Patterns and development of floral asymmetry in Senna (Leguminosae, Cassiinae)

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Abstract

The buzz-pollinated genus Senna (Leguminosae) is outstanding for including species with monosymmetric flowers and species with diverse asymmetric, enantiomorphic (enantiostylos) flowers. To recognize patterns of homology, we dissected the floral symmetry character complex and explored corolla morphology in 60 Senna species and studied floral development of four enantiomorphic species. The asymmetry morph of a flower is correlated with the direction of spiral calyx aestivation. We recognized five patterns of floral asymmetry, resulting from different combinations of six structural elements: deflection of the carpel, deflection of the median abaxial stamen, deflection or modification in size of one lateral abaxial stamen, and modification in shape and size of one or both lower petals. Prominent corolla asymmetry begins in the earl-stage bud (unequal development of lower petals). Androecium asymmetry begins either in the midstage bud (unequal development of thecae in median abaxial stamen; twisting of androecium) or at anthesis (stamen deflection). Gynoecium asymmetry begins in early bud (primordium off the median plane, ventral slit laterally oriented) or midstage to late bud (carpel deflection). In enantiostylos flowers, pronouncedly concave and robust petals of both monosymmetric and asymmetric corollas likely function to ricochet and direct pollen flow during buzz pollination. Occurrence of particular combinations of structural elements of floral symmetry in the subclades is shown.
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senna (Leguminosae, Cassiinae) 1

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The buzz-pollinated genus Senna (Leguminosae) is outstanding for including species with monosymmetric flowers and species with diverse asymmetric, enantiomorphic (enantiostyloous) flowers. To recognize patterns of homology, we dissected the floral symmetry character complex and explored corolla morphology in 60 Senna species and studied floral development of four enantiomorphic species. The asymmetry morph of a flower is correlated with the direction of spiral calyx aestivation. We recognized five patterns of floral asymmetry, resulting from different combinations of six structural elements: deflection of the carpel, deflection of the median abaxial stamen, deflection or modification in size of one lateral abaxial stamen, and modification in shape and size of one or both lower petals. Prominent corolla asymmetry begins in the early-stage bud (unequal development of lower petals). Androecium asymmetry begins either in the midstage bud (unequal development of thecae in median abaxial stamen; twisting of androecium) or at anthesis (stamen deflection). Gynoecium asymmetry begins in early bud (primordium off the median plane, ventral slit laterally oriented) or midstage to late bud (carpel deflection). In enantiostyloous flowers, pronouncedly concave and robust petals of both monosymmetric and asymmetric corollas likely function to ricochet and direct pollen flow during buzz pollination. Occurrence of particular combinations of structural elements of floral symmetry in the subclades is shown.

Key words: buzz pollination; enantiomorphy; enantiostyly; floral asymmetry; floral development; functional morphology; homology; petal venation.

Asymmetric flowers are rare in angiosperms and are known to occur mostly within large families or orders with predominantly monosymmetric (zygomorphic) flowers (e.g., Leguminosae, Lamiales, Orchidaceae, Zingiberales) and only exceptionally in basal angiosperms (e.g., Winteraceae; Endress, 1999). Enantiomorphy is a special kind of floral asymmetry in which flowers have two mirror-image morphs. Commonly in enantiomorphic flowers, the style is deflected to the left or to the right of the median plane, a condition known as enantiostyly, which occurs in at least ten angiosperm families of both monocots and dicots (Jesson, 2002) and seems to have evolved from monosymmetry multiple times (Jesson and Barrett, 2003). Left- vs. right-styled flowers may occur on different individuals (i.e., diomorphic enantiostyly) or on the same plant (i.e., monomorphic enantiostyly; see Jesson and Barrett, 2003, for an overview).

The development of enantiostyloous flowers has been explored in few taxa (Tucker, 1996, 1999; Jesson et al., 2003), whereas the genetics (Jesson and Barrett, 2002a, b) or role of enantiostyly in pollination biology (e.g., Delgado Salinas and Sousa Sánchez, 1977; Dulberger, 1981; Gottsberger and Silberbauer-Gottsberger, 1988) has been the focus of others. The large genus Senna (Cassinae, Leguminosae; ca. 350 species, Randell and Barlow, 1998) is exceptional for displaying both species with monosymmetric flowers and species with enantiomorphic flowers (monomorphic), in which the gynoecium, androecium, and corolla contribute to the floral asymmetry (Marazzi et al., 2006, 2007). Senna thus represents an ideal example to study floral asymmetry.

Floral whorls in Senna affect floral structure and symmetry in various ways (Marazzi et al., 2006, 2007). The gynoecium is formed by a single carpel, as is typical for legumes, and is usually long, arcuate, and point-tipped with a chambered (enclosed receptive surface) or a craterlike stigma (receptive surface not enclosed; Owens and Lewis, 1989; Dulberger et al., 1994; Endress, 1994; Tucker, 1996; Marazzi et al., 2007). Unlike most other enantiostyloous taxa, in Sena, not only the style, but the entire carpel is deflected to the side. The androecium consists of two five-merous whorls, is highly diverse, and has fascinated researchers for a long time (e.g., Müller, 1883; Venkatesh, 1957; Lasseigne, 1979; Tucker, 1991; Marazzi et al., 2007). Of the mostly seven fertile stamens, only the three abaxial ones appear to be involved in floral asymmetry. The corolla is yellow and more or less differentiated into three upper (i.e., standard petal and wing petals) and two lower petals (i.e., keel petals in papilionoids). In several enantiostyloous species, the upper petals are more or less reduced and the lower ones concave and/or modified in shape and size (Irwin and Barneby, 1982; Marazzi et al., 2006).

Expression of floral asymmetry during development in Sena species with highly asymmetric flowers has not been investigated before. Floral development has been studied in detail only in one species, S. didymobotrya (Tucker, 1996), which has enantiostyloous flowers with monosymmetric androecium and corolla. This species was part of a comparative study of Sena, Cassia sensu stricto (s.s), and Chamaecrista (Tucker, 1996), the three genera of subtribe Cassiinae (Irwin and Barneby, 1981, 1982). Flowers of Cassia s.s. are monosymmetric, whereas Chamaecrista species have asymmetric, enantiostyloous flowers (Irwin and Barneby, 1982; Tucker, 1996). Cassiinae have superficially similar flowers at anthesis due to the same pollination syndrome, but differ in early floral development (e.g., sequence of petal initiation, asymmetric initiation,
overlap between whorls, time of carpel initiation, etc.; Tucker, 1996, 1997). Dulberger (1981) observed that in *S. didynamobotrya* deflection of the carpel occurs 6–12 h before anthesis. In other enantioistylous species, style deflection occurs either in the bud or at the beginning of anthesis (Jessor et al., 2003).

Enantioistyly has usually been correlated with buzz pollination by pollen-collecting bees, which vibrate the anthers to extract and collect the pollen for larval provision (e.g., Buchmann, 1974, 1983). Rarely, enantioistylous flowers offer nectar and are not buzz-pollinated (e.g., species of *Wachendorfia*, *Haemodoraceae*; see Vogel, 1998). Although enantioistyly was commonly interpreted as promoting cross-pollination, its functional significance has long been debated (e.g., Todd, 1882; Ornduff and Dulberger, 1978; Dulberger, 1981; Fenster, 1995; Jessor and Barrett, 2002b). In buzz-pollinated flowers, enantioistyly is correlated with other floral features that likely have evolved in relation to the unusual pollination mode, including poricidal anthers (i.e., dehiscence restricted to apical pores) and heteranthery (i.e., different kinds of stamens in a flower), which are also found in *Senna* (e.g., Buchmann, 1974; Delgado Salinas and Sousa Sánchez, 1977; Dulberger, 1981; Gottsberger and Silberbauer-Gottsberger, 1988; Owens and Lewis, 1989; Dulberger et al., 1994). The role of these features and of enantioistyly in the pollination biology of *Senna* has been investigated only in a few species (Buchmann, 1974; Delgado Salinas and Sousa Sánchez, 1977; Fontanelle, 1979; Dulberger, 1981; Gottsberger and Silberbauer-Gottsberger, 1988; Carvalho and Oliveira, 2003; Laporta, 2003; Westerkamp, 2004). Implications for pollination biology of specialized anther dehiscence patterns are discussed by Marazzi et al. (2007).

In *Senna*, various kinds of enantioistyly, often with the androecium and corolla also affecting the floral asymmetry, appear to occur and characterize the major clades II–VI recognized by Marazzi et al. (2006) (Fig. 4A). The existence of different kinds of asymmetric flowers and the independent switches to these kinds inferred from the molecular phylogeny suggest that asymmetric flowers may have originated many times and may not be strictly homologous (Marazzi et al., 2006). Floral (a)symmetry in *Senna* involves several potentially independent structural elements. To understand the evolution of asymmetry, we must first obtain a clear understanding of the various elements. Therefore, in the current study, we investigated the diversity and patterns of floral (a)symmetry in the genus, and in particular, the patterns in corolla morphology and development of floral asymmetry. We addressed the following specific questions: (1) What patterns of floral asymmetry can be identified in *Senna*? (2) What patterns can be recognized in the diversity of petal form? (3) Do the investigated features provide any synapomorphies congruent with the new infrageneric relationships supported by the molecular phylogeny of *Senna* (Marazzi et al., 2006)? (4) How do species with different patterns of floral asymmetry differ in development? (5) What are the implications of our results with regard to our current understanding of pollination biology?

**MATERIALS AND METHODS**

*Species studied*—We studied 60 *Senna* species (one or more individuals per species) and two *Cassia* species, representing the sister genus of *Senna* (Marazzi et al., 2006). The *Senna* species studied represent all major clades and subclades of the molecular phylogeny of the genus of Marazzi et al. (2006) based on 81 *Senna* species and the diversity of morphological patterns observed during field collection (including color photographs of flowering individuals by the first author) and in subsequent morphological investigations (Marazzi et al., 2007). Most samples were collected in the field in Argentina, Australia, Bolivia, Brazil, Mexico, Panama, Paraguay, South Africa, and the United States, and a few were received from European and Australian botanic gardens. Fifty-seven *Senna* species were investigated with stereomicroscopy (SM), and three species, *S. martiana* (Benth.), H. S. Irwin & Barneby, *S. subulata* (Griseb.), H. S. Irwin & Barneby, and *S. cf. velatina* (Vogel) H. S. Irwin & Barneby, were studied from color photographs of their flowers. In addition 26 species of *Senna* and the two *Cassia* species were selected for detailed investigations on petal shape and venation of anthetic flowers. Four *Senna* species with asymmetric flowers were selected for developmental studies with scanning electron microscopy (SEM): *S. aciphylla* (clade IVa), *S. mucronifera* (clade IVb), *S. couchii* (clade VI), and *S. wisliczenii* (clade III). A list of the specimens studied and voucher information are given in the Appendix.

**Morphological investigation**—Flowers at anthesis and buds of different stages were fixed and stored in 70% ethanol. For investigating petal shape and venation, petals of 1–2 selected anthetic flowers were flattened between two glass slides with the ventral side downward. The slides were then immersed in 70% ethanol and photographed with an Axioscam HRC digital camera (Carl Zeiss AG, Oberkochen, Germany) mounted on a Stemi SV11 stereomicroscope (Carl Zeiss AG). For the developmental study of each selected species, 2–10 buds per developmental stage were studied with SEM (early bud = from organ initiation to beginning of organ differentiation; midstage bud = at organ differentiation; late bud = from end of organ differentiation to growth of differentiated organ). Standard specimen preparation procedures were used for osmium tetroxide-impregnated SEM samples. Several other midstage to late buds were examined with SM. In addition, 2–3 floral buds at midstage of each species were selected for serial sectioning. They were embedded in Kulzer’s Technovit 7100 (Kulzer & Co., Germany) and sectioned with a Microm HM 335 rotary microtome (Microm International GmbH, Walldorf, Germany) and conventional micromerite knife (grade D); transverse section (TS) series were cut at 7 µm, stained with ruthenium red and toluidine blue (Weber and Igersheim, 1994), and mounted in Histomount (National Diagnostics, Atlanta, Georgia, USA) on glass slides. Fixed floral material and slides are deposited at the Institute of Systematic Botany of the University of Zurich (Z), Switzerland.

**RESULTS**

**Diversity of floral symmetry and petals**—In all studied *Senna* species, the sepal is arranged either in a clockwise or counterclockwise spiral, which means that monosymmetric flowers of *Senna* also have an enantiomorphical calyx. In the two *Cassia* species studied, the corolla is monosymmetric; the petals all have nearly the same size and form (but the lower petals are slightly concave) and a single main vein, which extends up to the petal tip (Fig. 1A). In the following paragraphs we describe floral symmetry and petal diversity in the major clades of *Senna* (Marazzi et al., 2006; see also Table 1 and Fig. 4A–D).

**Clade I**—Flowers are monosymmetric. The gynoecium may be slightly deflected to the side in some flowers of an individual with otherwise monosymmetric flowers, but because the deflection is only slight and inconsistent in these species, their flowers are not considered truly enantiostylos. Upper and lower petals have similar forms, but the lower petals are slightly larger than the upper ones (Fig. 1B, C). All petals are only slightly concave (Fig. 2A, B). Petals have a single main vein, which does not extend up to the petal tip.

**Clade II**—Flowers are asymmetric, with the gynoecium deflected to the side in all species investigated, while androecium and corolla are monosymmetric. Upper and lower petals have more or less the same shape, but the upper petals are wider (*S. paradidyma*, Fig. 1D) or slightly smaller (*S. didynamobotrya*, Fig. 1E) than the lower ones. All petals are concave (*S. alata,
Fig. 1. Petal diversity in species of major clades and subclades of Senna and in Cassia javanica (clades in Fig. 4). (A) Cassia javanica; (B) Senna polyantha (clade I); (C) S. silvestris var. guaranitica (I); (D) S. paradictyon (II); (E) S. didymobotrya (II); (F) S. unijuga (III); (G) S. wislizeni (III); (H) S. mollissima (III); (H') close up of venation of standard petal; (I) S. aciphylla (IVa); (J) S. mucronifera (IVb); (K) S. uniflora (V); (L) S. cana var. calva (V); (M) S. acuruensis var. acuruensis (VI); (N) S. tondzii (VI); (O) S. pallida (VI); (P) S. chacoensis (VIa); (Q) S. villosa (VIIb); (R) S. hirsuta (VIIa). Some petals torn during flattening process (arrows). Dotted lines indicate missing parts of petal tissue.
Clade III—Flowers are asymmetric, with the gynoecium deflected to the side in all species investigated. The androecium is nearly monosymmetric (species of subclade IIIb, *S. spectabilis*) or the median and one lateral abaxial stamen are deflected to the opposite side of the gynoecium (species of subclade IIIa). The
corolla is asymmetric whereby the upper petals are not reduced (S. spectabilis, S. unijuga, Fig. 1F; S. wislizeni, Fig. 1G), or moderately reduced (S. atomaria, Fig. 2F; S. mollissima, Fig. 1H), and one lower petal (S. atomaria, S. mollissima, Fig. 1H; S. spectabilis, not shown) or both lower petals (S. unijuga, Figs. 1F, 2G; S. wislizeni, Figs. 1G, 2H) are modified in shape and size, i.e., the blade is highly asymmetric, concave and foot-shaped, and in addition, these two petals differ from each other (Figs. 1F–H). The standard petal is stalkless in S. mollissima (Fig. 1H). Upper petals have three main veins (S. unijuga, Fig. 1F; in S. wislizeni, Fig. 1G, the median vein is more conspicuous than the lateral ones), and the lower petals have apparently only two main veins (S. unijuga, Fig. 1F; S. wislizeni, Fig. 1G), or all petals have a single main vein, except the standard petal, in which two main veins form a double strand (S. mollissima, Figs. 1H, H′). In strongly modified petals, venation is particularly robust, and the basal part of the main veins is united (Figs. 1F, G), or many robust secondary veins extend from the basal part of the single main vein (Fig. 1H).

Clade IV—Flowers are asymmetric with the gynoecium deflected to the side in all species investigated. This clade includes S. skinneri plus a clade of two subclades IVa and IVb (Marazzi et al., 2006). The androecium of subclade IVa is asymmetric: all stamens are fertile and are arranged slightly irregularly (S. aciphylla, Fig. 2I; S. artemisioides, Fig. 2J), and one lateral abaxial stamen may be larger than the others (S. artemisioides, Fig. 2J; S. odorata, not shown). Seneca skinneri and species of subclade IVb have seven fertile stamens, except for S. hayesiana with only the four middle stamens fertile (see Fig. 4E). The androecium is asymmetric, with only the median abaxial stamen deflected to the opposite side of the deflected gynoecium (S. skinneri, Fig. 2K; species of subclade IVb, Figs. 2L–N) or it is nearly monosymmetric (S. dariensis var. hypoglauca, S. hayesiana, Fig. 2O; S. quinquangulata, Fig. 2P). The corolla is asymmetric in most species (subclade IVa, Figs. 2I, J; species of subclade IVb and S. skinneri, Figs. 2K–N), or, rarely, it is nearly monosymmetric (S. dariensis var. hypoglauca, S. hayesiana, Fig. 2O; S. quinquangulata, Fig. 2P; S. rizzinitii). In asymmetric corollas, the upper petals are not reduced, and one or both lower petals are concave, but not modified in shape and size (species of subclade IVa, Figs. 1I, 2I–J; species of subclade IVb, Fig. 2K, N), or one or both are concave and foot-shaped (species of subclade IVb, Figs. 1J, 2L, M). The standard petal may be emarginate or bilobed (species of subclade IVb*, Fig. 1J). Petals have three main veins (Figs. 1I, J). In strongly modified petals, venation is particularly robust, and the basal part of the main veins is united (Fig. 1J).

Clade V—Flowers are asymmetric, with the gynoecium deflected to the side in all species investigated. The androecium is nearly monosymmetric in species with the median abaxial stamen smaller than the lateral abaxial ones (S. cf. velutina, Fig. 3A), or it is asymmetric in species with three similar abaxial stamens, and the median abaxial stamen is deflected to the opposite side of the gynoecium (S. cana var. calva, S. uniflora, Fig. 3B). The corolla is nearly monosymmetric (S. cf. velutina, Fig. 3A; S. uniflora, Figs. 1K, 3B), or slightly asymmetric, with one lower petal concave and slightly modified in shape and size (S. cana var. calva, Fig. 1L). The standard petal may be emarginate (Fig. 1L). Petals have three main veins (Fig. 1L), or in S. uniflora, they apparently have only a single main vein (Fig. 1K). In the lower petal that is modified, venation is slightly more robust than in the other petals, but the basal part of the main veins appears to be free (Fig. 1L).

Clade VI—Flowers are asymmetric. The androecium is asymmetric in all species investigated: all three abaxial stamens are deflected to the side opposite the gynoecium (S. aversiflora, Figs. 3D; S. holwayana, Fig. 3E; S. pallida, Fig. 3I; S. tonduzii, Fig. 3F); or the median abaxial stamen is deflected, and the lateral abaxial stamen on the side of the gynoecium is conspicuously shorter than the other two (S. acuruensis var. acuruensis, Fig. 3G; S. acuruensis var. catingae, S. multijuga var. lindleyana, S. multijuga var. multijuga, Fig. 3H); or the lateral abaxial stamens oppose the gynoecium is conspicuously longer than the other two abaxial stamens, which are not deflected (species of subclade VIa, Figs. 3J–L). In S. pallida, almost all flowers have all three abaxial stamens deflected to one side, but we also observed a few flowers with the two lateral abaxial stamens deflected to one side and the median abaxial stamen to the other side. The corolla is asymmetric. Upper petals are highly reduced (S. acuruensis var. acuruensis, Fig. 1M; S. tonduzii, Fig. 1N), moderately reduced (S. pallida, Figs. 1O, 3I), or almost not reduced (S. aversiflora, Fig. 3D; S. holwayana, S. multijuga var. multijuga, Fig. 3H; S. aphylla, Fig. 3J; S. chacoensis, Figs. 1P, 3K; S. rigida, Fig. 3L). In reduced upper petals, the standard petal is the most reduced, whereas the lateral ones are similar to one another (S. acuruensis var. acuruensis, Fig. 1M), or the lateral petal opposite the gynoecium is smaller than the other lateral upper petal (S. pallida, Figs. 1O, 3I; S. tonduzii Fig. 1N). The lower petal opposite the gynoecium is concave and foot-shaped in all species investigated, whereas the other lower petal is concave and modified in size, but not foot-shaped, and only slightly asymmetric (S. aversiflora, Fig. 3D; S. holwayana, Fig. 3E; S. acuruensis var. acuruensis, Figs. 1M, 3G; S. acuruensis var. catingae, S. multijuga var. multijuga, Fig. 3H; S. pallida, Figs. 1O, 3I; S. aphylla, Fig. 3J; S. chacoensis, Figs. 1P, 3K; S. rigida, Fig. 3L), or it is strongly asymmetric (S. tonduzii, Figs. 1N, 3F). Petals have three main veins (Figs. 1M–P), except for highly reduced upper petals, which have only one main vein (Figs. 1M, N).

Clade VII—Flowers are monosymmetric in both subclades VIIa and VIIb. In some flowers of subclade VIIa, the gynoecium may be slightly deflected to the side, but because the deflection is only slight and inconsistent in these species, their flowers are not considered enantiostylos. Upper and lower petals have similar shapes (S. apiculata, S. armata, S. birestris, S. villosa, Figs. 1Q, 3P), or the lower petals are slightly longer and thinner than the upper ones and are concave (S. hisruta, Figs. 1R, 3M; S. septemtrionalis, Figs. 3N; S. subulata, Fig. 3O). In S. villosa, the petals are short-stalked (Fig. 1Q). The standard petal is emarginate (Figs. 1Q, R, 3M–P; not in S. apiculata and S. armata, both of subclade VIIb). The blade of the upper lateral petals is monosymmetric (e.g., S. hisruta, Fig. 1R) or slightly asymmetric, forming two mirror-image petals (e.g., S. pendula). Petals have three main veins (Fig. 1Q, R).

Floral development—We focus on the developmental stages at which the floral asymmetry becomes apparent especially in the corolla and androecium, and additionally consider calyx and corolla aestivation (i.e., overlapping of flanks of perianth organs in bud). We studied young floral stages with the SEM and midstage floral buds with transverse microtome sections of representatives of four clades (III, IVa, IVb, and VI) that are
characterized by asymmetric flowers: *S. wislizeni*, clade III (Figs. 4F, 5); *S. aciphylla*, subclade IVa (Figs. 4G, 6); *S. mucronifera*, subclade IVb (Fig. 7; TS not illustrated but similar to Fig. 4F); and *S. tonduzii*, clade VI (Figs. 4H, 8).

The sepals are always initiated in spiral sequence with the first sepal median abaxial (e.g., Fig. 5A), corresponding to a quincuncial calyx aestivation (we did not illustrate the complete sequence of sepal initiation). We found a correspondence between the direction of spiral calyx aestivation and the direction of deflection of the carpel at anthesis in all species studied developmentally: a clockwise spiral (i.e., fifth sepal on the right side) corresponds to a right floral morph, while a counterclockwise spiral (i.e., fifth sepal on the left side) corresponds to a left floral morph (Fig. 4D). Therefore, the calyx aestivation allows the prediction of the floral morph in buds.

*Senna wislizeni* (clade III)—In anthetic flowers of *S. wislizeni*, the carpel is deflected to the side, and the median and one...
Fig. 4. Patterns of floral symmetry and their distribution within *Senna*, petal diversity, corolla and calyx aestivation, floral diagram, and transverse sections (TS) of floral buds of species studied developmentally. In the phylogenetic tree, bootstrap values are above and clade numbers below the branches. Major clades represented by boxes, subclades separated by dashed lines, and other subclades supported by Marazzi et al. (2007) indicated by a vertical bold line. Relationships within clades or subclades are not shown. Only species studied in this article are listed (species in the same order as in Fig. 2 in Marazzi et al., 2006). Species in bold were selected for the developmental study. Diagrams of corolla aestivation, floral diagram and all TS represent right floral morphs. (A) Patterns 1–6 of floral symmetry (see Table 1; based on flowers of *S. siamea* [clade I], *S. didymobotrya* [II], *S. atomaria* [III], *S. mucronifera* [IV], *S. chacoensis* [VIa], *S. tonduzii* [VI], respectively) and their distribution on the molecular phylogenetic tree of *Senna* (and the sister *Cassia*; simplified from Fig. 2 in Marazzi et al., 2006). White boxes indicate floral monosymmetry; boxes shaded in gray indicate floral asymmetry. (B) Patterns of petal diversity (see Table 1 for abbreviations). (C) Patterns of corolla aestivation. (D) Direction of calyx aestivation and floral morph. (E) General floral diagram of *Senna*. (F) *S. wislizeni* (III); three adaxial staminodes. (G) *S. aciphylla* (IVA); all stamens fertile. (H) *S. tonduzii* (VI); level of TS in bud above the highly
lateral abaxial stamen are deflected to the opposite side; the corolla is asymmetric, with the upper petals not reduced and both lower petals concave and foot-shaped. Blade modification is more conspicuous in the lower petal opposite the deflected carpel (Figs. 1G, 2H).

Lower and upper petals develop unequally; they thus differ in size early in development, and the corolla is asymmetric (Fig. 5B). Organs of the outer androecial whorl are initiated when petals start to develop (Fig. 5C), while organs of the inner androecial whorl are initiated after the organs of the outer whorl start to develop (compare Fig. 5E, F). The carpel is initiated as a bulge in the center of the bud during initiation of the organs of the outer androecial whorl (Fig. 5C, E).

Shortly after petal initiation, one lower petal begins to differentiate into a foot-like shape (Fig. 5D). Corolla aestivation is quincuncial (see Fig. 4C), with the lateral upper petals covering the standard petal and also the lower petals (Fig. 5D). The androecium is still monosymmetric after all organs of the outer androecial whorl have been initiated (Fig. 5E). With subsequent anther development, the androecium becomes asymmetric because the stamens and staminodes of the outer androecial whorl appear to be arranged in a twisted pattern, i.e., with the anther tips of the middle and median abaxial stamens touching (and slightly overlapping) the side of one neighboring anther tip (Fig. 5F). This twisted pattern disappears with development of the abaxial stamens of the inner whorl (Fig. 5G). Differentiation of the thecae in the median abaxial stamen is unequal, one theca becoming larger than the other one (Fig. 5G–I). In the midstage bud, stamens of the inner and outer whorls are of different size (Fig. 5H, K). In the late bud, all middle stamens are of similar size, while the median abaxial stamen is the largest of the abaxial stamens (Fig. 5I, L). During anther differentiation, the carpel becomes arcuate and is still in the plane of floral monosymmetry up to midstage bud (Fig. 5G, H, J, K), while it appears slightly deflected in late bud (Fig. 5I, L).

*Senna aciphylla* (clade IVa)—In anthetic flowers of *S. aciphylla*, the carpel is deflected to the side, all stamens are fertile and deflected in an irregular manner, and the corolla is asymmetric, with the upper petals not reduced and one lower petal concave, but not modified in shape and size (Fig. 1I, 2I).

Sepals are initiated in spiral sequence, which is reflected in a quincuncial calyx aestivation (Fig. 6A, B). The two lower petals and one lateral upper petal are initiated before the two remaining upper petals (Fig. 6C). Initiation of these upper petals nearly overlaps with the initiation of the stamens of the outer androecial whorl, except that one of the two adaxial stamens is initiated later in front of the fifth sepal, between the two last initiated upper petals (Fig. 6C). Abaxial stamens of the inner androecial whorl are initiated before the middle and adaxial stamens (Fig. 6D). The carpel is initiated after the stamens of the outer androecial whorl and abaxial stamens of the inner whorl but before the middle and adaxial stamens of the inner whorl (Fig. 6D).

Shortly after petal initiation, the lower petals are already larger than the upper petals, and, although the upper petals are of different size, the corolla appears nearly monosymmetric (Fig. 6D). Subsequently, the upper petals reach a similar size, and corolla aestivation becomes quincuncial (nearly quincuncial in Fig. 6E, but see TS in Fig. 4G and aestivation diagram in Fig. 4E). During anther development, one middle and the two adaxial stamens of the outer androecial whorl appear to be arranged in a twisted pattern (Fig. 6F, G, J). This twisted pattern disappears with development of the abaxial stamens of the inner whorl in midstage bud (Fig. 6H). At this stage, anther differentiation (and anther tip elongation) first begins in the stamens of the outer whorl and in the abaxial stamens of the inner whorl (Fig. 6H, I, K). Stamens of the outer whorl are larger than those of the inner whorl also in late bud (Fig. 6I, L). Although differentiation of the thecae in the median abaxial stamen is slightly unequal, and one theca thus becomes larger than the other one, the androecium still appears to be nearly monosymmetric, but in late bud becomes irregularly asymmetric (Fig. 6H, I), likely because of space constraints and small differences in the sizes of the stamens (see Fig. 6K, L). The gynoecium appears asymmetric in early bud because the ventral slit is oriented slightly laterally and appears either to the left in buds with clockwise calyx aestivation or to the right in buds with counterclockwise calyx aestivation (Fig. 6E, F). During anther differentiation, the carpel becomes arcuate and appears slightly deflected in midstage bud (Fig. 6H, I).

*Senna mucronifera* (clade IVb)—In anthetic flowers of *S. mucronifera*, the carpel is deflected to the side; the androecium is asymmetric, with the median abaxial stamen deflected to the opposite side; and the corolla is asymmetric, with the upper petals not reduced and both lower petals concave (one is only slightly asymmetric and the other is foot-shaped) (Fig. 1J, 2M).

The median abaxial sepal is first initiated (Fig. 7A). The lower petals are initiated slightly before the upper petals (Fig. 7B) and grow to different sizes (Fig. 7C); the corolla is thus early asymmetric. The organs of the outer androecial whorl are initiated when the petals begin to develop (Fig. 7C), whereas the organs of the inner androecial whorl are initiated after the organs of the outer whorl begin to develop (compare Fig. 7C, D). Carpels are initiated after initiation of the organs of the outer androecial whorl (not illustrated, but compare Fig. 7C, D).

Shortly after petal initiation, one lower petal becomes foot-shaped (Fig. 7C, D). Aestivation of the corolla is cochlear ascending (Fig. 7E). The androecium is nearly monosymmetric after the organs of both outer and inner androecial whorls have been initiated (Fig. 7F). With subsequent anther development, the androecium becomes asymmetric because differentiation of the thecae in the median abaxial stamen is unequal; one theca becomes larger than the other (Fig. 7F–I). Stamens are all of nearly the same size in early bud, only the median abaxial stamen is much larger (Fig. 7F). In midstage bud, the three abaxial stamens become much larger than the four middle stamens and the three adaxial stamnodes (Fig. 7G, H, J, K). However, at this stage, the stamens of the inner whorl are still slightly smaller than those of the outer whorl and become similar in size in late bud (Fig. 7I, L). In late bud, the anther tips of the abaxial stamens begin to elongate. During anther differentiation in midstage bud, the carpel becomes arcuate and appears only slightly reduced adaxial staminodes and upper petals. For clarity, middle stamens are indicated in all TS. Abbreviations: ab, abaxial stamen of inner androecial whorl (iaw); ad, adaxial stamen of iaw; ad′, adaxial stamen of oaw; m, middle stamen of iaw; m′, middle stamen of oaw; LP, lower petals; S, sepals; UP, upper petals; UPS, standard petal. Scale bars = 1 cm.
Senna tonduzii (clade VI)—In anthetic flowers of _S. tonduzii_, the carpel is deflected to the side; the androecium is asymmetric, with all the abaxial stamens deflected to the opposite side of the carpel; and the corolla is asymmetric, with the upper petals highly reduced and one lower petal concave and foot-shaped, the other petal with a strongly asymmetric blade (Figs. 1N, 3F). Stamen union occurs in _S. tonduzii_ but in no other _Senna_ species studied. The filaments of the three adaxial staminodes and four middle stamens are united (see Marazzi et al., 2007).

The median abaxial sepal is initiated first (Fig. 8A). The two lower and one of the upper petals appear to be initiated before the two upper petals adjacent to the fifth sepal (Fig. 8B). The lower petals are of slightly different size; the corolla is thus early asymmetric (Fig. 8B). The organs of the outer androecial whorl are initiated before the last two upper petal initials begin to develop (Fig. 8C), whereas the organs of the inner androecial whorl are initiated when organs of the outer whorl begin to develop (compare Figs. 8B, E). The carpel is initiated after initiation of the organs of the inner androecial whorl, and, interestingly, it appears to be displaced from the median plane of floral symmetry (Fig. 8E).

Shortly after petal initiation, one of the lower petals, which are conspicuously larger than the upper ones, begins to become foot-shaped, and the other lower petal also becomes asymmetric (Fig. 8C, D). Corolla aestivation seems not to be cochlear ascending, but the upper petals appear in a partial contort pattern (Fig. 8H). The androecium is nearly monosymmetric after all its organs have been initiated (Fig. 8E, F). Later, the androecium becomes asymmetric because unequal differentiation of the thecae in the median abaxial stamen results in one become larger than the other (Fig. 8G). The stamens are all approximately similar in size in early bud, except for the adaxial staminodes, which remain much smaller (Fig. 8G). In midstage bud, the three abaxial stamens become larger than the middle stamens (Fig. 8I). However, at this stage, the stamens of the inner whorl, especially the middle ones, are still smaller than those of the other whorl, but they become almost equal in size in late bud (Fig. 8K). During anther differentiation, the androecium becomes twisted and is thus asymmetric (compare Fig. 8G, I, J). Elongation of the anther tips begins in late bud (Fig. 8J–L). Filament union begins in late midstage bud (Fig. 8K, L). During anther differentiation in midstage bud, the carpel becomes arcuate and deflected (Fig. 8I). The deflection becomes stronger in late bud (Fig. 8J, K).

**DISCUSSION**

**Patterns of floral (a)symmetry**—About half of the approximately 350 species of _Senna_ have asymmetric, enantiostylovous flowers, with both left and right morphs on the same plant (Irwin and Barneby, 1982). In our study, the morph of a flower is correlated with the direction of spiral calyx aestivation: a clockwise spiral corresponds to a right morph and a counterclockwise spiral to a left morph (Fig. 4D). Interestingly, in _S. aciphylla_ the spiral calyx aestivation appears to be correlated with the lateral orientation of the ventral slit in early gynoecium development, which means that the floral morph is also correlated with the ventral slit orientation: slit oriented to the left = right morph; slit oriented to the right = left morph (see Fig. 6E, 8). The morph can thus be predicted by observing the calyx aestivation in the floral bud. Whether such a correlation occurs in other monomorphic enantiostylovous genera with pentamerosous flowers has, to our knowledge, not been investigated. Similarly, the two androecium asymmetry morphs in _Convolvulus_ species (_Convolvulaceae_) are related to the direction of calyx aestivation (Endress, 1999). An enantiomorphic calyx is, however, present in all _Senna_ flowers, including the monosymmetric ones. Species with asymmetric flowers occur in clades II–VI, while those with monosymmetric flowers characterize clades I and VII.

The first sepal is always in median abaxial position, although a subtending bract is well developed, while bracteoles appear to be absent (Tucker, 1996), except in _S. paradoctylon_ (Irwin and Barneby, 1982). In fact, bracteoles may be initiated and then suppressed, as was found in several papilionoids (Prenner, 2004a) and in our preliminary SEM studies of _Senna_ species (unpublished data); bracteoles can also be completely absent, as in many other legumes (Sokoloff et al., 2007).

We recognized six major patterns of floral (a)symmetry, which we describe from the simplest to the most complex (Table 1; Fig. 4A, patterns 1–6). Pattern 1 corresponds to floral monosymmetry (although a slight, inconsistent gynoecium deflection can be observed in some flowers). The petals are usually flat (_Senna_ clades I and VII, _Cassia_), or rarely, the lower petals may be concave (species of subclade VIIa). Pattern 2, the simplest pattern of floral asymmetry, involves the lateral deflection of the gynoecium only, while the androecium and corolla are monosymmetric (clades II, few species of subclade IVb). In pattern 3, floral asymmetry additionally involves the corolla, whereas the androecium is nearly monosymmetric (subclade IIIa) or slightly irregular (species of clade IVa). This androecial irregularity does not pertain to lateral deflection of stamens nor to a conspicuous size modification of one of the lateral abaxial stamens (discussed later), but rather to small differences in size among all stamens and space constraints during development. Corolla asymmetry is due to concavity of the lower petal opposite the deflected carpel (e.g., _S. aciphylla_, clade IVa; Fig. 2). In pattern 4, floral asymmetry additionally involves the deflection of the median abaxial stamen (_S. skinneri_, species of clades IVb, V, VI), and in pattern 5 the modification in size of one lateral abaxial stamen either opposite the deflected carpel (species of subclades IVa and VIa) or on the same side (e.g., _S. multijuga var. multijuga_, clade VI; Fig. 3H). The corolla has an array of modifications especially of the lower petals, from one lower petal concave to both lower petals highly concave and modified in size and shape, i.e., foot-shaped. In addition, in pattern 5 the upper petals may be reduced (e.g., _S. acuruensis var. acuruensis_, clade VI; Figs. 1M, 3G). In pattern 6, the most complex pattern of asymmetry, the deflection of the carpel and both the median and one lateral abaxial stamens and the modification of the size and shape of the lower petals contribute to the floral asymmetry (species of clades III, VI). The asymmetric corollas are diverse: the upper petals are not reduced and one lower petal (e.g., _S. aversiflora_ of clade VI; Fig. 3D) or both lower petals (e.g., _S. wislizeni_ of subclade IIIa; Figs. 1G, 2H) are foot-shaped, or, alternatively, the upper petals are reduced, one lower petal is foot-shaped and the other lower petal is either concave and almost monosymmetric (e.g., _S. pallida_, clade VI; Figs. 1O, 3I), or flat and asymmetric (e.g., _S. tonduzii_, clade VI; Figs. 1N, 3F). Also, in flowers in which both lower petals are foot-shaped, these two differ from each other in size.
Fig. 5. SEM of floral development of *Senna wislizeni* (clade III) (clades in Fig. 4). Subtending bract removed in all flowers; one to all sepals removed in B–L; one to all petals removed in D–L. Flowers with adaxial side up in A–I. Right floral morph in B–F, left floral morph in G–L. Asterisk indicates gynoecium. (A) Initiation of first sepal (S1). (B) Quincuncial aestivation of calyx (S1–S5), initiation of petals (arrows). (C) Unequal development of lower petals (LP); initiation of organs of outer androecial whorl (arrows). (D) Quincuncial corolla aestivation; shape differentiation of one (left) lower petal. (E) Outer androecial whorl and carpel. (F) Initiation of organs of inner androecial whorl (arrows). (G) Differentiation of organs of outer androecial whorl into adaxial staminodes (ad°), middle stamens (m°), and abaxial stamens (ab°); unequal development of lateral abaxial stamens of inner androecial whorl (arrows) vs. other organs of the same whorl. (H) Differentiation of anther tips and lateral furrows; organs of inner androecial whorl partially hidden (arrows); carpel arcuate and in median plane of floral symmetry. (I) Anther differentiation in midstage bud. (J) Adaxial view of G. (K) Adaxial view of H. (L) Adaxial view of I; late stage of anther development, with the median abaxial stamen (arrow) largest; orifice of stigmatic chamber below asterisk. Scale bars in A = 125 µm, in B–L = 250 µm.
Fig. 6. SEM of floral development of *Senna aciphylla* (clade IVa) (clades in Fig. 4). Subtending bract removed in all flowers; four or all sepals removed in C–L; all petals removed in F–L. Flowers with adaxial side up in A–I. Right floral morph in A, E, left floral morph in B–D, F–L. (A) Spiral sequence of first three sepals (S1–S4) and initiation fifth sepal (arrow). (B) Quincuncial aestivation of calyx (S1–S5). (C) Development of lower petals (LP) and one lateral upper petal (on the right), and initiation of other upper petals; initiation of four stamens of outer androecial whorl (arrows). (D) Unequal development of petals; development of stamens of outer androecial whorl (ab°, m°, ad°) and abaxial organs of inner whorl (arrows); androecium nearly monosymmetric; initiation of carpel (asterisk). (E) Quincuncial corolla aestivation; oblique direction of ventral slit of carpel (asterisk). (F) Differentiation of stamens of outer androecial whorl; development of abaxial organs of inner whorl (ab). (G) Differentiation of stamens of outer androecial whorl and of abaxial organs of inner whorl. (H) Differentiation of anther tips and lateral furrows in midstage bud; organs of inner androecial whorl partially hidden (arrows); androecium nearly monosymmetric; carpel arcuate and laterally deflected. (I) Late stage of anther differentiation; carpel laterally deflected. (J) Adaxial view of G. (K) Adaxial view of H. (L) Lateral/adaxial view of I. Scale bars = 250 µm.
Fig. 7. SEM of floral development of *Senna mucronifera* (clade IVb) (clades in Fig. 4). Subtending bract removed in all flowers; two to all sepals removed in B–L; one to all petals removed in D, F–L. Flowers with adaxial side up in A–I. Right floral morph in C, D, F, G, I, J, L; left floral morph in A, B, E, H, K. (A) Initiation of first and second sepal (S1, S2). (B) Quincuncial calyx aestivation (S1–S5), initiation of petals (arrows). (C) Unequal differentiation of lower petals (LP) vs. upper petals (UP); initiation of organs of outer androecial whorl (arrows). (D) Differentiation of one lower petal into foot-shaped organ; development of abaxial organ of the inner androecial whorl (arrow). (E) Quincuncial corolla aestivation. (F) Development of organs of both androecial whorls (ab°, ab, m°, m, ab°, arrow); development of carpel (asterisk). (G) Differentiation of organs of androecial whorls into adaxial staminodes (ad°, median arrow), middle stamens (m°, lateral arrows), and abaxial stamens (ab°, ab); carpel arcuate. (H) Differentiation of anther tips and lateral furrows; unequal growth of middle and adaxial organs vs. abaxial organs of inner androecial whorl (arrows). (I) Anther differentiation in late midstage bud; carpel slightly deflected. (J) Adaxial view of G. (K) Adaxial view of H; orifice of stigmatic chamber below asterisk. (L) Adaxial view of I. Scale bars in A = 125 µm, in B–L = 250 µm. Abbreviations as in Fig. 4.
Fig. 8. SEM of floral development of Senna tonduzii (clade VI) (clades in Fig. 4). Subtending bract removed in all flowers; four or all sepals removed in B–L; three to all petals removed in E–G, I–L. Flowers with adaxial side up in A–I. Right floral morph in A–C, left floral morph in D–L. (A) Spiral initiation sequence of first four sepals (S1–S4). (B) Unequal development of lower (LP) and upper petals (UP); organs of outer androecial whorl initiated (arrows). (C) Shape differentiation in lower petals; development of organs of outer androecial whorl (arrows). (D) Corolla aestivation. (E) Beginning of development of organs of inner androecial whorl (arrows); carpel initiation (asterisk). (F) Development of organs of both androecial whorls (ab°, ab, m°) and of upper petals; development of carpel (asterisk). (G) Differentiation of organs of androecial whorls into adaxial staminodes (ad°, ad), middle stamens (m°), and abaxial stamens (ab°, ab). (H) Unequal differentiation of upper vs. lower petals. (I) Early midstage of differentiation of anther tips and lateral furrows; carpel deflected. (J) Late stage of anther differentiation. Staminodes indicated by arrows; carpel strongly deflected. (K) Adaxial view of J; filament union indicated by arrowheads. (L) Lateral view of J; filament union indicated by arrowheads. Scale bars: in A–D, F–L = 250 µm, in E = 125 µm.
Finally, dissection of floral asymmetry allowed us to recognize at least six structural elements, involving five organs from three different floral whorls (Table 1) that in diverse combinations form the five patterns previously described: (1) deflection of the carpel (patterns 2–6); (3) deflection of the median abaxial stamen (patterns 4, 6); (3) deflection (pattern 6) or, rarely, (4) deflection (pattern 5) of one lateral abaxial stamen; and modification in size and shape of (5) one or (6) both lower petals (patterns 3–6).

**Patterns of petal diversity**—Diversity in the corolla is particularly interesting in *Senna* because petals have undergone diverse morphological modifications (Table 1; Fig. 4B). They include: (1) reduction of upper petals (clades IIb, VII, VI, excluding VIa), (2) emarginate or bilobed shape of standard petal (clades V, VII and species of IV), (3) concavity of the standard petal (clade II), (4) concavity of lower petals (species of clades III–VII), and (5) enlargement and modification into asymmetric shape of lower petals (clades III, VI, and species of clade IVb). Our results do not support Tucker’s (1997, p. 160) observation that the enlarged petal in *Senna* is a lateral upper (“wing”) petal. The latter two petal modifications contribute to most of the diversity observed in corolla asymmetry. In the first kind, the upper petals may be unequally reduced, i.e., the lateral upper petals are of slightly different size, but this unequal reduction only weakly affects floral asymmetry. Moreover, they are often partially hidden by the enlarged lower petals. Strong petal modification causing asymmetric corollas is found also in the lower petals of *Chamaecrista* (Tucker, 1996, 1997). However, in some species of this genus, one upper lateral petal may be strongly modified to enclose the stamens (Okpon, 1969).

Petal venation in *Senna* is unusually diverse (Fig. 1). In most species, petals have three veins, but in a few species of the basal lineages of *Senna* and in *Cassia javanica*, petals have a single main vein. Also, petals of the small-flowered *S. uniflora* (clade V, Fig. 1K) and the highly reduced upper petals in a few species of subclade VI (Fig. 1M) have a single main vein, probably because of the reduction in petal size. Rarely, there are two main veins in highly modified, asymmetric lower petals (Fig. 1F, G) or in the standard petal (Fig. 1H, H'). The veins are particularly strong in highly concave and asymmetric lower petals (Figs. 1F–H, J, M–P), and rarely also in the standard petal (Fig. 1D, E).

**Implications for systematics of Senna**—Patterns of floral (a)symmetry and petal morphology are constant within a few clades suggested by molecular analyses (Marazzi et al., 2006). Pattern 1 (i.e., floral monosymmetry) is constant in clades I and VII, pattern 2 in clade II, pattern 4 in clade V, pattern 5 in subclade VIa (equivalent to series *Aphyllae*), and emarginate standard petal in subclades IVb* (equivalent to series *Trigonelloideae*) and VIa (see Table 1 and Fig. 4A). In addition, petal venation is constant in clade I (one main vein) and in clades IV–VII (three main veins). Compared to floral features not affecting floral (a)symmetry (Marazzi et al., 2007), the structural elements involved in floral (a)symmetry studied here are more evolutionarily flexible and provide less support for the major clades and subclades of *Senna* (Marazzi et al., 2006) and the current series of the genus (Irwin and Barneby, 1982).

**Floral development and expression of floral asymmetry**—The high diversity in patterns of floral asymmetry observed in

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**Table 1.** Six patterns of floral symmetry in *Senna* based on different combinations of character states of structural elements and distribution of these patterns within *Senna* (see Fig. 4A; after Marazzi et al., 2006, 2007). Characters (i.e., structural elements) and character states for symmetry of gynoecium (0, carpel in plane of floral monosymmetry; 1, carpel deflected to the side); androecium, median abaxial stamen (0, organ not deflected; 1, organ deflected) and lateral abaxial stamen (0, organ not deflected or modified in size; 1, organ deflected or modified in size); and corolla (0, petals not involved in floral asymmetry; 1, petals involved in floral asymmetry). See Fig. 4B for petal shapes. Clades after Marazzi et al. (2006, 2007).

<table>
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<tr>
<th>Pattern</th>
<th>Character states</th>
<th>Petal shape LP</th>
<th>Petal shape UP</th>
<th>Distribution in <em>Senna</em></th>
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<td>N</td>
<td>IIIa</td>
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Abbreviations used: C, concave; F, almost flat and open; LP, lower petals; LPoc, lower petal opposite the deflected carpel; LPsc, lower petal on side of carpel; M, monosymmetric; N, not reduced, standard petal not emarginate; N°, not reduced, standard petal emarginate; R, reduced; SS, modified in size and shape; UP, upper petals.
Senna, in addition to monosymmetry, likely reflects diverse patterns of floral development. Floral development was previously known in detail from only one species, *S. didymobotrya* (Tucker, 1996), a species of clade II with deflected carpel but monosymmetric androecium and corolla. We investigated the floral development of another species with moderately asymmetric flowers (*S. aciphylla*, Fig. 6, clade IVa) and, for the first time, species with strongly asymmetric flowers (*S. wislizeni*, clade III, Figs. 2H, 5; *S. mucronifera*, clade IVb, Figs. 2M, 7; and *S. tonduzii*, clade VI, Figs. 3F, 8).

**Organogenesis**—The first sepal initiated is always median abaxial, and the others follow in spiral sequence (this study; Tucker, 1996). Petals are also initiated in spiral sequence but almost simultaneously. Petals are initially equal (*S. didymobotrya*, Tucker, 1996), or unequal with the lower petals larger than the upper (*S. mucronifera*, *S. wislizeni*, and *S. tonduzii*, this study), or the upper petals are initially unequal but later become of similar size (*S. aciphylla*, this study). The organs of the outer androecial whorl are initiated after initiation of all petals (*S. wislizeni*, this study; *S. didymobotrya*, Tucker, 1996), or their initiation overlaps with petal initiation (*S. aciphylla*, this study). In both androecial whors, the organs are initiated in unidirectional order, from abaxial to adaxial. The carpel is initiated before any stamens (*S. didymobotrya*, Tucker, 1996), or unequal with the lower petals larger than the upper (*S. mucronifera*, *S. wislizeni*, and *S. tonduzii*, this study), or the upper petals are initially unequal but later become of similar size (*S. aciphylla*, this study). The organs of the outer androecial whorl are initiated after initiation of all petals (*S. wislizeni*, this study; *S. didymobotrya*, Tucker, 1996), or their initiation overlaps with petal initiation (*S. aciphylla*, this study).

In both androecial whors, the organs are initiated in unidirectional order, from abaxial to adaxial. The carpel is initiated before any stamens (*S. didymobotrya*, Tucker, 1996), or after the outer androecial organs (*S. aciphylla*, *S. mucronifera*, and *S. wislizeni*, this study), or after inner abaxial androecial organs (*S. tonduzii*, this study). Tucker (1996) cursorily mentions an organogenesis similar to that of *S. didymobotrya* in *S. artemisioides* (clade IVa), *S. bicapsularis* (clade VIIa), *S. obtusifolia* (clade IVb), *S. occidentalis* (clade VIIa), and *S. surattensis* (clade uncertain).

In contrast to *Senna* and most caesalpinioïds, the first initiated sepal is lateral abaxial in *Cassia javanica* (Tucker, 1996) and some other caesalpinioïds (Tucker, 1992, 1998, 2001, 2002; Kantz, 1996). Spiral sequence of sepal and petal initiation combined with unidirectional stamen initiation, as in *Senna*, corresponds to one of the common patterns found in caesalpinioïds, whereas another common pattern is spiral sequence of sepal and petal initiation combined with unidirectional petal and stamen initiation, which occurs in *Cassia* and *Chamaecrista*, for example (Tucker, 1996). A similar range of variation in timing of carpel initiation as observed in the *Senna* species studied here appears to be present in *Cassia* and *Chamaecrista* (Tucker, 1996).

**Organ development**—The sepal enlarges in the sequence of their spiral initiation (this study; Tucker, 1996). The petals reach an equal size early (*S. aciphylla*, this study; *S. didymobotrya*, Tucker, 1996), or they remain unequal until the onset of petal overlapping (*S. auriculata*, *S. bicapsularis*, *S. xfloribunda*, and *S. obtusifolia*, Tucker, 1996) or up to anthesis (*S. mucronifera*, *S. tonduzii*, and *S. wislizeni*, this study). Two patterns of corolla aestivation occur (Fig. 4C): (1) cochlear ascending, as typical of most caesalpinioïds (*S. auriculata*, *S. bicapsularis*, *S. corymbosa*, *S. lindeheimeriana*, *S. multijuga*, *S. pallida*, *S. pendula*, and *S. surattensis*, Tucker, 1996), and (2) quincuncial (*S. aciphylla*, *S. mucronifera*, *S. wislizeni*, and *S. tonduzii*, this study; and *S. alata*, *S. artemisioides*, *S. didymobotrya*, *S. polypylla*, *S. quinquangulata*, and *S. racemosa*, Tucker, 1996). The two patterns are probably dependant on the speed of petal growth: early enlarging petals maintain the pattern of their spiral initiation sequence resulting in quincuncial aestivation, whereas late enlarging petals are influenced by the developing floral monosymmetry, which results in a cochlear ascending aestivation. In early development, the median abaxial stamen enlarges faster than the other organs of the outer androecial whorl (*S. mucronifera*, *S. wislizeni*, and *S. tonduzii*, this study; *S. didymobotrya*, Tucker, 1996) or almost as fast as the other organs of the same whorl (*S. aciphylla*, this study). In all species studied, the middle and adaxial organs of the inner androecial whorl remain smaller than their counterparts of the outer whorl up to late-stage bud. In midstage bud, anthers begin to differentiate, and anther tips of abaxial stamens begin to elongate. The three abaxial stamens become similar in size and larger than the middle ones (*S. mucronifera* and *S. tonduzii*, this study), or the median abaxial one remains smaller than the lateral ones but is larger than the middle ones (*S. didymobotrya*, Tucker, 1996). Size difference between the abaxial and middle stamens may appear only in late bud (*S. wislizeni*, this study).

The carpel becomes arcuate and covered by hairs during midstage bud, and its stigmatic chamber is formed. The hairs fringing the stigmatic orifice develop in late bud.

**Expression of floral asymmetry**—The time at which floral asymmetry becomes evident during development differs according to the pattern of floral asymmetry at anthesis (patterns 1–6, Table 1, Fig. 4A). In enantiostyly *Senna* species, floral asymmetry involves either carpel deflection only or also stamen deflection or modification in size, and petal modification in size and shape (Table 1). Interestingly, flowers of all studied species with quincuncial corolla aestivation are enantiostylyous. In contrast, those of most species with cochlear ascending corolla aestivation are monosymmetric. In general, ascending or descending cochlear patterns prevail in monosymmetric flowers of large clades of core eudicots, such as Leguminosae and Lamiales (Endress, 1994). However, both patterns, cochlear and quincuncial, appear to occur also in *Chamaecrista* (Okpon, 1969; Tucker, 1996). More species should be studied in *Senna*, including also species of the nonrepresented clades I and V, to test whether a quincuncial corolla aestivation is restricted to asymmetric, enantiostylyous flowers.

Floral asymmetry appears at different developmental stages in the different floral whors of *Senna*. Prominent corolla asymmetry is expressed in early bud; the lower petals become modified in shape and size when they begin to develop (Figs. 5C, D, 7C, D, 8C, D). Asymmetry in the androecium is expressed in early midstage bud, when the size of the thecae in the median abaxial stamen becomes unequal (Figs. 5F, 7F, 8G). In addition, the androecium in *S. tonduzii* becomes conspicuously twisted during anther differentiation (Figs. 8G, I, J). A twisted pattern is also observed during development of the outer androecial whorl in *S. aciphylla* (Fig. 6F, G, J) and *S. wislizeni* (Fig. 5F), but it later disappears. Deflection of abaxial stamens to the side takes place only at anthesis. Asymmetry in the gynoecium of *S. tonduzii* appears to be expressed early in development; the carpel primordium appears to be displaced from the median plane of the flower (Fig. 8E). In *S. aciphylla*, the ventral slit of the carpel is oriented slightly obliquely in early bud (Fig. 6E, F), as found in some other caesalpinioïds with monosymmetric flowers (e.g., *Bauhinia malabarica*, Tucker, 1988; *Ceratonia siliqua*, Tucker, 1992; *Cassia javanica*, Tucker, 1996). It would be interesting to know whether the early asymmetries in the gynoecium of *Senna* species are related to the deflection of the carpel (enantiostyly), which appears to occur in midstage bud (*S. aciphylla*, Fig. 6H, I; *S. mucronifera*, Fig. 7I, K, L; *S. tonduzii*, Fig. 8H–L) or late bud (*S. didymobotrya*, Tucker, 1997; *S. wislizeni*, Fig. 5I, L). In other
enantiostyly of families (mostly monocots), enantiostyly is expressed late in development: the style becomes deflected in late bud (Wachendorfia paniculata, Dilatris corymbosa, and Philydrum lanuginosum) or only at anthesis (Cyanella lutea, Monochoria australasica, species of Heteranthera, and Solanum rostratum) (Jesson et al., 2003). This is also the case in enantiostyly genera of Gesneriaceae (Sainpaulia and Streptocarpus, Harrison et al., 1999; Q. C. B. Cronk, University of British Columbia, Vancouver, Canada, personal communication).

In caesalpinioiids, floral symmetry varies from nearly poly- symmetric to moderately or pronounced monosymmetric (Tucker, 2003) and asymmetric (Senna, Chamaecrista, and Labichea; Tucker, 1996, 1997, 1998; Marazzi et al., 2006). Whereas in Senna most of the floral asymmetry is expressed in the midstage bud or later, in Chamaecrista fasciculata the entire organogenesis is asymmetric: the floral asymmetry in the androecium and corolla is expressed at early stages by precocious organ initiation on one side (left or right; Tucker, 1996, 1999). A similar asymmetrical initiation was found in Schotia africana (Tucker, 2001) but in contrast to Chamaecrista, asymmetry does not persist in the flower at anthesis; it disappears during organ development. Also in Labichea lanceolata, which is distantly related to Senna (Bruneau et al., 2001) and characterized by reduced number of floral organs and dissimilar stamens, floral asymmetry is expressed very early in development, including an asymmetric floral apex and an asymmetric order of organ initiation (Tucker, 1998). The androecium of several mono- symmetric papilionoids is also asymmetric in early developmental stages because the adaxial antesepalous stamen is formed to the left or right of the median plane (Prenner, 2004b).

The asymmetrically curved or coiled keel, enclosing the asymmetric androecium and gynoecium of some papilionoids (Phaseolinae, Vicieae) is usually the result of late ontogeny (Tucker, 1999), as shown for Lathyrus lattifolius (Prenner, 2003) and Vigna caracalla (Troll, 1951; Prenner, 2003).

Implications for pollination biology—Enantiostyly is restricted to buzz-pollinated flowers, in which other features (such as poricidal anther dehiscence, heteranthey, and pointed stigmas) evolved in relation to the unusual pollination biology (e.g., Buchmann, 1983). In Senna, pollen-collecting bees extract pollen by vibrating the middle “feeding” stamens, which they clasp with their legs (e.g., Buchmann, 1974; Delgado Salinas and Sousa Sánchez, 1977; Dulberger, 1981; Gottsberger and Silberbauer-Gottsberger, 1988; Westerkamp, 2004). The abaxial “pollinating” stamens are usually longer and display a higher diversity in anther dehiscence specialization than feeding stamens (Marazzi et al., 2007). Most species of Senna have a long and arcuate carpel with an extremely small, chambered or crater-like stigma (Marazzi et al., 2007). Dulberger et al. (1994) suggested that the diversity in inflection of the style tip and stigma position and orientation evolved in relation to the specific size and positioning of the bees visiting the flowers. However, different lengths and inflections of the entire carpel may also be associated with different sizes of bees. The morphology of the carpel (i.e., straight or arcuate, median or deflected) may also be related to which body part of the bee approaches or touches the stigma, thus suggesting a functional significance for enantiostyly (e.g., Jesson et al., 2003; Jesson and Barrett, 2005).

Enantiostyly has commonly been regarded as a device to promote outcrossing (Todd, 1882) because pollen of a left floral morph is deposited on a place on the body of bees that corresponds to the position of the stigma in a right floral morph, and vice versa. In monomorphic enantiostyly taxa, such as Senna, the presence of both left and right floral morphs on the same plant and the observation that many of these plants are self-compatible indicate that geitonogamous self-pollination between different morphs is possible. However, compared to monosymmetry, enantiostyly appears to function to reduce geitonogamous pollen transfer (Jesson and Barrett, 2003, 2005).

Specifically, Jesson and Barrett (2003) suggested that enantiostyly associated with heteranthery and the deflection of a pollinating anther to the opposite side of the style may function to increase the precision of cross-pollen transfer and to reduce interference of stigmas and anthers within or between flowers on the same plant. Other authors have suggested that enantiostyly may only facilitate the access of the pollen-collecting bees to the middle anthers, which the bees clasp and vibrate, forcing the bees to adopt a position that results in a greater pollen removal (Westerkamp, 2004) and also protecting the gynoecium from damage by buzzing bees (Dulberger, 1981; Dulberger et al., 1994).

Diverse floral (a)symmetry patterns in Senna, including complex enantiostyly with highly asymmetric androecium and corolla, seem to be especially involved in pollen dispersal. Different pointing directions of anther pores appear to be related with different directions of pollen release (Marazzi et al., 2007). Most anthers release pollen directly toward the floral center and thus toward the bees. During buzzing, vibrational energy is transmitted either from the thorax of the bee (clasping the middle stamens) to the flower and thus to other floral parts, such as the abaxial pollinating stamens, the carpel, and petals (Buchmann and Hurley, 1978; Westerkamp, 2004) or by the body of the bee touching the pollinating stamens (Endress, 1997). In highly asymmetric flowers, anther pores of the abaxial pollinating stamens are usually directed toward the lower petals (Marazzi et al., 2007). These petals are positioned in such a way that pollen loss is avoided: they are highly concave, foot-shaped, and/or asymmetric, and they partially surround the pollinating stamens (Figs. 2F–H, L, M, 3D–L). Therefore, when bees buzz these flowers, pollen from the pollinating stamens is released toward the lower petals; vibration of these lower petals helps the pollen ricochet and finally adhere to the bees (e.g., Delgado Salinas and Sousa Sánchez, 1977; Westerkamp, 2004). We observed that in species of clade II, with enantiostyly flowers and monosymmetric corolla, the standard petal is pronouncedly concave and partially encloses the floral reproductive organs (Fig. 2C–E). In these flowers, the two large pollinating stamens are curved upward, and their anther pores are directed toward the standard petal (Marazzi et al., 2007; Fig. 2C–E). Therefore, the released pollen flow likely ricochets off the standard petal in a similar way, as described for flowers with concave and asymmetric lower petals. The particularly robust venation typical of both the highly concave standard petal and the asymmetric lower petals (Fig. 1D, E, and Figs. 1F–H, J, M–P, respectively), and their almost sessile shape, may be adaptations for efficiently transmitting the vibrations produced by the buzzing bees from the middle stamens (on which the bees clasp) to the concave petal blade.

Conclusion—Many kinds of floral asymmetry exist in angiosperms, which are expressed at different times during development and which may affect one or more floral whorls in diverse ways, such as asymmetric position of organ initiation, unequal organ differentiation, and deflection to one side. Floral
symmetry is composed of several structural elements and is thus best interpreted as a character complex rather than a single character. Because patterns of floral symmetry may not be strictly homologous, the elements involved in the floral symmetry should be treated individually if used for phylogenetic hypotheses (Bruneau, 1997; Herendeen et al., 2003) or for optimization studies, such as ancestral character state reconstruction (Marazzi et al., 2006). In Senna, complexity of floral symmetry is particularly evident. The genus includes not only monoosymmetric flowers, but also several kinds of asymmetric flowers with different organs of different floral whorls contributing to the floral asymmetry, and unrelated species have superficially similar asymmetric flowers. Detailed knowledge on the diverse floral morphology is a precondition for hypotheses on the evolution of floral asymmetry in Senna. In addition to reconstructing the evolution of each floral structural element involved in the floral (a)symmetry, testing for correlations among structural elements would allow us to recognize to what degree they evolved together or independently from each other.

LITERATURE CITED


Kantz, K. E. 1996. Floral development in the caesalpinioide tribe Caesalpinioideae (Fabaceae). Ph.D. dissertation, Louisiana State University, Baton Rouge, Louisiana, USA.


APPENDIX. Taxa used in this study, source, and voucher information. Clades or subclades of Senna by Marazzi et al. (2006) and sections by Irwin and Barneby (1982) (AS, Astr oxid; CH, Chamaefstula; PA, Paradictyon; PE, Peiranista; PS, Psilorhegma; SE, Senna). Acronyms of herbaria or botanical gardens: CBG = ANBG = Australian National Botanic Gardens; BGB = Botanic Garden of the University of Basel; BGZ = Botanic Garden of the University of Munich; BGZ = Botanic Garden of the University of Zurich; CTES = Instituto de Botánica del Nordeste de Corrientes; PMA = Parque Nacional de Panamá; STRI = Smithsonian Tropical Research Institute, Balboa; Z = Herbarium of the University of Zurich and Botanic Garden. Cult. = specimen from cultivated plants.

TAXON: Clade, Section [given only for Senna species]; Voucher specimen, Source, Herbarium.

Cassia fistula L.; Cult.: Endress 5007, Australia, Queensland, Brisbane, Z. C. javanica L.; Cult.: Endress 6411, Australia, Queensland, Brisbane, Z.

Senna aciphylla (Benth.) Randell; IVa, PS; Cult.; CGB 990061, CBG, Z. S. acuchenus var. acuchenus (Benth.) H.S. Irwin & Barneby; VI, PE; Wild; Conceição & Marazzi AC1125, Brazil, Bahia, HUEFS, Z. S. acuchenus var. catenae (Harms) H.S. Irwin & Barneby; VI, PE; Wild; Queiroz & Marazzi LQ 9177, Brazil, Bahia, HUEFS, Z. S. acuchenus var. catenae (Harms) H.S. Irwin & Barneby; VI, PE; Wild; Queiroz & Marazzi LQ 9205, Brazil, Bahia, HUEFS, Z. S. alata (L.) Roxb.; II, SE; Wild; Marazzi et al. BM626, Paraguay, Caaguazú, PY, CTEZ, Z. S. aphylla (Cav.) H.S. Irwin & Barneby; VI, PE; Wild; Marazzi et al. BM0084, Argentina, Santiago del Estero, CTEZ, Z. S. apiculata (M. Martens & Galeotti) H.S. Irwin & Barneby; V II, CH; Wild; Marazzi & Flores BM1170, Mexico, Puebla, MEXU, Z. S. armata (S. Watson) H.S. Irwin & Barneby; V II, CH; Wild; Schönberger IST51, USA, California, Z. S. arteniosioides (DC.) Randell; IVa, PS; Cult. s.n. BGZ; Marazzi BM001, Z. S. atomaria (L.) H.S. Irwin & Barneby; III, PE; Wild; Marazzi & Marazzi BM0173, Mexico, Oaxaca, MEXU, Z. S. averissifera (Herbert) H.S. Irwin & Barneby; VI, PE; Wild; Queiroz & Marazzi LQ 9204, Brazil, Bahia, HUEFS, Z. S. barclayana (Sweet) Randell; V II, CH; Cult. BGCT 2003376; Marazzi BM136, garden, Z. S. bistorolis (Hook.) H.S. Irwin & Barneby; V II, CH; Wild; Marazzi et al. BM090, Argentina, Tucumán, CTEZ, Z. S. cana var. calva H.S. Irwin & Barneby; V, CH; Wild; Conceição & Marazzi 1132, Brazil, Bahia, HUEFS, Z. S. cernua (Balb.) H.S. Irwin & Barneby; V II, CH; Wild; Marazzi et al. BM007, Paraguay, Caaguazú, PY, CTEZ, Z. S. chacoënsis (L.) Bravo H.S. Irwin & Barneby; V II, SE; Wild; Marazzi et al. BM626, Paraguay, Caaguazú, PY, CTEZ, Z. S. chacoënsis (L.) Roxb.; II, SE; Wild; Marazzi et al. BM626, Paraguay, Caaguazú, PY, CTEZ, Z. S. chlorocala (Harms) H.S. Irwin & Barneby; IVb, CH; Wild; Marazzi et al. BM129, Argentina, Salta, CTEZ, Z. S. corymbosa (Lam.) H.S. Irwin & Barneby; V II, CH; Cult. in private garden; Marazzi et al. BM103, Argentina, Tucumán, CTEZ, Z. S. crassiramea (Benth.) H.S. Irwin & Barneby; VI, PE; Wild; Marazzi et al. BM120, Argentina, Jujuy, CTEZ, Z. S. dairiensis var. hypoglauca H.S. Irwin & Barneby; V II, CH; Wild; Marazzi & Alvarez BM153, Republic of Panama, Cochlé, PMA, STRI, Z. S. didymobotrya (Fresen.) H.S. Irwin & Barneby; II, SE; Cult. BGZ 19700009; Marazzi BM002, Z. S. hayesiana (Britton & Rose) H.S. Irwin & Barneby; IVb, CH; Wild; Marazzi & Alvarez BM150, Republic of Panama, Panamá, PMA, STRI, Z. S. hilariana (Benth.) H.S. Irwin & Barneby; V II, CH; Wild; Marazzi et al. BM027, Paraguay, Alto Paraná, PY, CTEZ, Z. S. hirsuta var. leptocarpa (Benth.) H.S. Irwin & Barneby; V II, CH; Wild; Marazzi et al. BM065, Paraguay, San Pedro, V II, CH; V II, CH; Wild; Marazzi et al. BM115, Argentina, Salta, CTEZ, Z. S. holwayana var. holwayana (Rose) H.S. Irwin & Barneby; V, VI; Wild; Marazzi & Flores BM161, Mexico, Puebla, MEXU, Z. S. italica Mill.; II, SE; Wild; Zeitschmann 4345, Republic of South Africa, Free State, NMB, Z. S. macranthera var. nervosa (Vogel) H.S. Irwin & Barneby; IVb, CH; Cult. at the roadside; Marazzi et al. BM082, Paraguay, Caaguazú, PY, CTEZ, Z. S. mollissima (Willd.) H.S. Irwin & Barneby; III, PE; Wild; Marazzi & Flores BM181, Mexico, Oaxaca, MEXU, Z. S. morongii (Britton) H.S. Irwin & Barneby; V II, CH; Wild; Marazzi et al. BM130, Argentina, Salta, CTEZ, Z. S. mucronifera (Benth.) H.S. Irwin & Barneby; IVb, CH; Wild; Marazzi et al. BM019, Paraguay, Caaguazú, PY, CTEZ, Z. S. multijuga var. lindleyana (Gardner) H.S. Irwin & Barneby; V, VI; Wild; Queiroz & Marazzi LP 9226, Brazil, Bahia, HUEFS, Z. S. multijuga var. multijuga (Rich.) H.S. Irwin & Barneby; VI, PE; Cult. in private garden; Marazzi & Alvarez BM151, Republic of Panama, Panamá, PMA, STRI, Z. S. nicaraguensis (Benth.) H.S. Irwin & Barneby; II, SE; Wild; Marazzi & Flores BM185, Mexico, Chiapas, MEXU, Z. S. obtusifolia (L.) H.S. Irwin & Barneby; IVb, CH; Wild; Marazzi et al. BM024, Paraguay, Caaguazú, PY, CTEZ, Z. S. occidentalis (L.)
S. odorata (Morris) Randell; IVa, PS; Cult. ANBG 68349; s.n., CBG.
S. pallida (Vahl) H.S. Irwin & Barneby; VI, PE; Wild; Marazzi & Flores BM178, Mexico, Oaxaca, MEXU, Z.
S. paradictyon (Vogel) H.S. Irwin & Barneby; II, PA; Wild; Marazzi et al. BM028, Paraguay, Alto Paraná, PY, CTES, Z.
S. pendula (Willd.) H.S. Irwin & Barneby; VIIa, CH; Wild; Marazzi et al. BM117, Argentina, Salta, CTES, Z.
S. pilifera var. pilifera (Vogel) H.S. Irwin & Barneby; IVb, CH; Wild; Marazzi et al. BM011, Paraguay, Caaguazú, PY, CTES, Z.
S. pinheiroi H.S. Irwin & Barneby; IVb, CH; Wild; Queiroz 9210, Brazil, Bahia, HUEFS.
S. pleurocarpa (F. Muell.) Randell; II, SE; cultivated in BGZ from Seed Bank KPBG 930575; Demarc. 12081, Australia, Western Australia, unk.
S. polyantha (Collard.) H.S. Irwin & Barneby; I, CH; Wild; Marazzi & Flores BM172, Mexico, Oaxaca, MEXU, Z.
S. purpusii (Brandegee) H.S. Irwin & Barneby; VIIa, CH; Cult. BGB 3585/96-P; Marazzi BM004, Z.
S. quinquangulata (Rich.) H.S. Irwin & Barneby; IVb, CH; Wild; Queiroz & Marazzi LQ 9220, Brazil, Bahia, HUEFS, Z.
S. rigida (Hieron.) H.S. Irwin & Barneby; VI, PE; Wild; Marazzi et al. BM108, Argentina, Salta, CTES, Z.
S. robinifolia (Benth.) H.S. Irwin & Barneby; VI, PE; Cult. BGM 98/3500w; Marazzi BM005, Z.
S. rizzinii H.S. Irwin & Barneby; IVb, CH; Wild; Conceição & Marazzi 1126, Brazil, Bahia, HUEFS, Z.
S. rugosa (G. Don) H.S. Irwin & Barneby; IVb, CH; Wild; Queiroz & Marazzi LQ 9181, Brazil, Bahia, HUEFS.
S. septentrionalis (Viviani) H.S. Irwin & Barneby; VIIa, CH; Cult. BGM s.n.; Marazzi BM140, Z.
S. siamea (Lam.) H.S. Irwin & Barneby; I, CH; Cult., Causeway, Panamá City; Marazzi & Álvarez BM137, Republic of Panama, Panamá, PMA, STRI, Z.
S. silvestris var. guaranitica (Chodat & Hassl.) H.S. Irwin & Barneby; I, CH; Wild; Marazzi et al. BM068, Paraguay, San Pedro, PY, CTES, Z.
S. skinneri (Benth.) H.S. Irwin & Barneby; IV, CH; Wild; Marazzi et al. BM176, Mexico, Oaxaca, MEXU, Z.
S. spectabilis (DC.) H.S. Irwin & Barneby; III, PE; Wild; Marazzi & Flores BM187, Mexico, Oaxaca, MEXU, Z.
S. unijuga (Rose) H.S. Irwin & Barneby; III, PE; Wild; Marazzi & Flores BM186, Mexico, Chiapas, MEXU, Z.
S. villosa (Mill.) H.S. Irwin & Barneby; VIIb, AS; Wild; Marazzi & Flores BM174, Mexico, Oaxaca, MEXU, Z.
S. williamsii (Britton & Rose) H.S. Irwin & Barneby; VI, PE; Wild; Marazzi & Alvarez BM158, Republic of Panama, Panamá, PMA, STRI, Z.
S. wislizeni (A. Gray) H.S. Irwin & Barneby; III, PE; Wild; Marazzi & Flores BM169, Mexico, Puebla, MEXU, Z.