MORPHOLOGICAL NOTES ON THE GENUS CASSIA: II & III*

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II: Stomatal Distribution and Morphology

According to Solereder (1908), stomata are present in most Caesalpinioideae only on the lower surface of the leaflet, but in *Cassia* numerous stomata are found on the upper leaflet surfaces. Solereder (1908) and Metcalfe & Chalk (1950) stated that the arrangement of the subsidiary cells varies even within a single species, distinct types having been observed side by side in a single leaf in certain instances. This observation is true of *C. pleurocarpa* (Fig. 2, a, b) and *C. latopetiolata* where paracytic stomata occur on the adaxial surfaces and both paracytic and actinocytic stomata occur on the abaxial surfaces. In nearly all the species with paracytic stomata, the subsidiary cells accompanying each stoma are unequal in size.

In order to establish the pattern of stomatal distribution and morphology in *Cassia*, many species belonging to different subgenera and sections as recognised by Bentham (1871) were examined. The results are listed in table I.

It became evident that apart from paracytic stomata which are common to all subgenera as previously reported, there are certain species where the stomata are surrounded by a variable number of subsidiary cells, sometimes forming a ring round each stoma. These stomata are described as tending to be actinocytic. The actinocytic stomata have so far been found in subgenus *Senna*, where they are confined to certain sections.

The epidermis from living specimens of *C. mimosoides*, *C. aeschynomene*, Botanic Garden, Edinburgh, was examined; in all other cases, herbarium specimens were used.

The distribution of stomata on leaflets, sepal, corolla and fruit of the species examined is given in table I. The stomatal types are also indicated, as is their presence or absence on the adaxial and abaxial surfaces of the leaflets and other organs.

TERMINOLOGY:— a. Paracytic is used here loosely for all cases where each stoma is accompanied on either side by one subsidiary cell. These are more or less parallel to the long axis of the stomatal aperture or pore and guard cells. These subsidiary cells may be of the same size or different sizes.

b. Actinocytic is used here in a slightly sub-standard sense for all cases where each stoma is surrounded by a variable number of subsidiary cells. The term actinocytic was applied originally to stomata surrounded by radiating subsidiary cells as seen in surface view (Metcalfe 1950). As illustrated in fig. 2, b–e, the subsidiary cells do not exhibit a very pronounced radiate arrangement in relation to the guard cells, but they may still be termed actinocytic.

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* Continued from Notes R.B.G. Edinb. 29: 185–195 (1969).

TABLE I

Distribution of stomata

P = paracytic stomata present, A = actinocytic stomata present,
— = stomata absent, ne = organ not examined.

	Leaflets		Sepal both surfaces	Fruit
	adaxial	abaxial		
SUBGENUS CASSIA				
C. fistula L.	—	P	P	P
C. brewsteri F. Muell.	—	P	P	ne
C. grandis L. f.	—	P	P	P
C. leptophylla Vog.	—	P	P	ne
C. sieberana DC.	—	P	P	P
C. nodosa Hamilt. ex Roxb.	—	P	P	P
C. abbreviata Oliv.	—	P	P	P
C. javanica L.	—	P	P	P
C. roxburghii DC.	—	P	P	P
C. renigera Wall. ex Benth.	—	P	P	P
C. bakeriana Craib	—	P	P	ne
SUBGENUS SENNA				
Section SENNA				
C. stipulacea Ait.	—	P	P	ne
C. hookeriana Gill.	P	P	P	ne
C. cumingii Hook. et Arn.	A	A	P	ne
C. arnottiana Gill.	A	A	P	ne
C. arequipensis Meyen	A	A	P	ne
C. latopetiolata Domb.	P	A	P	ne
C. versicolor Meyen	—	P	P	ne
C. coquimbensis Vog.	P	P	P	ne
C. bahamensis Mill.	P	P	P	ne
C. aphylla Cav.	A			ne
	}	from stem epidermis		ne
C. crassiramea Benth.	A			ne
C. leiophylla Vog.	P	P	P	ne
C. multiflora Mart. & Gal.	P	P	P	ne
C. biflora L.	P	P	P	ne
C. polyphylla Jacq.	P	P	P	ne
C. trachypus Mart.	—	P	P	ne
C. multijuga Rich.	—	P	P	ne
C. auriculata L.	P	P	P	P
C. wislizeni Gray	P	P	P	P
C. galeottiana Martens	—	A	P	P
C. polyantha Moc. & Sess.	A	A	P	P
C. emarginata L.	—	P	P	P
C. atomaria L.	—	P	P	P
C. sylvestris Vell.	—	P	P	P
C. racemosa Mill.	—	P	P	P
C. garettiana Craib	—	P	P	P
C. siamea Lam.	—	P	P	P
C. montana Heyne	—	P	P	ne
C. timorensis DC.	—	P	P	P
C. alata L.	P	P	P	P
C. reticulata Willd.	P	P	P	P
C. notabilis F. Muell.	P	P	P	P
C. venusta F. Muell.	P	P	P	P
C. didymobotrya Fres.	P	P	P	P
C. paradictyon Vog.	P	P	P	ne
C. podocarpa Guill. & Perr.	—	P	P	ne

	Leaflets		Sepal	Fruit
	adaxial	abaxial	both surfaces	
C. nicaraguensis Benth.	P	P	P	ne
C. pleurocarpa F. Muell.	P	A	P	ne
C. adenensis Benth.	P	P	P	ne
C. obovata Collad.	P	P	P	A
C. holosericea Fres.	P	P	P	A
C. angustifolia Vahl	P	P	P	A
Section CHAMAEFISTULA				
C. macrophylla Kunth	—	P	P	ne
C. affinis Benth.	—	P	P	ne
C. oxyphylla Kunth	P?	P	P	ne
C. bacillaris L. f.	—	P	P	P
C. viminea L.	—	P	P	ne
C. rugosa Don	—	P	P	P
C. splendida Vog.	—	P	P	ne
C. bicapsularis L.	P	P	P	P
C. corymbosa Lam.	P	P	P	P
C. laevigata Willd.	—	P	P	P
C. tomentosa L. f.	ne	ne	P	P
C. petersiana Bolle	—	P	P	ne
C. goratensis Fres.	P	P	P	P
C. spectabilis DC.	—	P	P	ne
C. pumilo Gray	P	P	P	P
C. roemeriana Scheele	P	P	P	P
C. crotalarioides Kunth	P	P	P	P
C. bauhinioides Gray	P	P	P	ne
C. lindheimeriana Scheele	P	P	P	P
C. covesii Gray	P	P	P	P
Section ONCOLOBIUM				
C. sulcata DC.	P	P	P	P
C. leptocarpa Benth.	P	P	P	P
C. occidentalis L.	P	P	P	P
C. sophera L.	P	P	P	P
C. hirsuta L.	P	P	P	P
C. marylandica L.	P	P	P	P
C. ligustrina L.	P	P	P	P
Section PROSOSPERMA				
C. tora L.	P	P	P	P
C. pilifera Vog.	P	P	P	P
C. villosa Mill.	—	P	P	P
C. dysophylla Benth.	A	A	P	P
Section PSILORHEGMA				
C. divaricata Nees & Bl.	P	P	P	ne
C. surattensis Burm. f.	P	P	P	P
C. retusa Vog.	P	P	P	P, A
C. costata Bailey & White	P	P	P	P
C. chatelainiana Gaud.	P, A	P, A	P	P, A
C. glutinosa DC.	A	A	P	A
C. pruinosa F. Muell.	A	A	A	A
C. phyllodinea R. Br.	A	A	P	P, A
C. nemophila Cunn. ex Vog. var. coriaceae (Benth.) Symon	A	A	ne	ne
C. artemisioides Gaud.	A	A	P	A
C. sturtii R. Br.	A	A	P	A

	Leaflets		Sepal both surfaces	Fruit
	adaxial	abaxial		
C. desolata F. Muell.	A	A	ne	ne
C. oligophylla F. Muell.	A	A	ne	A
C. helmsii Symon	A	A	ne	ne
C. eremophila C. Cunn.	A	A	ne	ne
Subgenus Lasiorhegma				
Section Lasiorhegma				
C. absus L.	P	P	P	P
C. punctata Vog.	P	P	P	ne
C. barbata Nees & Mart.	P	P	P	ne
C. unijuga Rose	P	P	P	ne
C. dalbergiifolia Benth.	P	P	P	ne
C. carthartica Mart.	P	P	P	ne
Section Apoucouita				
C. apoucouita Aubl.	—	P	P	ne
C. adiantifolia Benth.	—	P	P	ne
Section Xerocalyx				
C. diphylla L.	P	P	P	P
C. tetraphylla Desv.	P	P	P	P
C. chartacea Irwin	P	P	P	P
C. langsdorffii Kunth	P	P	P	P
C. curvifolia Vog.	P	P	P	P
C. piribebuiensis Chodat & Hassler	P	P	P	P
Section Chamaecrista				
C. calycioides DC.	P	P	P	P
C. tagera L.	P	P	P	P
C. pilosa L.	P	P	P	P
C. trichopoda Benth.	P	P	P	P
C. pumila Lam.	P	P	P	P
C. cordistipula Mart.	P	P	P	P
C. grantii Oliv.	P	P	P	P
C. rotundifolia Pers.	P	P	P	P
C. grammica Spreng.	P	P	P	P
C. serpens L.	P	P	P	P
C. flexuosa L.	P	P	P	P
C. venulosa Benth.	P	P	P	P
C. parvistipula Benth.	P	P	P	P
C. chamaecrista L.	P	P	P	P
C. flavicoma L.	P	P	P	P
C. virgata Swartz	P	P	P	P
C. glandulosa L.	P	P	P	P
C. stenocarpa Vog.	P	P	P	P
C. nigricans Vahl	P	P	P	P
C. brevifolia Lam.	P	P	P	P
C. nictitans L.	P	P	P	P
C. zambesica Oliv.	P	P	P	P
C. patellaria DC.	P	P	P	P
C. mimosoides L. (s. l.)	P	P	P	P
C. aeschynomene DC.	P	P	P	P
C. comosa (E. Mey.) Vog.	P	P	P	P
C. kirkii Oliv.	P	P	P	P
C. falcinella Oliv.	P	P	P	P
C. concinna Benth.	P	P	P	P
C. tristicula H.B.K.	P	P	P	P

	Leaflets		Sepal both surfaces	Fruit
	adaxial	abaxial		
C. hildebrandtii Vatke	P	P	P	P
C. fallacina Chiov.	P	P	P	P
C. fenarolii Mendonça & Torre	P	P	P	P
C. gracilior (Ghesq.) Steyaert	P	P	P	P
C. wittei Ghesq.	P	P	P	P
C. quarrei (Ghesq.) Steyaert	P	P	P	P
C. hochstetteri Ghesq.	P	P	P	P
C. exilis Vatke	P	P	P	P
C. ghesquiereana Brenan	P	P	P	P
C. jaegeri Keay	P	P	P	P
C. brachypoda Benth.	P	P	P	P
C. usambarensis Taub.	P	P	P	P

TAXONOMIC CONCLUSIONS:—Within the genus, the basic type of stomatal apparatus is paracytic, and various gradations towards the anomocytic condition are found in such organs as the fruit, corolla and anther. The condition where the stomata are surrounded by many subsidiary cells (actinocytic) is here considered as probably derived from the paracytic.

Jalan (1962) investigated the ontogeny of the stomata in *Schisandra grandiflora* where a similar arrangement of subsidiary cells as in some *Cassia* species was observed. He found that due to longitudinal or transverse divisions in one or both of the subsidiary cells, the stomata become surrounded by five or six cells. The large number of cells (sometimes up to six or seven) surrounding the guard cells arise in this manner. That the same explanation could possibly hold for similar cells arrangement found in *Cassia* is reinforced by the fact that in *C. pleurocarpa* and other species, two, three, four, or five subsidiary cells were found in the same leaflet epidermis. In this and other species, it is possible that the many subsidiary cells arise by transverse or longitudinal division of one or both subsidiary cells. This is illustrated in fig. 2, b–e.

Actinocytic stomata are confined to subgenus *Senna* especially sect. *Psilorhegma* which are plants of tropical and subtropical Australia, SE Asia and islands of the Pacific.

Abaxial stomata are present on the leaflets in all the species. In the subgenus *Cassia* and in sect. *Apoucouita* of the subgenus *Lasiorhegma*, adaxial stomata are absent. The species in these groups are predominantly trees. Sections *Lasiorhegma* and *Chamaecrista* in subgenus *Lasiorhegma* have adaxial and abaxial stomata, while in subgenus *Senna* adaxial stomata occur in some species but are absent in others.

Sepal and corolla stomata are very widespread in the genus and probably occur in all the species. In the corolla of those species that I have examined, the stomata are paracytic, though the arrangement of subsidiary cells shows gradations towards the anomocytic condition. These are illustrated in fig. 1, g–i.

Stomata occur on the anthers (mainly located along the connective walls of the anther lobes) of *C. mimosoides* and *C. aechynomene*. These are illustrated in Fig. 1, e, f. These stomata are again paracytic although they show gradations towards the anomocytic condition. The occurrence of stomata on the anthers may be of limited distribution in the genus. Stomata have not been found on the filaments.

A primary division of the genus into three groups based on stamen and fruit structure was adopted by Bentham (1871) in establishing the subgenera *Fistula* (*Cassia*), *Senna*, and *Lasiorhegma*. From Table I, it appears that this division is broadly confirmed by patterns of stomatal distribution on the leaflets. This is summarised as follows:—

Subgenera	Stomatal type	Leaflet		No. of spp.	Habit
		adaxial	abaxial		
Cassia	Paracytic	—	+	20	Trees
Senna	Paracytic or .... actinocytic	±	+	about 278	Trees, shrubs, herbs.
Lasiorhegma					
Sect. *Apoucouita*	Paracytic	—	+	6	Trees.
Other sections	Paracytic	+	+	370	Shrubs and herbs.

If the absence of adaxial stomata is of general occurrence in section *Apoucouita*, this will be an additional character for the separation of the section from other related sections.

Stomatal morphology may be useful, in combination with other characters, for the grouping of species into sections and series.

Bentham (1871) recognised two series in sect. *Psilorhegma:* a. series *Interglandulosae* with ovate oblong or short glands between the lowest pair of leaflets or many pairs; b. series *Subverrucosae* with rather obscure glands which are sometimes absent. This division is confirmed by stomatal morphology. All the species of series *Interglandulosae* that I have examined possess paracytic stomata except *C. chatelainiana* with actinocytic stomata. On the other hand, all the species of series *Subverrucosae* that I have examined possess actinocytic stomata. *C. chatelainiana* could thus be transferred on the basis of stomatal morphology from series *Interglandulosae* to series *Subverrucosae*. It has small cylindrical glands on long stalks between all or the lower pair of leaflets, and this distinguishes it from other species of series *Subverrucosae* which have obscure glands on their rachides. Symon (1966) suggests that *C. chatelainiana* is closely related to *C. glutinosa* and *C. pruinosa* (both species are in series *Subverrucosae* and have actinocytic stomata) and its transfer to series *Subverrucosae* is probably justified.

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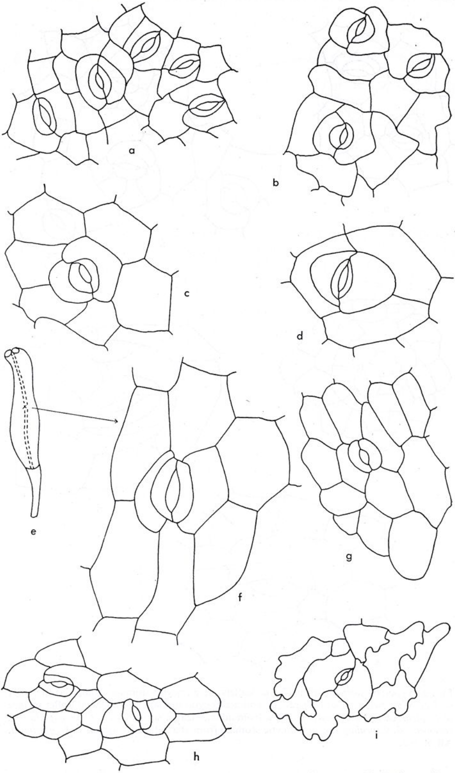

FIG. 1. Stomata from different organs in *Cassia*. a, stomata from abaxial leaflet surface of *C. fistula;* stomata from adaxial leaflet surfaces of b, *C. sophera*, c, *C. ligustrina*, d, *C. punctata*, e, location of stomata along the connective of anther wall in *C. mimosoides*, f, stomata from anther of *C. mimosoides;* stomata from g, petal of *C. laevigata*, h, sepal of *C. laevigata*, i, *C. rotundifolia* petal. All × 400.

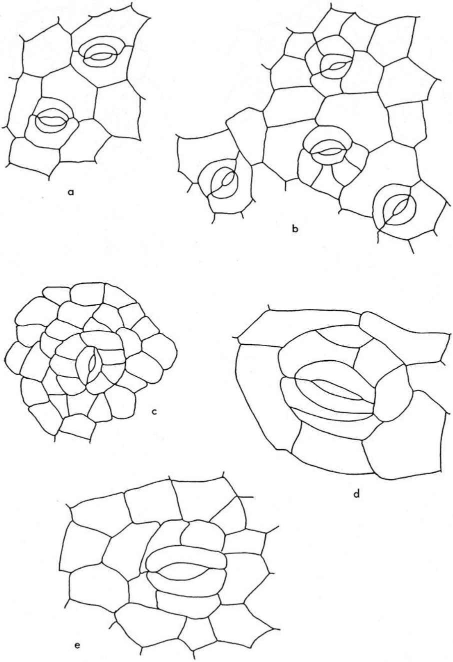

Fig. 2. Types of stomata from *Cassia* leaflets. a, paracytic stomata from adaxial leaflet surface of *C. pleurocarpa*; b, paracytic and actinocytic stomata from abaxial leaflet surface of *C. pleurocarpa*; actinocytic stomata from adaxial leaflet surfaces of c, *C. nemophila* var. *coriaceae*, d, *C. pruinosa;* e, actinocytic stomata from abaxial leaflet surface of *C. glutinosa*. All × 400.

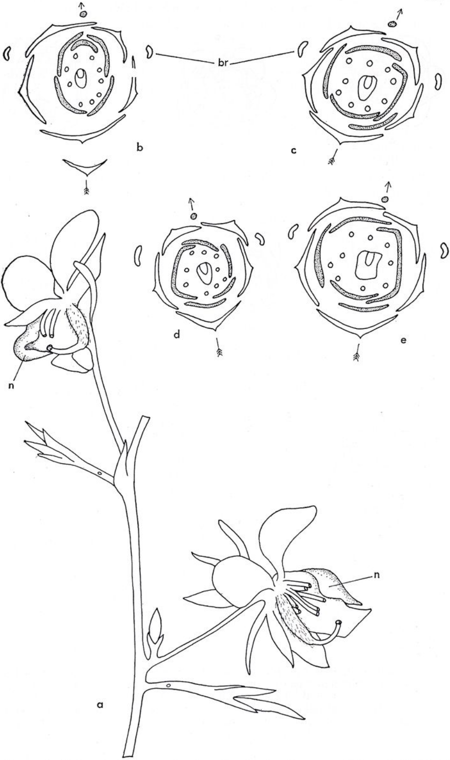

FIG. 3. Aestivation in *Cassia*. a, *C. mimosoides* showing flowers on right and left sides of stem inflorescence in relation to the view of the axis. b, Caesalpinioid aestivation (ascending imbrication), e.g. *C. fistula*. c, Irregular imbrication in *C. mimosoides*. d, *C. mimosoides* flower from left side of stem inflorescence. e, *C. mimosoides* flower from right side of stem inflorescence. n, navicular petal; br, bracteole.

FIG. 4. Floral ontogeny in *C. mimosoides*, showing camera lucida drawings (a–g) of the transverse sections of flower bud at successive stages of development. In stages a–d, note the early development of the large navicular petal (n) which ultimately disrupts the ascending imbricate aestivation (× 30); h shows details of g, and in this stage, at a higher level than the rest, the staminode(s) no longer appears (× 60).

III: Floral ontogeny and aestivation

The subfamily Caesalpinioideae is usually distinguished from other subfamilies of Leguminosae by the adaxial petal being interior in bud (ascending imbrication), in addition to other characters. When specimens of *C. mimosoides* and *C. nigricans* grown at the Royal Botanic Garden, Edinburgh, came to flower, the observed aestivation appeared different from the typical Caesalpinioid pattern.

In section *Chamaecrista*, to which these species belong, the floral structure is complicated by certain peculiarities: first, the flower is twisted on its pedicel and inclined at an angle; secondly, the style and ovary are positioned laterally on one side of the flower, the stamens on the other; thirdly, the direction of inclination of flower and the lateral positioning of style and stamens are reversed on opposite sides of the stem, so that the flowers on the right are a mirror image of those on the left (cf. Irwin 1964, pp. 32–33). This condition is illustrated in fig. 3, a. In each flower one petal is considerably enlarged, and because of its shape this is referred to henceforth as the navicular petal.

These peculiarities of the fully developed flower made it necessary to carry out the investigation of the floral structure and aestivation by sectioning young flower buds.

Serial sections of the flower buds of the following species were examined: *C. fistula*, *C. javanica*, *C. renigera*, *C. roxburghii*, *C. abbreviata*, *C. grandis*, *C. nodosa* and *C. absus*. The aestivation in these species agrees with the typical Caesalpinioid pattern. This is illustrated in fig. 3, b. It is to be noticed that the dorsal petal lies opposite the upper, ovuliferous margin of the ovary, while the ventral sepal lies opposite the lower sterile margin. The dorsal petal is also wholly internal in aestivation, being overlapped by the upper edges of the lateral petals. This arrangement is the characteristic ascending imbrication of subfamily Caesalpinioideae.

In *C. mimosoides*, *C. nigricans*, *C. kirkii*, *C. flexuosa*, *C. nictitans*, *C. patellaria*, all belonging to section *Chamaecrista*, there is a departure from this arrangement. Here the aestivation is irregularly imbricate, the dorsal petal being no longer overlapped on both margins. This condition is illustrated in fig. 3, c–e, from which it is clear that the large navicular petal is a lateral one. The small dorsal petal can be clearly identified by its position opposite the dorsal margin of the ovary. The central plane of the flower still runs through ventral sepal, ovary margins and dorsal petal. The obliqueness of the figure is due to the twisting of the flower on its pedicel. When a series of young flower buds are sectioned, the course of development can be followed. The sepal primordia are, of course, the first to be initiated. Then come the petal primordia, the navicular petal primordium appearing first. The rate of growth of this primordium considerably exceeds that of other petals and it seems very probable that it is the relatively early development of this large petal that disrupts the ascending imbricate aestivation that is usually found in *Cassia*. It may be noted also that the primordia of the three large stamens appear before those of the seven small ones, which also lag behind in further development. The important developmental stages of the floral primordia are illustrated in fig. 4.

If the change from the characteristic ascending imbrication of Caesalpinioideae to irregular imbrication which has been observed in some species of section *Chamaecrista* is widespread in the section, this may be helpful (when combined with other characters of the section, some of which were listed by Greene 1897—but cf. comments by Irwin, 1964) in the determination of the sectional or generic status of section *Chamaecrista*.

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