). The midvein can be sunken, flush or prominulous on the upper surface (Landrum, 2017; Oliveira *et al.*, 2017). Secondary veins vary from four to 22 (Landrum, 2017; this study). The secondary venation is predominantly brochidodromous but can be so throughout the leaf or only apically, with the basal veins acrodromous or camptodromous; tertiary venation is admedial reticulate and the ultimate marginal venation can be in complete or incomplete arches, or fimbriate (Cardoso and Sajo, 2006; Fank-de-Carvalho *et al.*, 2007; Oliveira *et al.*, 2017).

Considering the high abundance and diversity of *Psidium*, relatively few anatomical studies of the leaves have been conducted in the genus (see Gomes *et al.*, 2009 for a review; Al-Edany and Al-Saadi, 2012; Oliveira *et al.*, 2017; Endringer, 2020). Amongst leaf anatomical characters common to the genus, we can highlight a uniseriate epidermis and cuticle; hypostomatic leaves (amphistomatic in *P. ratterianum* Proença and Soares-Silva, Proença *et al.*, 2010); paracytic stomata; and tector trichomes that are abundant on the abaxial surface and rare on the adaxial surface (rarely absent on the adaxial surface). The mesophile is dorsiventral with 1–3 layers of palisade parenchyma on each side and a compact arrangement of spongy parenchyma. The hypodermis is formed by two continuous layers on the adaxial surface. The vascular bundle of the midvein is bicolateral and protected by lignified fibres. Sub-epidermal secretory cavities and prismatic crystals occur throughout the mesophyll (Soares-Silva and Proença, 2008; Gomes *et al.*, 2009; Endringer, 2020).

Reproductive biology

Psidium is mainly bee pollinated and mammal dispersed (Nic Lughadha and Proença, 1996; Gressler *et al.*, 2006). Pollination is by large (Apidae: Bombinae; Anthophoridae: Xylocopinae) or small (Apidae: Ceratini, Meliponinae; Colletidae; Oxaeidae) bees. Phenological strategy is steady state (Gentry, 1974), i.e. a few flowers open per day during a more or less prolonged flowering period (Proença and Gibbs, 1994). Several short, synchronized episodes of flowering per year were recorded for *P. guineense* Sw. (Suárez and Esquivel, 1987) while *P. acidum* (DC.) Landrum flowers throughout the year (Falcão *et al.*, 1992). Flowers are white, aromatic, with many anthers and a single style with a punctiform, funnel-shaped or capitate stigma (Proença *et al.*, 2010; Landrum, 2017). In *P. cattleyanum*, pollen is released as a mixture of monads and tetrads (Patel *et al.*, 1984).

Psidium firmum O.Berg is completely self-compatible, but the PERS (pre-emergent reproductive success; Wiens, 1984) range (4.6–12.7) found does not suggest habitual selfing (Proença and Gibbs, 1994). This study of *P. firmum* looked at the reproductive biology of eight sympatric species of Neotropical Myrtaceae in six genera and found two unusual characters in *P. firmum* that were not present in any of the other species: (1) the length of the styles varied within a plant so that some flowers had the stigmas raised 1–2 mm above the anthers, while others had the stigma at the same level as the anthers; and (2) cross-pollen tubes had penetrated ovules 48 and 72 h after pollination while at 72 h self-pollen tubes had still not penetrated the ovules. This suggests two possibilities: fruit set from self-pollinations results from either preferential self-exclusion or facultative apomixis. Preferential self-exclusion has been suggested to occur in *Clarkia unguiculata* Lindl. (Onagraceae, Myrtales). *Clarkia unguiculata* is a totally self-compatible species in which the use of a genetic marker (flower colour) showed that 58–100 % of the progeny of mixed self and cross pollen was outcrossed (Bowman, 1987); the author suggested that this was because the cross-pollen tubes grew faster and were responsible for most of the fertilizations. Apomixis has been recently recorded in *P. cattleyanum* and found to be through diplospory,

an unusual and previously unrecorded pathway in Myrtaceae (Souza-Pérez and Speroni, 2017), possibly conforming to the most common type of diplospory, the *Antennaria* type (Nogler, 1984). Apomixis had been previously reported in Myrtaceae but from non-Neotropical genera and following other pathways. In *Syzygium* (Tribe Syzygieae), apomixis occurs through adventitious embryony (Thurlby *et al.*, 2012, and references therein) and in *Callistemon* (Tribe Melaleuceae) through apospory (Rye, 1979). Urquía *et al.* (2020) suggested that the levels of clonal diversity found in populations of *P. galapagaeum* Hook.f. are best explained by clonal or asexual reproduction rather than by random mating between related plants. Most species of *Psidium* are hermaphrodites, but *Psidium ovale* (Spreng.) Burret is andromonoeicious, with both male and hermaphrodite flowers in the same plant (Soares-Silva and Proença, 2006).

The range of dispersal agents in *Psidium* was the widest recorded in a review of Neotropical Myrtaceae that included 115 species (Gressler *et al.*, 2006), with nine out of the possible ten classes of dispersers recorded: ants, bats, birds, fish, carnivorous mammals, lizards, marsupials, monkeys and ungulates; their study did not record rodents, but rodent dispersal has also been recorded (Nic Lughadha and Proença, 1996; Alvarenga and Talamoni, 2006). Mammal dispersal is probably dominant, with a few species with small, wine-coloured fruit that suggest bird dispersal, such as *P. ovale*, *P. macahense* O.Berg, *P. ganevii* Landrum & Funch, *P. cauliflorum* Landrum & Sobral and *P. grazielae* Tuler & M.C.Souza (Soares-Silva and Proença 2006; Tuler *et al.*, 2017b; Stadnik *et al.*, 2018). In *P. guajava*, *P. cauliflorum* and *P. grazielae*, the fruits are reddish internally. Half-eaten fruits are thus very conspicuous to birds, and one of us (C.E.B.P.) has observed parrots returning to the same half-eaten fruits of *P. guajava* to feed, while V.G.S. (see also Staggemeier *et al.*, 2017) observed that *P. cattleyanum* is consumed by large birds such as jays, e.g. *Cyanocorax caeruleus* (Vieillot, 1818) that remove whole fruits but also by smaller tanagers, e.g. *Rhamphocelos carbo* (Pallas, 1764), and thrushes, e.g. *Turdus rufiventris* (Vieillot, 1818), that peck at the fruits, consuming bits of flesh and presumably a few seeds. *Psidium cattleyanum* showed a keystone functional role in sustaining the fauna in a tropical forest in Southern Brazil (Pizo, 2002; Staggemeier *et al.*, 2017): its many small seeds scattered in the pulp of a medium to large fruit allowed dispersal by a wide range of vertebrate frugivores from small birds to medium sized mammals. Cauliflory has evolved albeit rarely; it is known in two species, *P. cauliflorum* and *P. grazielae.* Cauliflory has been suggested to be associated with bat dispersal (van der Pijl, 1982) and also with increased visibility of flowers to pollinators (Wallace, 1878; Warren *et al.*, 1997).

Floral morphology and anatomy

Flowers vary markedly in calyx structure and mode of anthesis, from completely closed buds that open by tearing or by a calyptra, to partially closed lobes, to free, shallow lobes. This plasticity is also found in other genera of Myrtaceae (Vasconcelos *et al.*, 2017a; Giaretta *et al.*, 2019). Besides this, flowers vary in size (4–13 mm long), bud shape and number of stamens (from approx. 80 to 720), number of locules (2–6) and ovules per locule (from approx. 3 to 180). Anthers vary by an order of magnitude in size, from 0.3 to 3 mm, and usually have an apical gland and a few smaller glands scattered along the connective, although some species have no glands and species with long anthers may have many scattered glands (Landrum, 2017; Vasconcelos *et al.*, 2019).

Floral vasculature was found to be of the 'consistent eight bundle' type in *P. cattleyanum* and *P. guineense* (Pimentel *et al.*, 2014). The presence of sclereids in the pericarp of the fruits has been recorded in several genera of Myrteae (Galan *et al.*, 2016; Pittarelli *et al.*, 2021, and references therein). However, *Psidium* is apparently the only genus in Tribe Myrteae (based on three studies that together looked at 34 species in 13 genera; Proença, 1991; Pimentel *et al.*, 2014; Pittarelli *et al.*, 2021) to consistently have isodiametric sclereids (stone cells) in the ovarian walls of the flower. Stone cells are found in the ovary of *P. cattleyanum, P. guineense,* and *P. firmum* (Proença, 1991; Pimentel *et al.*, 2014); they also occur in three closely related species of *Campomanesia* of the 'guazumifolia' complex, but were absent in nine other members of *Campomanesia* (Pittarelli *et al.*, 2021). However, these studies did not include all Myrteae genera, or even all nine genera in the subtribe Pimentinae to which *Psidium* belongs (Lucas *et al.*, 2019): *Curitiba* Salywon & Landrum, *Legrandia* Kausel, *Mosiera* Small and *Pimenta* Lindl. have not been investigated. Stone cells were hypothesized to offer protection to ovules and seeds (Pimentel *et al.*, 2014), an idea that is compatible with the theory presented by one of us (Proença, 1991) that they act as a mechanical barrier against oviposition by fruit flies (Tephritidae), notorious predators of guavas and other Myrtaceous fruit crops (Malavasi and Morgante, 1980; Burk, 1983; Malavasi *et al.*, 1983). Stone cells in the ovary occur in other fleshy fruited Myrtales, such as Australasian mega-diverse *Syzygium* (tribe Syzygieae, Myrtaceae; Schmid, 1972; Pimentel *et al.*, 2014, and references therein) and *Mouriri* Aubl. (Melastomataceae; Morley, 1976).

Placentation and fruit morphology

Although tribe Myrteae is invariably fleshy fruited (Wilson *et al.*, 2005), *Psidium* is the only genus to have not only fleshy fruit walls but also fleshy, developing placentas. In all other Myrteae genera, fruit fleshiness is exclusively due to the development of ovarian tissue, i.e. the thickness and fleshiness of the fruit wall. In the Myrtales, a fleshy placenta is also found in *Melastoma* L. and *Miconia* Ruiz & Pav. (Melastomataceae; Clausing *et al.*, 2000).

The placentation of *Psidium* is of the (putatively plesiomorphic) carpellate type (Pimentel *et al.*, 2014). It has been described as either axillary or parietal, and also as bilamellate, extrusive, intrusive, lamellate or peltate (Berg, 1857; Landrum and Sobral, 2006; Soares-Silva and Proença, 2008). This can be attributed to the fact that the margins of the carpels can be deeply intrusive into the locule or hardly so, and are sometimes incompletely coalescent, so that, in some cross-sections, placentation appears parietal and in others (at different levels) axillary. The placental lamellae can bear one, two or many series of ovules. The placental lamellae can be linear, bilobed, scutellate, peltate or U-shaped. To complicate matters furthermore, the lamellae can be straight, or curve either outwards or inwards to accommodate the ovules in the locule. If

the placental lamellae curve outwards, a tangential cut of the locule will show the ovules, which will appear as one or two neat series or, if the series are more numerous or the lamellae are less developed, a cluster of ovules like a bunch of grapes, sometimes described as mound like (Landrum, 2017). If the placental lamellae curve inwards (sometimes called reflexed), a tangential cut will show the smooth lamellae – only the outer series of ovules will be perceptible; other series, if present, will be hidden from view.

Seed morphology

Psidium seeds can be as few as one per fruit (rarely, and never in most of the fruits in any one species; Tuler *et al.*, 2021) or up to 325 (Landrum, 2017). They are 2–10 mm long and have bony seed coats from (5)8 to 30 cells thick at the narrowest point, in which the cells of the outer layer are pulpy and the inner thick-walled, elongated, somewhat ragged, and superimposed at one of the ends, giving the seed an opaque surface (Landrum and Sharp, 1989). This contrasts with other Myrteae genera with bony seed coats in which the cells are hexagonal and abutting; these genera have shiny seed coats, such as *Amomyrtella*, *Calycolpus*, *Mosiera*, *Myrrhinium* Schott, *Ugni* Turcz. (Landrum and Sharp, 1989) and *Accara* Landrum (Landrum, 1990). In species in which seeds develop imbedded in placental tissue, such as *P. guajava* and *P. guineense*, most are reniform and smooth (Landrum *et al.*, 1995); if there are edges, these are rounded and not sharp. If placentas do not develop into fleshy tissue, seeds tend to be more angular probably due to contact during development.

The bony seed coat has a plug-like operculum that in contact with water allows seeds to imbibe water, which is followed by the radicle pushing out the opercular plug and germinating through the aperture. The operculum can be shiny and mammiliform or dull and somewhat sunken (Tuler *et al.*, 2016; Landrum, 2017). Seeds of *P. guineense* are non-dormant and show a typical three phase imbibition pattern but were able to germinate after 1 year of storage (dos Santos *et al.*, 2015).

Cytogenetics

Psidium has the highest levels of polyploidy of any Neotropical Myrtaceae genus (Costa, 2009). In fact, it is the only Neotropical genus in which the diploid $2n = 22$ appears to be rare, although most species have not yet been sampled. A total of 100 counts of 15 species (approx. 15 % of the genus) have been made (Supplementary data Table S2). Three species had a single count that was the diploid number (Moussel, 1965; Tuler *et al.*, 2019a; Silveira *et al.*, 2021), six species had a single count that was a polyploid number, while all other species had more than one count. Total counts were 100, but these were heavily biased (77 %) towards three species: *P. cattleyanum* (36 counts; exclusively polyploid; Atchison, 1947; Smith-White, 1948; Hirano and Nakazone, 1969; Singhal *et al.*, 1984; Medina, 2014; de Souza *et al.*, 2015), *P. guajava* (30 counts; mixed ploidy but predominantly diploid; Kumar and Ranade, 1952; Sharma and Majumdar, 1957; D'Cruz and Rao, 1962; Roy and Jha, 1962; Raman *et al.*, 1971; Majumder and Mukherjee, 1972; Srivastava, 1977; Singhal *et al.*, 1980, 1984; Vijayakumar

and Subramanian, 1985; Pedrosa *et al.*, 1999; Marques *et al.*, 2016) and *P. guineense* (11 counts; Hirano and Nakazone, 1969; Srivastava, 1970; Chakraborti *et al.*, 2010; de Souza *et al.*, 2015; Marques *et al.*, 2016; Tuler *et al.*, 2019a; mixed ploidy but predominantly tetraploid). Diploid counts appear to be associated with narrow geographic distributions in general (Dar *et al.*, 2020) and also in *Psidium* and *Eugenia* (Silveira *et al.*, 2016; Tuler *et al.*, 2019a). If this hypothesis is true, it suggests that *P. guajava* might have been originally a rather narrowly distributed species whose range has been expanded by man, while crossing with *P. guineense* as suggested by Landrum *et al.* (1995) may have increased its invasive potential. A study of genetic diversity in *P. galapagaeum*, endemic to the Galapagos Islands, suggests it is an allopolyploid (Urquía *et al.*, 2020).

Importance to humans

The main utility of the genus *Psidium* to man are the edible fruits of guava (*P. guajava*). Guava fruits can be very rich in antioxidants, flavonoids and vitamin C (230–1426 mg 100 g^{-1} fresh fruit depending upon the cultivar and environmental conditions; Vaughan and Geissler, 1997; Luximon-Ramma *et al.*, 2003), and are consumed as fresh fruit, or industrialized in the form of juice drinks, jams, compotes, sweets, ice creams, fruit salads, biscuit fillings and tarts. The guava is a widely cultivated tropical fruit tree. During the 21st century, major producers for the world market have been Bangladesh, Brazil, China, Colombia, Egypt, India, Indonesia, Mexico, Nigeria, Pakistan, Phillipines, Thailand and the USA (Vaughan and Geissler, 1997; Pariona, 2017).

Also occasionally cultivated are *P. cattleyanum*, *P. guineense* (Vaughan and Geissler, 1997) and *P. friedrichsthalianum* O.Berg (Rojas-Gómez *et al.* 2020). These species have smaller fruits than the guava but exhibit similar fruit qualities. *Psidium cattleyanum* has shiny, yellow, deep pink or wine-coloured fruits, and *P. guineense* has thin-skinned yellow-green fruits which are juicier than guavas, while the fruits of *P. friedrichsthalianum* are also yellow-green and very tart. These latter species are commercialized on a small scale in local markets in Brazil and Costa Rica. In Cuba, a liqueur is made from the wild fruits of *P. salutare* (Kunth) O.Berg (Liogier, 1953).

Commercial guava orchards have recently suffered severely from guava decline, a disease caused by co-infection of the roots by species of *Meloidogyne enterolobii*, a nematode, with *Fusarium solani*, a fungus (Pereira *et al.*, 2009; Carneiro *et al.*, 2011; Gomes *et al.*, 2011). Investigations into possible sources of resistance to this disease in the *P. guajava* gene pool have found it to be either absent (Cardoso *et al.*, 2017) or borderline in a few genotypes (Cavalcanti Júnior *et al.*, 2020). *Psidium cattleyanum* Sabine is resistant to infection by *Meloidogyne* (de Almeida *et al.*, 2009; Marques *et al.*, 2012), but techniques such as its use as root stock and intraspecific crosses with *P. guajava* have failed (Cardoso *et al.*, 2017), which the authors attributed to possible differences in ploidy levels between these two species. *Psidium myrtoides* and *P. acidum* are also resistant (Marques *et al.*, 2012), and approx. 10 % of genotypes of *P. guineense* investigated were found to be resistant (Cavalcanti Júnior *et al*., 2020). Therefore, the phylogenetic affinities of *P. guajava* are of particular importance to direct research into guava decline.

Invasiveness

Psidium cattleyanum, *P. guajava* and *P. guineense* are aggressive, pioneer species that have become naturalized throughout the tropics and are considered globally widespread invaders (Richardson and Rejmánek, 2011). Fragile island ecosystems seem particularly susceptible. In Hawaii, Mauritius, the Phillipines, the Galapagos and the Seychelles, they have become major pests that are successfully outcompeting the native endemic flora. A colonization study in Hawaii has shown that *P. cattleyanum* was the most abundant understorey tree beneath old *Eucalyptus* plantations, even though they were surrounded by native rain forest (Harrington and Ewell, 1997); it is listed as one of the 100 worst invasive alien species in the Global Invasive Species Database (2013). In the Galápagos, *P. guajava* forms large populations (Jackson, 1995) and is considered one of the greatest threats to local biodiversity (Urquía *et al.*, 2019).

However, in some situations, the presence of guavas may be advantageous in secondary vegetation. A study on relative abundance of five species of arboreal mammals (macaque, langur, two flying squirrels and one giant squirrel) in forest fragments in India suggested that the presence of guava trees (that produce fruits that support a wide spectrum of birds and mammals) was beneficial (Umapathy and Kumar, 2000). Another study, in Ecuador, showed that abandoned pastures with guava tree canopies were apparently in a state of active succession to revert to forest, while open pastures were in a state of arrested succession, dominated by a few aggressive herbaceous or shrubby species (Zahawi and Augspurger, 1999).

Phylogenetic structure

Psidium emerges as a monophyletic genus, although with poor support (PP = 0.73) when the sister genus *Myrrhinium* Schott is included in the analysis. This is congruent with the results of Vasconcelos *et al.* (2017*b*) in which five species of *Psidium* were included in an inclusive phylogeny of Tribe Myrteae. The *Psidium* ML phylogenetic tree for which sequences of all four regions were available (restricted analysis) was almost fully resolved (Fig. 1). This tree is herein referred to as the backbone tree and major clades are congruent with the more inclusive ML tree (Fig. 2) and with the BI tree (Fig. 3), both of which included 30 species (45 accessions) that corresponds to about a third of the accepted species in the genus. Ten other species (Supplementary data Table S3) are present only in the single region trees that are available as Supplementary data Fig. S1 (ETS), Fig. S2 (ITS), Fig. S3 (*ndh*F) and Fig. S4 (*psb*A–*trn*H).

We identified four major clades in *Psidium* (Fig. 4). We propose to treat these clades as formal taxonomic sections with the following structure: section *Psidium* [section *Obversifolia* (section *Apertiflora* + section *Mitranthes*)]. Section *Psidium* has two strongly supported subclades that we treat as subsections: sub-section *Psidium* and sub-section *Albotomentosa*. This structure and the monophyly of these clades are supported by previous phylogenetic analyses in Myrtaceae, all of which included a smaller number of species of *Psidium*. Previous studies using Sanger sequencing that support the clades were focused on: (1) Tribe Myrteae (five species of *Psidium*; seven molecular regions; Vasconcelos *et al.*, 2017*b*); (2) the re-establishment of

P. macahense O.Berg [17 species of *Psidium* (originally 18 but the identity of voucher *Pietro s.n.* RB595299 has been changed to *P.* aff. *cattleyanum*); three molecular regions; Tuler *et al.*, 2019*b*]; and (3) the Greater Antilles flora [originally seven species of *Psidium* (eight since we accept *Calyptrogenia biflora* as a synonym of *Psidium amplexicaule*; Landrum, 2017); three molecular regions, Flickinger *et al.*, 2020].

In our study, the nuclear markers ITS and ETS both showed high levels of correct section identification, with good bootstrap values for sections and few misclassified species. The chloroplast intergenic spacer *psb*A–*trn*H showed a strongly conserved identity within section *Apertiflora* but poor internal structuring, while the other sections showed high variability; this region may be evolving too fast to be very informative for the whole of the genus. The chloroplast *ndh*F gene, that expresses NADH-plastoquinone oxidoreductase, as might be expected, showed low variability and low bootstrap values. One of its most informative regions was a 9 bp region (GTTTATTAA), commonly present in other genera of Myrteae such as *Calycolpus*, *Myrceugenia*, *Mosiera* and *Myrtus*, but frequently lost in *Psidium*. This 9 bp region was almost always present in the basal section *Psidium* (except for *P. guajava* and one accession of *P. guineense*), but was lost in all species except one each of sections *Obversifolia*, *Mitranthes* and *Apertiflora*.

Evolution, diversity and distribution

Psidium underwent an accelerated rate of diversification from approx. 25 million years ago (mya; under macrofossil calibration) or from approx. 17 mya (under fossil pollen calibration) up to the present (Vasconcelos *et al.*, 2017*b*). *Eugenia* L. and *Psidium* were the only Myrteae genera to show an abrupt increase in diversification rate at the crown (explosive radiation). However, while in the older *Eugenia*, diversification rates have gradually decreased over the last 10–20 million years, in the younger *Psidium* they have remained high (Fig. 5). Analyses of diversification through time using molecular phylogenies have been recently criticized (Louca and Pennell, 2020), so these results must be interpreted with care, and a wider sample of *Psidium* is desirable.

Eugenia and *Psidium* are the Neotropical genera of Myrtaceae with the highest rates of polyploidy (Costa *et al.*, 2008). Polyploidy is apparently rare in *Myrcia*, the second largest genus of Neotropical Myrtaceae (two polyploid populations out of 22 counts of 14 species; Forni-Martins and Martins, 2000; Costa and Forni-Martins, 2007; Amorim *et al.*, 2012; Silveira *et al.*, 2021). *Eugenia* and *Psidium* are also the genera with the highest diversity of fruit size and colour. *Eugenia* does not vary greatly in fruit seediness (1–4 seeds are the norm), while *Psidium* does. Also, *Eugenia* has a thin or crustaceous seed coat while *Psidium* has a thick bony seed coat with an operculum. Opercula are not unique to *Psidium*; they are also found in other genera in Subtribe Ugniinae such as *Mosiera*, *Myrteola* and *Ugni* (Landrum and Sharp, 1989; Salywon and Landrum, 2014), and in Subtribe Pimentinae, such as *Pimenta pseudocaryophyllus* (Gomes) Landrum and *Curitiba prismatica* (Landrum and Sharp, 1989; Salywon and Landrum, 2007) and in *Amomyrtella* (unplaced; Lucas *et al.*, 2019).
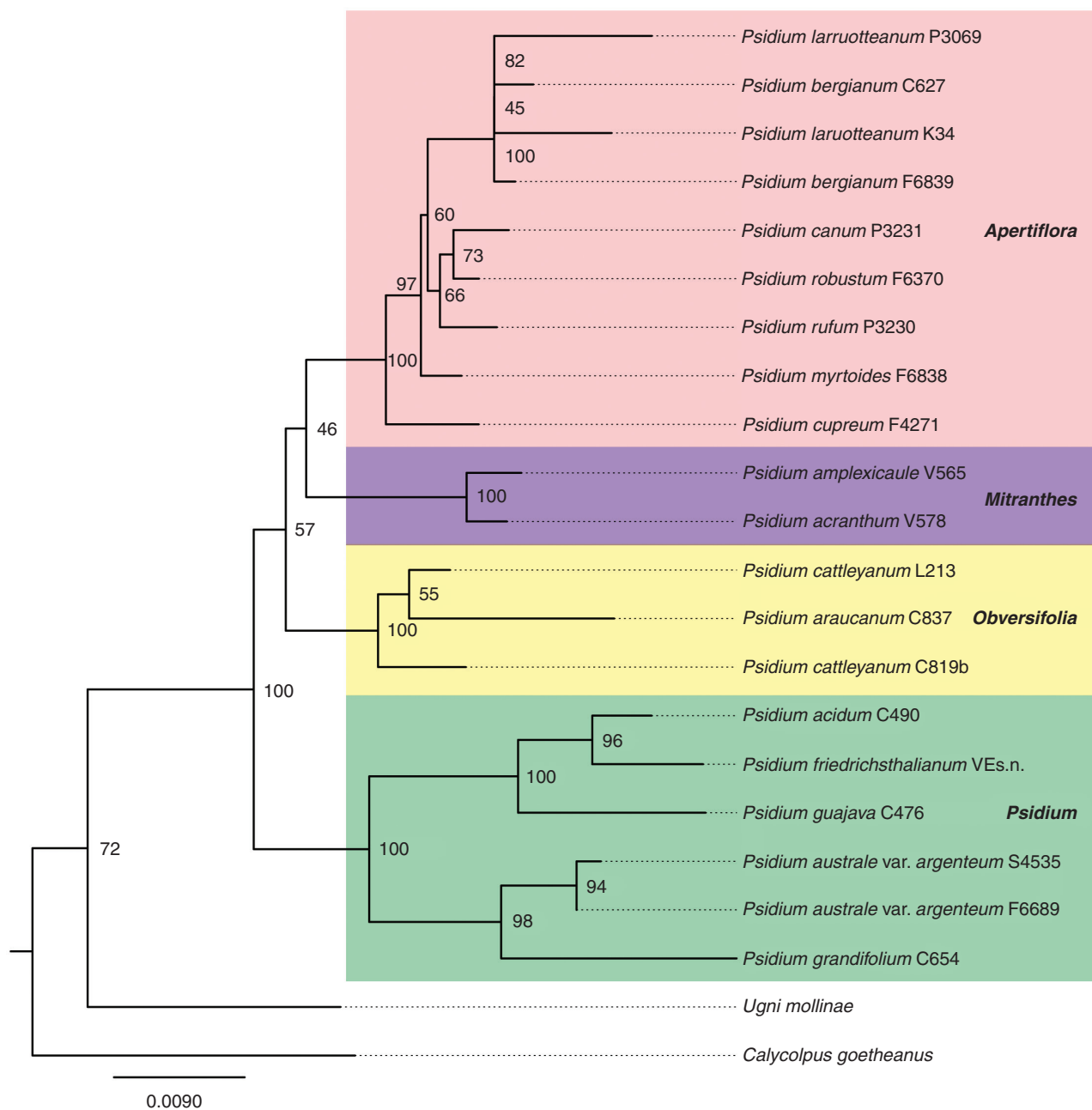
FIG. 1. Maximum likelihood phylogenetic tree of *Psidium* L. with 16 species (20 accessions). Only species with all four regions (ETS, ITS, *ndh*F and *trn*H–*psb*A) are included (backbone tree). Numbers to the right of nodes are bootstrap values. Section names are to the right of clades. Vouchers are identified by the first letter of the first collector's surname and number. For complete voucher data, see Supplementary data Tables S1 and S3.

Psidium is, however, the only genus to combine operculate seeds with both bird (Snow, 1981) and a wide range of other dispersal agents, including mammals (Pizo, 2002; Gressler *et al.*, 2006).

The combination of a wide range of dispersal agents, a wide range of seediness, operculate seeds that can exhibit long-term mechanical dormancy, stone cells in the ovarian tissue, polyploidy and apomixis is tentatively proposed as the main drivers behind the rapid rates of diversification in *Psidium*, as well as the ability to adapt to many different habitats. Polyploidy can break self-incompatibility (Richards, 1997; Miller and Venable, 2000), facilitate plant invasions, increase flower, fruit and seed size, and propitiate niche shifts by increasing drought tolerance (ter Beest *et al.*, 2012). Speciation in *Psidium* seems to have occurred mostly by such niche shifts through vegetative specialization and adaptation to different dispersal agents. This is reflected in the great variation in plant architecture and leaf prefoliation, shape, textures, venation and anatomy, seed number and seed size found within the genus (Rotman, 1976; Landrum, 2005, 2017; Proença *et al.*, 2010, 2013, and references therein). Apomixis facilitates range expansion by generating clonal populations (Hojsgaard and Hörandl, 2015) and has been recorded in

FIG. 2. Maximum likelihood phylogenetic tree of *Psidium* L. with 31 species (45 accessions). Numbers to the right of nodes are bootstrap values. Section names are to the right of clades. Vouchers are identified by the first letter of the first collector's surname and number. For complete voucher data, see Supplementary data Tables S1 and S3.

two megadiverse Myrtalean genera: *Syzygium* (Myrtaceae), the most species rich genus in the family (Govaerts *et al.*, 2008), and *Miconia* (Melastomataceae), the most species-rich woody genus with an exclusively Neotropical distribution (Goldenberg *et al.*, 2013).

Infra-generic classification

Three of the four clades identified in the phylogeny were found to mirror three of the six sections proposed by Berg (1857) in *Flora Brasiliensis* (Table 1). The alignment of Berg's

sections with these three major clades in our phylogeny was mostly accurate: a relatively small percentage (9–16 % depending on the section) of his names were misclassified. The exception was the artificial sect. *Rigidifolia* in which the three species were not found to be closely related. Since Berg indicated no type species, judicious lectotypification that would reflect phylogenetic structure was undertaken. To ensure that the infra-generic structure is congruent with the phylogeny, we have recognized two of Berg's sections, reduced two of them to subsections and synonymized two of them. The genus *Mitranthes* O.Berg, a synonym of *Psidium*, was raised to section level as the fourth section.
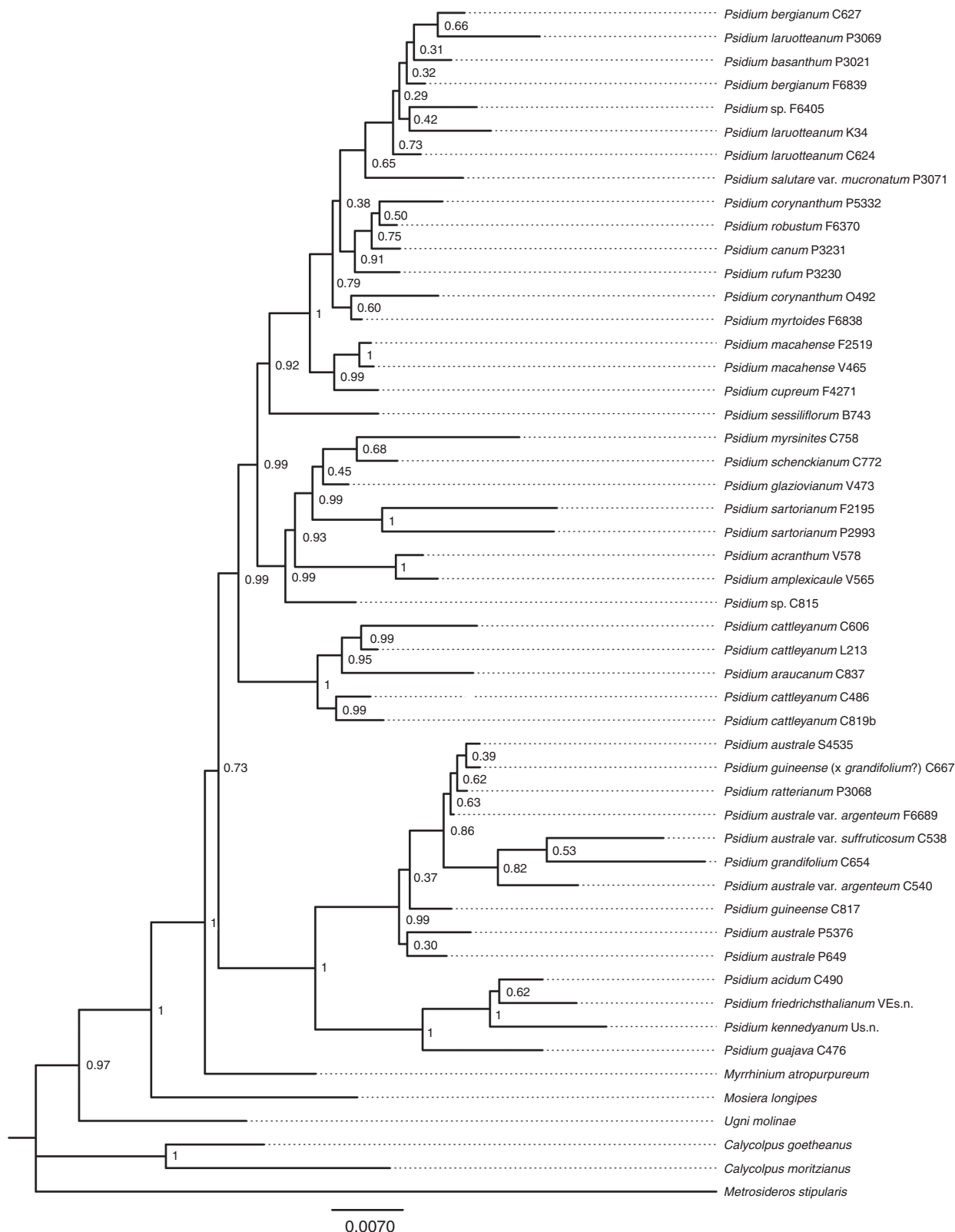
FIG. 3. Bayesian inference phylogenetic tree of *Psidium* L. with 31 species (45 accessions). Posterior probability (PP) values are to the right of nodes. PP values are presented with two digits (additional digits removed without approximation). For complete voucher data, see Supplementary data Tables S1 and S3.
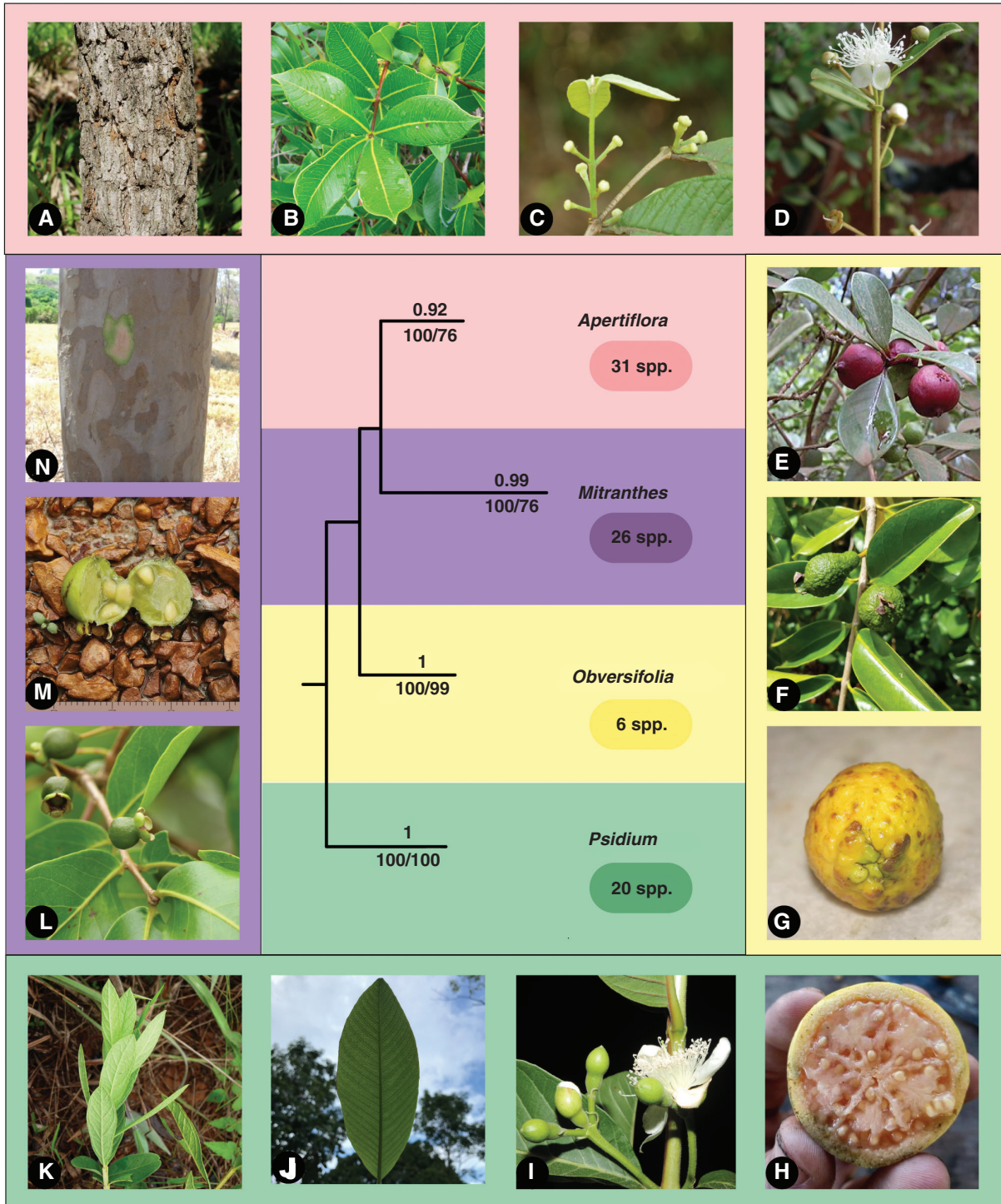
Fig. 4. Diagnostic characters of *Psidium* sections. Border colours indicate sections. Pink = section *Apertiflora*: (A) fissured bark [*P. laruotteanum*; Proença 3019 (UB)]; (B) venation forming a distinct marginal vein [*P. laruotteanum*; Kuhlmann 34 (UB)]; (C) auxotelic racemes [*P. cupreum*; Faria 10009 (UB)]; (D) open floral buds, stamens few and hemispherically distributed, anthers small [*P. basanthum*; Proença 3022 (UB)]. Yellow = section *Obversifolia*: (E) large red fruit with thick, torn calyx lobes (*P. cattleyanum*; photograph Forest & Kim Starr); (F) compressed branches and fleshy leaves [*P. gaudichaudiaum*; Tuler 637 (RB)]; (G) large yellow fruit (*P. ubatubense*; photograph Henry M. Alexandre). Green = section *Psidium*: (H) large fruit with well-developed fleshy placentas [*P. guineense*; Tuler 625 (RB)]; (I) dichasia, floral buds closed, many stamens at same level, anthers large (*Psidium guajava*; photograph Amelia C. Tuler); J. brochydodromous venation with arches (*P. guajava*; photograph Carolyn E.B. Proença); (K). quadrangular branches [*Psidium ratterianum*; Proença 3016 (UB)]. Purple = section *Mitranthes*: (L) camptodromous, inconspicuous venation and small fruit (*Psidium myrsinites*; photograph Stephen A. Harris); (M) seeds few per fruit (*Psidium myrsinites*; photograph Maurício Mercadante); (N) bark smooth and thinly peeling [*P. sartorianum*; Proença *et al.* 2993 (UB)].
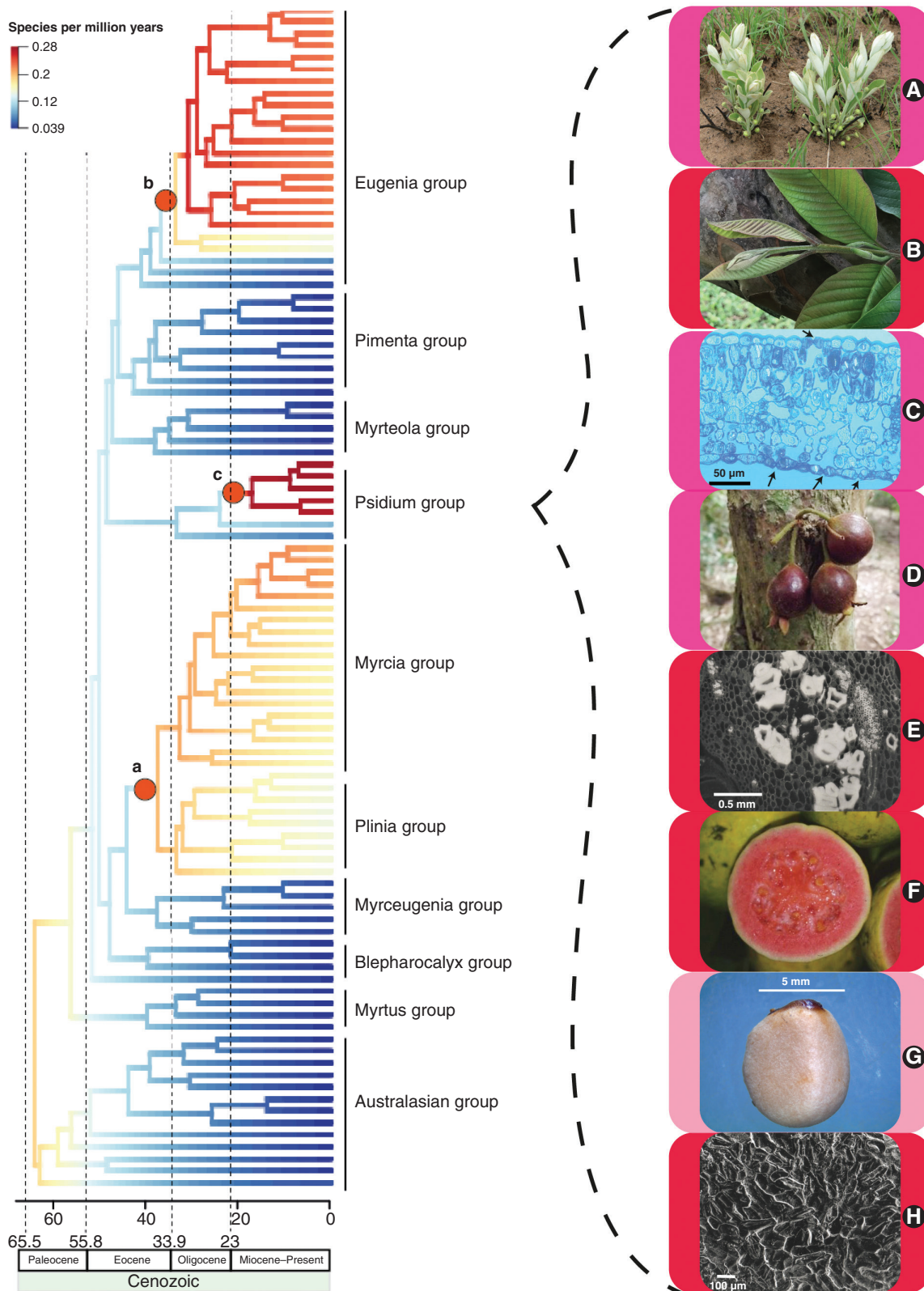
FIG. 5. Distinguishing morpho-anatomic characters in *Psidium* and their occurrence in Tribe Myrteae. (A) Hemixyle habit with lignotuber [*P. bergianum*; Wood 26934 (USZ)]; (B) variability in leaf pre-foliation and architecture (*P. guajava*; photograph CEBP); (C) amphistomatic leaves with arrows showing stomata [*P. ratterianum;* Proença *et al.* 3016 (UB)]; (D) fruit size, colour and seediness [*P. cauliflorum*; Tuler 480 (RB)]; (E) stone cell belt (white) in the ovary [*P. firmum*; Proença 610 (HEPH)]; (F) fruits with fleshy placentas (*P. guajava*; photograph CEBP); (G) bony seeds with operculum (black) [*P. rotundidiscum*; Faria *et al.* 4160 (UB)]; (H) seeds with pulpy testa of irregular, superimposed cells [*P. firmum*; Proença 638 (HEPH)]. Red = restricted to *Psidium*; deep pink = restricted to one to three large genera in tribe Myrteae; pale pink = restricted to a few genera in Tribe Myrteae. Photographs by first collectors in vouchered material except (C) (microphotograph by Suzanne Fank de Carvalho). Phylogeny showing diversification in Myrteae reproduced from Vasconcelos *et al.* (2017b) in accordance with the STM Permissions Guidelines, 28 April 28 2021).

TABLE 1. *Sections of* Psidium *proposed by* Berg (1857) *with original diagnostic characters showing species chosen as lectotypes*

Section	Leaf characters	Bud characters	Ovary locules	Names * not originally included (a current synonym was listed)
Apertiflora 37 original names 20 current species (11 sampled) 2 names in other genera† 31 names correctly classified (84 %)	Membranous or rigid, entire, never tomentose	Open, 4-5 crenate or dentate and later deeply split, calyx campanulate	2-7	**P. australe** (*anceps, suffruticosum*) √ **M** **P. basanthum** √ **P. cupreum** √ **P. decussatum** **P. densicomum** (*ovatifolium*) **P. firmum** **P. grandifolium** (*rubescens, sericeum*) √ **M** * **P. guineense** (*ypanemense*) √ **M** **P. guyanense** (*umbrosum*) **P. hians** (*nutans, refractum*) **P. laruotteanum** (*aerugineum, glaucescens, pohlianum*) √ **P. myrsinites** (*gardnerianum, myrsinoides*) √ **M** **P. myrtoides** √ **chosen LECTOTYPE** *P. langsdorffii* **P. oblongatum** **P. rhombeum** **P. rufum** (*macrospermum, widgrenianum*) √ **P. riparium** (*maranhense, mengahiense, paraense, sieberianum*) √ **P. striatulum** (*turbiniflorum*) √
Rigidifolia 3 original names 3 current species (2 sampled) Species not closely related	Sometimes obverse, rigid or barely rigid when mature, entire, venation obsolete, glabrous	Closed	2-4	* **P. guyanense** (*donianum*) √ **P. macahense** √ **chosenLECTOTYPE** **P. oligospermum** √
Obversifolia 9 original names 6 current species (3 sampled) 6 names probably correctly classified (91 %)	O coriaceous, entire, venation tenuous, glabrous or nearly so	4-5 toothed at apex	3-6	**P. australe** √ **M** * **P. cattleyanum** (*coriaceum, obovatum, variabile*) √ **chosen LECTOTYPE** *P. itanareense* * **P. gaudichadianum** (*sellowianum*) *P. oblongifolium* **P. robustum** √ **M**
Costata 7 original names 2 current species (1 sampled) 6 names correctly classified (86 %)	Cartaceous or coriaceous, entire, venation costate, glabrous or velutinous on the undersurface, or albo-tomentose	Closed	3-5	**P. guajava** √ **chosen LECTOTYPE** **P. guineense* (*araça, ooideum, polycarpon, sorocabense, sprucei*) √ *P. inaequilaterum*
Albotomentosa 10 original names 4 current species (4 sampled) 9 names correctly classified (90 %)	Coriaceous, usually obverse, venation costate, densely white tomentose on the undersurface	With apical gap (*hiantibus*)	2-5	**P. australe var. argenteum* (*cuneatum*) √ **P. grandifolium** (*albidum, incanescens, cinereum, lacteum, riedelianum, microcarpum*) √ **chosen LECTOTYPE** **P. laruotteanum** √ **M** **P. guineense* (*multiflorum, radicans*) √
Crenatifolia 7 original names 4 current species (2 sampled)	annual, membranous, slightly crenulate, venation tenuous	closed at first	2-4	**P. acutangulum** **P. australe var. sufruticosum* (*alatum*) √ **chosen LECTOTYPE** **P. striatulum** (*leptocladum, paraense, persicifolium*) √ **P. maribense**

Bold = currently accepted species; synonyms in parenthesis; √ = species sampled in the inclusive ML and BI phylogeny (Figs 2 and 3); M = misclassified by Berg according to the phylogeny. Some accepted species appear in more than one section (e.g. *P. guineense*) because Berg accepted current synonyms as good species and put them into different sections.

†Berg (1857) included *Psidium campomanesioides* O.Berg, a synonym of *Calycolpus calophyllus* (Kunth) O.Berg and *Psidium elegans* DC., now recognized as *Accara elegans* (DC.) Landrum in this section.

Taxonomic treatment

Psidium L. *Species Plantarum* 470. 1753. Type: *P. guajava* L.
Guajava P. Miller, Gard. Dict. Abr. ed. 4. 28 Jan 1754.
Cuiavus C. J. Trew, Pl. Sel. Pinx. Ehret 4: 12. 1754.
Guaiava Adanson, Fam. 2: 88, 563 ('Guiava'). Jul–Aug 1763.

1. *Psidium* L. sect. *Psidium*, Typus: *P. guajava* L.

Calyptropsidium O.Berg, Linnaea 27: 347, 349. Jan 1856 ('1854'). Typus: *C. friedrichsthalianum* O.Berg.
Psidium sect. *Costata* O.Berg, Fl. Bras. 14(1): 396. Typus: *P. guajava* L. (Lectotype here designated), *nom. illeg.* to be substituted for *Psidium* sect. *Psidium*
Psidium sect. *Crenatifolia* O.Berg, Fl. Bras. 14(1): 407. Typus: *Psidium alatum* O.Berg (Lectotype here designated) = *Psidium australe* var. *suffruticosum* (O.Berg) Landrum, *syn. nov.*

Diagnosis. Trees, shrubs or sub-shrubs. Bark smooth and thinly exfoliating in strips in trees. Young branches frequently quadrangular or alate, at least distally when young. Leaf venation not forming a clear marginal vein that runs parallel to the margin from the base (see sub-sections). Leaves coriaceous or chartaceous. Inflorescence axillary, solitary flowers or a three-flowered dichasium, rarely a raceme; average flower size 20–35 mm in diameter. Buds usually completely to partially closed with round, pentagonal or stellate apical pore or gap, rarely open. Calyx tearing or calyptrate at anthesis. Stamens rarely less than 150 and up to 720; anthers 0,5–1(–3) mm, usually with an apical gland and few to many smaller glands along the connective. Ovary locules (2)3–5(6); ovules (2)4–8-seriate per placental arm, the placental arms intrusive or extrusive. Fruits green, yellow-green or yellow when mature, never red or crimson, sometimes with a crimson flush when maturing, large for the genus, (1–)1,5–3(–6) cm in diameter, with well-developed fleshy placentas. Seeds (6)50–80(–325) per fruit, (2)3–5(–9) mm, geniculate, angular, reniform or lenticulate.

Phylogenetic support. Section *Psidium* clade has maximum support (BS = 100) in the four region ML backbone tree with six accessions (five species). In the inclusive trees with 14 accessions (eight species), the clade also has maximum support (BS = 100; PP = 1) in the ML tree and in the BI tree. The single region ML trees have between seven and 14 accessions. ETS supports the clade (BS = 84) with the additional inclusion of two single region species *P. striatulum* Mart. ex DC. and *P. kennedyanum* Morong, but two accessions emerge in weak, external clades. ITS (BS = 99) supports the clade with one species misclassified within it (*P. firmum*). The *psb*A–*trn*H region provides support for this clade: most of the accessions are in two clades (BS = 100 and 90) although they are not sisters and one accession is external to both. The *ndh*F chloroplast region does not support this clade; accessions are scattered.

Comments. Quadrangular young branches are common (not universal) in this section and are a good morphological marker; de Candolle (1828) was the first to observe this character and used it in his key in *Prodromus*. Pre-foliation is conduplicate; other vegetative morphological markers are the two venation types (see sub-sections for a detailed description) that are not of the typical Myrtaceae type, and the larger number of stamens, locules and

ovules. The placental arms are well developed and frequently curve outwards, with ovules usually 4–8 seriate per placental arm. *Psidium guajava* and *P. guineense*, both members of this section, can be hybridized artificially and probably do so in the wild as postulated based on morphological studies of putative hybrid swarms in several South American localities (Landrum *et al.*, 1995). Polyploidy is common in this section (in both sub-sections) and is discussed in more detail under the sub-sections.

a. *Psidium* sect. *Psidium*. subsect. *Psidium* – Type species: *P. guajava* L.

Diagnosis. Shrubs or trees to at least 18 m. Leaves usually glabrescent, sometimes with a crenulate margin. Venation brochydodromous. Calyx lobes free to partially coalescent to completely coalescent (bud closed), tearing slightly to completely between the calyx lobes at anthesis, or calyptrate. Stamens approx. (100–)150–250(–720); anthers 0,7–1,5(–3) mm. Ovary locules (2–)4(–6); ovules approx. (30–)50–90(–180) per locule. Fruits (7–)15–50(–60 mm); seeds (45–)60–100(–325) per fruit, (2)3–5(9) mm, geniculate, angular or reniform.

Phylogenetic support. Sub-section *Psidium* showed maximum support (BS = 100) in the four region ML backbone tree with three accessions (three species), in the inclusive ML tree (BS = 100) and in the Bayesian tree (PP = 1), both with four accessions (four species). Sub-section *Psidium* showed the highest support over the whole tree as well as high or maximum resolution between species. The single region ML trees had either three or four accessions. ETS supported (BS = 99) a clade with three of the four accessions of section *Psidium*; the fourth, *P. guajava*, emerged in sister sub-section *Albotomentosa*, sister to the remainder of that clade. ITS showed maximum support (BS = 100) for sub-section *Psidium*. The *ndh*F chloroplast region supported (BS = 70) the sub-section, with two accessions (*P. guineense* and *P. australe*, both of sub-section *albotomentosa* emerging as misclassified by Berg (1857) within the clade. The *psb*A–*trn*H region supported the clade (BS = 100) with three accessions.

Comments. Pre-foliation in section *Psidium* is conduplicate *sensu* Cullen (1978), i.e. the leaf is folded inwards along the midrib, but in *P. guajava* the adaxial surfaces are appressed, sometimes until the leaf reaches more than half its fully expanded length (Fig. 5B). The separation can also be earlier, when leaves are about a third of their mature length. This specialized leaf pre-foliation is associated with young leaf protection due to increased fracture toughness, a thicker edge that acts as a deterrent to leaf larvae that eat inwards, and by exposing only the better protected abaxial surface during leaf expansion (Grubb and Jackson, 2007, and references therein). Interestingly, glandular trichomes (not present in other species of *Psidium*) were observed on the petioles and abaxial surface of *P. guajava* (Cardoso *et al.*, 2009; Al-Edany and Al-Saadi, 2012). Glandular trichomes are very rare in tribe Myrteae, i.e. they were found in only one species of *Myrceugenia* in a study of 17 genera (44 species; four species of *Psidium* not including *P. guajava*) of Neotropical Myrtaceae (Cardoso *et al.*, 2009). Although conduplicate pre=foliation is present in *P. guineense* and *P. friedrichsthalianum* (that also belong to this section) the adaxial leaf surfaces are apparently always free.

b. *Psidium* sect. *Psidium* subsect. *Albotomentosa* (O.Berg) Tuler & Proença, *stat. nov.* – Type species: *P. grandifolium* (Lectotype here designated).

Diagnosis. Small trees, shrubs or sub-shrubs 0.3–6 m. Leaves frequently covered with whitish, tawny or rufous indumentum on the abaxial surface; venation acrodromous–brochydodromous (see comments below). Calyx lobes nearly free to partially coalescent to completely coalescent (bud closed), tearing slightly to completely between the calyx lobes at anthesis, never calyptrate. Stamens approx. 100–300(–560); anthers 0,5–1(–1,2) mm. Ovary locules (2)3(–5); ovules approx. 20–100(–120) per locule. Fruits 8–30 mm. Seeds approx. (6–)15–80(–234) per fruit.

Phylogenetic support. Sub-section *Albotomentosa* has been informally recognized by botanists as a morphological group, e.g. the *P. grandifolium* complex *sensu* Landrum (2005). The sub-section was highly supported (BS = 98) in the four region ML backbone tree with three accessions (three species). In the inclusive trees the sub-section also had high support (BS = 86) both in the ML tree and in the Bayesian tree (PP = 0.99) with ten accessions (four species). The single region ML trees had between five and 11 accessions. ETS supports (BS = 99) the section with eight accessions plus an additional species, *P. striatulum*, but two accessions (*P. australe* var. *suffruticosum* and one of the accessions of *P. grandifolium*) emerged external to the clade. ITS supports (BS = 100) the clade with one species misclassified by Berg (1857) within it (*P. firmum*). The *ndh*F region does not support the clade; accessions are scattered. The *psb*A–*trn*H region supports the clade (BS = 90) with one accession misclassified by Berg (1857) (*P. australe*). Although subsection *Albotomentosa* is highly supported, resolution between species was poor. This suggests this clade has only recently diversified, as was found for some other savanna genera (Simon *et al.*, 2009; Inglis and Cavalcanti, 2018). Rapid, recent diversification was suggested by these authors to have been driven by habitat changes associated with the rise of inflammable C$_4$ grasses during the last 5 million years.

Comments. This small sub-section has successfully occupied non-forested areas such as savannas and other grass-dominated habitats (Landrum, 2005; Tuler *et al.*, 2021); both plants and fruits are usually smaller than in its sister clade sub-section *Psidium*. The venation type of sub-section *Albotomentosa* is unusual in Neotropical Myrtaceae and restricted to this clade in *Psidium* and to *Campomanesia* (Cardoso and Sajo, 2006). This was classified as acrodromous–brochydodromous/last marginals forming arches/intramarginal vein absent/tertiary venation ramified admedial (Cardoso and Sajo, 2006). *Psidium ratterianum* is amphistomatic (Proença *et al.*, 2010), a derived condition associated with high CO$_2$ leaf conductance and fast growth of herbaceous plants in high-light and high-altitude conditions (Mott *et al.*, 1982; Muir, 2015). *Eucalyptus globulus* Labill. (another amphistomatic Myrtaceae) can independently regulate closure of leaf stomata on the different leaf surfaces, with changes in temperature, humidity and irradiance inducing differential closure (Richardson *et al.*, 2017) that allow plants to fine-tune their response to environmental conditions. Further investigation into leaf anatomy and leaf physiology in this section is desirable. Ploidy levels are poorly known in sub-section *Albotomentosa* if compared with sub-section *Psidium*. Four counts are available: 2*n* = 44 for *P. australe* and *P. guineense*, *n* approx. 33 for *P. grandifolium* and 2*n* = 22 for *P. ratterianum* (Costa and Forni-Martins, 2006; Silveira *et al.*, 2021), suggesting that polyploidy is at least not uncommon.

2. *Psidium* sect. *Obversifolia* O.Berg, Fl. Bras. – Type: *P. cattleyanum* Sabine (Lectotype here designated).

Diagnosis. Trees or large shrubs. Bark smooth and thinly exfoliating in trees. Young branches compressed; leaf venation camptodromous at base, the distal veins with arched loops or sometimes forming a clear marginal vein, but not with the typical Myrtaceous marginal vein that runs along the whole margin starting at the base, frequently obovate, glabrous, crass when fresh and somewhat lustrous above. Inflorescence axillary, uniflorous or in short racemes. Buds open, partially closed to completely closed; stamens approx. 180–400, locules 3–5; placentation peltate, ovules 10–35 per locule. Fruits green, yellow or deep crimson when mature, 20–45 mm, with well-developed fleshy placentas. Seeds 30–60.

Comments. Section *Obversifolia* is supported by three accessions (two species) in the four region ML (BS = 100) backbone tree. In the inclusive trees, it includes five accessions (two species) and is strongly supported in the ML tree (BS = 99) and in the Bayesian tree (PP = 1). The single region ML trees have between four and five accessions. ETS (BS = 49) and ITS (BS = 63) regions provided weak to good support for this section, with the first suggesting two possible new inclusions: *Psidium* sp. nov. from Bahia, Brazil and *P. minutiflorum* Urban & Ekman from Piauí, Brazil. Neither of the chloroplast regions (*ndh*F and *psb*A) supports this section.

The thick, rubbery leaves (empirically observed in the field by author A.C.T.) in *P. cattleyanum* of this clade are supported by leaf anatomy (Gomes *et al.*, 2009) and by a study of comparative leaf anatomy and morphology (Boeger and Wisniewski, 2003) in lowland tropical forest in Paraná, Southern Brazil. Boeger and Wisniewski (2003) investigated leaf thickness of 16 species of trees (in ten Angiosperm families) at three different successional stages; *P. cattleyanum* (native to the area) was present in two of these stages and showed above-average leaf thickness in both. The thick leaves in *P. cattleyanum* were due to the well-developed adaxial epidermis and the thick palisade parenchyma, not to cuticles or spongy parenchyma that showed low or average values. *Psidium cattleyanum* has 2–3 layers of palisade parenchyma on each side (Arruda and Fontenelle, 1994; Endringer, 2020) an unusual character in Neotropical Myrtaceae (Gomes *et al.*, 2009). However, other species of the section have not had their leaf anatomy studied.

The five accessions in the inclusive tree are one of *P. araucanum* and four of *P. cattleyanum* (two of P. *cattleyanum* var. *cattleyanum*, the red-fruited variety, and two of *P. cattleyanum* var. *lucidum*, the yellow-fruited variety). Our results provide some support that the two varieties be recognized at species level due to the position of *P. araucanum* (Fig. 1) as sister to *P. cattleyanum* var. *cattleyanum* (BS = 55 and PP = 0.95). Previous studies have found differences of putative taxonomic significance between the yellow-fruited and the red-fruited varieties (Table 2). The thickness of the collapsed phloem and organization of cristaliferous series in the bark are considered taxonomically significant characters that are not

TABLE 2. *Cytogenetic and morphological characteristics of* Psidium cattleyanum *Sabine*

Character	var. *cattleyanum*	var. *lucidum*	Reference
	(red fruits)	(yellow fruits)	
Chromosome numbers	44, 88, 77, 132	33, 44, 55, 66, 77, 88, 98, 99, 110, 132	Éder-Silva *et al.* (2007); Raseira and Raseira (1996); Machado (2016)
Bark: phloematic tissue	Organized and uniform	Disorganized and irregular	Rocha *et al.* (2008)
Bark: collapsed phloem	2129 µm thick	1656 µm thick	Rocha *et al.* (2008)
Bark: cristaliferous series	Single side of ray	Surrounding ray	Rocha *et al.* (2008)
Bark: angle of sieve plates	152	159	Rocha *et al.* (2008)
Fruit: anthocyanins (cyanidin)	Yes (deep red)	No (yellow)	Biegelmeyer *et al.* (2011)
Fruit: polyphenols	501 mg 100 g^{-1}	292 mg 100 g^{-1}	Biegelmeyer *et al.* (2011)
Fruit: vitamin C (ascorbic acid)	242 µg g^{-1} f. wt	200 µg g^{-1} f. wt	Luximon-Ramma *et al.* (2003)
Flavonoids	100 mg 100 g^{-1}	35 mg 100 g^{-1}	Biegelmeyer *et al.* (2011)

influenced by environmental conditions (Roth, 1981). *Psidium cattleyanum* shows disporic apomixis (Raseira and Raseira, 1996; Souza-Pérez and Speroni, 2017). Machado (2016) found that seeds from the same fruit showed different levels of ploidy.

Psidium cattleyanum. is characterized by absolute polyploidy (no diploid counts, 2n = 22, have been recorded in a total of 36 counts; Supplementary data Table S2). Considering the two varieties of *P. cattleyanum* separately permits a novel interpretation of the cytogeographic study of 17 populations of *P. cattleyanum* done by Machado (2016). That author found nine different cytotypes, and both varieties had a similar range of cytotypes. The diploid 2n = 22 was not found in the study and n = 33 was found only in *P. cattleyanum* var. *lucidum*, the yellow-fruited variety (Machado, 2016). The yellow-fruited variety populations were almost all coastal (only one was not) with conserved levels of ploidy per population and cytogeographic segregation. The lower levels of ploidy (44, 66 and 77) were restricted to the colder, wetter, more southerly populations of São Paulo, Paraná and Santa Catarina, and the higher levels (98, 110 and 132) to the warmer, drier, more northerly populations of Rio de Janeiro, Espírito Santo, Bahia and Paraíba (Éder-Silva *et al.*, 2007; Machado, 2016). The red-fruited variety, on the other hand, occurred in colder, wetter, inland habitats at higher altitudes in São Paulo and Paraná, with low and high ploidy levels coexisting in the same population. The red-fruited variety was sympatric with the yellow-fruited variety; no pure, red-fruited populations were found. Why is *P. cattleyanum* not as invasive in Brazil, where it is native (although identified as a pioneer species; Boeger and Wisniewski, 2003), as in other parts of the tropics? Although identified as a pioneer species, it is not as problematic in Brazil as elsewhere in the tropics. Machado (2016) showed that, in Brazil, red-fruited populations were (1) mixed with yellow-fruited populations and (2) showed no cytogeographic segregation. It is possible that the chance introduction of a well-adapted plant with an even polyploid number into a favourable habitat with available niche and low levels of competition (common in island habitats; Denslow, 2003) could be the trigger to its hyperinvasiveness. Since *P. cattleyanum* is apomictic (Souza-Perez and Speroni, 2017), founder populations could be established from this single plant, whose descendants would later cross sexually and produce many fertile seeds.

3. *Psidium* sect. *Apertiflora* O.Berg – Type species: *P. myrtoides* O.Berg (Lectotype here designated).

Psidium sect. *Rigidifolia* O.Berg – Type species: *Psidium macahense* O.Berg (Lectotype here designated), *syn. nov.*

Corynemyrtus (Kiaerskou) Mattos, Loefgrenia 10: 1. Mai 1963. Type: *C. corynantha* (Kiaerskou) Mattos (*Myrtus corynantha* Kiaerskou) *Myrtus* subgen. *Corynemyrtus* Kiaerskou, Enum. Myrt. Brasil. 39: 18. 1893.

Diagnosis. Trees, shrubs, sub-shrubs or hemixyles. Bark smooth or rough, exfoliating in rings, flakes, scales or plaques in trees. Young branches terete or compressed; venation brochydodromous usually forming a clear, crenate to almost straight marginal vein that runs closely parallel to the margin. Inflorescence axillary or terminal (rarely cauliflorous), uniflorous, raceme or auxotelic raceme; dichasia rare. Buds usually open, tearing into five or rarely four lobes (flowers tetramerous: *P. macahense* O.Berg; Tuler *et al.*, 2019b) or a mixture of tetramerous and pentamerous (Landrum, 2017); stamens (100–)125–200(–320); locules 2–3(–5); ovules 1–2(3) seriate per placental arm. Fruits green, yellow or crimson when mature, usually small for the genus (8–)10–25(–34) mm, with poorly developed placentas when mature; seeds (1–)4–20(–50).

Phylogenetic support. Several of the species in this section have been recognized as the *Psidium salutare* complex (Landrum, 2003). Section *Apertiflora* has maximum support (BS = 100) in the four region ML backbone tree with nine accessions (six species). In the inclusive trees it has high support in the ML analysis (BS = 76) and moderate support in the Bayesian analysis (PP = 0.92), with 18 accessions (13 species). The single region ML trees have between ten and 19 accessions. ETS supports (BS = 95) the section, with one accession misclassified by Berg (1857) and two new inclusions: *P. ovale* (Sprengel) Burret and *P. dictyophyllum* Urban & Ekman. ITS supports the section (BS = 72), with one accession misclassified by Berg (1857). The *psb*A chloroplast region supports (BS = 75) the clade with no misclassifications and the additional inclusion of two accessions of *P. robustum*. The *ndh*F region provides average support (BS = 62) for this clade, with two accessions emerging external to the clade. *Psidioum sessiliflorum* (Landrum) Proença & Tuler emerged as sister to the rest of the clade on a long branch that also reduced its BS support from 89 to 76. Morphologically, *P. sessiliflorum* fits section *Apertiflora* well, and the three sequences are well aligned with other species of the section. Possibly the long branch is caused by a combination of the ETS sequence being exceptionally short, and a unique 17 bp insertion in the *psb*A region.

Comments. This is the most species-rich section of the genus. It has diversified mostly in the Atlantic Forest and the South

American savannahs and grasslands. In the Atlantic Forest, plants are large trees or shrubs in which the bark is frequently (not always) rough or scaly, only rarely smooth and guava-like as in other sections. In savannahs and grasslands, species have adapted to seasonal drought and fire by the scaly bark becoming thick and corky (in arboreal species; Fig. 4A) or by adopting an hemixyle habit (i.e. sub-shrubs that resprout from underground lignotubers; Fig. 5A), in a similar way as in *Psidium* subsect. *Albotomentosa*. The tendency for flowers to be produced in auxotelic racemes observed in trees (Fig. 4C) has resulted in hemixyles that resprout after fire or drought by producing flowers at the proximal nodes and vegetative growth at distal nodes (Fig. 5A). The strongest morphological marker for this clade is the open flower buds with clear calyx lobes and minimal tearing or none at anthesis. It shares with its sister section *Mitranthes* a reduction in the number of locules, ovules and seeds. In these two sections, 2–3 loculate ovaries with one- or two-seriate ovules are the norm, with few exceptions. Seeds produced per fruit are on average fewer, with the lowest values of seeds per fruit almost always below ten.

4. *Psidium* sect. *Mitranthes* (O.Berg) Tuler & Proença, *stat. nov.* – Type species: *P. brownianum* DC.

Mitranthes O.Berg, Linnaea 27: 136 (in clave), 316. Jan 1856 ('1854'). *M. browniana* (DC.) O.Berg (*Psidium brownianum* DC.) (Lectotype; see Pfeiffer, Nom. 2: 327. 9 Mai 1873).
Mitropsidium Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15: 488 (1941). Typus: *M. pittieri* Burret

Diagnosis. Trees or shrubs. Leaves not fleshy when fresh, usually cartaceous or coriaceous. Branches compressed; venation brochydodromous or camptodromous, rarely forming a clear marginal vein, sometimes inconspicuous. Inflorescence axillary or terminal, uniflorous or rarely in simple three-flowered dichasia or in short racemes. Floral buds very variable, open, partially closed or completely closed, if closed tearing at anthesis or with a calyptra. Stamens (80–)100–200(–270); anthers 0,3–0,5(–0,9) mm with a single apical gland or with 1–5(–17) smaller glands on the connective. Ovary locules 2–3(4); ovules (3–)5–30(–44) per locule, uniseriate or biseriate. Fruits smallish for the genus, green, yellow-green or black mature, with poorly developed placentas (Fig. 4). Seeds (1–)4–20(–23) per fruit, externally rounded and pressed against the fruit wall and internally faceted where developing seeds abut or rounded and immersed in a fleshy endocarp.

Phylogenetic support. Section *Mitranthes* is highly supported (BS = 100) in the four region ML with two accessions (two species). In the inclusive trees with eight accessions (seven species) it is highly supported in the ML tree (BS = 76) and in the Bayesian tree (PP = 0.99). The single region ML trees have between three and seven accessions. ETS (BS = 95) supported the clade with four accessions, but three other accessions were misclassified. ITS (BS = 89) and the chloroplast region *psb*A (BS = 61) supported the clade with no misclassifications. The chloroplast region *ndh*F did not support the clade; accessions were scattered.

Comments. This section has successfully colonized the Atlantic Forest, Dry Forests throughout South America and the South American Dry Diagonal (*Caatinga* and *Cerrado*). There are apparently no sub-shrubs or hemixyles; plants are trees or large shrubs. It has also dispersed into the Caribbean where there are apparently several closely related species (Flickinger *et al.*, 2020). Pre-foliation is weakly (*P. myrsinites*) to strongly (*P. schenckianum*) revolute. Leaf venation camptodromous–brochydodromous/last marginals forming complete or incomplete arches/intramarginal vein absent/tertiary venation ramified admedial or more rarely brochidodromous (Cardoso and Sajo, 2006; Oliveira *et al.*, 2017). We have not been able to find chromosome counts for any species of this section. Anatomically, *P. oligospermum* lacks tector trichomes on the adaxial epidermis, a condition also common in its sister clade, *Psidium* sect. *Apertiflora*. It shares with its sister section *Apertiflora* a reduction in the number of locules, ovules and seeds (see discussion under that section).

Conclusion

Information gaps identified in morphology are on pre-foliation, the occurrence of colleters, staminal development, placentation and floral anatomy in general throughout the genus; records are patchy. Studies are in general biased towards sections *Psidium* and *Obversifolia* where the economically important species are. Scattered evidence suggests that stone cells in the ovary, apomixis and polyploidy occur across the genus. Stone cells in the ovary have been recorded in three species from different clades. Chromosome counts or studies of reproductive biology within section *Mitranthes* are non-existent, and few in section *Apertiflora*.

A comprehensive phylogenetic study of *Psidium* would undoubtedly bring a better focus to the preliminary understanding of how the genus evolved and diversified that has come to light in the present study. Recognition of the major clades/sections should facilitate this task by allowing in-depth studies of the sections separately, particularly of sections *Psidium* and *Obversifolia*, which present problems that are challenges to humanity in the areas of food security and biodiversity conservation. The approximately ten species of *Psidium* that are restricted to the western South American highlands of Colombia, Ecuador, Peru and Venezuela are absent from our phylogeny and their sampling would be of particular biogeographical interest. Many American genera of Myrtaceae are restricted either to Western (Andean) or Eastern South America (Govaerts *et al.*, 2008). The few genera that occur in both areas, such as *Myrcianthes* and *Myrceugenia* have been found to have a strong East/West dichotomy in recent phylogenetic studies (Murillo *et al.*, 2012; Vasconcelos *et al.*, 2017b). The same could be said for the Caribbean species, since our sample from this area was small (three species) and the Caribbean is quite diverse for Myrtaceae, with species putatively endemic to Jamaica, Hispaniola and Cuba (Flickinger *et al.*, 2020).

Relationships between species within *Psidium* sect. *Psidium* subsect. *Albotomentosa* and the *Psidium* sect. *Apertiflora* clades that have occupied the South American savannas and grasslands are very unclear, as can be seen in the trees with different accessions of *P. australe*, *P. bergianum* and *P. laruotteanum* emerging on different (albeit close) branches, i.e. not as sister taxa. These have been considered complexes of closely related

species (Landrum, 2005, 2021) so the lack of resolution is not surprising. If *Psidium* is a rapidly evolving genus, it is possible that these clades are recently evolved or evolving and that a genomic approach will be necessary to clarify their relationships. The two accessions of *P. corynanthum* that emerged separately could likewise be an artefact of poor resolution in section *Apertiflora* (these two accessions shared two regions, the ETS and *ndh*F) and are in separate, low bootstrap clades.

Many authors have alluded to the close morphological similarity between *P. guajava* and *P. guineense* (Landrum *et al.*, 1995; Marques *et al.*, 2016; Landrum, 2021). These two species share similar leaf venation, inflorescences, closed floral buds, flowers with many stamens, elongated anthers and fruits with many small seeds, and are frequently misidentified as each other in herbaria (Arévalo-Marín *et al.*, 2021). It has been widely believed that *P. guajava* and *P. guineense* would emerge as closely related, as was found by Salywon (2003) based only on ITS1 + ITS2. Our study has shown this not to be the case. The closest relatives of *P. guajava* are *P. acidum*, *P. friedrichsthalianum* and *P. kennedyanum*, not *P. guineense*. Although members of the same section, *P. guajava* and *P. guineense* belong to separate sister clades. These two species have apparently undergone parallel morphological evolution; we believe this parallelism could be associated with their similar invasive qualities.

The list of species with their probable sections (Supplementary data Table S1) is tentative. Thirty-five species have not had any DNA sequences generated and have thus been assigned to sections based on morphology; nine species with unclear affinities have not been attributed to a section. Twenty-five names were considered of uncertain status. The high degree of homoplasy, convergence and parallelism that appears to occur within *Psidium*, particularly between sister sections *Apertiflora* and *Mitranthes*, makes this a hazardous exercise. We have been conservative in only attributing species to sections when there was either strong molecular evidence, some molecular evidence combined with morphology or overwhelming morphological evidence. We hope this study will guide and encourage future work in this fascinating genus.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Table S1: list of accepted species in *Psidium* with probable sections, voucher specimens and bootstrap support for the section in molecular phylogenies, and references. Table S2: species with available chromosome counts, with section, count, reference, and voucher and geographic information when available. Table S3: species included in the phylogeny with GenBank accession numbers, voucher information and geographic data. Figure. S1: maximum likelihood single region tree (ETS). Figure S2: maximum likelihood single region tree (ITS). Figure S3: maximum likelihood single region tree (*ndh*F). Figure S4: maximum likelihood single region tree (*psb*A–*trn*H).

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