RESEARCH PAPER

Enantiostylous types of Cassiinae species (Fabaceae-Caesalpinioideae)

N. M. Almeida[1], V. M. Cotarelli[2], D. P. Souza[2], R. R. Novo[1], J. A. Siqueira Filho[2,3], P. E. Oliveira[4] & C. C. Castro[5]

1 Programa de Pós-Graduação em Botânica, Universidade Federal Rural de Pernambuco, Recife, Brazil
2 Universidade Federal do Vale do São Francisco, Petrolina, Brazil
3 Centro de Referência Para Recuperação de Áreas Degradadas, Universidade Federal do Vale do São Francisco, Petrolina, Brazil
4 Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Brazil
5 Unidade Acadêmica de Garanhuns, Universidade Federal Rural de Pernambuco, Garanhuns, Brazil

ABSTRACT

Species of the subtribe Cassiinae present a wide diversity of floral types. Until recently it was considered that this diversity did not extend to their reproductive mechanisms. However, studies have recorded some variations in the enantiostylous pattern in this plant group. This study aims to investigate the morphological and functional variations of enantiostyly in species of the subtribe Cassiinae. Additionally, it proposes the recognition of enantiostylous types (ET) based on pollen deposition and capture mode. Morphological data were collected in fresh and fixed (alcohol 70%) buds and flowers, and also using photos and rehydrated material from herbarium sheets, for a total of 59 species. The parameters used to establish the ETs were pollination type, nature of pollen deposition on the pollinator body, deposition type, number of petals involved in pollen deposition, and pollen pathway. Morpho-functional features allowed the recognition of seven enantiostylous types (Flexuosa, Cana, Macranthera, Martiana, Amiciella, Repens and Ramosa) that present several levels of complexity. The type Ramosa was the most common and the Cana type was the least common. The types Repens, Martiana and Flexuosa do not have reciprocal pollen deposition, thus species with these types may be considered atypical. The groups resulting from similarity analysis partially coincide with the clades proposed in phylogenetic studies of Cassiinae. The recognition of functional ETs is important for understanding the evolution of reproductive strategies of Cassiinae species, and indicates an interesting line of investigation of enantiostyly in other plant groups.

INTRODUCTION

Conflict between sexual functions in angiosperm hermaphrodite flowers, such possible self-pollination and autogamy, has select temporal (dichogamous) or spatial (herkogamous) mechanisms to optimise pollen flow and allogamy (Webb & Lloyd 1986; Barrett 2010). Enantiostyly is a form of reciprocal herkogamy in which there are two floral morphs that differ reciprocally in the arrangement of androecium and gynoecium in a left–right axis (Barrett 2002). In some cases, morphological differences in the petals direct pollen deposition on the pollinator body (Almeida *et al.* 2013; de Almeida *et al.* 2013). Enantiostyly favours pollen transfer between reciprocal floral morphs of different individuals – dimorphic enantiostyly (Todd 1882; Knuth 1906; Irwin & Barneby 1976) or within the same individual – monomorphic enantiostyly (Dulberger 1981; Gottsberger & Silberbauer-Gottsberger 1988; Bahadur *et al.* 1990; Fenster 1995; Laporta 2005). Intermorph pollination occurs because there is a coincidence between floral morphs in the area of pollen deposition and capture on the pollinator body.

The Cassiinae subtribe (Fabaceae), which includes the genera *Cassia* L., *Chamaecrista* Moench. and *Senna* Mill., has a high diversity of floral morphologies, such as the occurrence of anthers with different forms and functions (heteranthery) and also different petals acting upon the pollen flow, where many species are enantiostylous (Irwin & Barneby 1982; Dulberger *et al.* 1994; Tucker 1996; Marazzi *et al.* 2006, 2007; Marazzi & Endress 2008). Within this wide spectrum of floral forms, it is accepted that enantiostyly does not vary very much in its functionality among species (Gottsberger & Silberbauer-Gottsberger 1988; Carvalho & Oliveira 2003; Ribeiro & Lovato 2004; Westerkamp 2004; Laporta 2005; Urrutia & Hokche 2008; Almeida 2012). Some recorded variations, however, have been related to mechanisms of pollen deposition from the anthers to the pollinator body, and its capture by the stigma from the pollinator body (Carvalho & Oliveira 2003; Westerkamp 2004; Almeida 2012; Almeida *et al.* 2013; de Almeida *et al.* 2013).

The morphological diversity of flowers in monomorphic enantiostylous species of Cassiinae results in functional variations related to the site of pollen deposition (nothotribic or esternotribic), mode of pollen deposition on the pollinator body (direct or indirect) and the specificity or reciprocity on which pollen is deposited (Carvalho & Oliveira 2003; Westerkamp 2004; Laporta 2005; Almeida *et al.* 2013; de Almeida *et al.*

2013). Moreover, secondary features, such as the pathway of pollen grains that is sometimes driven by the petals to reach the pollinator body, have been recorded (Westerkamp 2004; Almeida 2012; Almeida *et al.* 2013; de Almeida *et al.* 2013).

Although pioneering studies started a century ago, enantiostyly is relatively little understood (Thorp & Estes 1975; Jesson & Barrett 2002), and distinguishing enantiostylous types (ET) remains superficial. Besides the arrangement in monomorphic or dimorphic types, enantiostylous species are also classified as (i) random, when floral morphs are randomly distributed within the same individual or non-random when there is a pattern of morph distribution within individuals (Barrett 2002); and (ii) reciprocal when the stamens are opposite to the gynoecium or non-reciprocal when there is no such arrangement (Jesson & Barrett 2003).

The positioning of sexual elements and petal morphology are important in delimiting groups of Cassiinae species (Marazzi & Endress 2008). Based on floral morphology analysis, species of *Chamaecrista* and *Senna* have been grouped in sections and series by Irwin & Barneby (1982). More recently, studies of macromolecular characters support new arrangements to that previous classification (Marazzi *et al.* 2006; Conceição *et al.* 2009). In all these classifications, however, there has not been consideration of features related to enantiostyly.

This study aims to (i) describe the morphological and functional floral features of enantiostylous Cassiinae species; (ii) suggest an arrangement of these species within enantiostyly types (ETs); and (iii) investigate whether these ET groups in Cassiinae species are supported by the two most recent phylogenetic reconstructions proposed for the subtribe Cassiinae.

MATERIAL AND METHODS

We evaluated 59 Cassiinae species (Table 1) using fresh and fixed (alcohol 70%) buds and flowers. We also used photos and material deposited at the Vale do São Francisco Herbarium (HVASF). A total of 30 species was analysed using fresh, fixed material and photos, 16 using herbarium material and photos, and 13 using herbarium material only. When necessary, herbarium material was rehydrated for observation of floral structures. Seven species (*Chamaecrista flexuosa*, *Senna cana*, *S. macranthera* var, *pudibunda*, *S. martiana*, *C. amiciella*, *C. repens* and *C. ramosa)* were selected as models for the enantiostylous types (ET) based on previous studies (Almeida 2012; Souza *et al.* 2012; Almeida *et al.* 2013; de Almeida *et al.* 2013; N. M. Almeida, unpublished data).

The establishment of ETs was based on five morpho-functional features of flowers: (i) Site of deposition – Deposition and capture of pollen on/from the dorsum (nothotribic) or the venter (esternotribic) of the pollinators; (ii) Reciprocity – Pollen deposited by the anthers on the same side of contact with the stigma (non-reciprocal) or on the opposite side (reciprocal); (iii) Mode of deposition – Pollen deposition on the pollinator body made directly by the anthers (direct) or by one or more petals (indirect); (iv) Number of petals involved with pollen deposition – No or one petal touches the pollinator on the site that is opposite to that contacted by the stigma (one), or more than one petal touches the pollinator on the side that is opposite to that contacted by the stigma (group); and (v) Pollen pathway – pollen deposition can be done by the anthers (direct) or mediated by a petal or group of petals (indirect).

Pollen obligatorily runs through all extension of the petal(s) before deposition on the side opposite to the stigma (looping; de Almeida *et al.* 2013), or pollen is ejected from the pores and briefly rebounds to one or more petals before reaching the opposite side of the pollinator body (ricochet; Westerkamp 2004; Almeida unpublished data). The distribution of the species in ETs was analysed with a Jaccard similarity analysis, using the PAST statistical tool (Hammer *et al.* 2001).

RESULTS

The similarity analysis of morpho-functional features of flowers allowed recognition of seven ETs (Fig. 1). We used the specific epithet of a model species to denominate each type (Fig. 2).

1 Flexuosa (*Chamaecrista flexuosa*; Esternotribic, non-reciprocal and direct). The pollen is deposited on pollinator venter through direct contact between the anther and the pollinator's body. The deposition is non-reciprocal because the anthers are positioned at the flower centre (Fig. 2A).

2 Cana (*Senna cana*; Nothotribic, non-reciprocal and direct). The pollen is deposited at the dorsum through direct contact with the pollinator's body. The deposition is non-reciprocal because a group of anthers is positioned on the same side of the flower and opposite to the stigma (Fig. 2B).

3 Macranthera (*Senna macranthera* var. *pudibunda*; Nothotribic, reciprocal and direct). The pollen is deposited on the dorsum through direct contact with the pollinator's body. The deposition is reciprocal because the pollination anthers are opposite to the stigma (Fig. 2C).

4 Martiana (*Senna martiana*; Nothotribic, non-reciprocal, indirect and ricochet on one petal). The pollen grains are deposited on the dorsal portion of the pollinator after rebounding from a petal (Ricochet; Westerkamp 2004). The deposition is non-reciprocal because a group of anthers is positioned on the same side of the flower and opposite to the stigma (Fig. 2D).

5 Amiciella (*Chamaecrista amiciella*; Nothotribic, reciprocal, indirect, looping made by one petal). The pollen grains are deposited on the dorsal portion of the pollinator after they have run through all the extension of a modified, tube-shaped petal (Looping; de Almeida *et al.* 2013). The pollen produced by the pollination anthers is deposited opposite to the stigma (Fig. 2E).

6 Repens (*Chamaecrista repens*; Nothotribic, non-reciprocal, indirect (looping made by a group of petals). The pollen grains are deposited on the dorsum after they run through all the extension of a structure similar to an arc made by a modified petal and a posterior petal. The deposition is non-reciprocal because a group of anthers is positioned on the same side of the flower, and is opposite to the stigma (Fig. 2F).

7 Ramosa (*Chamaecrista ramosa*; Nothotribic, reciprocal, indirect (looping made by a group of petals). The pollen grains are deposited on the dorsum after they have run through all the extension of a structure similar to an arc made by a modified petal (falcate petal) and two posterior petals (Almeida *et al.* 2013). The pollen produced by the pollination anthers is only deposited opposite to the stigma (Fig. 2G).

Type (7) was the most common, recorded in 20 species (32% of the total) distributed in *Chamaecrista* (19) and *Senna*

Table 1. Cassiinae species, their respective abbreviations and origin of material used.

| species	species abbreviations	origin of material	voucher (HVASF)
Chamaecrista acosmifolia var. *acosmifolia*	*Ch. acvac*	fresh/fixed/photography	N.M. Almeida 522, 25/04/2013
Chamaecrista amiciella	*Ch. ami*	fresh/fixed/photography	N.M. Almeida 519, 10/04/2013
Chamaecrista blanchetii	*Ch. bla*	herbarium	Marcondes Oliveira 4249, 28/05/2009
Chamaecrista brachystachya	*Ch. bra*	herbarium/photography	D.P. Souza 075, 18/12/2013
Chamaecrista brevicalyx	*Ch. bre*	herbarium/photography	V.M. Cotarelli 1691, 12/04/2012
Chamaecrista calycioides	*Ch. cal*	fresh/fixed/photography	V.M. Cotarelli 1853, 19/06/2012
Chamaecrista carobinha	*Ch. car*	herbarium/photography	J. Paula-Souza 9975, 10/07/2009
Chamaecrista curvifolia	*Ch. cur*	herbarium	F. Socolowski 156, 03/09/2012
Chamaecrista desvauxii var. *graminea*	*Ch. devgr*	herbarium/photography	J.A. Siqueira Filho 1813, 22/09/2006
Chamaecrista desvauxii var. *latifolia*	*Ch. devla*	herbarium	Marcondes Oliveira3605, 07/10/2008
Chamaecrista duckeana	*Ch. duc*	herbarium	J.R. Maciel 1008, 28/04/2009
Chamaecrista eitenorum	*Ch. eit*	herbarium/photography	Marcondes Oliveira 3606, 07/10/2008
Chamaecrista fagonioides	*Ch. fag*	fresh/fixed/photography	Marcondes Oliveira 4614, 20/01/2010
Chamaecrista fagonioides var. *macrocalyx*	*Ch. fagvma*	herbarium/photography	J.A. Siqueira Filho 1763, 21/09/2006
Chamaecrista flexuosa	*Ch. fle*	fresh/fixed/photography	Marcondes Oliveira 3607, 07/10/2008
Chamaecrista hispidula	*Ch. his*	herbarium	Marcondes Oliveira 3424, 11/06/2008
Chamaecrista jacobinae	*Ch. jac*	herbarium/photography	Marcondes Oliveira 4657, 27/01/2010
Chamaecrista linearis	*Ch. lin*	herbarium/photography	V.M. Cotarelli 1486, 14/03/2012
Chamaecrista pascuorum	*Ch. pas*	herbarium	Marcondes Oliveira 3508, 11/09/2008
Chamaecrista ramosa	*Ch. ram*	fresh/fixed/photography	C.R.S. Oliveira 129, 25/01/2012
Chamaecrista repens	*Ch. rep*	fresh/fixed/photography	V.M. Cotarelli 1563, 10/04/2012
Chamaecrista rotundifolia var. *grandiflora*	*Ch. rotvgr*	fresh/fixed/photography	J.A. Siqueira Filho 2373, 15/07/2010
Chamaecrista rotundifolia var. *rotundifolia*	*Ch. rotvro*	fresh/fixed/photography	N.M. Almeida 527, 26/04/2013
Chamaecrista serpens var. *serpens*	*Ch. sevse*	fresh/fixed/photography	N.M. Almeida 509, 10/04/2013
Chamaecrista sp1.	*Ch. sp1*	herbarium/photography	N.M. Almeida529, 21/12/2011
Chamaecrista sp2.	*Ch. sp2*	herbarium	N.M.P. Braga 118, 14/06/2012
Chamaecrista supplex	*Ch. sup*	fresh/fixed/photography	N.M. Almeida 520, 11/04/2013
Chamaecrista tenuisepala	*Ch. ten*	fresh/fixed/photography	N.M. Almeida 516, 10/04/2013
Chamaecrista zygophylloides var. *colligans*	*Ch. zyvco*	fresh/fixed/photography	V.D. Silva 078, 28/01/2009
Senna acuruensis	*Se. acu*	fresh/fixed/photography	A.C.P. Oliveira 1878, 08/11/2012
Senna acutisepala	*Se. acut*	fresh/fixed/photography	P.B. Schwartsburd 2425, 27/03/2011
Senna alata	*Se. all*	fresh/fixed/photography	N.M. Almeida 390, 12/12/2012
Senna aversiflora	*Se. ave*	herbarium	Marcondes Oliveira 3578, 12/09/2008
Senna bracteosa	*Se. bra*	herbarium/photography	Marcondes Oliveira 4001, 27/04/2009
Senna cana	*Se. can*	fresh/fixed/photography	V.M. Cotarelli 786, 01/07/2011
Senna catingae	*Se. cat*	herbarium	A.C.P. Oliveira 2811, 10/07/2013
Senna cearensis	*Se. cea*	herbarium	Marcondes Oliveira 4154, 25/05/2009
Senna gardneri	*Se. gar*	herbarium/photography	J.A. Siqueira Filho 2050, 26/05/2009
Senna georgica	*Se. geo*	herbarium/photography	L.M. Nascimento 752, 17/11/2008
Senna lechriosperma	*Se. lec*	fresh/fixed/photography	V.M. Cotarelli 1791, 05/06/2012
Senna macranthera	*Se. mac*	fresh/fixed/photography	A.C.P. Oliveira 2500, 07/05/2013
Senna macranthera var. *micans*	*Se. mavmi*	fresh/fixed/photography	N.M. Almeida 526, 25/04/2013
Senna macranthera var. *pudibunda*	*Se. mavpu*	fresh/fixed/photography	Marcondes Oliveira 2966, 19/07/2007
Senna macranthera var. *striata*	*Se. mavst*	fresh/fixed/photography	Marcondes Oliveira 3684, 11/10/2008
Senna martiana	*Se. mar*	fresh/fixed/photography	N.M. Almeida 269, 04/09/2012
Senna obtusifolia	*Se. obt*	fresh/fixed/photography	N.M. Almeida 510, 10/04/2013
Senna pendula	*Se. pen*	herbarium/photography	F. Socolowski 127, 01/08/2012
Senna quinquangulata	*Se. qui*	herbarium	L.M. Nascimento 675, 17/04/2008
Senna rizzinii	*Se. riz*	fresh/fixed/photography	N.M. Almeida 523, 25/04/2013
Senna siameae	*Se. sia*	fresh/fixed/photography	A.C.P. Oliveira 2339, 28/01/2013
Senna silvestris	*Se. sil*	fresh/fixed/photography	D. Araújo 690, 27/05/2009
Senna sp1.	*Se. sp*	fresh/fixed/photography	No Voucher
Senna spectabilis	*Se. spe*	fresh/fixed/photography	N.M. Almeida 373, 11/12/2012
Senna spectabilis var. *excelsa*	*Se. spvex*	herbarium	N.M. Almeida 294, 19/11/2012
Senna splendida var. *gloriosa*	*Se. splvgl*	fresh/fixed/photography	J.V.A. Ferreira 067, 30/05/2011
Senna splendida var. *splendida*	*Se. splvsp*	fresh/fixed/photography	N.M. Almeida 525, 25/04/2013
Senna trachypus	*Se. tra*	fresh/fixed/photography	N.M. Almeida 224, 29/08/2012
Senna tropica	*Se. tro*	herbarium	Marcondes Oliveira 4750, 27/01/2010
Senna uniflora	*Se. uni*	fresh/fixed/photography	V.M. Cotarelli 1627, 11/04/2012
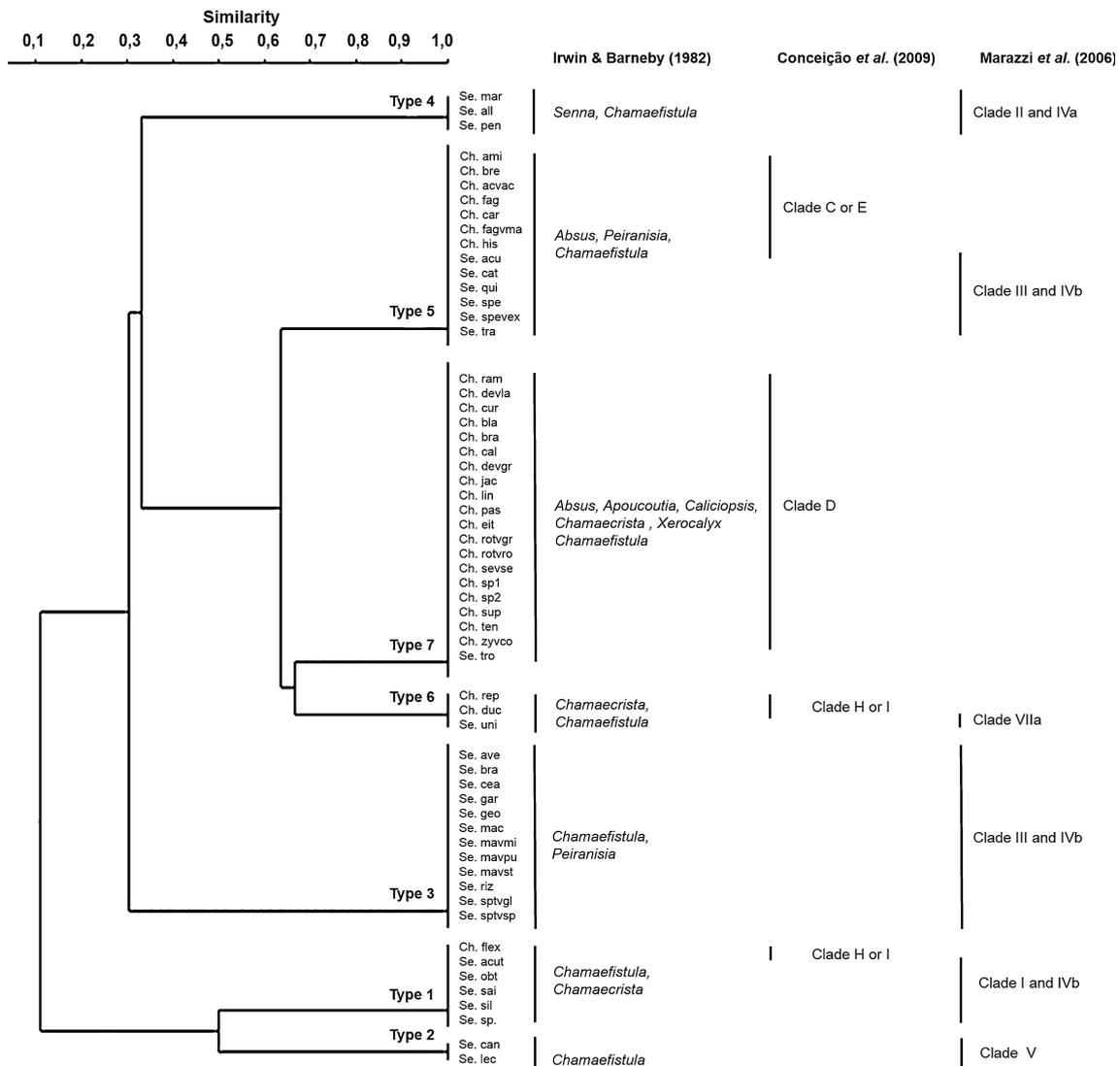
Fig. 1. Classification of enantiostylous Cassiinae species based on similarity (Jaccard) analyses of morphological and functional features of flowers. The names grouped on the right represent sections of *Senna* and *Chamaecrista* based on Irwin & Barneby (1982), classification proposed for *Chamaecrista* by Conceição *et al.* (2009) and for *Senna* by Marazzi *et al.* (2006).

(one). The Cana type (2) was less common and was observed only in *S. cana* and *S. lechriosperma* (3.2%; Fig. 1). The types Martiana (4) and Repens (6) were recorded in three species each (5%), Flexuosa (1) in six species (9.6%), Macranthera (3) in 12 species (19.5%) and Amiciella (5) in 13 species (21%). The types Macranthera (3), Cana (2) and Martiana (4) were observed only in *Senna* species, and the type Flexuosa (1) was restricted to the model species *Chamaecrista flexuosa* (Fig. 1). The highest similarity was recorded between the types Ramosa (7) and Repens (6), which also showed a secondary level of similarity with the type Amiciella (5); Fig. 1; among the most frequent types observed in *Senna*, types (1) and (2) were the most similar (Fig. 1).

DISCUSSION

The identification of seven enantiostylous types with different levels of complexity reflects the morphological diversity of

Cassiinae flowers and represents distinct strategies of pollen capture and deposition on the pollinator body (Irwin & Barneby 1982; Dulberger *et al.* 1994; Tucker 1996; Marazzi *et al.* 2006, 2007; Marazzi & Endress 2008; Almeida *et al.* 2013; de Almeida *et al.* 2013). Some of the enantiostylous types (ETs) are related to unusual strategies of pollen deposition upon the pollinator's body. The Ramosa type may be considered the most complex because deposition and capture of pollen occur indirectly at opposite sides of the pollinator body by means of a looping that is made by the pollen grains along the inner surface of a group of petals, as observed in the model species (de Almeida *et al.* 2013). The Amiciella type is considered the second most complex since it presents the same mechanisms observed in the Ramosa type except the use of a group of petals (only one petal plays that role); this is the only type that was shared by *Chamaecrista* and *Senna* species. Although some *Senna* species present high level of complexity, most present less complex enantiostyly: some do not have indirect pollen deposition (Carv-
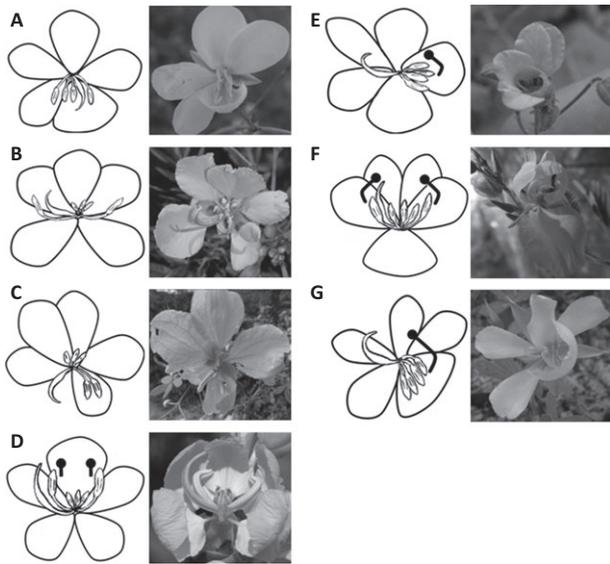
Fig. 2. Flowers and enantiostylous types of Cassiinae species. Schemes show the relative position of stamens and gynoecium. A: *Chamaecrista ramosa* (Ramosa type); B: *Senna cana* (Cana type); C: *C. amiciella* (Amiciella type); D: *S. macranthera* var. *pudibunda* (Macranthera type); E: *C. repens* (Repens type); F: *S. martiana* (Martiana type); G: *C. flexuosa* (Flexuosa type). Lines indicate the route of pollen grains, and circles show the final area of contact of pollen grains with the petals.

alho & Oliveira 2003; Laporta 2005; Almeida 2012) and in others the deposition is not reciprocal (Almeida unpublished data).

The types Repens, Martiana and Flexuosa do not have reciprocal pollen deposition, thus these types may be considered atypical, similarly to *Chamaecrista flexuosa* (Almeida *et al.* 2013). This species constitutes the first report of atypical enantiostyly; it has a third floral morph presenting a centrally positioned style that results in enhancement of the area of pollen capture and deposition at the pollinator body (Almeida *et al.* 2013).

The role of petals for indirect deposition of pollen in specific locations of the pollinator's body reported in this study was previously described for species of the subtribe Cassiinae. The occurrence of ricochet using only one petal for pollen deposition was reported for species of *Cassia* and described as analogous to the laws of incidence of light, where incidence and reflection angles are similar (Westerkamp 2004). In the looping type of deposition in *Chamaecrista ramosa*, pollen grains roamed over an arc-shaped surface formed by a group of petals (Almeida *et al.* 2013). Similar mechanisms have been described for *Chamaecrista fasciculata* (Todd 1882) and *Senna multijuga* (Delgado & Souza 1977). The presence of a modified tube-shaped petal in *Chamaecrista hispidula*, which functions as an extension of the anthers (Gottsberger & Silberbauer-Gottsberger 1988), is similar to that found in the species of type Amiciella in this study.

Heteranthery was observed in species of different enantiostylous types, particularly noted for differences in size and position of the anthers in flowers (Carvalho & Oliveira 2003; Westerkamp 2004; Arceo-Gómez *et al.* 2010; Almeida *et al.* 2013; de Almeida *et al.* 2013). Heteranthery seems to have evolutionary relationships with enantiostylous species that have pollen flowers and is common in *Cassia*, *Senna* and *Chamaecrista* species (Vogel 1978; Buchmann 1983; Gottsberger & Silberbauer-Gottsberger 1988; Westerkamp 2004; Laporta 2005; Almeida 2012; Almeida *et al.* 2013; de Almeida *et al.* 2013). Besides enabling the deposition of pollen on specific locations of the body of pollinators and directly linked to the occurrence of enantiostyly, the presence of stamens with different functions (feeding and pollination) is essential to avoid the risk of pollen limitation (Vogel 1978; Barrett 2002; Vallejo-Marín *et al.* 2009).

It is interesting that, despite the high morphological diversity of Cassiinae flowers, no species presented esternotribic, direct and reciprocal pollen deposition. These features probably occur in the monomorphic enantiostylous species *Solanum rostratum* (Solanaceae; Todd 1882; Barrett 2002) and also in species of *Monochoria* (Pontederiaceae; Tang & Huang 2005) and *Wachendorfia* (Haemodoraceae; Jesson & Barrett 2002). Thus, the investigation of enantiostyly in plant groups other than the Cassiinae species may allow recognition of new ETs.

For *Chamaecrista* and *Senna* species, the morpho-functional characters of flowers that were used to establish the ETs seem to reflect taxonomic differences between genera, since species of both genera occur in a similar number only in the Amiciella type. The other types include species of only one genus. Moreover, species of the same ET are restricted to specific sections of *Chamaecrista* and *Senna*, as proposed by Irwin & Barneby (1982).

Moreover, there was similarity between the arrangement of *Chamaecrista* species in ETs and the arrangement based on morphological and molecular data for this genus (data from Irwin & Barneby 1982 and Conceição *et al.* 2009; Fig. 1). Species of the sections *Chamaecrista*, *Xerocalyx*, *Caliciopsis* and *Absus* (Irwin & Barneby 1982), which were included in the Ramosa type, are similar to the clade 'D' of Conceição *et al.* (2009); the difference is the presence of the section *Apoucoutia*, which is represented by only one species. Similarly, the clades 'H' and 'I' are similar to the ETs Repens and Flexuosa because of the presence only of species of the section *Chamaecrista*. The Amiciella type is only represented by species of the section *Absus*, being similar to the clade 'C', except for the presence of one species of the section *Grimaldia*. However, Conceição *et al.* (2009) suggested the transference of the species in this section to the section *Absus*, which would lead to the Amiciella type and the clade 'C' having even more resemblance.

Following the same trend observed in *Chamaecrista* species, the ETs that have a higher number of *Senna* species are similar to the clades proposed in phylogenetic studies (Marazzi *et al.* 2006; Fig. 1). Some *Senna* species included in the type Amiciella represent part of the clade 'III', mainly regarding species of the section *Perianisia* (Irwin & Barneby 1982). Similarly, species included in the Macranthera type are represented in the clade 'IVb' (Marazzi *et al.* 2006) by species from the section *Chamaefistula* (Irwin & Barneby 1982). The types Cana and Flexuosa are similar to the clades 'V' and 'I' (Marazzi *et al.* 2006), respectively, in the presence of species that are shared exclusively in the section *Chamaefistula* (Irwin & Barneby 1982). The Martiana type is similar to the clade 'II' (Marazzi *et al.* 2006) because there are shared species with the section *Senna* (Irwin & Barneby 1982).

The current classification of enantiostyly is based on morph distribution among plants and tends to put together species with different flower morphology and diverse reproductive strategies. Classifying these species into monomorphic and dimorphic (Barrett *et al.* 2000), reciprocal and non-reciprocal

(Jesson & Barrett 2003) does not take into account important taxonomic and reproductive characters and does not define functionally similar groups. Even considering that different classifications may serve different purposes, and no one classification is definitive, our review of the proposed functional ETs details more clearly the existence of different expressions of enantiostyly.

Our approach allowed organisation of the wide diversity of reproductive mechanisms evolved among the Cassiinae enantiostylous species into functional and meaningful categories. These classes of enantiostylous species seem to be consistent with taxonomic and functional reproductive traits. The recognition of different types of enantiostyly in the Cassiinae subtribe raises several possibilities for studying reproductive strategies of other enantiostylous plant groups.

ACKNOWLEDGEMENTS

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