CHARACTERIZING THE FREQUENCY, MORPHOLOGICAL GRADIENT, AND DISTRIBUTION OF DIOECY IN *MICONIA* (MELASTOMATACEAE)

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Dioecy has evolved many times independently within the angiosperms. The distribution, frequency of occurrence, and floral morphology of dioecious angiosperms constitute the foundations for comparative studies of dioecy, yet for many groups they are still poorly characterized. We assessed species of *Miconia* for the presence of a dioecious reproductive system, characterized the floral morphology for staminate and pistillate flowers, and used herbarium records to analyze patterns of distribution and elevational range. We find that dioecious *Miconia* represent an uncommon case of a mismatched stage of organ abortion between staminate and pistillate flowers, with functionally pistillate flower morphology being largely consistent across species and morphological expression in functionally staminate flowers varying from near-absent gynoecia to slight reductions in gynoecia. We identify 60 dioecious species and 15 putatively dioecious species within *Miconia* that are distributed primarily in montane habitats between 1000 and 3500 m in the Andes, parts of Central America, and the Caribbean. Our results double the last known count of dioecy in *Miconia* and highlight the gradient of vestigial morphology in staminate flowers. Last, we provide discussion on the significance of dioecy in relation to floral development, pollination, and ecology in *Miconia*.

Keywords: staminate, pistillate, unisexual, tropical diversity, natural history collections, herbarium.

Online enhancement: appendix.

Introduction

Understanding the evolution of dioecy, a reproductive system defined by unisexual flowers on separate staminate and pistillate plants, is an important line of inquiry in biology, as the system has far-reaching effects on gene flow, floral trait evolution, and diversification. Fundamentally, dioecy enforces outcrossing (Baker 1959; Lloyd 1975; Charlesworth and Charlesworth 1978) but can also serve as a means for sex-specific specialization and resource allocation (Darwin 1877; Bawa 1980; Freeman et al. 1997). The separation of floral sexual organs onto separate individuals allows for more reproductive effort for either pollen or ovule/fruit production. However, dioecy is rare across angiosperms, being found in only 6% of species and 7% of genera (Renner 2014). In spite of its relative rarity, it has a wide phylogenetic distribution (47% of angiosperm families) and is estimated to have evolved at least 800 times. Evolutionary pathways leading to dioecy include either directly from hermaphroditic ancestors or through intermediary systems such as gynodioecy, monoecy, and heterostyly (Charlesworth and Charlesworth 1978; Dufay et al. 2014; Henry et al. 2018). The effect of dioecy on diversification is not well understood and has traditionally been considered an evolutionary dead end (Heilbuth 2000; Heilbuth et al. 2001). Although dioecious species face obstacles, such as the obligation of pollen from one plant reaching the ovules of the other and only a single sex with the ability to bear progeny, the dead-end generality does not hold in all groups (Vamosi and Vamosi 2004; Käfer et al. 2014; Sabath et al. 2016).

The terminology used for reproductive systems in plants is fraught with inconsistencies, resulting in efforts that are aimed at promoting unified use among researchers in the field and that reflect our use of terms such as “gender,” “sex,” “male,” and “female” with respect to contemporary social uses (Neal and Anderson 2005; Cardoso et al. 2018; Oberle and Fairchild 2023; Pannell 2023). In our study, we assess dioecy and hermaphroditism from a morphological standpoint, specifically in the development and function of gametophytes (pollen, ovules) and the primary floral organs that allow for their dispersal and use in successful sexual reproduction (stamens, style, stigma). Therefore, we choose to use terms that reflect our morphological approach (Sakai et al. 1995; Cardoso et al. 2018). We use

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the term "unisexual" to refer to individuals or flowers that express a single sexual function, either through functional stamens and pollen (collectively called the androecium) or through functional stigma, style, and ovaries (collectively called the gynoecium). Flowers and individuals characterized by solely functioning androecia are referred to as staminate, while those characterized by solely functioning gynoecia are referred to as pistillate. Dioecious species are those in which each individual has only unisexual flowers that are either all staminate or all pistillate. Hermaphroditic species and individuals are those that have bisexual flowers with both functional androecium and functional gynoecium.

Traditionally, two morphological groups of unisexual flowers have been recognized (Darwin 1877; Heslop-Harrison 1957; Ainsworth 2000; Mitchell and Diggle 2005), differing by the stage of developmental arrest that results in unisexuality. Type I flowers initially develop as bisexual, and sex differentiation occurs after the abortion and loss of function of androecium in pistillate flowers and gynoecium in staminate flowers (Mitchell and Diggle 2005). Type I unisexuality is characterized by retention of some degree of nonfunctioning sexual organs, such as sterile stamens or underdeveloped gynoecium (e.g., *Asparagus* Tourn. ex L., *Clusia* Plum. ex L.; Mitchell and Diggle 2005; Diggle et al. 2011). In type II flowers, unisexuality is determined at the onset of floral development, with cell growth occurring only in the androecium in staminate flowers and in the gynoecium in pistillate flowers (e.g., *Euphorbia* L., *Salix* L.; Mitchell and Diggle 2005; Diggle et al. 2011). In studies of dioecious groups, morphological and anatomical analyses of type I and type II flowers yield valuable insight into the homology, ancestral condition, and plant-pollinator mechanisms of dioecious lineages (Anderson and Simon 1989; Knapp et al. 1998; Naiki and Kato 1999; Judkevich et al. 2022; Reis et al. 2023). Similarly, understanding the distribution of dioecy in geographic and ecological space has made important contributions to our understanding of how dioecious plants migrate and colonize new areas (Baker and Cox 1984; Sakai et al. 1995; Schlessman et al. 2014). An accurate circumscription of the extent, morphology, and distribution of dioecious groups serves as the backbone for placing these patterns in macroevolutionary contexts aiming to understand the origins, biogeography, diversification effects, and causal mechanisms of dioecy (Bawa 1980; Diggle et al. 2011; Drew and Sytsma 2013; Zhang et al. 2019). However, dioecy can be difficult to diagnose at times, often needing substantial collection efforts and dedicated time for morphological assessment of a species, especially for tropical species with narrow ecological niches. As a result, comprehensive characterization of the extent, floral morphology, and distribution of dioecy is lacking in many groups (Diggle et al. 2011) and more so in tropical lineages that are disproportionately understudied when compared to temperate systems (Collen et al. 2008; Vasconcelos 2023). One such group is the Neotropical genus *Miconia* Ruiz & Pav., in which dioecy has been reported but never thoroughly investigated (Renner 1989; Almeda and Dorr 2006).

Miconia is the largest genus in Melastomataceae, comprising about 1900 species spread throughout the Neotropics, and one of the most species-rich genera that occurs there (Ulloa Ulloa et al. 2022). The genus is generally defined by terminal or axillary inflorescences, flowers subtended by a single pair of bracteoles, anthers without pedoconnectives, and berry fruits (Michelangeli et al. 2022). Because of its diversity of sexual and asexual reproductive strategies, the genus has been increasingly used to investigate shifts in pollination systems, floral trait evolution, and asexual reproduction via apomixis (Goldenberg and Shepherd 1998; Goldenberg et al. 2008; Caetano et al. 2013, 2018; de Brito et al. 2016; Gavrutenko et al. 2020). The occurrence and distribution of dioecy in *Miconia*, however, has been overlooked and ill defined. Suspicions of dioecy in *Miconia* date as far back as 1850 (Naudin 1850) in the description of *M. abortiva* (now a synonym of *M. globuliflora*). However, Gleason (1946) was among the first to discuss sexual dimorphism in the flowers of *M. brachygyna*. He questioned the "long-styled and short-styled forms of plants" (Gleason 1946, p. 189) within it and related species and, notably, observed varying forms of reduced gynoecium in *Miconia* species with otherwise normal androecia. Some species had styles that were "permanently short," while others had styles that were "nearly aborted" (Gleason 1946, p. 189). It was not until two decades later that Wurdack (1964, pp. 173–174) explicitly used the term "dioecy" while describing staminate and pistillate specimens of *M. dioica*: staminate flowers with "ovarium abortivum non ovulatum" and pistillate flowers with "stamina abortiva." The first compilation of dioecious *Miconia* was a list of 37 dioecious *Miconia* and their countries of occurrence that was included in the species description of dioecious *M. amilcariana* Almeda & Dorr (2006). The authors concluded that these species mainly fall within *Miconia* section *Cremanium*, a group of ~228 woody shrubs and trees mostly found in wet and humid forests from southern Mexico and the Caribbean to the tropical Andes. Later species descriptions added an additional eight dioecious species, including one species in *Miconia* section *Amblyarrhena* (de Santiago Gómez 2010, 2012; Burke and Michelangeli 2013, 2018; de Santiago Gómez and Michelangeli 2016; Angulo and Michelangeli 2023). The sectional classification used throughout *Miconia*, although not phylogenetically accurate (Goldenberg 2008), is a useful tool in species identification and categorization and remains in use by many in the field. Most members of *Miconia* section *Cremanium* primarily belong to a larger clade of ~500 species (*Miconia* III; sensu Goldenberg et al. 2008), consisting of sections *Cremanium*, *Amblyahrrena*, and *Chaenopleura*.

The initial list of dioecious *Miconia* (Almeda and Dorr 2006) was critical in laying the foundation for documentation of the extent of occurrence of this reproductive system in the genus. However, it lacked many critical details, such as herbarium voucher references of staminate and pistillate plants, sex determination of type specimens, ecological information for dioecious species, and range of *Miconia* section *Cremanium* species examined for a reproductive system. The frequency of dioecy and its distribution in *Miconia* remains unclear, and there is no characterization of the staminate and pistillate flower morphology. This study uses a collections-based and morphological approach to address the knowledge gap of dioecy in *Miconia*. The objectives were to (*a*) describe the differential floral dimorphism in species of *Miconia* section *Cremanium* and identify the stage of developmental arrest in androecium and gynoecium; (*b*) document the extent of dioecy in *Miconia* section *Cremanium*, including voucher references for staminate and pistillate individuals; and (*c*) analyze patterns of dioecious *Miconia* in geographic and ecological space. We also identify remaining gaps in collections (i.e., absent staminate or pistillate collection for a species) and assign sexes to available type specimens.

Material and Methods

Floral morphology of herbarium specimens was assessed in 196 species. Although the focus was on species of *Miconia* section *Cremanium*, a cursory assessment of sections *Chaenopleura* and *Amblyarrhena* was also conducted. A reproductive system was assigned to species by assessing floral reproductive characters. This was completed by analyzing all available specimens at the NY and US herbaria as well as two species examined from COL specimens (acronyms following Thiers 2023) and examining digital and physical type specimens. The number of flowering specimens available for a species varied, with some widespread and well-collected species having several flowering specimens of both pistillate and staminate plants and with other lesser-known species having only a single flowering specimen available. In addition to the specimen analysis, we conducted a literature search for each species, reviewing publications for mentions of dioecy, heterostyly, or dioecious morphology (e.g., "anthers aborted," "style reduced"). Since many species were described without reference to their sexual floral dimorphism, we did not interpret a lack of dioecious characters in the descriptions as hermaphroditism.

Those species with individuals containing flowers with well-developed pistil and stamens were designated as hermaphroditic. Species with underdeveloped androecia or gynoecia were examined further, and when available, multiple flowers of at least two (where available) herbarium specimens were rehydrated, dissected, and photographed using a Nikon SMZ1500 with a DXM1200F digital camera. Dioecious species were defined as those containing unisexual staminate and pistillate flowers on separate individuals. In the absence of the respective counterpart to a staminate or pistillate plant digitally or otherwise, we did not assume that a species was dioecious. Pistillate flowers were identified by a lack of function in the androecium (collapsed anthers devoid of pollen). Pollen absence was verified under the same Nikon stereoscope for all sampled pistillate specimens and with a Hitachi SU3500 scanning electron microscope for nearly a dozen species. Staminate flowers were identified by lack of function in the gynoecium, as indicated by the degree of morphological development (reduced style/stigma and either underdeveloped ovules or an absence of ovules). In our analyses, we make the assumption that the unisexual specimens examined for each species are representative of the entire individual. That is, staminate flowers seen on an herbarium specimen indicate that the entire tree contains staminate flowers and is not indicative of monoecy (staminate and pistillate flowers on the same individual). We make this assumption based on personal observations in the field, where we have seen several species in which individuals contain either all staminate flowers or all pistillate flowers. Furthermore, observed duplicate herbarium specimens (different inflorescences from the same individual) all had the same floral morphology.

To determine the distribution and habitat of dioecious species, occurrence data for each species were extracted from the Global Biodiversity Information Facility (GBIF) database (https://doi.org/10.15468/dl.3zhzby) and cleaned using R and the R package CoordinateCleaner (Zizka et al. 2019; R Core Team 2021). Occurrences were filtered to contain only herbarium records, and points were removed if they were in the ocean or at the centroids of countries or provinces. Points located at herbaria or biodiversity centers were also removed. In the process of the study, several species contained herbarium specimens with both unisexual and hermaphroditic individuals, likely due to misidentification (see "Results" and "Discussion"). For these, occurrences were manually cleaned to include only unisexual individuals. Elevation ranges were obtained from GBIF occurrences of each species.

Results

Of 198 species assessed, 183 were assigned a reproductive system determination based on floral morphology. Hermaphroditism was determined in 123 species (list A1; lists A1, A2 are available online). Overall, 75 species were found to primarily contain unisexual individuals with either aborted androecia or aborted gynoecia or, in a single case, with only a mention of dioecy in the literature (table 1; list A2). Dioecy was determined in 60 species (both the staminate specimens and the pistillate specimens were identified), and an additional 14 species contained either only staminate specimens (seven species) or only pistillate specimens (seven species). With the assumption that gynodioecy and other less common reproductive systems are absent in the group, it is possible that all 75 species are dioecious, but more collections are needed to confirm this designation. All unisexual *Miconia* exhibit type I flowers, characterized by aborted vestigial organs in pistillate and staminate flowers that appear to have lost all or partial functionality after initial development. Differences in sex expression between staminate and pistillate flowers lie in the stamens, the style/stigma, the ovaries, and the ovules. These differences are unambiguous and often apparent to the naked eye in both the herbarium and the field (figs. 1, 2). A list of voucher specimens representing staminate and/or pistillate individuals for each species was generated (list A2). Fifty-five types were given a sex determination, and the rest were unavailable for visual examination, destroyed, or not in flower. In all species assessed, we found no compelling evidence of monoecy, gynodioecy, or other less common sexual systems, except in *M. glaberrima* and *M. bracteolata*, in which staminate, pistillate, and hermaphroditic individuals were identified (see below).

Five species had a mix of numerous unisexual and hermaphroditic individuals. For three of these (*M. rubens*, *M. coriacea*, and *M. globuliflora*), unisexual and hermaphroditic specimens displayed both disparate vegetative morphology and geographic distribution. For example, *M. globuliflora* contained hermaphroditic specimens in Central America, but specimens from the Caribbean were strictly staminate and pistillate. A closer look at the specimens from both regions revealed differences between their indument, nodal setae, and leaf margins. Similar discrepancies in vegetative characters and distribution between unisexual and hermaphroditic specimens were also found in *M. coriacea* and *M. rubens*. In *M. glaberrima*, staminate and pistillate specimens were found throughout southern Mexico, Honduras, and Guatemala, while hermaphroditic specimens were exclusive to Costa Rica. There were no consistent vegetative differences between specimens from any location. Differences between specimens from the two regions lie in the floral morphology, with the stigma in pistillate flowers of *M. glaberrima* being considerably more peltate than that in bisexual flowers of those specimens from Costa Rica. The type of *M. glaberrima* is pistillate. In *M. bracteolata*, there were no consistent vegetative differences between staminate, pistillate, and hermaphroditic specimens, with

Table 1

Distribution and Staminate Flower Morphology of Unisexual *Miconia*

Species	Distribution	Elevational range (m)	Staminate flower morphology
M. alpestris	Central America	2286–2804	Ia
M. amilcariana	Andes	1210–2600	Ia
M. aprica	Andes	1020–3405	Ic
M. atrofusca	Andes	1829–3379	Ia
M. biformis	Andes	1500–2400	Ia
M. boliviensis	Andes	1800–3250	Ic
M. brachyanthera	Andes	1166–2813	Ic
M. brachygyna	Andes	1000–3275	Ib
M. bracteolata	Andes	1456–3775	Ia
M. brevistylis	Andes	3160–3621	N/A
M. brittonii	Andes	1219–2780	Ic
M. burkeae	Andes	1500–2800	Ib
M. caerulea	Andes	1100–3362	Ia
M. cardenasiae	Andes	2088–2850	Ic
M. choriophylla	Andes	1200–2240	Ib
M. clathrantha	Andes	763–3200	Ib
M. coelestis	Andes	1524–3479	Ic
M. comosa	Andes	N/A	N/A
M. coriacea	Caribbean	900–1490	Ia
M. crassistigma	Andes	2250–3050	Ic
M. cyanocarpa	Andes	230–3200	Ia
M. dasyclada	Andes	1250–2500	Ib
M. demissifolia	Andes	2025–3479	N/A
M. densifolia	Andes	2000–2025	N/A
M. desportesii	Caribbean	1600–2150	N/A
M. dielsii	Andes	400–2400	Ib
M. dimorphotheca	Andes	2000–3576	Ic
M. dioica	Venezuelan tepuis	1760–2375	N/A
M. divergens	Andes	1281–2300	N/A
M. dumetosa	Andes	1975–2972	Ic
M. elongata	Andes	825–3362	Ib
M. farfanii	Andes	2850–3300	Ib
M. galactantha	Andes	1550–3650	Ib
M. glaberrima	Central America	2–3650	Ia
M. globuliflora	Caribbean	450–1395	Ia
M. glomerulifera	Andes	2350–2662	Ia
M. hemenostigma	Central America	290–3250	Ib
M. herzogii	Andes	2000–2800	N/A
M. hygrophila	Andes	1000–3476	Ic
M. lehmannii	Andes	450–3978	Ib
M. lilacina	Andes	1567–2590	N/A
M. lugubris	Andes	1900–2972	Ib
M. malatestae	Andes	2450–2600	Ib
M. mazatecana	Central America	1450–1760	Ic
M. micrantha	Andes	580–2698	Ib
M. micropetala	Andes	1550–3300	Ib
M. mimica	Andes	N/A	Ib
M. minuta	Andes	180–2525	Ib
M. molinopampana	Andes	2425–2875	Ic
M. myrtiformis	Andes	2200–2900	Ic
M. neblinensis	Brazilian tepuis	2650–2667	N/A
M. neei	Andes	2000–4032	Ib
M. oligotricha	Central America	480–3200	Ib
M. paradisica	Andes	2000–3028	N/A
M. paucartambensis	Andes	N/A	Ia
M. peruviana	Andes	N/A	N/A
M. polychaeta	Andes	1730–2720	Ib
M. polygama	Andes	2100–3400	Ia
M. portogallensis	Central America	2100–2830	Ia
M. pulverulenta	Andes	1600–3962	N/A

Table 1 (*Continued*)

Species	Distribution	Elevational range (m)	Staminate flower morphology
M. purulensis	Central America	1000–2727	Ib
M. reburrosa	Andes	1850–2600	Ib
M. rubens	Caribbean	850–2440	Ia
M. rufiramea	Andes	2663–3000	Ic
M. rugifolia	Andes	1730–3265	Ib
M. rzedowskii	Central America	1950–2740	Ib
M. saxatilis	Andes	N/A	Ib
M. sterilis	Central America	1950–3000	Ia
M. tabayensis	Andes	600–2625	Ia
M. thaminantha	Andes	1080–3014	Ib
M. trichogona	Andes	1829–3265	Ib
M. valida	Andes	2050–3350	N/A
M. vargasii	Andes	3400–3500	Ic
M. vitiflora	Andes	N/A	N/A
M. weberbaueri	Andes	1565–2423	Ib

Note. N/A = not available.

all three found widespread throughout the Andes of Colombia, Ecuador, and northern Peru. The stigma in pistillate flowers is significantly more peltate than the capitate stigmas of bisexual flowers.

Staminate Flower Morphology

Floral morphology in staminate flowers varies considerably across species but is consistent within species. Gynoecium development is arrested in various stages of floral development, ranging from a near-complete absence of style, stigma, ovaries, and ovules to having only a reduced style/stigma with the retention of ovules (table A1; tables A1, A2 are available online). Species were grouped based on the stage of arrested development in the gynoecium of staminate plants (types Ia, Ib, and Ic; fig. 1). Species with type Ia staminate flowers were characterized by a near absence of style, stigma, ovaries, and ovules (17 species; fig. 1*A*–1*C*). Varying degrees of remnants of vestigial ovary tissues (0.1–1 mm) and minute style primordia (<0.1–0.35 mm) were found in these specimens. Species with type Ib flowers displayed gynoecium development arrested after initial growth of the style and sometimes the ovules. These flowers have short styles (0.5–1 mm), punctiform stigmas, and ovaries that contain either no ovules or significantly underdeveloped ovules (28 species; fig. 1*D*–1*F*). The punctiform stigmas of these species were in stark contrast to the longer (2–4 mm), peltate to strongly capitate stigma of pistillate flowers. Underdeveloped ovules were fewer in number and/or smaller in size than their pistillate counterparts. Species with type Ic flowers were characterized by a similarly reduced style (1–2 mm) and stigma but with well-developed ovules similar in size to their pistillate counterparts (15 species; fig. 1*G*, 1*H*). Although a heterostyly/gynodioecious system could be argued for species with type Ic staminate morphology, we assume that the reduction in stigma and style interrupts normal pollen receptivity and germination, obstructing sexual reproduction.

It is important to note that the floral morphology observed in unisexual *Miconia* does not always fall neatly into a category. For example, some species (e.g., *M. rubens*) have no elongation of the style but miniscule remnants of ovule primordia (placed in type Ia), while others (e.g., *M. dumetosa*, type Ic) show well-developed ovules but in lesser amounts than their pistillate counterparts. No abnormalities were seen in the stamens and anthers of staminate flowers. The anthers of staminate flowers that were examined regularly contained pollen in both unopened buds and flowers at anthesis and were often larger than their pistillate counterparts. Several species showed stability in staminate morphology, but there were others in which only one plant was available for dissection. Whether this stability holds across all species is left to be investigated as more collections are made.

Pistillate Flower Morphology

Floral morphology between pistillate plants of dioecious species is consistent, with androecium development halted at the production of pollen. Pistillate flowers are characterized by a well-developed gynoecium accompanied with sterile stamens that are often, but not always, shorter than their staminate counterparts (fig. 1; table A1). Anthers are usually collapsed, and in all dissected flower samples, no pollen was seen in unopened buds or flowers at anthesis. The only exception is in *M. mazatecana* of *Miconia* section *Amblyarrhena*, in which the species description indicates individuals with staminate flowers with short styles and developed ovules and individuals with pistillate flowers with morphologically bisexual flowers containing sterile pollen (de Santiago Gómez 2010). Unfortunately, flowers of this species were not available for dissection to independently confirm this. No abnormalities were seen in the gynoecium of all pistillate flowers assessed. Styles were elongated with stigmas that were peltate to strongly capitate, and pistillate specimens were often observed with fruiting branches, indicating a functioning gynoecium.

Distribution and Elevational Range

Altogether, dioecious species inhabit a wide distribution between southern Mexico and northern South America, including the Caribbean (fig. 3). The tropical Andes are the most rich in dioecious species, with the cordilleras of Bolivia, Peru,

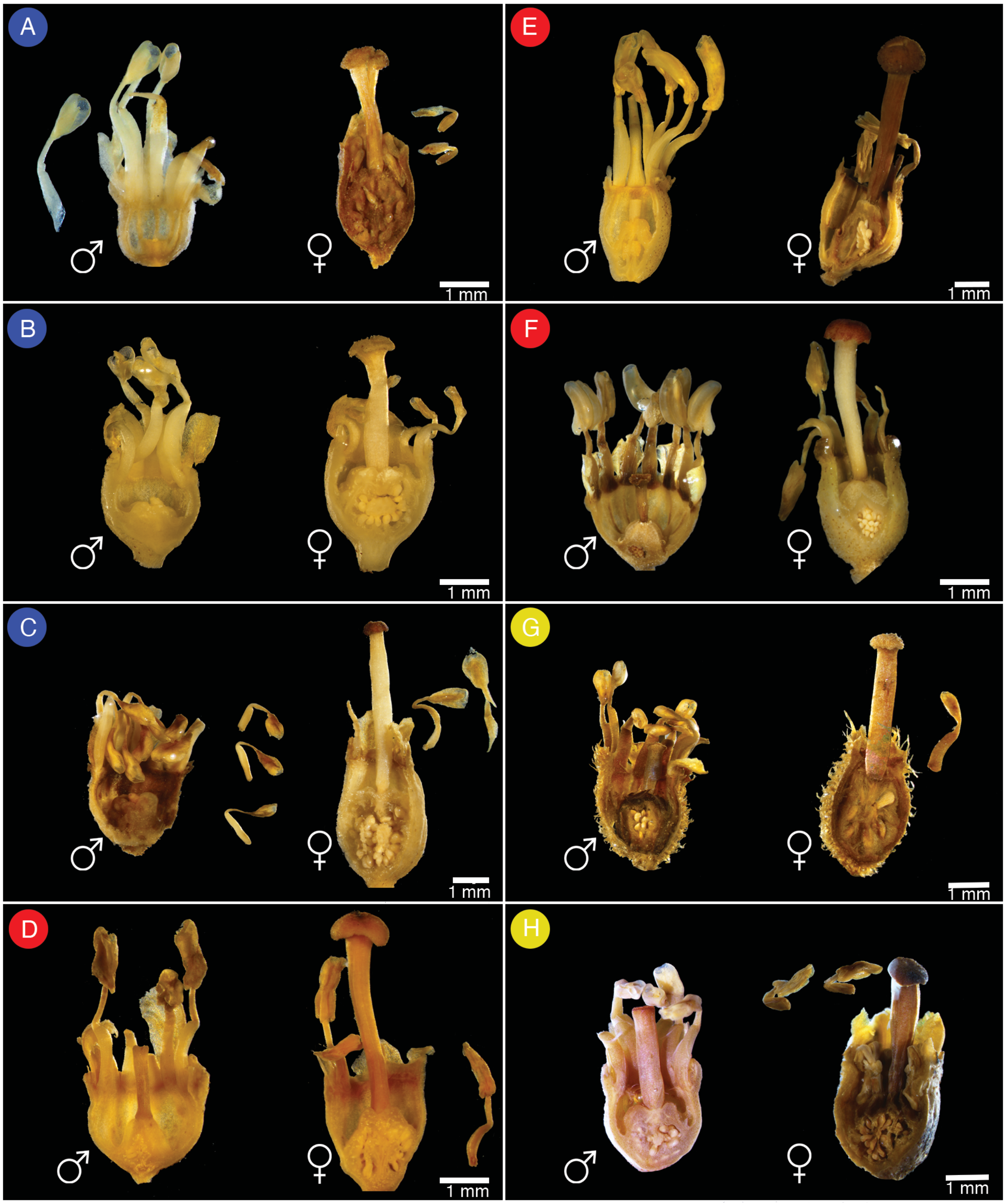

Fig. 1 Longitudinal sections of staminate (*left*) and pistillate (*right*) flowers from species containing staminate type Ia (blue; *A–C*), type Ib (red; *D–F*), and type Ic (yellow; *G*, *H*) flowers. *A*, *Miconia caerulea*. *B*, *Miconia rubens*. *C*, *Miconia polygama*. *D*, *Miconia trichogona*. *E*, *Miconia oligotricha*. *F*, *Miconia neei*. *G*, *Miconia brachyanthera*. *H*, *Miconia coelestis*.

Ecuador, Venezuela, and Colombia being home to 49 endemic dioecious species, with an additional 11 species in which only staminate or pistillate specimens were found. Eight dioecious species are known from southern Mexico to Nicaragua. In *M. purulensis* of Mexico, Guatemala, and Honduras, only staminate specimens were found. In the Caribbean, there are three dioecious species spread across the islands of the Greater and Lesser Antilles. Regardless of geographic location, dioecious

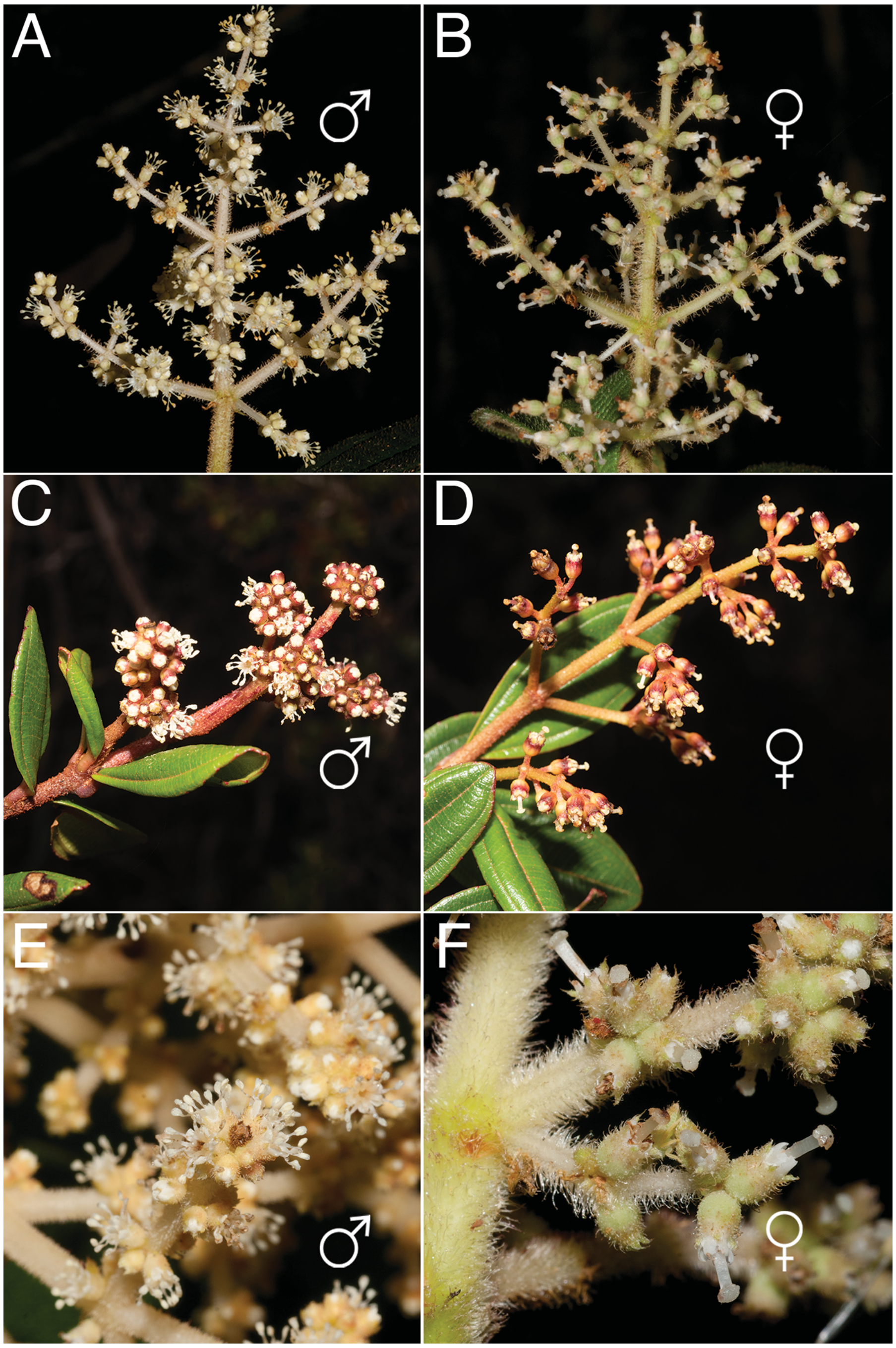

Fig. 2 Field photographs of staminate (*left*) and pistillate (*right*) individuals of dioecious *Miconia*. *A*, *B*, *Miconia caerulea*. *C*, *D*, *Miconia dumetosa*. *E*, *F*, *Miconia brachyanthera*. Photographs courtesy of F. A. Michelangeli.

Miconia are mostly found in humid montane forests between 1000 and 3500 m (table 1), with some species reaching high-elevation subalpine and alpine habitats (3500–4000 m). Fourteen species do make it into lowland mountain slopes below 1000 m, but none are endemic to these lower elevations. Dioecious species are absent from lowland Amazonia and, most notably, the humid montane forests of eastern Brazil (Mata Atlântica).

Discussion

Our results demonstrate that the occurrence of dioecy in Melastomataceae is much higher than previously recorded, with 60 confirmed dioecious species and 15 putatively dioecious species in *Miconia* section *Cremanium* and one dioecious species in *Miconia* section *Amblyarrhena*. This is an almost twofold increase from the last reported count of 37 species (Almeda and

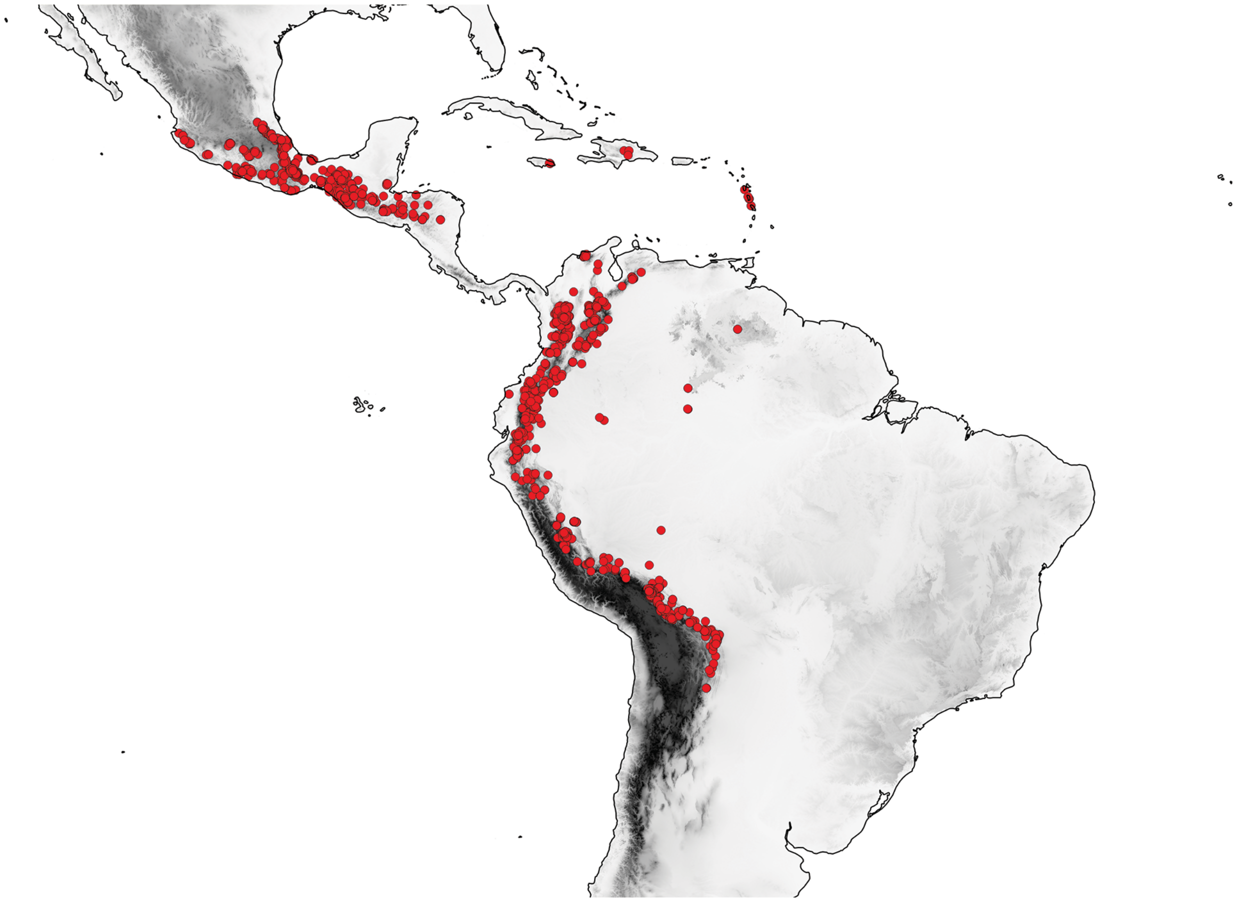

Fig. 3 Distribution of dioecious *Miconia* identified within this study. Each point corresponds to a collected specimen ($N = 4802$).

Dorr 2006) and represents 30% of all species within *Miconia* section *Cremanium* and 14% of species within the larger *Miconia* III clade (mainly, *Miconia* sections *Cremanium*, *Amblyarrhena*, and *Chaenopleura*). From the Almeda and Dorr (2006) list, we confirm dioecious systems in all species except *M. stenophylla* of section *Chaenopleura*. In the two specimens we examined for this species, we observed bisexual flowers with well-formed gynoecium and androecium in both.

The high frequency of dioecious species in a diverse clade points toward the success of dioecy in *Miconia*, but greater sampling and increased phylogenetic resolution are needed before the effects of dioecy on speciation and extinction can be understood. In Melastomataceae, similar reproductive systems with unisexuality, such as androdioecy and gynodioecy, have been documented or suspected (Bremer 1982; Burke and Michelangeli 2013; Mancera 2017; Stone 2017), but *Miconia* section *Cremanium* remains the only group in which dioecy has been found, apart from the two dioecious species in *Miconia* sections *Amblyarrhena* and *Miconia*. The latter species, *M. malatestae*, was erroneously placed in *Miconia* section *Miconia*, and its morphology coincides better with that of *Miconia* section *Cremanium* (Wurdack 1971).

In the five species in which hermaphroditic specimens were identified alongside unisexual specimens, we conclude that the hermaphroditic specimens for *M. rubens*, *M. coriacea*, and *M. globuliflora* are misidentified or possibly undescribed taxa because of the discrepancy in distribution and vegetative characters between hermaphroditic and unisexual specimens. Previous comparisons between specimens of *M. globuliflora* reached similar conclusions (Almeda 2009; F. Almeda, personal communication). In *M. glaberrima* and *M. bracteolata*, staminate, pistillate, and hermaphroditic individuals had no clear vegetative differences between them. If the geographically separate unisexual and hermaphroditic specimens of *M. glaberrima* were indeed a single species, that would imply a trioecious reproductive system, which is extremely rare in angiosperms. The sympatric specimens of *M. bracteolata* present a more compelling case of trioecy or perhaps “leaky” dioecy, in which dioecious populations have occasional bisexual individuals (Baker and Cox 1984), but hand-controlled pollination experiments testing compatibility are needed to confirm this.

The hermaphroditic majority of species in *Miconia* suggests that the ancestral flower for the group was bisexual and that unisexuality and dioecy are derived conditions. This is corroborated by the occurrence of type I unisexuality seen across all dioecious *Miconia*. Type I organ abortion can occur at various stages in floral development, from early in the formation of androecium or gynoecium primordia to postmeiosis loss of function in already-formed pollen or ovules (Ainsworth 2000; Diggle and Mitchell 2011), resulting in flowers retaining remnants of organs of the opposite sex. The only deviation to the consistent pistillate flower morphology in unisexual *Miconia* is in *M. mazatecana* of section *Amblyarrhena*, in which inaperturate pollen has been recorded in morphologically bisexual specimens (de Santiago Gómez 2010). Melastomataceae pollen is characteristically heterocolpate (Patel et al. 1984), leading the authors to conclude that the inaperturate pollen observed is sterile and that this species is cryptically dioecious. In contrast, the degree of development of gynoecium in staminate plants encompasses a wide morphological gradient ranging from near-complete abortion of the style and stigma (type Ia) to arrested development of the style and stigma after ovule development (type Ic; fig. 1). Separate analyses involving visualization of pollen germination and pollen tube growth have provided initial evidence that the stigma and style of type Ic flowers are nonfunctional, indicated by the absence of pollen germination observed in field-collected flowers of these species at different stages of anthesis (J. C. Angulo, A. S. Dellinger, and F. A. Michelangeli, unpublished data). Considering the gradient of morphology observed, it is possible that there is cryptic unisexuality in seemingly bisexual species of *Miconia*, in which the gynoecium or the androecium does not morphologically display loss of function but is nonetheless sterile by other means (i.e., nonfunctioning ovules, sterile pollen). Although this cannot be assessed using our methods, it should be considered in future research on reproduction within the group.

Floral ontogeny of Melastomataceae follows a sequential pattern beginning with sepals and followed by petals, carpels, and stamens (Basso-Alves et al. 2022). This implies that in dioecious *Miconia*, organ arrest in staminate plants occurs earlier in flower development than that in pistillate plants. This asynchronous developmental arrest between staminate and pistillate flowers is in contrast to unisexual flower development in most other angiosperms (Diggle et al. 2011), where conspecific staminate and pistillate flowers tend to exhibit organ abortion at the same developmental timing. Differences in the timing of organ abortion between closely related taxa, however, are common, as seen in the differential morphology of staminate plants between species of dioecious *Miconia* section *Cremanium*. The abortion of reproductive organs, leading to unisexuality, is achieved through several mechanisms, such as cell death, and controlled through a variety of genetic pathways that result in different or convergent floral morphologies (Mitchell and Diggle 2005; Henry et al. 2018). In unisexual *Miconia*, developmental interruption of gynoecium must occur either through different genetic pathways leading to our observed staminate morphologies or through the same pathway but at different times in development.

Our results show that dioecious *Miconia* mainly follow similar patterns of endemism and elevation throughout three regions in the Neotropics: the tropical Andes, the Caribbean, and parts of Central America. The distribution is similar to that of hermaphroditic members of *Miconia* sections *Cremanium*, *Amblyarrhena*, and *Chaenopleura*, except that there are several hermaphroditic species found throughout Costa Rica, Panama, and Brazil (Goldenberg et al. 2013) and no dioecious species are recorded in these countries. The two unisexual species that deviate from this distribution, *M. neblinensis* and *M. dioica*, are known from undercollected tepuis that could still harbor undescribed dioecious taxa. The disjunct distribution of dioecism, coupled with such variable floral morphology among species, alludes to multiple evolutionary origins of dioecy in *Miconia*, in contrast to previous suggestions of a single-origin scenario (Almeda and Dorr 2006). Although the most recent phylogenies of *Miconia* (Goldenberg et al. 2008; Gavrutenko et al. 2020) lack adequate sampling and resolution for the majority of these dioecious species, they indicate independent evolution of dioecy in the Andes and Central America, with dioecious species endemic to each region being interspersed throughout the phylogenies and nested within different and otherwise hermaphroditic clades. The different staminate floral morphologies (types Ia–Ic), however, do not seem to be conserved within specific clades.

Regardless of geographic location, unisexual *Miconia* are mostly found between 1000 and 3500 m. Several species reach elevations lower than 900 m, but none are endemic to lowland habitats. In contrast, the rest of the genus is found from sea level to subalpine habitats and often cooccurring with dioecious species above 1000 m. Elevational gradients have important implications for insect-pollinated dioecious species because of changes in pollinator abundance, activity, and composition with increasing elevation. At higher elevations, pollinators become scarce and are less active (Arroyo et al. 1982, 1983). Since insect-pollinated dioecious species are at a greater risk of reduced reproduction in environments with unpredictable pollination, it is expected that the frequency of dioecy would decrease with increasing elevation (Vamosi and Queenborough 2010). Melastomataceae are largely thought of as having a specialized bee-buzz pollination strategy in which bees vibrate pollen out of anthers, and this holds true for the majority of *Miconia* for which pollinators have been observed (Buchmann 1983; Renner 1989; Dellinger et al. 2022). This reliance on hymenopteran pollination would be another obstacle at higher elevations, where dipterans replace them as the dominant pollinators (Arroyo et al. 1982, 1983; Warren 1988). However, recent work has documented a generalist strategy in several species of *Miconia* section *Cremanium* (Kriebel and Zumbado 2014; de Brito et al. 2017; Manrique-Valderrama et al. 2022; J. C. Angulo, personal observation). These species offer nectar rather than pollen as an attractant to a variety of pollinator groups. Additionally, rather than the small apical pores suitable only to releasing pollen at a certain buzzing frequency, the anther pores in *Miconia* section *Cremanium* are larger and more suitable for pollen transfer onto nonbuzzing insects. This specialist to generalist shift in pollination is not unprecedented in *Miconia* (de Brito et al. 2016; Gavrutenko et al. 2020) and may be facilitating the success of dioecious *Miconia* in higher-elevation montane habitats. Unfortunately, formal documentations of pollinator observations, pollen-release mechanisms, and pollen-reward mechanisms are lacking in all dioecious *Miconia*.

Conclusions

This study contributes to the burgeoning understanding of diverse reproductive systems and strategies in *Miconia*. Our review of the literature shows that the paucity of research on dioecious *Miconia* has been in part due to a lack of documentation (table A2). The majority of *Miconia* presenting unisexuality were not originally described as dioecious, with only 19 species referred to as dioecious in the protologue. This highlights two issues: (1) the lack of information on basic biology and natural history for the vast majority of tropical species that prevents more detailed evolutionary studies and (2) the utility of biological collections (herbaria, in this case) to study morphological and evolutionary patterns. For example, when *M. cardenasiae* was recently described by two of us (Cardenas et al. 2014), even though we were fully aware of the more prevalent nature of dioecy in *Miconia*, we failed to recognize that this species was indeed dioecious. However, with a much larger number of collections now available, particularly with flowers in anthesis, it is now obvious that there are two different floral morphotypes.

Here, we generated the most comprehensive list of dioecious species in *Miconia* and highlighted the outstanding variation in floral morphology between dioecious species. Although our determinations could be reassessed in the future with increased field observations and sampling efforts, we believe that these designations serve as initial hypotheses based on available evidence. We hope that this study promotes future research on these plants, as dioecious *Miconia* represent a worthwhile system to test various hypotheses concerning the evolution of dioecy using phylogenetic and field-based approaches.

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