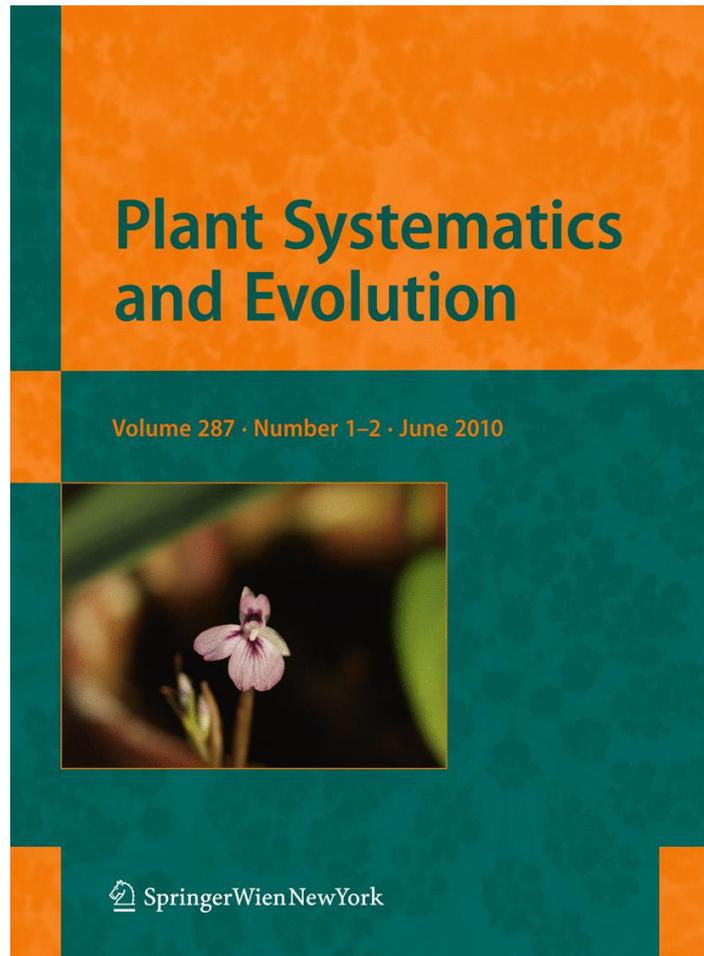


**ISSN 0378-2697, Volume 287, Combined 1-2**



**This article was published in the above mentioned Springer issue.  
The material, including all portions thereof, is protected by copyright;  
all rights are held exclusively by Springer Science + Business Media.  
The material is for personal use only;  
commercial use is not permitted.  
Unauthorized reproduction, transfer and/or use  
may be a violation of criminal as well as civil law.**

## *Planchonella*, first record of gynomonocy for the family Sapotaceae

Marcos Méndez · Jérôme Munzinger

Received: 21 October 2009 / Accepted: 29 March 2010 / Published online: 28 April 2010  
© Springer-Verlag 2010

**Abstract** Documenting nonhermaphroditic sexual systems, a task of major interest for evolutionary biology, is particularly problematic in rare or remote species, for which field sampling is difficult or field specimens or herbarium material is scarce. In addition to hermaphroditism, monoecy and dioecy have been reported in the family Sapotaceae. Nevertheless, the sexual system of some New Caledonian taxa currently included in the genus *Planchonella* remains vaguely characterized as having “bisexual and female flowers.” In the present study we investigate the significance of female flowers in *Planchonella endlicheri*, *P. laetevirens*, and *P. latihila*. We confirmed that *P. endlicheri* and *P. laetevirens* are gynomonocious in nature, and that *P. latihila* is gynomonocious at least when growing in a greenhouse. In addition, we found sexual dimorphism in floral size in *P. endlicheri*, namely a lower corolla length in female compared to bisexual flowers. Two kinds of position effects on floral sex were present in *P. endlicheri*. At the twig level, upper flowers had an increased probability of being female and at the inflorescence (fascicle) level, central flowers were predominantly female while lateral flowers were mainly bisexual. Our study illustrates how observational studies on rare or

remote species can improve our knowledge of sexual systems in plants and document relevant evolutionary patterns in sexual dimorphism and position effects of floral sex.

**Keywords** Flower size · Gynomonocy · *Planchonella* · Position effect · Sexual dimorphism · Sexual system

### Introduction

Many angiosperms are hermaphroditic, i.e., they bear exclusively bisexual flowers (Yampolsky and Yampolsky 1922). Nevertheless, sexual systems in which unisexual flowers are produced are widespread in angiosperms. For example, dioecy, i.e., separate male and female individuals, is present in about 175 families (Givnish 1982; Charlesworth 1985; Renner and Ricklefs 1995; M. Méndez unpubl. data) and monoecy, i.e., separate male and female flowers on the same individual, occurs in more than 130 families (Bertin 1993; Renner and Ricklefs 1995). Other sexual systems combine the presence of unisexual and bisexual flowers in different ways (Sakai and Weller 1999): male and bisexual flowers on the same individual (andromonoecy), female and bisexual flowers on the same individual (gynomonocy), male and bisexual flowers on different individuals (androdioecy), female and bisexual flowers on different individuals (gynodioecy). Of these, gynodioecy is the most widespread, being present in over 500 species in 50 families (Dem'yanova 1985). A major interest of evolutionary biology is to document the abundance of nonhermaphroditic sexual systems (Yampolsky and Yampolsky 1922; Renner and Ricklefs 1995) and to disentangle the causes of their evolution and maintenance (Charnov 1982).

An exhaustive documentation of nonhermaphroditic sexual systems is still pending for several reasons.

M. Méndez (✉)  
Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, C/Tulipán s/n., 28933 Móstoles, Madrid, Spain  
e-mail: marcos.mendez@urjc.es

J. Munzinger  
Laboratoire de Botanique et d'Écologie Végétale Appliquées,  
Herbarium NOU, IRD, UMR AMAP, New Caledonia 98848,  
France

J. Munzinger  
IRD, UMR AMAP, Montpellier 34000, France

Sometimes, misuse of the terminology in the floras leads to confusion (Parfitt 1985). But, above all, assessment of the sexual system has proven difficult for several species. For example, extreme dichogamy at the floral, branch, or plant levels has led to erroneous conclusions that a species was not hermaphroditic (Thompson and Gornall 1995) or to considering as dioecious species that are monoecious (Condon and Gilbert 1988). Detection of cryptic dioecy, in which individuals are morphologically hermaphroditic but functionally unisexual (Mayer and Charlesworth 1991), can also be difficult without detailed morphological and reproductive observations (Sawyer and Anderson 2000; Utteridge and Saunders 2001). Between-year variation in sexual expression, sometimes involving change from pure male/female to cosexuality, has also been a source of confusion (Poppendieck 1987; Manicacci and Després 2001; Ueno and Kadono 2001). Finally, sexual expression in some species defies inclusion in any of the existing typologies (El-Keblawy et al. 1995). All these problems are accentuated in rare or remote species, for which field sampling is difficult or field specimens or herbarium material is scarce.

The family Sapotaceae is said to have bisexual or unisexual flowers (Pennington 2004). Aubréville cited “polygamy” in several genera (Aubréville 1961a, b, 1963), and pointed out that female flowers are frequent at the generic level in America, but rare in Africa (Aubréville 1961a). Bisexual flowers predominate in tribes Mimuso-peae, Isonandreae, and Sideroxyloae, while in Chryso-phyllaeae monoecy and dioecy have been found, and dioecy predominates (Pennington 2004). Nevertheless, the sexual system of some Neotropical species or genera remains uncertain (Pennington 1990, 2004). This is also true for New Caledonian taxa currently included in the genus *Planchonella*. Many species in this genus, as currently circumscribed, have exclusively bisexual flowers (Pennington 2004), but Aubréville (1967) includes dioecy among the diagnostic features for *Pyriluma*, a New Caledonian endemic genus recently put in synonymy within *Planchonella* by Swenson et al. (2007b). Swenson et al. (2007b) suspect *Planchonella sphaerocarpa* Dubard to be dioecious. In addition, these authors consider several subclades in *Planchonella* and indicate “Flowers in species of subclade D2 are usually bisexual or female with reduced stamens, as in many species of *Planchonella*,” without more details. Female flowers have been reported by Aubréville (1967) in the New Caledonian endemic *Planchonella endlicheri* (Montrouz.) Guillaumin, *P. laetevirens* (Baill.) Pierre ex Dubard, *P. saligna* S. Moore, and *P. skottsbergii* Guillaumin. Female flowers have also been reported for *P. latihila* Munzinger & Swenson by Swenson et al. (2007a), and for *P. cauliflora* Munzinger & Swenson by Munzinger and Swenson (2009). Female flowers suggest

the presence of gynomonoeicy, but the short description by Aubréville and others does not allow other possibilities such as gynodioecy or even cryptic dioecy to be discarded, if apparently bisexual flowers are functionally male.

In the present study we investigate the significance of female flowers in *Planchonella endlicheri* [= *Bureavella endlicheri* (Montrouz.) Aubrév.; *Pouteria endlicheri* (Montrouz.) Baehni], *P. laetevirens* [= *Pouteria laetevirens* (Baill.) Baehni], and *P. latihila*. Information is provided about three aspects related to the presence of female flowers in these species. Firstly, we quantify to what extent female flowers are present in the populations and whether they occur together with bisexual flowers on the same individual or not. This allows us to assess whether gynomonoeicy or gynodioecy is present in the studied species. Secondly, we investigate the size of the female flowers compared to the bisexual ones. Sexual dimorphism in floral size has been documented for dioecious and monoecious species (Delph et al. 1996), as well as for some andromonoecious (Spalik and Woodell 1994; O'Brien 1994; Elle and Meagher 2000; Ushimaru et al. 2003a) and gynodioecious species (Baker 1948), but information for gynomonoeicy is very scarce (Bernardello et al. 1999). In addition, quantifying biomass allocation to floral structures can help to assess whether the gynoecium or the androecium is undeveloped (Solomon 1986; Emms 1993; Kaul et al. 2002). Thirdly, we recorded whether female flowers were arranged in specific positions along the twigs or within the inflorescences. Position effects on floral sex have been mainly reported for hermaphroditic species (Diggle 2003). However, some authors have suggested that male flowers are produced in “reproductively disadvantaged positions” of inflorescences in andromonoecious (Primack and Lloyd 1980; Emms 1993) and monoecious species (Heslop-Harrison 1972). Gynomonoeicy has been mostly neglected when studying position effects, although position effects are well known for gynomonoeious Asteraceae (Burt 1977) and are also present in other families (Lamiaceae: Heslop-Harrison 1957; Poaceae: Clayton and Renvoize 1986; Araceae: Grayum 1990). All in all, our work sheds light on the sexual system in *Planchonella* and can guide other botanists dealing with similar problems in remote or rare taxa.

## Materials and methods

### Study species and sampling sites

*Planchonella* was recently re-instated and re-circumscribed (Swenson et al. 2007a, b), and now encompasses several previously described small genera such as *Bureavella*, *Pyriluma*, and *Iteiluma*. *Planchonella* is a genus of trees or

shrubs, of about 100 species, centered in Southeast Asia and ranging to Tahiti and Hawaii. Eleven species were recently described from New Caledonia (Swenson et al. 2007a; Munzinger and Swenson 2009), where 36 species are currently known.

Species of the genus *Planchonella* have flowers with petals fused in a tubular, pentalobulated corolla. Stamens are fixed to the corolla (opposite to each lobe), and in addition to the stamens, five staminodes are present (fixed between lobes). Ovaries consist of five locules, each of them with an ovule. *Planchonella endlicheri* is a tree (10–20 m high) endemic to primary or secondary evergreen rainforests of the southern two-thirds of mainland New Caledonia and Ile des Pins, mostly on ultramafic rocks, but also on volcano-sedimentary substrates (Farino area). Flowering occurs in November–January. Flowers are borne in the axils of the leaves, in fascicles of 1–3 (5), with yellowish corollas of 4–9 mm length (Fig. 1a). *Planchonella laetevirens* is a treelet, which can become a tree more than 10 m high. It is restricted to the south of the main island, in primary or secondary evergreen forests on ultramafic substrate. Flowers are borne in axillary fascicles of 1–2, with white corollas (Fig. 1b). *Planchonella latihila* is a tree (up to 12 m high) endemic to primary or secondary evergreen rainforests on ultramafic substrate. Flowers are borne in the axils of the leaves, in fascicles of 1–6, with pale yellow corollas (Fig. 1c). Flowering of these last two species occurs in January–February.

For *P. endlicheri*, four sites covering a south-to-north transect of the distribution in the mainland New Caledonia were studied. From south to north the sites were (1) Kwé Binyi or ‘Kuebini’ (58K 706642 7537362, 10 m a.s.l.), where eight trees were sampled close to the old road near the river Kuebini, (2) Mont Koghi, where two trees were sampled by the road to Mont Koghi (58K 654751 7546988, 339 m a.s.l.) and five more in the surroundings of the Mont Koghi Hostel (58K 655252 7546648, 455 m a.s.l.), (3) Forêt Nord (58K 697340 7530003, 200 m a.s.l.), where two trees were sampled, and (4) Farino (58K 579761 7605652, 650 m a.s.l.), in the non-ultramafic area where *P. endlicheri* occurs, where 11 trees were sampled along a path.

For *P. laetevirens*, five trees were sampled at Fôret Cachée (58K 684734 7544497, 240 m a.s.l.).

Only two individuals are known from *P. latihila*, one in high Kwé west valley (58K 698452 7531559, 270 m a.s.l.), which was the only individual known for the description of the taxon (Swenson et al. 2007a) and one recently found at Grand Kaori Botanical Reserve (58K 695432 7533825, 210 m a.s.l.). Cuttings from the individual at Kwé west valley have been grown in the greenhouse at the Station de Recherches Maraîchères et Horticoles of the Neo-Caledonian Agronomic Institute (SRMH-IAC). Location of all sites is given as UTM coordinates.



**Fig. 1** Flowers of **a** *Planchonella endlicheri*, **b** *P. laetevirens*, and **c** *P. latihila*

#### Variables measured

The sexual system of *P. endlicheri* was studied in two ways. First, fallen corollas were collected under the trees in the four populations studied. Sex of the flower can be unambiguously inferred from the corolla because stamens are fused to the corolla. At Kuebini, corollas were sampled on 5 and 20 December 2007. At Mont Koghi, trees 1–3 were sampled on 8 and 28 December 2007 and trees 4–7 on 14 and 30 December 2007. At Forêt Nord, corollas were sampled on 20 January 2009. At Farino corollas were

sampled for five trees on 16 December 2007 and for two additional trees on 11 December 2008. Presence and number of stamens were recorded for all the corollas harvested. Overall, we scored 2,437 corollas (Table 1).

Second, one or two branches, bearing 2–21 twigs with flowers, were cut in the eight trees from Kuebini on 5 December 2007 and all the floral structures were examined in the lab. Seven to 21 twigs were examined per tree. Floral buds were dissected under a binocular microscope and scored for sex. The following stages were distinguished in the floral structures: scar of a fallen flower, female flower, bisexual flower, young fruit, and not scorable (mostly due to floral predation). Anthers were clearly visible even in small buds, thus allowing the scoring of all closed buds. Sex of young fruits could not be assessed due to the lack of corolla. Number and stage of floral structures per leaf axil were

noted. In addition, we ranked the position of the leaves bearing flowers or their remnants, from the bottom to the top of the twig, and we recorded the relative position of the floral structures in a given leaf axil. For the bisexual flowers, the number of stamens was recorded. A total of 88 twigs and 1,079 flowers and remnants of flowers were studied.

For *P. laetevirens* floral buds were directly collected from the trees on 10 January 2008 because corollas were not available and because the density of buds was too low to provide enough material by cutting branches. A total of 279 floral buds were scored. Fallen corollas and branches were sampled in the single individual of *P. latihila* at Grand Kaori, on 4 January 2008. A total of 6 corollas, 25 twigs and 129 floral structures were studied. In addition, 12 alcohol-preserved corollas from cuttings obtained from the individual at Kwé west valley were also examined.

**Table 1** Percentage ( $n$ ) of female flowers estimated from counts on twigs or fallen corollas in four populations of *Planchonella endlicheri*. Results of the  $G$  test for differences between sampling dates are also given

Plant	% Female flowers ( $n$ )			$G$	$df$	$P$
	Twigs	Fallen corollas (1st sampling date)	Fallen corollas (2nd sampling date)			
Kuebini						
1	42.9 (7)	–	0 (1)			
2	70.8 (48)	33.3 (36)	55.7 (79)	5.027	1	0.025
3	65.2 (118)	57.7 (52)	67.4 (135)	1.528	1	0.216
4	95.6 (69)	–	66.7 (51)			
5	36.3 (91)	44.4 (108) <sup>a</sup>	30.6 (49) <sup>a</sup>	2.892	1	0.089
6	33.6 (107)	–	–			
7	62.0 (71)	35.7 (171)	57.6 (92)	11.707	1	0.0006
8	77.4 (319)	64.7 (68)	73.3 (86)	1.304	1	0.253
Mont Koghi						
1	–	84.4 (45)	75.0 (64)	1.454	1	0.228
2	–	36.6 (112)	43.0 (79)	0.801	1	0.371
3	–	0 (5)	31.5 (54)			
4	–	40.5 (111)	19.7 (117)	12.015	1	0.0005
5	–	16.7 (174)	16.2 (136)	0.054	1	0.816
6	–	59.4 (64)	47.9 (71)	1.790	1	0.181
7	–	83.3 (6)	11.1 (18)			
Forêt Nord						
1	–	48.6 (72)	–			
2	–	30.8 (39)	–			
Farino						
1	–	23.1 (121)	–			
2	–	0 (5)	–			
3	–	39.0 (77)	–			
4	–	12.1 (33)	–			
5	–	26.3 (19)	–			
6	–	10.4 (67)	–			
7	–	25.0 (20)	–			

<sup>a</sup> Data for trees 5 and 6 combined. Due to the proximity of trees 5 and 6, fallen corollas could not be allocated to a specific tree

Length of unpredated fallen corollas was measured with a ruler to the next 0.5 mm (Kuebini) or scanned and length measured with ImageJ, to the nearest 0.1 mm (Mont Koghi, Forêt Nord, Farino). In Kuebini twigs, open or nearly open bisexual and female flowers were divided into corolla (plus stamens) and gynoecium, oven-dried at 50°C to constant mass, and weighed to the nearest 0.1 mg.

### Statistical analysis

Differences in frequencies were tested by means of the  $G$  test (Zar 1999). Differences between average values were tested with ANOVA after checking for normality and homoscedasticity (Levene test). Plant was considered as a random factor while sex was considered as a fixed factor. Correlations were tested by means of the Spearman correlation coefficient.

## Results

### Sexual system and floral sex ratios in *P. endlicheri*

Sampling of corollas under the trees showed the presence of both bisexual and female flowers in all trees but two (Table 1), in which the number of corollas fallen was very low. Dissection of floral buds taken from twigs confirmed the presence of female and bisexual flowers, including tree 1 at Kuebini (Table 1). Of 88 twigs examined, 14 (15.9%) bore only female flowers at the moment of scoring.

Based on fallen corollas, percentage of female flowers ranged from 10 to 84% (Table 1). Percentage of female flowers increased significantly on the second sampling date in two trees and decreased in one (Table 1). Based on dissection of floral buds collected from twigs, percentage of female flowers ranged from 33 to 96% (Table 1). No significant correlation was found between the percentage of female flowers estimated in different ways, but sample size ( $n = 5$  or  $6$ ) was too small to reach significance.

In addition to the presence of female flowers, deviation from the usual number of stamens (5) was also observed. Corollas with 1–7 stamens were present in all trees for which more than 10 bisexual corollas were harvested. The percentage of flowers deviating in stamen number from 5 ranged 8.7 to 25.8 (fallen corollas, both sampling dates combined) or 7.3–21.4 (twigs) at Kuebini, 6.5–18.8 (both sampling dates combined) at Mont Koghi, 18.5–18.9 at Forêt Nord, and 2.5–27.3 at Farino. Overall, around 10–19% of the corollas harvested had a number of stamens different from five (Table 2). In those corollas with fewer than five stamens, usually a staminode was present instead of a stamen; in a few cases, no trace of stamen was present.

### Position effects on floral sex in *P. endlicheri*

Twigs of *P. endlicheri* bore from 1 to 14 fascicles, with 5–8 being the most frequent number. Almost 57% of those fascicles bore two flowers, 31% bore one flower, and 11% bore three flowers. In less than 1% of the fascicles, four or five flowers were present. The percentage of fascicles with two flowers increased from bottom to the top of the twigs until fascicle 9 (Fig. 2). The percentage of fascicles with one flower was highest in the lower- and uppermost positions along the twig (Fig. 2). The percentage of fascicles with three or more flowers was highest in the lower part of the twigs and decreased to zero in the upper part of the twigs (Fig. 2).

A strong position effect in floral sex was found along the twigs (Fig. 3). From the bottom to the top of a twig, the percentage of bisexual flowers and developing fruits decreased ( $R_s = -1.000$  and  $-0.942$ , respectively;  $P < 0.0001$ ), while the percentage of female flowers increased ( $R_s = 1.000$ ;  $P < 0.0001$ ). A similar trend was found for each separate tree (results not shown), as well as for a separate analysis of fascicles with one, two, or more than two flowers (results not shown).

Within a fascicle, a strong position effect was found for pairs and triplets of flowers. In the case of pairs of flowers, careful observation of the floral peduncles allowed for embracing and embraced flowers to be distinguished. In 48 pairs in which one of the flowers was bisexual and the other one female, the female flower was embraced by the bisexual one in 100% of the cases. No case of embraced bisexual flower and embracing female flower was found. In 14 triplets of flowers in which bisexual and female flowers were present, the female flower was central in 12 cases, and in the other two, the central and one lateral flower were female and the remaining flower was bisexual. No case with central bisexual and lateral female flowers was found.

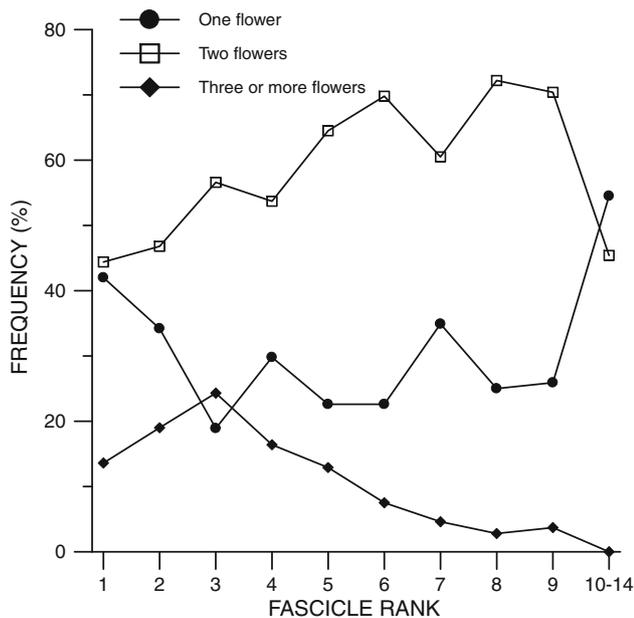
### Corolla size in *P. endlicheri*

The size of the fallen corollas ranged from 4 to 8 mm (Fig. 4). At the four populations, corollas of female flowers were significantly shorter than those of bisexual flowers ( $F_{1,4} = 421.347$ ,  $P < 0.0001$ ;  $F_{1,4} = 565.503$ ,  $P < 0.0001$ ;  $F_{1,1} = 165.527$ ,  $P = 0.049$ ;  $F_{1,4} = 116.785$ ,  $P = 0.0004$  for Kuebini, Mont Koghi, Forêt Nord, and Farino, respectively; Fig. 4). However, except in Forêt Nord ( $P = 0.068$ ) corolla length significantly differed among plants in a given population ( $F_{4,425} = 62.853$ ,  $P < 0.0001$ ;  $F_{4,529} = 18.538$ ,  $P < 0.0001$ ;  $F_{4,165} = 11.283$ ,  $P < 0.0001$  for Kuebini, Mont Koghi, and Farino, respectively, Fig. 4), so that female flowers in a given tree could be as large as bisexual flowers on another tree (e.g., Kuebini vs. Farino; Fig. 4). At Mont Koghi, the size of the flowers significantly

**Table 2** Percentage of flowers with different number of stamens in three populations of *P. endlicheri*

No. of stamens	Kuebini		Mont Koghi	Forêt Nord	Farino
	Fallen corollas ( <i>n</i> = 420)	Twigs ( <i>n</i> = 290)	Fallen corollas ( <i>n</i> = 638)	Fallen corollas ( <i>n</i> = 111)	Fallen corollas ( <i>n</i> = 241)
1	1.43	2.41	1.25	1.56	2.49
2	1.43	3.10	0.78	0.00	1.25
3	3.33	1.38	0.94	10.94	1.24
4	6.19	3.45	2.51	6.25	4.15
5	84.76	87.24	89.81	81.25	89.22
6	2.62	2.41	4.54	0.00	1.66
7	0.24	0.00	0.16	0.00	0.00

For fallen corollas at Kuebini and Mont Koghi, both sampling dates have been pooled

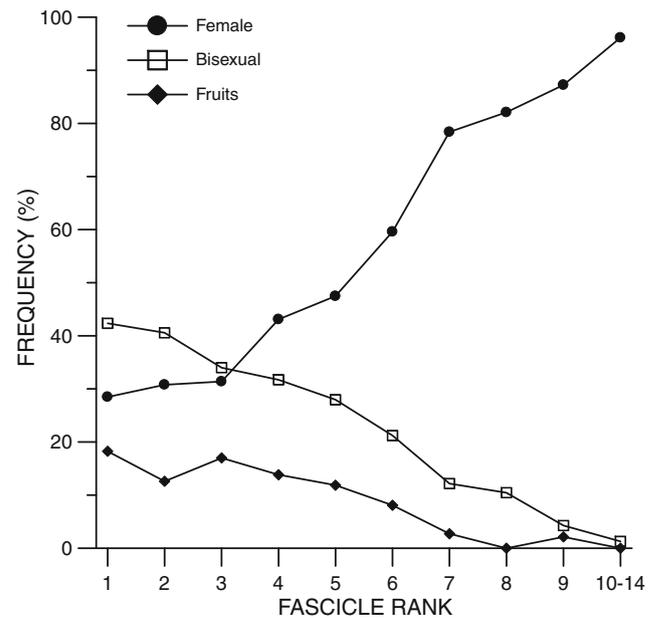
**Fig. 2** Percentage of fascicles with one, two, or three or more flowers along flowering twigs of *P. endlicheri*. Fascicles are numbered from the base to the top of the twigs

increased from the first to the second sampling date ( $F_{1,4} = 32.928$ ,  $P = 0.005$ ), but in a tree-specific way, as indicated by a significant interaction between tree and sampling date ( $F_{4,529} = 8.627$ ,  $P < 0.0001$ ).

At Kuebini, corolla dry mass of bisexual flowers was higher than corolla mass of female flowers (Table 3). In addition, the gynoecium dry mass of bisexual flowers was higher than the gynoecium mass of female flowers (Table 3).

#### Sexual system of *P. laetevirens* and *P. latihila*

Floral buds of *P. laetevirens* had a very high rate of predation by insects and infection by an unknown pathogen. This substantially reduced our effective sample size, but female and bisexual flowers were found in three individuals

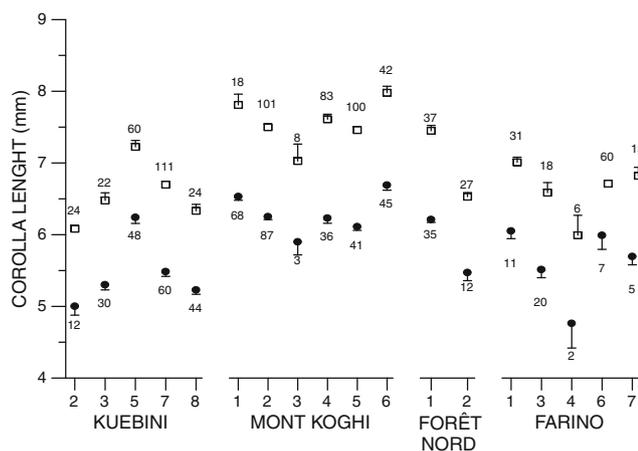
**Fig. 3** Variation in the percentage of female flowers, bisexual flowers, and developing fruits along the twigs. Fascicles are numbered from the base to the top of the twigs. Values at each fascicle do not add to 100% due to the presence of scars and nonscorable buds, which have not been included in the plot

of *P. laetevirens* for which more than 10 floral buds could be scored. Female flowers represented 30–80% of the flowers scored. In the other two individuals, female flowers (3–6), but not bisexual ones, were found.

In *P. latihila* at Grand Kaori, we only found bisexual flowers, aside from one female fallen corolla. Alcohol-preserved corollas from cuttings derived from the individual at high Kwé west valley revealed four female flowers and eight bisexual flowers.

#### Discussion

The present paper reports for the first time the presence of gynomonoeocism in Sapotaceae, where only hermaphroditism,



**Fig. 4** Average corolla length of female (black dots) and bisexual (open squares) flowers in four populations of *P. endlicheri*. Figures on the x axis indicate the code number of each tree. Bars indicate SE; bars smaller than the symbols are not indicated. Numbers close to the symbols indicate sample size

**Table 3** Average  $\pm$  SD (*n*) dry mass of corollas and gynoeceum in female and bisexual flowers of *P. endlicheri* from Kuebini

	Female	Bisexual	<i>F</i>	<i>df</i>	<i>P</i>
Corolla	6.3 $\pm$ 0.98 (14)	10.5 $\pm$ 1.26 (11)	86.157	1, 23	0.0001
Gynoeceum	3.2 $\pm$ 0.47 (14)	3.7 $\pm$ 0.52 (11)	7.066	1, 23	0.014

The results of the one-way ANOVA comparing both sexes are also provided

monoecy, and dioecy were known (Pennington 2004). We have confirmed that *P. endlicheri* and *P. laetevirens* are gynomonoeocious in nature, and that *P. latihila* is gynomonoeocious at least when growing in a greenhouse. Gynomonoeocy seems, therefore, also present in this last species although additional observations in the field will be necessary. Both female and bisexual flowers were present on the same individual in the three species, thus refuting the possibility of gynodioecy or cryptic dioecy. The presence of only female flowers in a few plants of *P. laetevirens* can be explained by the small sample size available. Cryptic dioecy is also unlikely because the gynoecea of bisexual flowers were well developed and even heavier than those of female flowers.

Gynomonoeocy is a rare sexual system in angiosperms (Yampolsky and Yampolsky 1922), with the exception of Asteraceae (Burt 1977), and has been considered as an intermediate evolutionary step in the pathway to monoecy (Bawa and Beach 1981). Monoecy and dioecy are present in neotropical *Pouteria* (Pennington 1990), from which *Planchonella* has been recently restored as an independent genus (Swenson et al. 2007b). As far as we know, no monoecy is present in *Planchonella*, and dioecy in *P. sphaerocarpa* and *P. dothioense* requires confirmation. A recent phylogenetic reconstruction of *Planchonella*

(Swenson et al. 2007a) indicates that the three species studied here belong to different subclades and suggests that gynomonoeocy has evolved independently from hermaphroditism within this genus. It is tempting to suggest a connection between gynomonoeocy and island endemism, as has been proposed for the evolution of dioecy (Thomson and Barrett 1981; Sakai et al. 1995). Nevertheless, further assessment of the sexual system within *Planchonella*, both in New Caledonia and other territories, is required before we can properly assess the commonness of gynomonoeocy in this genus and its evolutionary meaning within Sapotaceae.

We found sexual dimorphism in floral size in *P. endlicheri*, namely a shorter corolla in female compared to bisexual flowers. Sexual dimorphism in flower size has been mainly studied in dioecious and monoecious species (Delph et al. 1996). Delph et al. (1996) found that male flowers had larger corollas than female flowers in temperate plants, while in tropical plants cases of larger male corollas were as common as cases of larger female corollas. For gynodioecious plants, bisexual flowers are larger than female flowers (Eckhart 1999). Unisexual flowers are smaller in andromonoecious taxa, compared to bisexual flowers (Huang 2003; Ushimaru et al. 2003b; see, however, Manicacci and Després 2001). Information for gynomonoeocious taxa is very scarce. Baker (1948) made a first compilation for gynodioecious and gynomonoeocious plants, but almost or all species listed in his Table 1 are actually gynodioecious. The scattered literature suggests that female flowers are shorter than bisexual ones (*Lactoris*: Bernardello et al. 1999) or have lower dry mass (*Solidago*: Wise et al. 2008).

Eckhart (1999) reviewed the hypotheses accounting for sexual dimorphism in flower size. Most of these hypotheses deal with dioecy and gynodioecy. The extent to which those hypotheses are relevant for monoecy, andromonoecy, or gynomonoeocy has yet to be tested. In particular, further studies in gynomonoeocious taxa are required to assess whether pollinator attraction is higher in bisexual compared to female flowers, as claimed by the “male-competition” hypothesis, or whether lack of stamens involves a developmental decrease in corolla size, as claimed by the “developmental-correlation” hypothesis.

We found two kinds of position effects on floral sex for *P. endlicheri*, at the twig and at the fascicle level. Broad evidence exists for a decrease in allocation to female sexual structures and/or increase in allocation to male sexual structures along linear inflorescences in hermaphroditic species (reviewed in Diggle 2003; see also Ishii 2004). However, position effects on floral sex in nonhermaphroditic sexual systems have been scarcely studied. The position effects found here depart from the most documented pattern. The position effect at the twig level is puzzling. In *P. endlicheri*, our data on fruits indicate that

flowers open from the bottom to the top of the twigs. In addition, flowers are protandrous because stamens are already open in the bud (M. Méndez, personal observation). For protandrous species, Brunet and Charlesworth (1995) predict that sexual allocation should be biased towards femaleness early in the flowering season and towards maleness later on. This is exactly the opposite of the pattern found. An upper position of female flowers on the twigs could increase outcrossing if pollinators forage from the top to the bottom of the twigs (McKone et al. 1995). Unfortunately, no observations on pollinators could be made to test this hypothesis, due to the inaccessibility of the canopy in *P. endlicheri*.

Position effect on floral sex at the fascicle level seems easier to explain. We suggest that the pattern found is similar to the “king flower” present in apple trees, where the central flower in a cluster is most likely to set fruit (Black et al. 2000). Presumably, apical dominance makes the terminal flower a stronger sink for resources (Black et al. 2000). In *P. endlicheri*, the embraced flower of a fascicle would also have first access to resources, and this could have influenced its specialization as a female flower. Nevertheless, a proper test of this hypothesis would require documenting the relative probability of setting fruits for female and bisexual flowers.

Summarizing, we have documented for the first time the presence of gynomonoeicy in the family Sapotaceae. In addition, gynomonoeicy in *Planchonella endlicheri* is coupled to a clear sexual dimorphism in corolla length and to two kinds of position effects on floral sex. Our study illustrates how observational studies on rare or remote species can improve our knowledge of sexual systems in plants and document relevant evolutionary patterns in sexual dimorphism and position effects of floral sex.

**Acknowledgments** M.M. thanks Ulf Swenson for first pointing to the presence of female flowers in *Planchonella* and for advice on the study species. We thank Patrick Taton (Koghi Parc Aventure) for access to *P. endlicheri* within their property, Maeva Guyomar for help with the field work, and Laure Barrabé and Gilles Dagostini (IRD-NOU) and Marion Beauvallet (CIRAD) for collecting fallen corollas. Gildas Gateblé (SRMH-IAC) kindly provided us corollas from *P. latihila* cuttings. South Province's Direction de l'Environnement (DENV) provided collecting permits. *Planchonella endlicheri* is studied as a plant model for the ANR ULTRABIO program research.

## References

- Aubréville A (1961a) Notes sur des Poutériées américaines. *Adansonia* 1:150–191
- Aubréville A (1961b) Notes sur les Sapotacées africaines et sud-américaines. *Adansonia* 1:6–38
- Aubréville A (1963) Notes sur des Sapotacées africaines. *Adansonia* 3:227–231
- Aubréville A (1967) Flore de la Nouvelle-Calédonie et dépendances. I. Sapotacées. Muséum National d'Histoire Naturelle, Paris
- Baker HG (1948) Corolla-size in gynodioecious and gynomonoeious species of flowering plants. *Proc Leeds Phil Lit Soc* 5:136–139
- Bawa KS, Beach JH (1981) Evolution of sexual systems in flowering plants. *Ann Missouri Bot Gard* 68:254–274
- Bernardello G, Anderson GJ, López P, Cleland MA, Stuessy TF, Crawford DJ (1999) Reproductive biology of *Lactoris fernandeziana* (Lactoridaceae). *Am J Bot* 86:829–840
- Bertin RI (1993) Incidence of monoecy and dichogamy in relation to self-fertilization in angiosperms. *Am J Bot* 80:557–560
- Black L, Bukovac MJ, Stopar M (2000) Intraspecific fruit competition and position influence fruit size at harvest and response to chemical thinning agents in spur-type ‘Delicious’ apple. *Acta Horti* 527:119–125
- Burt BL (1977) Aspects of diversification in the capitulum. In: Heywood VH, Harborne JB (eds) *The biology and chemistry of the Compositae*, vol I. Academic Press, London, pp 41–59
- Charlesworth D (1985) Distribution of dioecy and self-incompatibility in angiosperms. In: Greenwood PJ, Harvey PH, Slatkin M (eds) *Evolution: essays in honour of John Maynard Smith*. Cambridge University Press, Cambridge, pp 237–268
- Charnov EL (1982) *The theory of sex allocation*. Princeton University Press, Princeton
- Clayton WD, Renvoize SA (1986) *Genera graminum: grasses of the world*. Royal Botanic Gardens, Kew
- Condon MA, Gilbert LE (1988) Sex expression of *Gurania* and *Psiguria* (Cucurbitaceae): Neotropical vines that change sex. *Am J Bot* 75:875–884
- Delph LF, Galloway LF, Stanton ML (1996) Sexual dimorphism in flower size. *Am Nat* 148:299–320
- Dem'yanova AEI (1985) Distribution of gynodioecy in flowering plants. *Bot Zhur* 70:1289–1301
- Diggle PK (2003) Architectural effects on floral form and function: a review. In: Stuessy T, Hörandl E, Mayer V (eds) *Deep morphology: toward a renaissance of morphology in plant systematics*. Koeltz, Königstein, pp 63–80
- Eckhart VM (1999) Sexual dimorphism in flowers and inflorescences. In: Geber MA, Dawson TE, Delph LF (eds) *Gender and sexual dimorphism in flowering plants*. Springer, Berlin, pp 123–148
- El-Keblawy A, Lovett-Doust J, Lovett-Doust L, Shaltout KH (1995) Labile sex expression and dynamics of gender in *Thymelaea hirsuta*. *Ecoscience* 2:55–66
- Elle E, Meagher TR (2000) Sex allocation and reproductive success in the andromonoecious perennial *Solanum carolinense* (Solanaceae). II. Paternity and functional gender. *Am Nat* 156:622–636
- Emms SK (1993) Andromonoecy in *Zigadenus paniculatus* (Liliaceae): spatial and temporal patterns of sex allocation. *Am J Bot* 80:914–923
- Givnish TJ (1982) Outcrossing versus ecological constraints in the evolution of dioecy. *Am Nat* 119:849–865
- Grayum MH (1990) Evolution and phylogeny of the Araceae. *Ann Missouri Bot Gard* 77:628–697
- Heslop-Harrison J (1957) The experimental modification of sex expression in flowering plants. *Biol Rev* 32:38–90
- Heslop-Harrison J (1972) Sexuality of angiosperms. In: Steward FC (ed) *Plant physiology: a treatise*. Vol. VI C: physiology of development: from seeds to sexuality. Academic Press, New York, pp 133–289
- Huang S-Q (2003) Flower dimorphism and the maintenance of andromonoecy in *Sagittaria guyanensis* ssp. *lappula* (Alismataceae). *New Phytol* 157:357–364
- Ishii HS (2004) Increase of male reproductive components with size in an animal-pollinated hermaphrodite, *Nartheicum asiaticum* (Liliaceae). *Funct Ecol* 18:130–137
- Kaul V, Sharma N, Koul AK (2002) Reproductive effort and sex allocation strategy in *Commelina benghalensis* L., a common monsoon weed. *Bot J Linn Soc* 140:403–413

- Manicacci D, Després L (2001) Male and hermaphrodite flowers in the alpine lily *Lloydia serotina*. *Can J Bot* 79:1107–1114
- Mayer SS, Charlesworth D (1991) Cryptic dioecy in flowering plants. *Trends Ecol Evol* 6:320–325
- McKone MJ, Ostertag R, Rauscher JT, Heiser DA, Russell FL (1995) An exception to Darwin's syndrome: floral position, protogyny, and insect visitation in *Besseyia bullii* (Scrophulariaceae). *Oecologia* 101:68–74
- Munzinger J, Swenson U (2009) Three new species of *Planchonella* (Sapotaceae) with a dichotomous and an online key to the genus in New Caledonia. *Adansonia* 31:175–189
- O'Brien SP (1994) Andromonoecy and fruit set in *Leptospermum myrsinoides* and *L. continentale* (Myrtaceae). *Aust J Bot* 42:751–762
- Parfitt BD (1985) Dioecy in North American Cactaceae: a review. *SIDA* 11:200–206
- Pennington TD (1990) Sapotaceae. *Flora Neotrop* 52:1–770
- Pennington TD (2004) Sapotaceae. In: Kubitzki K (ed) *The families and genera of vascular plants*, vol 6. Springer, Berlin, pp 390–421
- Poppendieck H-H (1987) Monoecy and sex changes in *Freycinetia* (Pandanaceae). *Ann Missouri Bot Gard* 74:314–320
- Primack RB, Lloyd DG (1980) Andromonoecy in the New Zealand montane shrub manuka, *Leptospermum scoparium* (Myrtaceae). *Am J Bot* 67:361–368
- Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants. *Am J Bot* 82:596–606
- Sakai AK, Weller SG (1999) Gender and sexual dimorphism in flowering plants: a review of terminology, biogeographic patterns, ecological correlates, and phylogenetic approaches. In: Geber MA, Dawson TE, Delph LF (eds) *Gender and sexual dimorphism in flowering plants*. Springer, Berlin, pp 1–31
- Sakai AK, Wagner WL, Ferguson DM, Herbst DR (1995) Origins of dioecy in the Hawaiian flora. *Ecology* 76:2517–2529
- Sawyer NW, Anderson GJ (2000) Dioecy in South American *Deprea* (Solanaceae). *Biotropica* 32:291–298
- Solomon BP (1986) Sexual allocation and andromonoecy: resource investment in male and hermaphroditic flowers of *Solanum carolinense* (Solanaceae). *Am J Bot* 73:1215–1221
- Spalik K, Woodell SRJ (1994) Regulation of pollen production in *Anthriscus sylvestris*, an andromonoecious species. *Int J Plant Sci* 155:750–754
- Swenson U, Munzinger J, Bartish I (2007a) Molecular phylogeny of *Planchonella* (Sapotaceae) and eight new species from New Caledonia. *Taxon* 56:329–354
- Swenson U, Bartish I, Munzinger J (2007b) Phylogeny, diagnostic characters, and generic limitation of Australasian Chrysophylloideae (Sapotaceae, Ericales): evidence from ITS sequence data and morphology. *Cladistics* 23:201–228
- Thompson PN, Gornall RJ (1995) Breeding systems in *Coriaria* (Coriariaceae). *Bot J Linn Soc* 117:293–304
- Thomson JD, Barrett SCH (1981) Selection for outcrossing, sexual selection, and the evolution of dioecy in plants. *Am Nat* 118:443–449
- Ueno S, Kadono Y (2001) Monoecious plants of *Myriophyllum ussuriense* (Regel) Maxim. in Japan. *J Plant Res* 114:375–376
- Ushimaru A, Itagaki T, Ishii HS (2003a) Floral correlations in an andromonoecious species, *Commelina communis* (Commelinaceae). *Plant Species Biol* 18:103–106
- Ushimaru A, Itagaki T, Ishii HS (2003b) Variation in floral organ size depends on function: a test with *Commelina communis*, an andromonoecious species. *Evol Ecol Res* 5:615–622
- Utteridge TMA, Saunders RMK (2001) Sexual dimorphism and functional dioecy in *Maesa perlaris* and *M. japonica* (Maesaceae/Myrsinaceae). *Biotropica* 33:368–374
- Wise MJ, Coffey LE, Abrahamson WG (2008) Nutrient stress and gall flies interact to affect floral-sex ratio in gynomonoeocious *Solidago altissima*. *Am J Bot* 95:1233–1239
- Yampolsky C, Yampolsky H (1922) Distribution of sex forms in the phanerogamic flora. *Bibl Genet* 3:1–62
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice-Hall, Upper Saddle River