STUDIES ON EXTRAFLORAL NECTARIES OF THE LEGUMINALES

I. Papilionaceae, with a Discussion on the Systematics of the Leguminales

by Bharati Bhattacharyya* *and* J. K. Maheshwari,† *Department of Botany, University of Delhi, Delhi*

(Communicated by B. M. Johri, F.N.A.)

(Received 7 October 1969; after revision 20 May 1970)

Extrafloral nectaries are found in the tribes Vicieae, Phaseoleae, Galegeae, Trifolieae, Hedysareae, Dalbergieae, Genisteae and Loteae. They are absent in the tribes Podalyrieae, Sophoreae and Swartzieae. Unlike the subfamilies Mimosoideae and Caesalpinioideae, extrafloral nectaries are rather uncommon in the subfamily Papilionatae (Syn. Faboideae; Lotoideae; Papilionoideae). The present study has been made on the genera *Rhynchosia* Lour., *Cajanus* DC., *Eriosema* DC., *Psoralea* Linn., *Moghania* St. Hill and *Vicia* Linn. In the investigated genera, nectaries develop from a solitary initial cell which undergoes a transverse division. The structure of nectaries in *Vicia faba* Linn. and *Rhynchosia minima* DC. is somewhat similar; they are non-vascularized and do not contain crystals. According to the present survey, the genus *Rhynchosia* Lour. is divisible into three groups: (i) without nectaries, (ii) nectaries only on dorsal surface of leaf, and (iii) nectaries on both the surfaces of leaf. The nectaries of Mimosoideae and Caesalpinioideae possess complex structures and are distinguishable into three zones—(i) secretory zone, (ii) thick-walled zone, and (iii) vascular zone. On the contrary, the nectaries of Papilionatae appear to be simple glandular bodies in genera like *Rhynchosia* and *Vicia*. A comparative study of the distribution, morphology and anatomy of extrafloral nectaries, shows that these provide reliable taxonomic characters for delimiting the taxa at subgeneric, specific and varietal levels, as in *Acacia*, *Albizia*, *Pithecellobium* and *Cassia*. In a brief discussion on the disputed status of the taxon Leguminosae, an evidence is presented to show that the subfamilies Mimosoideae, Caesalpinioideae and Papilionatae deserve the rank of families under a separate Order Leguminales (Nom. alt.: Fabales). Further, it would be worth while to replace the Ordinal name Leguminosae by Leguminales or Fabales; the former name being also used for one of the component families, Fabaceae or Papilionaceae (*see* Articles 17 and 69, ed. Lanjouw ICBN, 1966).

Introduction

The papers in this series are intended to give a detailed account of the morphology, anatomy and taxonomic significance of extrafloral nectaries

Present address: * Lecturer, Gargi College, New Delhi 24.
† Assistant Director, National Botanic Gardens, Lucknow 1.

in the Mimosaceae, Caesalpiniaceae and Papilionaceae. The present paper deals with the extrafloral nectaries in the Papilionaceae, together with a discussion on the systematics of the Leguminosae.

Unlike Mimosaceae and Caesalpiniaceae, extrafloral nectaries are rather uncommon in the Papilionaceae. The nectaries occur in the tribes Vicieae, Phaseoleae (subtribes Cajaninae, Erythrininae, etc.), Galegeae, Trifolieae, Hedysareae, Dalbergieae, Genisteae and Loteae, while they are absent in the tribes Podalyrieae, Sophoreae and Swartzieae.

Material and Methods

The living and herbarium materials of species belonging to the genera *Rhynchosia* Lour., *Cajanus* DC., *Eriosema* DC., *Psoralea* Linn., *Moghania* St. Hill and *Vicia* Linn. were examined in this study. Shoot tips, young axillary buds and leaves were fixed in F.A.A. (formalin-acetic acid-alcohol). The material was cut at 8–10 μ, after following the usual methods of dehydration, infiltration and embedding. The sections were stained with safranin-fast green and in the combination of safranin, crystal violet and orange G.

Squash preparations of the glandular tissues were made for cytological studies. These were stained with 1 per cent acetocarmine. The leaves of *Rhynchosia* Lour. were cleared by following Foster's technique (1950). These were stained in 1 per cent solution of safranin, prepared in a mixture of absolute alcohol and xylol (1 : 1), and mounted in Canada balsam.

Herbarium specimens of *Rhynchosia* Lour. were obtained from different herbaria to study the distribution of nectaries.

Observations

In the tribe Vicieae, nectaries are found in some species of the genus *Vicia* Linn. In *V. faba* Linn., the nectaries form blackish spots on the ventral surface of the stipules. The spots are whitish-green in younger stages, but become dark-coloured at maturity.

The tribe Phaseoleae comprises 5 subtribes, viz. Cajaninae, Erythrininae, Phaseolinae, Galactinae and Glycininae. The members of the subtribe Cajaninae are characterized by the presence of gland-dotted leaves, e.g. *Atylosia* W. and A., *Cajanus* DC. (Fig. 1 *J*), *Cylista* Ait., *Dunbaria* W. and A., *Eriosema* DC.,

Fig. 1 *A–O*. *Rhynchosia* spp., *Psoralea* spp. and *Moghania* spp. Semidiagrammatic representation of leaves and branches showing distribution of extrafloral nectaries. (*n*, nectary). *A–E*, *H*, *J*, *N*, *O*, lower surface of gland-dotted leaves; *M*, upper surface of gland-dotted leaves; *G*, *I*, *K*, *Ka*, *L*, lower and upper surfaces of gland-dotted leaves; *F*, nectaries apparently invisible. *A*, *Rhynchosia minima* DC. ×0·32. *B*, *R. nummularia* DC. ×0·32. *C*, *R. falconeri* Baker. ×0·32. *D*, *R. capitata* DC. ×0·32. *E*, *R. viscosa* DC. ×0·32. *F*, *R. filipes* Benth. ×0·32. *G*, *R. avensis* Benth. ×0·32. *H*, *R. suaveolens* DC. ×0·32. *I*, *R. cana* DC. ×0·32. *J*, *Cajanus cajan* Millsp. ×0·32. *K* and *Ka*, *Psoralea corylifolia* Linn. ×0·32. *L*, *P. subacaulis* Torr. and Gray. ×0·32. *M*, *P. psoralioides* (Walt.) Cory. ×0·32. *N*, *Moghania fruticulosa* (Wall. ex Benth.) Mukerjee. ×0·32. *O*, *Moghania* sp. ×0·32.

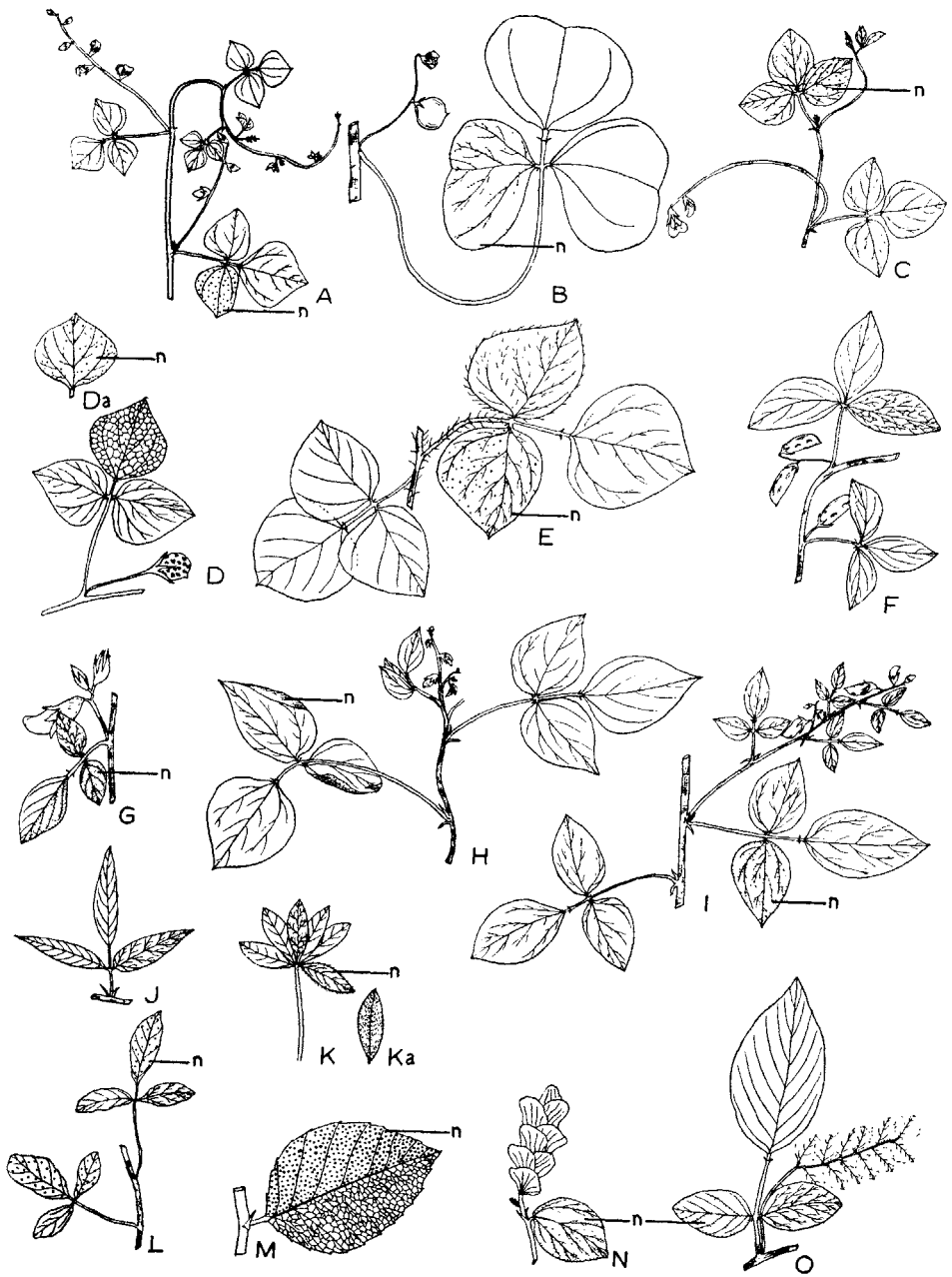

FIG. 1

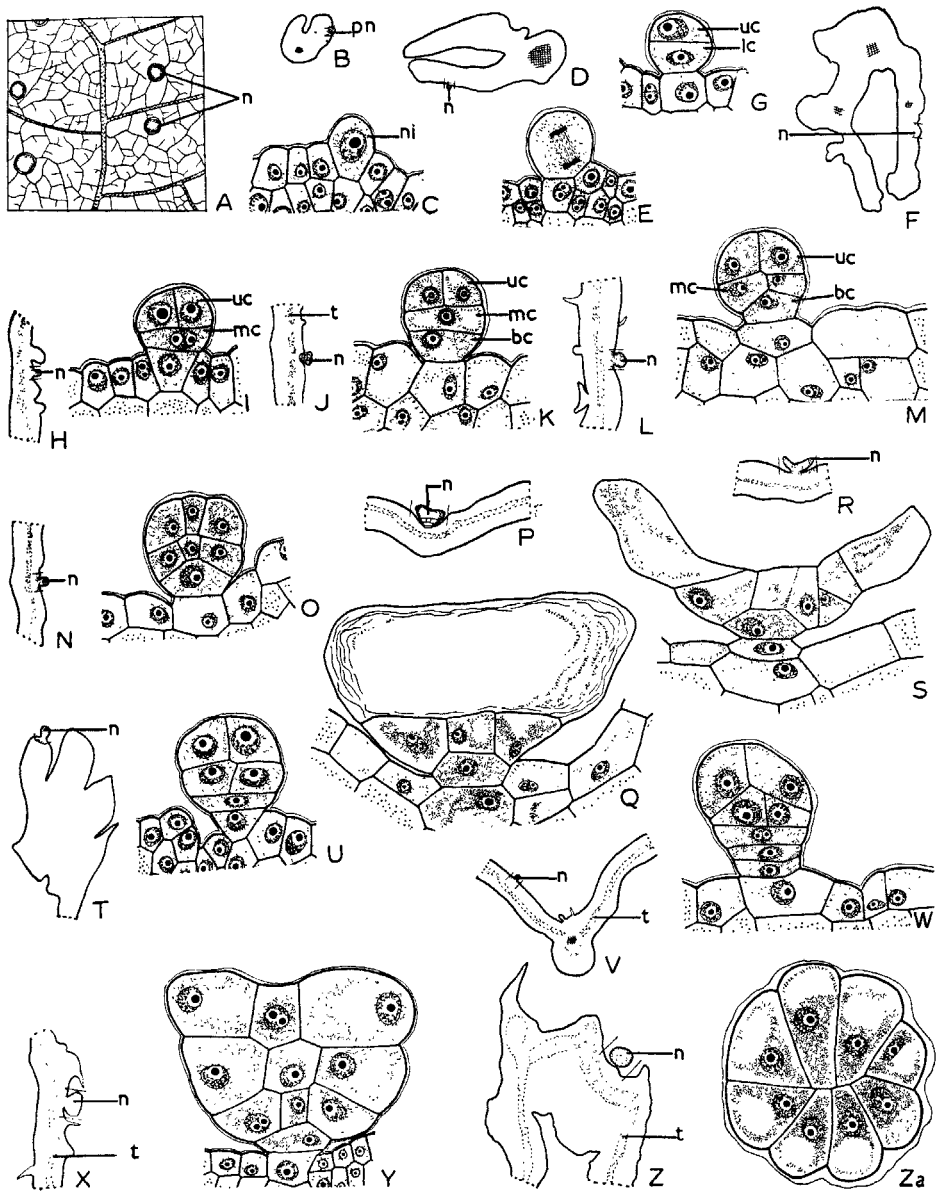
A
n
B
pn
C
ni
D
n
E
F
n
G
uc
lc
H
n
I
uc
mc
J
t
n
K
uc
mc
bc
L
n
M
uc
mc
bc
N
n
O
P
n
Q
R
n
S
T
n
U
V
n
t
W
X
n
t
Y
Z
n
t
Za

FIG. 2

Moghania St. Hill (Fig. 1 *N*, *O*), *Psoralea* Linn. (Fig. 1 *K–M*) and *Rhynchosia* Lour. (Fig. 1 *A–I*).

Rhynchosia Lour.

The species of *Rhynchosia* Lour. are characterized by pinnately trifoliolate leaves and densely hairy, nectariferous leaflets. The nectaries can be examined only when the hairs are scraped off.

In Indian floras, 22 species of *Rhynchosia* Lour. are described. Of these, we studied herbarium specimens of 18 species and fresh materials of 2 species.

On the basis of the present study, the genus *Rhynchosia* Lour. is divisible into three groups as follows:

Group I—Nectaries absent: *Rhynchosia filipes* Benth. (Fig. 1 *F*), *R. pilosa* Wall. ex Baker and *R. pseudo-cajan* Cambess.

Group II—Nectaries present on lower surface of leaf: *Rhynchosia acutissima* Thwaites, *R. capitata* DC. (Fig. 1 *D*), *R. cyanosperma* Benth., *R. densiflora* DC., *R. falconeri* Baker (Fig. 1 *C*), *R. minima* DC. (Fig. 1 *A*), *R. nummularia* DC. (Fig. 1 *B*), *R. rufescens* DC., *R. suaveolens* DC. (Fig. 1 *H*) and *R. viscosa* DC. (Fig. 1 *E*).

Group III—Nectaries present on both surfaces of leaf: *Rhynchosia avensis* Benth. ex Baker (Fig. 1 *G*) and *R. cana* DC. (Fig. 1 *I*).

The structure and development of the nectaries have been worked out in *Rhynchosia minima* DC.

Rhynchosia minima DC. is characterized by the presence of nectaries which appear as minute dots on the lower surface of leaflets. In early hours of the morning, secretion occurs in the form of glistening drops.

The cleared leaves showed that the nectaries are discoid (Fig. 2 *A*). They are compactly arranged in young leaflets but become sparse in older leaflets.

Fig. 2 *A–Za*. *Rhynchosia minima* DC. Development and structure of extrafloral nectaries. (*bc*, basal cell; *lc*, lower cell; *mc*, middle cell; *n*, nectary; *ni*, nectary initial; *pn*, position of nectary; *t*, tannin-filled cells; *uc*, upper cell). *A*, portion of a cleared leaf showing distribution of nectaries in surface view. ×42·4. *B*, (v.s.) young leaf indicating the position of nectary. ×70. *C*, one-celled nectary initial. ×768. *D*, (v.s.) young leaf; note the position of nectary on the lower surface of leaflet. ×70. *E*, first division of nectary initial. ×768. *F*, outline diagram for Fig. 2 *G* to show the position of nectary on leaflet. ×70. *G*, 2-celled nectary. ×768. *H*, portion of leaf in v.s.; note the position of nectary (*n*). ×70. *I*, 3-celled nectary. ×768. *J*, outline diagram of a 3-celled nectary. ×70. *K*, 4-celled nectary made up of 2 upper cells, a middle and a basal cell. ×768. *L*, portion of leaf (v.s.) to show the position of nectary. ×70. *M*, 5-celled nectary with 2 tiers of 2 cells each, and a basal cell. ×768. *N*, position of nectary on the surface of leaf (v.s.). ×70. *O*, 7-celled nectary showing 2 tiers of 3 cells each, and a basal cell. ×768. *P*, outline diagram for Fig. 2 *S*. ×70. *Q*, mature nectary showing remnants of cytoplasm in the upper tier; the cell walls have become disorganized. ×768. *R*, portion of leaf in (v.s.) showing the position of nectary. ×70. *S*, enlarged view of nectary. ×768. *T–Za*, abnormal development of nectary. *T*, outline diagram for Fig. 2 *U*. ×70. *U*, nectary showing 2 basal cells. ×768. *V*, young leaf (v.s.) showing the position of nectary. ×42·4. *W*, nectary with 3 basal cells. ×768. *X*, outline diagram for Fig. 2 *Y*; note the position of nectary. ×70. *Y*, mature nectary showing 3 layers of 3 cells each, subtended by a single cell. ×768. *Z*, (v.s.) leaf showing position of nectary. ×70. *Za*, (t.s.) apical region of nectary. ×768.

The nectaries are not associated with the vein endings of the leaflets. The vascular connection also could not be traced between the nectary and the vasculature of the leaf. A layer of cells, 1 or 2 layers below the epidermis, is filled with tannin (Fig. 2 *J*).

One of the enlarged epidermal cells of the leaf becomes densely cytoplasmic and shows a prominent nucleus (Fig. 2 *B*, *C*). This cell becomes the nectary initial. It divides transversely (Fig. 2 *D*, *E*) resulting in a 2-celled structure (Fig. 2 *F*, *G*). The upper cell of the 2-celled nectary (*uc*) undergoes a vertical division. Thus, a 3-celled structure comprising of a lower tier of one cell and an upper tier of 2 cells is formed (Fig. 2 *H*, *I*). The lower cell (*lc*) divides transversely producing a basal cell (*bc*) and a middle cell (*mc*) (Fig. 2 *J*, *K*). A vertical wall is laid down in the middle cell (Fig. 2 *L*, *M*). Thus, 5 cells disposed in 3 tiers are formed—a basal tier with 1 cell, a middle tier and an upper tier each with 2 juxtaposed cells (Fig. 2 *M*). One of the cells in the middle as well as in the upper tier divides vertically. This results in a 7-celled structure showing 2 tiers of 3 cells each, both subtended by the basal cell (Fig. 2 *N*, *O*).

In some instances, a different mode of development was observed. After the 5-celled stage in which 1 basal cell, and a middle and upper tier of 2 cells each are present, the basal cell (*bc*) undergoes 2 successive transverse divisions (Fig. 2 *T*–*W*). This results in the formation of a 7-celled structure showing from below 3 tiers of 1 cell each and 2 tiers each of 2 juxtaposed cells (Fig. 2 *V*, *W*). One of the cells in the 2 upper tiers divides anticlinally resulting in 3 cells in both the tiers. The uppermost cell of the 3 basal tiers also undergoes 2 successive vertical divisions so that the third tier from above also comprises 3 cells (Fig. 2 *X*, *Y*). A transverse section of the nectary at this stage shows 8 cells (Fig. 2 *Z*, *Za*). The cells are vacuolated and possess large, prominent nuclei. A thick cuticle is present on the surface of the nectary (Fig. 2 *Za*). At maturity, the cells of the upper 2 tiers degenerate and a cavity is formed. The lowermost tier of 3 cells and the basal cell remain intact (Fig. 2 *P*–*S*). The crystals are wanting in the tissues of both leaf and nectary.

Vicia Linn.

Of the 3 species available in Delhi, only one species, *V. faba* Linn., has been worked out in detail.

Vicia faba Linn.—Extrafloral nectaries occur in the form of prominent blackish spots on the ventral surface of the stipules (Fig. 3 *A*).

The nectaries of *V. faba* Linn. consist of an aggregation of numerous glands intermingled with unicellular hairs (Fig. 3 *G*, *H*). The glands are provided with a 4-celled body and a single-celled stalk. The body cells of the glands are stained deeply with safranin, whereas the stalk cell and the unicellular hairs take up the normal stain of safranin and fast green.

In a transection of developing stipule passing through the nectary, 10 to 12 papillate cells appear to protrude beyond the epidermis. These are the nectary initials which together form the nectary glands. The nectary initials are densely cytoplasmic and possess large nuclei (Fig. 3 *B*, *C*). Each initial cell undergoes a transverse division giving rise to a 2-celled structure (Fig. 3 *D*). However, the divisions are not synchronous in all the initial cells. Thus, the various stages of cell division in the nectary initials can be observed simultaneously. The lower cell (*lc*) of the resulting 2-celled structure is smaller than the upper cell (*uc*). The upper cell usually divides transversely resulting in a 3-celled body with the uppermost cell designated *ac*, the middle cell *mc* and the lowermost *lc* (Fig. 3 *E*). The lowermost cell or the basal cell is the smallest and does not divide further. The uppermost cell (*ac*) and the middle cell (*mc*) divide vertically (Fig. 3 *F*) resulting in a 5-celled structure with 2 tiers of 2 cells each, both subtended by a basal cell. Sometimes, however, the division in the upper cell is at first vertical and then transverse (Fig. 3 *G*). Thus, only a 5-celled structure is formed.

The crystals are lacking in the cells of the nectaries.

The nectaries of *Vicia faba* Linn. and *Rhynchosia minima* DC. are more or less similar. In *Vicia faba* Linn., the nectaries are aggregated in a shallow depression, while those of *Rhynchosia minima* DC. are scattered. The ontogeny of the nectaries of *V. faba* Linn. is also similar to that of the nectaries of *R. minima* DC. However, they differ mainly in the number of body cells, i.e. 4 cells in *Vicia faba* Linn. and 11–12 cells in *Rhynchosia minima* DC. Schwendt (1907) remarked that the structure of nectaries of *Vicia faba* Linn. is comparable with that of *Gossypium brasiliense* Macfad. The 5-celled structures have been variously termed by different workers as glands, hairs and trichomes. Solereder (1908) mentioned that the nectaries of *Vicia* Linn. 'consist of a group of numerous shortly stalked glandular hairs, provided with a 1 to 4-celled head'. Zimmermann (1932) classified the nectaries of *V. faba* Linn. along with those of Malvaceae among the trichomes. Metcalfe and Chalk (1950) remarked on the nectaries of *Vicia* Linn. as 'composed of stalked glands mixed with clothing hairs'. According to Janda (1937), the nectaries of malvaceous taxa resemble with those of *Vicia* Linn., both being trichomes. However, the present observations on the nectaries of *Vicia faba* Linn. show that there is only a superficial resemblance between the two groups.

The development of nectar glands was studied from squash preparations of nectariferous tissue after staining with 1 per cent acetocarmine (Fig. 3 *I–O*).

A General Discussion on the Taxonomic Significance of Extrafloral Nectaries in Leguminales

A vast fund of information is available on the morphology, anatomy and physiology of extrafloral nectaries in many families (Schnell *et al.* 1963).

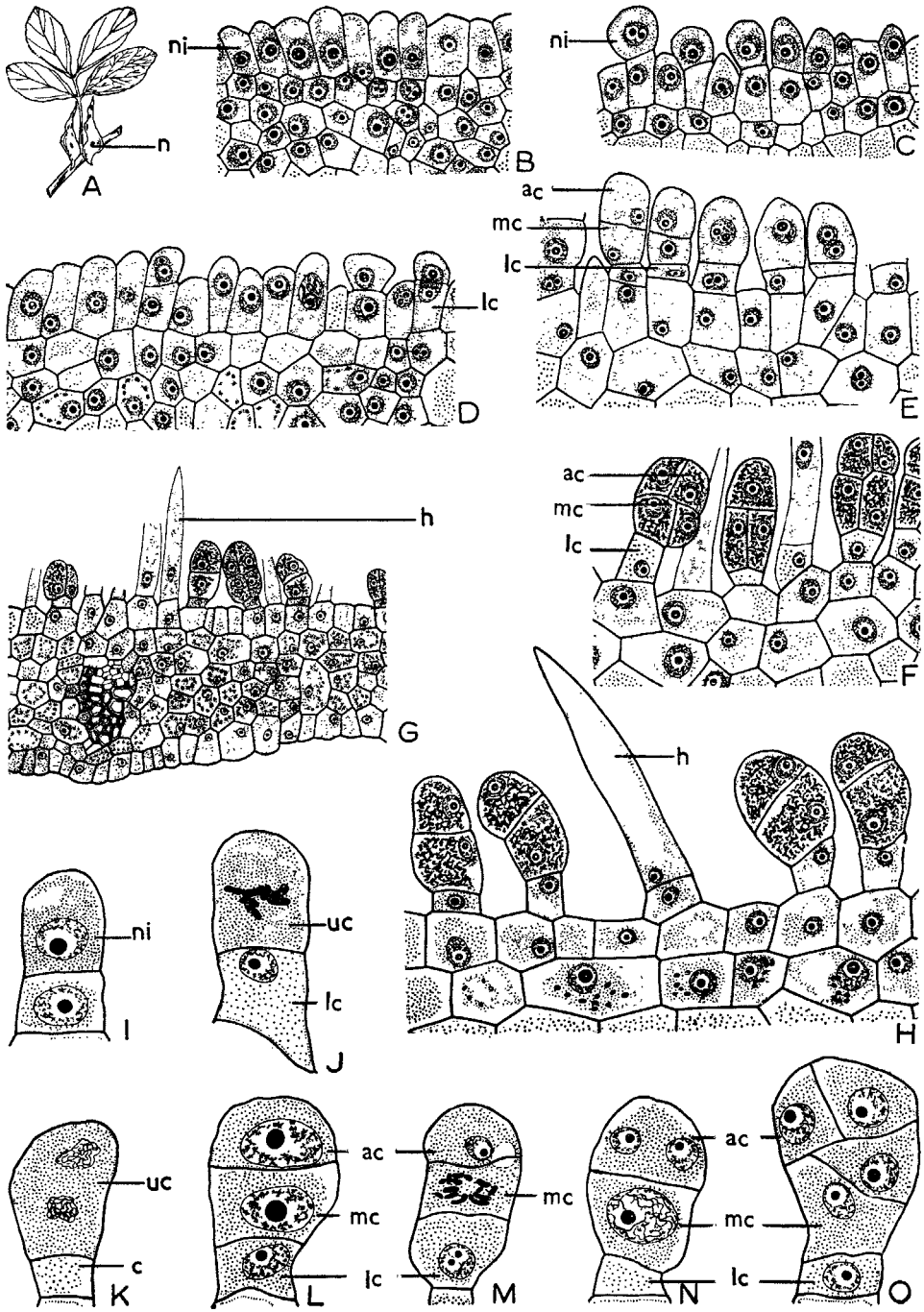
A
n
ni
B
ni
C
ac
mc
lc
D
lc
E
ac
mc
lc
F
h
G
h
H
ni
I
uc
lc
J
uc
c
K
ac
mc
lc
L
mc
M
ac
mc
lc
N
ac
mc
lc
O

FIG. 3

In the following pages, the structure and organization of extrafloral nectaries in the three taxa, viz. Mimosoideae, Caesalpinioideae and Papilionatae, have been considered in the light of structure and organization of nectaries in other families. A comparative data on distribution, morphology and anatomy of extrafloral nectaries have been collected with a view to elucidating the circumscription of the taxon Leguminosae (*see* Table III). Some of the earlier workers like Parker (1929) and Seibert (1948) mentioned about the usefulness of extrafloral nectaries in the identification of taxa at the specific level. In the Leguminosae, these have been demonstrated to provide a reliable taxonomic character for delineating the taxa, particularly at subgeneric and to some extent at specific levels. It is only in some instances that variations in their number and distribution have been recorded. This aspect has also been considered in the present study.

Structure and Organization of the Nectaries

As already described in earlier pages, the nectary initial arises from a solitary epidermal cell in all the investigated genera of the Leguminosae. However, in *Acacia modesta* Wall., 1 to 3 epidermal cells begin to behave as nectary initials, but ultimately only one of the cells contributes to the formation of nectary, while the others undergo vertical divisions and add to the epidermis. Extrafloral nectaries originating from single-celled epidermal initial have also been reported in *Duranta plumieri* Jacq. (Maheshwari 1954), *Gmelina arborea* Roxb., *Holmskioldia sanguinea* Retz., *Clerodendrum aculeatum* Griseb. and *Petrea volubilis* Linn. (Chavan and Deshmukh 1960, 1963, 1964*a*, *b*), and *Clerodendrum japonicum* Sweet (Maheshwari and Chakrabarty 1966). However, Reed's (1923) observations are contrary to these reports. According to him, more than one epidermal cell contributes to form a nectary in *Ricinus communis* Linn.

The division in the initial cell is transverse in the members of Verbenaceae (Maheshwari 1954; Chavan and Deshmukh 1960, 1963, 1964*a*, *b*; Maheshwari and Chakrabarty 1966). Salisbury (1909) and Reed (1923) reported in *Polygonum* and *Ricinus* respectively that the division is longitudinal. In leguminous plants, we have observed both longitudinal and transverse divisions. In *Acacia modesta* Wall., *Dichrostachys cinerea* W. and A., *Prosopis juliflora* DC. (Mimosoideae), *Rhynchosia minima* DC. and *Vicia faba* Linn.

FIG. 3 *A–O*. *Vicia faba* Linn. Development of extrafloral nectaries. (*ac*, uppermost cell; *h*, hair; *lc*, lower cell; *mc*, middle cell; *n*, nectary; *ni*, nectary initial; *uc*, upper cell). *A*, leaf with nectaries on the stipules. ×0·43. *B*, nectary initials (these resemble ordinary epidermal cells). ×320·6. *C*, same, later stage. ×320·6. *D*, 2-celled trichomes. ×320·6. *E*, 3-celled trichomes. ×320·6. *F*, 4 and 5-celled glandular trichomes. The cells are filled with tannin. ×320·6. *G*, (t.s.) stipule passing through nectariferous tissue; note the glandular trichomes and elongated, unicellular hairs. ×216·4. *H*, enlarged view of mature nectary. ×320·6. *I–O*, different stages of development of glandular trichomes in *Vicia faba*. ×832.

(Papilionatae), the nectary initial undergoes a transverse division. *Leucaena leucocephala* Wit (Mimosoideae) is the solitary example in which the nectary initial divides vertically. In *Prosopis juliflora* DC., both the conditions have been observed, although the transverse division is more common.

The nectaries of Mimosoideae and Caesalpinioideae could be distinguished into 3 zones: (i) secretory zone, (ii) thick-walled zone and (iii) vascular zone. The secretory zone is formed by thin-walled, densely cytoplasmic, polygonal cells. The thick-walled zone comprises cells with scanty cytoplasm and thickenings along the tangential and radial walls. The vascular zone is composed of xylem, phloem and sclerenchymatous pericycle. On the contrary, the nectaries of Papilionatae are simple, stalked, glandular bodies arranged either singly as in *Rhynchosia* Lour. or aggregated as in *Vicia faba* Linn. Their organization, similar to that of Mimosoideae and Caesalpinioideae, is also known in Cucurbitaceae and Verbenaceae (Chakravarty 1948, 1951; Chavan and Deshmukh 1960, 1964*b*), although the structure of the 3 zones in latter families differs greatly from that in Mimosoideae and Caesalpinioideae (*see* Table I).

TABLE I

Structure of extrafloral nectaries in Cucurbitaceae, Verbenaceae, Mimosoideae and Caesalpinioideae

	Cucurbitaceae	Verbenaceae	Mimosoideae	Caesalpinioideae
Secretory zone	6–12 layers; cells polygonal	1–2 layers; cells palisade-like	5–6 layers; cells polygonal	8–10 layers; cells polygonal
Thick-walled zone	1-layered; cells bilaterally thickened	1-layered; cells bilaterally thickened	2 to 3-layered, rarely 4 to 5-layered; cells radially and tangentially thickened	2 to 3-layered; cells radially and tangentially thickened
Vascular zone	Not known	Not known	Present	Present

Vasculature of Nectaries

The extrafloral nectaries in the subfamilies Mimosoideae and Caesalpinioideae are usually supplied by lateral bundles of the petiole except in *Acacia farnesiana* Willd. and *Albizia lebbeck* Benth. In the latter case, both the ventral bundles and the lateral bundles provide vascular supply to the nectaries. In the genera *Acacia*, *Albizia*, *Dichrostachys* and *Prosopis*, the sclerenchymatous sheath encircling the vascular bundles in the petiole extends also into the nectary as is reported earlier in *Dichrostachys glomerata* (Schnell *et al.* 1963).

The three types of vascular elements have been found in the nectaries: (i) phloem, (ii) phloem and xylem and (iii) predominantly xylem elements (*see* Frey-Wyssling and Agthe 1950). Frei (1955) examined 160 species of dicotyledonous plants and reported the presence of phloem elements in the nectaries of 91 species, phloem and xylem elements in 12 species and absence of vascular elements in 57 species. The non-vascularized nectaries are usually small and are situated close to the vascular tissues of the organ bearing the nectary. We have observed both xylem and phloem in the nectaries of *Acacia, Albizia, Desmanthus, Dichrostachys, Pithecellobium, Prosopis* (Mimosoideae) and *Cassia* (Caesalpinioideae). Amongst all the leguminous members, *Leucaena leucocephala* Wit is the sole example in which the vascular zone comprises only phloem and parenchymatous cells. The xylem elements are restricted near the lower limit of the vascular zone. Thus, in the subfamilies Mimosoideae and Caesalpinioideae, 2 modes of vascular supply are encountered, one represented by only phloem as in *Leucaena leucocephala* Wit and the other represented by xylem and phloem as in the genera *Acacia, Cassia,* etc. The nectaries are non-vascularized in the investigated genera of the subfamily Papilionatae.

In the present study, we have observed that crystals of various shapes occur in the tissues of the nectary. The rhomboidal crystals are usually observed in several members of the subfamily Mimosoideae; in *Desmanthus virgatus* Willd. linear crystals are also found. However, in some species of *Cassia* belonging to the subfamily Caesalpinioideae, druses are of frequent occurrence. In *C. occidentalis* Linn., both the druses and rhomboidal crystals are found. In *C. pumila* Lamk. and in the subfamily Papilionatae, the crystals are lacking. In contrast to our observations, Schnell *et al.* (1963) did not make any mention of the presence of crystals in the subfamilies Mimosoideae and Caesalpinioideae, although their occurrence in the cells of the secretory zone has been reported in several other families.

Taxonomic Value of Extrafloral Nectaries

Extrafloral nectaries have proved useful in the classification of taxa at both generic and specific levels. For example, the bignoniaceous genera *Pachyptera* and *Pseudocalymma* differ from other genera in the family in possessing petiolar nectaries (*see* Seibert 1948). Thus, Seibert (1948) recognized 10 kinds of nectaries in the family Bignoniaceae; the common ones are caeliac, interpetiolar, neuroaxillary, petiolar and stipular nectaries.

In the Leguminosae, extrafloral nectaries have proved useful in the delineation of taxa at subgeneric, specific and to a limited extent at varietal levels. The applicability of the extrafloral nectaries at various taxonomic levels and their limitations are discussed below.

Subgeneric level—De Wit (1955) delineated the three subgenera of *Cassia*, i.e. *Cassia*, *Senna* and *Lasiorhegma*, on the basis of extrafloral nectaries. In the present investigation, a further subgrouping of the subgenus *Senna* has been made. Thus, in subgenus *Senna* the extrafloral nectaries are either absent or present in different positions on the leaf. In one section they occur on the petiole whereas in the other they are found in between the pairs of pinnae. The key, thus, aids in an easier identification of the species belonging to the two sections of subgenus *Senna*.

Dimitri and Alberti (1954) keyed out the genus *Cassia* into two groups, one characterized by the presence and the other by the absence of extrafloral nectaries. In the first group, the nectaries are present either between the pairs of pinnae (e.g. *C. bicapsularis* Linn., *C. hookeriana* Gill., *C. floribunda* Cav., *C. corymbosa* Lamk., *C. multijuga* Rich. and *C. tora* Linn.) or on the petiole (e.g. *C. leptocarpa* Benth., *C. sophera* Linn.). The species like *Cassia alata* Linn., *C. carnaval* and *C. fistula* Linn. belong to the second group.

In the present study, more than 30 wild and cultivated species of *Cassia* were examined. The subgenus *Cassia* lacks extrafloral nectaries. The basic pattern followed for classifying the subgenus *Senna* is that of Dimitri and Alberti (1954) which was used for the Argentinian species of *Cassia*. Thus, the subgenus *Senna* has been divided into two groups on the basis of presence or absence of extrafloral nectaries. The group in which extrafloral nectaries are present is further divisible into two sections depending on the position of nectaries:

Section A—Nectaries present on the petiole,

Section B—Nectaries present in between the pairs of pinnae (*see* Chakrabarty 1968).

The subgenus *Lasiorhegma* comprises of species which possess petiolar nectaries; the latter may be either stipitate or sessile.

Species level—In several floristic treatments, the exact relationship of the two taxa, *C. obtusifolia* Linn. and *C. tora* Linn., is not indicated. These taxa are treated either as distinct species (Linnaeus 1753; Roxburgh 1832; De Wit 1955; Mall 1957; Brenan 1958; Irwin and Turner 1960; Shah and Nanda 1962) or as synonyms with *C. tora* Linn. as the valid name (Bentham 1871; Hooker 1878). According to Haines (1922), the species *C. obtusifolia* Linn. should be treated as a variety of *C. tora* Linn. Although some variations in the number of nectaries in *C. obtusifolia* Linn. have been observed (Irwin and Turner 1960), the two taxa can be distinguished by the shape and colour of nectaries. In *C. obtusifolia* Linn., the nectaries are curved with a linear, beak-like structure at its tip. These are usually orange-coloured and are supported on a greenish stalk. In *C. tora* Linn., the nectaries are pale yellow, straight and taper at the ends. The shape of the nectary is also helpful in the determination of many other taxa, e.g. species of *Acacia* belonging to the group *Caesia* (Chakrabarty 1968).

In some instances, the position of nectary is a taxonomic evidence for delineation of species. For example, the presence of interjugal nectaries, i.e. nectaries on internodal regions of rachis in both *Acacia decurrens* Willd. and *A. mollissima* Willd., distinguishes them from other species of *Acacia*.

In the present study, the number and distribution of nectaries have been found to be important features in the determination of species belonging to the genera *Albizia* and *Pithecellobium* (Chakrabarty 1968).

Varietal level—In one instance, the number of extrafloral nectaries has been found useful in distinguishing two related varieties. In *C. surattensis* Burm. f. var. *surattensis*, 1 or 2 nectaries occur between the lower two pairs of pinnae whereas in *C. surattensis* Burm. f. var *suffruticosa* (Koen. ex Roth) Chatterjee, more than two acropetally arranged nectaries occur between three or four pairs of leaflets.

Limitations—In contrast to the facts discussed above, there are some instances where the extrafloral nectaries could hardly be used as a taxonomic criterion, e.g. *Cassia occidentalis* Linn. The number and position of nectaries vary considerably in this species. In some of the Indian floras (Hooker 1878; Duthie 1903; Haines 1922; Gamble 1918), the taxon *C. occidentalis* Linn. is reported to possess a solitary large nectary at the base of petiole. The plants investigated by us, however, showed considerable variation in their position and sometimes even in the number of nectaries. The occurrence of a large petiolar nectary in *C. occidentalis* Linn. was not found to be a constant feature and is, therefore, of limited taxonomic value. Likewise, a detailed study of the nectaries of *Rhynchosia* has shown that these features are of limited value in taxonomy.

Although the position of extrafloral nectaries is constant in some species of *Acacia* and *Cassia*, there is no rigidity in the location of nectaries in other cases. In *Acacia leucophloea* Willd., the number of nectaries in a leaf varies from 1 to 4 (Fig. 4 *A*). The subspecies *A. nilotica* subsp. *indica* Brenan lacks petiolar nectaries but 1 or 2 jugal nectaries are present in between the pairs of pinnae (Fig. 4 *C*). In *A. modesta* Wall., nearly half of the examined leaves showed invariably a petiolar nectary (Fig. 4 *B*). In the other half, the number varied from 0 to 6. In *A. catechu* Willd., the leaf invariably bears a solitary petiolar nectary but the number of jugal nectaries varies from 1 to 6. A similar analysis of leaves of *Albizia amara* Boiv. showed that although the number of nectaries ranges from 1 to 3, the distribution of nectaries is variable (Fig. 5 *A*). In *Leucaena leucocephala* Wit, a nectary is usually present on the rachis. In addition, another nectary may occur between the pair of pinnae at one or both the ends (Fig. 5 *B*). In *Prosopis juliflora* DC., the number of jugal nectaries varies with the number of pairs of pinnae (Fig. 5 *C*).

It is, therefore, concluded that unlike the family Bignoniaceae, in Leguminosae the nectaries do not form a valid taxonomic character at the generic

level, particularly in *Acacia*, *Cassia* and *Rhynchosia*. However, when combined with other criteria, it forms an useful character at subgeneric levels and often at specific levels.

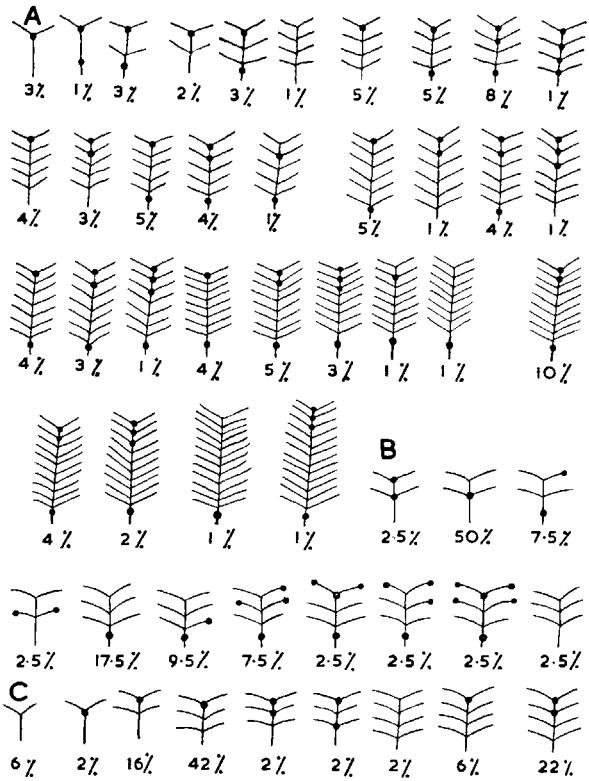

FIG. 4 *A–C*. *Albizia amara* Boivin, *Leucaena leucocephala* (Lamk.) de Wit and *Prosopis juliflora* (Sw.) DC. Diagrammatic representation to show the variation in position and distribution of extrafloral nectaries. *A*, *Albizia amara*—87·5 per cent leaves showed 1 petiolar nectary and 1–9 pairs of pinnae; 16·5 per cent leaves showed 7 pairs of pinnae and 1 petiolar nectary. *B*, *Leucaena leucocephala*—3·7 per cent leaves showed 2 nectaries between 2 pairs of pinnae; 14·6 per cent leaves showed 1 petiolar nectary. *C*, *Prosopis juliflora*—15 per cent leaves showed 3 pairs of pinnae with 1 nectary between each pair.

Status of the taxon Leguminosae—A good deal of comparative data on the botany of the Leguminosae are available (De Candolle 1825*a*; Rangaswamy and Chakrabarty 1966). It is, therefore, not surprising if the status of this large taxon comprising of more than 12,000 species and 600 genera is disputed. As early as 1789, de Jussieu coined the name Leguminosae for a group which today constitutes one of the largest and most important taxa of flowering

plants. The familial name Leguminosae has been retained by the ICBN as an alternate name for the Fabaceae or Papilionaceae (ed. Lanjouw ICBN, 1961, 1966). Whether the taxon Leguminosae represents a family comprising three subfamilies or an order including three families is still debated (*see* Table II). In recent taxonomic treatments, there is a general tendency to upgrade the subfamilies, Mimosoideae, Caesalpinioideae and Papilionatae, to the rank of families and to treat the taxon Leguminosae as a separate Order Leguminales

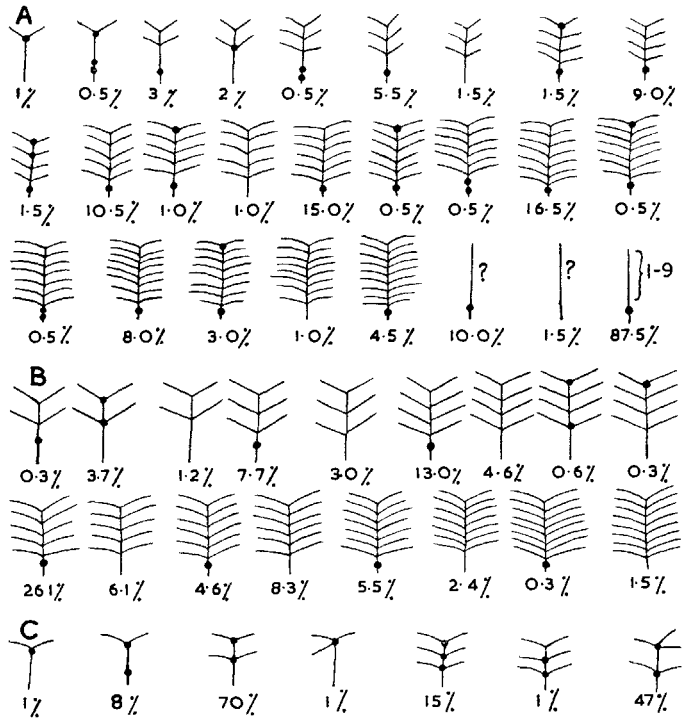

FIG. 5 *A–C*. *Acacia leucophloea* (Roxb.) Willd., *A. modesta* Wall. and *A. nilotica* (Linn.) Del. subsp. *indica* Brenan. Diagrammatic representation to show the variation in position and distribution of extrafloral nectaries. *A*, *Acacia leucophloea*—10 per cent leaves consist of 9 pairs of pinnae and show 1 petiolar nectary and 2 nectaries between the 2 uppermost pairs of pinnae. *B*, *A. modesta*—50 per cent leaves consist of 2 pairs of pinnae with a nectary between the lower pair of pinnae. *C*, *A. nilotica* subsp. *indica*—42 per cent leaves possess 3 pairs of pinnae and a nectary between the uppermost pair of pinnae; 22 per cent leaves showed 4 pairs of pinnae and 2 nectaries between the 2 uppermost pairs of pinnae.

(nom. alt.: Fabales). Further, the name Leguminosae had previously been used for one of the component families, Papilionaceae (*see* Jones 1955). In order to avoid duplication of names, Jones (1955) proposed the change of the

Ordinal name Leguminosae to Leguminales with a view to accommodating and providing an equal status for the four families, Mimosaceae, Caesalpiniaceae, Krameriaceae and Papilionaceae.

TABLE II

The Leguminosae—its status and circumscription

Taxon	Status	Investigators
Leguminosae	Family (cited as 'Order')	De Jussieu (1789); De Candolle (1825*b*); Bentham and Hooker (1865)
Leguminosae	Order (cited as 'Class')	*Brown (1814)
Fabaceae	Family (cited as 'Order')	Lindley (1853)
Leguminosae nom. cons. (nom. alt.: Fabaceae vel Papilionaceae)	Family	Taubert (1891); Rendle (1952); Bullock (1959); Lanjouw, ICBN (1961, 1966); Wilbur (1963); Melchior (1964); Rudd (1968)
Leguminosae	Order	*Warming (1879); Small (1903); *Britton and Brown (1913); Hutchinson (1926); Metcalfe and Chalk (1950)
Leguminales	Order	Jones (1955); Hutchinson (1959)
Fabales	Order	Takhtajan (1959); Barkley (1967)

* For literature references *see* Jones (1955).

Table III gives a comparative account of the distribution, morphology and anatomy of the nectaries of Mimosoideae, Caesalpinioideae and Papilionatae.

CONCLUSIONS

While in several instances, the position, shape, size, colour and number of nectaries have proved useful in taxonomic delimitations, in others these could hardly be used in classification at supra- and infra-generic levels. For example, the nectaries do not provide useful criteria in distinguishing *Acacia catechu* Willd. from *A. ferruginea* DC., as the number of jugal nectaries shows considerable variation in both the species. In *A. bonariensis* Gill. and *A. canescens* Grah., two conical jugal nectaries occur which are more or less alike in external morphology. Similarly, the nectaries of *Albizia lophantha* Benth. and *A. pedicellata* Baker ex Benth. cannot be distinguished from each other, as both are characterized by the presence of a petiolar nectary only. Often there is no rigidity in the location of nectaries as in the case of *Acacia leucophloea* Willd., *A. modesta* Wall., *A. nilotica* subsp. *indica* Brenan, *Albizia amara* Boiv., *Leucaena leucocephala* Wit and *Prosopis juliflora* DC. An

TABLE III

Extrafloral nectaries of Mimosoideae, Caesalpinioideae and Papilionatae

	Mimosoideae	Caesalpinioideae	Papilionatae
Occurrence	Normally at the base of petiole or on the rachis in between the pairs of pinnae (exception: all over rachis, e.g. *Acacia decurrens*) (present work)	Normally on the rachis in between the pairs of pinnae; sometimes also petiolar (exceptions: on the phyllodes, e.g. *Cassia phyllodinea*; on the surface of the leaf, e.g. *C. atroglandulosa*) (present work)	Normally on leaf-surface; on the ventral surface of stipules of *Vicia* (exception: stipules and stipels modified into nectaries, e.g. *Erythrina* (present work)
Shape	Variable; cupuliform with or without a deep canal-like depression, e.g. *Prosopis juliflora* and *Leucaena leucocephala*; columnar, e.g. *Dichrostachys cinerea*; flat and discoid, e.g. *Acacia modesta*	Variable; narrow and cylindrical, e.g. *Cassia auriculata*; elongated, e.g. *C. hirsuta*, *C. floribunda*; subulate, e.g. *C. obtusifolia*, *C. surattensis*; rotundiform, e.g. *C. occidentalis*; stipitate, umbrella-shaped nectaries, e.g. *C. pumila*	More or less constant; small, single-layered, disc-like, glandular bodies; either sparsely arranged, e.g. *Rhynchosia*, *Cajanus*, *Cylista* and *Dunbaria*, or aggregated together, e.g. *Vicia faba*
Stipe	Usually sessile; stipitate in *Dichrostachys cinerea*; stipe many-celled	Sessile and stipitate; stipe many-celled	Stipitate; stipe 1-celled
Secretory zone	5 to 6-layered; cells polygonal	8 to 10-layered; cells polygonal	2-layered; cells not polygonal
Thick-walled zone	2 to 3-layered; sometimes 4 to 5-layered; cells radially and tangentially thickened	2 to 3-layered; cells radially and tangentially thickened	Absent
Vascular zone	Present	Present	Not distinct
Vascular supply	Lateral bundles provide vascular supply in most instances; ventral bundles also take part, e.g. *Acacia farnesiana*, *Albizia lebbeck*	Lateral bundles provide vascular supply	No vascular supply; nectaries situated close to the vascular tissue of the organ bearing the nectary
Crystals	Usually rhomboidal; linear in *Desmanthus virgatus*; crystals absent in *Albizia amara*	Usually druses; also rhomboidal in *C. occidentalis*; only rhomboidal in *C. dimidiata*; crystals absent in *C. pumila*	Absent
Tannin	Abundant	Abundant	Absent

extensive study of the internal morphology of nectaries is, therefore, needed to distinguish the various species-groups.

The artificial keys prepared for delineating the species belonging to the genera *Acacia, Albizia, Pithecellobium* and *Cassia* show that the exomorphological features of nectaries can be used as taxonomic criteria when applied in combination with other vegetative and floral characters.

In a brief discussion on the disputed status of the taxon, Leguminosae, an evidence is presented to show that the Mimosoideae, Caesalpinioideae and Papilionatae deserve the rank of families under a separate Order, Leguminales (Nom. alt.: Fabales).

Jones (1955) proposed the change of the Ordinal name Leguminosae to Leguminales. If one follows the International Code of Botanical Nomenclature, it seems justified to replace the Ordinal name Leguminosae by Leguminales or Fabales (Articles 17, 69, ed. Lanjouw ICBN, 1966).

Acknowledgements

The authors are grateful to Professor B. M. Johri for encouragement and to Dr. N. S. Rangaswamy for valuable suggestions.

References

Barkley, F. A. (1967). Outline Classification of Organisms. Hopkins Press, Providence.

Bentham, G. (1871). Revision of the genus *Cassia*. *Trans. Linn. Soc., Lond.*, **27**, 503–592.

Bentham, G., and Hooker, J. D. (1865). Genera Plantarum. Vol. I. London.

Brenan, J. P. M. (1958). New and noteworthy Cassias from tropical Africa. *Kew Bull.*, **13**, 231–252.

Bullock, A. A. (1959). Nomina Familiarum Conservanda Proposita. *Taxon*, **8**, 154–181.

Chakrabarty, B. (1968). Studies on extrafloral nectaries of the Leguminosae with a review on extrafloral nectaries. Ph.D. Thesis. Delhi Univ., India.

Chakravarty, H. L. (1948). Extrafloral glands of Cucurbitaceae. *Nature, Lond.*, **162**, 576.

——— (1951). Glandular probract in *Coccinia cordifolia* (Linn.) Cogn. *Sci. Cult.*, **17**, 225–226.

Chavan, A. R., and Deshmukh, Y. S. (1960). The ontogeny of extrafloral nectaries in the genus *Gmelina*. *J. Indian bot. Soc.*, **39**, 410–414.

——— (1963). A contribution to the floral organogeny and ontogeny of extrafloral nectaries in *Holmskioldia sanguinea* Retz. *J. Maharaja Sayajirao Univ. Baroda*, **12**, 31–37.

——— (1964*a*). Studies in organogeny and ontogeny—IV. A study of the floral organogeny and ontogeny of extrafloral nectaries in the genus *Clerodendron*. *J. Maharaja Sayajirao Univ. Baroda*, **13**, 27–29.

——— (1964*b*). Studies in organogeny and ontogeny—V. A study of the floral organogeny and ontogeny of the extrafloral nectaries in *Petrea volubilis* L. *J. Maharaja Sayajirao Univ. Baroda*, **13**, 63–67.

De Candolle, A. P. (1825*a*). Mémoires sur la Famille des Légumineuses. Paris (facsimile ed. Lehre 1966).

——— (1825*b*). Prodromus Systematis Naturalis Regni Vegetabilis. Part II. Paris.

De Jussieu, A. L. (1789). Genera Plantarum (with an introduction by F. A. Stafleu). Paris (facsimile ed. Weinheim 1964).

De Wit, H. C. D. (1955). A revision of the genus '*Cassia*' (Caesalp.) as occurring in Malaysia. *Webbia*, **11**, 197–292.

Dimitri, M. J., and Alberti, F. R. (1954). Las especies del Genero *Cassia* cultivadas en la Argentina. *Revta Invest. agric., B. Aires*, **8**, 5–34.

Duthie, J. F. (1903). Flora of the Upper Gangetic Plain and of the Adjacent Siwalik and sub-Himalayan Tracts. Vol. I. (Reprinted ed. B.S.I., 1960). Calcutta.

Foster, A. S. (1950). Techniques for the study of venation patterns in the leaves of Angiosperms. *Proc. 7th int. bot. Congr., Stockholm*, 586–587.

Frei, E. (1955). Die Innervierung der floralen Nektarien dikotyler Pflanzenfamilien. *Ber. schweiz. bot. Ges.*, **65**, 60–114.

Frey-Wyssling, A., and Agthe, C. (1950). Nektar ist ausgeschiedener Phloemsaft. *Verh. schweiz. naturf. Ges.*, **4**, 175–176.

Gamble, J. S. (1918). Flora of Presidency of Madras. Part 2. (Reprinted ed. B.S.I., 1957). Calcutta.

Haines, H. H. (1922). The Botany of Bihar and Orissa. Pt. 3. London.

Hooker, J. D. (1878). The Flora of British India. Vol. II. London.

Hutchinson, J. (1926). The Families of Flowering Plants. Vol. I. Dicotyledons. London.

——— (1959). The Families of Flowering Plant. Vol. I. Dicotyledons. London.

Irwin, H. S., and Turner, B. L. (1960). Chromosomal relationships and taxonomic considerations in the genus *Cassia*. *Am. J. Bot.*, **47**, 309–318.

Janda, C. (1937). Die extranuptialen Nektarien der Malvaceen. *Öst. bot. Z.*, **86**, 81–130.

Jones, G. N. (1955). Leguminales: a new Ordinal name. *Taxon*, **4**, 188–189.

Lanjouw, J. (ed.). (1961, 1966). International Code of Botanical Nomenclature. Utrecht, Netherlands.

Lindley, J. (1853). The Vegetable Kingdom, ed. 3. London.

Linnaeus, C. (1753). Species Plantarum. Stockholm.

Maheshwari, J. K. (1954). The structure and development of extrafloral nectaries in *Duranta plumieri* Jacq. *Phytomorphology*, **4**, 208–211.

Maheshwari, J. K., and Chakrabarty, B. (1966). Foliar nectaries of *Clerodendrum japonicum* (Thunb.) Sweet. *Phytomorphology*, **16**, 75–80.

Mall, L. P. (1957). Contribution to the autecology of *Cassia tora* Linn. and *C. obtusifolia* Linn. *J. Univ. Saugar*, **6** B, 35–54.

Melchior, H. (1964). A. Engler's Syllabus der Pflanzenfamilien. Band II. Berlin.

Metcalfe, C. R., and Chalk, L. (1950). Anatomy of the Dicotyledons. Vol. 2. Oxford.

Parker, R. N. (1929). Indian climbing Acacias of the *Caesia* group. *Indian Forester*, **55**, 325–333.

Rangaswamy, N. S., and Chakrabarty, B. (1966). The Leguminosae of Delhi—some studies on their morphology and taxonomy. *Bull. bot. Surv. India*, **8**, 25–41.

Reed, E. L. (1923). Extra-floral nectar glands of *Ricinus cummunis*. *Bot. Gaz.*, **76**, 102–106.

Rendle, A. B. (1952). The Classification of Flowering Plants. Vol. I. Dicotyledons. London.

Roxburgh, W. (1832). Flora Indica. Vol. 2. Serampore.

Rudd, V. E. (1968). Leguminosae of Mexico—Faboideae. I. Sophoreae and Podalyrieae. *Rhodora*, **70**, 492–532.

Salisbury, E. J. (1909). The extra-floral nectaries of the genus *Polygonum*. *Ann. Bot.*, **23**, 229–242.

Schnell, R., Cusset, G., and Quenum, M. (1963). Contribution a l'étude des glandes extra-florales chez quelques groupes de plantes tropicales *Revue gén. Bot.*, **70**, 269–342.

Schwendt, E. (1907). Zur Kenntnis der extrafloralen Nektarien. *Beih. bot. Zbl.*, **22**, 245–286.

Seibert, R. J. (1948). The use of glands in a taxonomic consideration of the family Bignoniaceae. *Ann. Mo. bot. Gdn.*, **35**, 123–136.

Shah, G. L., and Nanda, U. (1962). Studies on *Cassia tora* L. and *Cassia obtusifolia* L. in Bombay. *J. Soc. Indian Foresters*, **2**, 12–15.

Small, J. K. (1903). Flora of the Southeastern United States. New York.

Solereder, H. (1908). Systematic Anatomy of the Dicotyledons (Engl. Transl.). Vol. I. Oxford.

Takhtajan, A. (1959). Die Evolution der Angiospermen. Jena.

Taubert, P. (1891). Leguminosae. In Engler and Prantl, Die natürlichen Pflanzenfamilien, III, 3, 70–388. Leipzig.

Wilbur, R. L. (1963). The leguminous plants of North Carolina. *Bull. N. Carol. agric. Exp. Stn.*, No. 151, 1–294.

Zimmermann, J. G. (1932). Über die extrafloralen Nektarien der Angiospermen. *Beih. bot. Zbl.*, **49**, 99–196.