

EMBRYOLOGY AND PHYLOGENY OF THE TRIBE GALEGEEAE (PAPILIONOIDEAE)

V. SESHAVATHARAM

Department of Botany, Andhra University, Waltair (A. P.)

ABSTRACT

Embryology of eight species belonging to three genera namely *Tephrosia*, *Sesbania* and *Mundulea* of the tribe Galegeae of the Papilionoideae was studied. Based on the present observations and on available earlier information, the embryology and phylogeny of the tribe have been discussed. On embryological grounds the tribe Galegeae appears to be a heterogenous assemblage with marked resemblances to the tribes Dalbergieae, Phaseoleae and Hedysareae of the Papilionoideae. The Galegeae are characterised by—(i) 4-sporangiate anther, (ii) secretory tapetum of uninucleate cells, (iii) presence or absence of a nucellar cap, (iv) presence or absence of an incipient integumentary tapetum, (v) formation of a linear or 'T'-shaped tetrad or a 'Triad' during megasporogenesis, (vi) Polygonum or Allium type of embryo sac development, (vii) well developed barrier tissue, (viii) Nuclear endosperm with a chalazal haustorial extension, (ix) Onagrad, Asterad or Caryophyllad types of embryo development and (x) suspensor of variable form—the features that are also shared by the tribes Phaseoleae, Dalbergieae and Hedysareae.

Chromosomally too the group was considered to be heterogeneous having base counts of $x=5, 6, 7, 8, 10$ and 11 and it was earlier suggested that genera with base numbers of $x=10$ and 11 may be merged with the tribe Dalbergieae or else the two tribes be merged. These suggestions and the 'Galegeae Complex' of Turner and Fearing, are discussed in the light of the embryological and other morphological information available.

INTRODUCTION

The Galegeae are one of the largest tribes of the sub-family Papilionoideae with 65 genera and 3,200 species of diverse habits (RENDLE, 1925). Our knowledge on the embryology of the tribe is confined to the studies in 10 genera and 16 species only. The structure and development of the anther and pollen is known in *Indigofera enaephylla* = *I. linnii* (UNTAWALE & DESHPANDE, 1968), *I. pulchella* (MAKDE, 1971) and *Milletia ovalifolia* (PAL, 1960), where the development was shown to be normal with a secretory type of tapetum. Polygonum type of embryo sac development has been reported in *Cyamopsis psoralioides* (GREEN *et al.*, 1964), *Deubentonia punicea* (REMBERT, 1969), *Glycyrrhiza foetida* (VEILLET-BARTOSZEWSKA, 1956), *Indigofera enaephylla* (UNTAWALE & DESHPANDE, 1968), *I. pulchella* (MAKDE, 1971), *Milletia ovalifolia* (PAL, 1960), *Psoralea corylifolia* (JOSHI, 1938), *Robinia pseudoacacia* (REMBERT, 1969) and *Sesbania aculeata* (SALGARE, 1973) while Allium type of embryo sac development was recorded in *Wisteria sinensis* (REMBERT, 1967) only. Information on the endosperm development is available in *Glycyrrhiza foetida* (VEILLET-BARTOSZEWSKA, 1956), *Milletia ovalifolia* (PAL, 1960), *Sesbania aegyptiaca* = *S. sesban* and *S. grandiflora* (RAU, 1951a, 1951b), *Tephrosia purpurea* = *T. hamiltoni* and *T. procumbens* (RAU, 1951b) and in *T. villosa* (JOHRI & GARG, 1959). Embryo development has been recorded in *Astragalus glycyphyllus* (CRETE, 1951), *Colutea arborescens* (SOUEGES, 1951), *Cyamopsis psoralioides* (RAU, 1954), *Glycyrrhiza foetida* (VEILLET-BARTOSZEWSKA, 1956), *Milletia ovalifolia* (PAL, 1960), *Psoralea bituminosa* (SOUEGES, 1950) and *Sesbania aegyptiaca* and *S. grandiflora* (RAU, 1951b). Occasional polyembryony has been recorded in *Sesbania aculeata* by HAQUE (1946).

OBSERVATIONS

The structure and development of the anther and pollen, ovule and embryo sac, endosperm and embryo have been studied in four species of *Tephrosia* Pers., namely *T. maxima* Pers., *T. purpurea* (Linn) Pers., *T. procumbens* Hamm. and *T. strigosa* (Dale) Santapau & Mahesh., three species of *Sesbania* Scop., namely *S. procumbens* Wight & Arn., *S. aculeata* Poir., and *S. grandiflora* Pers., and *Mundulea sericea* (Willd) A. Cheval.

Since a detailed account of these observations will form the subject matter for a separate paper only a brief description is given here indicating the important features.

The anther wall comprises the epidermis, the fibrous endothecium and a variable number of middle layers. The secretory tapetum is uniseriate with uninucleate cells. The pollen is shed at the two or three celled stage. The archesporium in the ovule is hypodermal and is single celled in *Mundulea sericea*, *Sesbania procumbens*, *Tephrosia maxima*, *T. purpurea*, *T. strigosa* and *T. procumbens* while it is represented by a plate of 2 or 3 cells in *Sesbania grandiflora* and *S. aculeata*. Megasporogenesis occurs normally resulting in a linear or a 'T' shaped tetrad. But, in *Sesbania grandiflora* and *S. procumbens* only a 'Triad' is formed during megasporogenesis where the upper dyad fails to divide. The embryo sac development conforms to the Polygonum type in all the species investigated.

Endosperm development is *ab initio* nuclear with a variable chalazal haustorium.

Embryo development in *Tephrosia purpurea* and *T. maxima* conforms to the Euphorbia variation of the Onagrad type and to the Catalpa variation of the Onagrad type in *T. procumbens* while in *T. strigosa* it follows the 'Alysicarpus' variation (SESHAVATHARAM, 1969) erected under the Onagrad type of JOHANSEN (1950). Embryogeny in *Sesbania aculeata* and *S. procumbens* conforms to the Trifolium variation of the Onagrad type.

DISCUSSION

Considerable variation has been noticed in the tribe during megasporogenesis and the formation of megaspore tetrads. Information available on this aspect obtained from 15 species belonging to 9 genera of the tribe is summarised in Table 1.

A 'triad' with the upper dyad degenerating (monosporic embryo sac devt.) was observed (SESHAVATHARAM, 1969) in *S. procumbens* and *S. grandiflora* while a 'triad' with the upper dyad dividing and the lower functioning directly (bisporic embryo sac devt.) was recorded by REMBERT (1967) in certain ovules of *Wisteria sinensis*. REMBERT (1969, 1971) has laid much emphasis on the variation in the tetrad patterns in the Leguminosae and derived one type from the other. According to him type 'D' represented in Table I (pattern VII of REMBERT, 1971) is derived from a linear tetrad. A tribe that shows variation in tetrad patterns was considered by him to be advanced while that with least variation was believed to be primitive. Unfortunately REMBERT made such generalised observations based on very scanty data—for example in the tribe Galegeae his conclusions are based only on 5 genera and 5 species out of the 3,200 species belonging to 65 genera of the tribe and his 'generalised tetrad' (REMBERT, 1971, Fig. 2) was wrongly represented with five cells. However, my observations (SESHAVATHARAM, 1969) on 3 genera and 8 species of the tribe does not lend any support to such a view. If the triad shown as type 'D' in Table 1, is to be considered as a feature of advancement than a linear tetrad, then, this is associated in *Sesbania grandiflora* with two primitive characters—a multiple archesporium in the ovule and a massive anther wall—and thus appears, to be of independent origin than a derived condition.

The embryo sac development in all the investigated members of the tribe conforms to the Polygonum type, with the single exception of *Wisteria sinensis* (REMBERT, 1967) in which

Table 1

Type	Description	Recorded in
'A'	Linear tetrad with the chalazal megaspore functioning.	<i>Daubentonia punicea</i> (Rembert, 1969), <i>Milletia ovalifolia</i> (Pal, 1960), <i>Indigofera pulchella</i> (Makde, 1971), <i>Mundulea sericea</i> , <i>Sesbania aculeata</i> , <i>Tephrosia maxima</i> , <i>T. procumbens</i> , <i>T. strigosa</i> (Seshavatharam, 1969).
'B'	'T'-shaped tetrad with the chalazal megaspore functioning.	<i>Psoralea corylifolia</i> (Joshi, 1938), <i>Tephrosia purpurea</i> (Seshavatharam, 1969).
'C'	Inverted 'T' shaped tetrad with one of the two chalazal megaspores functioning.	<i>Robinia pseudoacacia</i> (Rembert, 1969).
'D'	Triad with the upper dyad degenerating after meiosis I with a transverse division in the lower dyad and the chalazal megaspore functioning.	<i>Wisteria sinensis</i> (Rembert, 1967), <i>Sesbania procumbens</i> and <i>S. grandiflora</i> (Seshavatharam, 1969).
'E'	Triad with the upper dyad undergoing transverse division and the lower dyad directly giving rise to the 2-n embryo sac (bisporic type).	<i>Wisteria sinensis</i> (Rembert, 1967).

the embryo sac development in some ovules follows the *Allium* type. Again REMBERT (1969) opines that bisporic type of embryo sac development is a derived condition and in support of his view mentions that it occurs in the four morphologically advanced tribes of the Papilionoideae—Genisteae, Viciae, Galegeae and Phaseoleae. But the available embryological data in the subfamily Papilionoideae do not support such a view since the bisporic development was recorded in some ovules of *Pongamia pinnata* belonging to the primitive tribe Dalbergieae (SESHVATHARAM, 1969). Moreover, there are no confirmed reports of bisporic development in the equally or even more advanced tribes like Trifolieae and Loteae.

Information regarding the variation met with in the embryo development in the different members of the tribe, based on the present observations and previous reports is summarised in Table 2. In thirteen out of fifteen species where embryogeny is known, the development conforms to the Onagrad type. The two exceptions are *Galega officinalis* showing the Caryophyllad type and *Psoralea bituminosa* showing the Asterad type (see Table 2). Caryophyllad type is of common occurrence in the subfamily in the tribes Viciae and Trifolieae which are considered to be more evolved than Galegeae on embryological grounds (SESHVATHARAM, 1969). The embryogeny in *Psoralea* is of particular interest because, it is the only species in the Papilionoideae so far known which shows the Geum variation of the Asterad type so characteristic of the Rosaceae, through which the Papilionoideae are believed to have evolved. Unfortunately, nothing is known regarding the embryology of the tribe Chrysobalanoideae of the Rosaceae, the supposed connecting link between the two families.

Table 2—Variation in the embryo development in Galegeae

Species investigated and author	Embryo type after Johansen (1950)	Embryo type after Soueges (1948)
<i>Astragalus glycochyllos</i> (Crete, 1951).	Trifolium variation of the Onagrad type	Period I, Series B1, Megarchetype VI.
<i>Colutea arborescens</i> (Soueges, 1951).	—do—	—do—
<i>Cyamopsis psoralioides</i> (Rau, 1954 ; Green <i>et al.</i> , 1964).	—do—	—do—
<i>Galega officinalis</i> (Soueges, 1949).	Medicago variation of the Caryophyllad type.	Period II, Series B1, Megarchetype VI.
<i>Glycyrrhiza foetida</i> (Veilct-Bartoszewska, 1956).	Trifolium variation (?) of the Onagrad type.	Period I, Series B1, Megarchetype VI.
<i>Milletia ovalifolia</i> (Pal, 1960).	Lotus variation (?) of the Onagrad type.	Period I, Series B1, Megarchetype VI (?).
<i>Psoralea bituminosa</i> (Soueges, 1950).	Geum variation of the Asterad type	Period I, Series B1, Megarchetype II.
<i>Sesbania aegyptiaca</i> (Rau, 1951).	Trifolium variation of the Onagrad type.	Period I, Series B1, Megarchetype VI.
<i>Sesbania grandiflora</i> (Rau, 1951).	—do—	—do—
<i>Sesbania aculeata</i> (Seshavatharam, 1969).	—do—	—do—
<i>Sesbania procumbens</i> (Seshavatharam, 1969).	—do—	—do—
<i>Tephrosia maxima</i> (Seshavatharam, 1969).	Euphorbia variation of the Onagrad type.	Period I, Series A2, Megarchetype IV.
<i>Tephrosia purpurea</i> (Seshavatharam, 1969).	—do—	—do—
<i>Tephrosia procumbens</i> (Seshavatharam, 1969).	Catalpa variation of the Onagrad type	—do—
<i>Tephrosia strigosa</i> (Seshavatharam, 1969).	Alysicarpus variation of the Onagrad type.	Period I, Series B2, Megarchetype IV.

Embryologically the tribe Galegeae appears to be a heterogeneous assemblage showing affinities to the other tribes like Dalbergieae, Phaseoleae and Hedysareae. Within the tribe Galegeae there is much variation in the embryological characters considered to be of taxonomic significance. These include (i) the number of middle layers in the anther tapetum ranging from one to four, (ii) pollen grains shed at the 2 or 3 celled stages, (iii) presence of a nucellar cap of 4 or 5 layers in some members, (iv) presence of an incipient integumentary tapetum in some members, (v) barrier tissue of thick walled cells or poorly

developed, some times free from the inner integument, (vi) suspensor of variable size and shape and (vii) Asterad, Onagrad or Caryophyllad types of embryo development. Some of the embryological characters of the Galegeae are also shared by Hedysareae, Phaseoleae and Dalbergieae. For example : (i) A massive microsporangium wall present in some Galegeae (e.g. *Sesbania*), is also present in some Dalbergieae (e.g. *Pterocarpus*), (ii) a nucellar cap of 4 to 5 layers present in Galegeae (e.g. *Sesbania*) is also present in some members of Phaseoleae and Dalbergieae (e.g. *Pterocarpus*), (iii) an incipient integumentary tapetum present in some Galegeae (e.g. *Tephrosia*) is also present in some Hedysareae (e.g. *Zornia*) while it is common among the Phaseoleae, (iv) the megaspore 'triad' present in some Galegeae (e.g. *Sesbania*) is also present in some Hedysareae (e.g. *Ougeinia*), and Dalbergieae (e.g. *Pongamia*) and (v) the Onagrad type of embryo development where $cb = iec + co + s$ is also seen in all the three tribes viz. Galegeae (e.g. *Tephrosia*), Phaseoleae (e.g. *Rhynchosia*, *Phaseolus*, *Teramnus*) and Dalbergieae (e.g. *Pongamia*). The new type of variation of the Onagrad type designated as the Alysicarpus variation and recorded in *Alysicarpus monilifer* of Hedysareae (SESHAVATHARAM, 1969) is also present in *Tephrosia strigosa* of Galegeae and *Rhynchosia suaveolens* of Phaseoleae. Thus, the tribes Galegeae, Phaseoleae, Hedysareae and Dalbergieae show some overlapping embryological characters. This also true of the morphological characters based on which the tribes are separated. Morphologically the tribe Galegeae are characterized by diadelphous stamens, dehiscent, non-jointed pod and imparipinnate leaves with entire leaflets. The tribe Hedysareae is distinguished from the Galegeae by the jointed pod, the Phaseoleae by pinnately 3-foliolate leaves and the Dalbergieae by indehiscent pod. In this connection it is interesting to note that BUKARAT (1952) based on purely exomorphic grounds removed several woody genera from the Galegeae and included them under the Dalbergieae. The tribe Galegeae appears to be heterogenous even cytologically having basic chromosome numbers of $x=5, 6, 7, 8, 10$ and 11 . GAMS (1926) considered the Galegeae to be a remarkably primitive tribe derived from the Sophoreae. This view was not supported by chromosomal study (SENN, 1938 ; TURNER & FEARING, 1959).

Among the subtribes of the Galegeae, Astragalineae, Colutineae and Indigeferineae have a base number of $x=7$ or 8 while the sub-tribe Robinineae (except *Sesbania*) and Tephrosineae have the base number $x=10$ or 11 . TURNER AND FEARING (1959) divided the Galegeae, on the basis of chromosome numbers, and aligned all the genera of the tribe having a base number of $x=10$ or 11 along with Phaseoleae, Hedysareae and Dalbergieae, while ATCHISON (1951) suggested the removal of all genera having a base number of $x=10$ or 11 from the tribe Galegeae and to be placed in the tribe Dalbergieae or for the complete merger of the two tribes. The available embryological evidence also reveals the heterogenous nature of these tribes and lends support to the views of Turner and Fearing. It is quite interesting to note some correlation between the uniformity in embryo development and chromosome numbers in some Galegeae. Thus in *Cyamopsis psoraloides* ($x=7$), *Sesbania grandiflora* ($x=6$), *S. aculeata* ($x=6$), *S. procumbens* ($x=6$), *Colutea arborescens* ($x=8$), and *Astragalus glycyphylus* ($x=8, 11, 12$) where the basic chromosome number is $6, 7$ or 8 the embryo development corresponds to Period I, Series B and Megarchetype VI with the derivatives of the basal cell contributing only to the suspensor, while in genera like *Tephrosia purpurea*, *T. maxima*, *T. pumila*, *T. strigosa* ($x=11$) and *Psoralea bituminosa* ($x=10$) with basic chromosome number of $x=10$ or 11 the embryogeny falls under Period I, Megarchetype IV or II, with the basal cell cb contributing to the root cap and root tip or even partly to the hypocotyl and radicle in addition to suspensor ($cb = phy + icc + iec + co + s$). *Galega officinalis* is so far the only member in the tribe where

the embryo development falls under the IIInd Period and shows resemblances to the members of the tribes Trifolieae, Genisteae and Viciae. But unfortunately there is no report on the chromosome numbers of this species. It is also interesting to note here that the genus *Galega* differs from the rest of the subtribe Tephrosineae in being eupulvinate (DORMER, 1946). Thus the available morphological, cytological and embryological evidences suggest the heterogenous nature of the tribe Galegeae.

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