STUDIES IN THE CLASSIFICATION AND AFFINITIES OF *ACANTHACEAE*

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SUMMARY

The present investigation mainly deals with the classification and affinities of Nelsonioideae, a little studied group in the family Acanthaceae. Its natural relationships are assessed in the light of data accummulated from the fields of morpho-anatomy, palynology, and embryology. That the group is definitely Acanthaceous has been proved by comparison and correlation of available evidence in relation to the closely allied families (Scrophulariaceae, Gesneriaceae, Acanthaceae, Pedaliaceae, and Bignoniaceae) of the order Bignoniales. Bremekamp's (1953) drastic suggestion for transferring Nelsonioideae to the vicinity of Rhinantheae (Scrophulariaceae) is therefore considered untenable.

After an investigation into the structure of Nelsonioideae, its generic interrelationships and taxonomic coherence into a distinct taxon are discussed. The subfamily status of this group has been abandoned in favour of a tribe (Nelsonieae) based on overall correlation and comparison of other subfamilies in the Acanthaceae. The natural affinities of Nelsonieae in and around the family Acanthaceae are also assessed.

Seven genera are recognized, their descriptions given (based on the observations of available species) and an artificial key to their identification is also provided. Infrageneric classification is attempted for _Staurogyne_ and _Elytraria_. Artificial keys to the identification of supraspecific taxa and species recognized, are interpolated at appropriate positions. Nearly all the species of _Staurogyne_ are referred to their respective sections, subsections, and series where possible. Two new sections are recognized in _Staurogyne_, 3 varieties are elevated to specific status, and 12 new species are described. The subgen. _Tetrandra_ in _Elytraria_ is recognized for the first time, and a new genus _Anisosepalum_ is described, documented, and circumscribed.

Only one species in Elytraria is recorded to be new to science.

An extensive exploration of anatomical and palynological characters is undertaken. The occurrence of bi-celled glandular hairs and diacytic stomata of mesogenous origin has been found to be as constant characters of Nelsonieae. Peltate scales (found in 4 genera) and foliar sclereids in species of Staurogyne and Elytraria are reported for the first time in this group.

The 'acicular fibres' which in the past were referred to as either 'large raphides' or 'raphidines', are proved to be ordinary fibres and not cell inclusions. They are also recorded here for the first time in all the Nelsonieae excepting Anisosepalum and Saintpauliopsis. Confirmatory evidence is provided for the occurrence of both 'tricolpate' and 'tricolporate' pollen grains in the Nelsonieae through the intermediacy of the prevalent 'tricolporoidate' (with ill-defined pore) condition.

Two species complexes are recognized - in both cases a need for further biosystematic, cytogenetical and field studies is stressed.

The work has been illustrated with line drawings (18 plates of figures) which are supplemented by photographic plates (17 plates with 124 photographs). Distributional data of the Nelsonieae and Staurogyne spatulata complex are presented on two maps. Efforts are also made to correlate the taxonomic data with those of phytogeography, and to elucidate the causes of disjunct distribution exhibited by many of the genera in this group (Nelsonieae).

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INTRODUCTION

I. INTRODUCTION

The family Acanthaceae (Jussieu, 1789) with its 250 genera and 2500 species (Willis, 7th ed. 1966) constitutes the ninth biggest family of the tropics and subtropics. It exhibits four main centres of distribution: Indo-Malaya, Africa, Brazil (South America), and Central America.

From time to time the Acanthaceae has been referred to as one of the closely allied families of the order 'Tubiflorae' (Engler & Diels, 1936), 'Personales' (Hutchinson, 1934), 'Personatae' (Linnaeus, 1751) or 'Scrophulariales' (Cronquist, 1968). Although the circumscriptions of the orders are mainly a phylogenetic concept and thus varys considerably from one authority to another, yet application of several names to a single order merely induces serious taxonomic confusion. Opinions might vary as to how many families of this great group (Sympetalae) should form an order depicting their natural as well as phylogenetic relationships. But available information on the phytochemistry of these families (Cf. Hegnauer, 1964; Gibbs, 1962 & 1965) support the original grouping of Engler & Diels (1936). Leaving apart the question of natural association of families into an order or orders which is beyond the scope of the present problem, one can conclude that the valid and earliest available ordinal name to the following interrelated families (Scrophulariaceae, Orobanchaceae, Gesneriaceae, Acanthaceae, Bignoniaceae and Pedaliaceae) is 'Bignoniales' (Cf. Thorne, 1968). Therefore, I have adopted Thorne's concept and circimscription of the order in the present text.

The delimitation of the family Acanthaceae as a natural one from other related families of the Sympetalae started early in the history of natural classification. In 1895 Lindau at first produced the world monograph of the family Acanthaceae in Engler's 'Pflanzenfamilien' 4: 274-374. Taking data from the comparative morphology, anatomy and palynology he subdivided the family into four subfamilies: 1. Nelsonioideae, 2. Mendoncioideae, 3. Thunbergioideae, and 4. Acanthoideae.

The outlines of Lindau's classification was generally accepted until 1908 when Van Tieghem proposed to erect a separate family Thunbergiaceae incorporating Lindau's first three subfamilies. But unfortunately he neither put forward valid arguments nor documentation for this change. Consequently, the working taxonomists could not support Tieghem's contention although many of them realized the taxonomic difficulties in the family.

Recently Bremekamp (1953), after supporting twice (1938, 1944) the outlines of Lindau's classification has come forward with a drastic conclusion regarding the naturalness of the family Acanthaceae. He has raised Thunbergioideae and Mendoncioideae to their respective family status (Thunbergiaceae and Mendonciaceae) and changed his earlier contention of treating the Nelsonioideae as a subtribe of Acantheae. Rather on the contrary, Bremekamp (1953, 1955c & 1965) has suggested the transfer of the Nelsonioideae as a tribe (Nelsonieae) of the Scrophulariaceae and placed in the vicinity of the Rhinantheae.

Although the present work is mainly concerned about the transference of the Nelsonioideae to Scrophulariaceae, it is realized that the problem, by its very nature, cannot be solved in isolation. As a result, during the course of this work many species and genera of various interrelated taxa other than the Nelsonioideae itself [e.g. Hiernia, Rhinanthus, Rhynchocorys, Isoplexis, Bacopa (all under Scrophulariaceae), Mendoncia (Mendoncioideae), Thunbergia (Thunbergioideae) and Andrographis, Bremekampia, Gymnacanthus, Phlogacanthus, Hygrophila, Synnema etc. of Acanthoideae] were also investigated. For the purpose of comparison family characters have been taken mostly from the recent textbooks and relevant papers in the journals, while the data of the Nelsonioideae and Andrographideae (excepting the embryological ones) are largely accumulated by author's own observations.

The Nelsonioideae as a taxonomic group has long been recognized by various authorities. But its natural affinity in terms of family relationship has not been clearly elucidated. Bentham & Hooker (1876) stated "Tribus Schrophularineis accendens, sed habitus et capsulae valvae concavae medio semiseptifera omnino Acanthacearum." Lindau (1894, 1895) too, failed to assess its natural relationship within or outside the family Acanthaceae although he for the first time attributed to this group a rank of subfamily within Acanthaceae.

This fluid taxonomic situation has resulted in many interesting changes as to the position of the Nelsonioideae in the overall context of family relationships within the order Bignoniales. As a result, one can find controversial reports about the affinities of the Nelsonioideae: some follow the tradition in keeping them under Acanthaceae but without adducing proper arguments, while many authorities believe that the Nelsonioideae is an intermediate group between the Acanthaceae and the Scrophulariaceae. On the other hand, its genera like Elytraria, Saintpauliopsis, and several species of Staurogyne have been in the past transferred back and forth several times from one family to another (among Acanthaceae, Scrophulariaceae and Gesneriaceae).

In this chaotic situation, where data from the fields of palaeobotany, cytogenetics, phytochemistry and pollination-ecology are entirely lacking, assessment of natural relationships largely depends on the comparative characters of morpho-anatomy, palynology, and embryology. As to whether the similarities among the taxonomic groups are due to common origin, parallelism or convergence poses a difficult question, the affinities of the group ascertained here are mostly on corroborative evidence. Probably most of the taxonomists believe that careful systematic investigation, together with correlation of all the available data from various fields of observations, in most cases, enable the investigator to recognize parallel developments or convergent evolution. Therefore it is assumed that the final conclusion about the relationship is neither biased nor affected by the similarities due to parallel developments or convergence.

The present work on the Nelsonioideae has been presented under five chapters of which the Chapter II deals with the structure of the group concerned. After an extensive discussion on the taxonomic importance of macro- and micro- (morpho-anatomical, palynological and embryological) characters of the various genera recognized their natural association into a coherent taxonomic unit has been pointed out. Generic interrelationships have been discussed and their descriptions together with a key to identification are provided. Evolutionary trends, ecological habitats and geographical distribution of the Nelsonioideae are discussed in a minimum. As the study is not intended to be a taxonomic revision, no formal description of any species apart from those which are described here as new to science is attempted. Infrageneric classification is provided in *Elytraria* and *Staurogyne*. In the former, Subgen. *Tetrandra* has been newly described while in the latter two new sections (Sect. *Tetrastichum* and Sect. *Zenkerina*) apart from the two other previously recognized by Bremekamp (1955) are created to incorporate all the species of this biggest pantropical genus of the Nelsonioideae. Artificial keys are provided at the appropriate places where further subdivision of the taxa was not possible.

I have mostly followed Bremekamp's (1955c) scheme of infrageneric classification in *Staurogyne*, but in some cases with emended circumscription of the recognized taxa and have tried to supplement morphological data with the anatomical ones, where possible. Although Bremekamp's three Subsections

(*Macrosepalae*, *Macrochlamydeae*, and *Microchlamydeae*) in the Sect. *Staurogyne* are recognized in the present classification, one might consider them to be slightly unnatural groupings. This is firstly because they are mainly distinguished by a single character (relative length of the calyx to that of the corolla), and secondly because a few border-line species (cf. Appendix, pp. 206) are encountered between *Macrosepalae* and *Microchlamydeae*. Notable examples are *St. vicina*, *St. diandra*, *St. subrosulata*, and *St. singularis*. The last two species, according to Bremekamp's classification, are placed under the Subsect. *Microchlamydeae*, but their apparently nearest relatives (*St. rosulata* and *St. inaequalis* respectively) on the basis of characters other than calyx/corolla ratio are placed under the Subsect. *Macrosepalae*.

The species (only a few in number) included under the Subsect. *Macrochlamydeae* are closely interrelated and the group seems to be well-defined. But, by and large, one can not help feeling that infrageneric classification in such groups having innumerable closely allied species tends to become artificial at least below the sectional level. Series classification is attempted, but as they are mostly based on single characters and often encounter intermediate species, no latin name is applied. In the Subsect. *Microchlamydeae* I could not succeed in recognizing any of Bremekamp's series as a result of which they have been dropped from the classification.

Chapter III and IV are of general nature and the former deals with the comparison of the Nelsonioideae with the Acanthaceae, Scrophulariaceae (mainly with the Rhinanthoideae) and other related families of the order Bignoniales. In Chapter IV a consideration of attributing family, subfamily or tribal status to this group (Nelsonioideae) has been assessed in the general affinity of Bignoniales. The decisions and their favourable arguments are also put forward.

Finally in the Appendix taxonomic notes are provided for one of the two species complexes recognized in the group. In both the complexes a need for future biosystematic works together with extensive field studies in unravelling these taxonomic problems is stressed. In Staurogyne, 3 varieties have been elevated to species ranks while 12 species are described here for the first time. Only one species of Elytraria is described as new to science, the specimens of which were referred to as E. acaulis by Benoist /cf. In: H. Humbert ed., Flore de Madagascar vol. 1 (182): 25 (1967)/.

The work is illustrated with line drawings (18 plates of figures) and two maps all of which are original, while the data are documented with numerous photographic plates (17 plates with 124 photographs).

To save the space and avoid repetition the genera are abbreviated in the following way: St. = Staurogyne, A. = Anisosepalum, O.=Ophiorrhiziphyllon, G. = Gynocraterium, Saint. = Saintpauliopsis, N. = Nelsonia, and E. = Elytraria. Varietal classification is not usually attempted but the valid names of the species together with their synonymy and appropriate authorities are cited in the general index (arranged according to alphabetical order). Only a few distinct varieties are recognized in the course of the present investigation. They are recorded under their appropriate species in the index but are not keyed out in the text. References to the relevant literature are also given in an extensive enumeration under bibliography.

SYNOPSIS OF SUBFAMILIES, TRIBES, AND SUBTRIBES IN ACANTHACEAE

In the introductory chapter I have already mentioned that the family Acanthaceae was originally subdivided by Lindau (1895) into four distinct subfamilies (cf. p.2). Most of Lindau's successors with the exception of Bremekamp, have accepted the customary definitions of these groups without recourse to a thorough critical investigation.

As the present studies necessitate the incorporation of Nelsonioideae as a tribe Nelsonieae under the subfamily Acanthoideae (cf. Chapter IV, pp. 184-186), it seems convenient to give at the beginning of this account a brief enumeration of the classification system substantiated and followed in the main text. This synopsis can act as a ready reference to the taxonomic position of those genera cited frequently in the text.

However, I should frankly admit that the tribes and subtribes adopted here are mostly based on Lindau's circumscription. Apart from the Andrographideae and Nelsonieae, I have limited knowledge about their distinctness and delimitation. This is owing to the fact that they lie beyond the scope of my present problem.

Only those genera which are cited in the present work are referred to each tribe or subtribe. They are arranged in alphabetical order and the type genera are indicated by an asterisk.

ACANTHACEAE

Subfam. 1.
Acanthoideae
(including Landau's
Nelsonioideae)

Subfam. 2.
Thunbergioideae
*_Thunbergia_ etc.

Subfam. 3.
Mendoncioideae
Gilletiella, &
*_Mendoncia_

Group A.
Imbricatae

Group B.
Contortae

Group A. Imbricatae

Tribe 1. Nelsonieae.
Anisosepalum
Elytraria
Gynocraterium
*_Nelsonia_
Ophiorrhiziphyllon
Saintpauliopsis and
Staurogyne

Tribe 2. Andrographideae
*_Andrographis_
Bremakampia
Gymnostachyum
Phlogacanthus etc.

Tribe 3. Asystasieae
*_Asystasia_ etc.

Tribe 4. Graptophylleae

Tribe 5. Pseuderanthemeae
Subtribe Pseuderantheminae
*_Pseuderanthemum_ etc.
Subtribe Diclipterinae

Tribe 6. Odontonemeae
Subtribe Odontoneminae
Subtribe Monotheciinae

Tribe 7. Acantheae
*_Acanthus_
Sclerochiton
Trichacanthus etc.

Tribe 8. Aphelandreae
Geissomerio
Stenandrium
Stenandriopsis etc.

Tribe 9. Isoglosseae

Subtribe Porphyrocominae

Subtribe Isoglossinae

Tribe 10. Justicieae

*_Justicia_ etc.

Group B. Contortae

Tribe 11. Trichanthereae

Gymnacanthus

Tribe 12. Hygrophileae

Asteracantha (=_Hygrophila_)

*_Hygrophila_

Nomaphila

Synnema etc.

Tribe 13. Louterideae

Tribe 14. Petalideae

Tribe 15. Strobilantheae

Tribe 16. Ruellieae

Eranthemum

*_Ruellia_ etc.

Tribe 17. Barlerieae

Lepidagathis etc.

STRUCTURE OF THE NELSONIOIDEAE

II. STRUCTURE OF THE NELSONIOIDEAE

A. Variation and taxonomic importance of selected macro-characters

HABIT:

The Nelsonioideae, although a small group, exhibit a remarkable diversity in habit. The genera are predominently erect or decumbent, herbaceous annuals, while perennial subshrubs and scrambling undershrubs are also frequent in Staurogyne, Ophiorrhiziphyllon, and Anisosepalum. Rosulate or subrosulate species are usually prevalent in Elytraria, but can also be found in several species of Staurogyne. Most of the Nelsonioideae are free-living plants with the exception of A. alboviolaceum var. gracilius, which is reported to be epiphytic.

The character of habit and duration proves to be useful in identification only when it is correlated with other features of taxonomic importance. As an example, I have raised a variety of St. polybotrya to specific status (St. cambodiana) after considering its perennial woody habit, elongated leaves, laxly elongated racemose inflorescence, and larger calyx lobes.

ROOT:

A tap root with secondary and tertiary branches is frequent as in Staurogyne, Ophiorrhiziphyllon, and others. Fibrous roots arising from a thickened perennating rhizome are quite common in Elytraria and Nelsonia, whereas many species (e.g. St. paludosa, Saint. lebrunii, A. alboviolaceum var. gracilius) of diverse genera produce adventitous roots from the nodes of their decumbent stems.

Sometimes these fibrous roots become fairly thickened and fleshy (e.g. in many species of Staurogyne, and populations of N. canescens inhabiting marshy habitats), while in E. tuberosa they are markedly transformed into fusiform tubers - a distinguishing feature of the species.

STEM:

The stem is generally herbaceous, sometimes undeveloped and rhizomatous giving a scapigerous or subscapegerous habit, the flowering stem arising from a radical rosette of leaves as in most *Elytraria*, a few species of *Staurogyne*, and occasionally found in *Saintpauliopsis*. Woody stem (particularly at the base) is commonly met with in Subsect. *Macrosepalae*, Ser. *C*. of *Staurogyne*, and in *Ophiorrhiziphyllon*, while many isolated species of the Sect. *Staurogyne*, a few species of *Elytraria*, and *A. humbertii* also exhibit the same feature.

Ridged stems are not so uncommon as in *St. spatulata*, *St. polybotrya* and others, but usually the stems are cylindrical, sometimes rooting at the nodes. Prominent articulation (swollen nodes) of the stems can be found in several species of *Staurogyne* (e.g. *St. polybotrya*, *St. paludosa* and others) and *E. madagascariensis*.

Branching is either monopodial of sympodial, sometimes none, but usually the branchlets are very few in number, particularly in forest-loving plants.

LEAVES:

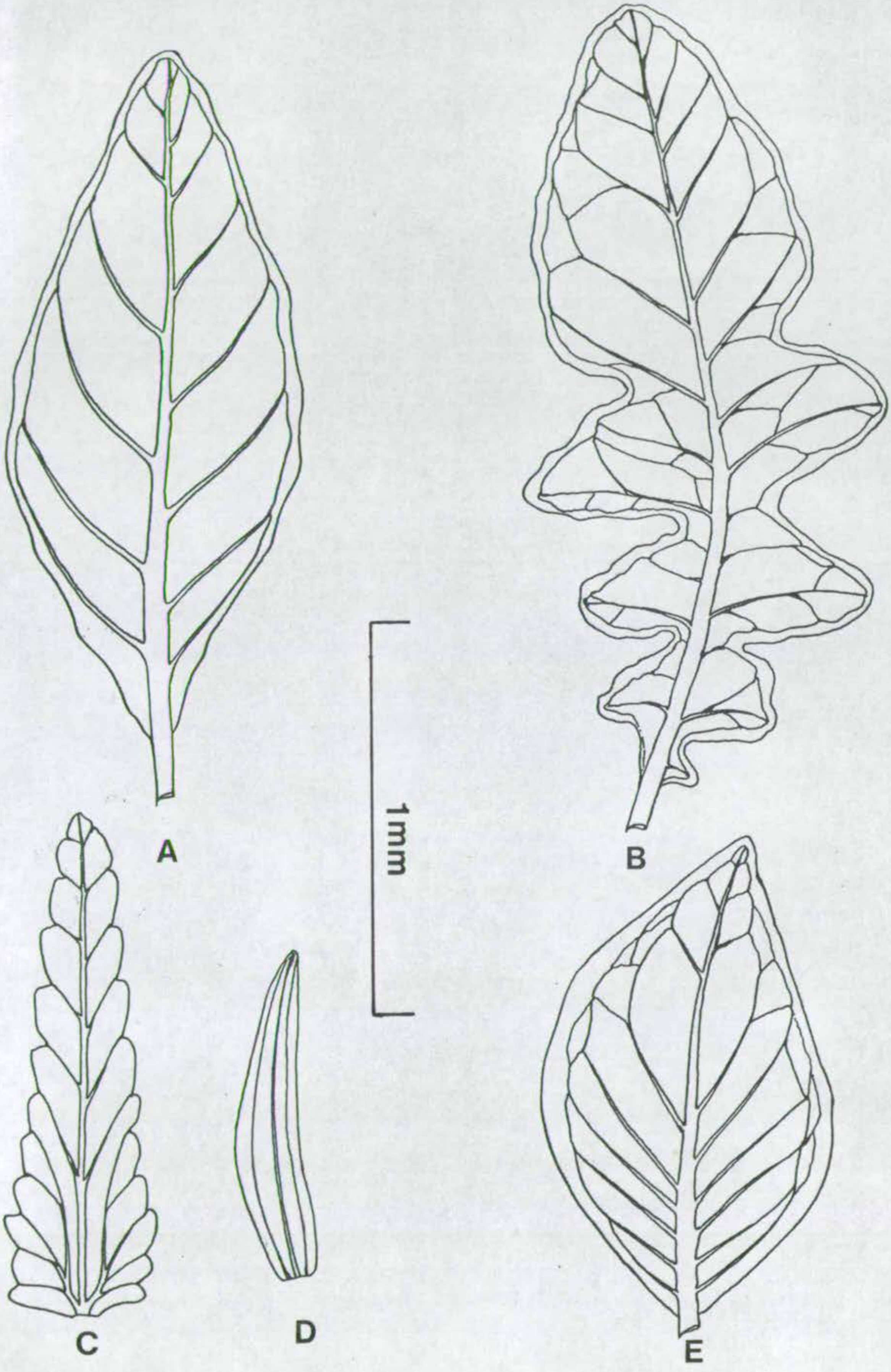
The leaves (at least the radical ones) are constantly herbaceous and dorsiventral. They afford numerous characters of taxonomic importance in generic and specific delimitations. Although alternate or subalternate leaves are often borne on the upper part of *N. canescens*, and several species of *Staurogyne*, opposite leaves are the rule in Nelsonioideae. Exceptions to this rule are *Elytraria* and *Saintpauliopsis* which bear mostly subalternate, subopposite or whorled (verticillate) leaves.

The particular shape, size, and indumentum of the leaves are proved to be reliable features in distinguishing closely allied species of *Staurogyne* and *Elytraria*. The leaves may range from the very inconspicuous size (e.g. 6-8 mm long) to extremely large type (up to 30 cm long) as in *E. macrophylla*. Petiolate (either long or short) leaves are commonly met with in all the genera, but subsessile or nearly sessile leaves are also not infrequent - especially in *Nelsonia*, *E. maritima*, and several *Staurogyne* species.

Fig. 1. TYPES OF VENATION AND THEIR COMPARISON

(Explanation in the text)

A & B = Nelsonioideae [A = *St. euryphylla*; B = *E. acaulis* var. *lyrata*]; C & D = Rhinanthoideae [C = *Rhinanthus*; D = *Odonites*], & E = Andrographideae [*Gymnostachyum*].



Fig·1·TYPES OF VENATION AND THEIR COMPARISON.

The leaves are mostly entire, subentire, repand or crenate, but in some populations of N. canescens and A. humbertii they are serrulate or lobed. On the other hand, E. acaulis var. lyrata and E. cubana are especially remarkable in their lyrate leaves which are markedly different from those of the other species of the genus.

An outstanding feature of the Nelsonioideae is their uniform type (pinnate venation) of venation in the leaves. The primary veins coming out from the midvein characteristically anastomose at the margin (Fig. 1. A,B). This can be referred to as 'camptodromous' type following the terminology of A. Kerner (1887) /cf. Stearn's Botanical Latin, 541, Fig. 40 (1966)/. In the lyrate or serrulate leaves the primary veins go directly into the lobes or dentations (Fig. 1. B) - the main pattern however, remains the same.

All these morphological features of the leaves are often correlated with those of reproductive organs of the various species in Elytraria and Staurogyne, but reverse is the case with Nelsonia (cf. Appendix "Notes on N. canescens complex" pp. 189-193).

INDUMENTUM:

Observations through a hand lens or a binocular microscope provide many characters of taxonomic importance, especially at the level of species delimitation. The hairs are either all non-glandular or sometimes mixed up with stalked glandular ones. These are not only restricted to the vegetative parts but are also visible on the reproductive organs. Their distribution, density, and nature are often a distinguishing feature of a particular species or genus e.g. Saintpauliopsis bears only eglandular hairs of distinctive type (Fig. 11. Cc). St. tenuispica is easily distinguished from its close ally St. merguensis by the total glandular hairiness of the inflorescence axis, and St. anigozanthus, St. hirsuta etc. possess both glandular and eglandular hairs on their stems, leaves, corolla (Fig. 6a. D) and capsules (Fig. 8 F). Both conspicuously or inconspicuously papillate leaves are often met with in several species of Staurogyne. These papillae may be either restricted to only one surface (e.g. St. paniculata var. glabrior possesses minute papillae only on the upper surface) or distributed on both surfaces (e.g. St. paludosa).

Genera like Staurogyne, Ophiorrhiziphyllon, Gynocraterium, and Anisosepalum are at once recognized from the rest of the Nelsonioideae by a common character hitherto unnoticed, i.e. the occurrence of round or oval, brownish-white, and thin 'peltate scales' (Fig. 11. B,B^1) on both surfaces of the leaves (mostly on the lower surface), occasionally found on the bracts, bracteoles, and even calyx lobes (e.g. Anisosepalum) too. Usually they look like minute scars on the leaf surface, but in the monotypic genus Gynocraterium they are reported to be "holes" (in fact these are also 'peltate scales' which are deeply seated into the epidermis) as mentioned by the collector.

INFLORESCENCE:

The inflorescence of the Nelsonioideae is fundamentally a raceme, although solitary axillary flowers (subtended by ordinary leaves instead of bracts) are occasionally found in Staurogyne (e.g. St. axillaris, St. anigozanthus, St. vauthieriana and Sect. Tetrastichum).

The genera like Nelsonia and Elytraria can be characterized by the constant possession of spicate inflorescences. The latter is almost unique in the Nelsonioideae in having one or more scapes (excepting E. madagascariensis which produces sessile spikes) which bear the flowering spikes at their apices.

Saintpauliopsis, a monotypic genus, is by far the most interesting in the nature of inflorescences: its floral axis divides characteristically in a 'scorpioid' (zig-zag) manner (after Lawrence, 1966), but the sequence of maturation (of flowers) is often inconstant. Staner (1934) while describing the genus for the first time reported the inflorescence to be a 'helicoid' cyme. Burtt (1958) on the other hand thought it to be a bractless raceme. All these confusions are in fact due to the minute inconspicuous bracts which are usually situated just below the calyx rim to which the two minute and hyaline bracteoles are attached, rarely further below (Pl. 11. F). As the branching tendency of the main floral axis remains impaired, the inflorescence is basically a raceme although superficially resembles a 'scorpioid' cyme. This is a remarkable example of inflorescence modification which has been described in the text as a modified raceme.

A considerable amount of morphological variations in the nature of inflorescence has taken place within the genus Staurogyne: all possible modifications (e.g. branched or unbranched types, laxly paniculate, condensed or subcapitate structures or spikes) of a true raceme have been recorded. All these characters of the inflorescence, apart from delimiting closely allied species, are also of utmost taxonomic use in the sectional classification of Staurogyne (cf. "Synopsis of Subgeneric, Sectional and Subsectional Classification" pp. 130-160).

The flowers of the Nelsonioideae are in general dichlamydeous, gamopetalous, hypogynous, bisexual and constantly zygomorphic at least in relation to androecium. Following the specific plan of the inflorescences (i.e. either raceme - condensed or subcapitate, panicle or spike) the flowers are either sessile (Elytraria, Nelsonia, and many species of Staurogyne) or distinctly pedicellate.

BRACTS:

The bracts of the Nelsonioideae exhibit remarkable diversities, especially in their shape, size, position and nature. They are constantly alternate and generally herbaceous in the group, excepting Elytraria which bears characteristically hard and scale-like bracts subtending the flowers: a character used in the generic delimitation.

Fig. 2. BRACT TYPES IN ELYTRARIA

(Explanation in the text: in each figure
both dorsal and ventral views are shown)

A = *E. nodosa*; B = *E. madagascariensis*;
C = *E. acaulis* var. *acaulis*; D= *E. marginata*;
E = *E. maritima*; F = *E. klugii*; G = *E. tuberosa*;
H = *E. bromoides*; I= *E. prolifera*; J = *E. planifolia*;
K = *E. shaferi*; L = *E. cubana*; M = *E. macrophylla*;
N = *E. caroliniensis*; & O = *E. imbricata*.

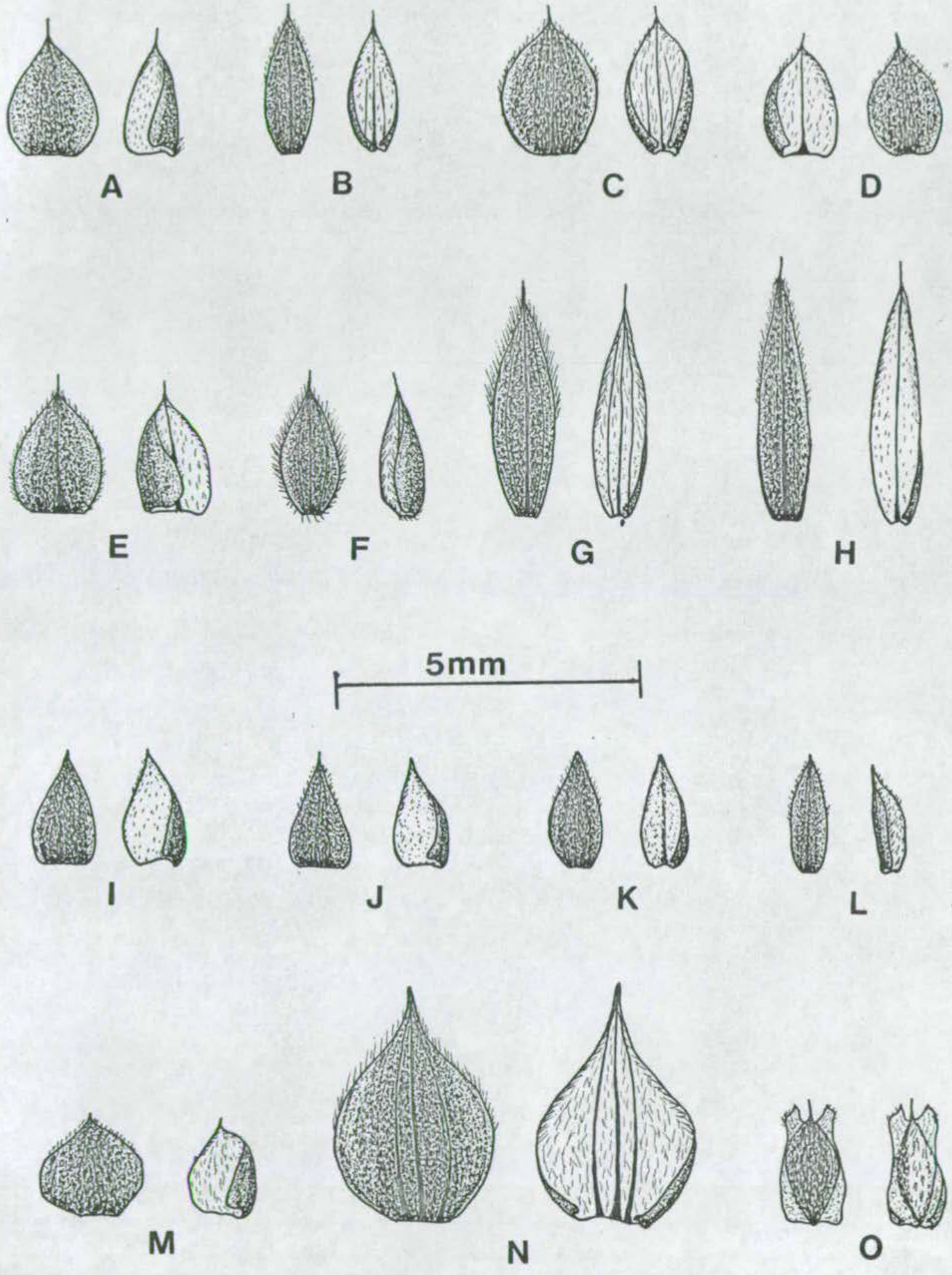


Fig. 2 - BRACT TYPES IN <u>ELYTRARIA</u>.

Bracts may either be strikingly different from those of the ordinary leaves or entirely alike. Particularly in the genus *Nelsonia*, and in Sect. *Tetrastichum* of *Staurogyne* the transformation of the leaves into bracts is gradually from below upwards, and there is no clearcut line between the two.

Similarly, the bract size is also variable from below upwards as in other racemose inflorescences where the bracts of lower mature flowers are always bigger than those of the upper young ones. But their relative length in association with the corresponding forms, if compared with the calyx lobes supply a good criterion for recognising many subsections of the genus *Staurogyne* (cf. "Synopsis of subgeneric, Sectional and Subsectional Classification" pp. 130-160).

Bracts may be either filiform and minute (e.g. *Saintpauliopsis* and many species of *Staurogyne*) [Fig. 3.*a*], triangular with (*Gynocraterium* and several species of *Staurogyne*) or without (Subsect. *Microchlamydeae* of Sect. *Staurogyne*) filiform tips, long and lanceolate (Subsect. *Macrosepalae* of Sect. *Staurogyne*, *Anisosepalum* and *Ophiorrhisiphyllon*) or leaf-like and mostly ovate or elliptic-lanceolate (*Nelsonia* [Fig. 4. A*a*] and Subsect. *Macrochlamydeae* of Sect. *Staurogyne*) [Fig. 3. M, *N*]. The shape, size, and nature of venation of these bracts provide a set of useful taxonomic characters for identifying various species of *Elytraria* (Fig. 2. A-O) [cf. key to species of *Elytraria* pp. 104-10*6*]. The position of the bracts is of particular significance in *Saintpauliopsis* (just below the calyx rim) by which one can be confident about the true nature of the Inflorescence. Although in other genera of the Nelsonioideae bracts are usually retained on the inflorescence axis proper, there are many isolated species in Staurogyne (eg. *St. brevicaulis*, *St. thyrsoidea* etc.) and *Anisosepalum* where a tendency to unite with the pedicel is highly pronounced (especially in *St. brevicaulis* they are united with pedicel up to the middle length).

Fig. 3. CALYX AND BRACT TYPES IN *STAUROGYNE*

(Explanation in the text: A-M = Calyx types;

a, b, m and n = Bracts)

A, a = *St. merguensis* (Subsect. *Microchlamydeae*); B, b = *St. racemosa* (Subsect. *Microchlamydeae*); C = *St. spatulata* (Sect. *Tetrastichum*); D = *St. paludosa* (Sect. *Zenkerina*); E = *St. capitata* (Sect. *Zenkerina*); F = *St. kamerunensis* (Sect. *Zenkerina*); G = *St. dolichocalyx* (Sect. *Zenkerina*); H = *St. griffithiana* [Ser. *A*. (*Heterosepalae*)]; I = *St. chapaensis* [Ser. *A*. (*Heterosepalae*)]; J = *St. mandioccana* (Ser. *C*); K = *St. versteegii* (Ser. *D*); L = *St. debilis* [Ser. *B* (*Isosepalae*)]; M = *St. densifolia* (Subsect. *Macrochlamydeae*), and N = *St. longibracteata* (Subsect. *Macrochlamydeae*).

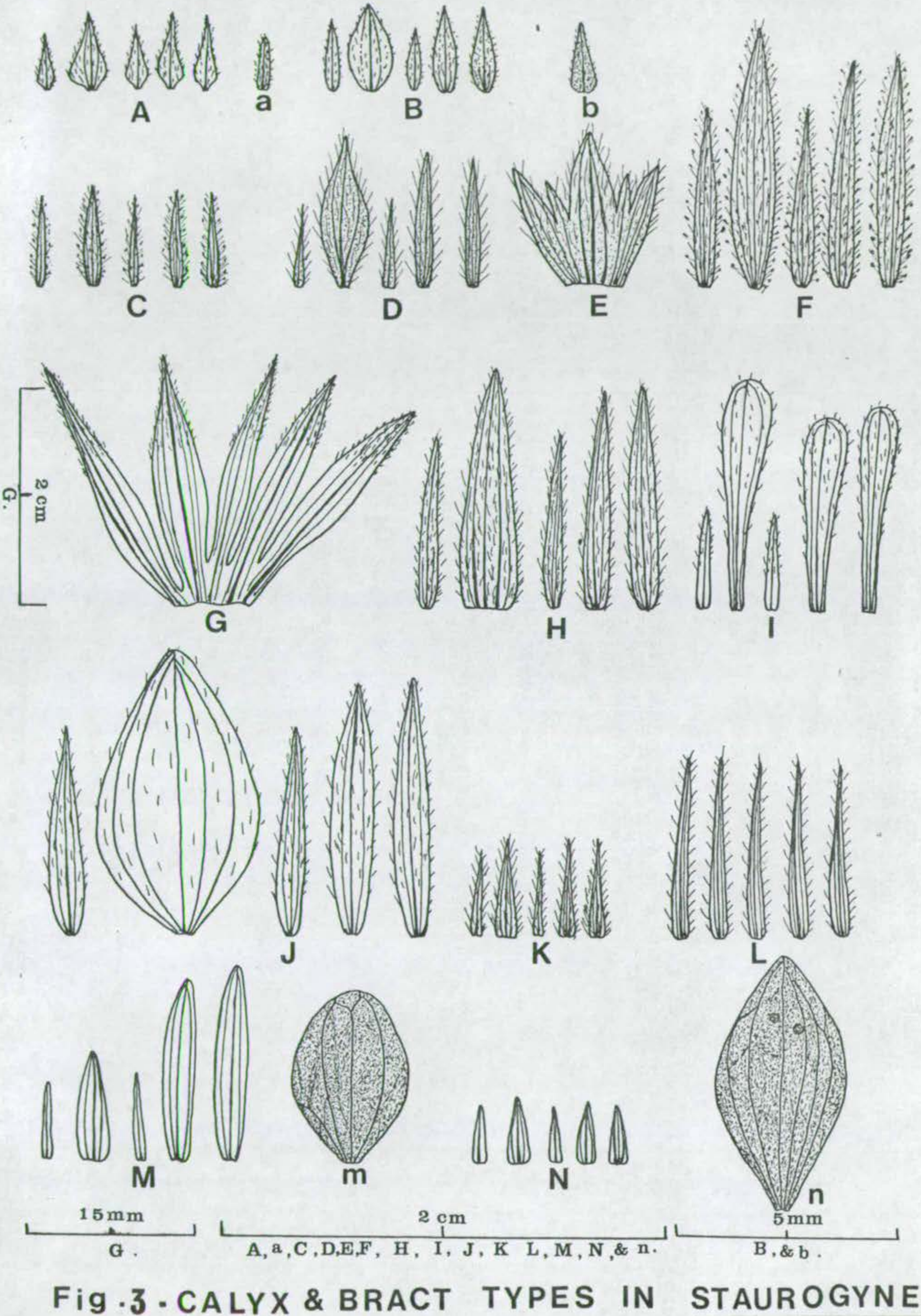


Fig. 3 - CALYX & BRACT TYPES IN STAUROGYNE.

BRACTEOLES:

The presence of a pair of persisting bracteoles to each flower is considered to be one of the distinguishing features of the Nelsonioideae (excepting Nelsonia) in comparison with most of the Acanthaceae. They are usually herbaceous, filiform, small or lanceolate and large, rarely lanceolate-spatulate (St. spatulata) in all the genera excepting Elytraria which is characterized by subherbaceous, keel-like, and aristate bracteoles.

The relative position of these constantly occurring opposite bracteoles is of particular significance in delimiting genera of the Nelsonioideae and several closely allied species of Staurogyne.

CALYX:

An outstanding feature of the order 'Bignoniales' lies in their persistent calyx. The Nelsonioideae happily conform with the generalization. The calyx members of the Nelsonioideae are usually united at least at the base, always with 'quincuncial' eastivation (Fig. 15. A). In five membered calyx the posterior and one of the two anterior lobes remain always outside, the two laterals being completely inside, and one of the anteriors remains both outside and inside (Fig. 15. A). But in genera like Elytraria (Fig. 4. C, D) and Nelsonia (Fig. 4.B), the two anteriors remain ± united to form an aestivation of four sepals out of which two (posterior and the anterior) remain outside and the two laterals remain inside.

While the extent of sepal connation at the base varies considerably in various genera and species of the Nelsonioideae, St. capitata forms a distinct calyx tube (sepals being united up to the middle, Fig. 3. E), probably of protective nature and could be involved in making the capsule indehiscent (Fig. 8. B).

The relative size in comparison to that of the corolla tube, shape, indumentum, and number of sepals are of considerable taxonomic value in the generic delimitations of the Nelsonioideae, and also useful at all levels in classifying the genus

Fig. 4. BRACT TYPES IN NELSONIA CANESCENS AND CALYX TYPES IN NELSONIOIDEAE (except *Staurogyne*)

(Explanation in the text)

Aa = *N. canescens*; B = *N. canescens*; C = American species of *Elytraria* (*E. bromoides*); D = Afro-Asiatic species of *Elytraria* (*E. madagascariensis*); E = *O. macrobotryum*; F = *G. guianense*; G = *Saint. lebrunii*, & H = *A. humbertii*(brl. = bracteole).

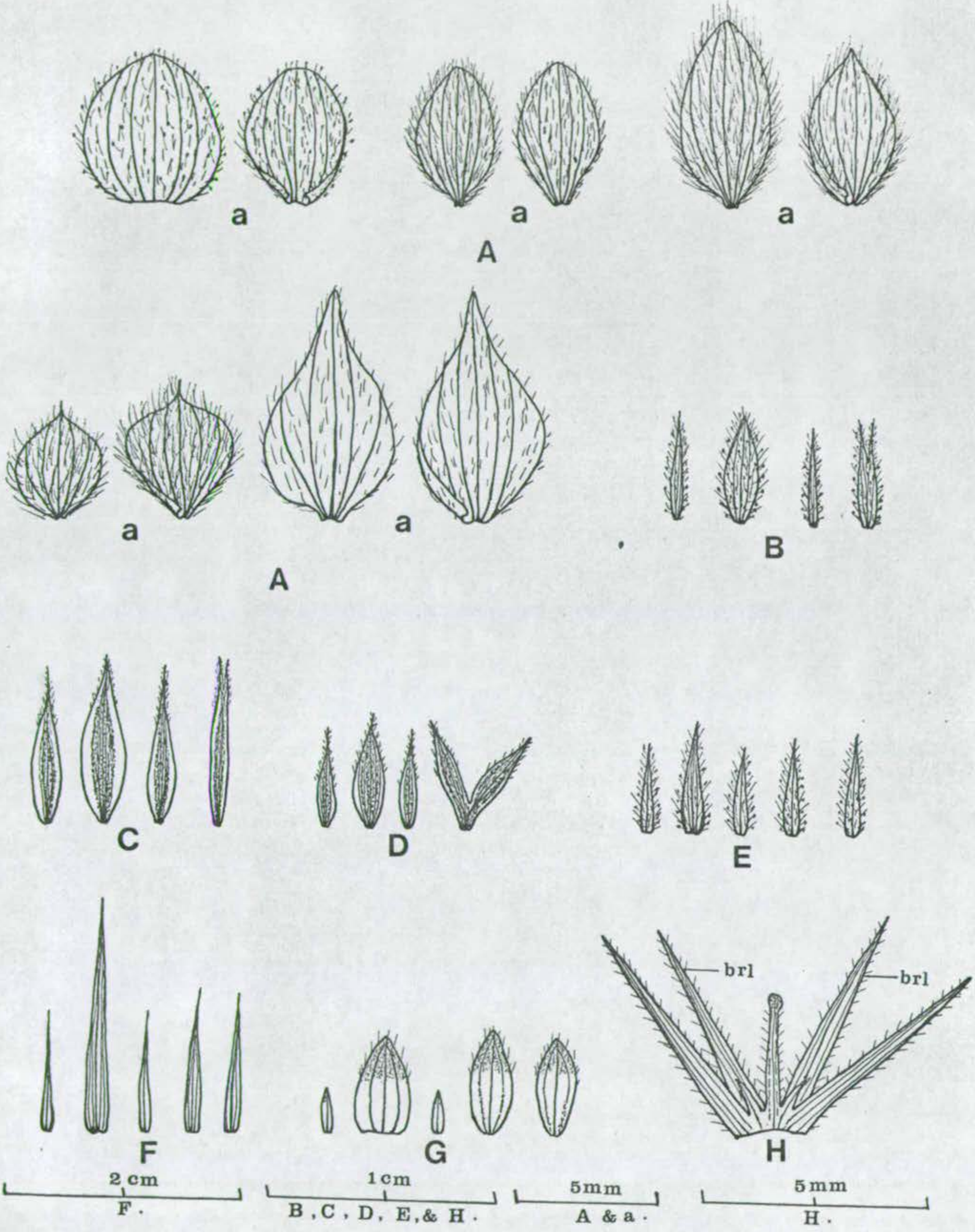


Fig. 4. BRACT TYPES IN *NELSONIA CANESCENS* & CALYX TYPES IN NELSONIOIDEAE (except *Staurogyne*)

Staurogyne. Subsimilar calyx lobes (posterior one being always very slightly longer and broader than the rest) are found in Ophiorrhiziphyllon (Fig. 4. E) and many Staurogyne species), while they are prominently dissimilar in Elytraria, Nelsonia, Anisosepalum (Fig. 4. H), Saintpauliopsis (Fig. 4. G), and many species of Staurogyne (Fig. 3. D,F,H,I,J, & M).

However, remarkable diversities are encountered in Staurogyne in the morphological nature of the calyx. In correlation with other characters of the bracts and stigma lobes, calyx types in Staurogyne provide numerous characters of taxonomic value which are useful in circumscribing its several subsections and series (cf. "Synopsis of Subgeneric, Sectional and Subsectional Classification" pp. 130-160).

The number of veins (either one, three, five or more) in the calyx lobes together with their shape and indumentum (either entirely glandular, eglandular or mixed) afford distinctive criteria, especially at the level of species identification. Similarly, the particular shape of the calyx lobes is also proved to be of utmost taxonomic value at the practical level of generic and specific delimitation.

The Nelsonioideae provide characteristically a five-membered calyx, but in genera like Nelsonia and Elytraria the number has been reduced to only four (Fig. 4. B, C). This phenomenon of progressive connation is obvious in all the American species of Elytraria where the two anterior lobes are united at least up to the middle (Fig. 4. C), but in Afro-Asiatic (including the Subgen. Tetrandra of Madagascar) species they are slightly united only at the base (Fig. 4. D) - the calyx looks at least superficially five-membered. Thus Benoist [cf. Flore De Madagascar ed H. Humbert 182 (1): 26 (1967)] while describing a new species of Elytraria (described as Tubiflora madagascariensis) reported the calyx to be of five sepals.

However, Nelsonia does not show any indication of early connation process -

Fig. 5. <u>TYPES OF COROLLA</u> (excepting <u>Staurogyne</u>)

(Explanation in the text: A-F' = Intact flowers;

a-f = Corollas split open after removing the calyces)

A, A', a = <u>N. canescens</u>; B, b = <u>E. bromoides</u>; B' = <u>E. maritima</u>;
b' = <u>E. madagascariensis</u>; C, c = <u>O. macrobotryum</u>;
D, d = <u>Saint. lebrunii</u>; E, e = <u>G. guianense</u>; F, f = <u>A. humbertii</u>,
& F' = <u>A. alboviolaceum</u>.

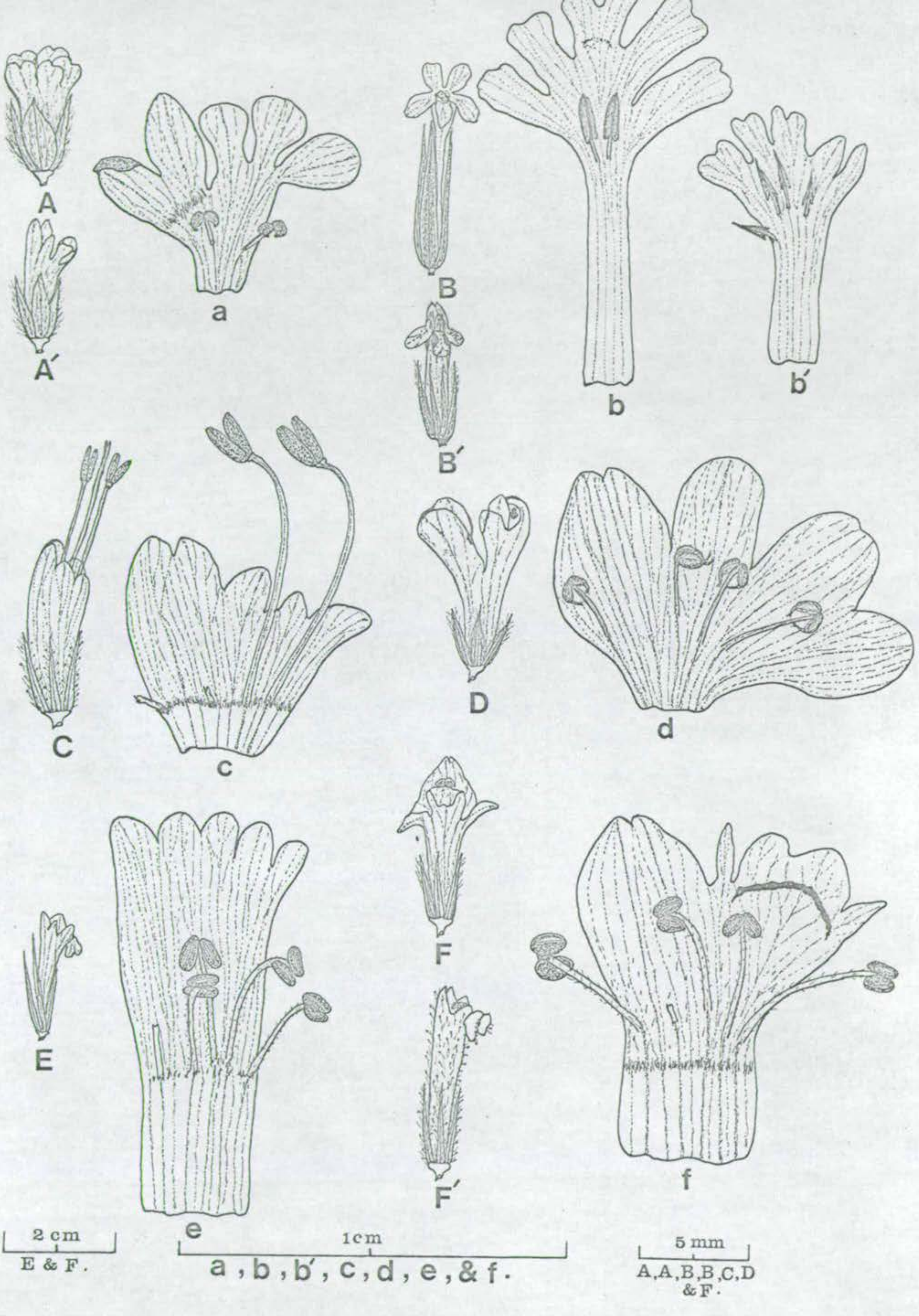


Fig ·5 - TYPES OF COROLLA (excepting *Staurogyne*).

probably it has attained its perfection in having a single anterior lobe which is slightly bifurcated at the apex only (Fig. 4. B).

COROLLA:

A sympetalous corolla, either of subactinomorphic or strongly zygomorphic nature is the rule in Nelsonioideae. Size differences are of considerable extent, especially in Staurogyne and Elytraria, but the form of corolla (either strongly zygomorphic, only subactinomorphic or both) is often characteristic of the genus, e.g. Elytraria, Ophiorrhiziphyllon, and Anisosepalum always possess strongly zygomorphic and bilabiate corollas (Fig. 5. B, B^1, C, & F, F^1), Gynocraterium bears remarkably slender, subactinomorphic corollas (Fig. 5. E), while both subactinomorphic and zygomorphic types occur widely in Staurogyne and Nelsonia (Fig. 6a, 6b, & 5. A, A^1).

In Staurogyne variation in corolla size is very great; flowers range from 6 mm (St. viscida) to 3 cm (e.g. St. anigozanthus, St. hirsuta etc.) in length. These large-flowered species are ± subshrubby in habit and produce a long, campanulate tube (Fig. 6a, D). Possibly this is an adaptation to specialized insect or bird pollination. However, isolated examples of species having bigger, prominent corollas are not so infrequent in the genus (e.g. St. longifolia, St. major, St. subcordata [Fig. 6a, B] ect.).

The number of lobes in the corolla is always five. They are often subsimilar in size and shape, particularly in the subactinomorphic (weakly bilabiate) corollas (Fig. 6a, d) but always remarkably dissimilar in the strongly zygomorphic flowers having distinct bilabiate corollas (Fig. 5. d). Corolla lobes are either elongate-lanceolate (Nelsonia, Elytraria and Gynocraterium), broadly lanceolate (Ophiorrhiziphyllon), or often suborbicular to orbicular in Staurogyne. In this respect, Anisosepalum is specially remarkable in having two minute, filiform lateral lobes in the lower lip of the corolla, accompanied by a broadly

Fig. 6a. TYPES OF COROLLA IN STAUROGYNE

(Explanation in the text: A-F = Intact flowers;
a-f = Corollas split open after removing the calyces)

A, a = St. spatulata (Sect. Tetrastichum); B, b = St. subcordata (Sect. Zenkerina); C, c = St. linearifolia Ser. D); D, d = St. hirsuta (Ser. C); E, e = St. debilis /Ser. B (Isosepalae)/, & F, f = St. coriacea (Ser. E).

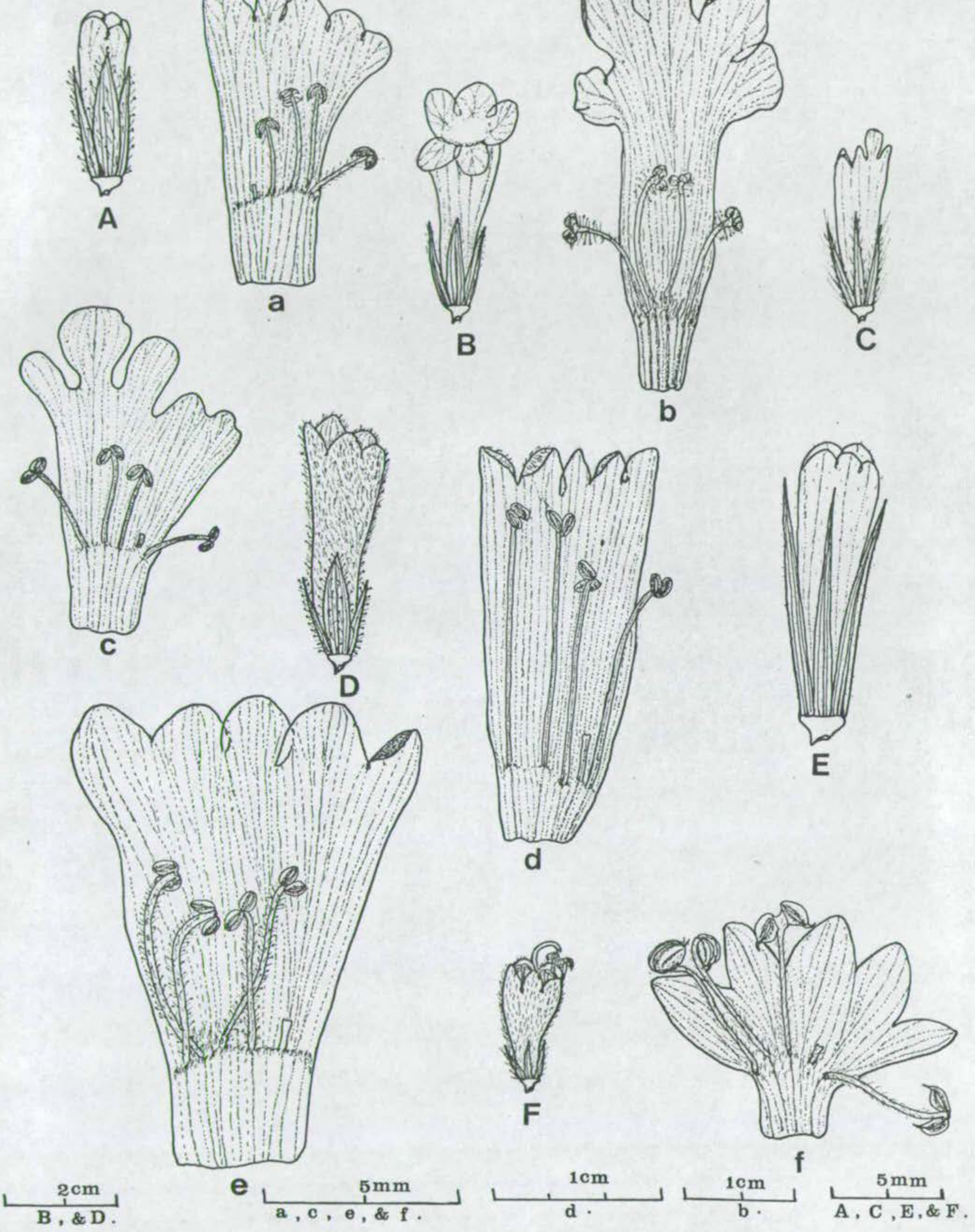


Fig. 6a - TYPES OF COROLLA IN STAUROGYNE.

ovate middle lobe. Its middle lobe possesses a characteristic 'palate' (Fig. 5. f) comparable to those of the other advanced tribes of the Acanthaceae (e.g. Asystasieae, Justicieae etc.) - probably adapted to bee pollination.

The aestivation of the corolla is characteristically 'descending imbricate' in all of the Nelsonioideae. This means that the middle (lower most) lobe of the lower lip constantly remains inside, while one of the upper lobes remains entirely outside, but the two upper lobes always cover the three lobes of the upper lip (Fig. 15. A).

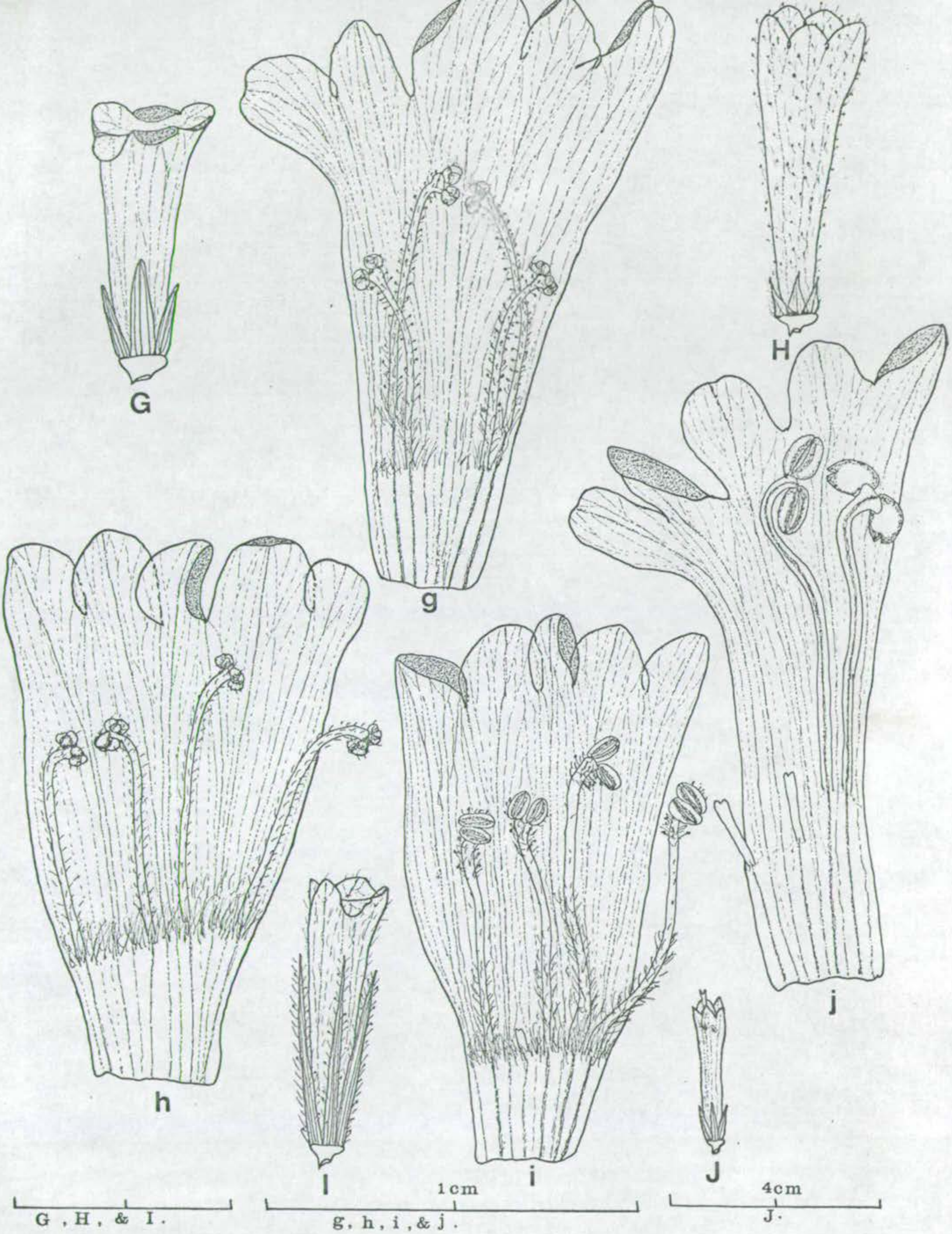
The corolla lobes and their tube may either be completely glabrous or hairy, often with prominent veins. Similarly, the corolla tube may be either glabrous or hairy inside, but usually it bears (excepting Ser. E, and many species of Staurogyne) a ring of eglandular hairs at the attachment of the staminal filaments. The density of these hairs in the ring and the type of indumentum (either wholly glandular, eglandular or both) are characteristics of particular species, and are therefore useful in taxonomic identification.

The form of the corolla tube is also diverse in Staurogyne (either campanulate, cylindrical with dilated upper portion or extremely slender tube-like), uniformly slender in Elytraria (Fig. 5. B, B^1), slender and tube-like with a dilated end in Gynocraterium (Fig. 5. E), while cylindrical and campanulate in the rest (Figs. 6a, 6b, & 5. A, C, D & F).

Yellow or yellowish-white colour largely predominates in the Nelsonioideae, but white flowers are also frequently met with in several species. Blue and mauve-coloured flowers are usually encountered in Elytraria, Nelsonia, and many Staurogyne species, whereas red-flowered species (e.g. St. grandiflora) are rarely found in the latter. Specialized nectar guides are usually not obvious in the flowers (of course, nectar may be present which is produced by the disc below the ovary), but occasional species (e.g. St. dolichocalyx) with agreeable fragrance indicates their preference for insect pollination.

Fig. 6b. TYPES OF COROLLA IN STAUROGYNE

(Explanation in the text: G-J = Intact flowers;
g-j = Corollas split open after removing the calyces)
G, g = *St. densifolia* (Subsect. *Macrochlamydeae*);
H, h = *St. merguensis* (Subsect. *Microchylamdeae*);
I, i = *St. sandakanica* (Sect. *Maschalanthus*), &
J, j = *St. diandra* (Subsect. *Microchlamydeae*).



Fig·6b·TYPES OF COROLLA IN STAUROGYNE.

ANDROECIUM:

Like many other sympetalous groups, Nelsonioideae possess typically didynamous zygomorphic androecium derived through the sterilization of the posterior fifth stamen (Fig. 15. A). This reduced fifth stamen is often represented by a small or long staminode in genera with four perfect stamens (e.g. Staurogyne and other related genera and Subgen. Tetrandra of Elytraria). The genus Ophiorrhiziphyllon and Subgen. Elytraria of Elytraria are always characterized by the presence of only two perfect stamens, usually accompanied by two minute or prominent staminodes owing to the sterilization of the upper longer pair of the didynamous stamens (Fig. 5. c). But Nelsonia represents a unique example having only two perfect stamens with no trace of staminodes (Fig. 5. a).

Staurogyne, a genus hitherto known to have always four perfect stamens, can also show a tendency to androecial reduction in the number of stamens. Thus St. diandra (Thailand) contains only two perfect stamens, often associated with two, rarely three staminodes (Fig. 6b. j).

Apart from the number of perfect stamens, particular anther shape with its connective and mode of dehiscence often provide useful taxonomic characters in generic delimitations within the Nelsonioideae (cf. "Key to Genera of the Nelsonioideae" pp. 89-90).

Most of the Nelsonioideae produce globose or subglobose anthers, but in Elytraria anthers are characteristically elongated (at least in mature flowers) - sometimes provided with small or long distal appendages (Fig. 7. K). Out of the two elongated anther lobes in Elytraria, one is often smaller than the other or one of them is placed a little higher up on the connective (Fig. 7. K, J). Other genera of the Nelsonioideae possess slightly dissimilar anther lobes, placed at the same level or slightly at different levels (Fig. 7. A, E, F, & G).

Fig. 7. TYPES OF STAMENS AND STIGMAS

(Explanation in the text: A-K = Stamens;

L(l)-R(r) = Stigmas)

A = *St. subcordata*; B = *St. diandra*; C = *St. spatulata*; D = *St. coriacea*; E = *Saint. lebrunii*; F = *O. macrobotryum*; G = *G. guianense*; H = *A. humbertii*; I, i = *N. canescens*; J = *E. caroliniensis*; j = *E. acaulis*; K = *E. madgascariensis*; L(l^1-l^8) = Stigmas in *Staurogyne* [l^1 = *St. argentea* (Ser. *A*); l^2 = *St. densifolia* (Subsect. *Macrochlamydeae*); l^3 = *St. hirsuta* (Ser. *C*); l^4 = *St. merguensis* (Subsect. *Microchlamydeae*); l^5 = *St. diander* (Subsect. *Microchlamydeae*); l^6 = *St. longibracteata* (Subsect. *Macrochlamydeae*); l^7 = *St. subcordata* (Sect. *Zenkerina*), and l^8 = *St. coriacea* (Ser. *E*)]; M = *O. macrobotryum*; N = *Saint. lebrunii*; O = *G. guianense*; P = *A. humbertii*; Q = *N. canescens*; and R(r) = *Elytraria*.

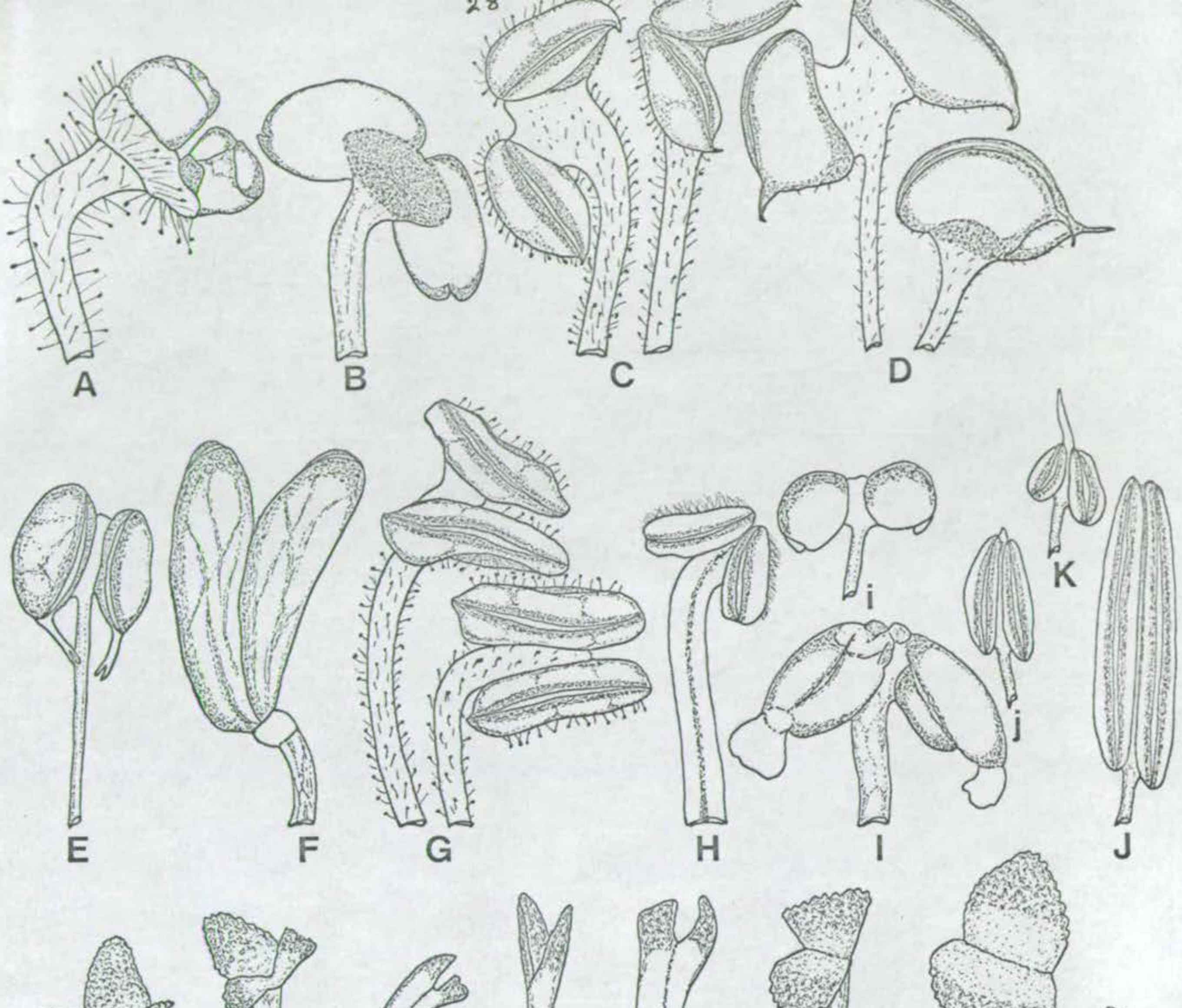


Fig ·7· TYPES OF STAMENS & STIGMAS·

In most of the *Elytraria* species the two anther lobes are joined together throughout their whole length and the connective is thin (Fig. 7. J, K), whereas in other genera they are united only at certain points - largely widened apart by their thickened wide connective (excepting only *Ophiorrhiziphyllon* where the connective is small - not wide apart) [Fig. 7. A-D, E, G, H & I].

Mostly the anther lobes are without any perceptible appendage, but apiculate, mucronulate or tailed anthers (referring to the base) are not infrequent in *Staurogyne* [e.g. *St. spatulata*, *St. coriacea* (Fig. 7. D), *St. rivularis* etc.]. *Saintpauliopsis* is quite remarkable for its anthers which are provided with long, slender tails - each tail being bifurcated at the apex (Fig. 7. E).

Usually the stamens are included and introrse in the Nelsonioideae, but subexserted stamens are also not rare in *Staurogyne* (cf. "Synopsis of Subgeneric, Sectional and Subsectional Classification" pp. 130-160) and *Elytraria*. Conversely, the genus *Ophiorrhiziphyllon* characteristically produces stamens which are much exserted from the mouth of the corolla tube (Fig. 5. C).

Staminal filaments in the Nelsonioideae are always placed alternately with the corolla lobes and are joined with the corolla tube, nearly at the base or to some extent higher up the tube. *St. petelotii* merits particular notice as it produces its filaments from nearly at the mouth of the corolla tube (at $\frac{3}{4}$ portion above the corolla tube). These filaments are extremely small in *Nelsonia* (Fig. 5. a) entirely glabrous in *Elytraria*, *Ophiorrhiziphyllon*, *Nelsonia*, *Anisosepalum*, *Saintpauliopsis*, and several species of *Staurogyne*. But most species of *Staurogyne* and the monotypic genus *Gynocraterium* possess filaments which are often hairy with either glandular or eglandular hairs, sometimes the anthers and the connectives also become hairy in many species. The characteristic hairs present on the staminal filaments (i.e. either entirely glandular, eglandular or both) sometimes provide taxonomic characters for identifying closely related species, especially in Staurogyne.

GYNOECIUM:

A bicarpellary, syncarpous, superior ovary is typically found in Nelsonioideae. The ovary may be cylindrical or obconical in shape, gradually or suddenly narrowed to form a style which is either slender and filiform or prominently thickened and hollow to some extent (e.g. many Staurogyne species).

The ovary is usually glabrous (e.g. Nelsonia, Elytraria, Saintpauliopsis, and Anisosepalum), but many species of Staurogyne (e.g. St. kamerunensis, St. anigozanthus and others) show pilosity on their ovaries which is mainly due to stalked glandular hairs in association with a few simple eglandular hairs.

Rao (1953) in an investigation of the floral anatomy of some 'Bicarpellatae' pointed out diverse features of the disc in the Acanthaceae (of course, without recourse to the studies of the Mendoncioideae and Nelsonioideae). He classified the disc into two broad categories: (1) the 'cushion' type, and (2) the 'annular' type. The disc of the Nelsonioideae conforms to the first category which is characterized by the complete fusion of the disc throughout its length with the floral axis. The disc may be either very small or insignificantly developed so that it is externally unrecognizable as such, and may appear as forming a portion of the ovary at the base (e.g. Nelsonia, Elytraria, and many other species of Staurogyne). In other genera the disc is often well-developed to form ± a swollen region above the insertion of the corolla. This has been described in the text as a 'cushion-shaped' disc, which is in fact, a swollen lump of tissue just below the base of the ovary.

The style is always simple, mostly glabrous, but minutely hairy from below upwards up to the middle in Gynocraterium and sparsely papillose in Anisosepalum. This character when correlated with others give support to their generic status in the Nelsonioideae.

The characters of the stigma in conjunction with other features of vegetative and reproductive parts have proved to be quite useful in classification and generic delimitations. Although the stigma characters occas~~i~~ionally encounter practical difficulties to observe them carefully in the herbarium sheets (owing to their fragile soft tissue at the stigmatic surfaces), nevertheless, they are of considerable taxonomic as well as biological importance hitherto unnoticed by the previous workers in the Nelsonioideae.

Most of the previous workers in the group have described the stigma of Elytraria as either shortly bilobed or unequal. It is true that the stigma is basically bilobed, but the lower lobe is always rather imperceptible, particularly in the dried flowers of the herbarium sheets. The upper lobe is always distinctive, often flattened and club-shaped which bends over the two or four stamens (Fig. 7. Rr).

The stigmas in the Nelsonioideae are usually included, but in Ophiorrhiziphyllon and a few species of Staurogyne they are either prominently exserted (Fig. 5. C) or slightly exserted (Fig. 6a. F) along with the stamens. However, subexserted or slightly exserted species may also occur in Elytraria and in a few American species of Staurogyne (e.g. St. anigozanthus, St. hirsuta etc.).

FRUITS:

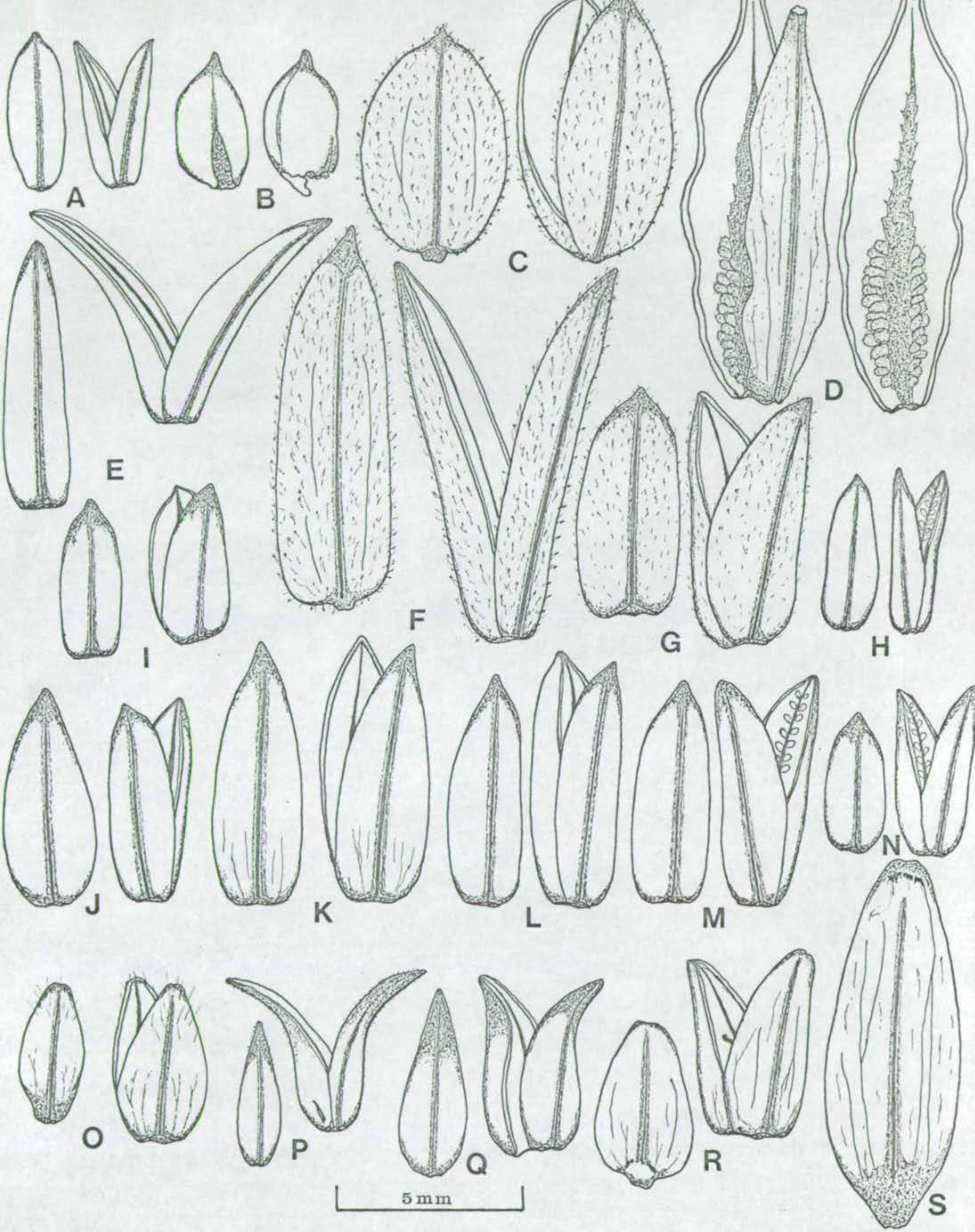
The characteristic fruit of the Nelsonioideae is a loculicidal capsule, usually dehiscing into two woody recurved valves after maturity. Only Sect. Zenkerina of Subgen. Tetrastichum under Staurogyne deserves special mention as its species bear tardily or irregularly dehiscent (rarely indehiscent) capsules (Fig. 8. B, C, & D).

The diversity of the capsule in its shape, size, indumentum, and nature of the apex provide features of taxonomic importance in the group. The tip of the capsule may be truncate or subtruncate (e.g. Saintpauliopsis and Anisosepalum

Fig. 8. TYPES OF FRUITS

(Explanation in the text: in each case [excepting D and *S*] two capsules are drawn - one before and the other after partial dehiscence)

A = *St. polybotrya* (Sect. *Tetrastichum*); B = *St. paludosa* (Sect. *Zenkerina*); C = *St. kamerunersis* (Sect. *Zenkerina*); D = *St. dolichocalyx* (Sect. *Zenkerina*); E = *St. argentea* [Ser. *A* (*Heterosepalae*)]; F = *St. anigozanthus* (Ser. *C*); G = *St. mandioccana* (Ser. *C*); H = *St. agrestis* (Ser. *D*); I = *St. coriacea* (Ser. *E*); J = *St. debilis* [Ser. *B* (*Isosepalae*)]; K = *St. longibracteata* (Subsect. *Macrochlamydeae*); L = *St. bullata* (Subsect. *Microchlamydeae*); M = *St. sandakanica* (Sect. *Maschalanthus*); N = *O. macrobotryum*; O = *Saint. lebrunii*; P = *N. canescens*; Q = *E. maritima*; R = *A. alboviolacum*, and S = *A. humbertii*.



Fig·8·TYPES OF FRUITS.

(Fig. 8. O-5), elsewhere in Elytraria and Nelsonia (Fig. 8. P, Q) gradually pointed to fine tips, possibly an adaptation to effective dispersal (cf. Rendel, 1925) by clinging to the fur of passing animals. This is probably possible by the fact that dehiscing valves usually retain a few seeds after the explosive severing of the capsule.

The variation in the capsule found in Staurogyne pertaining to its shape and size (Fig. 8. A-N) afford good criteria for recognizing closely allied species. All these capsules in conformity with their ovaries are usually glabrous or subglabrous (Fig. 8. A,B), but many species of diverse taxonomic relationships in Staurogyne produce distinctly hairy capsules (Fig. 8. C, F, G) provided with glandular and eglandular hairs. But in Saintpauliopsis the capsule bears only a few bristle-like eglandular hairs at the tip (Fig. 8. O).

Each dehiscing capsule valve contains either two (most of the Nelsonioideae) or four (only in Subgen. Tetrastichum of Staurogyne) rows of seeds (Fig. 8. M & D) borne alternately on thin (most of the Nelsonioideae) or thick (many Staurogyne species) placenta. The placenta in each case divides characteristically into two equal halves from the top to the base.

SEEDS:

Until now, the seeds of the Nelsonioideae have been described as globose or subglobose in outline and as always numerous in each capsule /cf. Lindau (1895), Bremekamp (1953) and others/. The statement regarding the number of seeds is true for a few genera (e.g. Staurogyne, Saintpauliopsis and Ophiorrhiziphyllon) of the Nelsonioideae, but the genera like Nelsonia, Elytraria, Gynocraterium, and Anisosepalum have ± a fixed number of seeds in their capsules.

This fixed number of seeds and their testa characters when correlated with other features of independent source, largely help in the generic delimitations. For example, Anisosepalum is unique in the Nelsonioideae in having (in each

Fig. 9. TYPES OF SEEDS

(Explanation in the text: A-I = Seed shape, size and surface; a-i = Bars, spines or hooks on the testa cells)

A, a = *St. spiciflora*; B, b = *St. paludosa*; C, c = *O. macrobotryum*; D, d = *Saint. lebrunii*; E = *A. humbertii*; F, f = *N. canescens*; G, g = *E. imbricata*; H = *E. maritima*, & I, i = *Andrographis echioides* [In each case of A-I both dorsal and ventral views are shown].

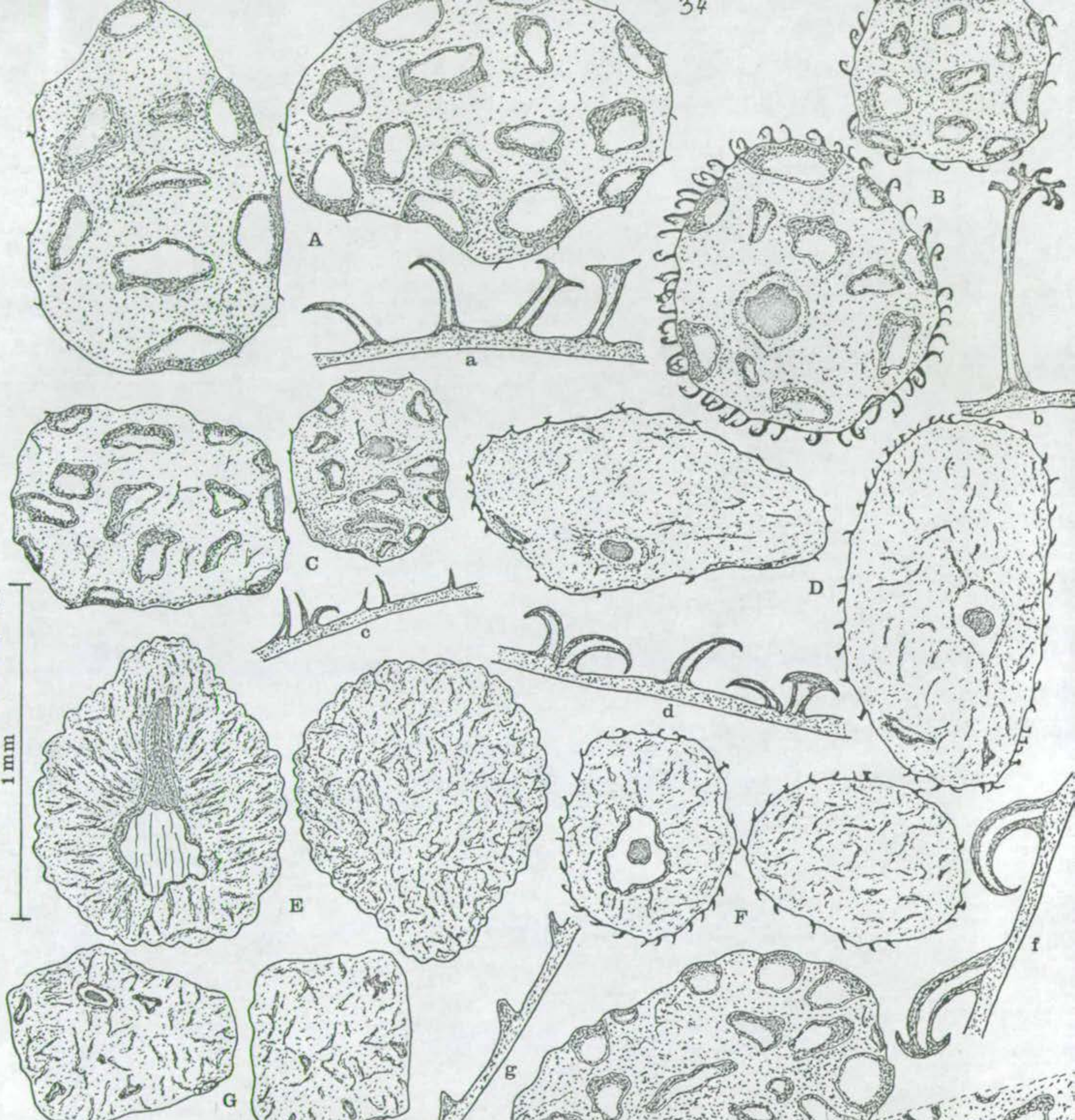


Fig. 9. TYPES OF SEEDS.

loculus) 6 or 8 larger seeds which are ventrally flattened (compressed), and have a characteristically large hilar excavation (Fig. 9. E). They are supported by unindurated retinacula which quickly fall off at maturity, while their testa is distinctly rugose (Fig. 9. E) but devoid of bars or hooks.

However, small hilar scars are also met with in *Nelsonia* (Fig. 9. F), and sometimes in the species of *Elytraria*, *Staurogyne* (Fig. 9. B, H) and *Saintpauliopsis* (Fig. 9. D). Papilliform retinacula are often perceptible in several species of *Elytraria* and *Staurogyne* (Fig. 8. D), but their usual absence in the group makes it unimportant for taxonomic classification.

All the Nelsonioideae apart from *Anisosepalum*, *Gynocraterium* (where seeds were not available), and *Elytraria* possess solid bars or hooks on their testa cells, some of which branch and rebranch at their extremities forming uncinate structures (Fig. 9. a, b). These were at first described by Kippist (1845) as "hammer-headed hairs" in *Nelsonia*: the statement was subsequently supported by Oersted (1854) and Lindau (1895). But Bremekamp (1953) has rightly pointed out that these, superficially resembling glochidiate hairs of the dome-shaped testa cells, are in fact provided with bars which straighten out elastically if the seeds are dipped into water for some time.

A uniform occurrence of solid bars or hooks on the testa cells of the Nelsonioideae (with the exception as cited above) invalidates the statement of Bremekamp (1953) in connection with *Staurogyne*, the seeds of which are described as only 'foveolate' without mentioning the bars or hooks.

The testa of the seeds in *Elytraria* is remarkably granular (the papillae can be of course, compared with the reduced solid bars, Fig. 9, g) accompanied by occasional irregular areas of depression, while that of *Staurogyne* and *Ophiorrhiziphyllon* is constantly 'foveolate' with sparsely distributed patches of irregular depressions (Fig. 9. A, B, & C).

The seeds are usually globose or subglobose in most of the genera in the Nelsonioideae, but this cannot be taken as a general rule since other types of seeds (e.g. round or obovate in Anisosepalum, oblong or suboblong with many faces in Saintpauliopsis, Elytraria, and many species of Staurogyne) are not so infrequent in the group. In a recent paper Long (1970) has described the seeds of Elytraria to be ± flattened (cf. pp. 279), while similar seeds are frequently encountered in various species of Staurogyne.

It seems that careful comparative studies of the seeds in the family Acanthaceae may in future yield fascinating taxonomic information which can be of value in the classification and generic delimitations of the family.

B. Studies in the micro-characters, their variation and taxonomic importance

The taxonomic importance of micro-characters has been emphasized much in recently published monographic work. A growing tendency among taxonomists is to explore new data and synthesize them into the framework of the existing classification. However, one should not overemphasize the value of micro-characters in comparison to that of the macro-morphological ones. It is only their correlation that counts much in the classificatory systems.

In the present investigation I have tried to focus particular attention on anatomical and palynological characters of the Nelsonioideae which have not previously been thoroughly studied.

MATERIALS AND METHODS

Anatomical studies into leaf, stem, root, fruits and seeds are all based on dried herbarium specimens excepting the developmental studies done on living plants.

Small pieces of dried specimens (any organ required for anatomical studies) were kept overnight in a dilute solution of about 10% KOH for softening. The concentration of KOH is varied depending on the texture of the original tissue concerned (i.e. either woody and hard or soft). Next morning the softened materials are thoroughly washed with water after decanting off entire KOH solution. If the materials are too dark owing to some chemical deposition, addition of a few drops of 25% H_2O_2 will oxidize and decolourize the tissues quickly. After thorough washing the materials are preserved in 70% FAA (Formalin: Acetic Acid: Alcohol) for hardening and become ready for sectioning within a couple of hours.

Histological studies into the root, stem, leaves (lamina and petiole), fruits, and seeds were all done by cutting hand sections from comparable regions.

All the available sheets have been examined and voucher specimens together with permanent slides are preserved at the University of Edinburgh, Taxonomy Section at the Royal Botanic Garden. The data obtained during this investigation are discussed under the following headlines:

ROOT

Root anatomy at the primary growth shows 6 or more radial vascular bundles, while in mature roots secondary growth is prominent. In O. macrobotryum the taproot shows growth rings in transverse section.

The cortex is usually parenchymatous, sometimes becoming slightly thickened at the outer layers, but in some fleshy roots of Nelsonia it possesses many conspicuous air chambers (Pl. 13.F).

STEM

The anatomy of the stem provides many taxonomic characters of importance in the group. These are particularly valuable for generic delimitations and also in the sectional classification of Staurogyne (cf. pp. 89-90 & 127-129).

The extent of hypodermis (either of 2 layers or many layers) can be used as one of the distinguishing criteria for the recognition of closely allied species. The parenchymatous cortex also varies in its thickness, depending mainly on the diameter of the stem, and the vascular bundles form a complete ring in the very early stages of primary growth.

TANNIN-CONTAINING CELLS

Method: Small pieces of tissues (softened previously by KOH and washed thoroughly) were fixed in alcoholic (7%) copper acetate for about 8-10 days. Hand sections were taken from these fixed tissues and placed in aqueous ferrous sulphate (0.5%) solution for about 3 minutes. This was followed by a thorough washing in water and the sections were ultimately treated with 70% alcohol and mounted in glycerine jelly. Tannin-containing cells showed positive reaction to become dark blue in colour (Peacock, 1955).

The cortical tissues of root, stem, and petiole in many species of Staurogyne, Elytraria, populations of Nelsonia, and the genus Ophiorrhiziphyllon possess few to many specialized thickened cells containing tanniferous substances. They superficially resemble young sclerified cells and their contents look granular in appearance. Although their nature and distribution do not appear to be of any taxonomic value in delimiting genera and species, yet their constant absence from other genera of the Nelsonioideae (e.g. Saintpauliopsis, Gynocraterium, and Anisosepalum) probably indicates some affinity amongst these genera compared to those which sometimes possess tannin-containing cells.

'ACICULAR FIBRES'

Thin elongated fibres ("resembling large raphides"!) named 'acicular fibres' (Russow, 1880) - a unique anatomical feature of Acanthaceae - are also constantly found in the Nelsonioideae except Anisosepalum and Saintpauliopsis. They are invariably present in the root, stem, petiole, and veins of the lamina (Pl. 1.A-H).

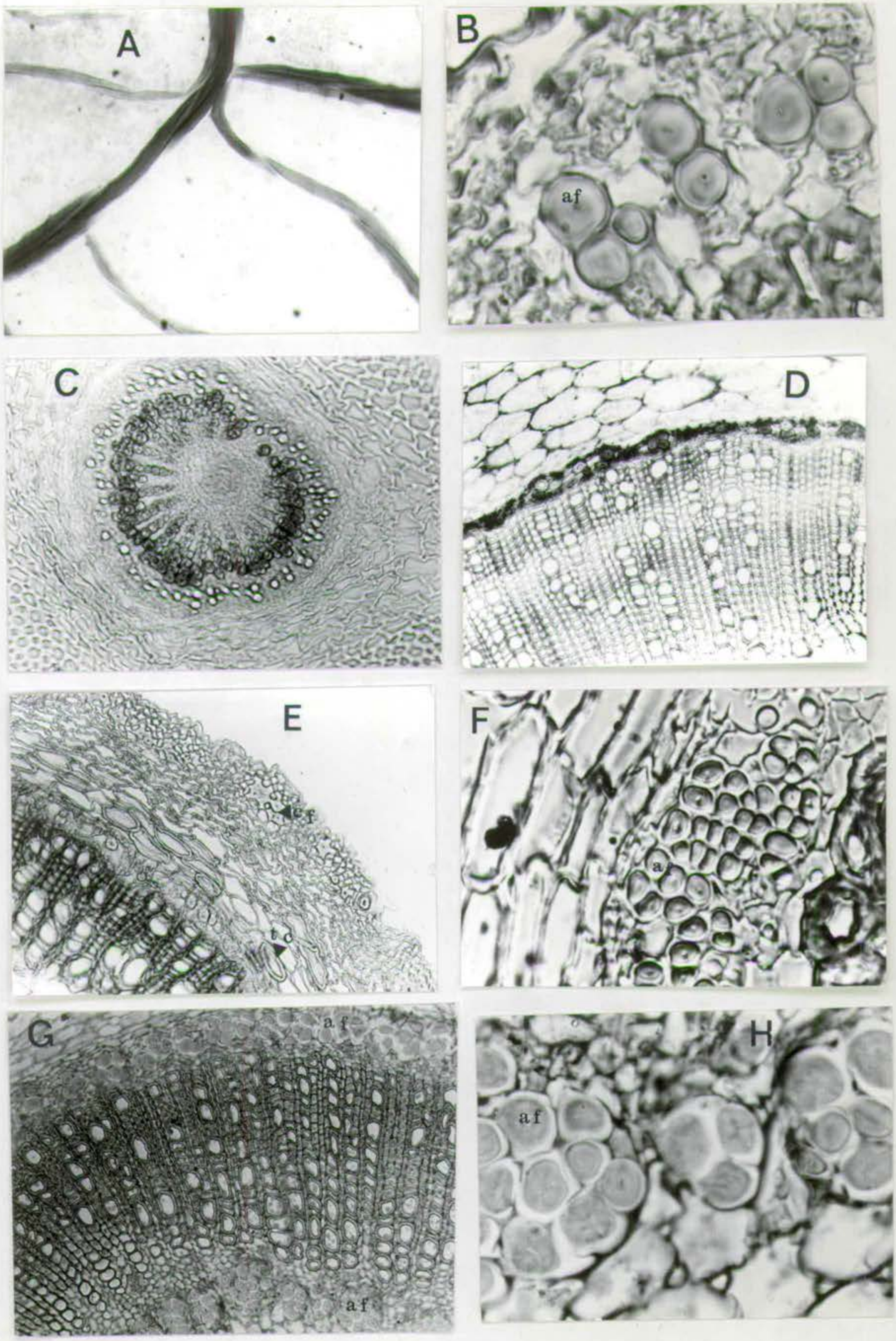
Available information on their nature and distribution within the family Acanthaceae is surprisingly scanty. But their occurrence has been reported so far in about 26 genera (cf. Metcalfe & Chalk, 1950 and Solereder, 1908). Bremekamp (1953) could not recognize these elements which he referred to as 'raphidines' in the Nelsonioideae (pp 537-538). But I have found these fibres invariably in the Nelsonioideae referred above and in Synnema, Gymnacanthus, Phlogacanthus, Bremekampia, and Acanthus.

These fibres (Fig. 12.D) occur either individually or in groups, usually in the phloem tissue surrounding the vascular cylinder of stem, root, petiole, and veins of the leaves. Their distribution and number vary enormously in the species of Staurogyne, while Nelsonia is unique in the Nelsonioideae for having 'acicular fibres' both in the phloem tissue of the vascular cylinder and also in

Pl. 1. '<u>ACICULAR FIBRES</u>' <u>IN NELSONIOIDEAE</u>

(Explanation in the text: A = cleared leaf,
and B-H = transverse sections)

A = A portion of leaf (lower epidermis removed) in <u>St. microphylla</u> (x 145); B = A portion of petiole in <u>St. longifolia</u> (x 650); C = Petiole in <u>E. macrophylla</u> (x 145); D = A portion of stem in <u>O. macrobotryum</u> (x 145); E = Part of stem in <u>N. canescens</u> (x 145); F = Vascular cylinder of root in <u>E. tuberosa</u> (x 650); G = A portion of stem in <u>N. canescens</u> (x 145, note the presence of 'acicular fibres' in the phloem and in the pith), and H = Part of the same - highly magnified (x 650). [af = 'acicular fibres'; cf = cortical fibres, and tc = tannin containing cells].



Pl.1.

the pith cells of the stem (Pl. I. E & 6).

Russow and Roulet were of the opinion that these fibres (especially the bundle of fibres) are derived from a mother cell which on repeated divisions produce numerous small cells adjacent to each other. The fibres lie freely in the cavity of this mother cell, since the primary lamellae of the 'acicular fibres' become resorbed during their development. As a result, they have been in the past always referred to as peculiar cell inclusions (raphides or 'raphidines').

To fill a gap in the knowledge of true nature regarding the 'acicular fibres' I endevoured to cut serial longitudinal sections of the shoot tips of N. canescens. Although I could not achieve successive stages in their development owing to the lack of suitable fresh materials, careful observations of numerous transverse sections under polarized light and high resolution of the compound microscope explicitly indicate that they are in fact phloem fibres - not cell inclusions. This can also be deduced from the fact that each of these fibres invariably possesses a thin primary wall of its own (Pl. I. F & H), they never occur at the meristematic region of the shoot apex, and there are numerous pits on their walls. Further, they can be transformed into cells superficially resembling sclereids in the veins and veinlets of St. microphylla (Pl. I. A).

However, these acicular fibres differ conspicuously from other ordinary phloem fibres found in the diverse plant families in their absolute size which is comparatively much smaller than that of the latter. In transverse sections occasionally they appear to be slightly separated from the primary wall and thus seem to lie freely in the cell lumen. This is of course, not a universal character of these fibres as there are many instances (Pl. I. B & D) where they are not separated from their primary walls. As these fibres are acicular in shape and also differ from the ordinary phloem fibres of many angiosperm families in their overall length (0.2-0.9 mm), the application of a separate name ('acicular fibres') to these peculiar phloem fibres of Acanthaceae seems to be justified.

Future studies into the development and distribution of acicular fibres might be profitable in understanding the generic relationship within the Acanthaceae and could be also useful in generic circumscription.

VESSEL ELEMENTS

Method: Jeffrey's method of maceration as outlined by Johansen (1940) was followed for the present investigation, but a quick method of staining was applied to save time. After decanting off the entire maceration fluid the materials were thoroughly washed with water several times and were left overnight in water. Next morning a small piece of stem was taken on a clean slide. By the help of a needle and a pair forceps only the vascular tissues were taken out under a binocular microscope. They were stained with safranin dissolved in methylated spirit for about 10-15 minutes and ultimately dehydrated thoroughly with absolute alcohol. Permanent slides were made by mounting the macerated tissues with euparal.

The vessel elements in the Nelsonioideae usually possess simple perforation plates at their transverse or oblique end walls. Occasionally these perforation plates are also observed on the side walls, especially in the species of Staurogyne. The secondary walls of these vessel members are either pitted, reticulate or annular, but in Saintpauliopsis they are always annular. The diameter of the vessel elements varies considerably from 21-54 μ in most of the Nelsonioideae, but in Saintpauliopsis it never exceeds 18 μ (12-18 μ). Future thorough studies in this direction might provide useful taxonomic and phylogenetic information.

NODAL ANATOMY

Serial transverse sections through the nodal region of the stem illustrate that the node in the Nelsonioideae is constantly unilacunar with one trace going into the petiole (Pl. I.C). Bremekamp emphasized the taxonomic importance of articulated (jointed together as separate units) stems in the family Acanthaceae. In fact the very characteristic swellings above the nodes of many Acanthaceous members (including Thunbergioideae and Mendoncioideae) can not be treated as homologous with the prominent swellings (articulations) of the nodes proper - often found in the plants bearing opposite leaves. Both articulated and non-articulated species can be met with in diverse genera like Staurogyne, Elytraria, Andrographis, Justicia and others. But none of the species in the tribes Andrographideae, Trichanthereae, Hygrophileae, and Nelsonioideae exhibit comparable swellings as encountered in many advanced members of the Acanthaceae.

Anatomical observations into these swollen regions above the nodes reveal the presence of a greater number of parenchymatous tissues in the pith and also in the cortex. Simultaneously a considerable increase in the collenchymatous cells is also noticed in the hypodermis. The vascular cylinders in these regions usually show weak secondary growth by having always a smaller extent of xylem tissue in comparison to that of the internodal region. Up to certain periods (earlier periods of shoot growth) the vascular cylinders in these swollen regions do not form complete rings of xylem tissue. These are probably responsible for rendering these regions (swellings) much softer than others.

This peculiar character of shoot swellings (particularly at mature living states) in Acanthaceous members may have some unknown physio-ecological significance which on further investigation might prove to be of taxonomic significance in tribal and generic delimitations.

Fig. 10. PETIOLE ANATOMY IN T.S. (transverse section)

(Explanation in the text: p = Periderm; pf = Pericyclic fibres; tc = Tannin containing cells; af = 'Acicular fibres', and w = Wing of the petiole)

A = *St. merguensis*; B = *St. obtusa*; C = *St. coriacea*; D = *St. paludosa*; E = *St. dasyphylla*; F = *St. rivularis*; G = *St. spatulata*; H = St. sp. (China); I = *Saint. lebrunii*; J = *N. canescens*; K = *E. nodosa*; L = *E. macrophylla*, and M = *E. madagascariensis*.

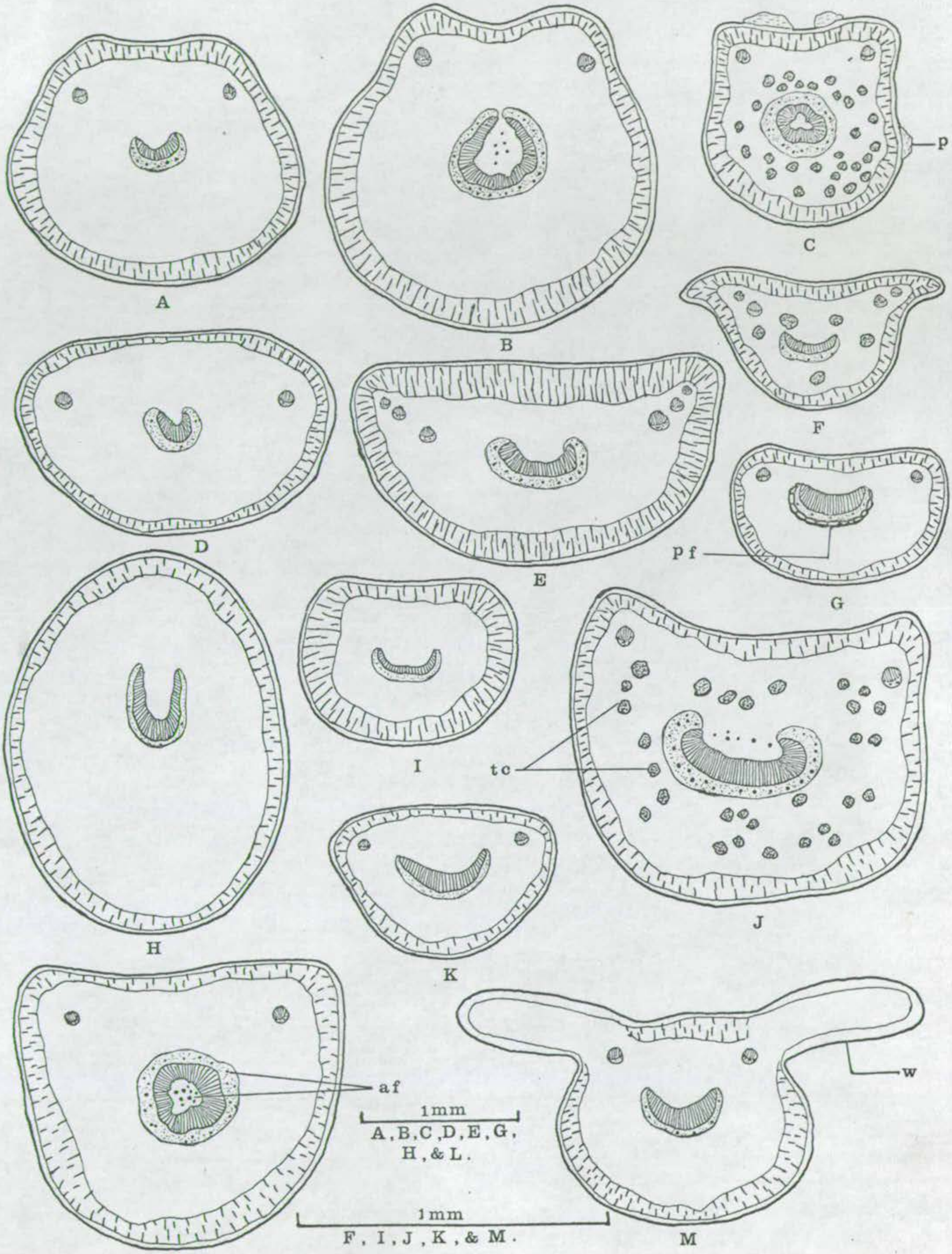


Fig ·10 ·PETIOLE ANATOMY IN T· S ·

PETIOLE

As the anatomical structure of the petiole varies considerably depending on the particular region from which the sections are cut, a constant comparable region (i.e. the distal end just below the base of the lamina) has been chosen for the study. Although the petiole anatomy does not help in the classification of Staurogyne, yet it is of taxonomic value at the level of species delimitation, especially when its characters are correlated with others.

Most of the Nelsonioideae possess a 3-traced petiole, the main bundle of which may be either of arc shape (Fig. 10) or ± round in outline (Fig. 10. C & L). Exceptions are St. rivularis (Fig. 10. F), N. canescens population and others containing four subsidiary bundles instead of the usual two, while St. dasyphylla (Fig. 10. E) is unique in having six subsidiary bundles (3 in each flank of the main vascular bundle). Further, Saintpauliopsis is characterised by a single-traced petiole (Fig. 10. I), but the condition may also be found rarely in Staurogyne (e.g. in an undescribed species from China) [Fig. 10. H].

The petioles are often non-winged, sometimes slightly winged in Staurogyne (e.g. St. rivularis, St. dasyphylla etc.) and populations of Nelsonia, while in E. madagascariensis conspicuously winged petiole (Fig. 10. M) is one of the distinctive features of the species.

The extent of collenchymatous tissue in the hypodermis of the petiole varies enormously from species to species [compare St. coriacea and St. paludosa (Fig. 10. C, D)], while a few populations of St. spatulata complex are outstanding in their petiole anatomy: the main vascular bundle is surrounded by a zone of pericyclic fibres (Fig. 10. G). The outer epidermis of the petiole in St. coriacea is ruptured at many places where periderm formation has been recorded (Fig. 10. C).

FOLIAR EPIDERMIS

Method: Small epidermal peelings can be easily obtained if the softened (by KOH)

Fig. 11. TYPES OF INDUMENTUM

(Explanation in the text)

A (a-a') = *Staurogyne* [a = eglandular hairs; a' = glandular hairs]; B, B', & Bb = 'Peltate Scales' [B = *St. spatulata*; B' = *A. humbertii*, & Bb = O. macrobotryum]; C (c-c') = *Saintpauliopsis* [c = eglandular hairs; c' = glandular hairs]; D (d-d') = *Nelsonia* [d = eglandular hairs; d' = glandular hairs]; E (e-e') = *Elytraria* [e = eglandular hairs; e' = glandular hairs], & F (f) = Bi-celled glandular hairs of the Nelsonioideae.

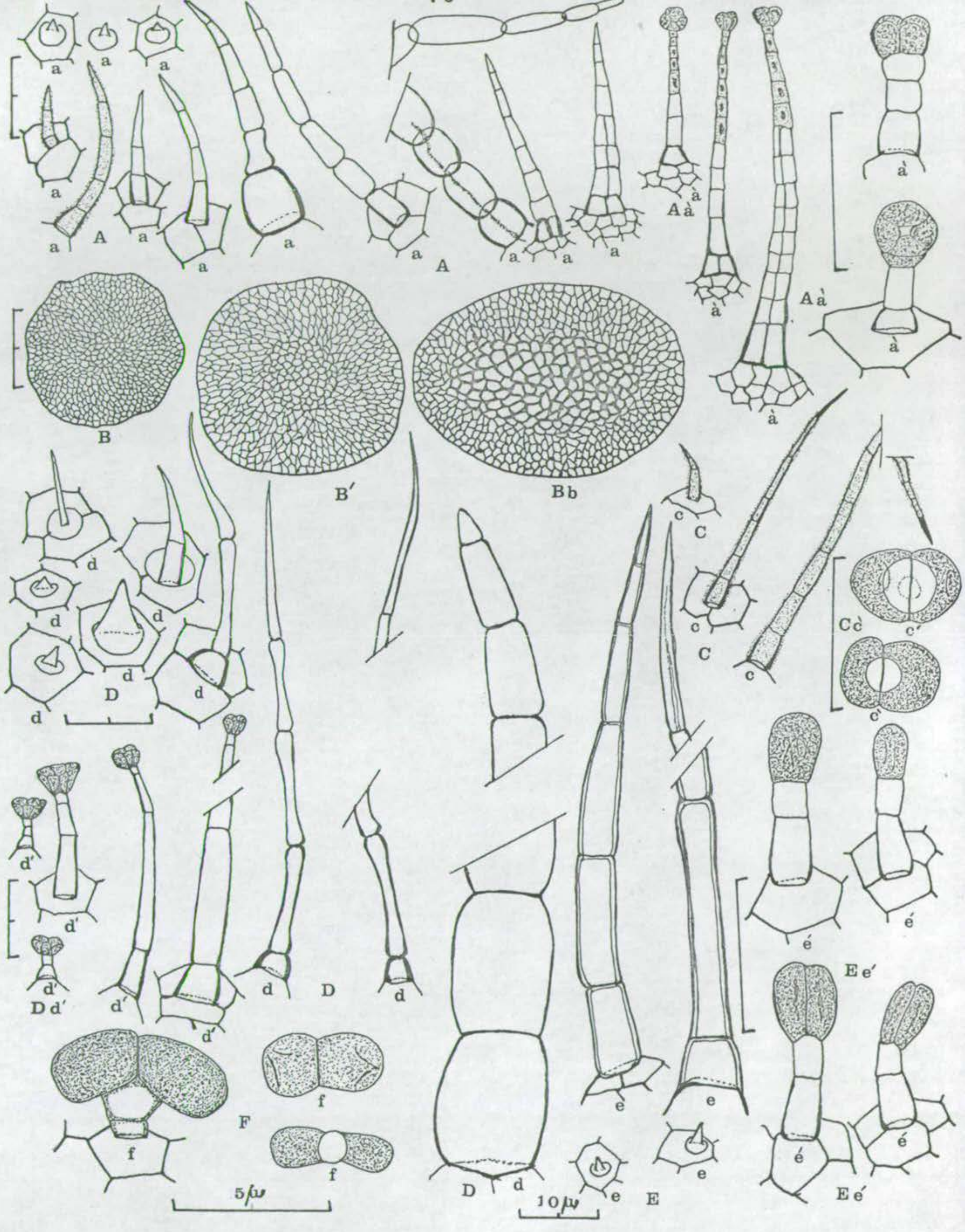


Fig.11.TYPES OF INDUMENTUM.

leaves are dipped into a solution of 25% H_2O_2 (concentration depends on the thickness of the leaves). They are washed in water, stained either with cotton blue dissolved in glycerine agar or with 50% alcoholic safranin dehydrated thoroughly, and ultimately mounted in euparal. But the best result obtained so far, proves that Delafield's iron haematoxylin is the most suitable stain for studying the epidermal peelings.

The epidermal cells in the Nelsonioideae are either rectangular, slightly irregular or markedly undulate in outline, always provided with broad lumens. Most of these cells possess moderately thickened or thin cell walls, but St. pedicellata (East Borneo) is remarkable in having profoundly thickened epidermal cells, the walls of which contain numerous pits (Pl. 3. C).

The characteristic Acanthaceous cystoliths are always absent from these cells as from all other tissues of the Nelsonioideae. However, in Elytraria abundant prismatic crystals of calcium oxalate are formed especially along the adjacent cells of the veins and veinlets (Pl. 3. E). Unlike the cystoliths they lie freely inside the lumen of the cells. Smaller crystals are rarely found in some species of Staurogyne, while they are entirely lacking in the rest of the Nelsonioideae.

INDUMENTUM

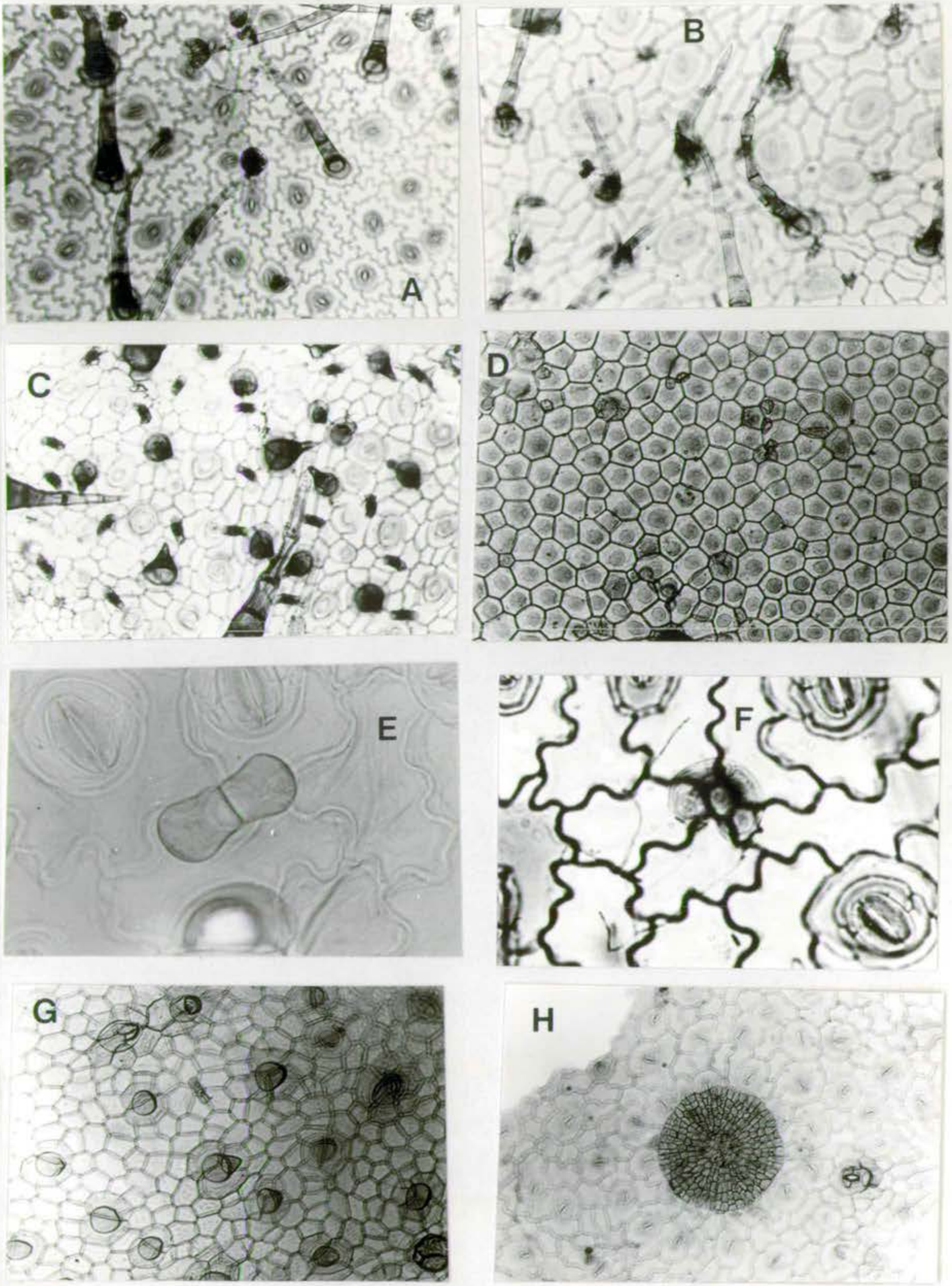
Basically two types of trichomes are recognized in the Nelsonioideae: multicellular, clothing simple type (eglandular), and the glandular type provided either with a bi-celled dumb-bell shaped [rarely 'C'-shaped, e.g. St. Vauthieriana (Pl. 2. F)] or 4 to 8-celled saucer-shaped head (Pl. 2. A).

These trichomes are usually uniseriate and smooth, but they are characteristically ornamented in Saintpauliopsis (Fig. 11. Cc) and in a few species of Staurogyne (Fig. 11. Aa). A few American species (e.g. St. anigozanthus, St. hirsuta and St. microphylla etc.) are worth mentioning in this respect as

Pl. 2. TYPES OF INDUMENTUM

(Explanation in the text; all photomicrographs are taken from the epidermal peelings; D and G = upper epidermis - the rest are lower epidermis)

A = St. vauthieriana (x 145); B = St. elongata (x 145); C = St. axillaris (x 145; note the papillae amongst long hairs); D = St. longifolia (x 145); E = Thunbergia laurifolia (Thunbergioideae; x 174 - note the bi-celled glandular hair); F = St. vauthieriana (x 174); G = St. singularis var. longipedicellata (x 145), and H = St. minarum (x 145).



Pl.2.

they possess trichomes (both glandular and eglandular) which are biseriate below and uniseriate above (Fig. 11. Aa & AÂ).

Sometimes the hairs in the Nelsonioideae are very short and undeveloped - thus giving an appearance of 'papillae' (not comparable with those formed by the direct prolongations of the epidermal cells) which may be either on both surfaces of the leaves /e.g. St. paludosa (Pl. 3. A)7 or restricted only to the upper surface, e.g. St. singularis var. longipedicellata (Pl. 2. G).

The commonly occurring bi-celled glandular hairs (Pl. 2.) of the Nelsonioideae deserve particular attention regarding their possible physiological function. Their stalk is made up of 2-3 small cells and the specialized head cells (2 in number), unlike many glandular (supposed to be of secretory or excretory function) hairs, do not contain a thick cytoplasm. If a fresh leaf is dipped for some time under water containing a drop of India ink and later on observed under the microscope, the distal ends of the head cells will be found to have accumulated the ink inside. India ink is not a dye, and only the head cells specifically absorb it, suggesting that these hairs have an absorptive function. This may be significant in the forest environment, enabling the plants to absorb the leachates of overhead canopy (cf. Tukey, 1966, 1969).

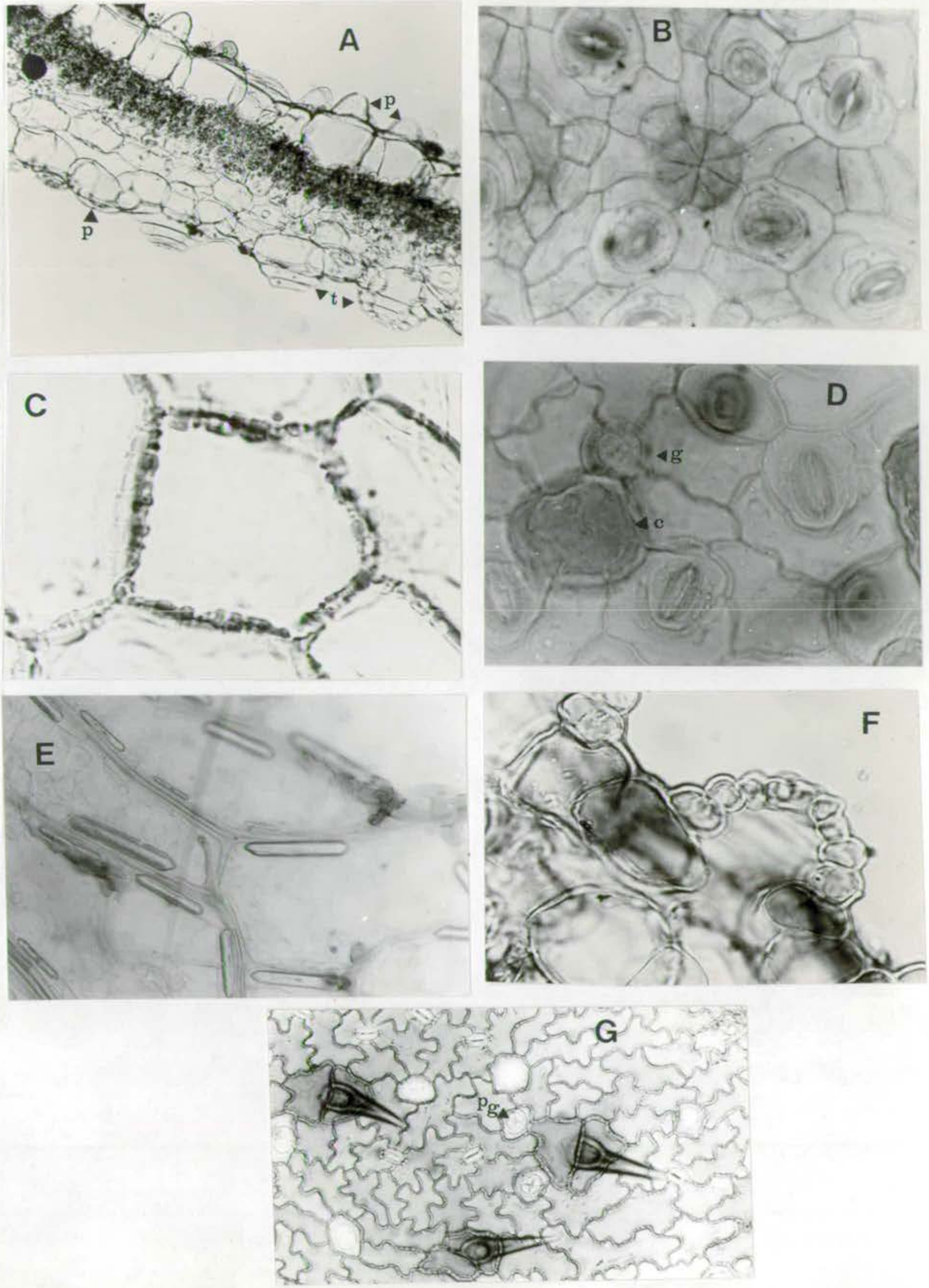
DEVELOPMENT OF BI-CELLED GLANDULAR HAIRS

Method: Observations on the development of stomata and likewise the glandular hairs necessitated the use of living fresh material from the green house of the Royal Botanic Garden, Edinburgh. Young, unfolded leaves of St. paludosa and E. maritima were collected in 3 : 1 (absolute alcohol: acetic acid) fixative and left for about 10-12 hours. They were then teased out on a clean slide with a drop of 1% acetocarmine by a flat-bottomed needle. Staining became intensified after repeatedly heating and cooling the slide over the flame of a spirit lamp. A cover slip was carefully placed over the teased out material before

Pl. 3. EPIDERMAL PEELINGS AND T.S. OF LEAVES

(Explanation in the text; A and D = transverse sections of the leaves; B, C, and E-G = epidermal peelings)

A = St. paludosa (x 174, mark the papillae and stomatal turrets); B = Phlogacanthus carviflorus (x 650); C = St. pedicellata (x 780; note the pits on the walls); D = Section through a stoma in St. paludosa (x 780; note the turet and its accompanying cells); E = E. shaferi (X 145); F = Andrographis rochii (x 650; cystoliths are present), and G = Rhinanthus cristagalli (x 145; note the 'anomocytic' stomata and characteristic 'peltate glands'). [pg = peltate gland; t = stomatal turets; p = papillae; g = gland, and c = cystolith].



Pl. 3.

the drop of acetocarmine completely dries up. The edges of the cover slip may be sealed off with rubber solution or cutex for making the slides permanent, but it is advisable to take photographs or make camera lucida drawings from the temporary mounts. The reason is obvious: the stain fades out quickly, and the acetocarmine dries up gradually to make the slide hazy.

The bi-celled glandular hair initial at first starts as a small, roundish protuberance on the epidermal cell. (Fig. 12. A_{1-2}). Soon after the prolongation of this outgrowth a dense cytoplasm along with a nucleus gradually becomes visible (Fig. 12. A_3). The first two successive divisions of this nucleus are unequal and periclinal (in relation to the horizontal plane of the epidermal cells) so that a row of three cells are formed (Fig. 12. A_6). Out of these three cells the topmost one becomes always the biggest and also contains the biggest nucleus. This cell now ultimately divides anticlinally (in relation to the epidermal cell) into more or less two equal cells (Fig. 12. A_{7-8}). At maturity, these two cells strikingly enlarge in their horizontal plane and thus ultimately become dumb-bell shaped in outline (Fig. 12. A_9).

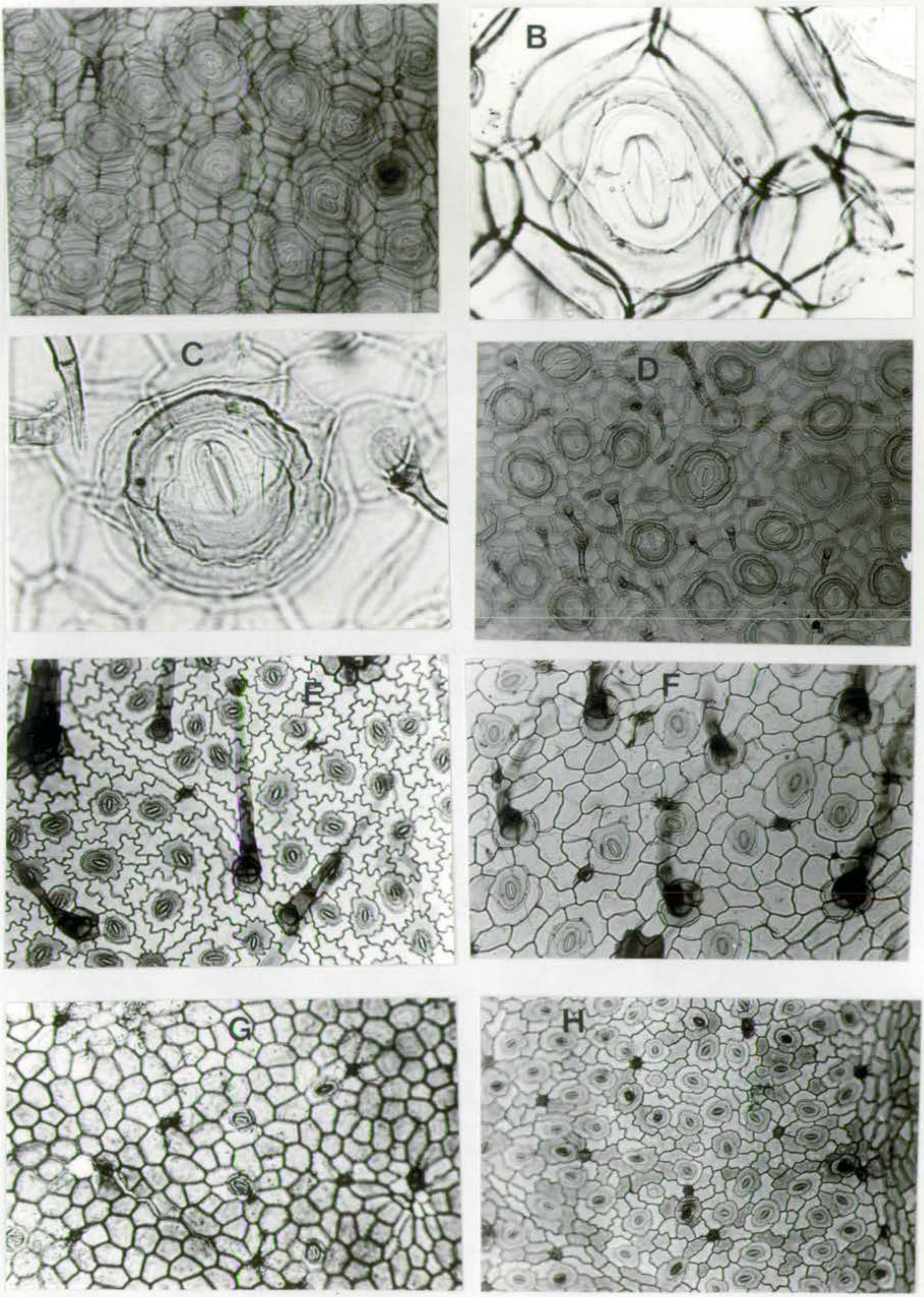
SCALES

The thin peltate scales so characteristic of Staurogyne, Gynocraterium, Ophiorrhiziphyllon and Anisosepalum are multicellular structures but without any perceptible stalk of their own (Fig. 11. B, B' & Bb; Pl.). They are usually attached to the epidermal cells by a group (ring) of comparatively thicker cells at the middle (Fig. 11. B-Bb); these cells also take up denser stain than others. The occurrence of scales in the Nelsonioideae is for the first time reported here and their taxonomic significance has also been discussed in the text.

Pl. 4. TYPES OF STOMATA IN STAUROGYNE

(Explanation in the text; A-D = 'double diacytic';
E-H = 'simple diacytic' - only G represents a peeling
of an upper epidermis - the rest from lower epidermis)

A = St. paludosa (x 145); B = St. paludosa (x 650);
C = St. obtusa (x 650); D = St. obtusa (x 145);
E = St. vauthieriana (x 145); F = St. shanica (x 145);
G = St. cambodiana (x 145), and H = St. minarum (x 145).

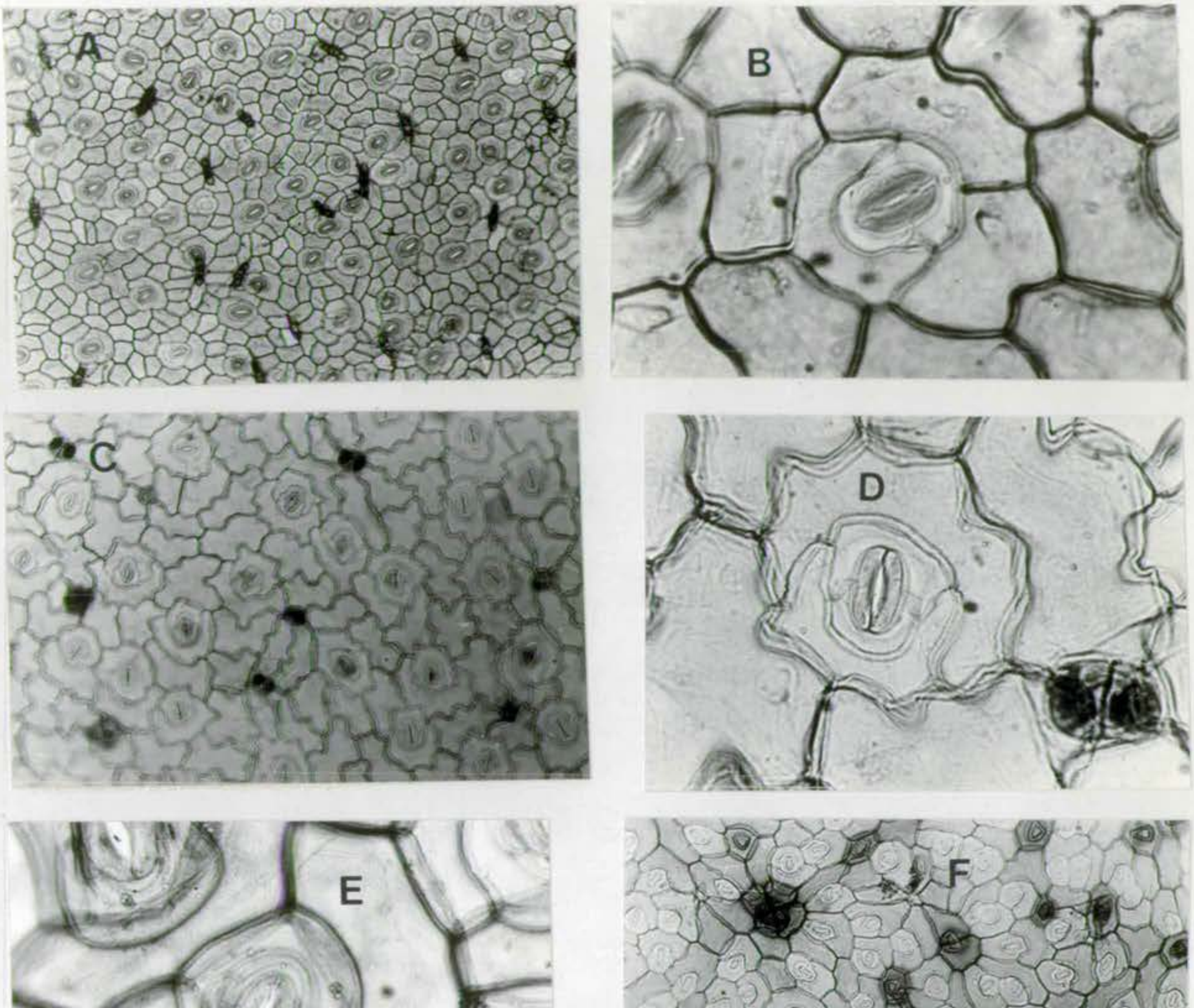


Pl.4.

Pl. 5. *STOMATAL TYPES IN NELSONIOIDEAE* [excepting *Staurogyne*], *LEPIDAGATHIS TRINERVIS* (Barlerieae and *MENDONCIA LINDAVIANA* (Mendonciordeae)

(Explanation in the text: in each photomicrograph a portion of the lower epidermal peeling is shown)

A = *O. macrobotryum* (x 145); B = *O. macrobotryum* (x 650); C = *Saint. lebrunii* (x 145); D = *Saint. lebrunii* (x 650); E = *N. canescens* (x 650); F = *E. caroliniensis* (x 145); G = *Lepidagathis trinervis* (x 650), and H = *Mendoncia lindaviana* (x 650).



Pl. 5.

STOMATA

Until now Paliwal (1964) & Inamdar's (1970) reports of the occurrence of 'diacytic' stomata in E. acualis are the only information at hand on the Nelsonioideae. However, they did not undertake any developmental studies of this species. In the present investigation I have explored all the available species of the Nelsonioideae supplemented by the developmental studies of E. maritima and St. paludosa.

The mature stomata in general are 'simple diacytic' (Pl.4. C,D), but 'double diacytic' types are also not infrequent in the Nelsonioideae. Populations of N. canescens (Pl. 5.E), E. shaferi, St. obtusa (Pl. 4. C,D) St. paludosa (Pl. 4.B) and other diversely related species illustrate this variation. These stomata often project above the level of epidermal cells and thereby look like 'turrets' (Pl. 3. A). On the other hand, 'simple diacytic' stomata are usually placed at the same level or slightly above the epidermal cells.

The stomata are mostly confined to the lower surface of the dorsiventral leaves, but occasionally they can also be found on the upper surface; the frequency is however exceedingly low (Pl. 4. G). Leaves (particularly at the upper portion) which are ± isobi-lateral, contain stomata on both surfaces: the frequency may either be equal or slightly different.

DEVELOPMENT OF STOMATA

The stomatal meristemoids are easily recognizable by their smaller size, denser cytoplasm, prominent nuclei and spheroidal or semi-lunar shape (Fig. 12. B, G; Pl. 6.C). The first division (periclinal) of the meristemoid cell in each case (Fig. 12. B_{2-3}, C_{2-3}) produces two unequal cells with two unequal nuclei. The cell containing smaller nucleus is the S_1 (first subsidiary cell) which later on enlarges quite considerably along with the meristemoid. The next division (which is also periclinal) of the cell containing bigger nucleus again

Fig. 12. DEVELOPMENT OF GLANDULAR HAIR

(Bi-celled) & STOMATA

(Explanation in the text)

A (1-9) = Development of bi-celled glandular hair in St. paludosa; B (1-8) = Development of 'simple diacytic' stomata in E. maritima, and C (1-10) = Development of 'double diacytic' stomata in St. paludosa. (SM = stomatal meristemoid; GMC = Guard mother cell; gc = Guard cell; so = stomatal opening; s_1, s_2, s_3, & s_4 = subsidiary cells - the numbers indicate their successive formation).

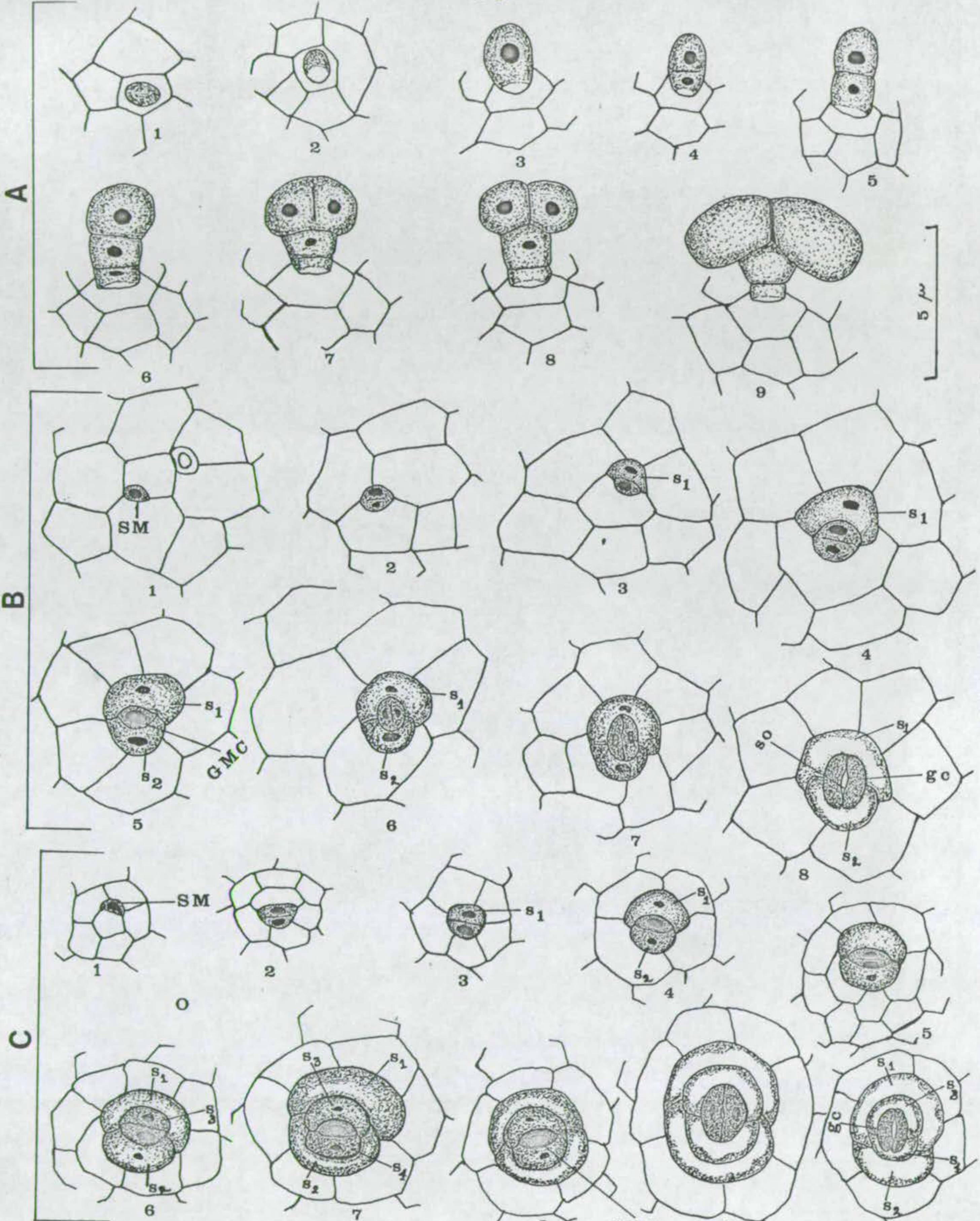


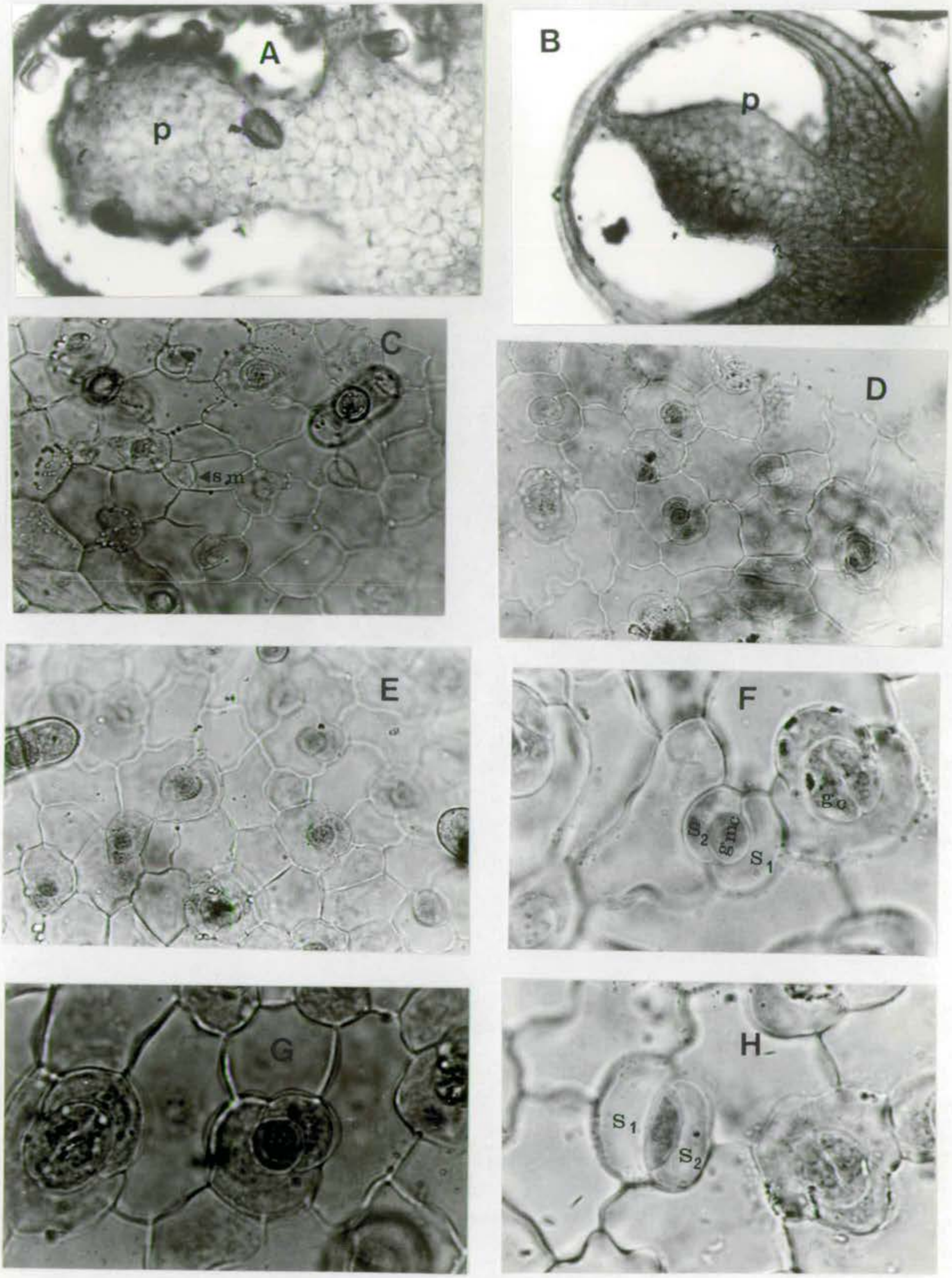
Fig.12. DEVELOPMENT OF GLANDULAR HAIR(bi-celled) & STOMATA.

Pl. 6. T.S. OF ANTHERS AND DEVELOPMENT OF SIMPLE DIACYTIC STOMATA

(Explanation in the text; A and B = transverse sections of anthers showing placentoids; C-H = stages in the development of simple diacytic stomata)

A = *Thunbergia laurifolia* (x 145; only one anther lobe is shown); B = *St. merguensis* (x 145; one anther lobe is shown), and C-H = *E. maritima* (C-E x 650) and (F-H x 1375).

[p = placentoid; gmc = guard mother cell; sm = stomatal meristemoid; S_1 = first subsidiary cell, S_2 = second subsidiary cell, and gc = guard cell].



Pl. 6.

produces two unequal cells out of which the middle one is lenticular in shape (the guard mother cell i.e. GMC) and the other cell (S_2 = second subsidiary cell) remains exactly opposite to the S_1 (Fig. 12. B_5 C_4; Pl. 6. G, H).

Up to this point stages are the same in both 'simple' and 'double' diacytic stomata. But in the formation of 'double diacytic' type the meristemoid cell divides (periclinally) twice more to form two other subsidiary cells (S_3 & S_4) /Fig. 12. C_{5-8}/ in a similar way as to the formation of S_1 and S_2 before the guard mother cell (GMC) divides anticlinally to form two crescentic guard cells in each case (Fig. 12. B_{6-7} C_9; Pl. 6.G). A small pore develops gradually at the middle region of the common wall and ultimately the mature guard cells become full of chloroplasts. In both cases, the subsidiary cells (either 2 or 4) remain at right angles to each other (or one another) in relation to the longitudinal axis of the guard cells (Fig. 12. B_8 C_{10}; Pl. 6.G). As the subsidiary cells (2 or 4) in both cases are derived from the stomatal initial (meristemoid cell) proper, the stomatal complexes are 'mesogenous' in origin.

Paliwal (1964) doubted the earlier contention of Pant & Mehra (1963) that the stomatal complex in some of the Acanthaceae could be formed by the successive five divisions of the meristemoid cell. But the present studies strongly support Pant & Mehra, who for the first time reported the occurrence of 'double diacytic' stomata in <u>Asteracantha longifolia</u> Nees (= <u>Hygrophila spinosa</u> T. And.), and they are also found in <u>Lepidagathis trinervis</u> Nees (Pl.5. G). This has also been confirmed by the recent independent work of Inamdar (1970).

Occasionally 'simple diacytic' stomata may either contain one or rarely two enlarged 'encircling' cells (as has been termed by Paliwal) which can not actually be treated as subsidiary cells. The reasons are obvious: their occurrence is not constant and their outer walls show similar undulations characteristic of the epidermal cells. They become specialized (enlarged) only to accommodate the enlarging subsidiary cells of the stomatal complex and are therefore an example of variation in the epidermal cells proper.

SCLEREIDS

Method: Small pieces of dried leaves from the herbarium sheets were at first soaked overnight in 20% KOH solution (thick leaves require a higher concentration) with a few drops of 25% H_2O_2. The softened materials after thorough washing by water were treated by the quick clearing technique used by Bokhari (1970). The morphological nature, orientation, and distribution of the sclereids were studied by both clearing technique and hand sectioning of the lamina at comparable regions (with midrib).

The data were also supplemented by the studies of macerated tissues following Jeffrey's method as outlined by Foster (1949). Staining and mounting were done according to Bokhari's modified technique (pp. 44).

Observation and Discussion: There has been no record for the occurrence of foliar sclereids in the Nelsonioideae. In an attempt to explore anatomical characters in the group I became interested in the morphology of sclereids, when I discovered them in St. merguensis during my investigation into the epidermal peelings. Subsequent studies into all the genera and species of the Nelsonioideae demonstrate that similar sclereids are also present in few other species of Staurogyne /e.g. St. cremostachya (Pl. 7. A), St. griffithiana (Pl. 7.D), and St. tenuispica (Pl. 7. C)/.

All these species possess 'diffuse astrosclereids' according to their topography. Regarding their taxonomic significance it is noted that St. merguensis and St. tenuispica belong to the Subsect. Microchlamydeae, while the other two remain in Subsect. Macrosepalae; of course, all in the same Sect. Staurogyne. Probably similar forms have arisen independently in the two taxonomic groups.

Fig. 13. TYPES OF SCLEREIDS & FIBRES (macerated).

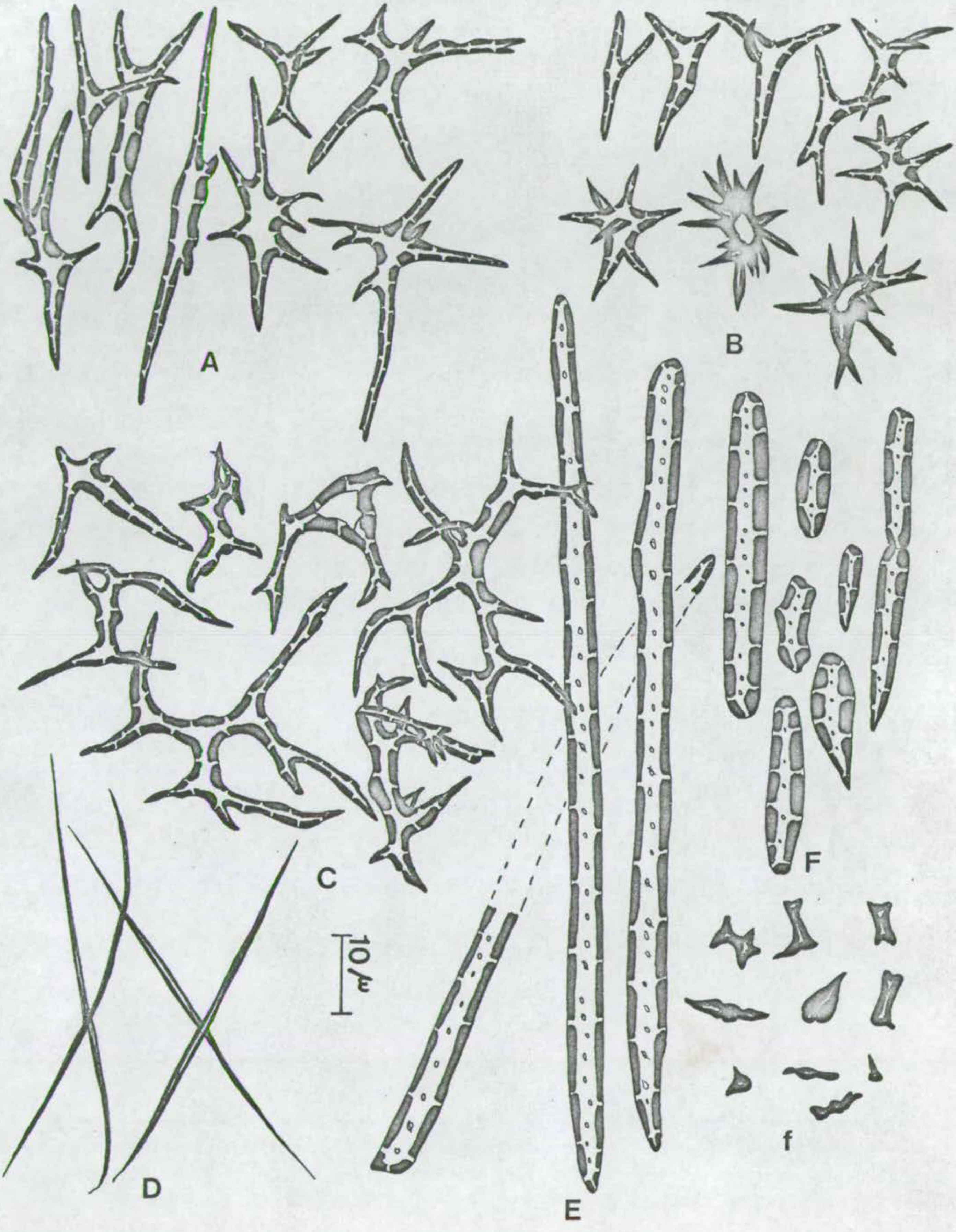
(Explanation in the text)

A = Foliar 'astrosclereids' in St. griffithiana;

B = Foliar 'astrosclereids' in St. oremostachya;

C = Foliar 'astrosclereids' in St. merguensis;

D = 'Acicular fibres' of the Nelsonioideae obtained from the macerated petiole; E = pericyclic fibres in the stem of Sect. Tetrastichum of Staurogyne, and F, f = Foliar sclereids in E. shaferi (F = Elongated 'macrosclereids' along the veins; f = smaller 'polymorphic sclereids' of the mesophyll).

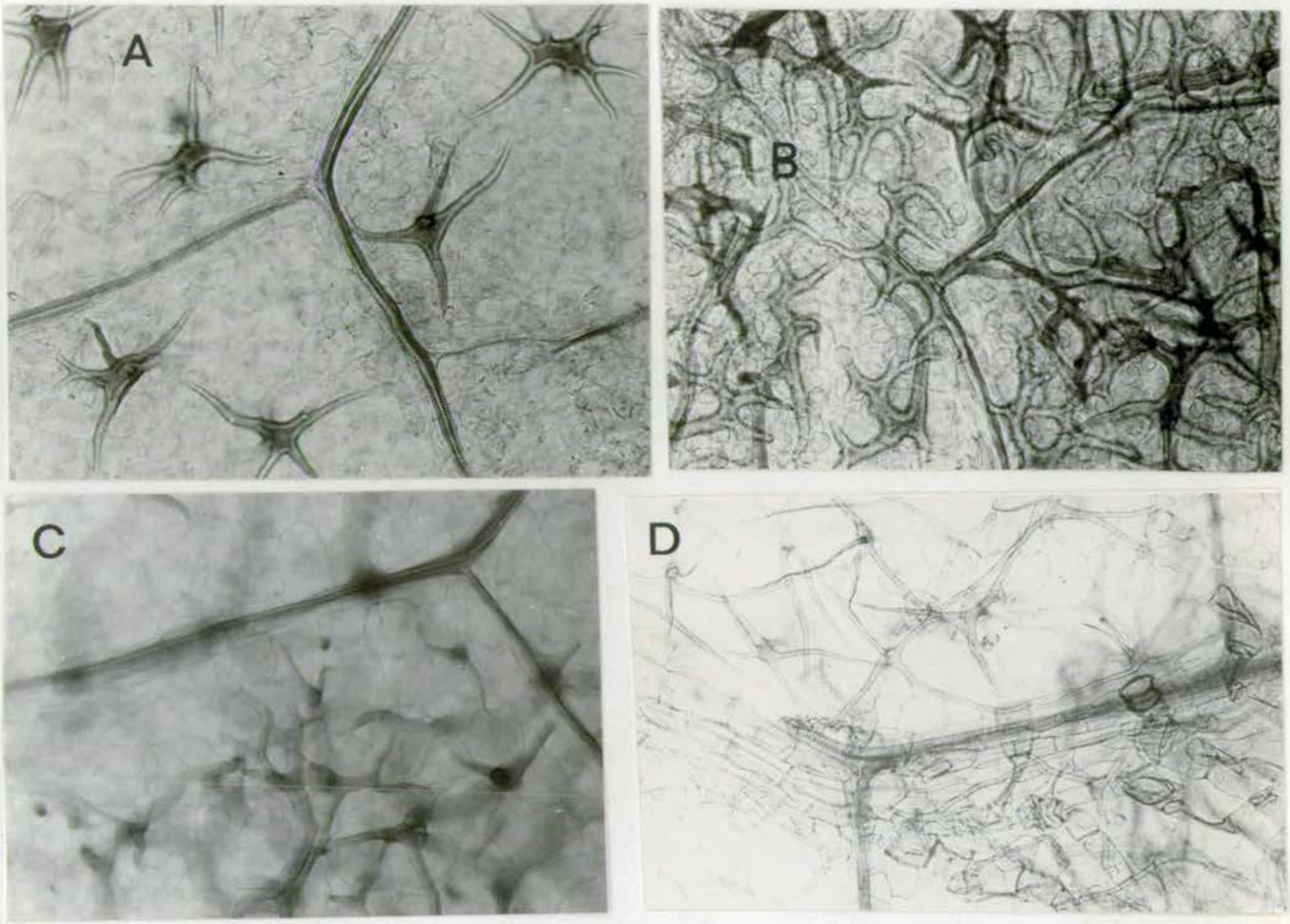


Fig·13·TYPES OF SCLEREIDS & FIBRES(macerated).

Pl. 7. SCLEREIDS IN *STAUROGYNE*

(Explanation in the text: in each photomicrograph only a portion of the cleared leaf is shown; A-D ='diffuse astrosclereids', and E-H = 'pseudoterminal' sclereids)

A = *St. cremostachya*; B = *St. merguensis*;
C = *St. tenuispica*; D = *St. griffithiana*;
E = *St. pedicellata*; F = *St. kerrii* (15287)
G = *St. aristata*; and H = St. kerrii (16307).
[A, B, and D = x 174, C and E-H = x 145].



Pl.7.

Size differences of the sclereids can be a guide in separating St. cremostachya (smaller types Fig. 13. B) from that of St. griffithiana (much longer sclereids, Fig. 13. A). The occurrence of similar foliar sclereids in these two species along with other morphological features clearly indicate their close affinities. Therefore, Bremekamp's (1953) remark about the relationships of St. cremostachya as an isolated species in the Ser. A (Heterosepalae) seems to be incorrect.

Conversely, size differences of sclereids between St. merguensis and St. tenuispica are not so great, but the former differs in having more complexly branched sclereids than the latter.

Species like St. aristata of the Subsect. Macrosepalae and St. pedicellata (E. Borneo), St. kerrii (Thailand) of Subsect. Microchlamydeae show a peculiar arrangement of sclereids which cannot be accommodated into strait jacket of terms depending on their topography. Most of these sclereids are strikingly elongated, less branched than those of the 'astrosclereids' and occur both at the extremities of the veinlets and also run parallel with the veins (Pl. 7. E-H). These are termed here 'pseudoterminal' sclereids.

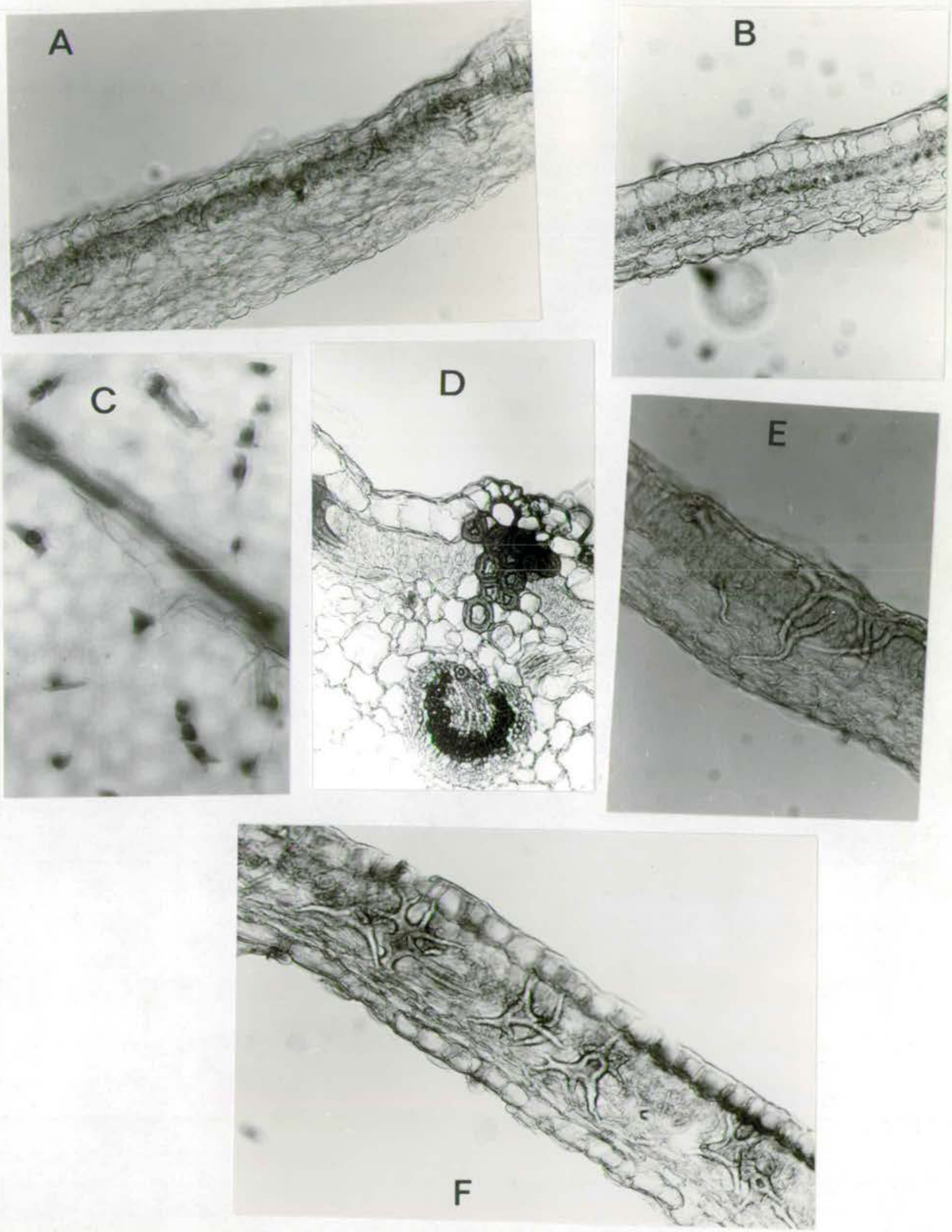
By far the most remarkable arrangement of sclereids has been encountered in E. shaferi. It is the only species of Elytraria which contains two types of sclereids - diffuse and parallel (Pl. 8. C) in the same leaf. The diffuse sclereids are very small, diversely shaped, often looking like small dots (Fig. 13. f), while the parallel type embraces unbranched, elongated, and ± bluntly pointed 'macrosclereids' (Fig. 13. F). Further, these elongated sclereids are also found in the t.s. of petiole (Pl. 8. D) as a patch of sclerified tissue on the adaxial surface just above the main vascular bundle.

The dorsiventral leaves of the Nelsonioideae as a rule show 2-3 layers of palisade parenchyma below the upper epidermis and 2-4 layers of spongy parenchyma above the lower epidermis. The sclereids are usually formed in

Pl. 8. SCLEREIDS IN LEAVES AND PETIOLE

(Explanation in the text: C = cleared leaf; A, B and D-F = transverse sections)

A = Leaf of St. tenuispica (x 145); B = Leaf of St. aristata (x 145); C = Leaf of E. shaferi (x 145; note the presence of two types of sclereids 'macrosclereids' along the veins - 'polymorphic' sclereids in the mesophyll); D = Petiole of E. shaferi (x 145; a group of 'macrosclereids' present at the dorsal side of the midrib); E = Leaf of St. merguensis (x 145), and F = Leaf of St. cremostachya (x 174).



Pl. 8.

the mesophyll (palisade + spongy tissue), often well extended into the spongy tissue, but sometimes found to protrude into the palisade tissue. In 'pseudo-terminal' type the sclereids are often seen just below the veins in t.s. (Pl. 3. C).

PLACENTOID IN ANTHERS

A placentoid (Chatin, 1870) is a long, parenchymatous tissue of the pollen sac at the place of dissepiment. It should not be mistaken with the surrounding inner tapetum or local thickening caused by cell-fragmentation or cell growth (Carniel, 1963).

Hartl (1963) surveyed the existence of placentoid in many families of the Sympetalae. He concluded that the families like Acanthaceae, Gesneriaceae and Orobanchaceae are possibly characterised by the constant presence of this tissue in their anthers, while Scrophulariaceae is intermediate in this respect (i.e. placentoid is absent from many genera and species).

In the present investigation I have found remarkably well-developed placentoid in transverse sections of the anthers in Thunbergia (Pl. 6. A), but ill-developed in St. merguensis (Pl. 6. B). This can be explained on the fact that anthers having elongated thecae connected throughout their length to the connective are probably best suited for the development of this tissue. However, lack of suitable fresh materials in Elytraria (producing elongated anthers) prevented me from further extension of this study.

POLLEN GRAINS

Acanthaceae is essentially a eurypalynous family. Perhaps it is unique in the angiosperms in having such a wide range of pollen morphological features. Bauer (1790-1840) was the first person to be interested in Acanthaceous pollen grains. Later on, detailed investigations were carried out by Bischoff (1833), Mohl (1836) and Fritzsche (1837). But it was Radlkofer (1883) who for the first time pointed out the taxonomic value of pollen grains in the classification of Acanthaceae. Lindau (1895) too realized the taxonomic importance of diverse pollen types in the family Acanthaceae and therefore attributed much significance to the criteria of pollen grains in classifying the Acanthaceae.

In the past few decades Bremekamp has contributed much to our knowledge of Acanthaceous pollen grains and the most recent work on the family is by Bhoj Raj (1961) who has investigated a poor sample (3 species of Staurogyne, one species of Elytraria and the monotypic genus Nelsonia) of the Nelsonioideae.

A critical investigation of the Nelsonioideae has been much neglected in all these previous works. Palynological contributions of the previous authors in this group are neither associated with good illustrations nor with photographs and sectioning. Pollen grains of this group are usually described as typically 'tricolpate', but a search into the relevant literature reveals at least three or four contradictory reports.

The present study is based on critical examination of fresh and acetolysed pollen grains of all the genera of the Nelsonioideae. Ultratome sections of the pollen grains have also been studied for obtaining a clear understanding of the sporoderm stratification and gross morphological features.

MATERIALS AND METHOD

Dry polliniferous material was taken out from the herbarium sheets and Erdtman's (1960) technique for acetolysis was followed. Permanent slides were made with the help of glycerine jelly (made according to Kissar's method) and sealed off with paraffin wax.

SECTIONING

Clean polliniferous material, either fresh or herbarium-dried, was boiled in a porcelain basin for a few minutes and crushed in it with a glass rod. A little bit of erythrosin powder was added to the boiling water to make the pollen grains coloured (pink). The debris was thrown away from the top and the settling pollen grains were collected in a specimen bottle with distilled water. Now the coloured pollen grains were transferred to a specimen tube (narrow-bottomed) containing boiling 4% agar solution so that the pollen grains settled down at the bottom overnight.

Next morning the solidified agar block with a mass of coloured pollen grains sticking at the bottom end was taken out and placed on a clean slide. By means of a sharp flattened needle numerous cubes of agar (with sticking pollen grains) of approximately 1 mm in diameter were cut and placed in a specimen bottle with ethanol for dehydration. Every change of the following series was made carefully by pipetting out the used solution.

Solution	No. of treatments	Duration
Ethanol 70%	2	15 minutes
" 90%	3	30 "
" 100%	4	15 "
Propylene oxide	2	15 "

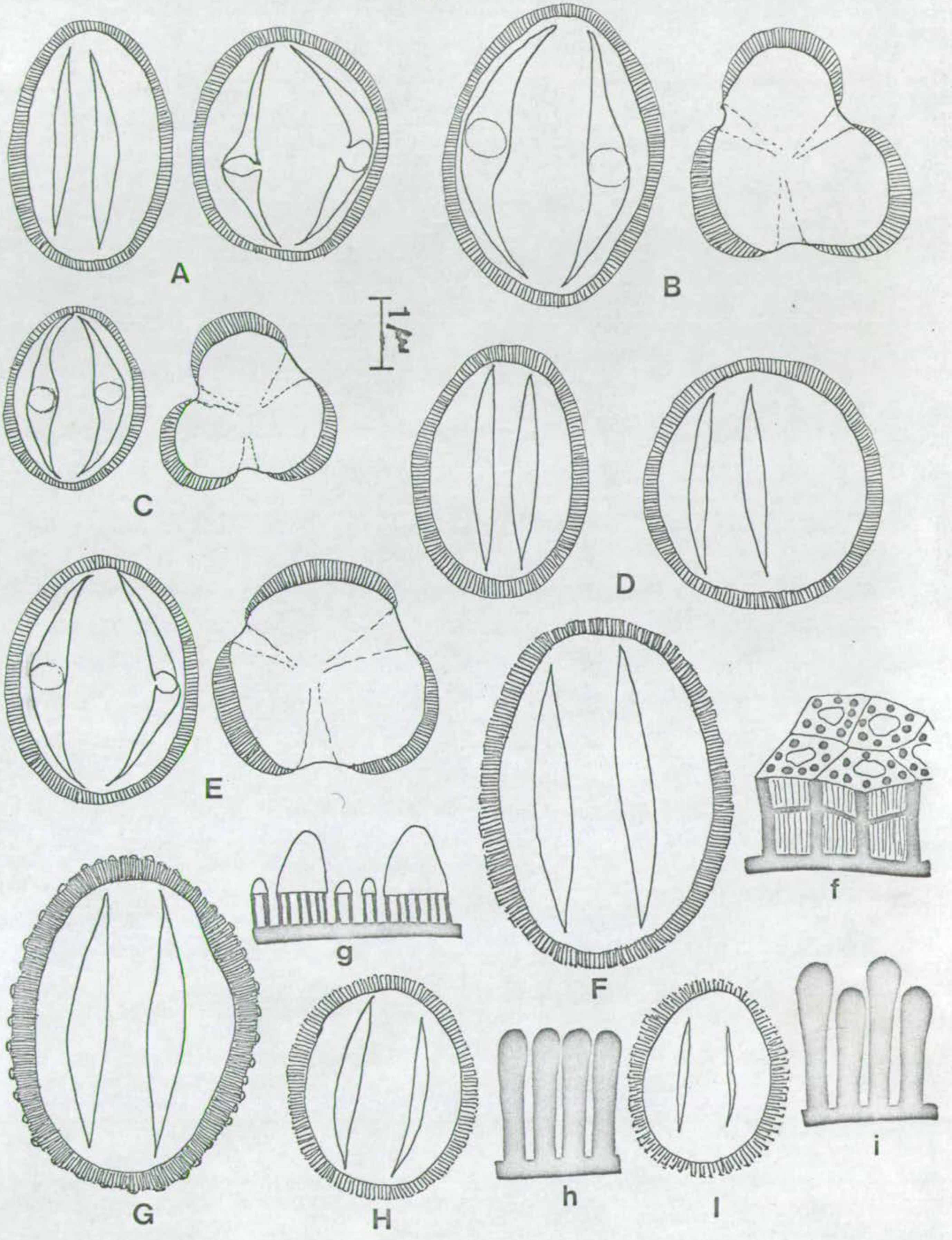
Then 25% araldite was added to 75% propylene oxide and the cubes were left overnight in this mixture. Next morning the cubes (2-3) were picked up by the pipette and placed into a capsule previously filled up ($\frac{3}{4}$ portion) with pure araldite. The capsule was then entirely filled up with more araldite and covered by the lid. Capsules prepared in this way were kept in the oven at 60°C for about 24 hours or more, depending on the hardening of the araldite.

After hardening, capsules were washed under running tap water and the solid blocks were taken out carefully. Sections were cut at 1.5μ on a Cambridge Ultratome. These were stained in 1% toluidene blue in 1% borax for about 3 minutes on a hot plate at 55°C and finally mounted in liquid paraffin. Microscopic photographs and electron micrographs were taken and are reproduced in the text (Pl. 10. G-I & Pl. 11. A-E).

Fig. 14. TYPES OF POLLEN GRAINS

(Explanation in the text: f-i = Diagrammatic representations of the patterns of sporoderm ornamentation)

A = St. *longibracteata*; B = *St. paludosa*; C = *O. macrobotryum*; D = *Saint. lebrunii*; E = *A. humbertii*; F, f = *E. marginata* (f = sporoderm ornamentation); G, g = *E. caroliniensis* (g = sporoderm ornamentation); H, h = *E. imbricata* (h = sporoderm ornamentation), and I, i = *E. acaulis* (i = sporoderm ornamentation).



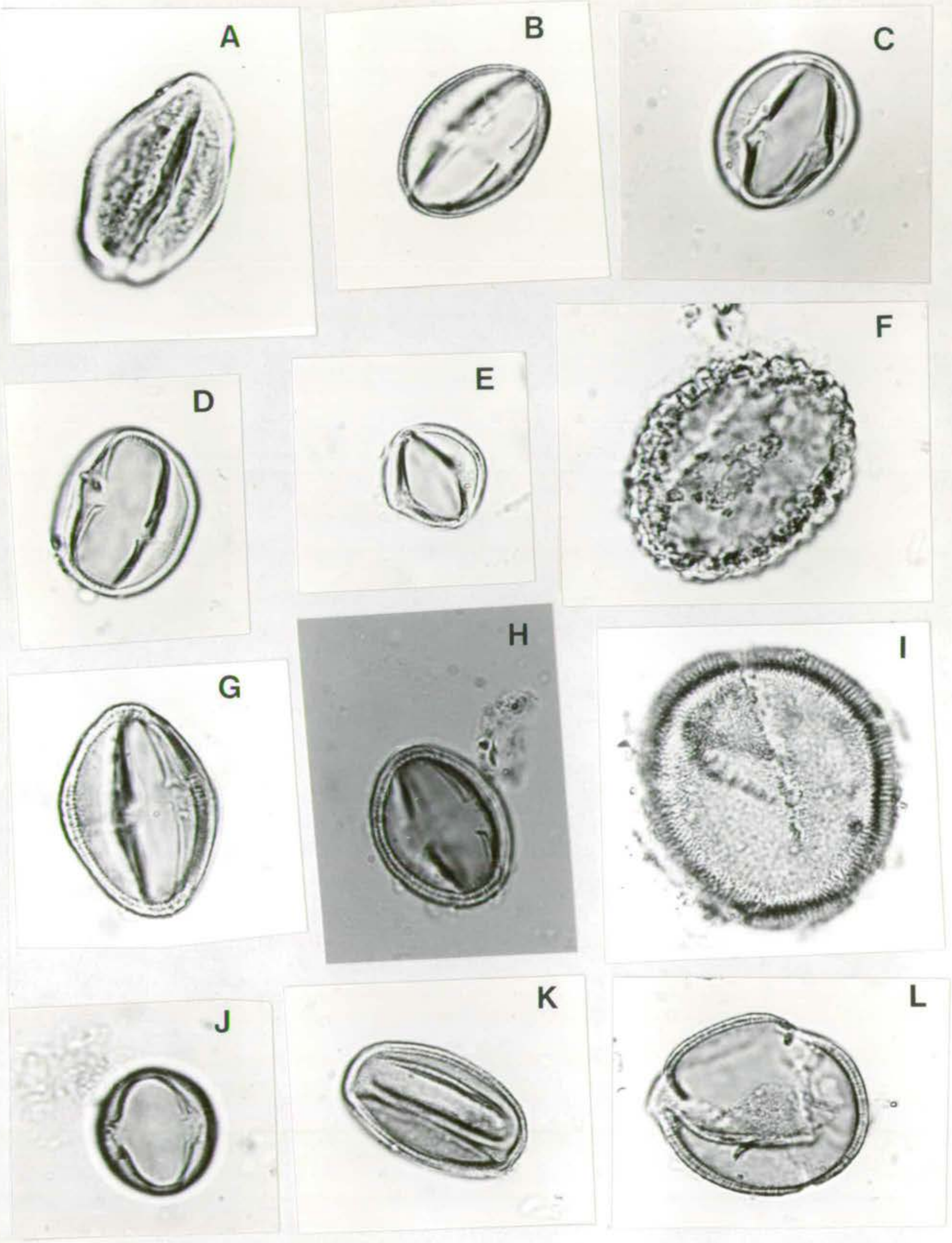
Fig·14·TYPES OF POLLEN GRAINS.

Pl. 9. POLLEN GRAINS IN THE NELSONIOIDEAE

[after acetolysis]

(Explanation in the text)

A = St. longibracteata (x 1,650); B = St. spatulata complex (x 1,650); C = O. macrobotryum (x 1,650); D = St. anigozanthus (x 1,375); E = St. linearifolia (x 1,375); F = E. caroliniensis (x 1,650); G = St. paludosa (x 1,375); H = N. canescens (x 1,650); I = E. imbricata (x 1,650); J = St. maclellandii (x 1,375); K = Saint. lebrunii (x 1,375), and L = St. lebrunii (optical view; x 1,375).



Pl.9.

Results and Discussion: The pollen grains of Nelsonioideae are ± uniform in shape. They are either ellipsoidal or roundish in outline. Size differences amongst the closely related species are not striking enough, but unrelated or distantly related species differ considerably in the size of their pollen grains. The biggest grains are found in *St. argentea* var. *angustifolia* (about 42-47/24-36 µ), while the smallest grains are met with in *N. canescens* (20-23/20-21µ), *St. repens* (18-25/16-18 µ), and *St. coriacea* 19-22/17-20 µ).

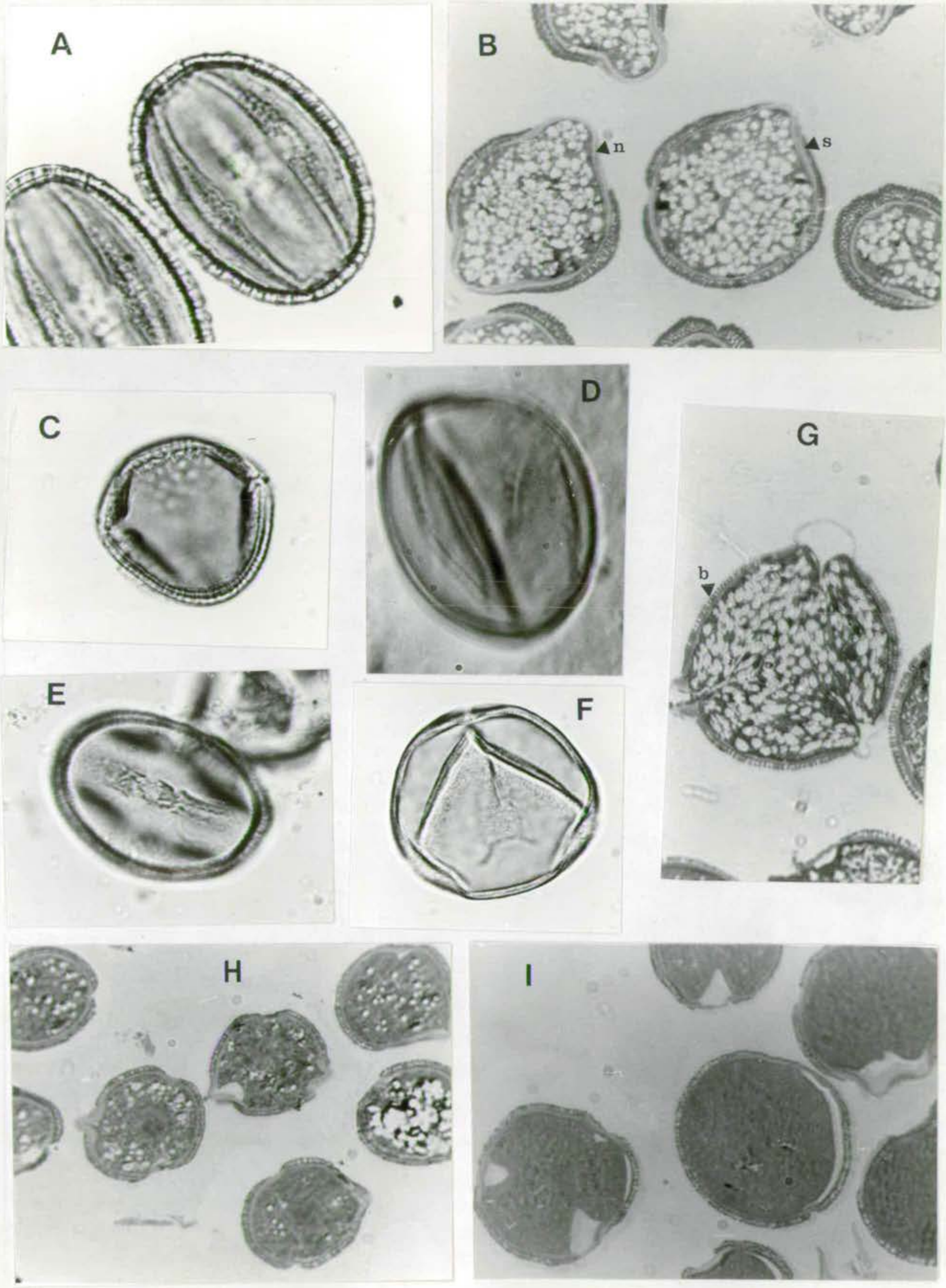
The Nelsonioideae are characterized by their free bacula (or columellae) of the sporoderm (Pl. 11) which may remain either singly or in groups. The sexine (primary exine) is sometimes differentiated into a thin layer known as pedium or foot layer (Pl.11.E). The nexine (secondary exine) is homogeneous excepting the gaps below the colpi (Pl.10.11). Sporoderm stratification (i.e. ornamentation and mode of arrangement of the columellae) is of taxonomic value in species delimitation of *Elytraria* (Fig. 14. t, g, h, & i), but any definite conclusion needs further studies of all the species so far described.

Typically 'tricolpate' pollen grains are recognized in Elytraria (Fig. 14. G-I. Pl. 9.F), *Saintpauliopsis* (Pl.9K), and *Gynocraterium*. Therefore, the statement of Johri & Singh (1959) regarding the occurrence of 'tricolporate' pollen grains in *E. acaulis* seems to be an observational error.

In the genera like *Nelsonia* (Pl. 9.H), *Ophiorrhisiphyllon* (Pl. 9.C), *Staurogyne* (Pl. 9.BD), and *Anisosepalum* (Fig. 14. E; Pl.10.E) an interesting trend has been noticed. Although typically 'tricolpate' pollen grains are not rare in *Staurogyne* (Fig. 14. A), most of the genera cited above possess pollen grains having colpi which appear ± broken at the middle region. Looking through the microscope in optical view a clear area is also obvious at this location. This gives an impression of a weakly defined pore in the colpus (can be referred to as an 'endoporus' after Retisma, 1970) [Fig. 14. B & C; Pl. 9 & 10].

Pl. 10. POLLEN GRAINS (after acetolysis)
AND THEIR SECTIONS

(Explanation in the text: A & C-F = acetolysed whole grains, B & G-I = ultratome sections of the pollen grains) A = Andrographis echioides (x 1,375); B = St. paludosa (x 1,650); C = Bremekampia tentaculata (x 1,375); D = Rhinanthus crista-galli (x 1,375); E = A. alboviolaceum (x 1,375; mark the resemblance with A); F = Rhinanthus crista-galli (optical view; x 1,375); G = N. canescens (x 1,650); H = O. macrobotryum (x 1,650), and I = A. humbertii (x 1,650) /n = nexine, s = sexine, and b = bacula/.



Pl.10.

Sections of pollen grains through the colpi clearly demonstrate the absence of nexine at these regions (Pl. 11), while the gap in the sexine is definitely due to the formation of the colpus. Whether these sections are in fact cut through the equatorial planes of the colpi is a difficult question to settle at the moment. But it is quite concievable why from time to time various authorities have put forward contradictory reports on the nature of Nelsonioideae pollen grains. Pioneer workers like Lindau (1893) himself described them as "typischer Spalten Pollen, Spalten sehr schmal, ohne Poren" and again (1895) as "Spalten Pollen mit Poren". Bhaduri (1944) also doubted the validity of the Nelsonioideae, as he observed similar pollen grains in *N. canescens* and *Andrographis paniculata* Nees. Mangenot & Ake Assi (1959) [pollen grains studied by Van Campo] also reported the occurrence of 'tricolporate' pollen grains in *St. paludosa*, while describing an alleged new genus *Staurogynopsis* under Nelsonioideae.

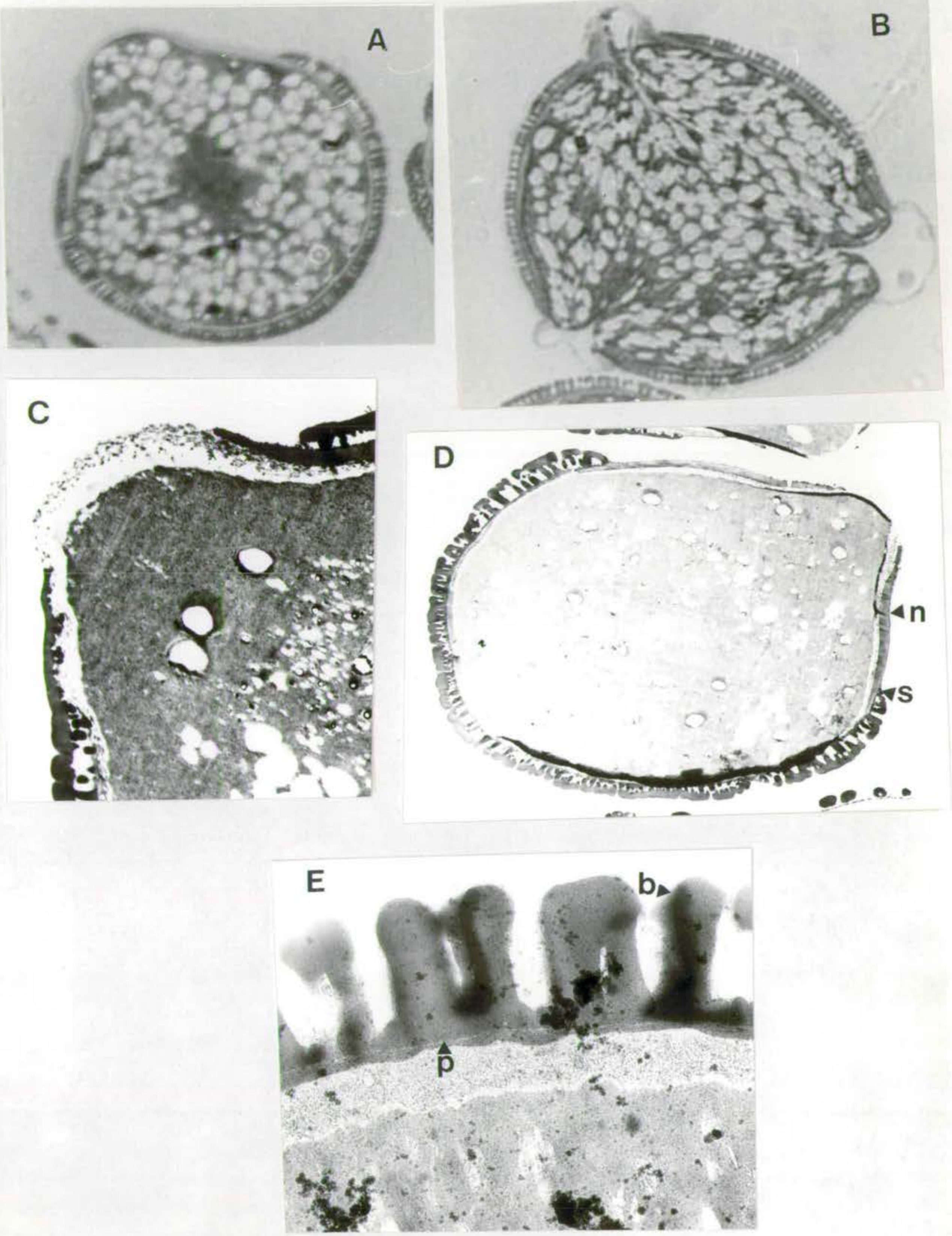
But all these reports of 'tricolporate' pollen grains in the Nelsonioideae have been refuted by the recent palynological survey of the Acanthaceae by Bhoj Raj. To contradict Raj's statement (i.e. the Nelsonioideae always possess 'tricolpate' pollen grains) the present critical studies of the fresh and acetolysed pollen grains of the Nelsonioideae taking a fair sample coupled with the Ultratome sectioning clearly reveal that the pollen grains of this group are basically 'tricolpate', but 'tricolporoidate' (after Erdtman, 1952) to 'tricolporate' types also occur widely in the Nelsonioideae.

Typically 'tricolpate' grains have been encountered in *Elytraria* (Fig. 14. F-I), *Saintpauliopsis* (Fig. 14. D), and *Gynocraterium* where the colpi do not show any further evolutionary developments in their structural features. But in the rest of the genera (e.g. *Staurogyne*, *Nelsonia*, *Ophiorrhiziphyllon* and *Anisosepalum*) a tendency can be easily recognized in the evolutionary development

Pl. 11. ULTRATOME SECTIONS OF POLLEN GRAINS

(Explanation in the text; A & B = photomicrographs;
C, D, & E = Electron photomicrographs)

A = St. paludosa (x 4,400); B = N. canescens (x 4,400);
C = St. paludosa (x 9,000); D = St. paludosa (x 3,750),
and E = A. humbertii (x 60,000) [n = nexine, s = sexine,
b = baculum, and p = pedium or foot layer.]



Pl.11.

of the colpi. In these genera the apertures are compound in structure and in each case the colpus tends to have a pore in the middle by which it shows a break and hyaline area at this location. That this is not an artifact has been proved by the critical observations on fresh pollen grains, mounted in water, lactophenol or glycerine.

This feature can be traced forward further in the tribe Andrographideae where the colpus bears a median constriction and an indistinct pore at the same location (Pl.10.A). This is according to Lindau a modified condition of 'tricolpate' pollen grains. Thus it is perhaps immaterial whether the weakly defined pores or breaks in the middle of 'tricolpate' pollen grains should be accommodated and described under a strait jacket of pollen morphological terms. It is undoubtedly an interesting finding in the Nelsonioideae, a sort of primitively 'tricolporate' (or 'tricolporoidate' of Erdtman) condition which probably has achieved further perfection in the relatively advanced tribe Andrographideae.

FRUIT ANATOMY

The anatomy of the fruit provides corroborative evidence in delimiting several genera of the Nelsonioideae. The particular type of cells and their arrangement in the pericarp of the capsule are the most useful from the taxonomic point of view.

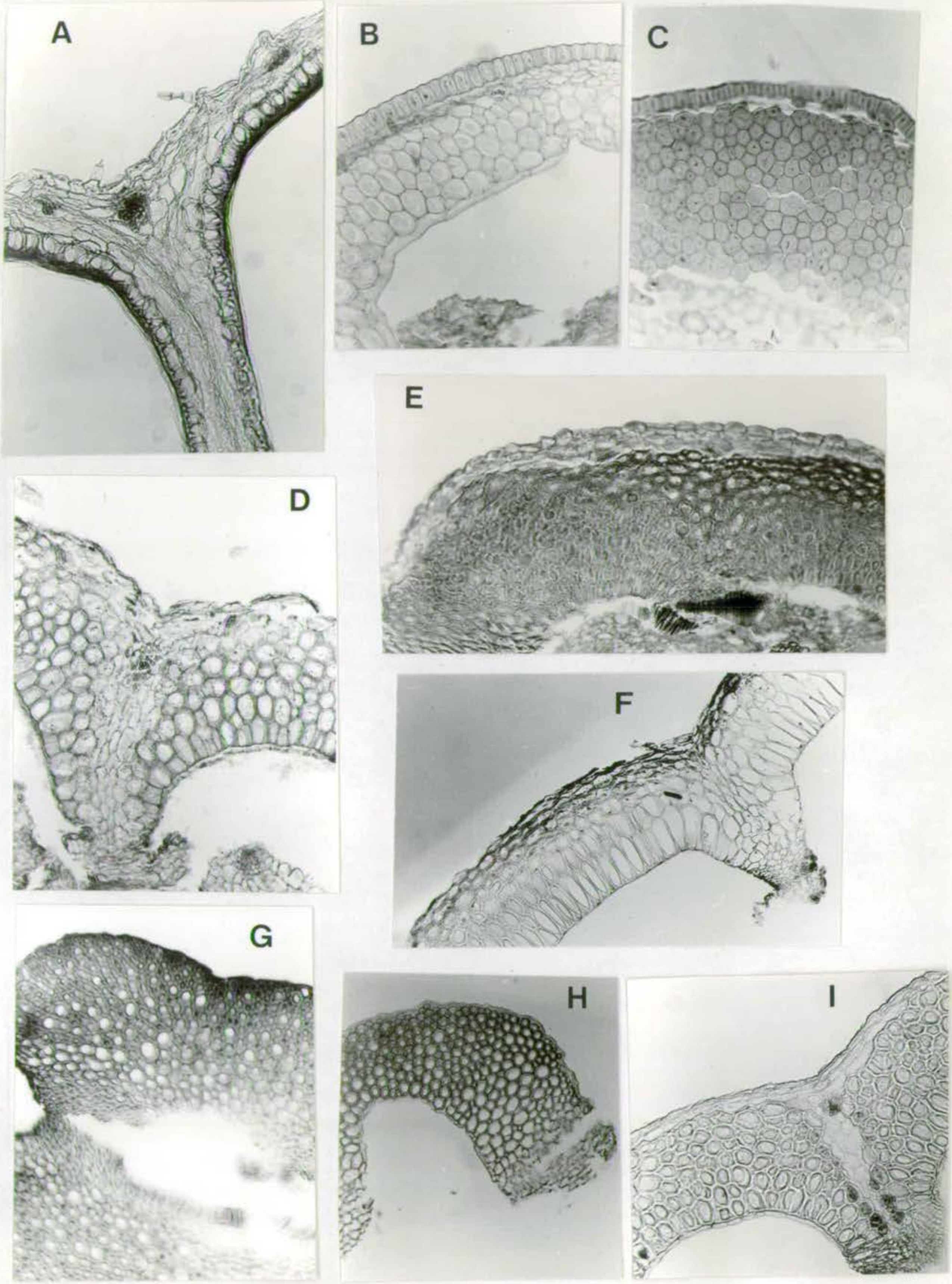
All the genera of this group usually possess an 'epicarp' which is made up of one layer of parenchymatous cells (can be also referred to as the outer epidermis) but Elytraria (Pl.12.E) is unique in having this layer entirely sclerified (with 'brachysclereids') except at the zone of dehiscence. The cuticle on this outer epidermis is as a rule smooth in the Nelsonioideae, but in Ophiorrhiziphyllon it is crenulate (Pl.12.D) in appearance.

The 'mesocarp' is entirely sclerified in Nelsonia (Pl.12.H), indistinguishable

Pl. 12. T.S. OF FRUITS AND THEIR TIPS

[Explanation in the text; C, E, & G = fruit tips; A, B, D, F, H, & I = fruits (capsule) - in each case a portion is shown only] All x 145

A = St. kamerunensis; B = E. acaulis; C = E. acaulis; D = O. macrobotryum; E = St. spiciflora; F = Saint. lebrunii; G = N. canescens; H = N. canescens, and I = O. macrobotryum.

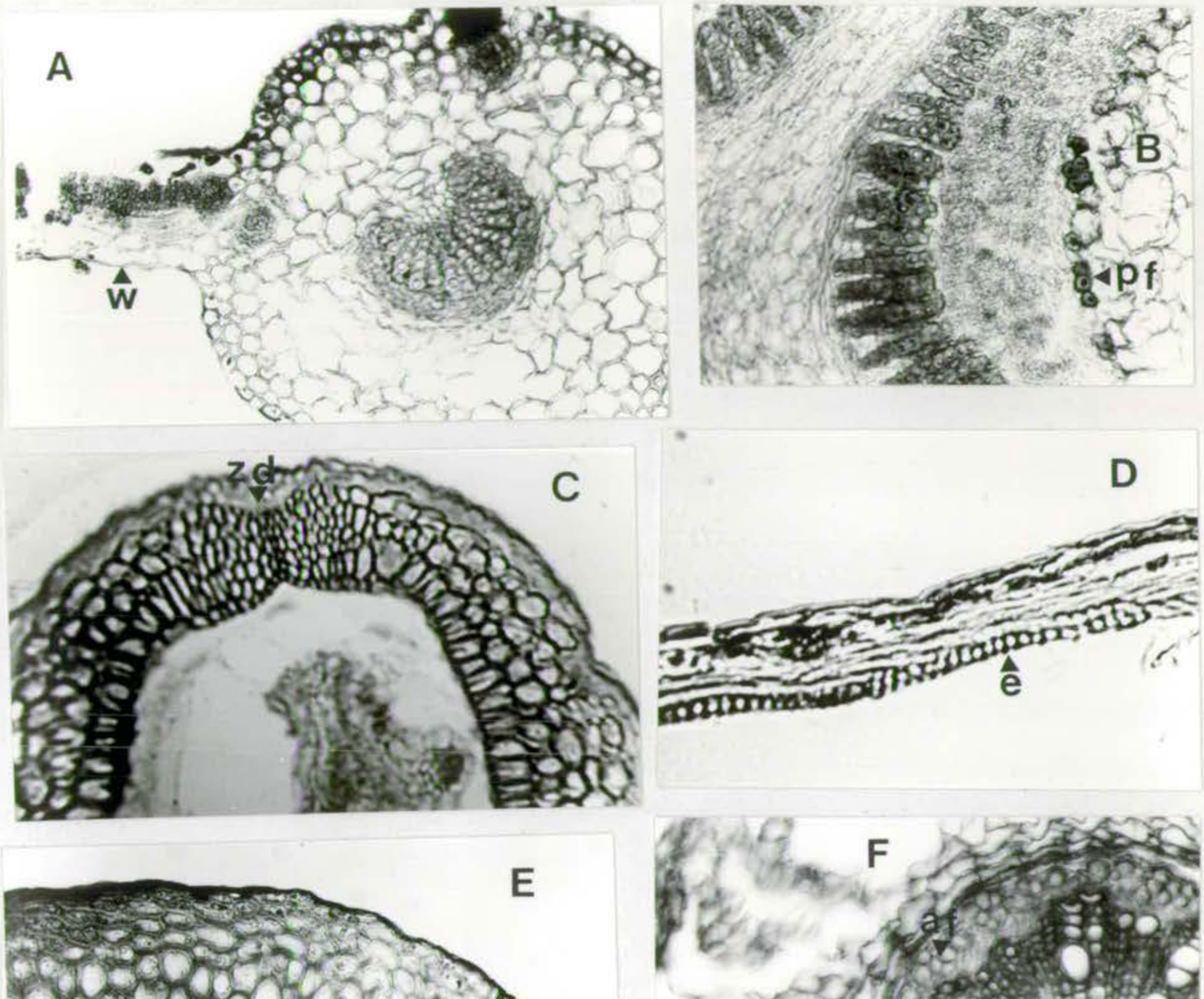


Pl.12.

Pl. 13. T.S. OF FRUITS, STEMS, PETIOLE, AND ROOT

(Explanation in the text; A = petiole; B, G & H = portions of stems; F = a part of root; C-E = portions of fruits /capsules/)

A = E. madagascariensis (x 145); B = E. madagascariensis (x 145); C = St. spiciflora (x 145); D = Rhinanthus crista-galli (x 232; note the parenchymatous tissues excepting the inner most sclerified endocarp); E = Saint. lebrunii (x 145; mesocarp indistinguishable); F = N. canescens (x 145; mark the prominent air chambers); G = Rhinanthus minor (x 145; no 'acicular fibres'), and H = N. canescens (x 145; note the presence of 'acicular fibres'). /w = wing; pf = pericyclic fibres; zd = zone of dehiscence; e = endocarp; ac = air chamber, and af = 'acicular fibres'/.



Pl.13.

in Saintpauliopsis (Pl. 12.F), while the rest of the genera possess 2-3 layers of parenchymatous cells (Pl. 12. A-E, G & I). The 'endocarp' is made up of only one layer (represented by the inner epidermis) of parenchymatous cells in Nelsonia (Pl. 12. G,H), indistinct in Saintpauliopsis (Pl. 12. F) and in others represented by many layers of thickened cells of which the layer adjacent to the inner epidermis becomes specialized (sclerified). In this respect, Sect. Zenkerina of Staurogyne deserves particular mention as its entire 'mesocarp' is either parenchymatous or the 'endocarp' bears 1-2 layers of sclerified cells adjacent to the inner epidermis (Pl. 12. A). On the other hand, in Elytraria the entire 'endocarp' (which is many layers thick) is exceedingly thickened and sclerified apart from a parenchymatous inner epidermis (Pl. 12. B).

The capsule tips are usually made up of sclerified cells which after dessication help in severing the two valves of the fruit (Pl. 12. C & H). This sclerification is much pronounced in Elytraria (Pl. 12. C) and Nelsonia (Pl. 12.H).

Lastly the macerated tissues of the fruits in these genera also demonstrate that there are considerable differences among them in the nature of their constituent pericarpial elements. For example, septate fibres are only found in Nelsonia (Pl. 15. A), while sclerified cells with scalariform thickenings can be met with in Staurogyne (Pl. 15. B), Elytraria (Pl. 15. C), and Nelsonia (Pl. 15.A). These are entirely absent from Siantpauliopsis (Pl. 15. D) and Rhinanthus (Scrophulariaceae) /Pl. 15. E/.

OVULES AND SEEDS

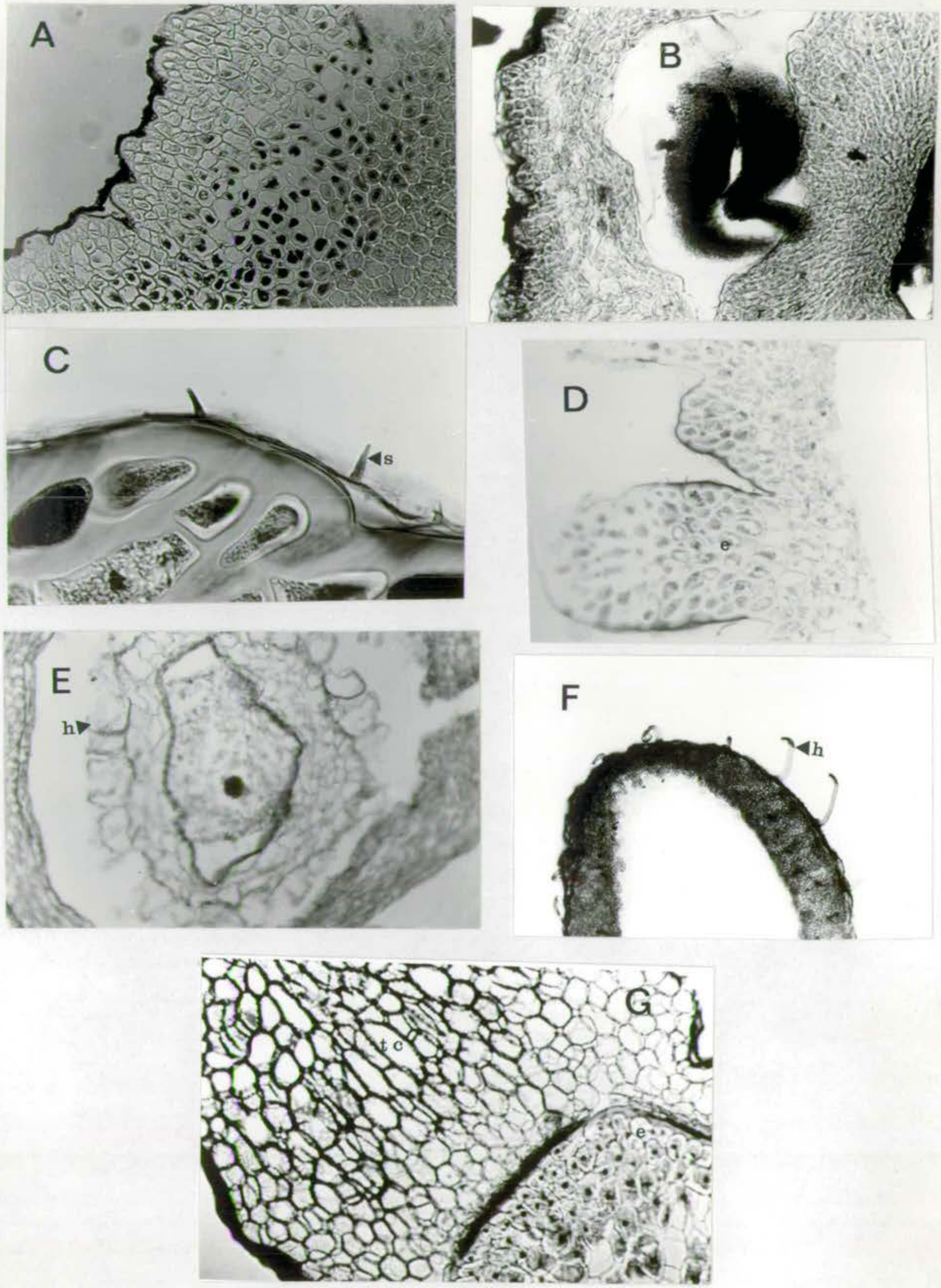
The number of ovules along with the number of placentas is of considerable taxonomic importance in the generic delimitation of the Nelsonioideae and also useful in the classification of Staurogyne. The ovules are as a rule unitegmic, tenuinucellate, either amphitropous or campylotropous - always obliquely oriented upwards and arranged in two or rarely four alternate rows in each loculus of

Pl. 14. T.S. OF SEEDS

(Explanation in the text)

A = *A. humbertii* (x 145); B = *A. humbertii* (x 145); C = *Andrographis echioides* (x 650; Acanthoideae); D = *Andrographis echioides* (x 145); E = *St. paludosa* (x 145); F = *N. canescens* (x 145; note the hooks on the testa), and G = *Rhinanthus crista-galli* (x 145; Rhinanthoideae-Scrophulariaceae).

[h = hook; tc = testa cells; s = spine, and e = endosperm].



Pl.14.

the ovary. The placentation is constantly 'axile' according to the classical interpretation. However, many of the genera (e.g. *Elytraria*, *Nelsonia* and *Saintpauliopsis*) and species sometimes may show unilocular condition at the upper portion of the ovary. Consequently, their placentation has been described in the past as 'parietal', but one should not make any general conclusion until serial sections of the entire ovary are examined. In fact, in all of these Nelsonioideae the ovary is strictly bilocular at least at the base.

Most species of *Elytraria* exhibit small funicular swellings. Similar swellings are also detectable in *Nelsonia* and many species of *Staurogyne*. In the past these have been referred to as 'papilliform retinacula' (funicular excrescences) the presence of which in the Nelsonioideae has been strongly rejected by Bremekamp (1965). It is a fact that many of the Nelsonioideae do not have perceptible swellings (papillae) on their funicles, but occasionally (e.g. *St. dolichocalyx*) /Fig. 8.D/ they can produce conspicuous projections fairly comparable to the reduced or undeveloped retinacula of other Acanthaceae. On the other hand, the genus *Anisosepalum* bears 'unindurated retinacula' (Fig. 8. R) supporting its seeds.

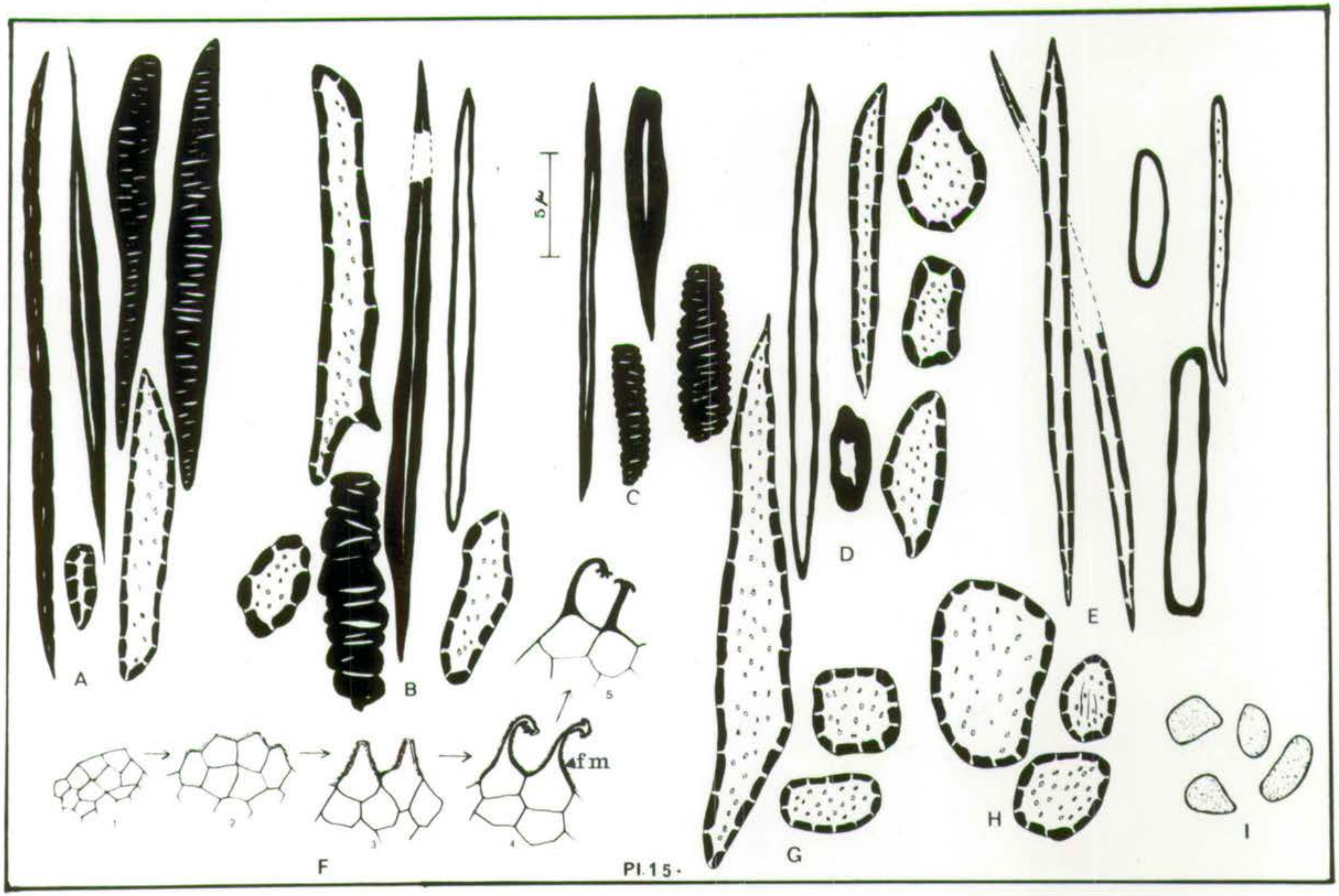
The testa of the Nelsonioideae is strikingly thin and its dome-shaped cells are entirely parenchymatous in nature (Pl.15.I). Apart from the rugose testa of *Anisosepalum* the Nelsonioideae are characterized by the possession of solid bars or hooks on their testa cells. (Fig. 9).

Lack of fresh materials did not allow me to investigate how these structures originate or what could be their exact chemical nature. However, observations into the ovules of various ages from the herbarium sheets (boiled in water for some time) indicate that these bars or hooks are in fact prolongations of the testa cells proper. They appear at first as small protuberances (Pl.15.F_1) which gradually enlarge; the walls at the beginning remain covered by a thin

Pl. 15.PERICARPIAL AND TESTA ELEMENTS (after maceration) AND STAGES IN THE DEVELOPMENT OF BARS OR HOOKS ON THE SEED TESTA

(Explanation in the text: A-E = pericarpial elements; G-I = testa cells of the seeds, and F_{1-5} = diagrammatic representations of the development of bars or hooks)

A = *Nelsonia*; B = *Staurogyne*; C = *Elytraria*; D = *Saintpauliopsis*; E = *Rhinanthus*; F_{1-5} = Stages in the development of hooks (or bars) on the testa cells of the Nelsonioideae (excepting *Anisosepalum*); G = *Rhinanthus*; H = *Rhyncochorys*, and I = Nelsonioideae /fm = film of mucilage/.



Pl.15.

film of mucilage (Pl. 15. F_{1-4}). Ultimately, some of these prolongations branch and rebranch at their extremities to give an appearance of 'hammers' or hooks (Pl. 15. F_5). At maturity, the seeds lose their mucilage entirely from these bars or hooks.

In Elytraria (Fig. 9. g) these prolongations are quite small and thus look like 'papillae' which are actually comparable with the smaller solid bars without any branching at their extremities.

The endosperm is as a rule persistent, fleshy (oily) and 'alveolate' (ruminate) in all the Nelsonioideae. The alveolation is caused by the depressions (irregular pits) on the testa cells (Fig. 9) and in some cases by the outward projections of the cells of the endosperm (e.g. Anisosepalum) /Pl. 16. B/.

The embryo of the Nelsonioideae may be either slightly 'bent' or 'spathulate' (after Martin, 1946) and on germination always produces two equal cotyledons.

GENERAL CONSIDERATIONS

COHERENCE OF THE NELSONIOIDEAE AS A TAXONOMIC GROUP

The subfamily Nelsonioideae are a small group of about 7 genera and 175 species (including the new ones described here), widely distributed in the tropics and subtropics of both worlds. Its genera exhibit remarkable diversities in the nature of morphological, anatomical, and palynological characters. But there is a fundamental unity and coherence of the group (Nelsonioideae) as a whole. Although the genera have diverged and evolved along separate lines of evolution, the basic plan of the group has remained more or less intact.

The Nelsonioideae can at once be recognized from allied groups by a combination of several important taxonomic characters - both exomorphic and endomorphic, macroscopic or microscopic. General characters of the group can be summed up as follows:

(1) plants without cystoliths but usually with 'acicular fibres' (excepting two genera),

(2) leaves mostly opposite, rarely alternate, subalternate or verticillate, always exstipulate and provided with pinnate venation the primary veins of which anastomose at the margin,

(3) occurrence of 'diacytic' stomata of 'mesogenous' origin,

(4) universal occurrence of bi-celled glandular hairs on the leaf epidermis,

(5) inflorescence fundamentally of racemose type,

(6) bracts, bracteoles, and calyx usually well developed, sometimes small in size - rarely the bracteoles are lost,

(7) corolla with 'descending imbricate' aestivation in buds,

(8) pollen grains usually of 'tricolpate' type, but manifesting a general tendency to be 'tricolporoidate' or 'tricolporate',

(9) six to numerous ovules, arranged in 2 or 4 alternate rows in each loculus of the ovary,

(10) embryo slightly 'bent' or 'spatulate' (after Martin, 1946),

(11) capsule always non-stipitate; if sterilisation occurs, it starts from the apex,

(12) capsule dehiscing loculicidally into two woody, recurved valves (rarely indehiscent),

(13) characteristic division of the placenta into two equal halves from the tip to the base,

(14) seeds usually small with a very thin testa and mostly provided with solid bars or hooks (excepting Anisosepalum), often without retinacula (in Anisosepalum retinacula are well developed but unindurated), but always with persistent 'alveolate' (ruminate) /after Hartl/ endosperm, and

(15) central chamber of the endosperm developing asymmetrically.

Slight divergence in any of these general characters outlined above surely reflects the evolutionary potential of the group concerned. To cite a few examples we can find tardily dehiscent or irregularly dehiscent capsules in the supposedly primitive subgen. Tetrastichum, Sect. Zenkerina of Staurogyne, while a modified type of racemose inflorescence (superficially resembling a 'scorpioid cyme') is encountered in Saintpauliopsis (cf. chapter II p. 14). The seeds of the Nelsonioideae are often small in size, usually provided with solid bars or hooks, but they are papillose (comparable to small solid bars) in Elytraria. Comparatively larger and fewer seeds with rugose testa (devoid of bars or hooks) occurring in Anisosepalum evidently show an evolutionary specialization. This tendency seems to be coupled with the simultaneous exploitation of the ecological amplitude, particularly in establishing the species and the genera in forest habitats. Prevalent occurrence of nearly all the advanced genera and species of Staurogyne accompanied by their larger and lesser number of seeds lucidly justifies the present contention.

This specialization is probably owing to an adaptation resulting out of the prevailing selective pressure for the accummulation of enough food materials necessary for better competition, especially at the crucial seedling stage of forest-loving plants. As a result, one can come across with a fact that all the advanced Nelsonioideae possess cotyledons which tend to be much bigger in size (e.g. Anisosepalum), indicating a possible but gradual elimination of the endosperm; - the immediate unfolding of the cotyledonary leaves for a greater photosynthetic surface especially at the seedling stage is far more useful in the prevailing ecological conditions of forest undergrowth communities.

Finally the pollen grains of the Nelsonioideae are basically 'tricolpate', but there is a general trend prevalent in the genera like Staurogyne, Nelsonia, Ophiorrhiziphyllon and Anisosepalum (Pl. 9) where 'tricolporoidate' condition is largely manifested. This can be interpreted as an intermediate step towards the evolution of typical 'tricolporate' pollen grains, usually characteristic of the higher related taxa.

Therefore, studies of the Nelsonioideae, a diverse but taxonomically coherent group, seems to be rewarding for the general assessment of its natural affinities with other families within the order 'Bignoniales' and might prove to be a source from which other related taxe might have evolved.

NUMBER OF GENERA IN THE NELSONIOIDEAE

The group originally designated as a tribe Nelsonieae [cf. Nees in Wall. Pl. As. Rar. 3: 75, 79-80 (1832) and Nees in DC., Prodr. 11: 62-79 (1847)] contained five genera. These were (1) Ebermaiera Nees, (2) Erythracanthus Nees,

(3) *Nelsonia* R. Br., (4) *Elytraria* Vahl, and a genus for which Nees used the name (5) *Adenosma* R. Br. (Scrophulariaceae).

The first two subsequently proved to be congeneric with *Staurogyne* Wall., while the placing of the fifth genus in this group was found to be incorrect, both taxonomically and nomenclaturally. The genus was in fact based on *Ruellia uliginosa* L., a species of quite different affinity (tribe Ruellieae) instead of the type species of Brown's genus. However, it was later on confirmed that the species referred to *Adenosma* by Nees actually belonged to a different genus - *Synnema* Benth. of the tribe Hygrophileae.

In Lindley's Introduct. Nat. Syst. ed. 2: 444 (1836) Nees added another genus-*Gymnacanthus* Nees - to this group. But subsequently [cf. DC., Prodr. 11: 219 (1847)] he came to a different conclusion by placing this genus in the tribe Trichanthereae and introducing a new but nomenclaturally illegitimate (a lat~~t~~er homonym!) name *Sclerocalyx* to it. As its capsule bears well developed indurated (woody) retinacula, the affinity cannot certainly be with the Nelsonioideae although it lacks cystoliths in various plant parts.

Spencer Moore's originally misplaced genus *Hiernia* S. Moore was also referred by Lindau (1895) to the Nelsonioideae, but it was later on pointed out by Engler & Gilg (1903) that *Hiernia* should be placed in the Scrophulariaceae - Gerardieae, and not far from *Gerardia* Benth. and *Xylocalyx* Balf. fil (cf. Carter, 1962). The peculiar woody united calyx, monothecal anthers, unilaterally beaked capsule not dehiscing into two woody recurved valves, and the 'anomocytic' stomata of *Hiernia* are entirely unknown in the Nelsonioideae.

At present *Staurogyne* Wall. is the biggest pantropical genus of the Nelsonioideae, while *Ophiorrhiziphyllon* Kurz, *Gynocraterium* Brem., *Saintpauliopsis* Staner, and *Anisosepalum* E. Hossain are a few smaller genera, either monotypic or ditypic. Tremendous morphological variations are encountered within the genus Staurogyne. Even two sympatric species often show remarkable morphological diversity, especially in habit, leaf shape, indumentum, stem and inflorescence character. Consequently this has led many contemporary taxonomists to create several new genera like Zenkerina Engl., Neozankerina Mildbr., and Staurogynopsis Mangenot & Ake Assi.

Engler (1897) primarily placed his genus Zenkerina in the Scrophulariaceae, but Hans Hallier (1903) rightly doubted the validity of this taxonomic conclusion by showing its natural affinities with Staurogyne. Thus Zenkerina was subsequently proved to be synonymous with Staurogyne and the necessary transfer was made by R. Benoist in 1913 (cf. Lecomte's Not. Syst. 2: 290).

Similarly Neozenkerina, at first described under Scrophulariaceae, has recently been found to be congeneric with Staurogyne by Heine/cf. Kew Bull. 16: 183 (1962)/. An isotype (although only at the vegetative stage) of Neozenkerina bicolor Mildbr., preserved at the Kew Herbarium, strikingly seems to be even synonymous with Staurogyne kameruenensis (Engl.) R. Ben.

Staurogynopsis is a genus of controversial nature consisting of two species out of which one was already described as Staurogyne capitata by E. A. Bruce /cf. Kew Bull. 285 (1935)/. On the other hand, Heine (1962) has already considered the genus Staurogynopsis to be congeneric with Staurogyne after giving some reasonable arguments. It is a fact that the two species (St. capitata and St. paludosa) referred to Staurogynopsis are a bit unusual in the Nelsonioideae in the nature of their irregularly dehiscent or indehiscent capsules. But similar comparable tardily dehiscent capsules are also met with in St. kamerunensis and St. dolichocalyx. Other points of resemblance are the general decumbent habit, stem rooting at the nodes, larger calyx lobes, similar corolla, and four rows of ovules in each loculus of the ovary. Therefore it is not advisable at the present moment ot keep a separate genus based on a single character (i.e. capsule indehiscence).

I have recognized altogether 7 genera in the present investigation of the Nelsonioideae. These are Staurogyne Wall., Ophiorrhiziphyllon Kurz, Saintpauliopsis Staner, Gynocraterium Brem., Anisosepalum E. Hossain, Nelsonia R. Br., and Elytraria Michx. Out of these above mentioned genera, Saintpauliopsis was at first erroneously described under Gesneriaceae. B.L. Burtt (1958) aptly transferred it to the Nelsonioideae but at the same time reduced the genus to a synonym of Staurogyne. No doubt Saintpauliopsis is closely related to Staurogyne, but there are numerous important differences too (cf. "Generic Interrelationships" pp. 84-88) which necessitate its recognition as a separate genus.

Ophiorrhiziphyllon and Gynocraterium are the only two monotypic genera with close affinity to Staurogyne, differing only in some minor characters of taxonomic importance. Although Anisosepalum is in fact a segregate genus of Staurogyne, containing two Central African species, it varies widely from the latter (cf. pp. 96-98). The remaining two genera, Nelsonia (monotypic) and Elytraria, are remarkably distinct within the Nelsonioideae and also pantropic in distribution.

GENERIC INTERRELATIONSHIPS

Although the number of genera in the Nelsonioideae is small (only 7), the genera are not all very closely related to one another. The basic plan of the group envisages that the Nelsonioideae might have originated in the past from a pentamerous, gamopetalous, multiovulate, and endospermic 'stock' - probably from a common "Scrophularian" ancestor. Zygomorphy in relation to stamens has been attained in the genera like Staurogyne, Saintpauliopsis, Gynocraterium, and Anisosepalum, possibly in one step by the sterilization of the posterior fifth stamen - often represented by a staminode.

Staurogyne is the largest, most diverse pantropical genus, while *Saintpauliopsis*, *Gynocraterium*, and *Ophiorrhiziphyllon* are monotypic with restricted distributions. The genus *Aniososepalum* is also a small one confined to Central Africa, but whatever be their range of distribution, all these genera form a close-knit group of interrelated taxa in one way or another.

Ophiorrhiziphyllon is so closely related to *Staurogyne* that it can only be recognized by some trivial characters, like the much exserted stamens with erect, elongated anthers (Fig.7.F) dehiscing by small slits at the tip, small connective, and crenulate cuticle (Pl.12.D) of the fruit epidermis. Previously it was separated from *Staurogyne* by three characters, viz. possession of two stamens with two staminodes, exserted stamens, and the anthers dehiscing by small slits. But the present study shows that nearly all of these differences break down one by one, as *St. coriacea*, *St. beddomei*, and others of the series *E* (Asiatic) possess shortly exserted stamens, while *St. diandra* (Tonkin) produces only two fertile stamens with 2 or 3 staminodes (Fig.6b.J). Both the genera possess numerous morphological, anatomical, and also palynological characters in common. Future cytogenetic studies might illuminate the question of whether *Ophiorrhiziphyllon* should be recognized as a separate genus, subgenus or a section of *Staurogyne*. For the present moment it is better to keep it as a separate genus although the differences are not of great magnitude.

The general tendency of the placenta in the Nelsonioideae to be divided into equal halves starts early in the developement of the ovary into mature fruit. This is also pronounced in *Saintpauliopsis* but nevertheless, its placentation is not 'parietal' according to the classic sense of the term. Serial transverse sections of the young ovary always reveal its bilocular condition at least at the base. Moreover, the occurrence of characteristically veined calyx lobes, loculicidal dehiscence of the fruit into woody recurved valves, and 'alveolate' endosperm are not features of Gesneriaceae but happily conform with the Nelsonioideae. From the viewpoint of general appearance, possession of four stamens, 14-20 ovules arranged in two alternate rows in each loculus of the ovary, and solid bars or hooks on the testa cells of the alveolate endospermic seeds, *Saintpauliopsis* is related to *Staurogyne*. On the other hand, there are numerous differences too (cf. "Generic Description" pp. 94-95). The genus *Saintpauliopsis* is rather unusual in the Nelsonioideae (excepting two undescribed species of *Staurogyne* from China) having a single trace in its petiole anatomy (Fig. 13.I), while it shows resemblance with *Anisosepalum* in the nature of bracteoles which are joined with the calyx rim to conceal the two minute lateral calyx lobes, and in the absence of 'acicular fibres' from various plant parts (Fi

The genus *Anisosepalum* contains only two species which were previously described under *Staurogyne*, but provides a good example of the evolutionary potentials present in the Nelsonioideae. It is of particular importance in possessing well-developed but unindurated retinacula supporting the seeds. The seeds are quite big, ovate in outline, and ventrally flattened with a rugose surface. The genus is especially remarkable in having a characteristic 'palate' on the lower lip of its bilabiate corolla, bracteoles joined with the calyx rim to conceal the two minute lateral calyx lobes, bifurcate stigma with upper lobe forked again, and the rugose seeds with a large hilar excavation (Fig. 9.E) supported by unindurated retinacula. *Anisosepalum* is no doubt distantly related to *Staurogyne* in the number of stamens (usually four), and in the possession of 'peltate scales' (Fig. 11.B^1) on the leaves and bracts. On the other hand it conforms anatomically (i.e. in the absence of 'acicular fibres' from various plant parts) with Saintpauliopsis but differs from the rest of the Nelsonioideae.

Further, it is noticealbe that Anisosepalum ahows affinity with Gynocraterium, especially in the number of ovules (6-8), and in the style character (hairiness at the base). However, it is quite interesting to observe that the very characteristic bilabiate corolla with a 'palate' on the lower lip, more or less comparable to Anisosepalum, is also met within other members of the advanced tribes of the Acanthaceae, like Asystasieae on one hand, and Hygrophileae (e.g. Synnema) on the other.

The remaining two genera, Nelsonia and Elytraria are remarkably distinct from the rest of the Nelsonioideae. Nelsonia is a monotypic genus which has successfully exploited its weedy character to be cosmopolitan in distribution. However, individuals producing enormously long spikes superficially resembling those of Elytraria species are not rare in Nelsonia, but they never produce scale-leaves or scaly bracts comparable to those of Elytraria. Further, Nelsonia is strikingly distinct in having only two stamens with the anthers carrying a characteristic lid for dehiscence (Fig. 7. I), and in the complete absence of staminodes and bracteoles. It is also unique in the stem anatomy: 'acicular fibres' are always present in the phloem tissue surrounding the vascular cylinder, and also in the parenchymatous pith cells of the stem (Pl. 1. G). Presence of solid bars or hooks on the testa cells of the seed shows a resemblance in one direction to other interrelated genera (i.e. Staurogyne, Ophiorrhiziphyllon and others), while the calyx character (4-lobed) resembles that of Elytraria in another direction. At present, its natural affinities in the context of other related genera of the Nelsonioideae seems to be rather remote.

Elytraria is quite outstanding in its scapigerous habit or in the possession of a short or long stipe. Subgen. Tetrandra indicates that the ancestors of Elytraria might have possessed 4 stamens, but over and above, the genus is unique in the Nelsonioideae in having hard scale-leaves on the inflorescence axis, scaly bracts subtending the flowers, anthers with a long connective to which the elongated thecae are attached along their whole length, and papillate (granulate) testa of the seeds (Fig. 9.G). The pollen grains are simple 'tricolpate' (also found in Saintpauliopsis and Gynocraterium), whereas in the rest of the genera both 'tricolpate' and 'tricolporoidate' conditions are obvious. However, the natural affinity of Elytraria to any of the existing genera of the Nelsonioideae, by and large, seems to be quite remote or at least uncertain at the present moment.

AN ARTIFICIAL KEY TO THE GENERA OF THE NELSONIOIDEAE

1a. Bracteoles absent; androecium consisting of 2 fertile stamens; ~~no~~ staminode absent; dehiscing anthers with small lids at their apices ....6. Nelsonia

1b. Bracteoles always present; androecium consisting of 4 fertile stamens with 1 or 0 staminode, or 2 fertile stamens with 2 or 3 staminodes; dehiscing anthers never with lids at their apices.

 2a. Bracts usually at the top of the pedicel (not on the inflorescence axis); anther bases tailed, tails forked at their extremities ....3. Saintpauliopsis

 2b. Bracts usually at the base of the pedicel (on the inflorescence axis), sometimes joined up to the middle of the pedicel; anther bases usually entire, occasionally muticous, rarely with short, entire tails.

  3a. Bracts rigid, scale-like; rachis with few or numerous spirally arranged, sterile scale-leaves at the lower portion; calyx 4 partite, ~~but~~ the lower lobe sometimes deeply or shortly incised; seeds granulate ....7. Elytraria

  3b. Bracts always soft, herbaceous; rachis without scale-leaves; calyx 5 partite, lobes similar, dissimilar or sometimes the two laterals markedly smaller than the rest and remain covered by the adjoining bracteoles; seeds either rugose or foveolate with minute hooked processes.

   4a. Fertile stamens and the stigma much exserted; connective of the anther lobes small; anthers elongated and straight ....2. Ophiorrhiziphyllon

4b. Fertile stamens and the stigma usually included, sometimes slightly exserted; connective of the anther lobes wide and thickened; anthers globose and subglobose.

5a. Bracteoles joined with the receptacle to hide the two lateral calyx lobes; corolla with a characteristic 'palate' on the lower lip; stigma bifurcate with the upper lobe being forked again; seeds rugose, ventrally flattened with a deep hilar excavation, supported by unindurated retinacula ...... 5. *Anisosepalum*

5b. Bracteoles never joined with the receptacle to hide the two lateral calyx lobes; corolla never with a 'palate' on the lower lip; stigma crateriform or trifurcate and cruciate, sometimes deeply or shortly bifurcate, rarely lamellate; seeds foveolate with minute hooked processes, subglobose or angular with a small hilar mark; retinacula 0 or papilliform.

6a. Style shaggy at least at the base; stigma crateriform; seeds 6 in each loculus of the ovary, arranged in 2 rows

.... 4. *Gynocraterium*

6b. Style entirely glabrous; stigma trifurcate and cruciate, sometimes deeply or shortly bifurcate, rarely lamellate; seeds 12 to 60 in each loculus of the ovary, either arranged in 2 or 4 rows .... 1. *Staurogyne*

DESCRIPTION OF GENERA

1. STAUROGYNE Wallich, Pl. As. Rar. 2: 80 (1831) t. 186.

Syn.: Ebermaiera Nees in Wall., Pl. As. Rar. 3: 75, 79 (1832).
Erythracanthus Nees in Wall., Pl. As. Rar. 3: 75, 80 (1832).
Stiftia Pohl ex Nees in DC., Prodr. 11: 70 (1847), nom. nud.
Zenkerina Engl. in Bot.Jahrb. 23: 497 (1897).
Neozenkerina Mildbr.in Notizbl. Bot. Gart. Berlin 7: 491 (1921).
Staurogynopsis Mangenot & Ake Assi in Bull. Jard. Bot. Brux. 29: 27 (1959).

Erect, suberect, decumbent, prostrate or scandent herbs, sometimes subshrubby; provided with taproot system or soon replaced by adventitous roots; annual or perennial. Stem herbaceous or woody at the base, unbranched or few-branched to profusely branched, sympodial or monopodial, terete, cylindrical or rarely ridged and rectangular, sometimes provided with swollen (articulation) nodes and occasionally rooting at the nodes. Leaves mostly opposite, sometimes subopposite or alternate at the upper part, usually petiolate, sometimes subsessile or sessile, often sessile or subsessile above; shape, margin, and indumentum of the lamina various, rarely glabrous, usually provided with roundish, papery, 'peltate scales' (at least on the lower surface). Inflorescence in terminal or axillary and terminal racemes or spikes, pedunculate or sessile, unbranched or few-branched to laxly paniculate, rarely subcapitate; racemes usually well-defined, sometimes ill-defined (lower flowers subtended by ordinary leaves) or restricted only to the axillary branches ('brachyblasts') supported by one or two pairs of reduced leaves, thus keeping the growing apex vegetative throughout. Bracts herbaceous, usually 3-veined, sometimes 5 or 7-veined, rarely 1-veined, occasionally similar to the ordinary leaves but mostly different; usually on the inflorescence axis, rarely united up to the middle of the pedicel; lower ones usually opposite, upper ones alternate; size and shape variable. Bracteoles much below or near the top of the pedicel, herbaceous, 1 or 3-veined. Calyx deeply 5-lobed; lobes slightly united at the base, very rarely forming a tube, often dissimilar, sometimes subsimilar or similar in shape and size, occasionally very minute and inconspicuous. Corolla subactinomorphic or weakly bilabiate, sometimes distinctly bilabiate; tube short or long, cylindrical or widely campanulate; lobes subequal or dissimilar; colour variable. Stamens mostly 4, didynamous, rarely 2, often included, sometimes subexserted or slightly exserted; filaments usually hairy, occasionally glabrous, mostly arising from 1/4th, rarely from 3/4th portion of the corolla tube; anthers bithecous; thecae globose or subglobose, base obtuse or muticous, rarely with short tails, dehiscing by longitudinal slits; connective broad and thickened; pollen grains typically 'tricolpate', 'tricolporoidate' or 'tricolporate'. Staminodes usually 1, sometimes 0, rarely 2 or 3, either conspicuous or inconspicuous. Stigma often trifurcate and cruciate, occasionally deeply bifurcate and lamellate or with the lower lobe being always thickened or lobed, rarely with two short and similar lobes, either included or slightly exserted. Style simple, filiform and glabrous throughout. Ovary glabrous, subglabrous or hairy; disc small or well-developed and cushion-shaped. Ovules about 12-60 or more, arranged in 2 or 4 alternate rows in each loculus of the ovary. Capsule ovate-conical, elongate-ovate, elliptical, ellipsoidal or oblong-acuminate, tip always mucronate and rigid, usually dehiscing into woody recurved valves up to the base, occasionally tardily or irregularly dehiscent, very rarely indehiscent. Seeds subglobose; testa thin, foveolate (with irregular depressions) and provided with minute, solid, hooked processes, some of which are branched at their extremities; endosperm persistent, fleshy, and 'alveolate'.

Type: St. argentea Wall.

Recognised species about 142 with wide pantropical distribution, particularly in the Pacific islands and tropical America.

2. OPHIORRHIZIPHYLLON Kurz in Journ. As. Soc. Beng. 40 (2): 76 (1871).

Ascending erect, stout, mostly unbranched herbs, provided with taproot system. Stem cylindrical, herbaceous above, woody at the base. Leaves opposite and petiolate; lamina lanceolate or elliptic-lanceolate, either glabrous or subglabrous, rarely pilose above, pubescent below on the veins, always provided with brown, papery 'peltate scales' (at least on the lower surface). Inflorescence in terminal, rarely axillary branched or unbranched racemes, approaching towards spicate condition. Bracts herbaceous, triangular-linear or ensiform, 1-veined. Bracteoles minute, linear-acute, herbaceous, 1-veined. Calyx deeply 5-partite; lobes slightly united at the base, subsimilar, posterior one 3-veined, always slightly longer and broader than the rest; others 1-veined. Corolla white, yellow or pinkish-red, distinctly bilabiate; lobes orbicular-obtuse. Stamens 2, always much exserted, filaments glabrous, arising nearly from the base of the corolla tube; anthers bithecous, thecae elongate and straight, dehiscing by small slits at the apices; connective small. Staminodes 2, always prominent, often bilobed at the apex. Pollen grains 'tricolporoidate' or 'tricolporate'. Stigma shortly bilobed, protruding; lobes usually small and subsimilar. Style glabrous, filiform. Ovary glabrous; disc cushion-shaped. Ovules about 14-18, arranged in two alternate rows in each loculus of the ovary; retinacula inconspicuous. Capsule oblong-acute, tip mucronulate, dehiscing loculicidally into two woody recurved valves up to the base. Seeds subglobose; testa thin, provided with minute, solid hooks; endosperm persistent, fleshy and 'alveolate'.

Type: O. macrobotryum Kurz.

Monotypic; confined to lower Burma, South China (Yunnan), Laos, and Thailand.

3. SAINTPAULIOPSIS Staner in Bull. Jard. Bot. Brux. 13: 8 (1934).

Prostrate, decumbent or ascending, subrosulate herbs, probably perennial, mostly provided with adventitous roots. Stem herbaceous, cylindrical, differentiated into nodes and internodes, often rooting at the nodes, branched or unbranched. Leaves opposite, forming a rosette of 6-8 from the ramification of the branch or simple opposite, long-petiolate; lamina subglabrous or sparsely pilose. Inflorescence in terminal or axillary modified raceme, producing flowers in a zig-zag manner (superficially resembling a 'scorpioid' cyme); peduncle long and slender. Bracts usually just below the calyx rim, rarely a bit further below, often carried away by the pedicel to its apex, minute and herbaceous. Bracteoles minute, herbaceous, joined with the calyx rim to conceal the two inconspicuous and hyaline lateral calyx lobes. Calyx 5-partite; lobes slightly united at the base, dissimilar, posterior one being the biggest and also broadest than the rest; laterals inconspicuous, 1-veined; others 3-veined. Corolla white, bilabiate; lobes orbicular-obtuse. Stamens 4, didynamous, included, filaments glabrous, arising from $\frac{1}{3}$ portion of the corolla tube; anthers bithecous, thecae subglobose, dehiscing by slits, provided with filiform appendage (tail) at the base, each tail forked at the apex. Staminode 1 or 0, usually hyaline and inconspicuous. Pollen grains typically 'tricolpate'. Stigma deeply bilobed. Style filiform, glabrous. Ovary glabrous; disc swollen, cushion-shaped. Ovules about 14-20, arranged in two alternate rows in each loculus of the ovary; retinacula 0. Capsule ovate-acute, tip subtruncate, dehiscing loculicidally into two woody recurved valves up to the base. Seeds suboblong or subglobose;

testa thin, provided with minute, solid hooks; endosperm persistent, fleshy and 'alveolate'.

Type: Saint. lebrunii Staner

Monotypic; distributed in Gabon, Belgian Congo (Kiuu), Burundi, and Madagascar.

4. GYNOCRATERIUM Bremekamp in Kew Bull. 1939 (10): 557 (1940).

Erect herbs. Stem herbaceous, slightly rectangular. Leaves opposite, petiolate; lamina subentire or repand, subglabrous on both surfaces, lower surface provided with cup-like, brown, 'peltate scales' looking like pores. Inflorescence in terminal, dense, sessile, unbranched spikes. Bracts and bracteoles long, linear-ensiform, herbaceous, bracts 5-veined, bracteoles 3-veined. Calyx deeply 5-partite; lobes slightly united at the base, prominently dissimilar, all narrowly linear-triangular, gradually ending in narrow points (filiform); posterior lobe 5-veined, laterals 1-veined and the anteriors 3-veined. Corolla subactinomorphic; tube cylindrical below, infundibuliform above; lobes small, orbicular, subequal. Stamens 4, didynamous, included; filaments minutely glandular hairy, arising from $\frac{1}{3}$ portion of the corolla tube; anthers bithecous, thecae ovoid, base minutely apiculate, dehiscing by longitudinal slits; connective small. Staminode 1, often prominent and filiform. Pollen grains 'tricolpate'. Stigma crateriform. Style filiform, glabrous above, minutely hairy below. Ovary minutely hairy at the top; disc small, cushion-shaped. Ovules 6 in two alternate rows in each loculus of the ovary; funiculus long and thickened at the hilar region. Seeds not seen.

Type: G. guianense Brem.

Monotypic; endemic to British Guiana.

5. *ANISOSEPALUM* E. Hossain, *gen. nov.*; maxime ut *Staurogyne* Wall;, sed bracteolis ad calycem adnatis, corollis palatis propriis praeditis, ovulis paucioribus, seminibus rugosis et forma stigmatis ab ea facile distinguenda.

Herbae erectae vel suffrutices repentes, terrestres vel epiphyticae, aliquando ad nodos radicantes, annuae vel perennes. Folia omnia opposita, integra parum lobata vel serrulata. Flores tres usque numerosi in racemos terminales vel terminales et axillares laxos vel condensatos dispositi. Bracteae herbaceae, liberae vel usque ad medium pedicellum connatae. Bracteolae magnae, herbaceae, ad apicem pedicelli insertae lobos laterales calycis occultantes. Calyx 5-partitus; lobi basi connati manifeste inaequales; laterales minuti, hyalini, uninervi; ceteri trinervi. Corolla infundibuliformis, manifeste bilabiata; labium superum cucullatum et ad apicem leviter bilabiatum; labium inferum trilobatum, lobis valde inaequalibus; lobus medius latissimus palato elevato praeditus. Stamina 4, didynama, inclusa; antherae thecae subglobosae, biloculares; connectiva lata et incrassata. Grana pollinis 'tricolporoidata' vel 'tricolporata'. Staminodium 1 vel 0. Discus annularis, pulviniformis. Ovarium glabrum, ovulis 6-8 utroque loculo in seriebus duobus dispositis. Stylus sparsim papillosus. Stigma profunde bifurcatum; lobus superus iterum bifurcatus. Capsula oblonga, obtusa vel acuta, non-stipitata, ad apicem subtruncata, parte superiore sterili, in valvos duos lignosos recurvatos loculicide dehiscens. Semina obovata, atra, ventraliter leviter compressa, omnia retinaculo non-indurato suffulta; retinacula tempore dehiscentiae dessicata et lapsa; testae rugosae, excavationibus hili magnis instructae; endospermium copiosum et alveolatum. Typus generis: *A. humbertii* (Mildbr.) E. Hossain, *comb. nov.* (Syn: *St. humbertii* Mildbr.) Species duas in Africa Centrale.

The new genus is without doubt closely related to *Staurogyne* Wall. In fact, the two species referred to here under the genus Anisosepalum were originally described as the species of Staurogyne. This is really interesting in the sense that there have been a number of genera published under this group which later on proved to be synonmous with the pantropical and the most varied genus Staurogyne. But unfortunately nobody has yet focussed attention towards the validity of placing these two species under Staurogyne .

Thorough morphological and anatomical studies of the group throughout its geographical range have revealed that these two Central African species differ widely from the rest of the genuine Staurogyne species. They are at once distinguished by the calyx, corolla, stigma and seed characters.

In the form of calyx the new genus approaches Saintpauliopsis, another African monotypic genus, but differs in the characteristics of inflorescence, corolla, stamens, number of ovules per loculus of the ovary, and seed surface.

A bilabiate corolla is also met with some of the American species of Staurogyne but none of them is provided with a 'palate' on the lower lip of the corolla. The number of ovules per loculus of the ovary varies from 12 to ∞ in Staurogyne, while in the new genus they are only 6-8, supported by unindurated retinacula in mature capsule. Further, the seeds in Anisosepalum (new genus) are slightly flattened at the ventral side and the testa is rugose with a large hilar excavation. All other genera of this group (excluding Elytraria which possesses reduced bars on the testa cells) possess seeds which are provided with solid hooks on their testa cells.

Anatomically the new genus (Anisosepalum) and Saintpauliopsis share a common character, i.e. the absence of 'acicular fibres' in the various plant parts, while the rest of the genera in this group always possess 'acicular fribes' in roots, stems, petioles, and veins. The occurrence of 'peltate scales' on the leaf lamina (particularly on the lower surface) and sometimes on the bracts and bracteoles is also characteristic only of the following genera: Staurogyne, Ophiorrhiziphyllon, Gynocraterium and Anisosepalum (new genus).

In the nature of pollen grains (either 'tricolporoidate' or 'tricolporate') also, the genus Anisosepalum shows resemblance to Staurogyne, Ophiorrhiziphyllon, and surprisingly to Nelsonia which is in fact distantly related to this alliance. Corroborative evidence clearly indicate that Staurogyne, Ophiorrhiziphyllon, Gynocraterium, Saintpauliopsis and Anisosepalum form a complex but closely interrelated group of genera within the Nelsonioideae.

Key to species:

1a. Calyx lobes longer; corolla widely campanulate above; capsule 7 mm to 1 cm long .... humbertii

1b. Calyx lobes much smaller; corolla forming a long, cylindrical tube, campanulate only at the top; capsule never more than 5 mm long .... alboviolaceum

6. NELSONIA R. Brown, Prodr. Fl. Nov. Holl. 1: 480 (1810).

Herbs erect, prostrate, scandent or decumbent, branched or unbranched, annual or perennial, provided with taproot system or soon replaced by adventitous roots, rarely fleshy and fibrous. Stem herbaceous, cylindrical, sometimes woody at the base. Lower leaves always opposite, upper leaves sometimes opposite or alternate, petiolate or subsessile, entire, serrulate or repand, indumentum variable in texture, size and density, rarely subglabrous on the upper surface. Inflorescence in terminal or terminal and axillary spikes; peduncle well-developed or none. Bracts herbaceous, pinnately or palmately veined, alternately arranged. Bracteoles 0. Calyx deeply 4-partite; lobes dissimilar; posterior one slightly bigger and broader than the rest, anterior lobe slightly or prominently bilobed at the apex; all hairy with glandular and eglandular hairs. Corolla subactinomorphic or bilabiate; lobes subobtuse. Stamens 2, included; anthers bithecous; thecae globose or subglobose, dehiscing by apical lids; connective wide; filaments short and glabrous. Staminodes 0. Pollen grains 'tricolporoidate' or 'tricolporate'. Stigma bilobed and capitate or deeply bifurcate, included. Style small, filiform and glabrous. Ovary glabrous; disc inconspicuous. Ovules about 4-10, arranged in two alternate rows in each loculus of the ovary, rarely 1 or 2 becoming mature, others aborted; retinacula papilliform or inconspicuous. Capsule ovate-elongate, tip pointed, dehiscing loculicidally into two woody, recurved valves up to the base. Seeds globose, provided with a hilar scar; testa thin, ornamented with solid hooks some of which are branched at their extremities giving an appearance of 'hammers'; endosperm persistent and 'alveolate'.

Type: *N. campestris* R. Br. = *N. canescens* (Lam.) Spreng. [Rousillom 53 (1789), Senegal (P. herb. Lamarck, holo. *Justicia canescens* Lam.! ex. Guinea), iso. in herb. Jussieu; Cat. No. 5773!]. Monotypic; at first palaeotropic, later on pantropic in distribution.

7. *ELYTRARIA* Michaux, Fl. bor. Amer. 1: 8 (1803), *nom. cons.*

Syn: *Tubiflora* J. F. Gmel., Syst. Pl. 2: 27 (1791), *nom. rejiciend.*

Herbs erect or decumbent, much branched or unbranched, scapigerous, subrosulate or with central stem giving rise to one or numerous rosettes, mostly perennial, sometimes annual, provided with taproots or soon replaced by adventitous roots in the acaulescent species, sometimes tuberously thickened. Stem rhizomatous or prominent, cylindrical, herbaceous or prominently articulated and woody at the base. Leaves alternate, subalternate or verticillate, petiolate or subsessile; lamina entire, repand, crenate, deeply lobed or lyrate. Inflorescence in terminal or terminal and axillary branched or unbranched spikes, borne on long or short scape having alternate or spirally arranged, rigid, clasping scale-leaves, rarely the spikes being sessile. Bracts alternate or spirally arranged, rigid, aristate and scale-like, veins parallel. Bracteoles concave, aristate and boat-shaped. Calyx deeply 4-partite; lobes dissimilar, anterior lobe either slightly forked at the apex or deeply bilobed nearly to the base; all usually hyaline or subhyaline. Corolla bilabiate; tube cylindrical; lobes narrow. Stamens 4 or 2, included or subexserted; filaments short, glabrous, inserted much above the base of the corolla tube; thecae elongated or subglobose (at least in buds), dehiscing by longitudinal slits; connective long, either produced into distal appendage or not. Staminodes usually 2 or 1, sometimes 0, often very small and inconspicuous. Pollen grains typically 'tricolpate'. Stigma included or subexserted, bilobed; lobes markedly unequal with the lower lobe often indistinct; upper lobe always flattened and club-shaped. Style long, filiform, and glabrous. Ovary glabrous; disc undeveloped or slightly developed at the base of the ovary. Ovules about 4-12, arranged in two alternate rows in each loculus; retinacula papilliform or inconspicuous. Capsule ovate-conical or ellipsoid-conical, tip pointed, dehiscing loculicidally into two woody, recurved valves up to the base. Seeds subglobose or provided with many faces; testa thin and granulate (the papillae are in fact comparable to solid bars); endosperm persistent and 'alveolate'.

Type: E. virgata Michx., nom. illeg. /= E. caroliniensis (J.F. Gmel.) Pers./.

Species about 15, pantropical in distribution.

Subgen. Elytraria.

Erect or decumbent, usually unbranched, rarely branched herbs, scapigerous, subrosulate or with a central stem giving rise to one or numerous rosettes, either perennial or annual. Stem rhizomatous or prominent, forming a long or short stipe, usually herbaceous, occasionally woody at the base. Leaves mostly alternate or subalternate, rarely verticillate, petiolate or subsessile;

lamina entire, repand, crenate, deeply lobed or lyrate. Inflorescence in terminal or terminal and axillary, branched or unbranched spikes, borne on long or short scapes having alternate or spirally arranged, rigid, clasping scale leaves. Calyx deeply 4-partite; lobes dissimilar, anterior lobe mostly with slight bifurcated apex, occasionally deeply bilobed nearly to the base. Perfect stamens always 2, included or subexserted; anthers with elongated thecae, both thecae joined together throughout their length to the connective but placed at different levels; connective usually not produced into distal appendage, rarely with mucronulate point. Staminodes usually 2, sometimes 0. ovules about 6-12, arranged in two alternate rows in each loculus of the ovary. Capsule and seeds similar to the genus. Type: *E. virgata* Michx., *nom. illeg.* [= *E. caroliniensis* (J.F. Gmel.) Pers.].

Species about 13, pantropical in distribution but mostly found in America, none in Madagascar.

Subgen. *Tetrandra* E. Hossain, *subgen. nov.*

Herbae perennes, multiramosae. Caulis ad basin lignosus, prominenter articulatus. Folia verticillata, 2-6 ad nodum orientia, petiolata; lamina lanceolata vel late lanceolato-spatulata. Inflorescentia spicata, sessilis vel pedunculata, terminalis vel axillaris; rhachides (scapi) 1-4 ad quamque nodum orientes, pilis ceaspitosis instructi; inferne foliis squamiformibus, sterilibus amplectantibus paucis vel numerosis instructi. Bracteae squamiformes, aristatae. Calyx profunde quadri-partitus, lobo antico fere ad basi bifurcato. Stamina 4, inclusa; thecae antherarum in floribus maturis elongatae, in alabastro subglobosae, appendice distali semper prominente. Staminodium 1 vel 0, inconspicuum. Ovarium ovulis in utroque loculo circa 4-6 in series duas dispositis. Capsula et semina generi similia.

Typus: Subgeneris: *E. madagascariensis* (R. Ben.) E. Hossain, *comb. nov.*

Reasons for creating a new Subgen. (*Tetrandra*) of *Elytraria*..

The two species (viz. E. madagascariensis and E. nodosa) referred to Subgen. Tetrandra undoubtedly agree to the structural plan of Elytraria. But in considering their overall taxonomic affinities within the framework of the genus, it becomes really difficult to ascertain their close relatives. Features like the perennial, woody habit, prominently articulated stems, and the occurrence of verticillate leaves are quite remarkable. Moreover, these two species share a common character hitherto unknown in any other species of Elytraria, i.e. the presence of four fertile stamens with subglobose anther lobes (at least in buds) provided with prominent apical appendages.

Anatomically, these two species are usually distinguished by a zone of isolated pericyclic fibres encircling the vascular cylinder of the stem in t.s. (Pl.13.B). This feature seems to be one of the primitive ones in the Nelsonioideae, as it is also found in the primitive Sect. Tetrastichum (Fig.13,E) of Staurogyne.

However, in the general habit, the Subgen. Tetrandra superficially resembles E. imbricata, a widely distributed species of America and Malaysia. But from the taxonomic point of view, the Subgen. Tetrandra shows at least a remote affinity with the existing Afro-Asiatic species, especially in the leaf arrangement, and in the lobing of the anterior calyx lobe.

All the existing species of Elytraria produce spikes which are borne on scapes, clothed with numerous rigid scale-leaves, but E. madagascariensis possesses entirely sessile spikes bearing a few (2-3) sterile bracts at the base. A close relative of the above-mentioned species is E. nodosa, which on the other hand, produces long sterile scapes to push its flowering spikes further up. This is the prevailing characteristic in Elytraria species. Therefore an evolutionary trend can be easily traced out within the genus - the gradual sterilization of the lower part of the spikes to form the scapes. Simultaneously, the number of fertile stamens has also been reduced from 4 to 2 in the highly advanced species of Elytraria.

Finally, these two species (E. madagascariensis and E. nodosa) are of great phytogeographic importance. They are confined to Madagascar and also possess many primitive features in common, in the general context of the genus Elytraria. Thus it can be assumed that these two species are in fact 'relicts' of the past ancestral 'stock' of Elytraria, which aptly merit a Subgenus of their own.

AN ARTIFICIAL KEY TO SUBGENERA AND SPECIES OF

ELYTRARIA

1a. Fertile stamens 4; anthers subglobose (particularly in unopened flowers), connective produced upwards to form an apical appendage; capsule with 4-6 seeds in each loculus; Pericyclic fibres present apart from the 'acicular fibres' in the phloem tissue of the stem in t.s.; [species confined to Madagascar] .... Subgen. Tetrandra

- 2a. Inflorescence sessile with only a few sterile bracts below; bracts elliptic-lanceolate, puberulous; bracteoles minutely glandular hairy on the keel .... madagascariensis
- 2b. Inflorescence with long peduncle, covered by many sterile scale-leaves; bracts ovate, glabrous; bracteoles ciliate on the keel .... nodosa

1b. Fertile stamens 2; anthers elongated, no apical appendage of the connective present; capsule with 4-12 seeds in each loculus; pericyclic fibres absent but 'acicular fibres' present in t.s. of the stem; [species of Asia, Africa, and America]...... Subgen. Elytraria

- 3a. Anterior calyx lobe deeply bifurcated, nearly to the base; [species of Asia and Africa.]
  - 4a. Caulescent or acaulescent herbs; leaves alternate or subopposite; peduncle of the inflorescence densely covered by scale-leaves .... acaulis
  - 4b. Herbs with distinct stipe below; leaves verticillate; peduncle of the inflorescence with sparsely distributed scale-leaves.
    - 5a. Prostrate, much branched herbs with distinct nodes and internodes; leaves ± sessile .... maritima

5b. Erect, unbranched or less branched herbs, without distinct nodes and internodes; leaves subsessile or with distinct petiole .... marginata

3b. Anterior calyx lobe only bipartite at the apex; [species confined to America.]

6a. Plants with several stipitate rosettes arising from a central stem or the rosettes sometimes replaced by shoots with ± distinct internodes; at least the uppermost bracts of the inflorescence tridentate .... imbricata

6b. Plant with a single sessile or subsessile rosette; bracts never tridentate.

7a. Species with taproot system; leaves obovate; bracts rhombic-ovate with spiniform tips .... macrophylla

7b. Species with fibrous root system, roots sometimes fusiform; leaves ovate, elliptic-lanceolate or linear-oblong; bracts ovate or elliptic.

8a. Scape usually long, virgate with scale-leaves having long, aristate, recurved tips; bracts 3-6 mm wide .... caroliniensis

8b. Scape usually short with scale-leaves having acute or acuminate points; bracts always less than 3 mm wide.

9a. Bracts with distinct mid-vein protruding into a prominent aristate awn at the tip; always 3-veined.

10a. Leaf base cordate or subcordate; petiole with foliaceous wings at the distal end. Roots tuberous .... tuberosa

10b. Leaf base obtuse or attenuate, petiole simple.

11a. Leaves broadly elliptic, 1-5 cm broad; upper surface glabrous except at the costa and the veins; bracts broadly elliptic, up to 5 mm long .... klugii

11b. Leaves narrowly lanceolate, 5 mm to 2.5 cm broad; upper surface puberulent or rarely associated with sparse strigae; bracts narrowly elliptic, up to 9 mm long .... bromoides

9b. Bracts with indistinct mid-vein, either truncate or pointed at the apex - never provided with awns; veins obscure.

12a. Upper surface of the leaves papillose and pilose; bract truncate at apex; petiolar and foliar sclereids present .... shaferi

12b. Upper surface of the leaves either glabrous or subglabrous, rarely with the mid-veins being pilose; bract acute or acuminate at apex; petiolar and foliar sclereids absent.

13a. Plant proliferous in habit; leaves very thin and shining; inflorescence proliferous; bracts puberulent ...... prolifera

13b. Plant never proliferous in habit; leaves thick, non-shining; inflorescence never proliferous; bracts glabrous.

14a. Leaves entire or repand, rarely crenate, typically ovate; upper surface glabrous or puberulent, never rugose .... planifolia

14b. Leaves strongly crenate, oblong-linear or narrowly oblong-ovate; upper surface rugose with pilose mid-vein .... cubana

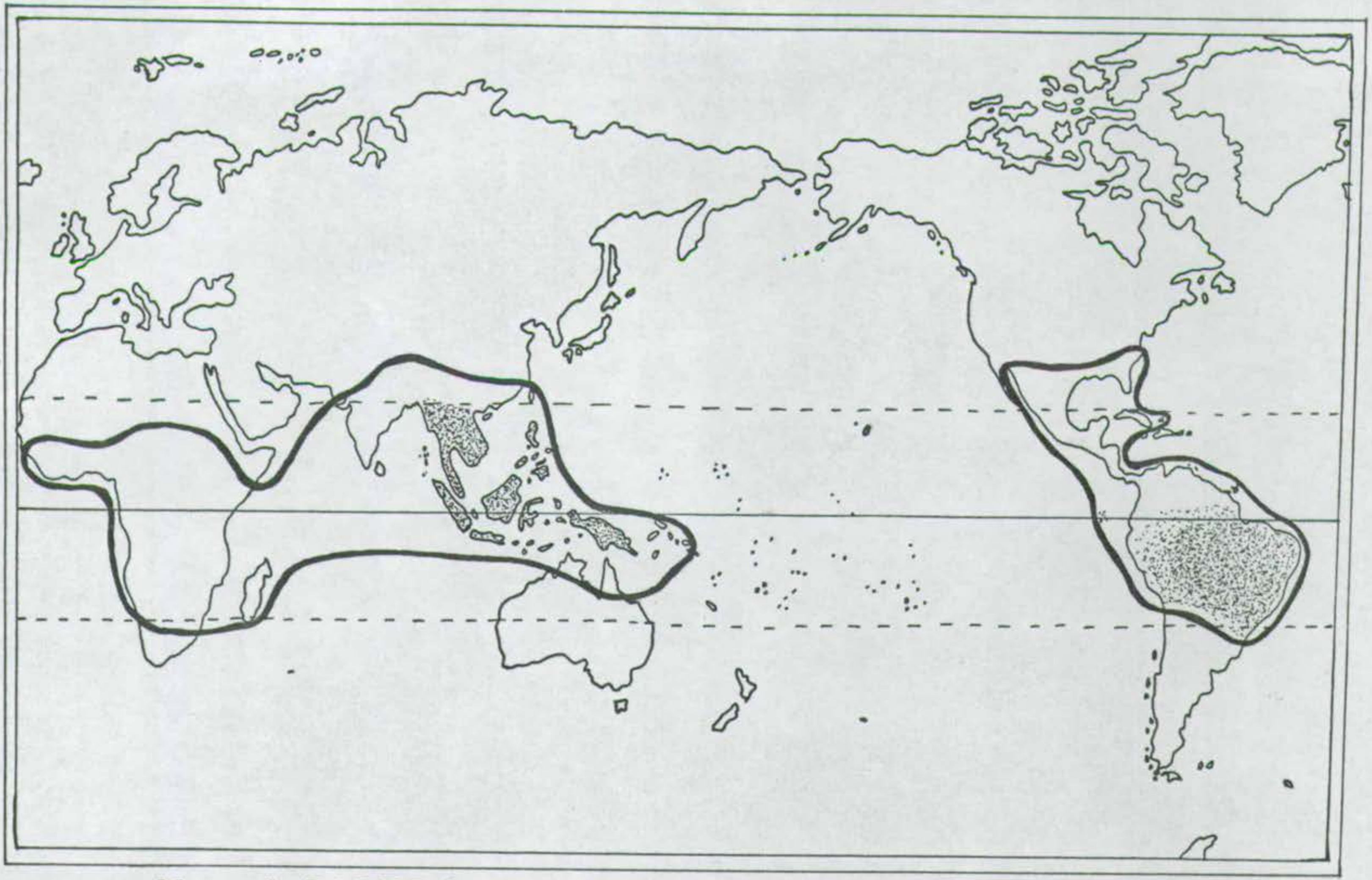
ECOLOGICAL HABITATS AND GEOGRAPHICAL DISTRIBUTION

Ecological Habitats: Most Nelsonioideae occur as weeds of forest floor in the tropics and subtropics. Apart from a few gregarious species like St. paludosa, St. capitata (both of them quickly multiply by vegetative reproduction) and the monospecific genus Nelsonia, many of them tend to grow in isolated patches of small populations, often containing a few individuals only. Whether it is due to ill adaptation, severe competition or a combination of both is difficult to ascertain at the present state of our knowledge.

Considerable habitat variation is encountered in E. imbricata, E. marginata and N. canescens. The genus Nelsonia in particular grows in any concievable habitat and is consequently adapted to extreme biotic pressure, fire and grazing effects. On the other hand, E. caroliniensis grows in the bottomlands, pine barrens, and is also found on calcareous gravel or wet rocky soil.

Nearly all the species of the Subgen. Tetrastichum, Sect. Tetrastichum grow as weeds of the rice fields and open pastures, while desert plants are only encountered in the genus Elytraria. For intangible physiological and structural reasons the Nelsonioideae seems to be adapted to diverse habitats like open pastures (dry or marshy), forest floors, and specialized habitat like the deserts.

Geographical Distribution: The distributional data together with its resulting patterns in any taxonomic group become more useful when considered from the evolutionary and ecological viewpoints of the whole family. The great taxonomic distinctness of the genera like Elytraria and Nelsonia may be due to an ancient evolution and diversification which could be traced back in the early geological times if fossil evidence of these groups were recovered. A noteworthy fact about the Nelsonioideae lies in their discontinuous (disjunct) distribution (Map 1. pp 108). Out of the seven genera recognized in the group, three are disjunct pantropical, while the fourth one shows discontinuous distribution in Africa and Madagascar.



Map.1. DISTRIBUTION OF THE NELSONIOIDEAE (With Two Centres Of Diversity). Shown Stippled.

The term disjunct (or discontinuous) distribution refers to the occurrence of a genus in two or more separate geographical areas which are often widely separated. The present distributional range of the Nelsonioideae clearly exhibits that its members are mainly confined to the tropics and subtropics of both worlds including the isolated islands in the belt (Map 1. pp. 108). Two distinct centres of abundance (or diversity) depending on the concentration of species are recognized: Brazil and Indo-Malayan territory. Representatives of the Nelsonioideae are fairly common in Africa, while the genus Nelsonia and Staurogyne (only St. spatulata complex) have extended their range to some extent in the northern parts of Australia.

In America one species of Elytraria (E. caroliniensis) can be found in certain parts of North America. The species of Staurogyne and Elytraria are ± common in Central America (Mexico), but they are mostly abundant in South America - particularly in Brazil.

On the other hand, greatest concentration of the Nelsonioideae is found in Indo-Malayan region (mainly Burma, Thailand, Cambodia) together with the Malayan Archipelago (mostly Borneo, Sumatra, Java, New Guinea and Philippines). Only a few species of Staurogyne are found in Africa which are mostly distributed in the south west tropical parts of the continent (of course, excepting Madagascar). Conversely, the genera like Elytraria (3 species) and Nelsonia are widely distributed throughout the continent (excepting the northern and southern extremities) and are also represented in Madagascar (by 2 endemic species of Elytraria and Nelsonia).

Small genera like Ophiorrhiziphyllon, Gynocraterium, Saintpauliopsis and Anisosepalum exhibit mostly a restricted distribution. Out of the first three monotypic genera Gynocraterium is endemic to British Guiana (South America), Ophiorrhiziphyllon is restricted to Burma, Thailand and South China, while

Saintpauliopsis is found in Gabon, Belgian Congo (Kivu and Lake Kivu), Burundi, and Madagascar. The genus Anisosepalum with its two species is entirely central African in distribution.

It is realized that any widely occurring genus in the southern Hemisphere will obviously exhibit disjunct distribution owing to its very nature of land mass distribution in this region. These anomalies (i.e. widely separated species groups in the same genus) in plant distribution commonly invite speculations in relation to present-day geography. But it is nevertheless one of the most difficult and unsettled questions of phylogeny as to whether these disjunct genera (or groups) are the outcome of polyphyletic or monophyletic origin.

It is of utmost taxonomic and phytogeographic importance that the American species of Staurogyne, although some of them look morphologically a bit different from the Asiatic ones, taxonomically belong to the same Sect. Staurogyne, and even in the same Subsect. Macrosepalae Brem. (cf. pp. 139-154). However, two distinct series can be recognized amongst the American species, viz. one having a distinctly bilabiate, minute corolla associated with herbaceous habit, and the other having a subactinomorphic, showy, large corolla accompanied by subshrubby habit. Probably these are the two separate lines of evolutionary diversification of the genus concerned, effected by adaptive radiation, prolonged isolation, and exploitation of the specialized pollinators. In this regard, however, it is noteworthy that both weakly bilabiate and showy large corollas are also met with in several unrelated species of the Asiatic Staurogyne.

Consequently, the present distribution of the biggest pantropical genus (Staurogyne) of the Nelsonioideae cannot be explained without undue speculations. Long distance dispersal is not possible for this type of transpacific disjunct distribution. Moreover, the plants in this group are not provided with any special mechanism for wide dispersal of the diaspores. Although long distance dispersal can be possible between the oceanic islands, by and large, it provides no satisfactory explanation to the continental disjunctions. A land bridge of any sort is geologically impossible, while the 'drift' theory ('sialic transport' or 'continental conveyance', Schopf. 1970) is also untenable in this particular example.

Increasing evidence from newly discovered fossils, convection currents in the earth's mantle, rock magnetism, mid-oceanic ridges, and sea-floor spreading have served to strengthen the theory of 'Continental drift' which is probably useful in the plausible explanation to the present-day distribution of Elytraria. The taxonomy of this genus indicates that the species either common to both Africa and Indo-Malaya or only restricted to Africa are in fact closely allied to one another. The American species (many in number), on the other hand, show affinities to those of Africa. As a result, the concept of a previous supercontinent (Gondwana land mass) is not against the distribution pattern and taxonomy of Elytraria.

The situation in Nelsonia is slightly different, but its distribution can also be envisaged in the light of 'drift' theory. The species complex (N. canescens, cf. pp. 189) of this genus poses a taxonomic problem itself. At present, with a broad concept of species in the genus it is visualized that South American specimens (described in the past as N. pohlii and N. bruelloides) are remarkably similar to those of the African specimens (described before in the name of N. bruelloides). This indicates that probably South America in the past geological times (possibly late Triassic!) was in free communication with the continent of Africa. Therefore, African N. canescens could extend its distributional range into the New World. Whether the American specimens are of recent introductions or of past continuous distribution in the land mass of Gondwana supercontinent is a debatable question. But weedy habit and prolific development of N. canescens in the Old World, particularly in Indo-Malayan and African territories, suggest that Nelsonia was probably at first palaeotropic and later on became pantropic in distribution. Its presence throughout the tropics and subtropics of both worlds (including Madagascar), but excepting the area in between Malayan Peninsula and New Guinea, rather supports the contention of Bentham (1869) [which was questioned by Bremekamp, 1955] who in fact intended to imply that it was introduced into the New World by saying "already abundant in several parts of tropical America."

The subject of plant geography is an adjunct to taxonomy, but greatly needs synthesis and correlation of other data obtained from various fields before making any generalization or conclusion. To unravel the past history, origin, and centres of diversification of any plant group for explaining its present-day distribution in the land masses of southern Hemisphere, data from the fields of ecogeography, palaeoclimatology, geology and palaeobotany are badly needed.

A BRIEF DISCUSSION ON THE EVOLUTIONARY TRENDS WITHIN NELSONIOIDEAE

It is often believed that ancestral conditions and trends of specialization (evolutionary trends) can be recognized in any living or fossil plant group when comprehensive systematic investigations are carried out. However, in absence of relevant data, particularly from palaeontology, ecogeography, cytogenetics and geological history, recognition of such evolutionary trends may prove to be mere speculation. Moreover, a remarkable prevalence of parallel and convergent evolution in habit, function, and structure quite elegantly reflects a relatively limited means of effective reproduction and 'adaptive radiation' which the angiosperms have in their disposal. Thus a single character can evolve independently at the same time or in different chronological times in different angiosperm taxa of various taxonomic affinities.

But it is a common belief that in any taxonomic group, characters of diverse nature - either primitive or advanced, usually tend to occur together (cf. Sporne, 1948). From the correlation values, features of a particular group can be assessed as either primitive or advanced, judged in the overall taxonomic information available. Thus from the extensive studies of the taxonomic structure of the Nelsonioideae a group of species (viz. subgen. Tetrastichum, sect. Tetrastichum) in the genus Staurogyne emerge to be the more primitive in having a maximum correlation of supposedly primitive characters. Depending on these characters which are stated below, the evolutionary trends (specializations) are traced out and discussed in various organs and tissues of the Nelsonioideae.

(1) Plants occurring in sunny, open situations.

(2) Presence of isolated pericylic fibres (apart from the usual 'acicular

fibres' in the phloem tissue) surrounding the vascular cylinder in t.s. of the stem.

(3) Occurrence of simple 'diacytic' stomata in the leaf-lamina which is devoid of any specialized mechanical element (e.g. sclerieds).

(4) Inflorescence an ill-defined terminal or axillary raceme, i.e. at least the lower flowers are solitary and axillary (subtended by ordinary leaves instead of bracts).

(5) Presence of bracts and bracteoles which are always herbaceous and distinct; bracteoles never joined with the calyx rim.

(6) Calyx with five unequal lobes, slightly united at the base, and the corolla being subactinomorphic with five dissimilar lobes.

(7) Stamens four, zygomorphic and didynamous with the posterior one being transformed into a staminode.

(8) Ovules about 60 or more, arranged in four alternate rows in each loculus of the ovary.

(9) Fruits typically capsular, dehiscing loculicidally into two woody recurved valves up to the base.

(10) Seeds are numerous, comparatively smaller in size, globose or subglobose in outline, provided with solid bars or hooks on the testa cells.

HABIT AND HABITAT

Studies of the Nelsonioideae from the point of distributional range and morpho-anatomy suggest that the group is basically herbaceous and mostly occur as forest undergrowth in shady, moist habitats. Apparantly primitive species are found in the genus Staurogyne, subgen. Tetrastichum. The species of the Sect. Tetrastichum (cf. Synopsis of Subgeneric, Sectional and Subsectional classification, pp. 126) usually occur in open sunny situations with a few occasional outliers in the forests. This in association with their prevalent perennial habit indicates that the Nelsonioideae might have originated at first in open habitats while adoption of sciadophily in forest habitats is a successful but secondary adaptation to the available ecological niches.

STEM

From the anatomical point of view the stem also provides evidence of evolutionary importance. A trend in reduction of the pericyclic fibres (constantly found in Sect. Tetrastichum) is clearly manifested in the related but comparatively more advanced sections, subgenera, and genera of the Nelsonioideae.

Further, the occurrence of 'acicular fibres' (Pl. 1) in the phloem tissue of the vascular cylinder reveals another interesting trend of evolutionary reduction. They are invariably present in all the genera of the group excepting Saintpauliopsis and Anisosepalum which seem to have lost the 'acicular fibres' during their evolutionary history.

However, it is also undeniable that in the specialization of this particular anatomical feature Nelsonia represents an offshoot having 'acicular fibres' in both the phloem and the pith cells of the vascular cylinder (Pl. 1. G).

LEAF

Leaf anatomy does not provide any clear-cut evolutionary specialization. But it is observed that 'double diacytic' stomata have evolved independently in E. shaferi, N. canescens (some populations), and several unrelated species of Staurogyne (Pl. 4. A, B), whereas 'simple diacytic' stomata are the rule in Nelsonioideae. It is however worth mentioning that the former type of stomata never occurs in the species of the Sect. Tetrastichum. Probably the variation is due to habitat preferences, but it is entirely uncertain to have definite conclusion at the present state of our knowledge.

Fig. 15. FLORAL DIAGRAMS & EVOLUTIONARY TRENDS IN INFLORESCENCES

(Explanation in the text: all figures diagrammatic)
A = Floral diagram of the Nelsonioideae; B = Floral diagram of the Rhinanthoideae, and C (1-11) = Evolutionary trends in the inflorescence of the Nelsonioideae [1-7 = *Staurogyne* (1, 2 = Sect. *Tetrastichum*; 3 = Sect. *Maschalanthus*; 4, 5 & 6 = Sect. *Zenkerina*, and 2, 4, 5, 6 & 7 = Sect. *Staurogyne*); 8, 9 = *Elytraria*; 8 = *Nelsonia*; 4 = *Ophiorrhiziphyllon*; 4, 5 & 6 = *Anisosepalum*; 6 = *Gynocraterium*, and 10, 11 = *Saintpauliopsis*].

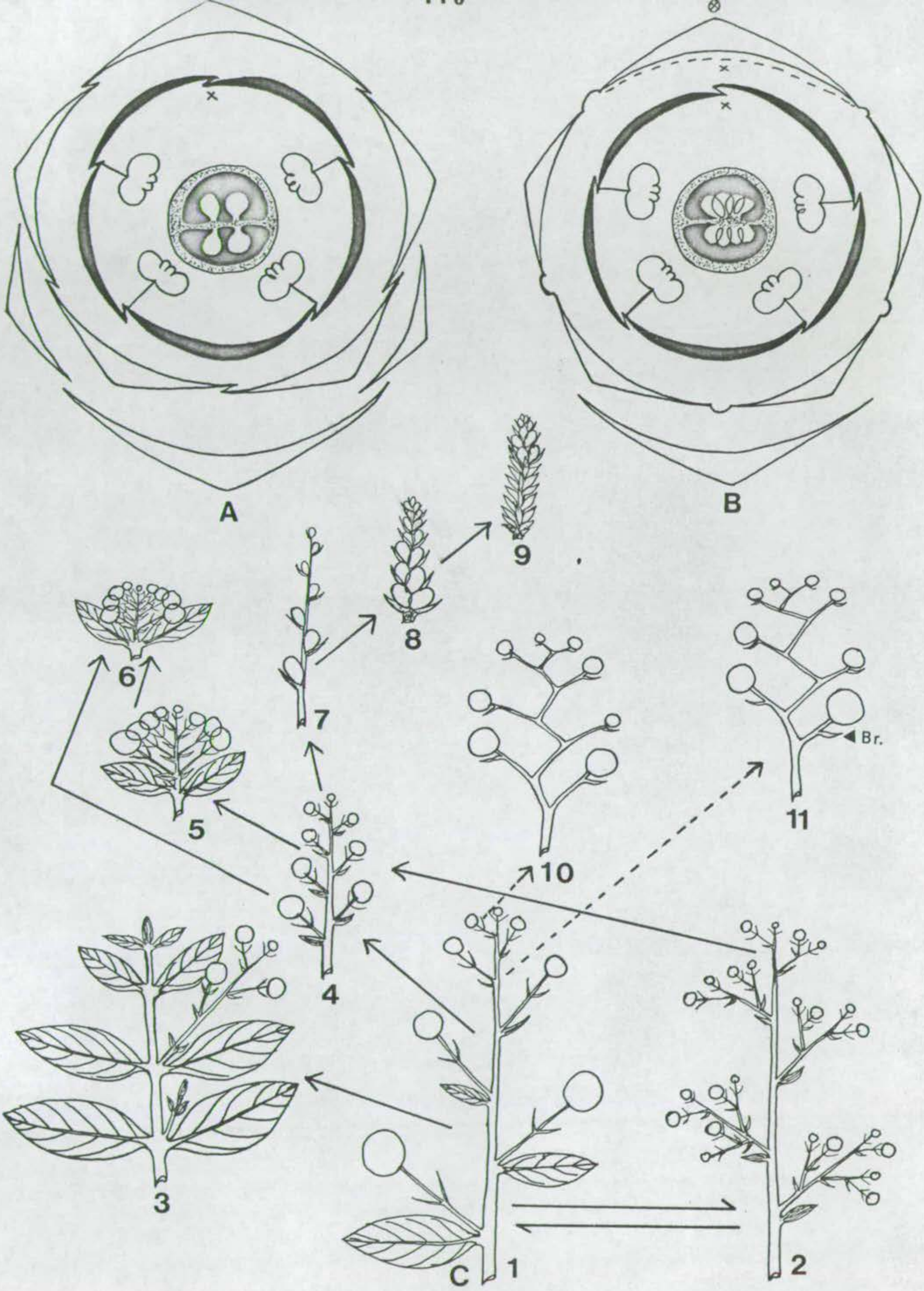


Fig. 15. FLORAL DIAGRAMS & EVOLUTIONARY TRENDS IN INFLORESCENCE.

Pl. 16. PRINCIPAL TYPES OF INFLORESCENCES IN STAUROGYNE

(Explanation in the text; arranged according to their probable evolutionary trends; all photographs taken from the herbarium sheets)

A = St. spatulata complex (Sect. Tetrastichum);
B = St. maclellandii (Sect. Tetrastichum);
C = St. paludosa (Sect. Zenkerina - inflorescence capitate); D = St. papuana (Sect. Staurogyne);
E = St. versteegii (Sect. Staurogyne - inflorescence capitate), and F = St. axillaris (Sect. Maschalanthus - note the impaired growth of the main shoot apex).

Pl.16. PRINCIPAL TYPES OF INFLORESCENCES IN STAUROGYNE.

Similarly, sclereids (mechanical elements) have evolved separately in several species of *Staurogyne*, and only in *E. shaferi* (Pl.8.C). It is often difficult to interpret as to how these anatomical characters evolve in a particular group where necessary correlation does not exist among other features of evolutionary advancement. Nevertheless, it is noteworthy that the occurrence of sclereids in the leaf lamina is always restricted to those species which are considered to be relatively more advanced in the context of the genus concerned. Consequently, it can be presumed that the outstanding specialization of the leaf tissue (i.e. sclereid formation) in Nelsonioideae is a secondary adaptation.

INFLORESCENCE

It is often difficult to interpret variations in the structure of the inflorescence as evolutionary specializations. But in the Nelsonioideae, one can safely conclude that its basic type of inflorescence is a raceme. While ill-defined racemose inflorescence is usually found in the primitive Sect. *Tetrastichum* of *Staurogyne*, condensed racemes, spikes, and panicles are also frequently met with in several species of unrelated taxa. These types of inflorescences are usually terminal or terminal and axillary. But in the Sect. *Maschalanthus* of the Subgen. *Staurogyne* they are entirely restricted to axillary branches - the main short apex remains always vegetative (Pl. 16.F).

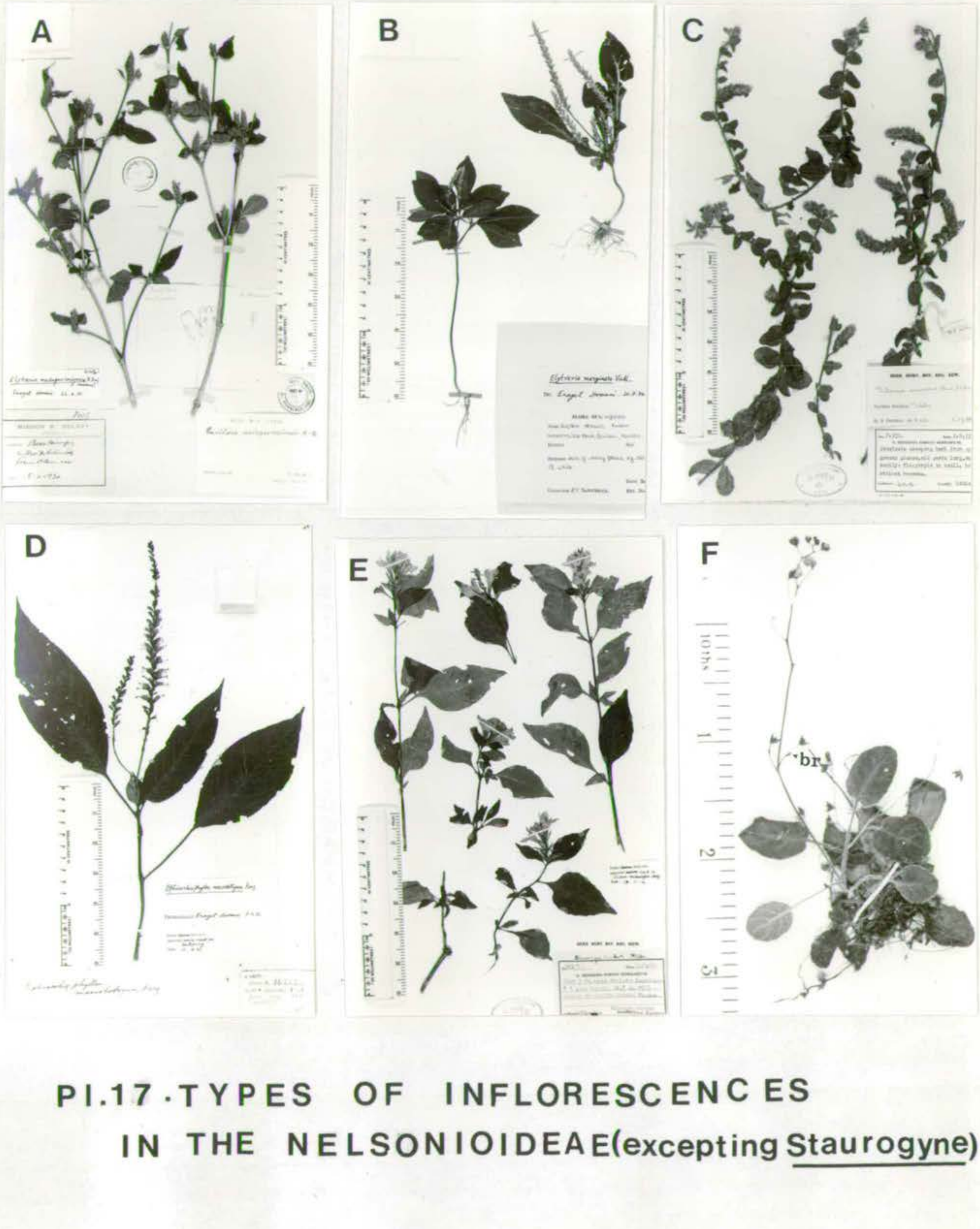
On the other hand, a constant process of sterilization in the lower part of the spike occurs in *Elytraria* (Subgen. *Tetrandra*) while *Saintpauliopsis* has attained quite independently a modified type of racemose inflorescence (Pl. 17.E), superficially resembling a 'scorpioid cyme' (after Lawrence, 1966).

By and large, the evolutionary specialization in the nature of the inflorescence in Nelsonioideae does not properly correlate with other specialized features of its various taxonomic entities. But however reticulate the

Pl. 17. TYPES OF INFLORESCENCES IN THE NELSONIOIDEAE (excepting *Staurogyne*)

(Explanation in the text; all photographs taken from the herbarium sheets).

A = *E. madagascariensis* (sessile spikes); B = *E. marginata* (note the sterile peduncle at the base of the spike); C = *H. canescens*; D = *O. macrobotryum*; E = *A. humbertii* (condensed spikes or racemes); F = *Saint. lebrunii* (mark the position of bracts which are on the pedicels or at the top of them - never on the inflorescence axis proper; flowering in a sigzag manner is also worth noticing; br = bract).



Pl.17 · TYPES OF INFLORESCENCES IN THE NELSONIOIDEAE(excepting Staurogyne).

variation is, it is nevertheless not too difficult to imagine the derivation of one type of inflorescence from another, taking the racemose type as a starting point in the Nelsonioideae (cf. Fig. 15.C).

BRACTS AND BRACTEOLES

Bracts and bracteoles are highly specialized in Elytraria where they are rigid and scale-like. A notable feature is the variation in the herbaceous type, especially in Staurogyne, e.g. leaf-like and large in Subsect. Macrochlamydeae, narrow and linear or lanceolate in Subsect. Macrosepalae, while minute and inconspicuous in Subsect. Microchlamydeae and also in Saintpauliopsis.

Bracteoles are universally present in the group except Nelsonia, which is unique in Nelsonioideae in having lost its bracteoles entirely. The bracteoles may be either near the base or at the top of the pedicel, but an interesting adaptation has taken place in the genera Saintpauliopsis and Anisosepalum where the two bracteoles are joined with the calyx rim to conceal the two minute lateral calyx lobes.

CALYX

Calyx characters show that the group fundamentally bears a 5-partite calyx with the lobes often united at the base. Evolutionary specialisation in the direction of elaboration has taken place in Sect. Staurogyne, Subsect. Macrosepalae, while reduction is manifested in Subsect. Macrochlamydeae and Microchlamydeae. An independent evolutionary line has been attained in one species, St. capitata of Sect. Zenkerina (Subgen. Tetrastichum of Staurogyne), where the calyx lobes are united up to the middle to form a distinct calyx tube (Fig. 3.E).

Sepals are either dissimilar, subsimilar or exactly similar, but a remarkable reduction restricted only to the lateral calyx lobes evidently arisen independently in two different genera, e.g. Saintpauliopsis and Anisosepalum which are not closely related in other features. Probably in these cases the protective function of the two lateral calyx lobes (necessary for the young ovary) has been switched over to the bigger bracteoles which are joined in the rim, resulting in more effective protection. The tendency probably attained its perfection in the subfamilies Thunbergioideae and Mendoncioideae, where the calyx is extremely reduced into a mere fimbriated rim and the bracteoles have become enormously enlarged (like spathaceous bracts) for effective protection of the bud and the ovary.

Conversely, reduction in the number of calyx lobes has taken place quite independently in two different genera, e.g. Nelsonia and Elytraria. Studies of the primitive species in Elytraria (Subgen. Tetrandra) illustrate the fact that the reduction in the number of calyx lobes from five to four has been achieved by the gradual fusion of the two anterior lobes. This fusion process which starts from below upwards, has attained its perfection in the advanced species of Elytraria and in particular, Nelsonia. Parallel developments have also occurred in the genera (e.g. Veronica) of the Scrophulariaceae.

COROLLA

Relevant data from the pollination biology are entirely lacking in the Nelsonioideae. Consequently the functional evolution of the corolla is often difficult to explain. Whatever may be the situation, some courses of corolla specialization are not too difficult to envisage taking Staurogyne Sect. Tetrastichum to be the most primitive. Thus from a subactinomorphic smaller corolla, one can find a weakly bilabiate and comparatively bigger corolla in the related Sect. Zenkerina (Fig.6a.B). This phenomenon is also prevalent in the various sections and subsections of Subgen. Staurogyne. The process of corolla elaboration has culminated in the strictly American Ser. C. of Subsect. Macrosepalae under Sect. Staurogyne. The development of a larger corolla with long, cylindrical or widely campanulate tube (Fig. 6a.D) is probably an adaptation to specialized insects or bird pollination.

On the other hand, distinctly bilabiate but smaller corolla has been independently established in another American Ser. *D.* of Subsect. *Macrosepalae*. This trend of corolla size reduction, accompanied by the occurrence of the bilabiate condition, is also pronounced in an Asiatic Ser. *E.* of the same Subsection and is probably culminated in *Ophiorrhisiphyllon* (Fig. £.Cc).

Smaller corolla, either bilabiate or subactinomorphic, can be found in *Nelsonia* and *Elytraria* which are relatively more advanced genera of the Nelsonioideae. But a unique variation of the corolla structure has been encountered in *Anisosepalum* (Fig. 5.F) where its distinctly bilabiate corolla bears a 'palate' on the lower lip (having two very narrow lateral lobes). This is probably an adaptation to specialized bee pollination which has evolved independently in various genera and tribes of the closely related families (e.g. Acanthaceae, Scrophulariaceae and Gesneriaceae).

STAMENS

A very clear-cut reductional trend in the number of stamens is recognizable in the Nelsonioideae. Starting from the basic number of four achieved through their ancestral history, sterilization has occurred in the two lateral stamens (the upper pair of the didynamous androecium). Genera like *Staurogyne*, *Gynocraterium*, *Saintpauliopsis*, *Anisosepalum* and the Subgen. *Tetrandra* of *Elytraria* all have four perfect stamens basically. Often these are associated with a small or well-developed staminode (representing the fifth posterior stamen) which reflects their ancestral pentamerous condition. From this, gradual elimination of the perfect stamens has been initiated at first in

St. diandra where 3 or 2 staminodes are frequent. The process shows its intermediate stages in most of the species in *Elytraria* and *Ophiorrhisiphyllon*, where remnants of only two staminodes are left. Its end point in the Nelsonioideae probably has been attained in *Nelsonia* where traces of staminodes are entirely eliminated (only two perfect stamens are left) [Fig. 5. a].

Stamens in the Nelsonioideae are mostly included, but a tendency towards exsertion from the mouth of the corolla tube has been established in the Ser. *E.* of Subsect. *Macrosepalae* under *Staurogyne*. Thus subexserted or slightly exserted stamens are frequently met with in the above-mentioned series, and also in some species of *Elytraria* (Fig.5.B^1). Possibly this is an adaptation for effective pollination which has achieved further perfection in *Ophiorrhisiphyllon* (Fig. 5.c) where the stamens are long-protruding.

In the Nelsonioideae anther lobes are predominantly subglobose or globose, whereas they are elongated on *Ophiorrhisiphyllon* and *Elytraria*. But the occurrence of subglobose anthers in Subgen *Tetrandra* of *Elytraria*, at least in the bud condition, clearly indicates that the elongated anthers can be obtained from the subglobose ones through evolutionary changes.

POLLEN GRAINS

No definite correlation in respect to evolutionary advancement of the taxa and the corresponding specialization in the pollen grains has been notcied in the Nelsonioideae. Basically the pollen grains are prolate and 'tricolpate'. These are shown by genera *Elytraria*, *Gynocraterium*, *Saintpauliopsis*, and a few species of *Staurogyne*. But by and large, there is a prevalent tendency in the group, quite pronounced in *Nelsonia*, *Anisosepalum*, *Ophiorrhisiphyllon*, and most of the species of *Staurogyne* i.e. the pollen grains tend to be 'tricolporate' in nature through the intermediate step, referred to be as 'tricolporoidate' (Pl. 9.). The trend has been perfected in several other related tribes of the family Acanthaceae, e.g. Andrographideae.

STIGMA

A trifurcate and cruciate stigma seems to be the most primitive type in the Nelsonioideae, as it is mostly found in the primitive sections of Staurogyne. From this type possibly the bifurcate unequal type has evolved which is largely prevalent in the group. The lamellate stigma found in St. subcordata (Fig. 7.I[1]) and the crateriform type characteristic of Gynocraterium (Fig. 7.O) seem to be two independent lines of specialization.

Corroborative evidence indicates that simple bilobed, capitate or flattened club-shaped stigmas (with conspicuously unequal lobes: lower lobe being always imperceptible) are relatively more advanced than the previous types, as they are prevalent in advanced genera like Ophiorrhiziphyllon (Fig.7.M), Nelsonia (Fig.7.Q), and Elytraria (Fig. 7.R).

OVARY AND OVULES

Studies in the number of ovules per ovary, arranged in a specific number of alternate rows in each loculus, reveals an interesting trend of reduction both in the number of ovules and also in the number of rows per cell. In the Subgen. Staurogyne ovules are only 12-40, always arranged in two alternate rows in each loculus of the ovary - possibly achieved through evolutionary reduction in one step from the species containing four rows of ovules (Subgen. Tetrastichum). This reductional trend has been particularly prominent in the genera like Gynocraterium and Anisosepalum, where one can find only 6-8 ovules per loculus of the ovary.

The development of typical 'retinacula' supporting the seeds of other highly evolved Acanthaceae is not so clear-cut in the Nelsonioideae. But 'papilliform retinacula' occasionally arise in the species of Staurogyne (Fig. 8.D) and Elytraria, but it is a noteworthy fact that the evolution of the 'retinacula', by some means or other, is closely tied up with the lesser number of ovules in the ovary followed by the consequential enlargement of the seed size. This is fully apparent in Anisosepalum, where the seeds are supported by well-developed but 'unindurated (non-woody) retinacula', but of course not comparable to the hardened, hook-like structures of the highly advanced Acanthaceae.

FRUITS

The trends of specialization in the fruits of Nelsonioideae are rather complex. A clear-cut correlation in respect to the evolution of taxa and the corresponding increase in the fruit size is difficult to trace out. However, a general trend of gradual sterilization of the upper part of the fruit is largely evident in the species of Staurogyne, Nelsonia, Elytraria and Anisosepalum (Fig. 8.C, D, P. Q. & R).

Fundamentally, the fruit is a loculicidal capsule, dehiscing into two woody, recurved valves with the placenta being divided up to the base. But an interesting variation is shown by the Sect. Zenkerina (Subgen. Tetrastichum of Staurogyne) where the fruits are tardily or irregularly dehiscent. As the species of this section possess relatively advanced type of inflorescences (cf."Synopsis of Subgeneric, Sectional and Subsectional classification" pp. 130-160) and bigger seeds, I presume that the phenomenon of capsular indehiscence is a secondary adaptation in the group. Similar examples can be encountered in the Leguminosae, subfamily Papilionoideae (cf. Fahn & Zohary, 1955) and also in the Cruciferae (cf. Zohary, 1948).

SEEDS

The seeds are usually small, globose, subglobose or provided with many faces, rarely obovate. A general trend of increase in size coupled with the exploitation of the sciadophilous forest habitats is evident in the species of Staurogyne. Consequently one can come across numerous small seeds in the primitive Sect. Tetrastichum, most of which are the weeds of open, sunny habitats. The trend of seed size elaboration has been correspondingly correlated with the decrease in the number of seeds per loculus of the ovary, and ultimately has ended up in Anisosepalum where the seeds are much bigger and also slightly flattened (compressed) at the ventral side (Fig. 9.E).

The testa of the seeds in Nelsonioideae bears solid, hooked processes (Fig.9.a,b) which through the evolutionary course has been reduced in Elytraria (Fig. 9.g) and completely lost in Anisosepalum (Fig. 9.E).

Nearly all these above-mentioned trends of specialization can be explained on the basis of three principal phenomena viz. (1) reduction, (2) fusion, and (3) change in symmetry (Stebbins, 1950). All of them have a profound effect on the ontogeny of the organism and can be operative at any stage of life or level of time. They can work either in conjunction (two or all at the same time) or in isolation, but their effects become outstanding, especially when the processes are operative at the early ontogeny of the organism.

It is believed that the rate as well as the direction of evolution are largely variable in various taxonomic entities and the recognition of a specific direction of any evolutionary trend, in most cases depends largely on intuitive interpretations especially when fossil evidence is entirely lacking. Therefore, the courses (directions) of evolutionary specializations suggested here in the Nelsonioideae, should be evaluated with due caution.

KEY TO SUBGENERA, SECTIONS, SUBSECTIONS, AND SERIES OF *STAUROGYNE*

(Note: Key to species appears at the page number shown against each taxon)

1a. Ovules about 60 or more, arranged in 4 rows in each loculus of the ovary .... Subgen. *Tetrastichum*

2a. Inflorescence an ill-defined raceme or subcapitate (at least the lower flowers subtended by ordinary leaves), rarely paniculate; capsule dehiscing into two woody recurved valves; xylem cylinder always surrounded by isolated pericyclic fibres apart from the 'acicular fibres' in the phloem tissue .... Sect. I. *Tetrastichum*, pp. 131

2b. Inflorescence always well-defined (all flowers subtended by bracts), racemose or subcapitate; capsule tardily dehiscent or indehiscent; xylem cylinder without pericyclic fibres but with a few or numerous 'acicular fibres' in the phloem tissue .... Sect. II *Zenkerina*, pp. 137

1b. Ovules about 12-40, arranged in 2 rows in each loculus of the ovary .... Subgen. *Staurogyne*

Inflorescence usually well-developed, rarely in some species the lower flowers subtended by leaf-like bracts or leaves, either terminal or axillary, racemose, subcapitate, spicate or paniculate. Xylem cylinder never covered by pericyclic fibres, but usually with many 'acicular fibres' in the phloem tissue.

3a. At least some of the inflorescences borne on the main shoot apex or on the branch apex, i.e. the main shoot apex always terminated by an inflorescence .... Sect. III. *Staurogyne*

4a. Posterior calyx lobe usually more than or rarely equal to half as long as the connate part of the corolla

.... Subsect. 1. *Macrosepalae*

5a. Stamens and the stigma slightly exserted; stigma slightly bifurcate, lobes equal .... Ser. E, pp. 153

5b. Stamens and the stigma usually included, rarely subexserted; stigma usually trifurcate and cruciate - when bifurcate, lobes unequal; lower lobe usually much thickened and knob-like.

6a. Corolla distinctly bilabiate, usually less than 1 cm, long, rarely attaining up to 1 cm .... Ser. D, pp. 150

6b. Corolla subactinomorphic, usually more than 1 cm. long, very rarely up to 1 cm. or slightly less.

7a. Plants subshrubby in habit, tall in stature; posterior calyx lobe always much broader than the rest .... Ser. C, pp. 149

7b. Plants herbaceous in habit, sometimes woody at the base; posterior calyx lobe either equal to or slightly broader than the rest.

8a. Lateral calyx lobes always much narrower and usually shorter than the other ones

.... Ser. A. (Heterosepalae), pp. 140

8b. Calyx lobes all of the same kind, subsimilar or exactly similar in size, all 3-veined ... Ser. B. (Isosepalae), pp. 147

4b. Posterior calyx lobe always less than half as long as the connate part of the corolla.

9a. Bract several times as long as the calyx lobes or at least longer than the posterior and lateral calyx lobes

.... Subsect. 2. Macrochlamydeae, pp. 154

9b. Bract as long as or shorter than the calyx lobes

.... Subsect. 3. Microchlamydeae, pp. 156

3b. All inflorescences borne on the apices of axillary branches ('brachyblasts'), subtended by one, two or 0 pairs of reduced leaves, i.e. the main shoot apex always provided with a vegetative bud
.... Sect. IV. <u>Maschalanthus</u>, pp. 159

SYNOPSIS OF SUBGENERIC, SECTIONAL, SUBSECTIONAL AND SERIES CLASSIFICATION IN STAUROGYNE

Subgen. TETRASTICHUM Brem. in Reinwardtia 3: 166-167 (1955).

Branched or unbranched, erect or prostrate, decumbent herbs, mostly perennials, rarely annuals. Stem herbaceous, rarely woody at the base, sometimes rooting at the nodes. Upper leaves usually subopposite or alternate, rarely opposite, mostly provided with short petioles, sometimes subsessile. Inflorescence in ill-defined racemes (at least the lower flowers subtended by ordinary leaves) or in well-defined racemes (all flowers subtended by bracts), sometimes condensed and subcapitate, very rarely paniculate. Bracts usually narrow, sometimes leaf-like, always smaller or equal to the calyx lobes. Bracteoles narrow, linear or linear-lanceolate, usually shorter than the calyx lobes. Corolla subactinomorphic or weakly bilabiate. Stamens 4, always included, filaments hairy. Staminodes 1 or rarely 0. Stigma trifurcate and cruciate or deeply bifurcate with one lobe always smaller and thickened, rarely the lobes are lamellate. Ovules about 60 or more, arranged in 4 alternate rows in each loculus of the ovary. Capsule either dehiscing loculicidally into two woody recurved valves or tardily dehiscent, rarely irregularly dehiscent or indehiscent, elongate-ovate, oblong-acuminate, elliptic or narrowly ellipsoid. Type: St. spatulata (Bl.) Kds.

18 species; palaeotropic in distribution, found in open sunny habitats, often as weeds of rice fields, and sometimes as forest undergrowth which are sciadophilous.

Sect. I. Tetrastichum E. Hossian, sect. nov.; affinis Sectioni Zenkerinae sed foliis sursum suboppositis vel alternis leviter petiolatis vel subsessilibus, floribus racemos dispositis vel aliquando condensatis ex parte vel omnibus a foliis suffultis, inflorescentia terminali vel terminali et axillari raro paniculiformi et capsulis semper elongato-ovatis in valvas duas lignosas recurvatas loculicide dehiscentibus facile differt.

Herbae erectae vel decumbentes annuae vel perennes; plantae in locis apricis habitantes. Folia suprema subopposita vel alterna leviter petiolata vel subsessilia. Inflorescentiae racemosae raro paniculiformes vel aliquando floribus condensatis; flores ex parte vel omnes a foliis suffulti. Corolla plerumque minus 1 cm. longa, raro usque ad 1.2 cm. longa, subactinomorpha. Bases antherarum micronulati vel appendiculati, raro obtusi. Stigma trifurcatum et cruciatum, raro bifurcatum lobis inaequalibus instructum. Capsula semper elongato-ovata in valvas duas lignosas recurvatas usque ad basin loculicide dehiscens.

Stem anatomy: Isolated pericyclic fibres always present surrounding the vascular cylinder in t.s. of the stem (Fig.13.E) in addition to the 'acicular fibres' in the phloem tissue.

Typus sectionis: St. spatulata (Bl.) Kds.

13 species; distributed mainly in Asia - the species complex recognized extends up to Northern Australia.

Key to species: (Note: Species with double underlines in all the keys provided in the text refer to those which are not seen by the author).

1a. Inflorescence a well-defined panicle .... maclellandii

1b. Inflorescence an ill-defined (lower flowers subtended by ordinary leaves) raceme, sometimes condensed into spicate or subcapitate structure at the apex.

  2a. Anther bases without perceptible appendage (i.e. the bases are obtuse).

    3a. Plants slender and unbranched; leaves ovate-oblong ...... perpusilla

    3b. Plants stout and branched; leaves lanceolate or lanceolate-oblong .... polybotrya

2b. Anther bases mucronulate or shortly tailed, never obtuse.

4a. Trailing or prostrate herbs; all leaves (excepting those which subtend the flowers) opposite.

5a. Corolla 1.2-1.4 cm long .... *glutinosa*

5b. Corolla never more than 8 mm long .... *spatulata* complex

4b. Erect or slightly decumbent (at the base) herbs; upper leaves alternate or subalternate

6a. Stem cylindrical, usually very thickened and woody at the base; leaves narrowly linear-lanceolate and elongate .... *cambodiana*

6b. Stem angular, usually herbaceous and thin, rarely subherbaceous, leaves lanceolate, lanceolate-oblong or spathulate.

7a. Corolla 1 cm or more in length .... *neesii*

7b. Corolla often less than 8 mm long, rarely attaining up to 9 mm in length .... *spatulata* complex

TAXONOMIC NOTES ON *St. spatulata* (Bl.) Kds. COMPLEX

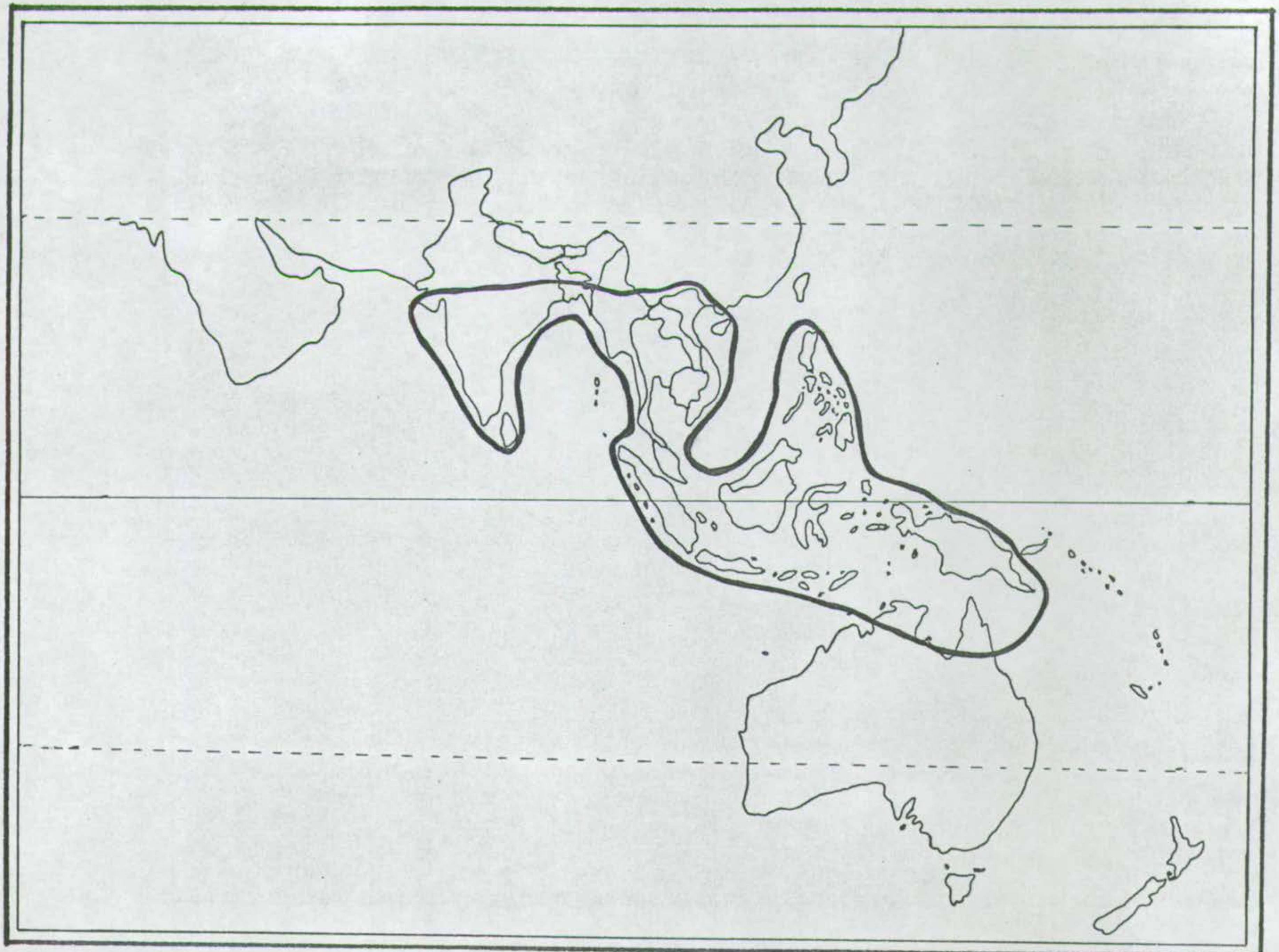
The species *St. glauca* (Nees) O. Kuntze was first described by Nees as *Ebermaiera glauca* [In: Hook., Comp. Bot. Mag. 2: 310 (1836)] and the necessary transfer was made by Kuntze [Rev. Gen. Pl. 1: 497 (1891)]. Clarke [Fl. Brit. Ind. 4: 396 (1884)] reduced the species *St. spatulata* (Bl.) Kds. to a variety of *St. glauca* which is according to our present nomenclatural rules a mistake. As the earliest epithet in this alliance is *spatulata* [*Adenosma spatulatum* Bl., Bijdr. Fl. Ned. Ind., 757 (1826)], the valid name should be *St. spatulata* (Bl.) Kds., Exkursionsfl. Java 3: 211 (1912).

In recent years many new species have been described in this alliance which are in most part based on a few specimens differing solely on their habit or external facies. Of course it is a fact that apart from St. maclellandii all the species of the Sect. Tetrastichum are very closely related to one another. They differ mostly in minor characters of flowers, inflorescences, leaves and habit. Usually they are found in rice fields and open pastures, rarely as forest undergrowths. As a result, most of these variations exhibited by these species seem to be rather plastic in nature and probably many of these minor variations are controlled by their habitats.

The present critical investigation into all the available sheets preserved in the British herbaria has revealed that many of these allegedly distinct species are in fact minor forms or varieties of a widely distributed weedy species (St. spatulata). Consequently I have reduced St. siamensis and St. flexicaulis to its synonymy. Of course the previous species had already been referred to by Benoist to be a minor form of this complex /cf. Bull. Soc. Bot. Paris 60: 267 (1913)_7 who preferred to keep it as a variety.

In my present account I have included St. rivularis, St. polycaulis, St. leptocaulis, St. latibracteata, St. viscida, and St. candelabrum in the complex but their subsequent nomenclatural changes are not attempted owing to lack of enough materials and especially the type specimens of the newly described species in the complex. Apparently the descriptions of these species do not differ considerably from the range of characters expressed by the complex.

The leaves may be either petiolate or subsessile, opposite at the base, alternate above or at least alternate at the flower-bearing apices. The lamina is either entire, repand or serrulate, glabrous, subglabrous or prominently hairy on both surfaces, rarely papillose. The shape and size also vary widely: they may be either lanceolate, lanceolate-spathulate or spathulate - sometimes two or more types occurring in the same plant. Bracts, bracteoles and calyx lobes are likewise variable in their shape and size which are constantly



Map.2. DISTRIBUTION OF Staurogyne spatulata(Bl.)Kds. COMPLEX.

hirtellous with glandular and eglandular hairs. Corolla size is not a suitable guide for recognizing a taxonomic entity as it varies enormously in the specimens of the same locality. Anther bases are always mucronulate or distinctly appendiculate. This is against the contention of Bremekamp (1955c) who could not recognize these minute appendages in St. viscida and others. He even doubted the validity of Wight's figure (in Ic. t. 1488) showing anther appendages in St. glauca (= spatulata).

The ovary may be either sparsely hairy at the apex or entirely glabrous, but there is no clear-cut break in this character depending on geographical distribution of the specimens [Bremekamp (1955c) pointed out that the Australian specimens of this complex vary from the rest of the Asiatic ones in their hairy ovary and capsules].

Distributional map (Map 2. pp. 134) shows that the complex is widely distributed in Indo-Malayan territory and has extended its range up to certain parts of northern Australia. The Australian specimens, although they do not vary taxonomically, yet resemble those of the Philippine islands (particularly St. rivularis) more closely than the specimens of Indo-Malaya. In this regard it is also noteworthy that many specimens from Madras and Ceylon look very similar to those of Australia, New Guinea, and Philippines.

Clarke at first regarded the Australian specimens to be a distinct species and thus gave a name (St. australica) to a herbarium sheet at Kew. But Bentham in his "Flora Australiensis" 4: 544 (1869) recognised them to be St. glauca which is widespread in Indo-Malaya. The present investigation supports Bentham's contention in so far as adopting a broader species concept until further information are available.

A better course seems to be to recognise this complex as a single species (St. spatulata) having two distinct subspecies based on geographical criteria.

The specimens occurring in New Guinea, Philippines, and Australia always possess well developed bracteoles which are constantly bigger than the calyx lobes. But on the other hand, the rest of the Indo-Malayan specimens usually possess narrower bracteoles; either all of them or at least the upper ones are always smaller or at best equal to the calyx lobes. Each of these subspecies may then be subdivided to form two or more varities depending on minor characters.

Future comprehensive studies incorporating morphological data, ecological observations, cultural and cytogenetic experiments might help in solving this critical and interesting taxonomic problem. The complex really needs further extensive investigation.

Sect. II. Zenkerina (Engl.) E. Hossain, stat. et comb. nov.

Syn: Zenkerina Engl., Bot. Jhrb. 23: 497 (1897).

Neozenkerina Mildbr. in Notizbl. Bot. Gart. Berlin 7: 491 (1921).

Staurogynopsis Mangenot & Ake Assi in Bull. Jard. Bot. Brux. 29: 27 (1959).

Valde affinis sectioni Tetrastico sed plantis manifeste perennibus, raro annuis, prostratis decumbentibus vel ascendentibus, inflorescentia floribus omnibus a bracteis suffultis terminali et axillari, racemis subsessilibus vel subcapitatis condensatis et capsulis oblongo-acuminatis ellipticis vel anguste ellipsoideis, alteruter tarde vel irregulariter dehiscentibus, raro indehiscentibus ab ea facile distinguenda.

Plantae prostratae, decumbentes vel ascendentes, perennes, raro annuae; sciadophilae. Folia omnia opposita, folia suprema interdum subsessilia, vulgo petiolis brevibus suffulta. Inflorescentia semper floribus omnibus a bracteis suffultis, terminalis vel terminalis et axillaris racemis subsessilibus vel subcapitatis condensatis. Corolla saepissime grandis, longitudine usque ad 2 cm vel magis semper ultra 1 cm longa attingens, leviter bilabiata vel subactinomorpha. Bases antherarum semper obtusae. Stigma trifurcatum et cruciatum vel profunde bifurcatum lobis lamellatis instructis. Capsula oblongo-acuminata, elliptica vel anguste ellipsoidea, alteruter tarde vel irregulariter dehiscens raro indehiscens.

Stem anatomy: Vascular cylinder always without pericyclic fibres but with 'acicular fibres' in the pholem.

Typus sectionis: St. kamerunensis (Engl.) R. Ben.

5 species; distributed in Africa and Indo-China.

Key to species:

1a. Corolla 3-3.8 cm long; stigma deeply bifurcate, lobes lamellate .... subcordata

1b. Corolla always less than 2 cm long; stigma usually trifurcate and cruciate, rarely bifurcate with unequal lobes.

  2a. Inflorescence a subcapitate and condensed raceme; capsule oblong-acuminate, never more than 4-5 mm long.

    3a. Calyx lobes joined up to the middle to form a tube .... capitata

    3b. Calyx lobes slightly united at the base, 5 partite .... paludosa

  2b. Inflorescence an elongate raceme; capsule elliptic or narrowly ellipsoid, usually 7-12 mm long.

    4a. Calyx lobes puberulent or sparsely pubescent, 1.6-2.2 cm long; capsule narrowly ellipsoid, never less than 10 mm long .... dolichocalyx

    4b. Calyx lobes hirtellous with glandular and eglandular hairs, never more than 1.2 cm long; capsule elliptic, never more than 7 mm long .... kamerunensis

Subgen. STAUROGYNE

Annual or perennial herb, occasionally subshrubby and woody at the base; plants sciadophilous and usually found as forest undergrowth. Leaves all opposite, sometimes rosulate or subrosulate, rarely the upper leaves being subopposite. Inflorescence in axillary and terminal or only terminal racemes, spikes or panicles, usually well defined (all flowers subtended by bracts), sometimes the racemes are entirely restricted to the axillary branches and thus keep the terminal (main shoot) apex vegetative althroughout. Bracts and bracteoles various, occasionally equal to, sometimes much bigger or smaller than the calyx lobes. Calyx lobes either markedly dissimilar or subsimilar, often strikingly similar in shape and size, usually bigger, occasionally smaller or rarely equal to half as long as the connate part of the corolla. Corolla subactinomorphic or distinctly bilabiate, length various, small indistinct or prominent and showy; tube cylindrical or infundibuliform. Stamens mostly 4, rarely 2, often included, sometimes slightly exserted; anther bases usually obtuse, rarely apiculate or with short tails. Staminodes often 1, rarely 0, 2 or 3. Stigma trifurcate and cruciate or deeply bifurcate with lower lobe always thickened or lobed, occasionally the lobes are short and similar, usually included, rarely subexserted. Ovules about 12-40, arranged in 2 alternate rows in each loculus of the ovary; retinacula papilliform or 0. Capsule elongate-ovate or ovate-conical, always with hard mucronulate tip, dehiscing loculicidally into two woody, recurved valves.

Stem anatomy: Pericyclic fibres never present surrounding the vascular cylinder in t.s. of the stem, but 'acicular fibres' always present in the phloem.

Type: St. argentea Wall.

Numerous species; pantropical in distribution.

Sect. III. Staurogyne

Inflorescence in axillary and terminal or only in terminal racemes or condensed into subcapitate structures, usually the main shoot apex terminating into a flowering branch at maturity, rarely in a few abnormal species of the subsect. Macrosepalae, ser. C. of America seem to have retained a reduced vegetative apex, occasionally provided with a few axillary, solitary flowers. Bracts and bracteoles various. Calyx lobes largely dissimilar, often subsimilar or similar in shape and size.

Type: St. argentea Wall.

Numerous species; distributed in tropical Asia and America, only one in Africa.

Subsect. 1. Macrosepalae Brem. in Reinwardtia 3: 176-177 (1955).

Stem monopodial or sympodial. Inflorescence various, peduncles usually shorter. Calyx lobes markedly unequal; laterals always much narrower and shorter than others or all equal in size and shape, at least the posterior lobe being always bigger than or equal to half as long as the connate part of the corolla. Bracts and bracteoles narrow, usually equal, subequal or slightly smaller than the calyx lobes. Stamens and stigmas usually included, sometimes subexserted or slightly exserted. Stigma lobes often trifurcate and cruciate, sometimes deeply bifurcate with unequal lobes, occasionally shortly bilobed with the lobes being equal or subequal.

Type: St. argentea Wall.

Numerous species; pantropical in distribution (only one in Africa).

Ser. A. /Heterosepalae Brem. in Reinwardtia 3: 181 (1951)_7.

Plants herbaceous, sometimes slightly woody at the base. Inflorescence in axillary and terminal or only in terminal spikes, racemes or condensed into subcapitate structures. Bracts and bracteoles narrow, either equal to or slightly smaller than the calyx lobes. Calyx lobes markedly dissimilar; laterals always much narrower and shorter than the rest, posterior lobe either equal to or slightly broader than the anterior ones. Stamens and stigma always included. Stigma trifurcate and cruciate, when deeply bifurcate - lobes unequal, lower lobe thickened or lobed.

Type: St. argentea Wall.

Species about 46, distributed in Indo-Malaya and Africa.

Key to species:

1a. Staminal filaments arise from $\frac{3}{4}$ portion of the corolla tube; calyx lobes (excepting the lateral two) spathulate........................ chapaensis

1b. Staminal filaments arise from $\frac{1}{3}$ portion of the corolla tube (i.e. slightly above thebase of the tube); calyx lobes linear, linear-lanceolate, lanceolate or filiform, rarely subspathulate.

2a. Calyx lobes filiform at least at the apices or sharply ended into aristate points.

3a. Inflorescence ± a lax raceme; flowers distinctly pedicellate.

4a. Lamina glabrous above; bracts, bracteoles and calyx lobes all filiform .... kingiana

4b. Lamina papillose above; bracts, bracteoles and calyx lobes lanceolate at the base, narrowed above into subulate (aristate) or filiform points .... longifolia

3b. Inflorescence a condensed spike, sometimes branched at the base; flowers always sessile.

5a. Leaves 6-8 cm broad; corolla about 2 cm long; stigma bifurcate and hollow; foliar sclereids present .... aristata

5b. Leaves never more than 4.5 cm broad; corolla up to 1.8 cm long; stigma trifurcate and cruciate; foliar sclereids absent.

6a. Lamina glabrous or sometimes puberulous above; awns of the calyx lobes about 5-6 mm long; capsule puberulous .... argentea

6b. Lamina sparsely strigulose or densely pilose above; calyx lobes shortly aristate (awns never more than 2 mm long); capsule glabrous.

7a. Herbs decumbent at the base; posterior calyx lobe up to 12.5 mm long, laterals 8-9 mm long .... setigera

7b. Herbs erect; posterior calyx lobes up to 8 mm long, laterals up to 3.5 mm long .... condensata

2b. Calyx lobes linear, linear-lanceolate or lanceolate, never filiform nor aristate at the apex, rarely subspathulate.

8a. Herbs rosulate or subrosulate with practically no stem or very short stem.

9a. Bracts 2-4 mm broad, joined with the pedicel up to some distance; calyx lobes pilose with very long, white and septate hairs .... brevicaulis

9b. Bracts always narrow, never more than 0.8 mm broad; usually free from the pedicel, rarely united at the base only; calyx lobes puberulous or pubescent.

10a. Inflorescence paniculate or laxly branched.

11a. Lamina glabrous above; calyx lobes 13-14 mm long; corolla 17-18 mm long .... amoena

11b. Lamina densely pubescent above; calyx lobes 5-6 mm long; corolla up to 8 mm long .... obtusa

10b. Inflorescence racemose, usually unbranched, rarely with 1-2 branches at the base.

12a. Lamina puberulous and papillose or puberulous and sparsely pilose on the veins above; flowers 8-9 mm long.

13a. Inflorescence axis densely white pubescent; calyx lobes 8-10 mm long, ciliate .... hainanensis

13b. Inflorescence axis puberulous; calyx lobes 5-6 mm long, puberulo-pubescent .... concinnula

12b. Lamina densely pubescent or tomentose above; flowers 12-15 mm long.

14a. Leaves oblanceolate, 5-9 cm long, 1.8-3.5 cm broad, base contracted; peduncle never less than 2.5 cm long .... rosulata

14b. Leaves obovate-oblong, up to 17.5 cm long, 10 cm broad; peduncle up to 6 mm long .... macrophylla

8b. Tall or dwarf herbs, sometimes decumbent at the base, always provided with prominent stems.

15a. Inflorescence paniculate or laxly branched raceme.

16a. Lamina glabrous or subglabrous above; posterior calyx lobe 6-7.5 mm long.

17a. Calyx lobes puberulous or subglabrous; corolla up to 8 mm long .... paniculata

17b. Calyx lobes densely hirtellous with glandular and eglandular hairs; corolla up to 14 mm long .... lasiobotrys

16b. Lamina pubescent or strewn with sparsely distributed septate hairs above; posterior calyx lobe 10-12 mm long.

18a. Leaves lanceolate or elliptic-lanceolate; corolla 2.8-3 cm long, dark purple .... atropurpurea

18b. Leaves oblong, broadly or narrowly elliptic; corolla never more than 2.1 cm long, either white or yellow.

19a. Calyx lobes linear, hirtellous with glistening white hairs; corolla up to 1.6 cm long, subglabrous outside .... simonsii

19b. Calyx lobes linear-lanceolate, densely pubescent with glandular and eglandular hairs; corolla up to 2.1 cm long, pubescent outside .... elongata

15b. Inflorescence racemose and unbranched, rarely with 1-2 short branches at the base, occasionally condensed and spicate.

20a. Upper surface of the leaves entirely glabrous or papillose, rarely provided with sparsely distributed minute strigae.

21a. Inflorescence drooping; corolla dark red, up to 2.6 cm long, glabrous inside .... grandiflora

21b. Inflorescence erect; corolla white or yellow, never more than 1.5 cm long, hairy at least at the attachment of the staminal filaments inside.

22a. Flowers entirely sessile; calyx lobes ciliate with long, septate, eglandular hairs .... malaccensis

22b. Flowers distinctly pedicellate; calyx lobes glabrous, subglabrous or ciliate with long, septate, glandular hairs.

23a. Inflorescence very much condensed; calyx lobes ciliate with long, septate, glandular hairs .... longeciliata

23b. Inflorescence usually a lax raceme, sometimes a bit crowded below; clayx lobes glabrous or subglabrous.

24a. Two anterior calyx lobes always bigger than the rest.

25a. Leaves distinctly papillose above; bracts nearly free from the pedicel; inflorescence lax ....shanica

25b. Leaves entirely glabrous above; bracts joined with the pedicel at least half the length; inflorescence dense .... inaequalis

24b. Two anterior calyx lobes either smaller than or equal to the posterior one.

26a. Lamina glabrous on both surfaces.

27a. Leaves gland-dotted (punctate) below; bracts lanceolate-obtuse .... punctata

27b. Leaves without gland dots; bracts linear-acute or filiform.

28a. Inflorescence few-flowered (2-6); corolla 1.3-1.7 cm long .... brachystachya

28b. Inflorescence many flowered; corolla never more than 1 cm long .... monticola

26b. Lamina glabrous or papillose above, pubescent or puberulous below at least on the veins.

29a. Bracts shorter than the bracteoles; flowers sessile .... novoguineensis

29b. Bracts either equal to or bigger than the bracteoles; flowers distinctly pedicellate.

30a. Inflorescence few-flowered (6-8); upper surface of the leaves papillose; bracts linear, free from the pedicels .... tenera

30b. Inflorescence many-flowered; upper surface of the leaves glabrous; bracts foliaceous and lanceolate, united to some extent with the pedicels.

31a. Flowers sessile or subsessile; bracts longer than the calyx lobes, 4.5 mm broad .... dispar

31b. Flowers distinctly pedicellate (2-5 mm); bracts either smaller than or equal to the calyx lobes, never more than 2 mm broad.

32a. Axis of the inflorescence pubescent; pedicels 1.5-2 mm long .... bella

32b. Axis of the inflorescence glabrous; pedicels 3-5 mm long .... subglabra

20b. Upper surface of the leaves strewn with septate, long or short hairs, either sparsely or densely distributed (pilose or velutinous), rarely puberulo-pubescent.

33a. Inflorescence very much condensed and subcapitate in form.

34a. Bracts puberulo-pubescent and ciliate at the margin; the lowest bract obovate or elliptic, 12 mm long and 7 mm broad; corolla 10 mm long .... subcapitata

34b. Bracts subglabrous; the lower bract lanceolate, 8 mm long and 2.5 mm broad; corolla 16-18 mm long .... incana

33b. Inflorescence usually lax, sometimes condensed into cylindrical spikes, never subcapitate.

35a. Corolla 2-4 cm long.

36a. Inflorescence 3-flowered; sepals 14 mm long, ciliate.. sesamoides

36b. Inflorescence many-flowered; sepals up to 10 mm long, hirtellous.

37a. Leaf base acute, inflorescence axis and calyx lobes hirtellous with glandular and eglandular hairs ...... major

37b. Leaf base rotundate; inflorescence axis and calyx lobes hirtellous with only eglandular hairs having bulbous bases; ovary glandular hairy .... arcuata

35b. Corolla 10-18.5 mm long.

38a. Lamina puberulo-pubescent above; inflorescence reflexed; foliar sclereids present .... cremostachya

38b. Lamina provided with long or short septate hairs above, either sparsely or densely distributed; inflorescence erect; foliar sclereids absent (excepting St. griffithiana).

39a. Upper surface of the leaves densely pilose or velutinous.

40a. Flowers sessile or subsessile; bracts lanceolate-spathulate; calyx lobes pubescent or puberulent .... velutina

40b. Flowers distinctly pedicellate (1.5-8 mm);bracts elliptic, lanceolate or linear; calyx lobes sparsely pubescent or hirtellous with glandular and eglandular hairs.

41a. Bracts joined with the pedicel to some length; calyx lobes sparsely pubescent; corolla up to 17 mm long; foliar sclereids present .... griffithiana

41b. Bracts free from the pedicel; calyx lobes hirtellous with glandular and eglandular hairs, corolla 10-12 mm long; foliar sclereids absent .... filipes

39b. Upper surface of the leaves sparsely strigulose or puberulo-strigosa.

42a. Bracts, bracteoles and calyx lobes hirtellous with only eglandular hairs; corolla up to 5 mm long.

43a. Leaves oblong, base rotundate .... ranaiensis

43b. Leaves lanceolate, oblanceolate or elliptic-lanceolate, base acute .... havilandii

42b. Bracts, bracteoles and calyx lobes hirtellous with glandular and eglandular hairs; corolla 8-11 mm long.

44a. Herbs provided with flowering runners; lower bracts obovate; capsule glabrous .... *zeylanica*

44b. Herbs with erect flowering branches; lower bracts oblong or lanceolate; capsule puberulous or pubescent.

  45a. Bracts joined with the pedicel to some length; inflorescence ± laxly racemose.

    46a. Leaves elliptic or elliptic-lanceolate; corolla broadly infundibuliform above; species of Africa .... *le-testuana*

    46b. Leaves elliptic-spathulate or lanceolate; corolla uniformly subactinomorphic; species of Asia .... *thyrsoidea*

  45b. Bracts free from the pedicel; inflorescence condensed and cylindric in structure .... *lanceolata*

Ser. B. [*Isosepalae* Brem. in Reinwardtia 3: 210 (1955)].

Calyx lobes all of the same shape and size, usually subsimilar, sometimes markedly similar, all 3-veined. All other characters similar to Ser. A.

Type: *St. jaherii* Brem.

9 species; distributed in Malaysia only.

Key to species:

1a. Inflorescence in triads which after anthesis takes lateral position; ovules about 12 in each loculus of the ovary .... *anomala*

1b. Inflorescence usually solitary and after anthesis always terminal; ovules about 25 or more in each loculus of the ovary.

  2a. Upper surface of the leaves densely or sparsely pilose.

    3a. Calyx lobes up to 6 mm long; peduncle, rachis and pedicels provided with glandular hairs .... *samarensis*

    3b. Calyx lobes 7-8 mm long; peduncle, rachis and pedicels possessing eglandular hairs.

4a. Bracts 3-5 mm long; calyx lobes densely hirsute .... panayensis

4b. Bracts 2-2.5 mm long; calyx lobes sparsely ciliate .... debilis

2b. Upper surface of the leaves glabrous, subglabrous, strigulose or minutely pubescent.

5a. Calyx lobes 12-17 mm long.

6a. Bracteoles larger; calyx lobes subglabrous; capsule 5 mm long .... amboinica

6b. Bracteoles smaller; calyx lobes conspicuously ciliate; capsule 8 mm long .... papuana

5b. Calyx lobes usually not more than 8 mm long, rarely up to 11 mm long.

7a. Lamina minutely pubescent, strigulose or papillose on the upper surface.

8a. Calyx lobes conspicuously ciliate.

9a. Leaves elliptic; pedicels 3.5-5 mm long .... ophiorrhizoides

9b. Leaves ovate-lanceolate or narrowly oblong; pedicels 2.5-3 mm long .... debilis

8b. Calyx lobes puberulous or entirely glabrous .... jaherii

7b. Lamina entirely glabrous on the upper surface.

10a. Calyx lobes 10-11 mm long; corolla 1.5-1.7 cm long ......jaherii

10b. Calyx lobes 7-8 mm long; corolla up to 1.2 cm long ...... debilis

Ser. C.

Plants subshrubby, often woody at the base. Inflorescence in branched or unbranched racemes, rarely in a few abnormal species some flowers are solitary at the axils and sometimes possess reduced vegetative apex on the main shoot. Corolla subactinomorphic, always more than 1 cm long, often showy. Calyx lobes markedly dissimilar; posterior lobe always much broader than the rest, usually bigger than or rarely equal to the bracts and bracteoles. Stamens and stigma usually included, rarely subexserted in a few abnormal specimens. Capsule always prominent, never less than 7 mm long.

Type: *St. anigozanthus* (Nees) O. Kuntze

Species about 10, confined to tropical America.

Key to species:

1a. Calyx lobes less than 1 cm long; corolla never more than 1.5 mm long .... *mandioccana*

1b. Calyx lobes much longer than 1 cm; corolla never less than 2.5 cm long.

  2a. Plant microphyllous; stem 0.5-1 cm in diameter; leaf lamina containing transformed 'acicular fibres' superficially resembling the sclereids .... *ericoides*

  2b. Plant macrophyllous; stem never less than 2 cm in diameter; leaf lamina containing the usual 'acicular fibres'

    3a. Upper surface of the lamina entirely glabrous or subglabrous, lower surface pubescent on the veins.

      4a. Bracts spathulate; calyx lobes pubescent with eglandular hairs; staminal filaments glabrous .... *minarum*

      4b. Bracts lanceolate; calyx lobes and corolla tube densely pubescent with glandular hairs; staminal filaments glandular hairy .... *brachiata*

    3b. Both surfaces of the lamina densely pilose or hirsute, rarely the upper surface being papillose.

      5a. All flowers subtended by bracts .... *hirsuta*

      5b. At least some of the lower flowers subtended by ordinary leaves.

6a. Calyx lobes covered with glandular and eglandular hairs .... warmingiana

6b. Calyx lobes covered with only glandular hairs.

  7a. Leaves oblong, apex obtuse; corolla up to 2.5 cm long .... glutinosa

  7b. Leaves lanceolate or elliptic-lanceolate, apex acute, corolla never less than 3 cm long.

    8a. Lamina pilose on the upper surface; bracteoles ± near the top of the pedicel.

      9a. Corolla tube pubescent outside with eglandular hairs; capsule never less than 1.4 cm long ....vauthieriana

      9b. Corolla tube pubescent outside with eglandular hairs; capsule never more than 1.1 cm long .... anigozanthus

    8b. Lamina puberulous excepting the hirsute veins on the upper surface; bracteoles much below the top of the pedicel ..... elegans

Ser. D.

Plants herbaceous, usually low in stature. Inflorescence in racemes or spikes, sometimes subcapitate, rarely paniculate. Calyx lobes dissimilar or subsimilar, usually equal to or slightly bigger than the bracts and bracteoles. Posterior calyx lobe is always slightly bigger and broader than the rest. Corolla distinctly bilabiate, usually less than 1 cm long. Stamens and stigma always included. Capsule usually less than 5 mm long, rarely attaining up to 5 mm.

Type: St. agrestis Leonard

Species many, confined to tropical America.

Key to species:

1a. Inflorescence capitate or subcapitate; flowers few (5 or less) in number.

2a. Bracteoles linear or linear-lanceolate; calyx lobes hirtellous with eglandular hairs.

3a. Leaves irregularly dentate or revolute at the margin; staminal filaments glabrous .... <u>versteegii</u>

3b. Leaves subentire or minutely repand; staminal filaments minutely glandular hairy .... <u>trinitensis</u>

2b. Bracteoles oval; calyx lobes glandular pubescent ...... <u>veronicifolia</u>

1b. Inflorescence a raceme or spike, sometimes condensed at the apex, rarely paniculate, flowers many.

4a. Leaves linear-elongate; lower lip of the corolla about 5 times as long as the upper lip .... <u>linearifolia</u>

4b. Leaves of other shapes excepting the above; lower lip of the corolla never more than 3 times as long as the upper lip.

5a. Corolla not profoundly bilabiate, ± infundibuliform above.

6a. Lower bracts very broad, up to 2.7 cm in diameter; posterior calyx lobe more than 1 cm long .... <u>eustachya</u>

6b. Lower bracts narrow, never more than 1 cm in width; posterior calyx lobe always less than 1 cm long.

7a. Bracts joined with the pedicel to some length; corolla up to 6.3 mm long. Plant stoloniferous .... <u>stolonifera</u>

7b. Bracts free from the pedicel; corolla never less than 7 mm long.

8a. Upper surface of the lamina papillose and sparsely strigose, inflorescence much elongated and lax .... <u>euryphylla</u>

8b. Upper surface of the lamina only papillose, inflorescence condensed and ovate at the apex .... <u>riedeliana</u>

5b. Corolla profoundly bilabiate, often small in size, ± cylindrical above.

9a. Plant erect from the base; branches numerous and fastigiate; inflorescence ± paniculate .... fastigiata

9b. Plant decumbent at the base, branches few or none, if any, they are not fastigiate; inflorescence a spike.

10a. Herbs with many sessile, reduced (microphyllous) leaves at the apex; inflorescence lax.

11a. Leaves hirsute with glandular and eglandular hairs; flowers pale pink or lavender in colour .... agrestis

11b. Leaves papillose or glabrous above, hirsute on the veins below, always with glandular hairs; flowers white.

12a. Lower leaves petiolate; calyx lobes glandular and eglandular pubescent .... diantheroides

12b. Lower leaves sessile or subsessile; calyx lobes eglandular hairy .... repens

10b. Herbs with all the leaves petiolate, a few may be subsessile above; inflorescence a condensed, cylindrical or ovoid spike.

13a. Creeping herbs; leaves entirely sessile .... fockeana

13b. Herbs decumbent only at the base, flowering shoots erect; leaves petiolate or rarely the upper ones subsessile.

14a. Calyx lobes villous with glandular and eglandular hairs.

15a. Upper surface of the lamina glabrescent; corolla never more than 5 mm long .... lepidagathoides

15b. Upper surface of the lamina pubescent; corolla 6.5 to 7 mm long.

16a. Leaves oblong; calyx lobes up to 5 mm long; capsule 4 mm long .... stahelii

16b. Leaves ovate-elliptic; calyx lobes 6-6.5 mm long; capsule 5 mm long .... miqueliana

14b. Calyx lobes villous with only eglandular hairs.

17a. Lamina ovate; calyx lobes 7 mm long; corolla 8 mm long .... wullschlageliana

17b. Lamina oblong-elliptic; calyx lobes up to 5 mm long; corolla about 5-6 mm long .... tenuicaulis

Ser. E.

Inflorescence in axillary and terminal or in terminal, unbranched or laxly branched racemes, often paniculiform. Bracts and bracteoles very minute, usually smaller or equal to the calyx lobes. Calyx lobes subsimilar in shape and size, either equal to or slightly bigger than half as long as the connate part of the corolla. Corolla weakly bilabiate. Stamens and stigma subexserted or slightly exserted. Stigma shortly bilobed; lobes equal or subequal.

Type: St. coriacea (T. And.) O. Kuntze

6 species; endemic to Thailand and Burma.

Key to species:

1a. Inflorescence a simple raceme, mostly unbranched.

2a. Axis of the inflorescence prominently hairy; sepals green .... hypoleuca

2b. Axis of the inflorescence glabrous or scabrid; sepals prominently red-tipped .... beddomei

1b. Inflorescence a panicle, either provided with a few or many branches.

3a. Leaves coriaceous; anther bases tailed .... coriacea

3b. Leaves herbaceous; anther bases obtuse or mucronulate.

4a. Plants with inconspicuous or short stems (never more than 2.5 cm long); lamina either pubescent or strigose on the upper surface .... gracilis

4b. Plants with prominent stems; upper surface of the lamina glabrous or subglabrous.

5a. Peduncle of the inflorescence up to 10 cm long; calyx lobes 2-3 mm long; corolla 3-4 mm long, pubescent outside ...... *parviflora*

5b. Peduncle of the inflorescence up to 4 cm long; calyx lobes (posterior and anterior) 6-8 mm long; corolla up to 10 mm long, glabrous outside .... *expansa*

Subsect 2. *Macrochlamydeae* Brem. in Reinwarditia 3: 222 (1955).

Stems unbranched or sympodial. Inflorescence in elongate, unbranched or laxly branched spikes, sometimes congested at the apex. Bracts several times as long as the calyx or at least longer than the posterior and lateral calyx lobes, usually ovate, obovate or elliptic-acute, herbaceous and leaf-like. Bracteoles narrow, similar to the calyx lobes. Calyx lobes small, unequal or subequal, either all or only the posterior and lateral lobes being smaller than half as long as the connate part of the corolla.

Type: *St. longispica* (Ridl.) Ridl.

7 species; distributed in Malaysia, Thailand, Burma and Indo-China.

Key to species:

1a. Corolla tube narrowly cylindrical, staminal filaments arise from $\frac{3}{4}$ portion above the base of the corolla tube .... *petelotii*

1b. Corolla tube widely campanulate; staminal filaments arise from $\frac{1}{4}$ portion above the base of the corolla tube.

2a. Bracts many times longer than the calyx lobes; inflorescence with a few or no sterile bracts on the peduncle; flowers never congested at the apex.

3a. Stem hirsute; calyx lobes glandular-punctate; corolla never more than 1.5cm long .... *cuneata*

3b. Stem glabrous or subglabrous; calyx lobes never glandular-punctate; corolla 1.8-2.5 cm long.

4a. Inflorescence profusely branched; bracts 3-veined; ovules about 18-20 in each loculus of the ovary .... longispica

4b. Inflorescence unbranched; bracts 5-veined; ovules about 36-40 in each loculus of the ovary .... longibracteata

2b. Bracts slightly longer than the posterior and lateral calyx lobes or only twice as long as all the calyx lobes; flowers congested at the apex.

5a. Stem hardly any, leaves 18-20 cm long; inflorescence branched above; bracts and calyx lobes provided with septate hairs .... helferi

5b. Stem prominent; leaves 6.5-17 cm long; inflorescence unbranched; bracts and calyx lobes glabrous.

6a. Stem with long internodes; leaves 14-17 cm long, densely pilose above; bracts 12 mm long .... latifolia

6b. Stem without perceptible internodes; leaves 6.5-10 cm long, glabrescent with sparsely distributed strigae above; bracts 6-7 mm long .... densifolia

Subsect. 3. Microchlamydeae Brem. in Reinwardtia 3: 223-224 (1955).

Rosulate, subrosulate or ascending erect herbs, sometimes woody at the base, rarely prostrate or decumbent. Inflorescence in terminal and axillary or in terminal spikes or racemes, unbranched, few-branched or laxly paniculate. Bracts and bracteoles usually very minute, smaller than or rarely equal to the calyx lobes. Calyx lobes unequal or subequal, usually minute, rarely conspicuous, often many times smaller than or rarely a bit smaller than half as long as the connate part of the corolla.

Type: St. merguensis (T. And.) O. Kuntze

Species 17; confined to Thailand, Indo-China and Malaysia.

Key to species:

1a. Stamens only 2; staminodes 2 or 3 .... diandra

1b. Stamens always 4; staminode 1 or 0.

  2a. Inflorescence a spike; flowers sessile or subsessile.

    3a. Lamina pubescent above; corolla puberulous outside, 10-11 mm long .... spiciformis

    3b. Lamina glabrous above; corolla glabrous outside, up to 18 mm long, never less than 15 mm in length .... spiciflora

  2b. Inflorescence racemose or paniculate; flowers conspicuously pedicellate.

    4a. Calyx lobes slightly shorter than half as long as the connate part of the corolla.

      5a. Inflorescence paniculate; lamina pilose on the upper surface.

        6a. Herbs rosulate; corolla bluish-purple, 1.6-1.8 cm long; foliar sclereids absent .... subrosulata

        6b. Herbs with prominent stems; corolla white with purple lobes, 1-1.2 cm long; 'pseudo-terminal' foliar sclereids present .... kerrii

      5b. Inflorescence in simple raceme, lamina glabrous or papillose on the upper surface.

        7a. Mature leaves papillose on the upper surface; pedicels of the flowers never less than 6 mm long; corolla lobes pink .... singularis

        7b. Mature leaves glabrous on the upper surface; pedicels of the flowers never more than 3 mm long; corolla lobes white.

8a. Lateral calyx lobes capitate and reddish at the apices; corolla glabrous outside; staminal filaments glabrous .... vicina

8b. Lateral calyx lobes acute and greenish at the apices; corolla puberulous outside; staminal filaments minutely glandular hairy .... citrina

4b. Calyx lobes at least twice as many times shorter than half as long as the connate part of the corolla.

9a. Tall herbs with prominent stems; leaves papillose on both surfaces .... racemosa

9b. Low herbs, rosulate or subrosulate (with short stems), rarely prostrate; leaves pubescent or pilose, never papillose on both surfaces.

10a. Plants totally prostrate; branching sympodial .... humifusa

10b. Plants erect or decumbent only at the base; branching monopodial.

11a. Mature leaves entirely glabrous at least on the upper surface.

12a. Inflorescence shortly pedunculate; corolla glabrous outside; foliar sclereids absent.

13a. Leaf base auriculate; calyx lobes 4-4.5 mm long; corolla 1.5-2 cm long .... balansae

13b. Leaf base contracted; calyx lobes 2.3-2.5 mm long; corolla about 1 cm long .... batuensis

12b. Inflorescence with a long peduncle; corolla puberulous or pubescent outside; foliar sclereids present.

14a. Inflorescence axis entirely glandular-hirtellous; calyx lobes 2-2.5 mm long; corolla 1.2-1.6 cm long .... tenuispica

14b. Inflorescence axis pubescent with eglandular hairs; calyx lobes 2.6-3.5 mm long; corolla 1.7-2 cm long .... merguensis

11b. Mature leaves pilose or provided with sparsely distributed, long, septate hairs, rarely puberulous on the upper surface.

15a. Herbs decumbent at the base; lamina lanceolate or elongate-lanceolate.

16a. Lamina puberulous on both surfaces; capsule up to 6.5 mm long; 'pseudo-terminal' foliar sclereids present .... pedicellata

16b. Lamina densely pilose on both surfaces; capsule up to 4 mm long; foliar sclereids absent .... burbidgei

15b. Herbs erect; leaves elliptic, elliptic-oblong or oblong.

17a. Leaves bullate on both surfaces; upper surface densely pilose, lower surface papillose; bracts nearly as long as the calyx lobes .... bullata

17b. Leaves flat on both surfaces; both surfaces densely pilose or provided with sparsely distributed, long, septate hairs; bracts half as long as the calyx lobes .... dasyphylla

Sect. IV. Maschalanthus Brem. in Reinwardtia 3: 237 (1955).

Stem usually monopodial, ascending erect, scandent or rarely attaining a climbing habit. Inflorescence in racemes, always restricted to the apices of short axillary branches ('brachyblasts'), occasionally the lower flowers solitary and axillary; main shoot apex remains always vegetative and vigorous. Bracts and bracteoles narrow, either equal or unequal to the calyx lobes. Calyx lobes subsimilar or similar in shape and size, always bigger than half as long as the connate part of the corolla. Corolla subactinomorphic, tube always infundibuliform.

Type: <u>St. axillaris</u> S. Moore

7 species; distributed in Indo-China, China, Borneo, Malayan Peninsula and Palawan Archipelago.

<u>Key to species</u>:

1a. Leaves linear-lanceolate or linear-elongate; inflorescence with 2-4 cm long, slender peduncle; calyx lobes subglabrous or puberulent with ciliolate margin.

  2a. Leaves linear-lanceolate; upper surface glabrous; calyx lobes subglabrous .... <u>capillipes</u>

  2b. Leaves linear-elongate; upper surface prominently papillose; calyx lobes puberulent .... <u>stenophylla</u>

1b. Leaves lanceolate, oblanceolate or lanceolate-oblong; inflorescence either sessile or subsessile, peduncle if present, never more than 1.5 cm long; calyx lobes usually hirtellous, rarely pubescent.

  3a. Scandent or climbing herbs, attaining up to 3-5 meter in height; calyx lobes 5-6 mm long; corolla 6-8 mm long .... <u>scandens</u>

  3b. Ascending erect or decumbent herbs; calyx lobes 8-16 mm long; corolla 1-2 cm long.

    4a. Calyx lobes 8-10 mm long, provided with only eglandular hairs; upper surface of the leaves papillose or pilose.

      5a. Inflorescence sessile or subsessile, few-flowered, lamina papillose on the upper surface .... <u>athroantha</u>

      5b. Inflorescence distinctly pedunculate, many-flowered; lamina pilose on the upper surface .... <u>merrillii</u>

    4b. Calyx lobes 12-16 mm long, provided with glandular and eglandular hairs; upper surface of the leaves papillose and strigulose.

6a. Inflorescence sessile or subsessile, strongly contracted; corolla 1.2-1.4 cm long; ovules about 26 in each loculus of the ovary .... axillaris

6b. Inflorescence distinctly pedunculate and lax; corolla 1.9-2 cm long; ovules about 36 in each loculus of the ovary .... sandakanica

III. "POOLED" CHARACTERS OF THE NELSONIOIDEAE AND COMPARISON WITH SCROPHULARIACEAE AND OTHER RELATED FAMILIES

The present investigation into the structure of the Nelsonioideae provides numerous characters of profound taxonomic importance. As a result, the group has been well-circumscribed as a taxonomic entity.

The available information on the structure of the Nelsonioideae evidently prove that they are typically exstipulate, sympetalous, and bicarpellate dicotyledons with subactinomorphic or zygomorphic corolla associated with oligomerous stamens. These are more or less the general characters of the order Bignoniales (Tubiflorae). But the characters which enlighten our ideas about the relationship of the Nelsonioideae in terms of family level classification are discussed in the following paragraphs:

1. Nelsonioideae are mostly free-living chlorophyllous herbs or subshrubs, rarely epiphytes. Most of the families in this affinity (e.g. Scrophulariaceae, Acanthaceae, Gesneriaceae and Pedaliaceae) are usually herbaceous, sometimes subshrubby, rarely arborescent (e.g. Bignoniaceae).

Available evidence demonstrates that specialized phenomena like parasitism and epiphytism have evolved several times in various taxonomic groups of diverse affinities. As a result we can find both hemiparasites and total parasites in several genera of the Scrophulariaceae: the Orobanchaceae are reported to be entirely obligate parasites. Similarly, epiphytism has also evolved independently in various Acanthaceous genera e.g. Asystasia and others.

Thus in respect of habit, Nelsonioideae do not provide any clear-cut affinity to any of the above-mentioned families. Nevertheless, they are quite different in this respect, particularly in comparison with the hemiparasitic Rhinanthoideae of the Scrophulariaceae to which the Nelsonioideae have been related by Bremekamp (1953).

2. The leaves in the Nelsonioideae are basically opposite, sometimes sub-alternate, rarely verticillate or alternate at the top. The leaf arrangement can not be of profound value in assessing relationship of the taxa, as both alternate and opposite types may occur in a single genus, and probably both types have evolved repeatedly in several angiosperm families. But a distinct character of the Nelsonioideae leaves lies in their usual petiolate nature: the petiole may be either short or long. The lamina bears basically pinnate venation (can be referred to as either 'Brochiodromous' or 'Camptodromous' after Kerner, 1887) the principal veins of which anastomose at the margin (Fig.I.A,B)

This is an outstanding difference when compared with those of the Rhinanthoideae. The leaves are always sessile, either alternate or opposite, accompanied by palmate or parallel venation (either 'Craspedromous' or 'Acrodromous' after Kerner) [Fig. I.C,D).

3. The constant occurrence of bi-celled glandular hairs (Pl. 2) on both surfaces of the leaf epidermis is one of the distinctive anatomical features of the Nelsonioideae. But the fact that they can evolve independently in several taxonomic groups of diverse affinities is clearly demonstrated by their repeated occurrence in Scrophulariaceae (e.g. Isoplexis), Gesneriaceae (e.g. Cyrtandra and others), Labiatae (e.g. Salvia), and Acanthaceae (e.g. Thunbergia).

Although the character is not so useful in assessing the family relationships of the Nelsonioideae, it provides one of the numerous differences in between the Rhinanthoideae and the Nelsonioideae. Conversely, a unique type of 'peltate gland' (Pl.2.H), so distinctive for the Rhinanthoideae, is entirely absent from the Nelsonioideae.

4. Mature stomata in the Nelsonioideae are always 'simple diacytic' or double-diacytic (a minor variation, possibly related to ecological conditions),

constantly of 'mesogenous' origin.

Studies of the stomatal complexes with their developmental history have often provided interesting clues to the solution of taxonomic problems (Stebbins & Khush, 1961). Notwithstanding the view as to which type is primitive in angiosperms, Nelsonioideae show a good indication of their affinities towards the Acanthaceae in this respect. The family Scrophulariaceae (e.g. Rhinanthus and others, Pl.3.G) mostly possess 'anomocytic' stomata while the Acanthaceae like Nelsonioideae are marked by having a 'diacytic' type of 'mesogenous' origin. Mullan (1933) for the first time reported the occurrence of 'paracytic' stomata in Lepidagathis trinervis Nees (also referred by Metcalfe & Chalk, pp. 1017), but the present reinvestigation of the species gives entirely negative result. In fact, the mature stomata of L. trinervis are of 'double-diacytic' type (Pl.5.G) representing a minor variation of the commonly occurring 'simple diacytic' stomata, and thus happily conforms with the generalization about the family Acanthaceae.

Other related families are of special notice in this respect: stomata largely 'anisocytic' in Gesneriaceae, often 'anomocytic' in Bignoniaceae with a few genera having 'paracytic' or 'diacytic' types, while they are usually 'anomocytic' in the Pedaliaceae (which have been suggested by Bremekamp (1942) to be merged with the Acanthaceae!).

5. 'Acicular fibres' peculiar only to the family Acanthaceae have also been found in the Nelsonioideae, excepting the genera Saintpauliopsis and Anisosepalum. Up till now, none of the other related families have been reported to have 'acicular fibres' in various plant parts. However, a sudden disappearance of this particular anatomical character from some of the closely related genera is difficult to explain at the present state of our knowledge. Even the selective significance of this peculiar type of fibres is also unknown or obscure, but by

and large their presence in the Nelsonioideae recalls the situation in the Acanthaceae.

6. The Nelsonioideae are characterised by their corolla aestivation which is 'descending imbricate': the middle lobe of the lower lip always remains inside (Fig.15.A). The variation in the corolla aestivation is mostly unexplainable in terms of selective pressure, but the way it varies in various families usually falls into distinct lines or groups. Sometimes it may come out as one of the distinguishing features between the families, subfamlies (e.g. Scrophularioideae and Rhinanthoideae in the Scrophulariaceae) and often genera or groups of genera.

A majority of the tribes and subtribes under the subfamily Acanthoideae possess 'imbricate aestivation' (with the middle lobe of the lower lip always remaining outside), while a considerable portion of the tribes, on the other hand, are characterised by the 'plicate' (rotate) aestivation of their corolla which is also constant in the subfamilies Thunbergioideae and Mendoncioideae. The tribe Andrographideae of the Acanthoideae is by far the most important in this respect: its genera mostly possess a similar corolla aestivation ('descending imbricate') like the Nelsonioideae but the genus Gymnostachyum is remarkable in having 'ascending imbricate' (the middle lobe of the lower lip remains always outside) type recalling the situation in other Acanthoideae.

'Imbricate aestivation' is also encountered in other related families, e.g. Scrophulariaceae (subfam. Scrophularioideae) and in the subfamily Rhinanthoideae corolla is always 'galeate' with mostly 'quincuncial' (either one or both the lateral lobes remaining outside) aestivation. Therefore, the affinity of the Nelsonioideae in respect of corolla aestivation seems to be more remote from the Rhinanthoideae.

7. The inflorescence is fundamentally a raceme in the Nelsonioideae: of course, a 'modified raceme' (Pl.17.F) superficially resembling a 'scorpioid cyme' is also found in Saintpauliopsis. The family Scrophulariaceae and also the Acanthaceae exhibit remarkable variations in the nature of inflorescence: both racemose and cymose types are frequently found in various genera of these two families.

Conversely, the family Gesneriaceae is characterized by a cymose inflorescence or axillary solitary flowers. Two other related families, e.g. Bignoniaceae and Pedaliaceae, usually possess 'dichasia', sometimes compounded into 'monochasia' or often with the flowers solitary in the axils. Thus in the nature of inflorescences Nelsonioideae may be related either to the Scrophulariaceae or to the Acanthaceae.

8. Flowers in the Nelsonioideae are mostly provided with prominent bracts and bracteoles: the bracteoles are usually opposite while the bracts are mostly alternate or subopposite. The prolific development of bracts and bracteoles in this group can only be compared to that of the Acanthaceae.

However, it is also noteworthy that similar bracts and bracteoles can be met with in some genera of the Scrophulariaceae. Bremekamp (1965) has pointed out the importance of alternate arrangement of the bracts in the Nelsonioideae in comparison to that of the Acanthaceae, which is said to be always opposite. This is, I think, an oversimplification, as many Acanthaceous genera (including the type genus Acanthus) embrace alternate bracts. Other families in this particular feature usually do not come into the picture.

9. The pollen grains of the Nelsonioideae are either typically 'tricolpate' or 'tricolporoidate' (having a weakly defined pore in the colpus) or 'tricolporate'. Both 'tricolpate' and 'tricolporate' pollen grains are frequently found in the Scrophulariaceae, while the Acanthaceae is remarkable in being entirely

'eurypalynous'. Various tribes and subtribes of the Acanthaceae are characterized by the particular type of pollen grains but one should not forget the occurrence of more than one type of pollen grains in a single genus, e.g. Pseuderanthemum and Eranthemum.

The recognized tendency of the pollen grains to be 'tricolporate' in nature, pronounced in the Nelsonioideae is of considerable taxonomic significance. Probably due to this evolutionary trend, the pollen grains seem to have attained further perfection in a relatively advanced tribe Andrographideae (Acanthaceae) where they are ± perfectly 'tricolporate' in nature (Pl. 10.A)

10. The placentation of the Nelsonioideae, in the classic sense of the term is 'axile', although in some textbooks [cf. Syllabus der Pflanzenfamilien ed. 2 (1964) and Cronquist's The Evolution and Classification of Flowering Plants (1968)] occurrence of 'parietal' placentation is reported in Elytraria (Nelsonioideae). From the embryological point of view, and according to Puri's (1952) proposals for the definition of the 'parietal' placentation, the family Acanthaceae provide interesting examples. Owing to this interpretation, Anima De (1967) has described the placentation of the Acanthoideae (true Acanthaceae of Bremekamp) as 'parietal'. On the other hand, following the scheme of classification given by Eames & McDaniels (1947) and Gunderson (1950) she has considered the placentation of the Acanthaceae as a "derived type of axile placentation".

The Nelsonioideae in this alliance is better suited to the Acanthaceae as they also possess a 'derived type of axile placentation', of course, if we follow the embryological definitions.

11. Ovules are 6 to numerous, arranged either in 2 or 4 alternate rows in each loculus of the ovary, always obliquely oriented upwards. In all the previous literature, Nelsonioideae have been characterized by the presence of numerous

ovules, a statement which is correct only for the three genera (Staurogyne Ophiorrhiziphyllon, and Saintpauliopsis). The present investigation has revealed a trend of evolutionary reduction in the number of ovules within the group, culminating in the genera like Gynocraterium (6 ovules) and Anisosepalum (6-8 ovules) /cf. "A brief discussion on the evolutionary trends within Nelsonioideae" pp. 1247.

A similar situation with 2 or 4 alternate rows of ovules can also be found in the tribe Hygrophileae (e.g. Synnema) of the Acanthaceae. Of course, a comparable reductional trend in the number of ovules is also pronounced in the Rhinanthoideae (Scrophulariaceae), but their ovules are not obliquely oriented upwards. Moreover, the placenta in the Nelsonioideae, either thick or thin, characteristically divided into two equal halves up to the base. Conversely, in the Rhinanthoideae placenta is usually much thickened and protruded, either remains intact or divides into two parts up to the middle. This division of the placenta into two equal halves up to the base is one of the most outstanding characters of the Acanthaceae, hitherto unknown in any other family of the Sympetalae.

12. The retinacular development is not so clear-cut in the Nelsonioideae. Ovules are usually supported by 'papilliform retinacula' or often without any conspicuous swelling on the funiculus. In this respect, Anisosepalum is particularly remarkable, as it contains a fewer number (6-8) of comparatively bigger seeds supported by 'unindurated (non woody) retinacula' (Fig. 8. R). Although these are not strictly comparable to those of the characteristic, woody and hook-like funicular excrescences ('jaculators' or 'retinacula') found in the advanced members of the subfamily Acanthoideae, yet they provide evidence that the formation of the 'retinacula' is somehow or other, tied up with a lesser number of comparatively bigger seeds per loculus of the capsule.

Many authorities have considered the occurrence of 'retinacula' as the most common and distinguishing feature of the Acanthaceae. But the statement seems to be an oversimplified generalization, as the subfamilies Thunbergioideae and Mendoncioideaeare entirely devoid of 'retinacula'. Even if we exclude these taxa from this comparison, there are numerous isolated genera (eg. *Trichacanthus*, *Hygrophila*, *Nomaphila*, *Synnema* and others) of the so-called true Acanthaceae (Acanthoideae) which also lack the characteristic hook-like 'retinacula' on their funicles. Further in the genus *Trichacanthus*, they are reported to be entirely obsolete.

The function of the 'retinacula' in their fully developed form is clearly conceivable, but their selective significance of evolutionary precursors are yet to be clarified. The above-mentioned genera and also the Nelsonioideae provide evidence that the evolutionary changes were well under way before the propulsive function was acquired.

Therefore, too much emphasis should not be given to this funicular character for the assessment of natural relationship within the family Acanthaceae, although their occurrence in either well-developed or reduced (papilliform) forms is pretty informative towards the evolutionary history of the group. Similar structures are entirely absent from any other angiosperm families.

13. Seeds of the Nelsonioideae are mainly globose, subglobose or elongated with many faces, but in *Anisosepalum* they are ovate and much bigger than others - slightly flattened (compressed) at the ventral surface. Bremekamp (1953, 1965) has pointed out the similarities in this respect to the Rhinanthoideae which have round, non-flattened (e.g. *Rhynchocorys*) or winged, flattened (e.g. *Rhinanthus*) seeds. Flattened, winged seeds are characteristic of numerous Bignoniaceous genera, but they are also not uncommon in other related families (e.g. Scrophulariaceae and Acanthaceae). That the true Acanthaceae always

possess flattened seeds is not correct, as diverse genera in the Acanthoideae (e.g. Acanthus, Synnema and others) also contain globose or semiglobose seeds.

The most remarkable feature of the Nelsonioideae seeds lies in their thin testa (Pl. 14. A, E) which is usually (excepting only Anisosepalum) provided with solid bars or hooks, more or less comparable to the prolongations (spines) of the testa cells in the tribe Andrographideae (e.g. Andrographis /Pl. 14. D7 and Phlogacanthus) of the Acanthaceae. In this respect, Gymnostachyum of the tribe Andrographideae deserves special mention as it bears similar solid bars like the Nelsonioideae on the testa cells of the seeds.

Ornamentations of the testa cells, including various types of hairs, scales or solid bars, are quite remarkably developed in the Acanthaceae, while the seeds are usually smooth in the Rhinanthoideae, Pedaliaceae and Gesneriaceae. The testa of the Rhinanthoid seeds is conspicuously thickened, mostly made up of sclerified cells (Pl. 15. G,H), while those of the Nelsonioideae are mostly parenchymatous (Pl. 15. I).

14. A unique character found in the seeds of the Nelsonioideae is the constant presence of persistent and fleshy endosperm. Bremekamp (1953, 1967) has attributed enormous importance to this particular feature while comparing the group with the rest of the Acanthaceae. It is of course, a fact that a greater portion of the Acanthoideae (true Acanthaceae) possesses exalbuminous seeds, while the Scrophulariaceae are characterized by the presence of albuminous seeds.

Present investigation has clearly established that the endosperm in the Nelsonioideae is always prominently 'alveolate' (Hartl, 1959), and thereby differs embryologically from that of the 'non alveolate' type found in the Rhinanthoideae (Pl. 14. G). However, it is worth noticing that similar 'alveolate' endosperm/also occurs in the supposedly primitive subfamily Scrophularioideae of the family Scrophulariaceae. Probably this is an ancestral character which has been retained by the primitive members of both the families (i.e. Scrophulariaceae and Acanthaceae), but the Scrophularioid members are entirely devoid of the characteristic placenta and capsular dehiscence found in the Nelsonioideae.

Other related families like Gesneriaceae and Pedaliaceae usually possess a thin or thick layer of endosperm, occasionally being exalbuminous, while Bignoniaceae is distinctly exalbuminous. In this context one should particularly notice that the family Acanthaceae is usually stated to be exalbuminous in all the existing textbooks. The fact that true Acanthaceous genera like Andrographis and Bremekampia (Haplanthus) also possess persistent endosperm in their seeds has often been overlooked.

Moreover, the endosperm of these genera is profoundly 'alveolate' resembling closely that of the Nelsonioideae. The fact that the plants with persistent endospermic seeds are primitive in the group is also suggested by the occurrence of exalbuminous seeds in the closely related but advanced genera (e.g. Phlogacanthus and Gymnostachyum) of the tribe Andrographideae. This is a remarkable finding which lends support to those who believe that the family Acanthaceae is more closely related to the Scrophulariaceae and Gesneriaceae than to the Bignoniaceae.

Further, it also suggests that these interrelated families probably in the past had a common origin: the 'stock' having more or less round seeds with persistent endosperm. Evolutionary changes have rendered them dorsally flattened or winged, simultaneously losing the endosperm coupled with reduction of the number of ovules per capsule.

15. Embryological resemblances, e.g. amphitropous, tenuinucellate and unitegmic ovules with 'polygonum' type of embryosac development in between the Nelsonioideae and the Rhinanthoideae are quite considerable. These are not extraordinary, as all these families (Scrophulariaceae, Acanthaceae, Gesneriaceae, Bignoniaceae,

Pedaliaceae and others) belong to a supposedly natural order. The most fundamental difference between the Nelsonioideae and the Rhinanthoideae (Scrophulariaceae) lies in the nature of endosperm development: the central chamber of the endosperm in the former grows asymmetrically, while in the latter it develops symmetrically.

Embryological data of other related families considered in the text are in fact alarmingly scanty, but available evidence clearly demonstrates that the asymmetrical development of the central chamber pertaining to the early ontogeny of the endosperm is a unique feature of the Acanthaceae.

A free nuclear phase of the endosperm is absent from both the Nelsonioideae and the Rhinanthoideae, but present in the tribe Andrographideae (Johri & Singh, 1959). Future studies in the embryogeny of Staurogyne (taking samples from both the advanced and primitive species) and Phlogacanthus species might reveal whether a free nuclear phase of the endosperm is in fact a later development or basic to the group.

16. The fruit of the Nelsonioideae is fundamentally a loculicidal capsule, dehiscing elastically or simply into two woody, recurved valves up to the base, rarely being indehiscent. Tardily dehiscent fruits are not entirely uncommon in the true Acanthaceae (e.g. Acanthus), but in general, loculicidal dehiscence of the fruit with woody, recurved valves up to the base is a feature which is exclusively Acanthaceous.

None of the related families exhibits such a unique type of fruit dehiscence (two valves quickly fall off from the pedicel) except in some of the Bignoniaceous genera which resemble superficially in their silique-like fruits to those of the Acanthaceae.

A closely related family Pedaliaceae is distinctive in its beaked or barbed loculicidal capsules or nuts, while in the Scrophulariaceae and Gesneriaceae various types of septicidal and loculicidal fruits are frequently met with; occasionally they are fleshy, indehiscent or berry-like.

Bremekamp (1965) has stressed that the general occurrence of a 'curiously structured' tip of the friuts found in the true Acanthaceae is lacking in the Nelsonioideae. Anatomical observations illustrate that the hard tip of the Acanthaceous fruits in fact possess many sclerified cells which after dessication help in the quick severing of the two valves of the fruit. A similar anatomical feature (presence of sclerified cells) has also been uniformly noticed in the Nelsonioideae, much pronounced in the genera like Nelsonia and Elytraria (Pl. 12. C,E, & H).

CONCLUSIONS ABOUT RELATIONSHIPS

The Nelsonioideae, as a taxonomic group, differs widely from the Rhinanthoideae (Scrophulariaceae) in several important characters discussed above. As a result, all the arguments put forward by Bremekamp (1953, 1965) for the transference of the Nelsonioideae to the Scrophulariaceae become unacceptable.

The present investigation elegantly circumscribes the limits of the family Acanthaceae by the constant occurrence of 'diacytic' stomata of 'mesogenous' origin, occasional presence of the 'acicular fibres', characteristic division of the placenta into two equal halves up to the base, and a unique dehiscence of the capsule into two woody recurved valves. To this an embryological feature may be added: the central chamber of the endosperm dividing asymmetrically in its early ontogeny. All these characters are happily compatible with the Nelsonioideae, but the characteristic dehiscence of the placenta and the fruit is missing from the subfamily Mendoncioideae (the fruit is a 1-2 seeded drupe).

From the inception of the Nelsonioideae as a taxonomic group, it has been kept isolated from other subdivisions of the family Acanthaceae. Usually it is treated as a primitive (starting) Acanthaceous group without any comment on their possible relationship with the rest of the Acanthaceae. Johri & Singh (1959) for the first time pointed out some of the embryological similarities in between the Nelsonioideae (Elytraria) and the Andrographideae. In this respect, it is also interesting to note that Bhaduri as far back as in 1924 observed resemblances in the nature of pollen grains in between Andrographis paniculata Nees and N. canescens.

The presence of 'descending imbricate' aestivation in the corolla (excepting Gymnostachyum of the Andrographideae which bears 'ascending imbricate' type) and the constant occurrence of the persistent, fleshy, 'alveolate' endosperm (excepting Phlogacanthus and Gymnostachyum) make these two groups (i.e. Nelsonioideae and Andrographideae) quite outstanding in the general affinities of the Acanthaceae as a whole.

Further, Andrographideae resembles Nelsonioideae in several other important features, e.g. occurrence of 'acicular fibres', thyrse or racemose type of inflorescence, nonstipitate or slightly stipitate capsules, and elongated or angular unflattened seeds (found in Andrographis and Bremekampia) supported by weakly developed 'retinacula' with minute, solid prolongations (spines) [found in Phlogacanthus and Andrographis] or bars (Gymnostachyum) of the testa cells.

The pollen grains of the two groups also show remarkable resemblance, as the 'tricolporoidate' condition prevalent in the Nelsonioideae is more or less comparable to that of 'weakly defined tricolporate' (with indistinct pore in the colpus) condition of the Andrographideae.

As a result, the necessary conclusion is that the Nelsonioideae is a basic, probably 'relict' group, but taxonomically most closely related to the tribe Andrographideae of the true Acanthaceae.

In this context it might be profitable to discuss briefly the relationships of two other subfamilies (Thunbergioideae and Mendoncioideae) of the Acanthaceae. Bremekamp (1953, 1965) has given family status to each of them, being largely influenced by the fruit and pollen grains character. His Thunbergiaceae has been characterized by the possession of a rostrate capsule having 1 or 2 semiglobose seeds in each loculus provided with a large hilar excavation at the ventral side, and 'grooved' pollen grains. On the other hand, the family Mendonciaceae has been circumscribed by the possession of unilocular, 1-2 seeded drupe, and 'tricolpate' pollen grains bearing very minute equatorial colpi.

The taxonomic significance of the pollen grain characters is highly appreciated especially when they are found to be correlated with other features. Acanthaceae is essentially an 'eurypalynous' family, and it has already been pointed out (pp. 166) that considerable morphological diversity in the nature of pollen grains may occur even within a single genus (e.g. Pseuderanthemum) of this family. One species, Thunbergia chrysops is particularly interesting in this aspect: the pollen grains are spiny /cf. Lindau in Engler's Pflanzenfamilien 4: 292 (1895) Fig. 116M/ and devoid of any 'groove' - so characteristic of the genus. Therefore, too much emphasis should not be given to such characters without corroborative evidence from other independent fields of observation for assessing the natural relationships of any taxonomic group.

A rostrate capsule of the Thunbergioideae and a drupe of the Mendoncioideae may at first sight look quite different morphologically from that of the typical capsule of the Acanthoideae and the Nelsonioideae. But if one considers this phenomenon from an evolutionary standpoint, it is not too difficult to obtain a

Fig. 16. DIAGRAMMATIC REPRESENTATION OF FRUIT SPECIALIZATION IN ACANTHACEAE

(Explanation in the text)

A = 'Prototype' found in Nelsonioideae, Hygrophileae, & Trichanthereae; B, C = Andrographideae & Hygrophileae; D = Advanced tribes of the Acanthoideae; E = Acantheae; F = Thunbergioideae, & G = Mendoncioideae.

drupe or a rostrate capsule from the typical capsular fruit present in the primitive Acanthoideae and in the Nelsonioideae. There are numerous examples in angiosperms where families or even genera predominently possess capsular fruits but have given rise to drupes (or berries) or vice versa through evolutionary changes, often expressed through simple orthogenetic changes.

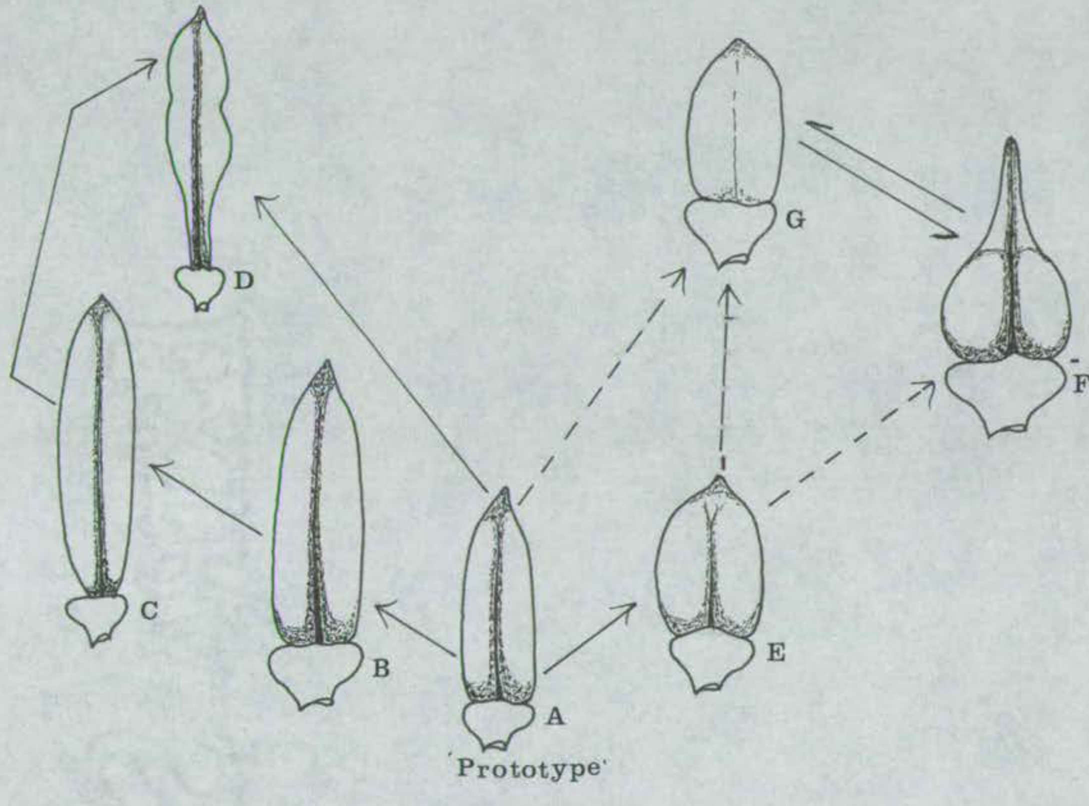


Fig.16.DIAGRAMMATIC REPRESENTATION OF FRUIT SPECIALIZATION IN ACANTHACEAE.

The unilocular condition of the ovary in some of the Mendoncioideae seems to be a derived condition from the bilocular type through the failure of the partition wall in the middle. Although not exactly similar but a comparable situation is well exemplified by the Orobanchaceae, where the unilocular ovary has evolved gradually from the typical, bilocular one (cf. Boeshore, 1920).

Bremekamp has adduced much importance to the shape of the seeds in various subfamilies of the Acanthaceae. It has been reported that the Acanthoideae (true Acanthaceae of Bremekamp) always possess flattened seeds, while the Nelsonioideae and the Thunbergioideae are characterized by the seeds which are globose or subglobose in outline. In this respect, the tribes Andrographideae (especially Andrographis and Bremekampia), Hygrophileae (Synnema) and Acantheae (Acanthus) provide important noteworthy examples. Seeds of these genera as cited above, are not certainly flattened; instead they are globose, semiglobose or elongated. Moreover, a similar excavation on the ventral side of the seeds found in the Thunbergioideae is also encountered in the seeds of Anisosepalum (Fig.9.E) and Nelsonia (Nelsonioideae) [Fig.9.F]

However, the two subfamilies Thunbergioideae and the Mendoncioideae are in fact closely allied to each other in several features, e.g. climbing or twinning (lianes) habit, absence of cystoliths, usually with anomalous structures in stem anatomy, reduced calyx but enlarged sheathing bracteoles, and general 'plicate' eastivation of the corolla.

Taxonomically these two groups differ from the rest of the Acanthaceae by their general habit and fruit character. But on the other hand, they also possess many characters in common with the rest of the Acanthaceae, e.g. usual heterophyly, occurrence of 'acicular fibres' in various plant parts, interrupted (in patches) hypoderm (either collenchymatous or sclerenchymatous), constant possession of 'diacytic' stomata, uniform occurrence of 'placentoid' (Pl. 6.A) in the anthers, and in the development of prominent disc around the ovary (a character, found particularly well-developed in the advanced Acanthaceae). Furthermore, the characteristic type of bi-celled glandular hairs found in the Nelsonioideae, are also present in the Thunbergioideae (Pl. 2.E). Both Thunbergioideae and Mendoncioideae produce exalbuminous seeds. This is also in conformity with the advanced Acanthoideae.

Therefore, I believe that all these groups probably have a common origin from which they have diverged in different evolutionary lines. Perhaps Thunbergioideae and Mendoncioideae represent two different but closely allied peaks of evolution within the family Acanthaceae. That they are relatively more advanced than many of the other Acanthaceae are evident by their habit, anatomical peculiarity, bigger but fewer number of semiglobose, exalbuminous seeds, and tardily dehiscent (Thunbergioideae) or indehiscent (drupes of the Mendoncioideae) fruits.

As far as these groups are taxonomically recognizable, attribution of subfamily rank seems to be quite reasonable and thus reflects the evolutionary potentialities of a diverse but basically natural family Acanthaceae of the tropical worlds.

Regarding the affinities of the Acanthaceae itself, one can never be entirely certain until all the necessary data are available, in and outside the closely related families considered here. Moreover, families like Acanthaceae, Bignoniaceae, Pedaliaceae, Scrophulariaceae, and Gesneriaceae with other smaller offshoot families are so closely interrelated that it is often difficult to conceive a separate origin for each of these families (this is against the contention of Hutchinson, 1959). Available evidence indicates that all these families are the outcome of specialized evolutionary trends in angiosperms, particularly adapted for insect pollination. In absence of fossil data, and other necessary evidence from various fields, it is practically impossible to assess whether the resemblances (especially at the level of families and orders) are actually due to common origin, or parallelism or convergence.

However, predictions about Acanthaceous ancestors and assessment of their phylogenetic relationships with other families have not been totally hindered by the lack of necessary data in the group concerned. Baillon (1866-'95) was in the opinion that the family Acanthaceae is related to both Scrophulariaceae and Labiatae on the basis of stamen morphology. He further related the Acanthaceae to the Bignoniaceae on the basis of calyx and fruit characters, and also traced its affinity with Boraginaceae and the Convolvulaceae in its nearly actinomorphic flowers.

In recent years, Hegnauer (1964) has provided phytochemical evidence (particularly in the common occurrence of Caffeic acid derivatives) for assessing the relationships with the Verbenaceae-Labiatae complex. This is also in accord with the view expressed by Wettstein (1935), who placed Acanthaceae in between Bignoniaceae and Verbenaceae.

On the other hand, Bessey (1915) considered the family Scrophulariaceae or groups ancestral to them as a common 'stock' for the derivation of the Acanthaceae. Most of the recent authors including Leonard (1951), Grant (1955), Takhtajan (1961), Melchior (1964), and Cronquist (1968) supported this contention with the implications that the Acanthaceae is an old, highly developed, and very natural group of the order Bignoniales (Tubiflorae). There is no doubt that certain parallel developments have taken place in the closely related Scrophulariaceae.

Ideas solely contrary to the above-mentioned monophyletic origin of the Acanthaceae have also been put forward from time to time. Thus Van Tieghem (1908), Bremekamp (1953, 1965), Bhoj Raj (1961), and Anima De (1966) are of the opinion that the original composition of the family is essentially artificial and presumably the subfamilies are polyphyletic in origin.

Notwithstanding with this view, cytologically all these subfamilies look rather closely related, although Mendoncioideae and Thunbergioideae have proved to be morphologically quite different from the rest of the Acanthaceae. Consequently, Grant (1955), who studied cytologically a fair sample of various subfamilies of the Acanthaceae (of course, the Nelsonioideae being poorly represented), came to the conclusion that there is no "cytological criterion" to separate the subfamilies and thereby elevate them to the status of individual families.

Judging all the pros and cons of the assessment of taxonomic affinities and status, the available evidence indicates that all these families (e.g. Scrophulariaceae, Gesneriaceae, Acanthaceae etc.) probably originated from a common 'stock' in the early diversification of the Sympetalae. Acanthaceae seems to be more closely allied to the Scrophulariaceae and the Pedaliaceae than to the Bignoniaceae to which it has long been related. Gesneriaceae is probably related to both Scrophulariaceae and the Acanthaceae, but placing of these three closely interrelated families in any horizontal classification (i.e. in a linear sequence) probably may not depict their actual relationship which might be of extradinarily reticulate in nature.

IV. TAXONOMIC TREATMENT OF THE NELSONIOIDESE

A consideration of family, subfamily or tribal status in the general affinity of 'Bignoniales'.

However unstable be the present angiosperm classification in practice at the higher hierarchical levels, there is a general agreement that a family should be as 'natural' as possible. But a natural family does not necessarily imply that its members will be easily separated or indentified from those of the other related families. Let us take the order 'Bignoniales' as an example: the families included here are so closely interrelated but mostly natural, that preparation of a convenient key to their identification is simply impossible until some of them are keyed out in more than one dichotomy. In this particular situation one must remember two very important points: if one believes that family differences in the order 'Bignoniales' should be of fundamental value, the order as a whole will end up with only one family; in a large and mentally unwieldy group an imperfect organization is better than no organization at all.

However, the present inconsistency of treatment prevalent at higher levels of angiosperm classification clearly reflects a depauperate store of correlated characters in the angiosperm for the characterization of its higher taxonomic groups. Evolutionary changes which result in better general adaptation, adoption of aquatic habits and specialized phenomena like mycotrophy, parasitism, and epiphytism have evolved several times in various unrelated families of angiosperms.

But on the other hand, it is also admitted that natural, recognizable groups of species, and groups of these groups exist in nature. Whether they are in essence synthetic or analytic constructions, depend mainly on the particular approach taken by the taxonomists. The rank which should be given to these groups are better to be judged on overall correlation of characters, size and coherence of the group concerned, and the extent of gap present in the variation chain.

The fact that the Nelsonioideae are recognisable as a taxonomic group is evident from the discussion on "Coherence of the Nelsonioideae as a taxonomic group" pp.79-81. The particular rank or category at which they should be accommodated is a matter of overall correlation of character comparisons made in the context of the family as a whole. Having numerous basic Acanthaceous features in common, the Nelsonioideae are definitely members of the family Acanthaceae (cf. Chapter III on "Conclusions about relationships" pp.172-179). As a result, the question of attributing a separate family status to the Nelsonioideae does not arise here.

The second possible rank is the subfamily at which the group has already been received by Lindau (1895) and for a long time followed by his successors. Bremekamp's uncertainty about the rank of this small group has been obvious by his contradictory opinions at different times. However, most people accept the group as a subfamily of controversial affinities within the Acanthaceae: some, of course, favour the opinion of considering them as a connecting link between the Scrophulariaceae and the Acanthaceae.

If we believe that attribution of rank to any taxonomically recognized group should depend on overall assessment of character correlation and amount of divergence from allied groups, the group should at the same time be easily circumscribed from its alliances. As there are no objective criteria laid down for recognizing subfamilies in any angiosperm family, I feel that one should assess the overall situation in broader evolutionary perspectives, so that the basic structure of the family can be easily visualized whatever subgroupsit may contain. In constructing a family one must remember only one thing: the natural association of groups, i.e. genera into tribes, tribes into subfamilies, and subfamilies into a family.

During this synthetic agglomeration process, some subfamilies might come out as more distinctive than some of the closely related families. This may be due to their great age and extinction boosted up by their evolutionary divergence. But elevation of these distinct subfamilies into separate families is not worthwhile, rather a temptation to academic botanists which should be checked until enough information unravels their true affinities or helps in the interpretation of evolutionary concepts.

Nearly all the taxonomic literature had followed the customary definition of the Nelsonioideae as a subfamily, as was put forward by Lindau in 1895. It has long been separated from the rest of the subfamilies by the following few characters, e.g. numerous ovules with papilliform retinacula, absence of cystoliths from the plant parts, and the presence of 'tricolpate' pollen grains.

Character comparison and correlation (pp. 161-179) provide ample evidence that the presence of numerous ovules can not be taken as a general character of the Nelsonioideae. Genera like <u>Nelsonia</u> (4-8 ovules per loculus), <u>Elytraria</u> (4-12), <u>Gynocraterium</u> (6), and <u>Anisosepalum</u> (6-8) remain out of consideration in this respect. Further in a multiovulate genus like <u>Staurogyne</u> one can find 60 or more ovules per loculus of the ovary in the subgen. <u>Tetrastichum</u>, while advanced species (e.g. <u>St. anomala</u>, <u>St. riedeliana</u>) of the subgen. <u>Staurogyne</u> may possess only twelve ovules instead. Reductional trend in the number of ovules, followed by at first reducing the number of placentas from 4 to 2, and simultaneously coupled with the sterilisation of the upper part of the capsule, is frequently found in the tribes (e.g. <u>Trichanthereae</u> and <u>Hygrophileae</u>) and the subfamily Thunbergioideae of the Acanthaceae which predominently produce non-stipitate (without sterile and solid lower part) capsules. On the contrary, other Acanthaceous tribes mostly perform this function (i.e. achieving fewer ovules in the capsule) by the constant sterilization of the lower part of the capsule.

Species with numerous ovules arranged in 4 alternate rows in each loculus as encountered in the Nelsonioideae (*Staurogyne* only) can also be found in a relatively primitive tribe Hygrophileae (e.g. *Synnema balsamica*) under the group Contortae. The minute and globose seeds of this species are also noteworthy, but they are devoid of endosperm, so characteristic of the Nelsonioideae.

The tribe Andrographideae deserves special mention in this respect. The members of this group usually possess 2-12 ovules per loculus of the ovary and the seeds in *Andrographis* and *Bremekampia* (*Haplanthus*) are also not typically flattened as other true Acanthaceae (cf. Bremekamp).

The constant presence of persistent endosperm in the seeds of the Nelsonioideae could have been used as a better key character than others hitherto used. But unfortunately, none of the earlier workers referred to this in the key. However, the character of endosperm should not be over emphasized in circumscribing the Nelsonioideae owing to the fact that genera like *Andrographis* and *Bremekampia* of the tribe Andrographideae also possess persistent 'alveolate' endosperm in their seeds. An advanced genus like *Phlogacanthus* of the tribe Andrographideae exhibits an evolutionary trend within the tribe itself which can be visualized by its exalbuminous seeds supported by prominent hook-like retinacula. Possibly *Phlogacanthus* has lost its endosperm through evolutionary changes, simultaneously coupled with the attainment of bigger, flattened (compressed) seeds - so characteristic of the Acanthaceae. These flattened light-weighted seeds in comparison to those of ovoid and heavy-weighted ones are definitely much better suited for quick and efficient dispersal by their supporting retinacula. On the other hand, loss of endosperm with the concommitant achievement of bigger cotyledons seems to be a prerequisite for successful competition (for more photosynthetic surface to receive more sunlight) in the seedling stage in the available forest habitats.

A common spot character of the Acanthaceae is the occurrence of cystoliths in various plant parts. No doubt it is a character of taxonomic value for the identification of many Acanthaceous members from those of the other closely related families, but its taxonomic use mainly lies in the tribal delimitations of the subfamily Acanthoideae. Instances of convergent evolution of cystoliths are also not infrequent, as they are found too in the unrelated families like Urticaceae and Moraceae.

Most of these phytochemical features are in fact expressions or end results of a long series of interconnected metabolic pathways. Elimination or restriction of any step of these chained processes might result in an entirely different product or might lead to the loss of particular metabolite. Thus the tribe Acantheae and Aphelandreae of the subfamily Acanthoideae entirely lack cystoliths from their tissues. Isolated genera or species in predominantly cystolith-bearing tribes or genera are not so infrequent in the family where cystoliths have been lost completely. The genera Haselhoffia, Gymnacanthus (Sclerocalyx), and one species of Cosmianthemum illustrate the fact beautifully. As a result, too much emphasis on the presence or absence of cytolitns should not be given until a thorough investigation into all the mambers of the tribes and subtribes is carried out.

Two other subfamilies-Mendoncioideae and Thunbergioideae also come into the picture in this respect. Both of them constantly lack cystoliths from the tissues, but the Nelsonioideae, although conforming to this character with the above-mentioned subfamilies, differs largely in several other features of taxonomic significance. The first three subfamilies (Nelsonioideae, Mendoncioideae, and Thunbergioidea) for a long time were considered to be closely related to each other, particularly in the absence of characteristic cystoliths and retinacula of the Acanthoideae.

It is remarkable that although many members of the Nelsonioideae show papilliform retinacula, the genus *Anisosepalum* possesses prominent unindurated ones supporting the seeds. Further, the characteristic (true) Acanthaceous retinacula are seen to be well-developed only in the advanced genera and tribes of the Acanthoideae: they are weakly developed in several isolated genera, and even reported to be obsolete in the genus *Trichacanthus*. The formation of characteristic, indurated (woody) retinacula efficient for successful seed dispersal seems to be tied up with two factors - the seed shape and the number. Thus primitive tribes like Trichanthereae, Hygrophileae and many genera of the Andrographideae which possess comparatively many seeds not typically flattened like those of the other Acanthoideae, simultaneously also show ill-developed retinacula supporting their seeds. Any overriding importance given to such loss characters (e.g. cystoliths and retinacula) for subdividing the family Acanthaceae is liable to produce an artificial classification. Similar examples of such loss characters are also quite frequent in several other angiosperm families. The occurrence of albinos in any species having mostly coloured flowers or the formation of discoid heads in a genus or species (e.g. *Senecio vulgaris* L.) which is largely characterized by the radiate heads, is mainly controlled by a single gene or a series of inter-linked genes. Therefore, taxonomic significance of such loss characters in classifying higher groups should be carefully evaluated although they might have enormous practical value for the purpose of indentification.

The pollen grains are said to be typically 'tricolpate' in the Nelsonioideae (Bremekamp; Bhoj Raj, 1961), although reports of 'tricolporoidate' (Erdtman, 1952) and 'tricolporate' (Bhaduri, 1944; Johri & Singh, 1959; Van Campo, 1959 and others) types are also not infrequent. The value of pollen grain characters in the taxonomy of a largely 'eurypalynous' family like Acanthaceae has long been appreciated, starting as early as 1883 (Radlkofer). But at the same time, it has been proved that too much emphasis on such characters without necessary sampling might lead to contradictory decisions about natural relationships. For example, we can cite Bhoj Raj (1961) who supported Bremekamp in transferring the Nelsonioideae to the vicinity of the Rhinanthoideae (Scrophulariaceae) depending on only pollen grains but without adducing necessary arguments.

It is to be noted that typically 'tricolpate' pollen grains are also encountered in the tribes Acantheae and Aphelandreae, apart from some of the Nelsonioideae (e.g. Elytraria, Saintpauliopsis, Gynocraterium and some species of Staurogyne) but most of the other genera e.g. Nelsonia, Ophiorrhiziphyllon, Anisosepalum, and numerous species of Staurogyne possess 'tricolporoidate' or 'tricolporate' pollen grains. Many of this type of pollen grains resemble strikingly those of the Andrographideae and thus indicate a probable evolutionary advancement in the nature of the pore which is slightly well-developed in a relatively advanced tribe like Andrographideae. Further, 'tricolporoidate' (an intermediate stage in between 'tricolpate' and 'tricolporate' types) condition can also be found in the genus Stenandrium and Stenandriopsis of the tribe Aphelandreae.

It can safely be concluded that character correlation and comparison eventually do not provide enough evidence in favour of recognizing the Nelsonioideae as a separate subfamily within the family Acanthaceae. Therefore, its status within the family is open to question which will be settled in the following pages.

DECISIONS

The above discussion in the light of available knowledge reveals that the family Acanthaceae should contain only three subfamilies, e.g. Mendoncioideae, Thunbergioideae, and Acanthoideae: the Nelsonioideae of Lindau (1895) should be merged with his Acanthoideae, as there is no clearcut break between the two.

According to Lindau's classification, Nelsonioideae easily fits into the framework of the Acanthoideae and remains as a tribe Nelsonieae at the starting position of the subfamily. It happily conforms with Lindau's Group II - Imbricatae which I think should be treated as much more primitive than his Group I - Contortae. It is due to the fact that the tribes Nelsonieae and Andrographideae (excepting Phlogacanthus and Gymnostachyum) possess persistent endosperm in their seeds while the rest of the Acanthaceae are reported to be exalbuminous.

Numerous seeds either without or supported by papilliform or ill-developed retinacula probably represent an ancestral condition so elegantly exhibited by the supposedly primitive tribes of both the Groups (e.g. Nelsonieae and Andrographideae of the Group - Imbricatae and Trichanthereae and Hygrophileae of the Group - Contortae). It is also striking that all these tribes are at the same time characterized by their prevalent elongated sessile capsules comparable to those of the Nelsonioideae and most of the Andrographideae. This type has been considered to be the basic type of capsule found in the Acanthaceae, from which other advanced types can be derived through evolutionary changes (pp. 175).

The type of corolla with its weak contorted aestivation of the smaller corolla lobes in the Trichanthereae and Hygrophileae (e.g. Synnema) makes it more plausible that the Imbricatae group with smaller corolla lobes (in supposedly primitive tribes) might have been the proginetors of the Contortae group. Features like the constant occurrence of cystoliths, highly evolved pollen types (banded or colporate) or absence of 'tricolpate' pollen grains, and the complete lack of endosperm from their seeds also suggests its advanced position within the family Acanthaceae.

To conclude this chapter I will summerize my decisions:

1. Nelsonioideae as a taxonomic group can be easily identified,
2. they are definitely Acanthaceous,
3. the subfamily Nelsonioideae (sensu Lindau) is merged with the Acanthoideae in favour of its status as a tribe Nelsonieae,
4. the tribe Nelsonieae is best placed in the neighbourhood of the tribe Andrographideae, as their relationships have been assessed in the light of available information within the family Acanthaceae.

In fact, the tribe Andrographideae can only be separated from the Nelsonieae by the absence of bi-celled glandular hairs on the leaf surface, presence of cystoliths in various plant parts, and the seeds which are supported by short or long, indurated retinacula.

APPENDIX

TAXONOMIC NOTES ON NELSONIA CANESCENS (LAM.) SPRENG. COMPLEX

The genus Nelsonia at first described by R. Brown contained two species, N. campestris and N. rotundifolia, both collected from tropical Australia. Sprengel (Syst. Veg. 1: 42 (1815)] rightly transferred Lamarck's Justicia canescens to Nelsonia R. Br., and later on Nees (1847) recognized altogether 5 species under the genus.

All these species were in fact based on minor variations pertaining to indumentum and leaf shape. As a result, Bentham recognized only one species in Nelsonia in his "Flora Australiensis" and contended that it was "a common tropical weed in Asia and Africa, and already abundant in several parts of tropical America".

However, Bremekamp (1955) has doubted the validity of Bentham's conclusion with particular emphasis on the absence of N. canescens from the Malay Archipelago. Recently in 1964 he has concluded that the Australian and New Guinean (Van Royen's collection) specimens are in reality quite different from others in several aspects - deserving the rank of two separate species. But he refrained from describing them as new to science owing to the unsatisfactory taxomony of other existing species of the genus concerned.

My observations on Nelsonia are based on the present investigation of rich collections preserved in the British and Continental herbaria. There is tremendous variation in all this material, particularly in habit, duration, indumentum, shape and size of the leaves (Fig.17.A-K) & bracts (Fig.4.Aa), size of the capsules, and number of perfect seeds in each loculus of the ovary. Often two specimens of the same locality but of different ecological habitats look morphologically so different that one can hardly believe that they belong to the same species.

Fig. 17. TYPES OF LEAVES IN NELSONIA CANESCENS

(Explanation in the text)

A = *N. canescens* var. *vestita*; B-F = *N. canescens* var. *canescens*; & I-K = *N. canescnes* variant. A.

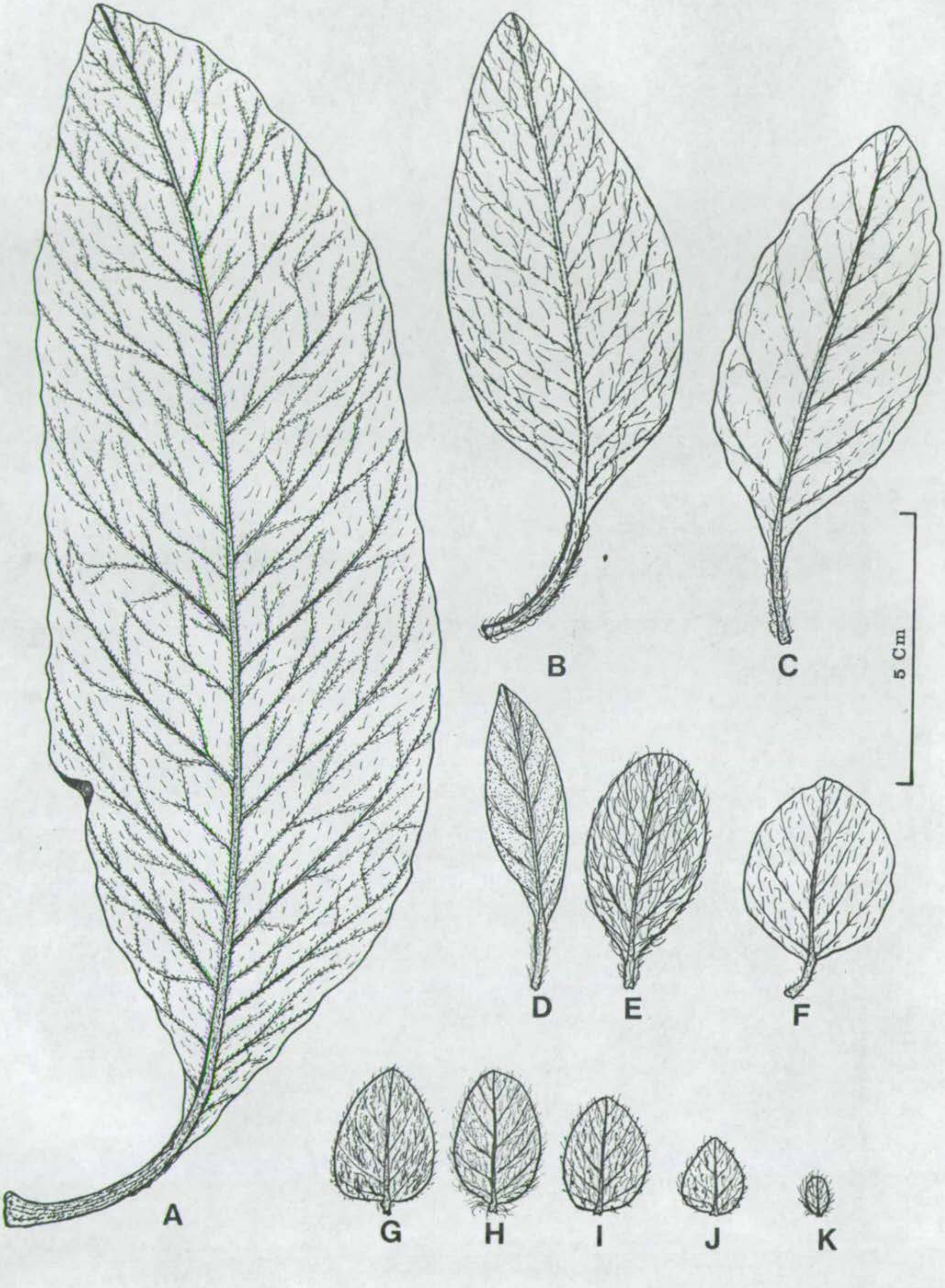


Fig.17. TYPES OF LEAVES IN N. CANESCENS.

Tiny erect herbs or prostrate, scandent or decumbent, branched or unbranched, long-stemmed herbs are frequently met with. They are either annual or biennial, some appear to be perennial too - often provided with taproot system or soon replaced by adventitous roots. In plants of marshy habitats these adventitous roots are quite fleshy and fibrous. Leaves can be either petiolate or subsessile (particularly the upper leaves seem to have reduced petioles through gradual reduction), entire, serrulate or repand. The size of the leaves is outstandingly variable (Fig. 17.A-K), ranging from a tiny, inconspicuous, nearly sessile (Fig. 17.G-K)ones to enormously large (up to 22 cm. long), petiolate ones (Fig. 17.A-F). Leaves of intermediate sizes are also frequent (Fig. 17.B-F).

The surface varies likewise in the nature and density of the indumentum: clothing type of hairs are usually multicellular, sometimes the individual cells being jointed and knee-like (Fig. 11.Dd); these are usually mixed with stalked (multicellular) glandular hairs - the heads consisting of either four or eight cells (Fig. 11.Dd^1), while on the epidermal peelings constant occurrence of bi-celled glandular hairs (Pl. 2.), so characteristic of the Nelsonioideae, are also encountered. Morphologically, the leaf surface may be either subglabrous or hairy with all sorts of intergrading densities of indumentum.

Anatomical variations relating to the nature of the stomata and presence/absence of collenchymatous fibres are also striking in several specimens. Usually the stomata are of 'simple diacytic' type, but in a few specimens 'double-diacytic' (Pl. 5.E) type is also recorded. Similarly, groups of collenchymatous fibres may be either present or absent in the t.s. of the stem (Pl. 1.E,G & H).

The inflorescence is usually a condensed spike, either terminal or axillary. The spikes often become elongated after anthesis, but in a few specimens they are comparatively much bigger in size and thus resemble at least superficially to those of <u>Elytraria</u> species. Bract's size varies profoundly even in the same spike, as the lower ones are usually bigger than those of the upper part of the spike. But the bracts afford numerous variations pertaining to their overall shapes (Fig. 4. Aa).

Conversely, if we examine the flowers and fruits of all these specimens of diverse facies, the variabilities come to a surprisingly low level. Plants with subactinomorphic (Fig.5.A) or weakly bilabiate (Fig.5.A^1) corolla are quite frequent, and the stigma may either be bilobed or capitate (Fig. 7.Q) or slightly bifurcate (Fig.7.Q) at the apex. There is a slight variation in the size of the capsule, but the shape is relatively constant. The number of ovules varies from 4-8 in each loculus of the ovary, but in a few specimens only one or two perfect seeds have been found (the others being aborted).

It is true that the Australian specimens hitherto referred to as *N. canescens* (=*N. campestris* R. Br.) possess subsessile or nearly sessile leaves, but similar leaves are also found in several specimens of Northern Rhodesia (Salisbury) and Indo-Pakistan subcontinent.

Uniform features of all these specimens are as follows: presence of 'acicular fibres' in both the phloem of the vascular bundle and also in the parenchymatous pith of the stem, complete absence of bracteoles, constantly 4-lobed calyx with the anterior one being forked at the apex, universal occurrence of capitate (either short or long) hairs on the bracts and calyx lobes [against the contention of Bremekamp (1964)], subactinomorphic or weakly bilabiate flimsy corolla with two included stamens, uniform anther structure (Fig.7.I,i), short and glabrous filaments, uniform pollen grains (either tricolporoidate or tricolporate), typically pointed capsule, and the seeds being ornamented with solid bars or hooks, some of which are branched at the extremities.

Although there is enormous variation in the morphological features as discussed above, there is practically no correlation among these characters.

Geographical distribution in association with other morphological characters also does not help in attributing subspecific rank to any subdivision of the species complex. No doubt it is an interesting point made by Bremekamp (1955, '64) that the genus is entirely absent from the area between the Malaysian Peninsula and New Guinea. But the occurrence of similar specimens (morpho-anatomically) in New Guinea, Australia, and Northern Rhodesia (Africa) should not be forgotten.

Abnormalities in the chromosome numbers have been recorded by Joseph (1964) in Nelsonia. Whether this is due to chromosomal rearrangements, aneuploidy, polyploidy or 'B' chromosomes is not yet definitely ascertained. Future biosystematic works on various populations of N. canescens can only prove whether minor variations of bracts and leaf shape are genetically fixed in the population or largely plastic owing to the changing habitats and environments.

At the present state of our knowledge one can conclude that the existing complex nature and unsatisfactory taxonomic situation in the genus Nelsonia are possibly due to its weedy tendencies. In lack of correlated characters I prefer to recognise only one species in Nelsonia having two minor varieties based on only leaf size.

It is of course, a bit difficult to believe that such an enormous amount of variability should be incorporated into the range of a single species. But in the absence of correlative characters recognition of many species on minor variations (mostly on single characters) largely reflects faulty taxonomy.

Cytotaxonomic and biosystematic investigation coupled with extensive field study are badly needed in the genus Nelsonia.

SPECIES DESCRIPTIONS IN STAUROGYNE AND ELYTRARIA WHICH ARE EITHER NEW TO SCIENCE OR NEW COMBINATIONS

/Note: Latin descriptions of the new species recognized here will be published within a short time; arranged according to the infrageneric classification followed in the text/.

1. Staurogyne cambodiana (R. Ben.) E. Hossain, stat. nov.

Syn: St. polybotrya (Nees) O. Kuntze var. cambodiana R. Ben. in Bull. Bot. Soc. France, 60: 267 (1913); Fl. Gen. Indo-China, 4: 628 (1935).

(Subgen. Tetrastichum, Sect. Tetrastichum)

Sparingly branched or unbranched, erect herbs, 10-16 cm, probably perennial. Stem woody at base, 1.5-4.5 mm thick, minutely pubescent, rarely glabrescent, distinctly articulated and ridged. Leaves sessile or subsessile; lamina 2.5-7 cm x 4-7 mm, elongate, narrowly oblanceolate-linear, margin repand, acute or subobtuse, both surfaces puberulent in young leaves, glabrous in mature ones. Inflorescence a terminal and axillary lax raceme, mostly on the apices of the branchlets. Flowers many or few, distinctly pedicellate, pedicels 1-2 mm, pubescent. Bracts, bracteoles, and calyx lobes hirtellous with glandular hairs, intermixed with a few simple, septate hairs. Lower bracts leaf-like, upper ones lanceolate-spathulate, subacute, 3-veined. Bracteoles 4-6 mm long, linear-lanceolate, acute, 3-veined. Calyx lobes dissimilar, all linear-lanceolate, acute; posterior lobe 8-9 mm x 0.8-1 mm, 5-veined; laterals 5.5-6 mm x 0.2-0.3 mm, 3-veined; anteriors 6-7.5 mm x 0.8-1 mm, 5-veined. Corolla glandular-puberulent outside, pubescent at the attachment of the filaments inside, 1-1.2 cm, 2-2.5 mm broad above, subactinomorphic. Stamens 4; filaments hirtellous with eglandular, septate hairs; anther bases mucronulate; staminode 1, very small and hyaline. Stigma trifurcate. Ovary glabrescent, ovules about 60, arranged in 4 rows in each loculus. Calsupe puberulent, 4.5-5 mm, up to 1.5 mm broad, oblong, mucronulate.

Type: INDO-CHINA: Kampong Soai, February, 1876, Hermand 404, 414 (P.)

LAOS: Expedition of Me-Kong, Kemarath, Thorel (P.)

Closely allied to St. polybotrya, but easily distinguished by its articulated, thick and woody stem, elongated narrowly lanceolate-linear leaves, elongated lax raceme, larger calyx lobes, and puberulent capsule.

2. Staurogyne dolichocalyx E. Hossain, sp. nov.

(Subgen. Tetrastichum, Sect. Zenkerina)

Erect herbs, 30 cm, semi-woody at base. Stem slightly ridged, glabrescent or tomentellous below, tomentose above, about 3.5 mm diam. at base, usually unbranched, sometimes provided with short, slender branches below, articulated. Leaves opposite, petiolate; petiole 1.5-4 cm, tomentose or tomentellous; lamina elliptic-lanceolate, 5-13 cm x 2-4.5 cm, entire, acute, attenuate at base, glabrous above, pubescent only on the veins below. Inflorescence a terminal or axillary, unbranched raceme, slightly nodding and elongated after fruiting. Flowers congested, very shortly pedicellate; pedicels 0.8-1 mm, up to 5 mm after fruiting, tomentose. Bracts narrowly lanceolate, acuminate, 3-veined, joined with the pedicel to some extent, pubescent. Bracteoles nearly at the top of the pedical, narrowly lanceolate, acuminate, pubescent. Calyx lobes sub-equal, all narrowly lanceolate, acuminate, 3-veined, puberulent or sparsely pubescent; posterior one 1.8-2.2 cm x 2-2.5 mm; laterals 1.6-2 cm x 1.2 mm; anteriors 1.8-2.1 cm x 1.8-2mm. Corolla light blue, fragrant, scabrid outside in bud; mature flowers not seen. Stamens 4, filaments hairy; staminode not seen. Stigma bifurcate. Ovary glabrous; ovules numerous (about 60 or more), arranged in 4 rows in each loculus; retinacula papilliform. Capsule narrowly ellipsoid, up to 1.2 cm, provided with an acute hard tip, tardily dehiscent; dehiscing valves shrink and become crimpled. Seeds small, angular-round or globose; testa foveolate with solid minute hooks.

Type: INDO-CHINA: Taai Wong Mo Shan & vicinity Chuk-phai, Ha-coi, Tonkin, October, 16-22, 1936, Tsang, W.T. 27028 (holo. E., iso. K.)

Indo-China: Taai Wong Mo Shan, near Chuk-phai, Ha-coi, Tonkin, May, 3 - June 22, 1939, Tsang, W.T. 2900 (E., P.)

This is a remarkable Asiatic species in Subgen. Tetrastichum, and can be at once identified by its large, narrowly-lanceolate, long-acuminate bracts, bracteoles and calyx lobes together with its large, ellipsoid-acuminate fruits.Its affinity with any other known Asiatic species of this subgenus is remote. But it approaches quite interestingly one species from Africa, e.g. St. kamerunensis.

These two species agree in their inflorescence, long bracts, bracteoles and calyx lobes associated with their tardily dehiscent fruit character. At present, with practically no cytogenetic data in the group, it is difficult to determine correctly whether this superficial resemblance does in fact reveal a close affinity of these two disjunct species in their evolutionary perspective.

/Note: All other species in Staurogyne belong to Subgen. Staurogyne/.

3. Staurogyne inaequalis E. Hossain, sp. nov.

/Sect. Staurogyne, Subsect. Macrosepalae, Ser. A (Heterosepalae)/.

Plant herbaceous, about 40 cm. Stem cylindrical, laxly branched, tomentose; branching sympodial. Leaves all opposite, petiolate; petiole 0.5-2 cm, tomentose or villous, lamina narrowly ovate-elliptic, elliptic-lanceolate or oblong-lanceolate, obtuse or subobtuse, base attenuate or obtuse, margin repand, upper surface glabrous, lower surface pubescent on the veins. Inflorescence in axillary and terminal, sessile or subsessile, dense raceme, always subtended by a pair of much reduced leaves at the base; peduncle short, 5 mm; rachis and peduncle white-tomentose. Flowers many, shortly pedicellate; pedicels 1-2 mm, tomentose. Bracts, bracteoles, and calyx lobes puberulous, sparsely

ciliolate at the margin. Bracts lanceolate-spathulate, 5-8 mm x 1.5-2 mm, slightly united with the pedicel at the base. Bracteoles at the top of the pedicel, 5-6 mm, linear-subspathulate. Calyx lobes profoundly dissimilar, anterior two lanceolate-subspathulate, others linear-lanceolate; posterior lobe up to 8 mm x 0.5-0.7 mm; laterals 5-6 mm x 0.4 mm; anteriors much prominent, up to 10 mm x 1.2-1.5 mm. Corolla white, subactinomorphic, 1.5-2 cm; tube 1.3-1.5 cm, about 4 mm broad above, glabrous outside, glandular pubescent at the attachment of the filaments inside. Stamens 4; filaments of the lower pair puberulent; staminode 1, small. Stigma trifurcate and cruciate. Ovary glabrous; ovules in two rows in each loculus. Capsule not seen.
Type: THAILAND: Phitsanulok, Phu Mieng Mountain, evergreen forest, alt. 1300 m, 27.7.1966, K. Larsen, T. Smitinand & E. Warncke 929 (holo. AAU).

Closely allied to St. shanica and also shows affinity with St. singularis of the Subsect. Microchlamydeae in having similar facies, much bigger anterior calyx lobes and the bracts which are slightly united to the pedicel at the base. St. inaequalis is at once recognized by its sessile or subsessile racemose inflorescences which are subtended by a pair of much reduced leaves, lanceolate-subspathulate bracteoles, bigger calyx lobes, smaller corolla, and characteristically longer anterior calyx lobes.

4. Staurogyne atropurpurea E. Hossain, sp. nov.

/Sect. Staurogyne, Subsect. Macrosepalae, Ser. A (Heterosepalae)7.

Plants subshrubby. Stem unbranched, brown and pubescent. Leaves petiolate; petiole pubescent, 2-3 cm, lamina lanceolate or elliptic-lanceolate, upper surface provided with sparsely distributed short strigae, lower surface puberulous or pubescent. Inflorescence a lax, drooping raceme, axillary or terminal, either unbranched or with 2-3 short branches at the base; peduncle white-tomentose with glandular and eglandular hairs. Flowers pedicellate, pedicels 1-2 mm.

Bracts, bracteoles and calyx lobes all densely hirtellous with long, septate eglandular hairs intermixed with glandular hairs. Bracts 6-8 mm, linear-lanceolate, acute. Bracteoles up to 6 mm, filiform, acute. Posterior calyx lobe up to 12 mm x 1 mm; laterals 8-8.5 mm x 0.5 mm; anteriors 11-12 mm x 0.5-0.7 mm, all linear-triangular, gradually ending into fine points. Corolla dark purple, 2.8-3 cm; tube 2.2-2.3 cm, glandular-pubescent outside, sparsely pubescent at the attachment of the filaments inside. Stamens 4, filaments glandular hairy; staminode 1, small. Style glabrous. Stigma deeply bifurcate; lower lobe smaller and thickened. Ovary glabrous, disc cushion-shaped; ovules in two rows in each loculus of the ovary. Capsule not seen. Type: THAILAND: Song Thaw, 1.11.1962, evergreen forest, alt. 800 m, Kai Larsen 9457 (holo. K.).

Related to St. lasiobotrys, but easily distinguished by its leaf indumentum, longer calyx lobes, and larger flowers with prominently dark purple corolla.

5. Staurogyne grandiflora E. Hossain, sp. nov.

[Sect. Staurogyne, Subsect. Macrosepalae, Ser. A (Heterosepalae)].

Unbranched, erect herb. Stem glabrescent below, brownish-puberulent above, 4.5 mm diam. Leaves opposite, petiolate; petiole 3-5 cm, glabrous below, minutely puberulent above; lamina 15-22 cm x 7-7.5 cm, broadly elliptic-lanceolate or oblong-lanceolate, acuminate, thin, base contracted, margin repand, glossy-green and glabrous above, grey white with minutely puberulent veins below. Inflorescence a terminal, drooping, few-branched lax raceme; peduncle short, 1 cm; rachis hirtellous with glandular and eglandular hairs. Flowers many, pedicellate, pedicels 2-3 mm, pubescent with glandular and eglandular hairs. Bracts, bracteoles, and calyx lobes hirtellous with glandular and eglandular hairs. Bracts linear-triangular, acute, 4-5 mm, 1-veined. Bracteoles at the top of the pedicel, similar to the bracts. Calyx lobes subsimilar;

laterals 9-9.5 mm x 0.5-0.7 mm, others 10-11 mm x 0.9-1 mm, all 3-veined, linear-triangular, acute. Corolla dark red, about 2.6 cm, up to 10.5 mm broad above, lobes 3-4 mm, glandular-puberulous outside, glabrous inside; tube contracted below, spreading above. Stamens 4, filaments sparsely hairy with minute glandular hairs; staminode 1.5 mm long, capitate at the apex. Stigma deeply bifurcate. Ovary glabrous, ovules about 34-36, arranged in two rows in each loculus. Capsule not seen.

Type: BURMA: Tavoy District, Kaleinaung Reserve, alt. 305 m, 28.1.1925, Ba Pe 833 (holo. K.).

This handsome species is well-marked in the genus for its enormously large, thin and glossy-green leaves. Its closest alley seems to be St. major from which it differs in its glabrescent stem and petiole, entirely glabrous upper surface of its remarkably large leaves, and the dark red corolla being glabrous inside.

6. Staurogyne aristata E. Hossain, sp. nov.

/Sect. Staurogyne, Subsect. Macrosepalae, Ser. A (Heterosepalae)/.

Monopodial herb, up to 18 cm. Stem minutely tomentose, 4.5 mm thick. Leaves opposite, petiolate; petiole 1-2.5 cm, brown-tomentose, slightly winged; lamina broadly elliptic, 14-16 cm x 6-8 cm, acute or subacute, entire or obscurely repand, glabrous above, minutely pubescent or puberulent on the veins below, brown. Inflorescence a terminal, subspicate, condensed, few-flowered raceme. Bracts and bracteoles up to 1.4 cm, linear-lanceolate, contracted into subulate points, puberulent; bracteoles at the top of the pedicel. Calyx lobes dissimilar, pubescent, margin ciliolate; laterals up to 8 mm, others up to 13.5 mm long, linear-lanceolate, contracted into subulate points (excepting the laterals). Corolla white, tube contracted at the base; spreading above, puberulent outside, bearded at the attachment of the filaments inside, about 2 cm, 6.5 mm broad above, lobes 3-4 mm. Stamens 4; filaments glandular-hirtellous; staminode 1, 1.3 mm, bilobed at the apex. Stigma bifurcate, hollow. Ovary glabrescent; ovules 24-28, arranged in two rows in each loculus. Capsule 5.5 mm, elongated, puberulent.

Type: THAILAND: Peninsular. Trang, Chowng, Ton Nam Pleie, alt. ca. 100 m, 14th November, T. Smitinand & E. C. Abbe 6139 (holo. K.) [Royal Forest Dept. No.24375].

Easily recognized by its broadly elliptic leaves which are glabrous above, condensed subspicate inflorescence, acute lateral calyx lobes, and bifurcate hollow stigma.

Morphologically - particularly in the characteristics of the bracts, bracteoles and calyx lobes - it resembles St. longifolia, and St. argentea. But the new species (St. aristata) is remarkably different from all other species of the Ser. Heterosepalae in its leaf anatomy, as it contains 'pseudo-terminal' sclereids in its leaf lamina.

7. Staurogyne filipes E. Hossain, sp. nov.

[Sect. Staurogyne, Subsect. Macrosepalae, Ser. A (Heterosepalae)].

Branched or unbranched herb, 12-35 cm. Stem tomentose, brown, 2.5-3 mm diam. Leaves all opposite, petiolate; petiole 0.5-4 cm, sparsely tomentose, brown; lamina 3-10.5 cm x 1-3 cm, lanceolate or elliptic-lanceolate, acute or subacute, entire or obscurely repand, ciliate or ciliolate, densely strigulose or pilose above, pubescent below. Inflorescence a lax raceme, unbranched, on axillary branches and terminal shoot apices, 6-8 flowered; rachis glandular-hirtellous, filiform. Flowers distinctly pedicellate, pedicels 2-8 mm, glandular-hirtellous or with glandular and eglandular hairs. Bracts, bracteoles and calyx lobes hirtellous with glandular and eglandular hairs. Bracts linear or linear-lanceolate, acute or subacute, 1-veined, 2.5-5.5 mm. Bracteoles nearly at the top of the pedicel, linear-acute, 3-5 mm, 1-veined. Calyx lobes subsimilar or dissimilar; laterals 4.5-6.5 mm, others 6.5-11 mm, all 3-veined. Corolla whitish or pale pink with purple lines on the throat, 10-12 mm, up to 4 mm broad above; tube slender below, spreading above, pubescent or glandular-pubescent outside, barbellate at the attachment of the filaments inside. Stamens 4, filaments glandular hairy with occasional eglandular hairs, staminode 1, 0.5 mm. Stigma trifurcate and cruciate. Ovary glabrous, ovules about 26-28, arranged in two rows in each loculus. Capsule puberulent, elongate-conical, about 5 mm long, mucronulate.

Two variants can be recognized: they are not given any formal latin name owing to the limited materials.

Variant A.

Pedicels 2-6 mm. Bracts linear-acute, 2.5-3.5 mm.

Type: LAOS: Muang Huang, Wiengchan, alt. c. 200 m, in evergreen bamboo forest, March 31st, 1932, A.F.G. Kerr 21771 (holo. K).

LAOS: Muang Huang, Wiengchan, alt. c. 200 m, in evergreen bamboo forest, 29th March, 1932, A.F.G. Kerr 20793 (BM, K).

Variant B.

Pedicels 6-8 mm. Bracts 4-5.5 mm, linear-lanceolate.

Type: THAILAND: Betang, Pattani, alt. c. 400 m, evergreen forest, August 1st, 1923, A.F.G. Kerr 7442 (holo. BM).

THAILAND: Betang, Pattani, alt. 400 m, evergreen forest, August 24th, 1923, A.F.G. Kerr 7920 (BM).

Apparently an isolated species of this area but to some extent approaching St. amoena, particularly in the nature of inflorescence, bracts, bracteoles and calyx characters. But St. filipes is quite distinct in the indumentum of its various parts, lanceolate or elliptic-lanceolate smaller leaves, smaller calyx, corolla and filiform rachis of the inflorescence.

8. Staurogyne microphylla (Nees) E. Hossain, stat. nov.

Syn: Ebermaiera minarum var. microphylla Nees in Mart., Fl. Bras. 9: 18 (1847).

Staurogyne ericoides Lindau in Engl., Bot. Jhrb. Biebl. 25 (60): 44 (1898).

(Sect. Staurogyne, Subsect. Macrosepalae, Ser. C.)

Subshrubby and woody at least below. Leaves shortly petiolate; petiole 2-7 mm, tomentose; lamina narrowly lanceolate or oblong-lanceolate, acute, 1.8-6 cm x 0.5-1 cm, attenuate below, upper surface either subglabrous with prominent veins or densely strigose, lower surface pubescent or densely strigose. Infrloescence a few-flowered (2-6) raceme, mostly terminal, rarely on branch apices. Flowers pedicellate, pedicels 5-8 mm. Bracts narrowly lanceolate, smaller than the calyx lobes, sparsely or densely pubescent with glandular and eglandular hairs. Bracteoles at the top of the pedicel, linear-lanceolate, hirsute with glandular and eglandular hairs. Calyx lobes largely dissimilar; posterior one lanceolate, up to 1.6 cm x 3 cm, laterals 1 cm, anteriors 1.2-1.4 cm, all hirtellous with mainly glandular intermixed with a few eglandular hairs. Corolla subactinomorphic, more than 3 cm, 5.5-6 mm broad above; tube cylindrical, up to 3 cm, densely pubescent outside, glabrous inside. Stamens 4; filaments glabrous; staminode 1, prominently long, sigmoid at the base, bilobed at the apex. Stigma subexserted, deeply bifurcate with the lower lobe again lobed at the apex. Ovary subglabrous; disc well developed; ovules in two rows in each loculus. Capsule hairy.

Type: BRAZIL: in ripa rivuli Tymbopeba, August, 1824, L. Reidel 467 (holo. Leningrad).

BRAZIL. Minas prope Alegria ad Caraca ad rivulos, A. Glaziou 15295 (K).

That the variety deserves a specific rank can be justified by its several distinguishing characters of taxonomic importance. Firstly, the leaves which are shortly petiolate and narrowly lanceolate or oblong-lanceolate in St. microphylla, but broadly lanceolate in St. minarum and provided with long petioles. Further, the smaller bracts, bracteoles and calyx lobes merit particular mention; they are mostly glandular hairy in the former, while entirely eglandular hairy in the latter.

Anatomically St. microphylla is unique amongst all of the American species, as it contains fusiform, much thickened, unbranched, short fibres running parallel with the veins of the leaf lamina (possibly transformed 'acicular fibres' of the phloem tissue) resembling superficially to be the sclereids of other species.

9. Staurogyne euryphylla E. Hossain, nom. nov.

Syn: Ebermaiera riedeliana Nees var. latifolia Nees in Mart., Fl. Bras. 9: 19 (1847), non St. latifolia Brem. (1969).

(Sect. Staurogyne, Subsect. Macrosepalae, Ser. D.)

Ascending, erect or decumbent herbs. Stem subherbaceous, pubescent below, tomentose above. Leaves shortly petiolate, petiole 0.8-2.5 cm, tomentose; lamina ovate-lanceolate, acute, 2-8.5 cm x 1-3 cm, base subcordate or sharply contracted, upper surface papillose and sparsely strigulose, lower surface sparsely papillose with pubescent veins. Inflorescence on axillary and terminal or only on terminal apices, densely spicate. Bracts prominent, lower ones leaf-like, elliptic-lanceolate, acute or subacute. Bracteoles at the top of the pedicel, linear-lanceolate. Calyx lobes largely dissimilar; laterals 5-6 mm, others 7-8 mm; posterior lobe elliptic-lanceolate, others linear or linear-oblanceolate. Bracts, bracteoles and calyx lobes covered with glandular and eglandular hairs. Corolla subactinomorphic, slightly bilabiate, 6-7 mm, 2 mm broad above, papillose and pubescent outside with glandular and eglandular hairs. Stigma deeply bifurcate with lower lobe again lobed at the apex. Ovary subglabrous; ovules about 12, arranged in two rows in each loculus. Capsule glandular hairy, oblong-conical, tip mucronulate, up to 4 mm x 2 mm.

Type: BRAZIL: Esparanga (Bahia), June 1822, L. Riedel /170/ (Leningrad): type of Ebermaiera riedeliana var. latifolia. Nees (1847), while describing St. riedeliana pointed out that the species is related to a widely occurring Asiatic species - St. glauca (= spatulata). This affinity is unlikely as the latter species bears 4 rows of ovules (about 60 or more) in each loculus of the ovary, possesses an ill-defined racemose inflorescences (lower flowers seem to be solitary and axillary), and shows isolated pericyclic fibres surrounding the vascular cylinder of the stem. In fact all the American species belong to the advanced Subgen. Staurogyne, none in the primitive Subgen. Tetrastichum.

The variety latifolia, originally described under the species St. riedeliana, actually differs from the latter species in many respects, especially in its facies, subherbaceous stem, broadly lanceolate leaves with subcordate or sharply contracted base, lamina being papillose on both surfaces, elongated spike (2-6 cm), and elliptic-lanceolate, acute bracts. Its specific status is thus clearly justified by the available evidence. As the specific epithet latifolia is already occupied, a new name (St. euryphylla) has been applied to this species.

10. Staurogyne longibracteata E. Hossain, sp. nov.

(Sect. Staurogyne, Subsect. Macrochlamydeae)

Erect herb, about 30-40 cm. Stem 2-3 mm diam., brownish, slightly woody at the base, clothed with minute hairs below, glabrous above. Leaves opposite, petiolate, petiole about 2-4 cm, glabrescent or with sparsely distributed minute brown hairs; lamina elliptic-lanceolate, 6-16 cm x 2-6 cm, acute, entire, base contracted or cuneate, glabrous, pale-green above, glabrescent, reddish-brown below, veins prominent on underside, usually with short brownish hairs.

Inflorescence a terminal spicate raceme, unbranched; peduncle short, up to 1 cm long, rachis glabrous. Flowers very shortly pedicellate, pedicels usually 1-2 mm, attaining up to 3 mm after fruiting. Bracts elliptic-lanceolate or elliptic-obovobate, obtuse or mucronulate, pale brown, 5-veined, 1-1.6 cm x 5-6.5 mm, glabrous. Bracteoles linear-lanceolate, acute, subacute, 3-veined, 6-8 mm x 0.5-1 mm, glabrous. Calyx lobes subequal, posterior one 3-3.5 mm x 1 mm; others 2-2.8 mm x 0.6-0.9 mm, all triangular, acute, glabrous. Corolla 1.8-2.5 cm, up to 6.5 mm broad above, glabrous outside, papillose inside, densely barbellate at the attachment of the filaments; lobes red, minutely hairy at the tip. Stamens 4; filaments and anthers glandular hairy; staminode small, ecapitate, 0.8-1 mm. Stigma broad, hollow, and bifurcate; upper lobe fimbriate, lower lobe again forked. Ovary glabrous, ovate-elongate, mucronulate, up to 7.5 mm x 2.5 mm, dehiscing into two woody recurved valves. Seeds globose; testa foveolate and provided with adpressed minute hooked processes.

Type: BURMA: Tavoy District, Hills West of Pungdow Power Station, Alt. 305 m, August, 1961, J. Keenan, U Tun Aung & R.H. Rule 940 (holo. E).

BURMA: Tenasserim Division: Tavoy District, Hillside West of Pungdow Power Station, alt. 671 m, August, 1961, J. Keenan, U Tun Aung & R.H. Rule 860 (E); ibid., Hills West of Pungdow Power Station, alt. 640 m, August, 1961, J. Keenan, et al. 801 (E); ibid., 2½ miles east of Pungdow Power Station, alt. 366 m, 22nd August, 1961, J. Keenan et al. 1121 (E).

Closely related to St. longispica and St. cuneata, but can be easily distinguished from the former by its elliptic-lanceolate or elliptic obovate, 5-veined bracts, unbranched, spicate racemose inflorescence and 36-40 ovules in each loculus of the ovary. From St. cuneata it differs in its bracts character, larger flowers, and glabrousness of the various parts.

11. Staurogyne subrosulata E. Hossain, sp. nov.

(Sect. Staurogyne, Subsect. Microchlamydeae)

Subrosulate herb, c. 30 cm (including the inflorescence). Stem tomentellous. Leaves petiolate; petiole 1-4 mm, tomentellous; lamina elliptic-oblanceolate, subacute, entire, puberulo-pubescent above, minutely puberulent below with tomentellous prominent veins, 7-15 cm x 4-6 cm, base contracted. Inflorescence terminal or subterminal; peduncles many, 4-6 cm, paniculately branched above, puberulent. Flowers lax, very shortly pedicellate; pedicels 0.5 - 1 mm, puberulent. Bracts and bracteoles triangular-lanceolate, acute, puberulous with ciliate margin, up to 2 mm x 0.8 mm. Bracts arise from the inflorescence axis; bracteoles nearly at the top of the pedicel. Calyx lobes elliptic-lanceolate, subequal, acute, 5.5-6 mm; posterior lobe 1-1.2 mm broad, anteriors 0.8 mm, and laterals 0.5 mm broad, all scabrid with ciliate margin. Corolla bluish-purple, 1.6-1.8 cm, up to 2.5 mm broad above, prominently hairy outside, pubescent at the attachment of the filaments inside; lobes 2-3 mm, orbicular-obtuse. Stamens 4, anthers hairy at the back, lobes mucronulate at the base; filaments glandular hairy; staminode 1, small, 0.5 mm, capitate. Stigma bifurcate and hollow, lower lobe forked again. Ovary glabrous, ovules in two rows in each loculus. Capsule not seen.

Type: THAILAND: Central. Sarika Falls at Nakhon Nyok, alt. 300 m, 14th August, 1968, Kai Larsen, T. Santisuk & E. Warncke 3398 (holo. AAU).

Its near relative is St. rosulata in a different Subsect. Macrosepalae from which it differs in its elliptic-oblanceolate leaves, much branched paniculiform inflorescence supported by long peduncles, triangular minute bracts and bracteoles with a prominently hairy corolla. Moreover, it is noteworthy that in St. rosulata, linear or linear-lanceolate bracts come out from the pedicel, but in St. subrosulata they arise from the inflorescence axis proper.

12. *Staurogyne diandra* E. Hossain, *sp. nov.*

(Sect. *Staurogyne*, Subsect. *Microchlamydeae*)

Suffruticose plant c. 64 cm. Stem woody at base, pubescent, 4 mm thick. Leaves all opposite, petiolate; petiole 1.5-6 cm long, pubescent; lamina 5-15 cm x 2.5-6 cm, elliptic-lanceolate, acute, margin obscurely repand, upper surface glabrous, lower surface glabrescent except the pubescent veins. Inflorescence a terminal, many flowered, lax raceme; peduncle 3.5 cm, axis pubescent. Flowers shortly pedicellate; pedicels 2-3 mm, minutely pubescent. Bracts and bracteoles linear-lanceolate, acute, glabrous; bracts 5-6 mm and bracteoles 4.5-5 mm. Calyx lobes dissimilar, all linear-triangular, acute, glabrous; posterior lobe 6-8 mm, 7-veined; anteriors 6-8.5 mm, 5-veined; laterals 5-6 mm, 3-veined. Corolla 2-2.5 cm, up to 5.5 mm broad above; lobes 2.5-3 mm, glabrous outside and inside. Stamens 2; filaments glabrous; staminodes 2 or 3, two always prominent, 3-4.5 mm, apex bifurcate. Stigma shortly bifurcate, slightly protruding out, one lobe smaller and thicker than the other. Ovary glabrous; ovules about 27-28, arranged in two rows in each loculus. Capsule not seen.

Type: INDO-CHINA: Tonkin, Chapa, alt. 1900 m, April, 1936, *Petelot* 5928 (holo.P).

Unique in the genus *Staurogyne* in having two fertile stamens and 2 or 3 staminodes. Apparently unrelated to any other species of the Subsect. *Microchlamydeae*. But it shows, however, a distinct morphological affinity with *St. vicina*, particularly in the nature of inflorescence and glabrous subactinomorphic corolla. At present its true relationship is uncertain.

13. *Staurogyne spiciformis* E. Hossain, *sp. nov.*

(Sect. *Staurogyne*, Subsect. *Microchlamydeae*)

Unbranched herb, 10-24 cm. Stem 1.5-2 mm diam., pubescent with brownish hairs. Leaves all opposite, petiolate; petiole 1-3cm, brownish-pubescent; lamina

oblong-elliptic, acute or subacute, base contracted, margin obscurely repand, minutely pubescent, 4-12 cm x 1.5-3.8 cm, upper surface minutely pubescent or puberulent, lower surface puberulent, densely pubescent on the veins. Inflorescence a terminal or axillary, densely spicate raceme, axis pubescent. Bracts linear-lanceolate, up to 4 mm, minutely pubescent, margin ciliolate. Bracteoles at the top of the pedicel, up to 2 mm, triangular-acute, minutely pubescent, margin ciliolate. Clayx lobes slightly dissimilar, all 3-veined, minutely pubescent, margin ciliolate; posterior lobe 2.8-3.5 mm, laterals 2.6-3 mm, and anteriors 3.5-4 mm, all linear-triangular, acute. Corolla subactinomorphic, 10-11.5 mm, up to 2.5-3.5 mm broad above; lobes 1.5-2.5 mm; tube slender below, spreading above, puberulent outside, hirtellous inside at the attachment of the filaments. Stamens 4; filaments minutely glandular-hairy; staminode 1, 0.3 mm, white. Stigma deeply bifurcate. Ovary glabrous; ovules 16-17, arranged in two rows in each loculus. Capsule not seen.
Type: CAMBODIA: Crescit prope rivus in montibus Epong, alt. 1200 m, June, 1870, L. Pierre 1075 (holo. P, iso. P).

Related to St. vicina, but easily distinguished by its leaves being pubescent or puberulent on both surfaces, spicate inflorescences, shortly pubescent-ciliolate calyx lobes, shorter puberulent corolla, and minutely glandular-hairy staminal filaments.

14. Staurogyne Kerrii E. Hossain, sp. nov.

(Sect. Staurogyne, Subsect. Microchlamydeae)

Branched or unbranched herb, 15-30 cm. Stem decumbent and woody at base, rooting at the nodes, sparsely pubescent below, tomentose-brown above. Leaves opposite, petiolate; petiole 1-5 cm, scarsely or densely tomentose; lamina elliptic, obovate or oblong, 5-10 cm x 2-4.5 cm, obtuse or subobtuse, subherbaceous, margin obscurely repand, ciliolate, base slightly unequal or subcordate, upper surface pilose, lower surface minutely pubescent, veins tomentose, greyish-brown. Inflorescence terminal or axillary, few-branched panicle; peduncle brownish-red, pubescent; rachis pubescent below, glandular-hirtellous at the top. Flowers many, shortly pedicellate, up to 2 mm after fruiting, pubescent. Bracts linear-lanceolate, acute, 2.5-3mm, minutely pubescent. Bracteoles at the top of the pedicel, linear-triangular, acute, 1.5-2 mm, minutely pubescent. Calyx lobes unequal, triangular-linear, acuminate, red-tipped, pubescent and ciliate with short glandular and eglandular hairs; laterals up to 3 mm, others 3.5-4 mm. Corolla white, 10-12 mm, up to 2.5 mm broad above; lobes purple, 1-1.5 mm, ciliolate outside; tube glandular-hirtellous outside, pubescent at the attachment of the filaments inside. Stamens 4; filaments glandular-hairy; staminode 1, prominent, 1 mm, capitate and bifurcate at the tip. Stigma bifurcate. Ovary glabrous; ovules in two rows in each loculus. Capsule not seen.

Type: THAILAND: Tasan. Chumpaun, alt. 150 m, December, 23, 1928, A.F.G. Kerr 16307 (holo. BM).

THAILAND: Klaung Hin Kao. Petalung, alt. c. 300 m, April 18, 1928, A.F.G. Kerr 15287 (BM).

Closely allied to St. merguensis and St. tenuispica, but differs in habit, pilose upper surface of the elliptic, obovate or oblong leaves, and triangular-linear, acuminate, pubescent and ciliate (both glandular and eglandular hairs) calyx lobes.

The most interesting aspect of St. kerrii lies in its leaf anatomy. Both St. merguensis and St. tenuispica possess 'diffuse astrosclereids' in their leaf-lamina, while St. kerrii contains 'pseudo-terminal', less branched sclereids. This type of sclereids is also found in St. aristata of the Subsect. Macrosepalae and in St. pedicellata of the Subsect. Microchlamydeae. However, both these species differ widely from *St. kerrii* in several important characters.

15. *Staurogyne pedicellata* E. Hossain, *sp. nov.*

(Sect. *Staurogyne*, Subsect. *Microchlamydeae*)

Unbranched, low herb, decumbent and woody at base, erect above, sometimes rooting at the nodes. Stem dark-brown, subglabrous and articulated. Leaves petiolate, all opposite; petiole 1-4 cm, dark brown, warty and sprasely strigulose; lamina narrowly oblong-lanceolate, 3-16 cm x 1-3.5 cm, entire or minutely repand, acute or subacute, both surfaces puberulent with sparsely strigulose veins, reddish-brown. Inflorescence a terminal, unbranched or few-branched pedunculate, lax, raceme; peduncle slightly shorter or longer than the internodes of the rachis; inflorescence axis densely pubescent. Flowers with long pedicels, largely unilateral after anthesis; pedicels 2.5-3.5 mm, after fruiting up to 5 mm. Bracts minute, 1-1.5 mm, triangular-acute, minutely pubescent. Bracteoles below the top of the pedicel, similar to the bracts. Calyx lobes subsimilar, all linear-triangular, acute, pubescent, 2-3 mm x 0.5 mm. Corolla about 1 cm, tube 9 mm, up to 2 mm broad above, slender and curved below, glandular-pubescent at base, scabrid above, barbellate at the attachment of filaments inside; lobes slightly violet inwards. Stamens 4; filaments glandular-hairy; staminode 1, prominent, 1.5 mm, capitate. Stigma trifurcate and cruciate. Ovary glabrous; ovules 20-22 in two rows in each loculus. Capsule elongate-conical, tip mucronulate, subglabrous, about 6.5 mm x 2.5 mm. Seeds subglobose, brownish-black; testa foveolate with minute, hooked processes. Type: EAST BORNEO: West Kutei, Mt. Palimasan near Tabang on Belajan River, alt. 500 m, 13 September, 1956, *A. Kostermans* 12998 (holo. Leiden, iso. K. Arn. Arb.).

Apparently an isolated species within the Subsect. *Microchlamydeae*. It is easily recognized by its narrowly oblong-lanceolate leaves which are puberulent on both surfaces, largely unilateral (after anthesis) flowers with long pedicels, and prominent staminode.

Possibly it bears a distant affinity with <u>St. humifusa</u>, but differs in many important characters. Anatomically, <u>St. pedicellata</u> is especially marked by its 'double diacytic' stomata, epidermal cells with remarkably pitted cell-walls (lower epidermal cells), and 'pseudo-terminal' sclereids in the leaf lamina.

16. <u>Elytraria nodosa</u> E. Hossain, <u>sp. nov.</u>

(Subgen. <u>Tetrandra</u>)

Much branched, probably perennial herb, c. 28 cm. Stem woody at base, 2-3 mm diam., prominently articulated with swollen nodes, glabrous below, pubescent above. Leaves verticellate, 2-4 arising from the node, petiolate; petiole 4-12 mm, minutely pubescent; lamina broadly lanceolate, very thin, sparsely pubescent on the veins below, puberulent above, 1. 5-5 cm x 0.8-2.2 cm. Inflorescence a spike, terminal and axillary; rachis (scape) 1-4, arising from each node having a tuft of bristle-like hairs, lower portion with numerous spirally arranged, sterile, ovate-acute, clasping, rigid, overlapping scale-leaves; flower-bearing inflorescence 0.5-1.4 mm x 3-4.5 mm. Bracts ovate, acute, concave, rigid, aristate, margin hyaline, minutely pubescent at the apex, glabrous outside, 4-5 mm x 3 mm. Bracteoles linear-lanceolate, aristate, concave, 3.5-4 mm x 0.5 mm, margin subhyaline, apex and the keel ciliate with septate hairs. Calyx lobes 4, lower lobe deeply bifurcate nearly to the base giving an impression of a 5-lobed calyx), all narrowly elliptic-lanceolate, scarious at the tip, apex ciliate with septate hairs, 4-4.5 mm; posterior lobe slightly broader than the rest. Corolla bilabiate, glabrous outside and inside. Stamens 4; filaments puberulous, inserted much above the base of the corolla tube; anthers alongated in mature flowers, subglobose in buds, two lobes placed at different levels; distal appendage prominent; staminode

1 or 0, very small and hyaline. Ovary glabrous; ovules 4-5 in each loculus. Capsule conical, about 3.5 mm, glabrous.

Type: MADAGASCAR: Voyage of M. Boivin, 1847-1852, Bernier herb. No. 289 (holo. P). MADAGASCAR: Goudot, Herb. Maire (P).

Closely related to another endemic species, E. madagascariensis but easily distinguished by its inflorescence having numerous sterile scale-leaves below, ovate glabrous bracts, and ciliate keel of the bracteoles.

These two specimens were cited by R. Benoist under Tubiflora acaulis in the "Flora of Madagascar" vol. 1 (182e): 25 (1967). The conserved name of the genus is Elytraria Michx., and the species E. acaulis is confined to Indo-Malaya and tropical Africa. It is a caulescent species with a short stem, having alternate and subalternate leaves, 2 fertile stamens, and 2 little staminodes. Benoist probably misidentified the above two Madagascar specimens as E. acaulis, owing to similaries in bract and calyx characters.

INDEX TO GENERA AND SPECIES SO FAR REFERRED TO THE NELSONIOIDEAE

[Only the recognized genera in the Nelsonioideae are numbered according to the text and their page numbers given. Species with asterisk marks are keyed out in the text; those with double underlines are not seen by the author; species with double asterisk marks refer to the monotypic ones recognized; genera and species cited after (=) sign refer to their valid names St. = *Staurogyne*; N. = Nelsonia; E. = *Elytraria*, and A. = *Anisosepalum*].

Ebermaiera Nees = Staurogyne

angustifolia T. And. = St. argentea var. angustifolia
argentea Nees = St. argentea
axillaris Nees = St. comosa (Nees) O. Kuntze = St. cremostachya
beddomei Clarke = St. beddomei
brachiata Hiern. = St. brachiata
concinnula Hance = St. concinnula
coriacea T. And. = St. coriacea
debilis T. And. = St. debilis
elegans Nees = St. elegans
elongata Nees = St. elongata
fastigiata Nees = St. fastigiata
glauca Nees = St. glauca = St. spatulata
glutinosa Wall. = St. glutinosa
gracilis T. And. = St. gracilis
gracilis Wawra = St. wawrana
griffithiana T. And. = St. griffithiana
helferi T And. = St. helferi
hirsuta Nees = St. hirsuta
humilis Nees = St. polybotrya var. humilis
humilis Miq. = St. miqueliana
incana (Bl.) Hassk. = St. incana
itatiaiae Wawra = St. itatiaiae
lanceolata (Bl.) Hassk. = St. lanceolata
lasiobotrys Nees = St. lasiobotrys
longifolia Nees = St. longifolia
longispica Ridl. = St. longispica

macahensis Glaz. on herbarium sheet = *St. mandioccana*; probably a form of variety
maclellandii T. And. = *St. maclellandii*
mandioccana Nees = *St. mandioccana*
merguensis T. And. = *St. merguensis*
minarum Nees = *St. minarum*
minarum Nees var. *microphylla* Nees = *St. microphylla*
neesii Vidal = *St. neesii*
nelsonioides Miq. = *Adenosma nelsonioides* (Miq.) Hall. f. ex Brem.
nitida Reichb. = *St. nitida* Clarke on herbarium sheet = non *Staurogyne*!
obtusa T. And. = *St. obtusa*
paniculata Wall. ex T. And. = *St. paniculata*
parviflora T. And. ex Clarke = *St. parviflora*
polybotrya Nees = *St. polybotrya*
racemosa (Roxb.) Miq. = *St. racemosa*
repens Nees = *St. repens*
riedeliana Nees = *St. riedeliana*
var. *latifolia* Nees = *St. euryphylla*
sanctae-catharinae Nees = non *Staurogyne*!
setigera Nees = *St. setigera*
simonsii T. And. = *St. simonsii*
spicata Ridl. on herbarium sheet = *St. spiciflora*
?*spiciflora* Miq. = *St. spiciflora*
staurogyne Nees = *St. argentea*
stolonifera Nees = *St. stolonifera*
subcapitata Clarke = *St. setigera*

subpaniculata Hassk. = St. elongata

trichocephala Miq. = St. setigera

thyrsoidea Nees = St. thyrsoidea

vauthieriana Nees = St. vauthieriana

velutina Nees = St. velutina

veronicifolia Nees = St. veronicifolia

warmingiana Hiern. = St. warmingiana

zeylanica Nees = St. zeylanica

Elytraria Michx. nom. cons. Gen. No. 7, pp. 99-106

*acaulis (L. f.) Lindau

var. lyrata (Vahl) Brem.

acuminata (Small) Cory = bromoides

amara Blanco = imbricata

angustifolia (Small) Leonard = caroliniensis var. angustifolia

apargifolia Nees = imbricata

*bromoides Oerst.

caulescens Ledeb. = imbricata

*caroliniensis (J.F. Gmel.) Pers.

var. angustifolia (Fernald) Blake

crenata Vahl = acaulis

crenata Vahl var. lyrata Vahl = acaulis var. lyrata

crenata Leonard = cubana

*cubana (Leonard) Alain

cupressina Nees = caroliniensis

fasciculata H.B.K. = imbricata

frondosa H.B.K. = imbricata

herbacea Michx. = caroliniensis

*_imbricata_ (Vahl) Pers.
indica Pers. = _acaulis_
*_klugii_ Leonard
lyrata Vahl = _E. acaulis_ var. _lyrata_
*_macrophylla_ Leonard
*_madagascariensis_ (R. Ben.) E. Hossain, _comb. nov._
*_marginata_ Vahl
*_maritima_ J.K. Morton
microstachya Oerst. = _imbricata_
*_nodosa_ E. Hossain, _sp. nov._
pachystachya Oerst. = _imbricata_
*_planifolia_ Leonard
*_prolifera_ Leonard
ramosa H.B.K. = _imbricata_
scorpioides Roem. & Schult. = _imbricata_
*_shaferi_ (P.Wilson) Leonard
squamosa (Jacq.) Lindau = _imbricata_
tridentata Vahl = _imbricata_
tridentata Vahl var. _wrightii_ Gomez = _shaferi_
*_tuberosa_ Leonard
vahliana Michx. = _caroliniensis_
virgata Michx. = _caroliniensis_
virgata Michx. var. _angustifolia_ Fernald = _caroliniensis_ var. _angustifolia_
virgata Michx. var. _vahliana_ Nees = _E. caroliniensis_

Erythracanthus Nees = _Staurogyne_
elongatus (Bl.) Nees = _St. elongata_

griffithianus Nees = *St. griffithiana*

obtusus Nees = *St. obtusa*

racemosus (Roxb.) Nees = *St. racemosa*

Geophila D. Don (Rubiaceae)

hirsuta Chev. = *St. paludosa*

Gynocraterium Brem. Gen. No. 4, pp. 95

***guianense* Brem.

Hiernia S. Moore (Scrophulariaceae)

angolensis S. Moore

Justicia Linn. (tribe Justiceae, Subfam. Acanthoideae)

acaulis L. f. = *Elytraria acaulis*

ajugoides L. Hamilt. = *Nelsonia canescens*

bengalensis Spreng. = *N. canescens*

brunelloides Lam. = *Hemigraphis brunelloides* (Lam.) Brem.

canescens Lam. = *N. canescens* (Lam.) Spreng.

imbricata Vahl = *E. imbricata*

lamiifolia Koen. = *N. canescens*

lamiifolia Roxb. = *N. canescens*

nummulariaefolia Vahl = *N. canescens*

origanoides Vahl = *N. canescens*

pentastachya L. Hamilt. = *N. canescens*

pusilla Pohl = *N. canescens*

tomentosa Roxb. = *N. canescens*

Lepidagathis Nees (tribe Barlerieae)

incana (Bl.) Nees = *Staurogyne incana*

Limnophila R. Br. (Scrophulariaceae)

viscida Ridl. = *St. viscida* (Ridl.) Brem.

- *Loxostigma* C.B. Clarke (Gesneriaceae)
  - *sesamoides* Hand.-Mazz. = *St. sesamoides*
- *Nelsonia* R. Br. Gen. No. 6, pp. 98-99
  - *albicans* Kunth = *canescens*
  - *campestris* R. Br. = *canescens*
    - var. *vestita* (Roem. & Schult.) Clarke = *canescens* var. *vestita*
  - ***canescens* (Lam.) Spreng.
    - var. vestita (Roem. & Schult.) E. Hossain, *comb. nov.*
  - *hirsuta* Roem. & Schult. = *Ruellia hirsuta*
  - *lamiifolia* Hochst = *canescens*
  - *lamiifolia* Roxb. = *canescens*
  - *nummulariaefolia* Roem. & Schult. = *canescens*
  - *origanoides* Roem. & Schult. = *canescens*
  - *origanoides* Hochst = *canescens*
  - *pohlii* Nees = *canescens*
  - *rotundifolia* R. Br. = *canescens*
  - *tomentosa* Willd. = *canescens*
  - *vestita* Roem. & Schult. = *canescens*
- *Neozenkerina* Mildbr. = *Staurogyne*
  - *bicolor* Mildbr. = *St. kamerunensis*
- *Ophiorrhiziphyllon* Kurz Gen. No. 3, pp. 93-94
  - *hypoleucum* R. Ben. = *St. hypoleuca* (R. Ben.) R. Ben.
  - *laxum* Lindau = *Justicia* sp.
  - ***macrobotryum* Kurz
  - *poilanei* R. Ben. = *macrobotryum* *syn. nov.*

Poecilocnemis Mart. ex Nees = _Geissomeria_ Lindl. & others

minarum Mart. = _Staurogyne minarum_

Ruellia L. (tribe Ruellieae)

comosa Wall. nom. nud. = _St. eremostachya_ Brem.

diffusa Vell. = _N. canescens_

incana Bl. = _St. incana_

racemosa Roxb. _St. racemosa_

Saintpauliopsis Staner Gen. No. 2, pp. 94-95

** _lebrunii_ Staner

Stachytarpheta Vahl (Verbenaceae)

squamosa Vahl = _Elytraria imbricata_

Staurogyne Wall. Gen. No. 1, pp. 91-93; 127-160

*_agrestis_ Leonard

alboviolacea R. Ben. = _Anisosepalum alboviolaceum_

Subsp. _grandiflora_ Napper = " subsp. _grandiflorum_

var. _gracilior_ Heine = _A. alboviolacea_ var. _gracilius_

*_amboinica_ Brem.

*_amoena_ R. Br.

angustifolia Wall. = _St. argentea_ var. _angustifolia_

*_anigozanthus_ (Nees) O. Kuntze

*_anomala_ Brem.

*_arcuata_ C.B. Clarke

*_argentea_ Wall.

var. _angustifolia_ (Wall.) E. Hossain, _stat. nov._

var. _breviaristata_ Imlay

*_aristata_ E. Hossain, _sp. nov._

*_athroantha_ Brem.

Staurogyne (contd.)

*atropurpurea E. Hossain, sp. nov.

*axillaris S. Moore

balabacensis Quisumb. = setigera var. grandis Brem.

*balansae R. Ben.

*batuensis Brem.

*beddomei (C.B. Clarke) O. Kuntze

*bella Brem.

var. longipedicellata Brem. = singularis var. longipedicellata

*brachiata (Hiern.) Leonard

*brachystachya R. Ben.

*brevicaulis R. Ben.

*bullata Brem.

*burbidgei C.B. Clarke ex Brem.

*cambodiana (R. Ben.) E. Hossain, stat. nov.

candelabrum Brem. = spatulata complex

*capillipes Brem.

*capitata E.A. Bruce

*chapaensis R. Ben.

ciliata Elm. = debilis var. ciliata

*citrina Ridl.

comosa (Wall.) O. Kuntze, nom. illeg. = cremostachya

*concinnula (Hance) O. Kuntze

*condensata Brem.

congoensis S. Moore = le-testuana

*coriacea (T. And.) O. Kuntze

*cremostachya Brem.

*cuneata Imlay

Staurogyne (contd.)

- *dasyphylla Brem.
- dasystachya Brem. = novoguineensis
- *debilis (T. And.) C.B. Clarke ex Merr.
  - var. ciliata (Elm.) E. Hossain, stat. nov.
  - var. pubifolia Brem.
  - var. longifolia Brem.
- *densifolia Brem.
- *diandra E. Hossain, sp. nov.
- *diantheroides Lindau
- *dispar Imlay
- *dolichocalyx E. Hossain, sp. nov.
- *elegans (Nees) O. Kuntze
- *elongata (Bl.) O. Kuntze
- ericoides Lindau = microphylla, syn. nov.
- *euryphylla E. Hossain, nom. nov.
- *eustachya Lindau
- *expansa Brem.
- *fastigiata (Nees) O. Kuntze
- *filipes E. Hoasain, sp. nov.
- flexicaulis Brem. = spatulata complex
- floribunda Rizzini in clavi, sine descri.
- *fockeana Brem.
- glauca (Nees) O. Kuntze = spatulata complex
  - var. spatulata C.B. Clarke = spatulata (Bl.) Kds.
- *glutinosa (Wall.) O. Kuntze
- *glutinosa Lindau, non Wall.

Staurogyne (contd.)

*gracilis (T. And.) O. Kuntze

*grandiflora E. Hossain, sp. nov.

*griffithiana (Nees) O. Kuntze

*hainanensis Merr. & Chun.

*havilandii C.B. Clarke ex Brem.

*helferi (T. And.) O. Kuntze

*hirsuta (Nees) O. Kuntze

humbertii Mildbr. = Anisosepalum humbertii

*humifusa Brem.

humilis (Nees) O. Kuntze = polybotrya var. humilis

*inaequalis E. Hossain, sp. nov.

*incana (Bl.) O. Kuntze

itatiaiae Wawra

*jaherii Brem.

var. kinabaluensis (Brem.) E. Hossain, stat. nov.

javanica Lindau = Pararuellia napifera (Zoll.) Brem.

*kamerunensis (Engl.) R. Ben.

*kerrii E. Hossain, sp. nov.

kinabaluensis Brem. = jaherii var. kinabaluensis

*kingiana C.B. Clarke

kradengensis Brem. = monticola, syn. nov.

*lanceolata (Bl.) O. Kuntze

*lasiobotrys (Nees) O. Kuntze

latibracteata Brem. = spatulata complex

*latifolia Brem.

lebrunii (Staner) B.L. Burtt = Saintpauliopsis lebrunii

Staurogyne (contd.)

*lepidagathoides Leonard

leptocaulis Brem. = spatulata complex

*leptocaulis Leonard, nom. illeg. = tenuicaulis E. Hossain, nom. nov.

*le-testuana R. Ben.

*linearifolia Brem.

*longeciliata Brem.

*longibracteata E. Hossain, sp. nov.

*longifolia (Nees) O. Kuntze

var. condensata Ridl. = condensata

*longispica (Ridl.) Ridl.

macahensis Glaziou on herbarium sheet = mandioccana

*maclellandii (T. And.) O. Kuntze

macrantha C.B. Clarke = Didissandra sp. (Gesneriaceae)

macrantha Lindau = vauthieriana

macrantha C.B. Clarke = Didymocarpus sp.

*macrophylla (T. And.) O. Kuntze

*major R. Ben.

*malaccensis C.B. Clarke

*mandioccana (Nees) O. Kuntze

maschalostachys Brem. = jaherii, syn. nov.

*merguensis (T. And.) O. Kuntze

*merrillii Brem.

*microphylla (Nees) E. Hossain, stat. nov.

*minarum (Nees) O. Kuntze

var. microphylla Nees = microphylla

minor (Kraenzl.) B.L. Burtt

Staurogyne (contd.)

*_miqueliana_ (Miq.) O. Kuntze
*_monticola_ R. Ben.
multiflora Brem. = _velutina_, _syn. nov._
*_neesii_ (Vidal) C.B. Clarke ex Merr.
  var. _thorelii_ R. Ben. = _polybotrya_ var. _thorelii_
*_novoguineensis_ (K. & H.) B.L. Burtt
nudispica (C.B. Clarke) Brem. = _Pararuellia nudispica_ (Clarke) Brem.
*_obtusa_ (Nees) O. Kuntze
*_ophiorrhizoides_ Elm.
palawanensis (Elm.) Brem. = _Gymnostachyum palawanense_
*_paludosa_ (Mangenot & Ake Assi) Heine
*_panayensis_ Brem.
*_paniculata_ (Wall.) O. Kuntze
*_papuana_ Laut.
*_parviflora_ (T. And.) O. Kuntze
pauper C.B. Clarke = _Phialacanthus pauper_ (Clarke) Brem.
*_pedicellata_ E. Hossain, _sp. nov._
*_perpusilla_ Henry & Balak.
*_petelotii_ R. Ben.
*_polybotrya_ (Nees) O. Kuntze
  var. _humilis_ (Nees) E. Hossain, _stat. nov._
  var. _thorelii_ (R. Ben.) E. Hossain, _comb. nov._
polycaulis Brem. = _spatulata_ complex
prianganensis Brem. = _subglabra_ var. _prianganensis_ Brem.
*_racemosa_ (Roxb.) O. Kuntze
*_ranaiensis_ Brem.

Staurogyne (contd.)

*repens (Nees) O. Kuntze

*riedeliana (Nees) O. Kuntze

var. latifolia (Nees) = euryphylla

rivularis Merr. = spatulata complex

*rosulata Brem.

*samarensis Brem.

*sandakanica Brem.

serrulata C.B. Clarke = Didymocarpus sp.

*sesanmoides (Hand.-Mazz.) B.L. Burtt

*setigera (Nees) O. Kuntze

setisepala C.B. Clarke = griffithiana

*shanica W.W. Smith

siamensis C.B. Clarke = spatulata complex

*simonsii (T. And.) O. Kuntze

*singularis Brem.

var. longipedicellata (Brem.) E. Hossain, comb. nov.

*spatulata (Bl.) Kds. - a species complex

*spiciflora (Miq.) Brem.

*spiciformis E. Hossain, sp. nov.

*stahelii Brem.

*stenophylla Merr. & Chun.

*stolonifera (Nees) O. Kuntze

*subcapitata Brem.

*subcordata R. Ben.

subcordata (Elm.) Brem. = Gymnostachyum subcordatum Elm.

*subglabra C.B. Clarke

Staurogyne (contd.)

*subrosulata E. Hossain, sp. nov.
*sundana Brem.
*tenera R. Ben.
*tenuicaulis E. Hossain, nom. nov.
*tenuispica Brem.
*trinitensis Leonard
*thyrsoidea (Nees) O. Kuntze
*vauthieriana (Nees) O. Kuntze
*velutina (Nees) E. Hossain, comb. nov.
*veronicifolia (Nees) O. Kuntze
*versteegii Brem.
*vicina R. Ben.
*warmingiana (Hiern.) Leonard
wawrana Leonard
*wulschlageliana Brem.
*zeylanica (Nees) O. Kuntze

Staurogynopsis Mangenot & Ake Assi = Staurogyne
maiana Mangenot & Ake Assi = St. capitata
paludosa Mangenot & Ake Assi = St. paludosa

Tubiflora J.F. Gmel. nom. rejiciend = Elytraria Michx.
acuminata Small = E. bromoides
angustifolia (Fernald) Small = E. caroliniensis var. angustifolia
caroliniensis (Walt.) Gmel. = E. cardiniensis
pachystachya O. Kuntze = E. imbricata
shaferi P. Wils. = E. shaferi
squamosa (Jacq.) O. Kuntze = E. imbricata

Verbena Linn.(Verbenaceae)

squamosa Jacq. = *E. imbricata*

Zahlbrucknera Pohl ex Nees = *Hygrophila* R. Br., *Staurogyne* Wall. & *Nelsonia* R.Br.

fruticosa Pohl = *St. mandioccana*

repens Pohl = *N. canescens*

Zenkerina Engl. = *Staurogyne* Wall.

kamerunensis = *St. kamerunensis*

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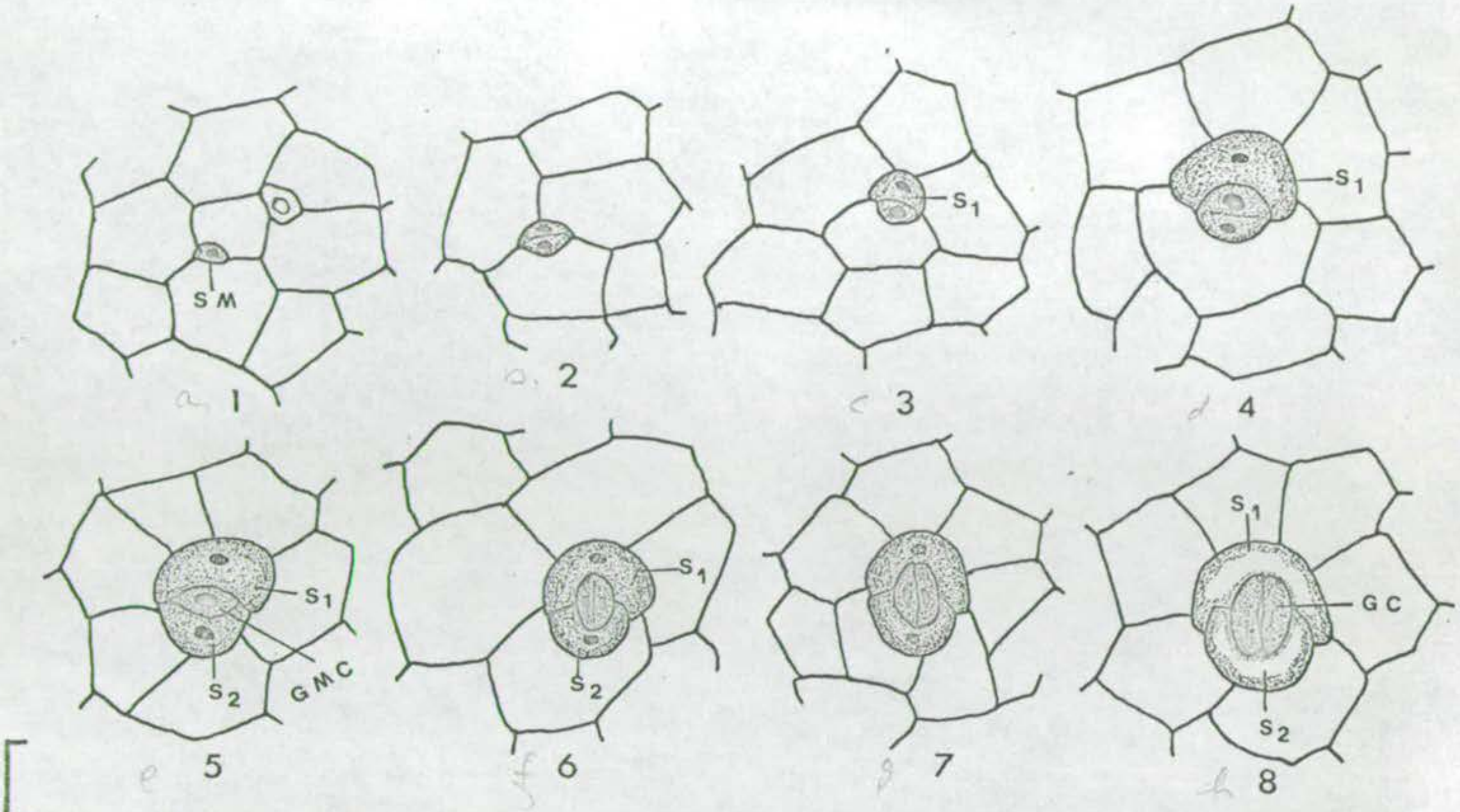

Fig. A. DEVELOPMENT OF SIMPLE DIACYTIC STOMA

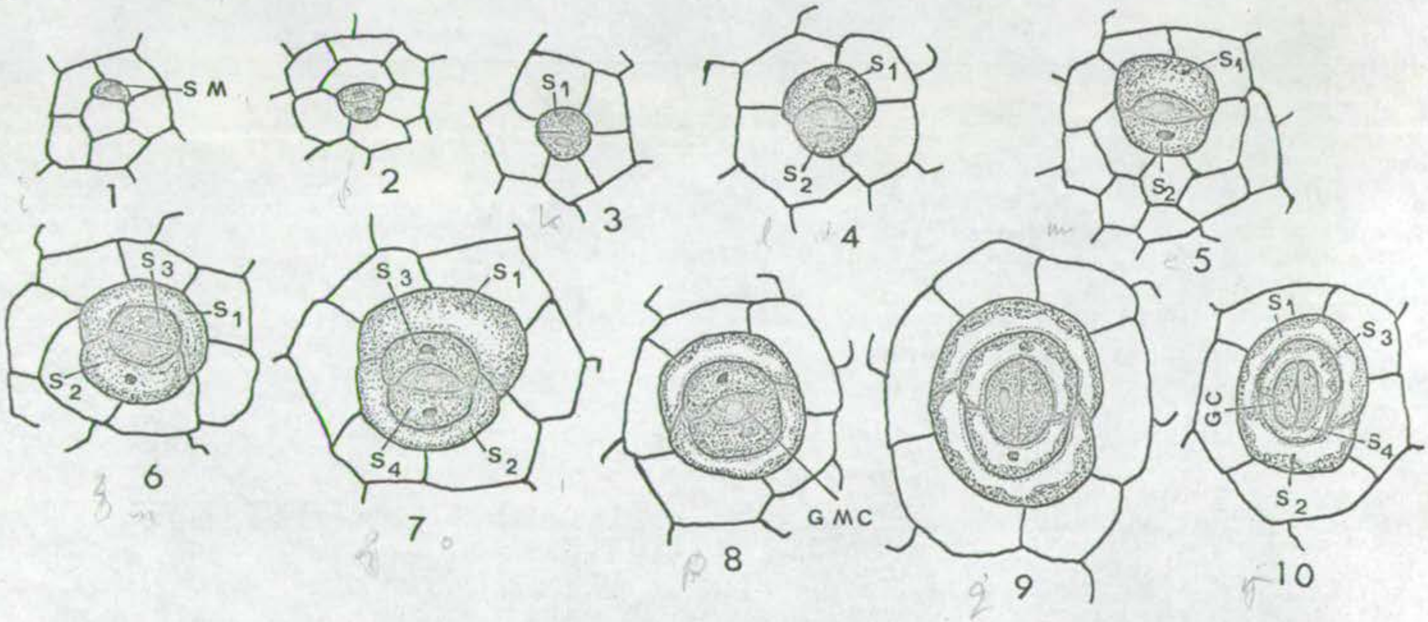

Fig. B. DEVELOPMENT OF DOUBLE DIACYTIC STOMA

ABSTRACT OF THESIS

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Title of Thesis Studies in the classification and affinities of Acanthaceae

SUMMARY

The present investigation mainly deals with the classification and affinities of Nelsonioideae, a little studied group in the family Acanthaceae. Its natural relationships are assessed in the light of data accummulated from the fields of morpho-anatomy, palynology, and embryology. That the group is definitely Acanthaceous has been proved by comparison and correlation of available evidence in relation to the closely allied families (Scrophulariaceae, Gesneriaceae, Acanthaceae, Pedaliaceae, and Bignoniaceae) of the order Bignoniales. Bremekamp's (1953) drastic suggestion for transferring Nelsonioideae to the vicinity of Rhinantheae (Scrophulariaceae) is therefore considered untenable.

After an investigation into the structure of Nelsonioideae, its generic interrelationships and taxonomic coherence into a distinct taxon are discussed. The subfamily status of this group has been abandoned in favour of a tribe (Nelsonieae) based on overall correlation and comparison of other subfamilies in the Acanthaceae. The natural affinities of Nelsonieae in and around the family Acanthaceae are also assessed.

Seven genera are recognized, their descriptions given (based on the observations of available species) and an artificial key to their identification is also provided. Infrageneric classification is attempted for Staurogyne and Elytraria. Artificial keys to the identification of supraspecific taxa and species recognized, are interpolated at appropriate positions. Nearly all the species of Staurogyne are referred to their respective sections, sub-sections, and series where possible. Two new sections are recognized in Staurogyne, 2 varieties are elevated to specific status, and 12 new species are described. The subgen. Tetrandra in Elytraria is recognized for the first time, and a new genus Anisosepalum is described, documented, and circumscribed. Only one species in Elytraria is recorded to be new to science.

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An extensive exploration of anatomical and palynological characters is undertaken. The occurrence of bi-celled glandular hairs and diacytic stomata of mesogenous origin has been found to be as constant characters of Nelsonieae. Peltate scales (found in 4 genera) and foliar sclereids in species of Staurogyne and Elytraria are reported for the first time in this group.

The 'acicular fibres' which in the past were referred to as either 'large raphides' or 'raphidines', are proved to be ordinary fibres and not cell inclusions. They are also recorded here for the first time in all the Nelsonieae excepting Anisosepalum and Saintpauliopsis. Confirmatory evidence is provided for the occurrence of both 'tricolpate' and 'tricolporate' pollen grains in the Nelsonieae through the intermediacy of the prevalent 'tricolporoidate' (with ill-defined pore) condition.

Two species complexes are recognized - in both cases a need for further biosystematic, cytogenetical and field studies is stressed.

The work has been illustrated with line drawings (18 plates of figures) which are supplemented by photographic plates (17 plates with 124 photographs). Distributional data of the Nelsonieae and Staurogyne spatulata complex are presented on two maps. Efforts are also made to correlate the taxonomic data with those of phytogeography, and to elucidate the causes of disjunct distribution exhibited by many of the genera in this group (Nelsonieae).