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Systematic Placement of Rapateaceae (Commelinales)

by

Miriam Colella

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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Abstract

Systematics And Placement of The Rapateaceae (Commelinales)

by

Myriam Colella-Franco

Chairman: Dr. Jack Valdovinos

A comparative morphological, anatomical, cytological, palynological and embryological study of the families Rapateaceae and Thurniaceae was undertaken in order to elucidate its systematic position within the order Commelinales. The overall morphology of the unifacial leaves of the Rapateaceae showed a pattern of localized meristematic activity and "arm chair" morphology during earlier stages, in both unifacial and cylindrical leaves. Shoot apex morphology and histology showed the typical monocotyledon pattern in which the leaf primordium encircles the vast majority of the apex surface. The shoot apex histology was surveyed in the family Thurniaceae and in members of the subfamilies Saxofridericioideae and Rapateoideae of the Rapateaceae; in both subfamilies there were little variations on the tunica-corpus layers. No unifacial leaves were observed in Thurniaceae. Stomatal differences observed among the two subfamilies are shape, size of the guard cells, length of the pore and ornamentation in the subsidiary cells. Inflorescence morphology showed two distinctive patterns among the two subfamilies. The inflorescence construction is monopodial in the Saxofridericioideae and monopodial and sympodial in Rapateoideae. Thurniaceae were always monopodial. Pollen studies showed variations at the subfamilial level that is in agreement with previous classifications.

The embryological studies showed that the embryo sac formation is of the monosporic type in all of the genera studied (***Shoenocephalium***, ***Kunhardtia***, ***Guacamaya***, ***Duckea***, and ***Monotrema***). Features such as anther and seed appendages, reproductive morphology, and anatomy showed variations at the genus and species level. Chromosome numbers in ***Cephalostemon*** are in agreement with those previously reported in the tribe Rapateoideae. The cladistic analysis confirmed the original placement of the Rapateaceae within the Commelinales, and the subdivision of the family into two subfamilies.

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I wish to express my thanks to the following people and institutions that made possible the completion of this project by helping me with ideas, spirit collections for anatomical studies, technical assistance and field trips. Dr. Barbara Palser (University of Massachusetts) who taught me embryology; Dr. David Burney (Fordham University) who showed me how to handle pollen samples; Mr. Mike Baxter (Lehman College), my friend and microscopy teacher; Victor Morales, Irene Morales and Mauricio Morales all members of my family that went to the field with me and helped me with my lab work, they endured years of sacrifice and my absence; Dr. Cynthia Morton who advised me in relation to pollen. Mr. John Pruski (Smithsonian Institution), Dr. Brian Boom (Director of Science at The New York Botanical Garden), Dr. Paul Berry (Univ. of Wisconsin) and Dr. Douglas Daly (The New York Botanical Garden) collected Rapateaceae in the field and brought them for my study; Dr. Dówn Frame from the Institute of Tropical Botany, Montpellier (France) for her critical comments; Joan Reid, executive assistant for the CUNY Biology program for encouragement

and compassion in the midst of turmoil; Dr. Dennis Stevenson (The New York Botanical Garden-CUNY) who helped me to present my findings at international congresses, to use his anatomical lab at The New York Botanical Garden and helped me with many creative ideas. Dr. Scott Mori (The New York Botanical Garden-CUNY) and Mrs. Miriam Fredrick (English Department at Lehman College-CUNY) for their helpful criticism of my manuscript. Dr. Thomas Jensen at Lehman College who allowed me use the facilities of his laboratory of Electron Microscopy and helped me in whatever academic needs I have during the time I left the Garden and started teaching at Lehman College. Dr. Jack Valdovinos, from Lehman College who has helped me with encouragement, optimism and trust in the most difficult moments, who has made the dream of defending becomes true.

The following institutions were pivotal to the completion of this project: The Venezuelan Corporation of Guayana (CVG) and TECMIN (Tecnica Minera), for the logistic facilities and moral support with field trips in remote areas of the Venezuelan Amazon; the people of Maroa (Guahibo tribe) in Amazonian state, Venezuela, and its sheriff. The Herbarium of the University Ezequiel Zamora (in Venezuela) and its curator, Dr. Basil Stergios, for processing my botanical collections and sending them from Venezuela to New York. Lehman College (CUNY) Electron Microscopy center; and The New York Botanical Garden herbarium and anatomical laboratory.

A graduate fellowship from The New York Botanical Garden made it possible for me to study the reproductive biology of communities of Rapateaceae in the Venezuelan Guayana. I am also grateful to the scientific staff and library staff at The New York Botanical Garden for being so helpful.

Table of Contents

List of Tables

List of Figures

Dedication

To Basilia, Othello, Mauricio and Irene, all of them the people I love

Introduction

The general interest that botanists have placed in the orders Commelinales and Juncales is based on several facts: the Commelinales have been hypothesized as one of the sister groups of the Poales (Dahlgren et al, 1985), and it is believed that they comprise a branch derived from a possible Asparagales or Bromeliflorae ancestor (outgroup) by the evolution and acquisition of novel characters (Stevenson & Laconte, 1995; Chase et al, 1995). The Juncales, are believed to be the sister group of the Cyperaceae (Dahlgren et al, 1985). The Commelinales and Juncales are very diverse with a somewhat restricted geographical distribution of some genera.

Dahlgren et al 1985, included the following families in Commelinales: Commelinaceae, Xyridaceae, Mayacaceae, Rapateaceae, and Eriocaulaceae, and Thurniaceae and Juncaceae were included in Juncales. Engler (1888) placed our present Commelinales, plus other families, (Thurniaceae and Bromeliaceae) in the Farinosae. Engler divided the Farinosae further into Bromeliineae (Thurniaceae, Rapateaceae, and Bromeliaceae) and

Enantioblastae (Xyridaceae, Mayacaceae, and Eriocaulaceae). Engler based his classification on the presence of starch in the endosperm. Today we base angiosperm classification on the use of multiple data that include morphological, cytological, phytochemical, embryological, and molecular features. The inclusion of multiple data provides a better resolution for the phylogeny of monocots, considering that the monocots are precisely rooted in the correct sister group, and the real plesiomorphies are properly established. Cronquist, (1981) placed the Commelinaceae, Mayacaceae, Xyridaceae and Rapateaceae under the Commelinales, the Eriocaulaceae were placed in their own order, and the Thurniaceae was placed in the Juncales.

The Englerian classification (Engler, 1964) inspired botanists and evolutionary biologists to believe that Rapateaceae and Bromeliaceae are related. Some molecular taxonomists believe, on the basis of similarities at the molecular level, that these two families are not too distant (Sitma & Givinish, pers. comm.). A combined analysis of the molecular and morphological data of the families of the Commelinales and Thurniaceae has proven to be helpful in understanding phylogenetic relationships among these families (Chase et al, 1993, 1995). One of the goals of the research described here has been to generate new morphological, anatomical, cytological, palynological, and embryological data for the families Thurniaceae, Rapateaceae, and Xyridaceae. Maguire's previous studies done on these families were analyzed by the author and the data were used to establish or test phylogenetic hypotheses of the relationships among the mentioned families, and to elucidate the placement of the Rapateaceae, Xyridaceae, and Thurniaceae (Fig. 78)

The Rapateacae were extensively studied by Maguire (1958, 1965) who proposed the division of the family into two subfamilies: Saxofridericioideae Maguire, and Rapateoideae Maguire, four tribes: Saxofridericieae Maguire, Schoenocephalieae Maguire, Rapateeae Endichler, and Monotremeae Maguire, and 16 genera. He based his classification mostly on macromorphological characters such as numbers of ovules per locule, placentation, seed size, seed shape, and seed appendages. Thus he recognized the following genera: Saxofridericia, Phelpsiella, Amphiphyllum, Stegolepis, Epidryos, Marahuacea, Kunhardtia, Guacamaya, and Schoenocephalium, all the genera with pluriovulate carpels with prismatic, pyramid-like or moon-like seeds and comprising the subfamily Saxofridericioideae. The remaining genera listed below have carpels with one seed per locule, basal or axial placentation, and ovoid or oblong seeds that may bear an appendage. These genera, Rapatea, Cephalostemon, Duckea, Spathanthus, Monotrema, Potarophytum, Windsorina, Maschalocephalus, belong to the subfamily Rapateoideae, Maguire's classification of the Rapateaceae, in particular the placement of Cephalostemon, was questioned by Steyermark (1988). In view of that criticism and the lack of a firm resolution of the phylogeny of the Rapateaceae, a comparative morphological, and embryological survey was undertaken for representative genera that belong to the four tribes (as described by Maguire), including Cephalostemon. The results of these studies will help to understand the phylogenetic relationships among genera and the position of the Rapateaceae, Thurniaceae, and Xyridaceae within the Commelinales.

Previous studies done on the anatomy of the Rapateaceae

The vegetative anatomy of Rapateaceae was first studied by Boubier (1895) and later by Solereder & Meyer (1925) and Carlquist (1966, 1969). Based on stem anatomy, Carlquist recognized the two subfamilies and four subtribes proposed by Maguire (1958). One of the important features of the subfamily Rapateoideae is the presence of tannin-filled parenchyma distributed idioblastically in both the cortex and the cylinder, however, this character is not present in some genera. The subfamily Saxofridericioideae is characterized by the presence of silica cells, and in some genera, the silica cells are associated with hypodermal fibrous strands. Tannin-filled parenchyma cells are present in both the cortex and central cylinder.

Carlquist (1966) also described the root anatomy. In general, he found that the roots have an epidermis, which is both thin-walled and lost from mature roots, or if persistent then it becomes suberized. The exodermis has a variable number of layers with hypodermal sclereids. The cortex may have tannin-filled cells found singly or in-groups. The middle cortex has spongy “arm parenchyma” The endodermis is commonly uniseriate and the degree of lignification is variable. The pericycle is either uniseriate or multiseriate. The stele is polyarch and xylem and phloem poles are numerous. Sclereids may be abundant in the medulla.

The degree of vessel specialization is related to the type of perforation plate. Thus, scalariform perforation plates are assumed to be more primitive than simple perforation plates. Cheadle & Kosakai (1980) and Carlquist (1966) reported the occurrence and specialization of vessels in Rapateaceae. They notice that vessels were absent in the rhizome, and, in some cases, they were absent in other organs such as leaves, roots, or scapes. Based on the degree of vessel specialization in the roots, it has been suggested that vessels in the roots of Monotremeae are more advanced, in the tribe Rapateeae they are intermediate, and in the tribe Saxofridericieae they are more primitive.

The lamina is dorsiventral or isobilateral. The mesophyll is usually differentiated into palisade and spongy tissue in the dorsiventral taxa.

Species with isobilateral blades have limited development of the palisade parenchyma on the abaxial as well as adaxial surface. The vascular bundles are simple and colateral, of the basic "graminean type" in larger veins.

Herbaria were the collections have been deposited

The first, and second set of my field plant and spirit collections were deposited in the following Herbaria: The New York Botanical Garden (NY, USA) and Herbarium of the Ezequiel Zamora University (PORT, Portuguesa state in Venezuela). Any additional duplicates were deposited in assorted herbaria of South America, Europe and USA. In appendix 1, I cited all the collections by collector (s) name and number utilized in the present research.

Phytogeography

The family Rapateaceae occurs mainly in tropical America, from Panama to Bolivia, and in West Africa (Fig. 1). In the Neotropics, the Rapateaceae live in a variety of habitats such as forest understory, seasonally flooded savannas, shrublands, open rocks and bogs; they can also be terrestrial, epiphytic or aquatic. In West Africa the genus Maschalocephalus occurs only on white sand savannas.

The size of these herbaceous plants is variable, thus individuals belonging to the genus Rapatea may be 50 cm tall or, as in the genera Saxofridericia or Stegolepis, the plants can be up to 3 mts. tall. The highest diversity at the generic and species level has been reported in the Guayana province (Maguire, 1958; Steyermark, 1983; Huber, 1988); comparatively, the Amazonian province shows less endemism. It is suggested that mainly micro and macro-evolutionary processes determined the geographic distribution and endemicity in Rapateaceae. Raven & Axelrod (1981) suggested that most of the families of the order Commelinales (Xyridaceae, Mayacaceae, Eriocaulaceae and Rapateaceae) differentiated in the Guayana shield.

Geology of the Guayana shield

The Guayana region is part of a Precambrian shield that was connected with Africa 100 million years ago. Africa and South America were a component of the southern Pangea, known as Godwana. The northern area of Godwana was formed by the north and south Godwana shields which eventually gave rise to the shields of Western Africa, Brazil and Guayana (Schubert & Huber, 1990). The geological continuity of the South American Precambrian shield was disrupted by the Amazon fracture that split the continent in two parts separated by the Amazon river basin; this fracture caused the separation of the South American shield into the Guayana and Brazilian Precambrian shield (Schuber & Huber, 1990). The Guayana shield has undergone several geomorphological episodes revealed by its present topography.

The basal and oldest portion of the Guayana shield consists of metamorphic and igneous rocks that were degraded over 500 m.y.a. (million years ago). Over this crystalline basement, a layer of sediments known as Roraima's Formation was deposited 1.6-1.7 m.y.a. Parts of this sediment were removed during erosion cycles leaving the sandstone outcrops exposed *(Formacion Roraima).* These sandstone or Tepuis arise at different altitudes above sea level. The word Tepui was used by the Pemon Indians to designate a particular type of mountain with a truncate or flat top.

The Venezuelan portion of the Guayana shield has several landscapes which range in altitude from 100-3000 mts. : the lowland plains, the piedmont, the intermediate uplands (100-1000 mts.) and, the mountainous highlands rising between 1000-3000 mts. Huber & Alarcon (1988), recognized altitude gradients and temperature gradients on those landscapes. They define a macrotermic belt with mean annual temperatures above 24 C, a mesotermic belt with mean annual temperatures between 12 and 24 C and a submicrotermic belt with temperatures between 6-12 C. Most of the area is subject to a high rainfall (2000-4000 mm per year), and has a very short or no dry season. The Rapateaceae have a wide range of distribution and they grow along the latitudinal gradient from 100 to 3000 mts.

Vegetation Types

In the Venezuelan Guayana, as in all other regions of the world there is an association between physiography, topography and vegetation. Huber & Alarcon (1988) distinguished several vegetation types in the lowlands and in the mountains and Tepui. Thus, in the highlands the following types are common: the evergreen forest, the shrublands, the meadows where some of these communities grow on bogs of variable age, and the pioneers. Huber & Alarcon concluded that lowland white-sand savannas are analogous ecosystems to high mountain herbaceous meadows on Tepui summits. The summits harbor a substantial number of endemic genera (ca. 39%); in three Tepui tops the degree of endemism at the species level is 50% at Roraima, 40% at Duida, and 40% at Chimanta.

The common vegetation types in the lowlands are the evergreen mesothermic forest, the shrublands, the Banas and the Caatingas. Banas and Caatingas differ from the surrounding evergreen forest in floristic composition, tree size, density, and degree of scleromorphism.

There seem to be an ecological preference here, and Rapateaceae shows diversification of many genera as suggested by the number of modern endemics in these communities. Although speciation has occurred in the highlands (Steyermark, 1979), and in the lowlands, several genera occupy intermediate range distributions. This would include Stegolepis, Kunhardtia, and Saxofridericia.

The lowland elements associated with Banas and Caatingas grow in the majority of the cases, on deep white-sand soils such as Spodosols or Quartzisaments. These soils which are at least 1-2 mts. deep, are very acidic and with very low nutrients content, they are characterized by: 1) high content of iron and aluminum, while iron is needed in small amounts, aluminum is always toxic for the plants, 2) they may be waterlogged in periods of copious rainfall but water evaporates and percolates quickly down through the sand, mimicking drought conditions in periods of little or no rainfall. These communities are described as "edaphic communities" (Medina, et al, 1984). These evergreen forests are relatively frequent along the Casiquiare-Rio Negro (Venezuelan Amazon) area, and harbor endemic genera and species of Rapateaceae such as: Duckea flava Mag., Schoenocephalium teretifolium, Guacamaya superba, Cephalostemon ridelianus, Rapatea longipes, Schoenocephalium cucullatum etc. Some genera such as Spathanthus and some species of Rapatea prefer the evergreen forest and understory.

Exclusively highland genera growing in many cases on bogs or sandy substrates are: Phelpsiella, Amphyphyllum and Marahuacea. These taxa show a narrow distribution or are endemic to only one Tepui summit. The occurrence of an endemic on a particular site is related with its ecology, physiology, history, and degree of isolation.

Pleistocene Climatic Changes

It is believed that historical events at the population level such as micro and macro-evolutionary processes, weather changes, geomorphologic process, and fluctuations in the abundance of pollinators or seed disperses have influenced the actual distribution of the Rapateaceae.

Steyermark (1979, 1988) suggested that the present distribution of numerous taxa on Tepui summits be related to the existence of Pleistocene refugia. He arrived at this conclusion based on the number of endemic and relictual taxa. He inferred that a proportion of the generic flora present on the Tepui summits reached its actual location as a result of immigration from other areas (Andes, Amazon, Guyana lowlands, etc.).

Schubert (1986, 1988) studied the Quaternary palynoflora of the Venezuelan Guayana, and postulated that the same paleoclimate could have promoted different biogeographical situations in different localities. Rull (1991) emphasized that the origin of the Tepui flora weather autochthonous or allochthonous is still unsettled. Rull concluded that additional paleoecological evidence does not support the refugia hypothesis proposed by Steyermark (1979, 1988). Rull surveyed several Tepui summits (mainly bogs) and lowland lakes. Using radio-carbon dating techniques he hypothesized that the age of the bogs oscillate between 2000-8000 YBP (years before present). During that time, quantitative floristic changes occurred and the species diversity remained almost constant. The rate of extinction was very low and climatic changes were not drastic. It was suggested by Rull (1991) that the climatic variation during certain periods (Holocene) induced intermediate perturbations that favored ecological succession over speciation processes. The palynological data of Rapateaceae shows that the species composition was very much like the present one (Rull, 1991).

An alternative hypothesis proposed by Huber (1995) relates the origin, distribution, and diversity of certain Tepui taxa, with their ecology and diversification. Thus, in the particular case of the Rapateaceae, Huber hypothesized that the family diversified exclusively within the Guayana region.

It seems probable to me that speciation events in Rapateaceae, whether allopatric or sympatric, may have occurred before the Holocene period and the separation between lowland and highland elements might have been established sometime before the Pleistocene.However, migration could occur in both directions. The ecological separation between lowland taxa and highland taxa seems to agree, to a certain extent, with the phylogenetic hypothesis (see chapter 7) about the evolutionary relationships of the different genera.

Thus, the subfamily Saxofridericioideae presents many plesiomorphic characters (Maguire, 1958) and most likely originated on the summits e.g. Phelpsiella, Marahuacea, Stegolepis and Amphiphyllum. The members of the tribe

Schoenocephalieae: Schoenocephalium, Guacamaya, and Kunhardtia diversified in the lowlands. The subfamily Rapateiodeae shows more synapomorphies and it could have originated in the lowlands. The presence of the genera Windsorina, Maschalocephalos, and Potarophyton (Tribe Monotremeae) outside the Venezuelan Guyana accounts for a peripheral diversification at the generic level. This subfamily probably originated in the lowlands and subsequently migrated through the rivers or speciated locally sympatrically or allopatrically. The genus Cephalostemon is very diverse in Brazil and it can be hypothesized that its actual distribution represents a relictual distribution with extinction in between the Venezuelan Guayana and the Brazilian Precambrian shield. Its geographic distribution possibly agrees with a secondary diversification center.

In any case, the data is still too scanty and better understanding is needed of the microevolutionary and macroevolutionary process at the population and species level in Rapateaceae.

Scale 1:134,000,000
Robinson Projection

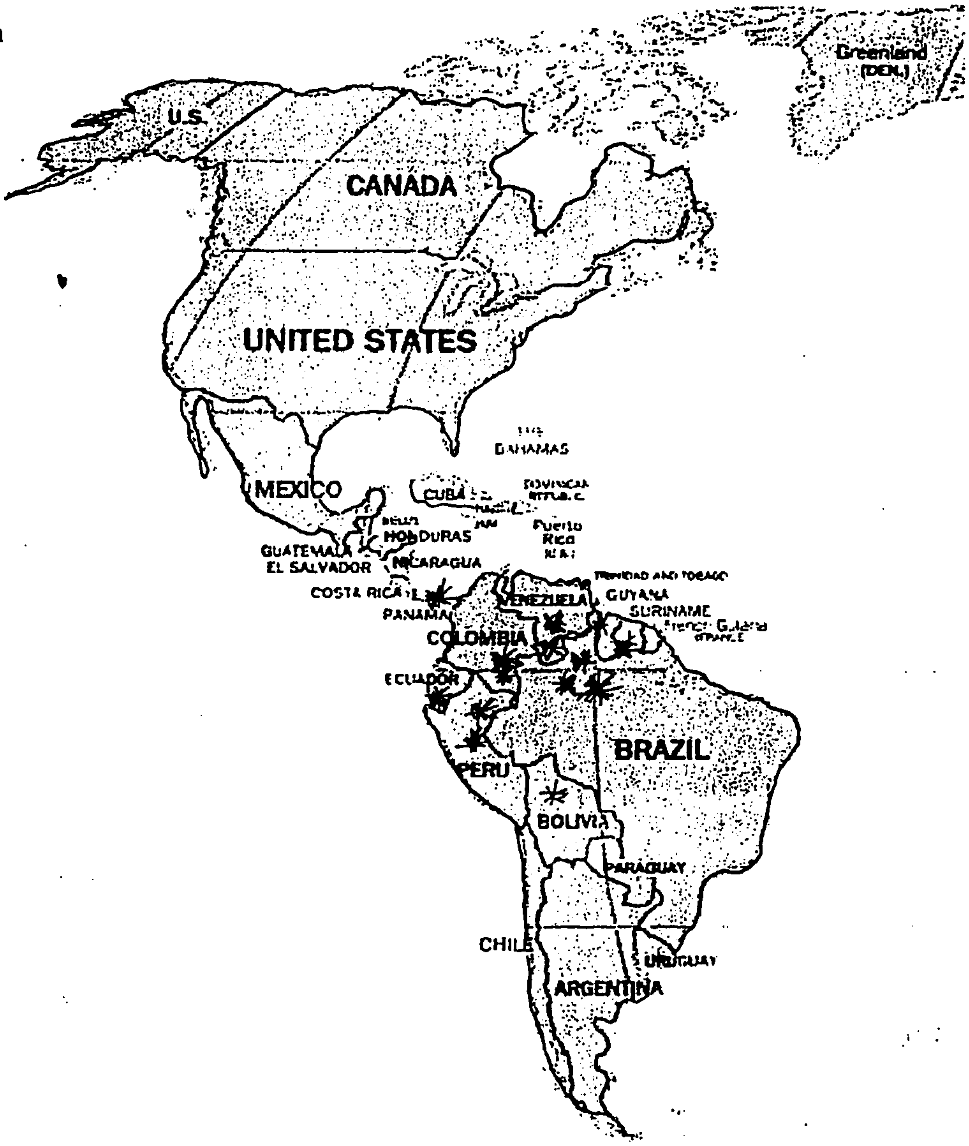


Fig. 1: Geographical distribution of Rapateaceae in the Neotropics . Countries are mark with asterisk.

Results

Chapter 1

General Morphology

The early morphological descriptions of the families Rapateaceae, Thurniaceae, and Xyridaceae by Martius (1847), Kornicke (1873), Pilger (1930), and Maguire (1958) emphasized the general aspects of floral morphology. These descriptions were applied mostly to taxonomic monographs, and features such as the ecology, morphology, anatomy, and the embryology of these two families were only briefly mentioned. While these botanists made note of the unifacial blades in Xyridaceae and the asymmetrical shape of the sheath and unifacial leaves of Rapateaceae, none of them attempted to study these characteristics. Important contributions to the knowledge about the anatomy of the above families were made by Solereder & Mayer (1929), Carlquist (1961, 1966, 1969), and Cutler (1965). More recently, Tieman (1986) and Venturelli & Bouman (1987) have described the embryology of selected genera of Rapateaceae and Abolboda in the Xyridaceae. The embryology of some of the remaining unstudied taxa is reported here. The embryology of the Thurniaceae is not well known.

Branching patterns of vegetative and reproductive axes, leaf ontogeny, and shoot apex organization is described here for the first time. There have been only a few studies that have used anatomical, morphological, and embryological data to address phylogenetic questions in Rapateaceae and Thurniaceae; none of them have applied cladistic analysis to determine of intrageneric or intrafamiliar relationships of these taxa. One of the goals of the present research is to elucidate phylogenetic relationships among the 16 genera of the Rapateaceae and the 2 species of the monotypic Thurniaceae using morphological, anatomical and embryological data.

Materials and Methods

Leaves and rhizomes of Rapateaceae and Thurniaceae were fixed in FAA (Formaline, Alcohol, and Acetic acid) for at least 24 hours. In order to remove the abundant mucilage, the material was washed in water several times. The material was then dehydrated by means of an ethanol-TBA series, embedded in paraplast, and sectioned at 8-10 um on a rotary microtome. The anatomical sections were stained with safranine-fast green or safraninechlorazol black. Freehand sections and permanent sections of reproductive parts of Thurniaceae, Xyridaceae, and Rapateaceae were also made using the same techniques. Where silica bodies were abundant, the tissues were treated with HF (10 %) for several days. In preparation for SEM, the material was critical point dried and gold coated.

RESULTS

Vegetative Anatomy and Morphology of Rapateaceae

From my field and lab observations, it was notice that the Rapateaceae are perennial rhizomatous herbs usually with clonal and sexual development. The rhizomes consist of two portions, one that is subterranean and branches sympodially, and another one that is aerial and branches monopodially. Size of the plants varies from 30 cm to 2 meters. Axillary buds, when present, are common in the nodal region, and exhibit preformation. Adventitious roots emerge from the internodes. The leaves are condensed in a pseudorosette, which is often unbranched and exhibits distichous or spirodistichous phyllotaxis. Monopodial axes tend to be more common in plants with distichous phyllotaxis (Halle et al, 1978). In most of the genera, the leaves are equitant, terete, and unifacial. The proximal portion consists of an open plicate, bifacial and mostly asymmetrical sheath, bearing in its distal part a unifacial blade with a midrib that is in many cases displaced towards the blade's margins. During their development, the plants produce abundant mucilage in the stems, leaves, and inflorescences.

During laboratory handling of the plant specimens, it was noticed that mucilage is secreted by specialized hairs or secretory cavities such as the ones found in the stem cortex. The ecological function (s) of the mucilage is not well known, but four possible hypothesis are suggested: 1) herbivore defense (insects mostly) because it is quite abundant in young organs; 2) protection against overheating, in particular for species growing in open or high altitude areas; 3) nutrient and water uptake, in particular for those species living in oligotrophic soils with variable water supply, and 4) a less probable correlation of the presence of mucilage in the inflorescences (a common occurrence) with a particular pollination syndrome. Epicuticular waxes were recorded in Rapatea and Maschalocephalus.

Shoot Apex in Rapateaceae

Studies of shoot apex organization at the subfamilial level and its taxonomic implications show that a trend of increasing distinction of zones does occur in other families such as in Moraceae subfamilies Moroideae and Conocephaloideae (Smith, 1963). In grasses, Brown (1958) reported a correlation between the number of tunica layers and certain other anatomical characters of systematic significance. However, Hara (1962) reported little correlation between shoot apex organization and taxonomic differences. In selected families of the order Ericales (Ericaeae, Empetraceae, Pyrolaceae, and Diapensiaceae), the shoot apices were uniform. Hara (1962) suggested that tunica stratification have little phyletic significance among these families. In some situations, there are seasonal changes in the number of tunica layers and they may vary with plastochronic changes. Increased stratification occurs at the apex over time, and it becomes more evident with age or nutritional status. The taxonomic significance of the changes in shoot apex organization in Rapateaceae and Thurniaceae is reported here for the first time.

According to my results, stratification of the shoot apex in members of the Rapateaceae subfamily Saxofridericioideae proved to be very similar. In Guacamaya superba (Fig. 2b, 2c), the shoot apex displays a tunica with three cell layers originating anticlinally while in the corpus, cell division occurs randomly. Procambrial strands penetrate the young leaves. There is some evidence for the activity of a primary thickening meristem (PTM) reported in some other monocots (Rudall, 1992). This apical meristem pattern is similar in Schoenocephalium teretifolium, Monotrema aemulans, and Duckea flava. The apical meristem of the axillary buds showed the same tunica-corpus organization, in Kunhardtia rhodantha (Fig. 3a). Variations in the anatomy of the shoot apex of Rapateaceae at the generic level seems to have very little taxonomic use however, more anatomical studies including many developmental stages need to be included.

The type and distribution of meristematic activity in the leaves has more taxonomic value, as there are differences in leaf morphology. Some species belonging to the genera Schoenocephalium and Duckea are distinct in having cylindrical unifacial leaves and a almost enclosed sheath. In contrast, Rapatea and Saxofridericia have a well differentiate sheath, petiole and blade. Many species belonging to these taxa have also unifacial leaves.

Branching Patterns in Rapateaceae

A greater understanding of the Rapateaceae gross morphology and branching pattern would be gained through studies that are more anatomical and analyses of populations of living plants. Unfortunately the natural populations are very small and many species occur in remote places. This situation created a problem regarding the amount of material available, and growing them in a green house proved to be extremely difficult as almost all individuals died.

In addition to the scapose inflorescence, the aerial stem in Rapateaceae bears several types of foliar appendages with the exception in Mashalocephalus with sessile inflorescences. Three types of leaves are distinguished: unifacial, bifacial, and intermediate with a well defined bifacial sheath and a rudimentary blade in the form of a tip. In the majority of the cases, the scape is enclosed by two or three intermediate leaves (prophyls on the inflorescence). Intermediate leaves are associated with the other leaves (unifacial or bifacial) and are quite often in axillary positions. This type of foliar appendage was briefly mentioned before by Maguire (1958). A diagrammatic representation of the aerial branching morphology of the Rapateacae and Thurniaceae based on the species studied is presented in Fig. 4. In the tribe Saxofridericioideae, the inflorescences are axillary (Fig. 4a), and Saxofridericia duidae has axillary buds. Terminal inflorescences with axillary buds near the end of the branch are common in the tribe Schoenocephalieae. The subfamily Rapateoideae is characterized by axillary inflorescences, although in Duckea spp. they are terminal. A common feature in the species studied is the presence of the "axillary unit" comprising both a vegetative and a reproductive bud located in the axis of the leaf (Figs, 4e, 4d).

Axillary buds are also common. The subfamily Rapateoideae shows more morphological variability than the subfamily Saxofridericioideae.

Rapatea spruceana carries the inflorescence on one side of the stem, and the axillary buds on the other side (Fig. 4c). Spathanthus unilateralis displays the axillary unit at the base of the aerial stem (Fig. 4d). In the genus Duckea, the inflorescence is also near the base of the stem, whereas the axillary unit is located towards the distal portion of the stem (Fig. 4c). Monotrema aemulans has supernumerary axillary buds, from the base of the old leaves, from which new branches arise (Fig. 4f). The maturation of the inflorescence is, as in most of the cases, acropetal.

The leaf: Unifacial and Bifacial Appendages

Ensiform or sword-shaped leaves are not uncommon in monocotyledonous plants, in particular in many members of the Iridaceae, Phormiaceae, Liliaceae, Cyperaceae, Rapateaceae. Kaplan (1975) pointed out that ensiform leaves differ from dorsiventral ones in: 1) absence of a true blade region; 2) flattening in the vertical plane rather than in the horizontal plane, and 3) radial rather than bifacial distribution of photosynthetic tissues. Fig. 3b, shows a cross section of a typical unifacial leaf in Monotrema aemulans.

In general, leaves originate on the flanks of the shoot apex where a local concentration of meristematic cells marks the beginning of leaf development. These cells grow to form a leaf buttress. The cells of the leaf buttress may be derived from the tunica alone or from the tunica and corpus.

The angiosperms exhibit an interesting variation in leaf morphology, ranging from unifacial, to partially unifacial, to completely dorsiventral leaves. Dale and Milthorpe (1981), pointed out that during early stages of leaf ontogeny, an apical meristem is usually established in bifacial (Fig. 5a) and unifacial (Fig. 5b) leaves. As growth progress, intercalary meristems become more important. By the time, the leaf primordium has reached a length of 80-200um marginal and submarginal meristems are established along the sides of the leaf (Figs. 5c, 5d). The growth of these meristems controls lamina formation in dorsiventral flattened leaves. In some monocotyledonous leaves, the marginal meristem is inhibited in the early stages of leaf ontogeny and the adaxial and basal meristem generates the majority of derivatives. Therefore, the overall morphology of the leaf is unifacial (Fig. 5d). The differential activity of adaxial and basal meristems produces a great variability in leaf shapes.

The primordium of a dicotyledoneous leaf is usually confined to a relatively narrow sector of the shoot circumference whereas in monocotyledonous leaves the primordium is initiated almost around if not in all the area of the shoot apex. The pattern of leaf formation in monocots is different from that of dicots. In the former, the proximal region of the leaf primordium gives rise to the blade and the sheath while the distal region gives rise to a precursor tip that, in the case of unifacial leaves, will develop into a unifacial segment. In dicots, the proximal region generates the base of the leaf and stipules, whereas the distal portion develops into the blade or phyllode as in the case of unifacial leaves (Kaplan, 1975).

Among unifacial leaves, there is also certain diversity in shapes. The leaf can have a bifacial sheath and a unifacial blade such in Rapateaceae, Phormiaceae (<u>Xeronema</u> <u>morei</u>), Xyridaceae, Iridaceae, Acoraceae etc., or it can be unifacial only in its distal portion (Vorlauferspitze) as in Agavaceae. In other examples, the leaves are cylindrical and the sheath may be missing, as in Juncaceae and Cyperaceae. An earlier explanation was suggested by DeCandolle (1827) and Arber (1922) who interpreted the unifacial leaf as a deblade expanded petiole or phyllode. A more recent contribution by Kaplan (1977) proved that leaf primordia are bifacial in origin and subsequent changes in meristematic activity during leaf development may produce a unifacial leaf.

Unifacial leaves in Rapateaceae

The youngest leaf primordium of the following genera: Monotrema, Spathanthus, Schoenocephalium, Guacamaya, Rapatea, and Duckea, originates as a circunferential expansion of the leaf around the shoot apex (Fig. 6e), the two lateral zones of the young sheath become confluent as they meet on the periphery of the shoot apex. At this point, the primordium is 125 nm tall. The common monocotyledonous feature of a sheathing leaf base is exhibited in early organogenesis of the apex region of Guacamaya superba. In subsequent stages, a sheath and a blade can be distinguished (Fig. 6f). A detail of the young leaf sheath is shown in Fig. 7. During this period, the young leaf looks like an "arm chair" (Figs. 6a, 6c. 6f) and this configuration has been reported in other unifacial monocotyledon leaves, e.g. in Juncaceae and Alliaceae (Kraehenbuehl, 1983).

The growth pattern of the asymmetrical sheath of some species of Rapateaceae, in particular Rapatea, Saxofridericia, and Stegolepis seems to be slightly different from that reported in other unifacial monocotyledons with leaves with symmetrical sheath sides (Kaplan, 1977). When the young leaf of Guacamaya superba is about 140 um tall (Fig. 7a), the sheath shows residual activity of the adaxial meristem, near the inception of the unifacial blade.

Most likely, some extra meristematic activity on one side of the sheath accounts for the asymmetrical growth of the sheath during leaf ontogeny. At maturity, half of the sheath is asymmetrical and may carry an auricle-like structure on its distal portion. The other half of the sheath merges with the blade, and bears the mid-rib which changes its orientation further up on the blade, towards the margins of the unifacial portion.

The genus Schoenocephalium deviates slightly from the developmental pattern of sheath-blade described above. This genus exhibits a sheath that is not totally open, and encloses the new leaf primordium during early organogenesis instead of showing an open sheath as in the other genera already studied (Figs. 6b, 6d). The unifacial blade in Schoenocephalium is cylindrical (arrows in Fig. 6d). The young leaf is bent at the tip. The same growth pattern has been described in the genus Juncus (Kraehenbuehl, 1983). Frequently a domed shoot apex characterizes monocotyledon leaf organogenesis and the first emergence is recognizable as a distinct leaf primordium. During this developmental stage, no buttress is distinguished (Steeves & Sussex, 1991). In Rapateaceae, subfamily Saxofridericioideae (Fig. 7e) the emergence of a leaf primordium is associated with a localized growth activity in the shoot apex. As the young appendage grows, it expands further from the apical dome, and mitotic activity seems more active on the abaxial side. In subsequent stages (Fig. 7a), the position of the shoot apex and the newly formed leaf primordium lies in the same plane (Figs. 7b, 7d). At this point, a new leaf primordium begins to form. The phyllotaxis of the young leaf is spirodistichous. The young leaves of Guacamaya are shown in Figs. 7d, 7e. The enclosed sheath of Schoenocephalium teretifoilum can be observed in Fig. 7f.

Vegetative Anatomy and Morphology of the Thurniaceae

The Thurniaceae are perennial, rhizomatous, semi-aquatic, colonial herbs that can be up to 2 mts. tall. The phyllotaxis is tristichous and the inflorescences are borne in the leaf axis. The leaves are bifacial, plicate, without a petiole, and with an open short sheath. Mucilage is present in small quantities, but no anatomical structure has been reported in association with its secretion. Mature stomata are of the paracytic type, although Cutler (1965) reported paracytic and tetracytic stomata. Stomata are in the intercostal areas of the leaves, and they are frequently located on the abaxial surface. Epicuticular waxes were found in Thurnia sphaerocephala (Rudge) Hook.f. and in T. polycephala Schnee.

The vegetative anatomy of the family Thurniaceae was first studied by Solereder & Meyer (1929) and later by Cutler (1965). The rhizome exhibits three main regions with an unusual orientation of the vascular bundles.

A very important anatomical feature, described for the first time in monocotyledons by Cutler (1965), is the presence of a particular type of inverted vascular bundle in Thurniaceae. Small inverted vascular bundles (subsidiary) are associated with the large vascular bundles. Silica bodies are reported in the epidermal cells. On anatomical grounds, Cutler (1965) indicated that the taxonomic position of the Thurniaceae was rather isolated. Inverted vascular bundles occur in equitant leaves but the xylem poles of these bundles face towards one another. This is not the case in the inverted vascular bundles of Thurniaceae.

This present morphological study did not attempt to resolve the histological processes related with the development of unifacial appendages, rather, an objective of this research was to elucidate the morphological changes of the leaves from their inception. When preserved plant material was available, a follow-up from early stages of leaf development was recorded.

Shoot Apex in Thurniaceae

The tunica is composed two layers of cells and the corpus shows cell division occurring in several planes. The young leaf primordium does not encircle the shoot apex in Thurniaceae as in Rapateceae, because the open Thurniaceae sheath is not folded or plicate (Fig. 9b). The primordium thickens towards the sides, and its distal portion has a hooded shape. As growth continues in the following stage, the young leaf displays a triangular shape with a hollow center and significant growth towards the periphery. Spike-like outgrowths are common along the margins, and are of epidermal origin (Fig. 9a). The margins of the older leaves bear the spikes.

A cross section of the stem (Fig. 8b) shows that phyllotaxis is tristichous. In this type of spatial design, the triangular leaves are easy to accommodate. The new leaf primordia (Fig. 8a) are about 37.5 um tall, and the next young leaf is 70 um tall. A comparison between the shoot apex and leaf morphology of the Rapateceae and Thurniaceae (Table 1) show that there are very few similarities among these families. This is due to the differences in primordium shape, leaf shape, and phyllotaxis. The inflorescences are always axillary in Thurniaceae whereas in Rapateaceae they are terminal or lateral. A morphological and anatomical resemblance between Thurniaceae and Pronium in the Juncaceae (Zimmermann & Tomlinson, 1968) can be noticed as the leaves, phyllotaxis, and shoot apex organization are similar. The phyllotaxis in Pronium is tristichous and the organization of the shoot apex and the growth of the young leaf look like that of Thurnia. These morphological similarities (among other features) with the Juncaceae favor the inclusion of the Thurniaceae in the Juncales according to Dahlgren et al (1985).

Branching Patterns in Thurniaceae

Studies of the branching pattern of the subterranean portion of the Thurniaceae are lacking. Here, it will be discuss the first description: the aerial axis is monopodial, and it bears bifacial leaves. Vestigial or transitional leaves are absent. The erect scape carries a series of mostly three enveloping bracts that originate at successive nodes, ending at the base of the inflorescence. In Thurnia polycephala the growth pattern of the inflorescences is sympodial, and several heads are borne on each inflorescence branch, whereas in T. sphaerocephala the growth pattern of the inflorescences is monopodial, and a single axis carries one globose head. A diagrammatic representation of the aerial branching pattern of Thurniaceae and Rapateaceae is provided in Fig. 4.

Table 1 summarizes the morphological features of both families. It can be concluded that the overall morphology and branching patterns of both families are not homologous, the Thurniaceae lacks axillary buds and scapose or sacciform spataceous bracts, and the axillary unit is absent.

Vegetative morphology in Rapateaceae and Thurniaceae

Table 2 summarizes features such as leaf types and vegetative morphology of all the genera of Rapateaceae studied and the two species of the family Thurniaceae. It can be noticed that there are important morphological differences between Thurniaceae and Rapateaceae. In Thurniaceae, the leaf sheath is open, the spathaceous bracts are absent, and the axillary buds too. In view of the fact that the inverted vascular bundles in Thurniaceae can be related to some kind of leaf unifaciality (Cutler, 1965; Tomlinson pers. comm.), and may evoke a certain ancestry with the unifacial leaf pattern in Rapateaceae, they can be interpreted as constituting a parallelism between these two families. In later chapters, more evidence based on reproductive morphology, and phylogeny indicates a distant ancestry between these two families. Moreover, the Rapateaceae do not share a great morphological resemblance with Thurniaceae. They may have evolved in similar ecological and geological conditions. Resemblance that is more recent may be due to evolutionary convergence. Future molecular data and cytological studies of the chromosomes during microsporogenesis may help to firmly verify our placement hypothesis of the Thurniaceae within the Juncales.

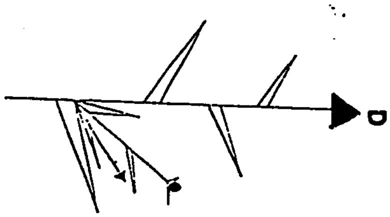
Fig. 2: Shoot apex of an axillary bud in : a) Kunhardtia rhodantha; (Colella, M. s/n); b) cross section in the young leaf of Monotrema aemulans (Colella et al, 1277), bar=0,8 mm.

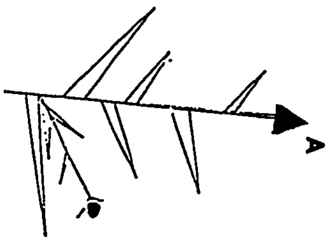

A
sh
P1
Sa
sh
B
sh
Sa
L1
C
Sa
L

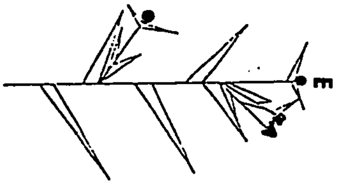
Fig. 3: Vegetative morphology of: a) Kunhardtia rhodantha (Berry, 4808); b) cross section in the young leaf of Monotrema aemulans, bar = 0.8 mm.


A
B

Fig. 4: Diagrammatic representation of vegetative morphology of: a) Saxofridericia duidae, b) tribe Schoenocephalieae; c) Rapatea spruceana; d) Spathanthus unilateralis; e) Duckea flava; f) Monotrema aemulans; Thurnia sphaerocephala (triangle =vegetative apex, sphere = inflorescence).


D


A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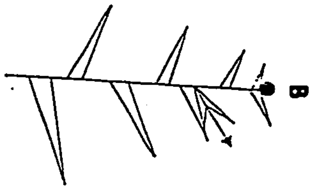
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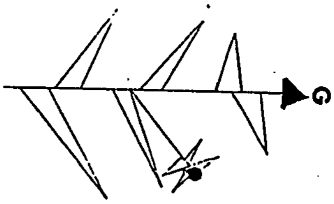
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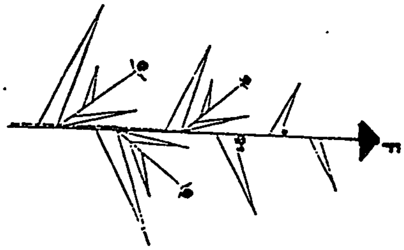
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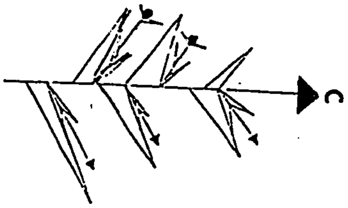

C

Fig. 5: Meristematic activity on a growing leaf: a) dicotyledon leaf and shoot apex; b) monocotyledon leaf and shoot apex; c) meristematic zones of a leaf; e) same as c but in the leaflet of compound leave (Adm = adaxial meristem, Am = apical meristem, Bm= basal meristem, Im = intercalary meristem, Lp = leaf primordium, Mm = marginal meristem, Pm = plate meristem. (From A. Bell, 1992).

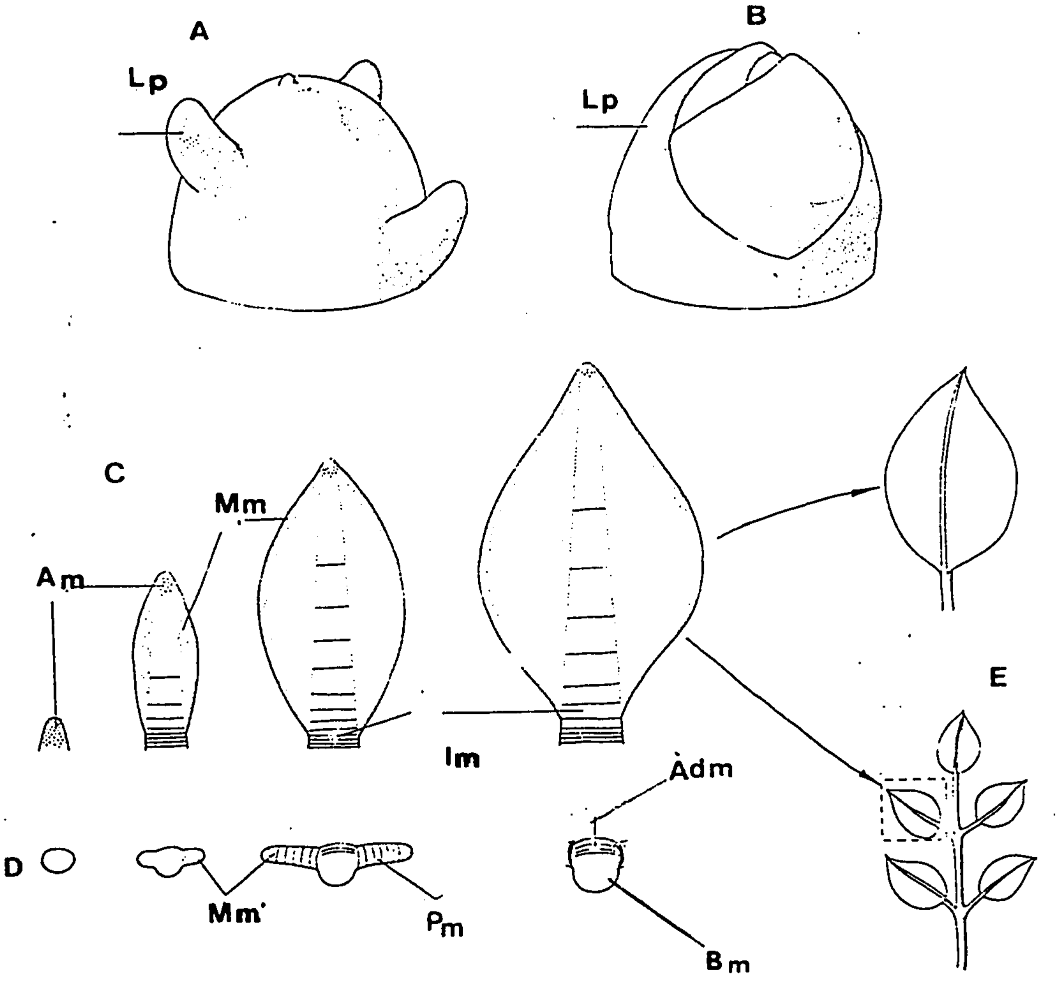
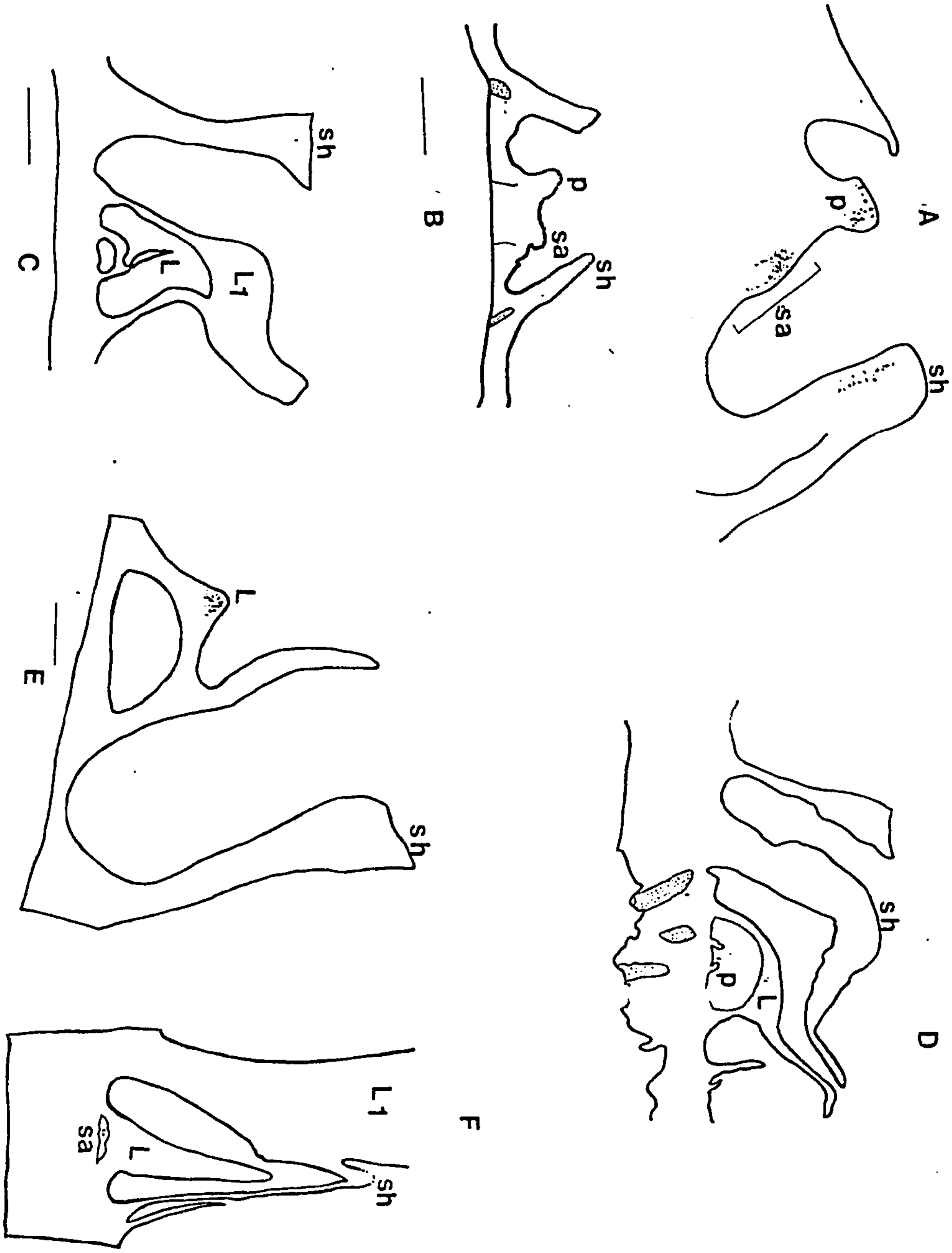

A
Lp
B
Lp
C
Mm
Am
Im
E
Adm
D
Mm'
Pm
Bm

Fig. 6: Shoot apex and leaf morphology in: a) Monotrema aemulans (Colella & Morales, 1276); b) Schoenocephalium teretifolium (Colella et al, 2123); c)Guacamaya superba (Colella & Morales, 1275); d) Schoenocephalium teretifolium; e) circunferential expansion of the leaf; f)Guacamaya superba, bar = 5 um.


A
B
C
D
E
F

Fig.7 : Diagram of the shoot apex and leaf morphology showing location of the meristematic activity in: a) Guacamaya superba (Colella, et Morales, 1275); b) Monotrema aemulans (Colella et Morales, 1276) c) Kunhardtia rhodantha (Colella s/n) d) Guacamaya superba; e) Rapatea longipes (Colella, 1774); f) Schoenocephalium teretifolium (Colella et al, 2123) bar = 0,5 mm.


A
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sa
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L1
L
D
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L
p
E
L
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F
L1
sh
L
sa

Fig. 8: Shoot apex and young leaf of Thurnia sphaerocephala (Colella et Morales, 1250); a) young leaf showing spines, bar = 5 um.

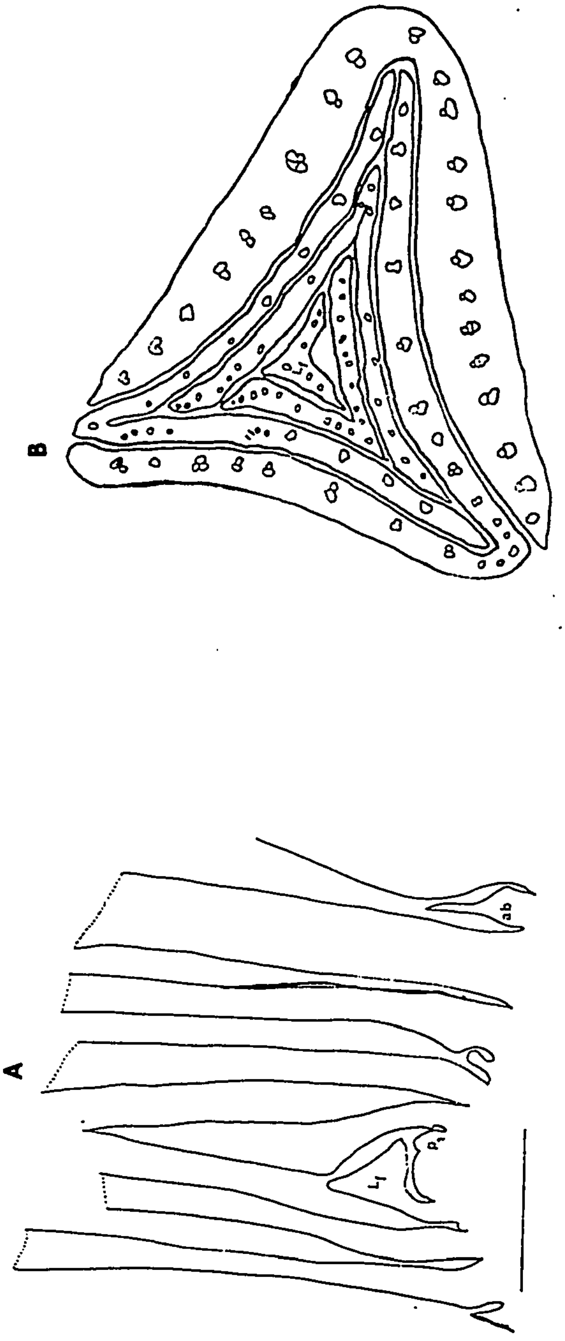

B
L1
A
ab
L1
p1

Fig. 9: Shoot apex and young leaf of Thurnia sphaerocephala (Colella et Morales, 1250); a) young leaf showing spines, bar = 5 um.

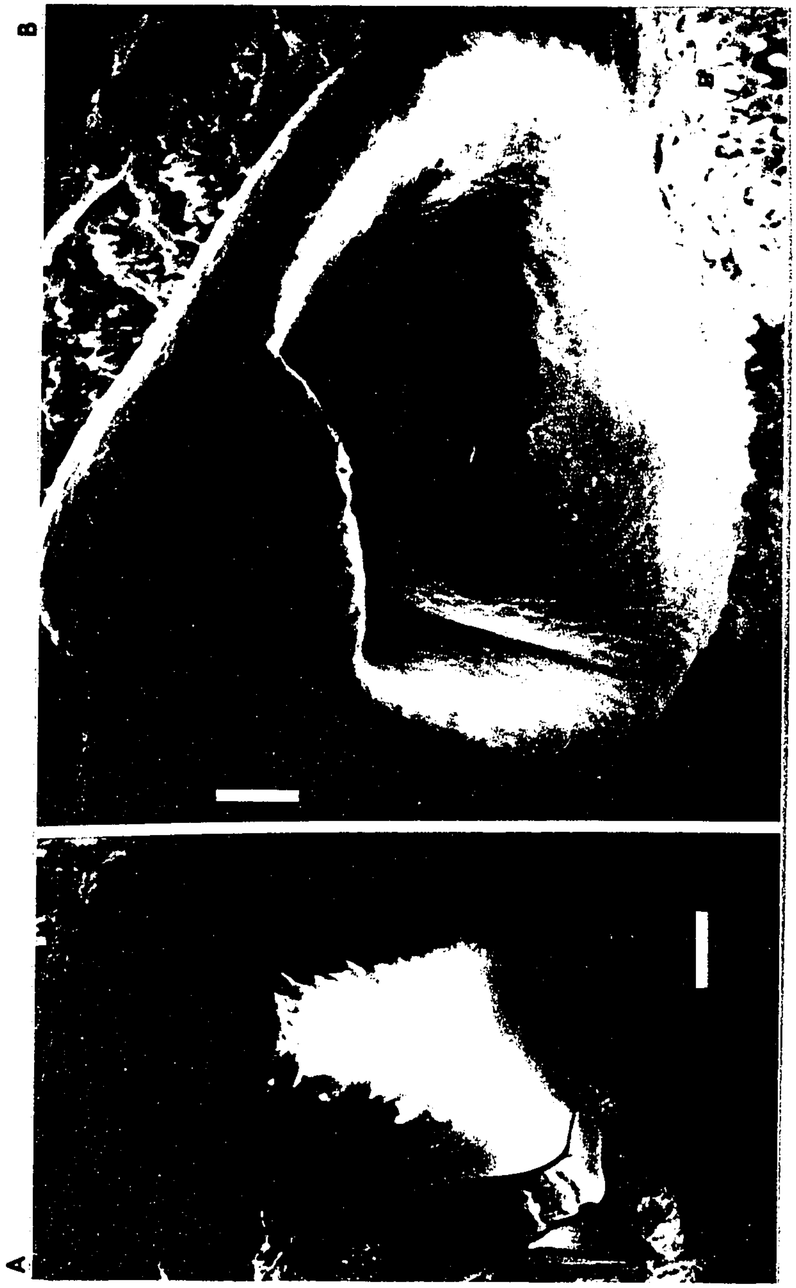

A
B

Table 1: Vegetative Morphology of Rapateceae and Thurniaceae

Vegetative Features	***Rapateaceae***	***Thurniaceae***
Leaf Morphology	mostly unifacial	bifacial, no petiole
Sheath	encircling shoot apex, plicate, mostly open	open, never encircling apex
Spines	only in Saxofridericia petiole	always on leaf margins
Shape of leaf primordium	chair-shaped	hood-shaped
Shape of shoot apex	domed	domed
Inflorescence Position	terminal or axillary	axillary

Table 1

Vegetative Morphology of Rapateaceae and Thurniaceae

Table 2: Leaf types in several genera of Rapateaceae and the genus Thurnia.

Legend: Taxa: genera; Inflorescence position (Inflo. position): Axillary or terminal; Leaf type: unifacial, bifacial, cylindrical; Spathaceous bracts: Sacciform, vestigial, fused, none; Sheath type: open, partially close, none; Habitat preference: wet or dry.

Taxa	**Inflo. Position**	**Leaf type**	**Axillary buds**	**Spatac. bracts**	**Sheath type**	**Habitat**
Saxofridericia	Axillary, few	Unifacial and bifacial	Lateral, few	Sacciform	Open	Dry, wet
Phelpsiella	Axillary, few	Unifacial	Unknown	Sacciform	Open	Dry, wet
Stegolepis	Axillary, many	Unifacial	Unknown	Vestigial or lacking	Open	Dry, wet
Amphiphyllum	Axillary, many	Unifacial	Unknown	Sacciform	Open	Dry, wet
Epidryos	Axillary, few	Unifacial	Unknown	Vestigial	Open	Epiphyte
Schoenocephalium	Terminal	Unifacial and cylindrical	Lateral, few	Small	Open or partially closed	Wet
Kunhardtia	Terminal	Unifacial	Lateral, few	Covering only the young inflores.	Open	Wet
Guacamaya	Terminal	Unifacial	Lateral, few	Sacciform	Open	Wet
Rapatea	Axillary	Bifacial and unifacial	Lateral, many	Fused at the base	Open	Mostly wet
Duckea	Axillary or terminal	Unifacila and cylindrical	Lateral, many	Inconspicuous	Open or partially closed	Wet
Spathanthus	Axillary	Unifacial	Lateral, many	Fused at base	Open	Wet
Monotrema	Axillary	Unifacial	Lateral, many	Inconspicuous	Open	Wet
Thurnia sphaerocephala	Axillary	Bifacial	Open	None	None	Aquatic
Thurnia polycephala	Axillary	Bifacial	Open	None	None	Aquatic

Table 2

Leaf Types

Chapter 2

Inflorescence Morphology

Inflorescences are shoot systems bearing flowers whose major function is reproduction. The study of inflorescence ontogeny helps to understand patterns, phylogenetic relationships and floral ecology among taxa. A detailed description of the inflorescence morphology of Rapateaceae, Thurniaceae and Xyridaceae has not yet been done. Despite the remoteness of the natural habitats of these families, the complexity of the compound globose inflorescence probably accounts for the lack of ontogenetic studies and more precise analysis of floral patterns. In order to elucidate the inflorescence morphology in Rapateaceae, careful dissections of the inflorescences were made and SEM pictures were taken of several floral stages. The anatomy of the inflorescences was diagramed.

An important distinction is made regarding branching development and sequencing. Thus, Bell (1991) recognizes two main types of branching patterns: 1) the cymose or sympodial (e.g cinncinus, thyrse), and 2) the racemose or monopodial (e.g spikes, umbells). Phylogenetic analyses and ontogenetic studies of the inflorescence give us some insights about the morphological processes that gave rise to the Rapateaceous cephalium. For a better understanding of the inflorescence morphology and branching pattern in the majority of Rapateaceae (cephalium made out of spikelets), Thurniaceae, Eriocaulaceae, and some Xyridaceae, it is suggested that a set of diverse and complex processes gave rise to a highly condensed floral system known as pseudanthium (Claussen, 1990). This type of transformation has also been reported to have occurred in many dicotyledoneous families (Troll, 1964; Weberling, 1991; Claussen, 1990).

The Pseudanthium

Claussen (1990) defines a pseudanthium as a type of floral transformation in which the attraction of the individual flowers gets reduced with an increase in aggregation. In the last stage of aggregation flowers form a new unit referred to as an inflorescence-blosom or a pseudanthium. The most important steps in floral transformation towards a pseudanthium are a) aggregation and inconspicuosness of individual flowers, b) floral differentiation, and c) integration of extrafloral bracts. Aggregation and inconspicuosness of flowers and bracts within or below the inflorescence often have a great impact on the design of the inflorescence-blosom (e.g spathaceous bracts in Rapateaceae and Commelinaceae). Pseudanthia can be derived from indeterminate or determinate inflorescences.

According to Troll (1964), indeterminate inflorescences originate from determinate inflorescences by truncation. An inflorescence is determinate when the growing point of it is transformed into a floral apex. They are indeterminate when the growing point never completes its development and produces lateral flowers or inflorescences (Weberling, 1991). The majority of the inflorescences studied in Rapateaceae, Thurniaceae, Xyridaceae (Tiemann, 1988) and Eriocaulaceae (Stutzel, 1984) are determinate.

Claussen (1990) suggests that if the individual flowers of the simple inflorescence are replaced by a complete inflorescence of the same branching pattern, then certain forms of the compound inflorescence be obtained. This type of branching can be repeated several times, so that third-order inflorescences or inflorescences of multiple order can result. The resulting inflorescence is a system with a multi-axial branching system. This process has taken place in several Commelinales (Commelinaceae, Eriocaulaceae, Xyridaceae, and Rapateaceae). The individual elements of the compound inflorescence are termed partial inflorescences (e.g the branches in a thyrse or in a raceme). Troll

(1964), suggested that determinate or indeterminate inflorescences tend to form pseudanthia.

The spikelet

The inflorescences of Rapateaceae have been interpreted as heads or capitula, or spikes of spikelets, and sometimes as a small collection of a few to several spikelets arranged in a variable fashion (Maguire, 1958). Our observations confirm that a spikelet is a modified spike with sterilization along the main axis and has a terminal flower (Fig. 56a). The mature spikelets are of a variable size, ranging from 0.5 cm (Monotrema sp.) up to 5 cm (Kunhardtia sp.). They consist of a variable number of coriaceous bracts arranged in spiral. Some are sessile or slightly pedicelate. The number and position of the prophylls is obscure by virtue of a spikelet condensation and packing in the cephalium; younger stages are needed for a better understanding of the phyllotactic patterns of the spikelet in the entire family.

Maguire (1958) enumerated the bracts of the spikelets and created categories in an orderly fashion, but this can be simplified by calling all of these bracts "spikelet bracts".

The number of spikelets is quite variable, and some genera may have species with a cephalium of about 100 or more spikelets (Stegolepis sp.and Saxofridericia sp., Spathanthus sp. Rapatea sp.) or just 1 to 3 spikelets per reduced cephalium (Stegolepis sp., Monotrema sp., and Epidryos sp.). Frequently two spathaceous bracts are located at the base of the inflorescence. Their degree of fusion, development and position is variable.

Infrageneric Inflorescence Types

It is suggested that the variability in inflorescence types in Rapateaceae are related to the probable existence of a common ancestor that had an inflorescence pattern with sympodial lateral branches in a monopodial main axis. Previous cladistic analysis done by Stevenson and Loconte (1995) showed that Commelinaceae was the first branch in the entire order. It can be suggest that the Commelinaceae retained a mixture of primitive and advanced characters in relation to the remaining Commelinales (Fig. 78). The inflorescences pattern of the family Commelinaceae are characterized by a type of inflorescence that consists of a monopodial ortogonal main axis with secondary lateral sympodial branches (thyrse and cincinnus). These sympodial branching may suggest an inflorescence ancestor for Rapateaceae. Although more ontogenetic studies with earlier inflorescence stages will help to understand the process better. The evidence gathered in this research, points towards the fact that the genera Windsorina and Maschalocephalus have the same type of monopodial-sympodial inflorescences as in Commelinaceae (Figs. 12, 13); the remaining genera showed a monopodial system in both primary and secondary inflorescence axis. It will be difficult on evolutionary grounds to think that the Rapateaceae developed two types of complex inflorescences -cymose and monopodial- simultaneously during the same evolutionary period.

It is suggested that the ancestor of Rapateaceae had a monopodial main axis with lateral sympodial branches, and in the course of evolution, two paths were developed. First, on one side the cephalium with monopodial branches derived by condensation of a sympodial inflorescence, and second, on the other side a different type of inflorescence, probably retained from its ancestor, the less common cymose ripidium which is sympodial (Fig. 11).

It was determined in the present research that the cephalium in Rapateaceae, (globose heads, capitulum etc.) is an assemblage of lateral branches -the spikelets- whose development starts at the base of the inflorescence, and ends in the upper part of it. At its base the younger spikelets sometimes never flower. The shape of the spikelets is probably being modified by possible changes that occurred in the meristematic activity of the inflorescence floral apex. During these changes, the spathaceous bracts can be totally or partially fused. On speculative grounds we can suggest that in the subfamily Saxofridericioideae the inflorescence peduncle developed in such a way that the base of the inflorescence is wider than the apex, and as a consequence the young inflorescence have a triangular resemblance. In later stages when all the spikelets are mature the cepahlium looks like a sphere. This is the case in Saxofridericia, some Stegolepis, Kunhardtia, Guacamaya, Schoenocephalium, Cephalostemon, Duckea, Monotrema, Potarophyton, and in a few species of Rapatea. In another possible variation of the peduncle, changes in the meristematic activity added more cells in the median plane and eventually the cephalium was transformed into an inflorescence with a predominantly ovoid shape. This is the case for the majority of the species of Rapatea. A third possible trend is the meristematic activity of the peduncle in which more cells are added in the transversal plane; further events lead to inflorescence axis elongation with the appearance of a spike of spikelets, as in the inflorescence of Spathanthus.

A detailed account of the inflorescences types among genera is presented for the first time in Table 3. The genera were enumerated following Maguire's phylogeny. Table 3 summarizes the position of the spathaceous bracts in relation with the lateral repetitive branches or paracladia, and the inflorescences shapes. A clear tendency of reduction in the complexity and shape (size too) of the inflorescence is seen in the genera Windsorina and Maschalocephalos. They depart from the cephaloid construction and have a more open branched system. The African genus Maschalocephalos has a little pedunculate and axial inflorescence with no evidence of multiple branching (Fig. 13). However, the Guianan genus Windsorina presents an elongated peduncle with many lateral branches (Fig. 12). The general shape of the remaining genera is that of a cephaloid or modifications of the cephaloid by reduction in the number of lateral branches or paracladia or by compression of the cephaloid in the median or transversal plane.

A Hypothetical Model of Inflorescence Construction

The author previously suggested that the inflorescences of the possible ancestor of the Rapateaceae could have a monopodial main axis with sympodial lateral branches.

In general, this ancestral type could have been a highly enriched thyrse or raceme with cymose lateral branches. These lateral branches suffered sterilization in their bracts. The sterile bracts of the previous flowers remained, and a terminal flower survived. Further aggregation and condensation reduced the size of the lateral axis, and this process gave rise to the spikelets. As for the cephaloid shape, more condensation and aggregation took place in the main axis to render the cephalium (Fig. 11).

Differences in inflorescence construction among the subfamilies Saxofridericioideae and Rapateoideae are presented in Fig. 10. Evidence of sympodial or cymose branching was not found in the genera Rapatea, Saxofridericia, Duckea and Monotrema; however, a more exhaustive survey may lead to different conclusions. A young cephalium with spirally arranged immature primordia of the spikelets of Saxofridericia aculeata is shown in Fig. 9. The apex is still active at the top of the inflorescence as young spikelets primordia are being added. At this particular stage, the basal spikelets were already mature and in pre-anthesis. The timing of the spikelets bracts remains unclear. A close view of terminal young Duckea junciformis flowers is shown in Fig. 14a. The sterile bracts were removed. The outermost three members of this whorl are the sepals and the innermost is the petals. Although eight phyllotactic patterns were observed in Stegolepis, the genus Saxofridericia has six phyllotactic patterns.

The inflorescence shape in Rapatea is an obconical cephalium that underwent elongation in the transversal plane; as a consequence it has a modified spikelet inception. In Fig. 10c the young spikelets are shown to have developed in a zigzag fashion and the inflorescence apex was less evident than in Saxofridericia. The spikelets in Rapatea did not seem to be spirally arranged and there were many glandular hairs at the base of the spathaceous bracts. In a mature inflorescence, the oldest spikelets are confined mostly to the center whereas the younger spikelets tend to be located on the sides.

Fully developed young cephalia of Duckea junciformis and Monotrema aemulans (Subfamily Rapateoideae) are shown in Fig. 14. The floral apex was exhausted by a terminal spikelet. The spikelets arrangement in Saxofridericia duidae (subfamily Saxofridericioideae) differs from that of Monotrema aemulans. In Duckea junciformis the oldest inflorescence remained in a lower branch; further development showed a tendency of clustering and to form sub-units of spikelets tightly packed as in

Monotrema aemulans (Fig. 14a).

No evidence of separate branching systems or floral sub-units was found in Saxofridericia duidae. Two separate floral sub-units can be seen in Fig. 14b of Monotrema aemulanas, with a narrow gap that separates the branches of the cephalium. The phyllotactic patterns in Monotrema and Duckea do not show the same pattern of contact parastichies as reported in Saxofridericia duidae.

In summary, important differences have been determined in inflorescence shape, size and developmental patterns among the subfamilies Saxofridericioideae and Rapateoideae. These data support the taxonomic separation of the two subfamilies proposed by Maguire (1958). It is suggested that, major modifications towards reduction in size of the head and of the spathaceous bracts, in the number of spikelets, and shifting in inflorescence branching system, were a more active processes in the tribe Monotremeae, and less active processes in the tribe Rapateeae. The subfamily Saxofridericioideae has a more homogeneous and stable construction, and reduction occurs only in the number of spikelets or spathaceous bracts.

Inflorescence Convergence

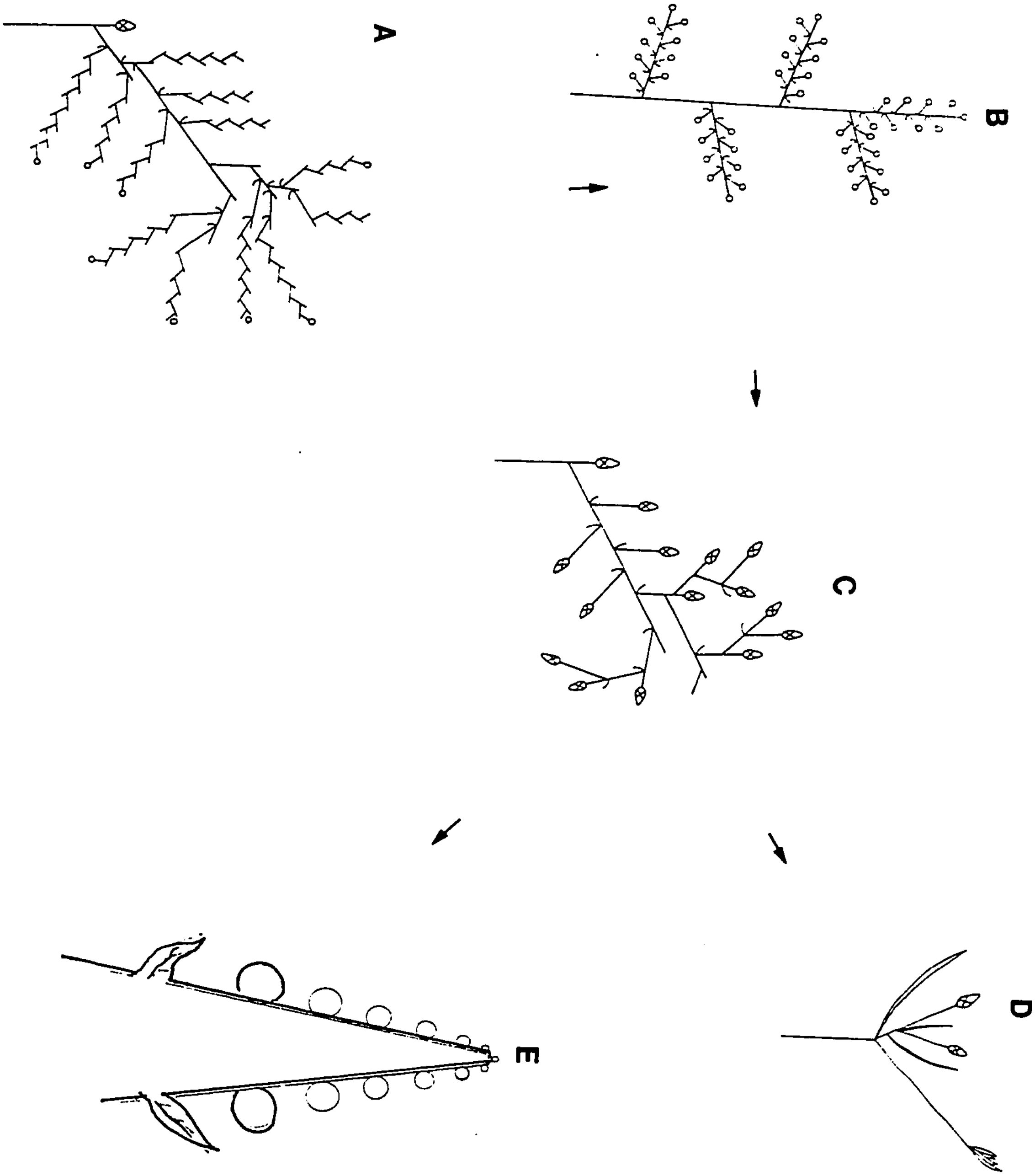
It can be suggested that there is an evolutionary convergence in the inflorescence structures of Rapateaceae and Thurniaceae. The acquisition of pseudanthia in both cases may suggest different pollination syndromes. The common inflorescence shape of the majority of Rapateaceae is that of a head or cepahalium made out of spikelets. In Thurniaceae the head is formed by single flowers, there is no evidence of spikelet formation and a few sterile and membranaceous bracts always surround the base of the flowers. Pollination syndromes in Rapateaceae are predominantly zoophylous although some wind pollination may occur. It is suggested that the genus Windsorina is most likely wind pollinated. Based on my preliminary field observations of the ratio of insect's presence/absence, frequency of pollinators, and floral morphology, I suggest that wind pollination is the common pollination syndrome in Thurniaceae. The green small flowers with inconspicuous brown-spotted tepals and long papillose stigmas with three stigmatic branches and very motile anthers recall a wind pollination syndrome reported in some Cyperaceae. We were unable to capture any insects due to the low frequency of insect visits. More field observations will hopefully render more reliable data.

The convergence in inflorescence shape in Thurniaceae and Rapateaceae it appears to be in relation to the morphology of pseudanthial processes. The adaptations of these inflorescence in relation to wind pollination syndrome are different, contradicting the general belief (Claussen, 1990) that pseudanthia evolved in order to make animal pollination more effective. The same can be said for the families with wind pollinated pseudanthia such as Juncaceae and Cyperaceae.

Fig. 10: Inflorescence apex: a) non-cymose floral apex of Saxofridericia duidae (Colella, 2206) (94x); b) Rapatea paludosa (Colella et Morales, 1272) detail of spiklet primordia (143 x); c) R. paludosa floral apex, showing young spathaceous bracts and glandular hairs, (94 x).


A
B
C

Fig. 11: Hypothetical floral transformation in Rapateaceae.


A
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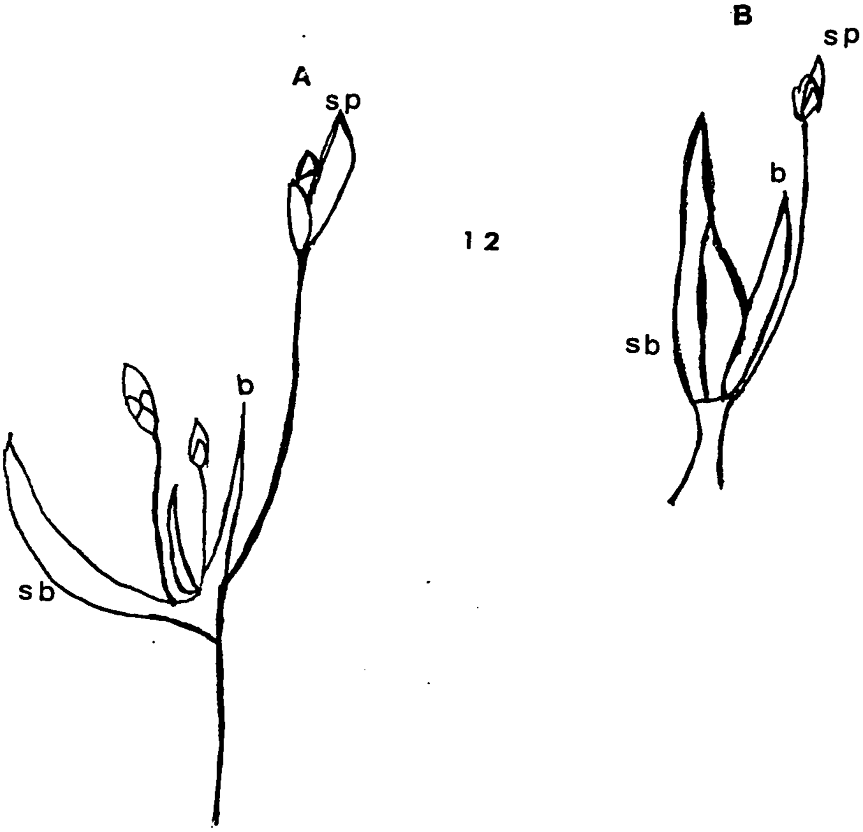
Figs. 12 and 13: Sympodial inflorescence construction in 12) Widsorina, and in 13 the same for Mashalocephalos. B=bract. Sb=subtending bract. Sp=spathaceous bract.



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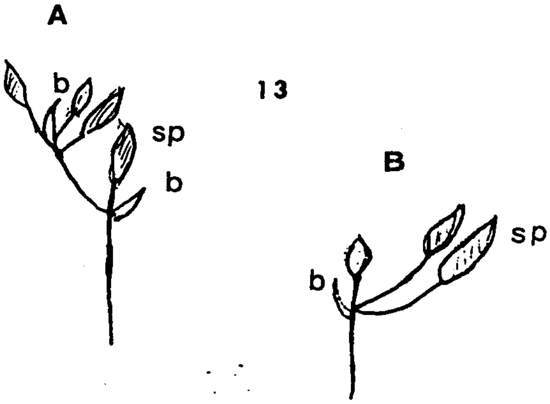

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Fig. 14: Inflorescence structure of: a) Duckea squarrosa (M. Colella, 2068) (45x); b) Monotrema aemulans (M. Colella et al 1276) (23x).


A
B

Table 3: Inflorescence Types

Inflorescence Types

Genus	*Spathaceous bracts*	*# of branches*	*Shape of pseudanthia*
Saxofridericia	2, paracladia	numerous	cephaloid
Phelpsiella	2	3-4	cephaloid
Amphiphyllum	2-4	5-7	pseudocephaloid
Epydros	absent	3-4	non-pseudanthious
Stegolepis	vestigial	1-many	cephaloid in many cases
Marahuacea	2	3	elongated in trasnversal plane
Kunhardtia	2	many	subconical
Guacamaya	2, paracladia penetrates them	many	subconical
Schoenocephalium	2, many		subconical/cephaloid
Rapatea	2, fused at the base	many	obconical, elongated in medial plane
Cephalostemon	2	1-9	pseudoglobose
Duckea	2	3-5	pseudoglobose

Genus	***Spathaceous Bracts***	***# of Branches***	***Shape of pseudanthia***
Spathanthus	1	many	elongated in medial
Monotrema	2-3	1-5	pseudoglobose
Potarophytum	2-4	4	pseudoglobose
Windsorina	no	many	non-pseudanthial
Maschalocephalus	no?	few	non-pseudanthial

Table 3: Inflorescences Types

Chapter 3

Pollen Morphology

The study of pollen morphology can have many implications related to evolution, taxonomic, medical, and economic aspects. Pollen for example is the main source of food for honey making. In a more evolutionary context Knox (1984) pointed out that the diversity in form and structure of pollen grains suggest that they have arisen by remarkable processes of adaptation to the environment or through coevolution processes with specific animal vectors. Pollen morphology has shown to be useful in determining taxonomic affinities at different hierarchical levels, depending on the group under consideration (Zavada, 1983). In addition, the study of pollen morphology, ultrastructure, and ontogeny has helped botanists to elucidate phylogenetic relationships among different taxa. In many cases considerable variation in shape, size, ornamentation patterns and ontogeny may occur among families. However some important variations are also reported at the generic and species level. Johri, et al. (1992) suggested that palynological data may contribute to a higher level systematics, however many taxonomic applications have focused on the relationships below family and between species and genera. Palynological characters are also complementary to other characters such as gross morphology, ultrastructure, ecology or plant molecular biology. In some examples the palynological data may agree or disagree with the existing classification.

The palynological studies on Rapateaceae done by Carlquist (1961) support Maguire's subfamily and tribal classification up to a certain extent. Carlquist concluded that variations in size, exine patterns, symmetry and aperture forms were different in the four tribes. Using conventional light microscopy and cytochemical techniques Carlquist (1961) published a complete and well-illustrated study on the pollen morphology of Rapateaceae. Earlier studies (Erdtman, 1952) were scanty, incomplete, and probably with some technical inadequacies. Using scanning electron microscopy, Zavada (1983) studied the pollen morphology of a few Rapateaceae. However all his grains collapsed, and with such grains it is difficult to detail sulcus morphology, size or exine pattern.

In order to understand the placement of the different genera of Rapateaceae and its relationships with some Commelinales I started a study of the pollen morphology of selected taxa of Rapateaceae, Thurniaceae, and Xyridaceae. Spore samples were taken from herbarium exsiccata at The New York Botanical Garden (Appendix 1) or from spirit material of my own field collections located at the Harding laboratory of The New York Botanical Garden (Appendix 1). Using light microscopy and SEM, features such as size, aperture type, shape, and exine sculpturing were studied. Pollen samples from individuals of the families Thurniaceae (Thurnia sphaerocephala Hook), Xyridaceae (Abolboda grandis), and Rapateaceae were analyzed. The following Rapateaceae were studied: Stegolepis squarrosa Maguire, Amphiphyllum schomburgkii Maguire, Kunhardtia rhodanta Maguire, Cephalostemon angustatus Malme, Duckea flava (Link) Maguire, and Monotrema xyridoides Gleason.

The most common techniques such as acetolysis and sonication for light and scanning electron microscopy (SEM) were used. SEM techniques require that the samples should be dehydrated, then critical point dried and finally gold coated. Light microscopy preparations were done with acetolized (Erdtman, 1952) and sonicated pollen, or from conventional anatomical preparations (using safranine and fast green as dies); pollen from spirit collections was sometimes mounted in glycerin jelly. Palynological terminology follows that of Ertdtman (1952).

Pollen Morphology: descriptions

Thurniaceae

The pollen of Thurnia spaerocephala Hook.f. and T. polycephala Scheene is in tetrahedral rhomboidal tetrads, they are monoaperturate, and the pore is lateral (Fig. 15 The sexine pattern is granulate and sometimes (Fig. 15d), the granulae are more dense towards the junction of the tetrads. The apertural region shows what can be interpreted as two openings but it needs confirmation (Figs. 15b, c, e, and arrows). The pollen grains did not tolerate acetolysis very well and future studies should involve the use of other techniques. The tetrads did not separate very well when acetolized. Erdtman (1952) described some of the features of Thurniaceae pollen. The systematic placement of the Thurniaceae has been near the Juncaceae with whom they also share some morphological features according to Cronquist (1981), Dahlgren et al (1985) or somehow nears the Rapateaceae according to Engler (1964). However on palynological grounds the pollen of Thurniaceae is more similar to that of Juncaceae than Rapateaceae.

Rapateaceae

Saxofridericioideae

The pollen morphology of some members of the two subfamilies was studied by selecting one or two representatives for each of the four tribes. No attempt was made to perform a careful statistical analysis of pollen size, shapes or apertures, as the approach was more qualitative. The species Stegelopis squarrosa Maguire and (Amphiphyllum) schomburgkii Maguire (Maguire) belong to the tribe Saxofridericieae. The genus Stegelopis along with Rapatea is one of the largest in numbers in the entire family.

An equatorial view of the proximal face shows that the elongate and elliptical spores of Stegolepis squarrosa are monosulcate (Fig. 19b). The sexine pattern is reticulate (Figs. 16a, c, and d,), and some grains showed flattened sides. The oblong spores of Amphiphyllum schomburgkii are monosulcate too, but the lumina between the walls narrows more than in Stegolepis squarrosa (Fig. 16b); the sulcus runs along the equatorial plane. In general, in spite of the minor differences in sexine patterns, shape and sulcus morphology, the pollen of both taxa does not look very different.

These palynological similarities are congruent with features such as morphology, phytogeography and embryology, suggesting an affinity between these two genera, which is in agreement with Carlquist (1961) who placed them together within the Saxofridericioideae. However, Maguire (1982), reported that the pollen of Amphiphyllum schomburgkii was asymmetric, oblong, strongly reticulate, and hemizonisulcate. We were unable to see any hemizonisulcate and strongly reticulate spores.

Schoenocephalieae

Carlquist (1961) suggested that semi-collapsed pollen may have a sulcus partially closed, and that could explain why some spores of the monosulcate pollen of Kunhartdia rhodanta Mag. present a sulcus that is a little wider than in the probably semi-collapsed Stegolepis squarrosa or Amphiphyllum shomburgkii. A polar view of the distal face shows some exine flakes in the aperture region (Fig. 16b). Contrary to what Carlquist (1961) reported the sulcus of Kunhartdia rhodantha does not narrow toward the ends and the sides are curved near the apertural area (Figs. 17a, b, c, and d); the overall shape is pseudo-elliptical. It has been reported that the pollen of Schoenocephalium is a mixture of spores with trichotomosulcate and monosulcate pollen (Carlquist, 1961). Sexine sculpturing in Kunhardtia is also reticulate but the pattern is intermediate between that of S. squarrosa and that of Amphiphyllum shomburgkii (Figs. 17c, b). Shape, sulcus and exine morphology between the tribes Saxofridericieae and Schoenocephalieae is somehow different but for a better understanding of pollen variability more complete surveys need to be done. Taxonomic affinities based on palynological data, only, should not be the unique criteria used as a support of the previous classification proposed by Maguire (1958).

Rapateoideae

This subfamily consists of two tribes (Rapateeae and Monotremeae) and eight genera. Morphological, anatomical, and embryological features (Maguire, 1958; Carlquist, 1961; Venturelli & Bouman, 1985; Tiemann, 1983) have been used as evidence for the segregation of this subfamily from the Saxofridericioideae. Pollen morphology also supports this separation. The genera Cephalostemon angustatus Malme and Duckea flava Maguire belong to the tribe Rapateeae, where the genus Rapatea is the largest in number in the entire subfamily. On palynological grounds, the pollen morphology of these genera looks different.

The spores of Duckea flava have a zonisulcate aperture (Figs. 18a, b, and 19a) with some exine flakes, and a thinner sexine in the aperture area. The overall shape of the mature pollen is elliptical, without evidences of flattening on the sides. Although the sculpturing in Duckea flava looks ornate, the sexine pattern is denser, a feature that is absent from previous described patterns. The reticulum is extremely narrow, and very little lumina are left between the walls, looking more like a scrobiculate pattern (Figs. 20a, b, and e). On Fig. 20b, a section of the spores shows the stratification of the exine.

The spores of Cephalostemon angustatus are elliptical, and probably zonisulcate (Figs. 21a, b). Although inadequate material was available the sexine pattern shows areas very smooth without walls or areas where the walls are present and a dense pattern with little lumina occurs. In the walled areas it reminds one of the Duckea flava sculpturing. It is suggested that an irregularly reticulate-orbiculate pattern occurs here and that the sculpturing in this genus requires further investigation. A few exine flakes were visible in the apertural area. Pollen kit and some other unnecessary particles were attached to the pollen grain.

The zonisulcate condition seems to be common in the entire tribe, with the exception of the disulcate genus Spathanthus Desv. perhaps this disulcate aperture can be interpreted as a condition derived from the zonisulcate through a narrowing of the central part of the aperture area (as it is the case in the tribe Monotremeae). Then further isolation of the two lateral apertures occurred until they became independent.

Monotremeae

The tribe Monotremae consists of four genera: Monotrema, Windsorina, Potarophytum, and the African monotypic disjunct Maschalocephalus (Maguire, 1958). Using SEM techniques, it was possible to study the pollen from herbarium material of Monotrema xyridoides Gleason. The spores of M. xyridoides are elliptical or slightly depressed in polar view (Figs. 20c, d), and monosulcate with a distinct modification in the sulcus. In Figs. 20d, and f, the aperture area narrows towards the center (polar view), and the sides may act as separate aperture regions for the future germination of the pollen grain. The sculpturing pattern is also derived from the reticulate type but the lumina are smaller like scrobiculi and small pits are located at the base of the lumina (Fig. 20). Carlquist (1961) reported the same type of pollen morphology (with minor variations) in the Monotremeae.

On palynological grounds there seems to be certain uniformity in the shape, sculpturing and aperture of the spores and these features may support 1) the separation of the Monotremeae from the Rapateeae, and 2) the Monotremeae assemblage proposed by Maguire (1958). On embryological grounds the most striking difference is that reported by Tiemann (1983) on the proliferation of antipodals (up to 40) in the genera Maschalocephalus and Potarophyton of the Monotremeae, a feature that seems absents in the remaining Rapateaceae. In spite of some morphological differences, there are some other important similarities between these four Monotremeae taxa, such as the presence of a chalazal appendage, similar embryology (Windsorina unknown), and floral morphology, and phytogeographical distribution as in the genera Windsorina and Potarophytum in the Potaro region of Guyana. However vegetative morphology is not well known in the entire tribe, and the embryology of the monotypic Windsorina has yet not been studied. It may be premature to comment on the possible affinities of these four genera and more research undoubtedly will bring a better understanding. However, based on the known similarities, they probably are a natural assemblage separate from the Rapateeae.

Affinities of the Rapateaceae with other families

Several authors (Carlquist, 1961; Venturelli & Bouman, 1988; Poole & Hunt, 1979; Erdtman, 1952; Maguire, 1958, 1982; Zavada, 1983) have studied the pollen morphology of the Commelinales, but with the exception of Carlquist very few publications focused on the comparative aspects of pollen morphology. Carlquist (1960) suggested that the pollen of Rapateaceae showed some similarities with that of the genus Xyris (Xyridaceae) probably because Xyris has the only sulcate (1-3 sulci), reticulate and bean-shaped spores in the entire family. However his contribution on the pollen of Xyridaceae was done using only light microscopy, and it lacks pictures and complete drawings of the entire spores of Xyris. Carlquist (1960) concentrated his palynological studies of the Xyridaceae on the genera Abolboda, Orectanthe, and Achlyphila, giving little importance to Xyris. Carlquist (1960) has suggested that in order to elucidate the palynological relationships among the Xyridaceae, more pollen analysis needs to be done on the genus Xyris. I will add that more pollen analysis is needed in the more recently described Xyridaceous genus Aratitiyopea Steyermark & Berry.

At this points in time the family Xyridaceae consists of the following genera: Abolboda, Achlyphila, Orectanthe, Aratitiyopea and Xyris. A modern study of the pollen morphology, and embryology of the Xyridaceae (the embryology of Orectanthe, Achlyphila and Aratitiyopea is unknown) is a very much needed task that will help to resolve the phylogenetic position of the Xyridaceae within the Commelinales. It will also help to test the hypothesized sister group relationships between Xyris and Mayaca. Novel morphological characters in the Xyridaceae will add more strength and consistency to future phylogenetic analysis of the Commelinales. A study of the pollen morphology and embryology of the Xyridaceae was beyond the scope of the present research. The pollen of Orectanthe, Abolboda and Achlyphila is inaperturate, spheroidal, and with a variable exine pattern that shows minute embedded pila with excrescencies laying on a thin exine. Thus, in addition to the pila, Carlquist (1960) reported the presence of funnel or spines in Abolboda spores, and knobs of different sizes in Orectanthe pollen. However, in Achlyphila, the knobs or the spines are absent but the pila are the largest of the family. None of the Rapateaceous pollen showed the above mentioned exine patterns; instead the pollen of the different genera are aperturate, generally reticulate, and elliptical to spheroid in shape (few times). No close resemblance was found between the spores of the Xyridaceae and Rapateaceae. The pollen of the monotypic Mayacaceae (Mayaca fluviatilis Aublet) is monosulcate, spheroid, and with a finely reticulate exine sculpturing (Venturelli & Bouman, 1986), as in Rapateaceae, the aperture area is covered by exine flakes. Zavada (1983) suggested that the pollen wall structure of Mayaca exhibit many similarities with the pollen wall found in some Commelinaceae. He reported that the exine of Rapateaceae varies from scabrate, minute scabrate (small projections), reticulate, psilate, and sometimes with a smooth surface. The only pseudo-spherical spores in Rapateaceae are those of Rapatea but the aperture is zonisulcate, and the exine pattern is reticulate. In general, not only the spores (Fig. 18c), but the anatomy, embryology and ecology of Mayacaceae and Rapateaceae are different to the extent that they should remain as separate and distinct families.

The spores of Rapateaceae have a particular resemblance with that of some Commelinaceae, a feature never discussed in previous publications. Most of the Commelinaceous pollen is monosulcate as in Rapateaceae, but Tinantia has an extended sulcus, and it can be said that is almost zonisulcate, a common feature of the subfamily Rapateoideae. Zebrina has three germinal apertures, and Schoenocephalium has been reported to be trichotomosulcate sometimes. On some occasions, the ovate shape with flattening sides and distal surface as in Gibasis, could be interpreted as analogue with that present in the Monotremeae. They also have an extended and wide sulcus, that may reached the sides as in Shoenocephalium and many Monotremeae. Showing a great variability in pollen size, the Commelinaceae have an exine pattern with spinulate-bacculate ektexine as in some Xyridaceae.

The Commelinaceae also present exine flakes in the aperture areas as in Rapateaceae and Mayacaeae. We should not dismissed that perhaps the above resemblance between the spores of Rapateaceae and Commelinaceae are due to parallelism, but it will be useful to test the resemblance hypothesis with a broad study on the comparative morphology, ontogeny and ultrastructure of the pollen in both families.

The pollen of Eriocaulaceae is spherical, spinulate and spiroaperturate. None of the

Rapateaceous pollen has any such features. Affinities of this family are more likely to be with Xyridaceae and Commelinaceae.

Fig. 15: Pollen of Thurnia sphaerocephala (Colella et Morales 1250) : a) SEM tetrads, bar= 5 um; b) acetolised tetrads (2000x); c) tetrads showing aperture (2000x); d) SEM showing sculpturing; e) polar view (1000x).


A
B
C
D
E

Fig. 16: Pollen of: a) Stegolepis squarrosa (Boom, 9372) sulcus view and exine pattern detail, bar= 5 um; b) Amphyphyllum shomburgkii (Maguire et al, 65564) exine pattern detail, c) same as b. sulcus detail; d) Stegolepis squarrosa polar view.


A
B
C
D

Fig. 17: Pollen of Kunhardtia rhodantha (Berry, 4808); polar view, distal face with exine flakes, bar= 5 um; b) equatorial view, proximal face, bar= 10 um; c) equatorial view, and distal face, bar= 10 um; d) polar view, distal face, bar= 5 um.

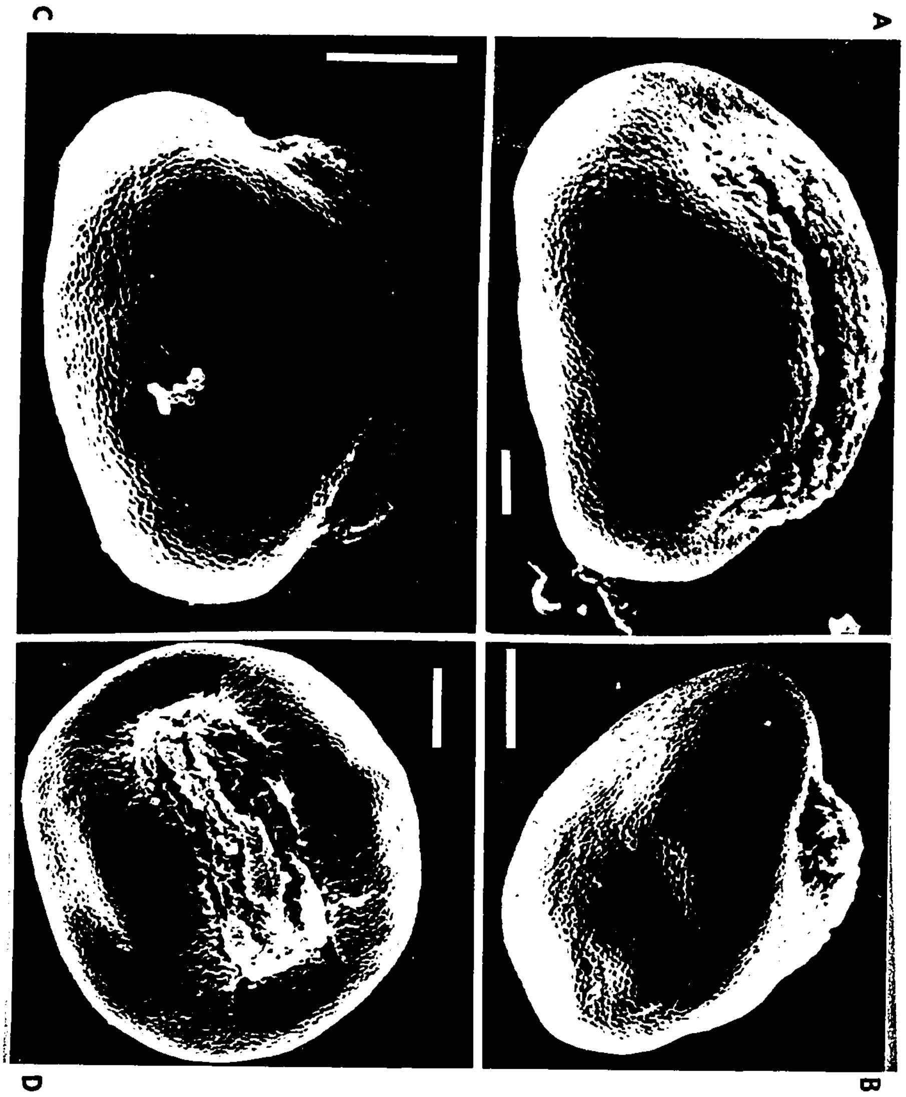
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Fig. 18: Pollen of: Duckea flava (Colella et al, 2068), a) sulcus view; b) equatorial view, bar= 10 um; c) Rapatea sp. nov. (Daly s/n) zonisulcate pollen showing exine pattern, bar= 7 um.

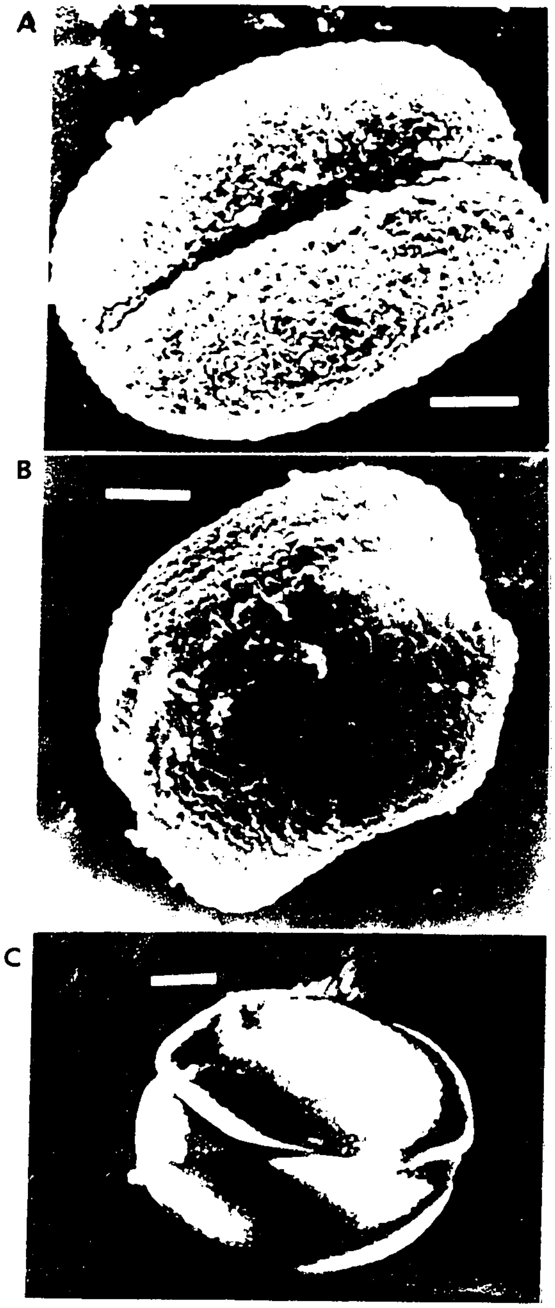
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Fig. 19: Pollen of: a) Duckea flava (M. Colella et al, 2068) equatorial and polar view, bar= 10 um; b) Stegolepis squarrosa (Boom, 9372)equatorial view, bar= 5 um.

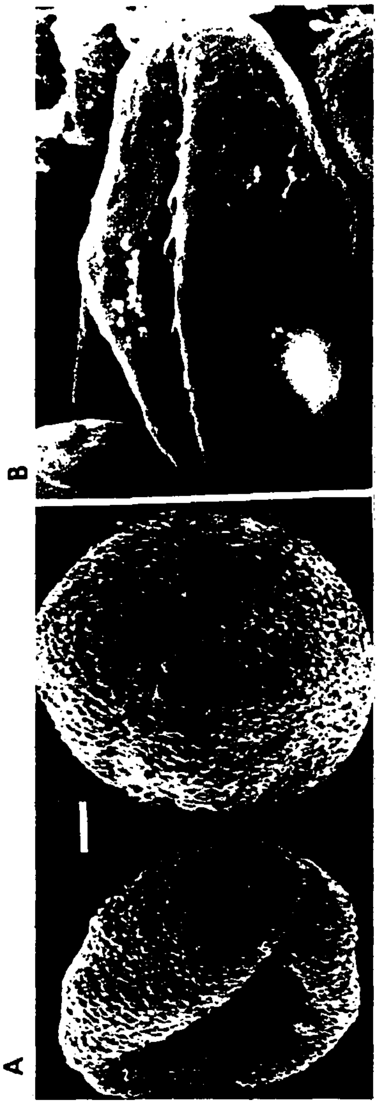
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Fig. 20: Pollen of a) equatorial view of Duckea flava (Colella, 2068); b) D. flava detail of the layers; c) Monotrema xyridoides (Pires, 14999) polar view, sculpture; d) M. xyridoides equatorial view; e) D. flava, zonisulcate pollen; f) M. xyridoides polar view. Bar= 10 um.

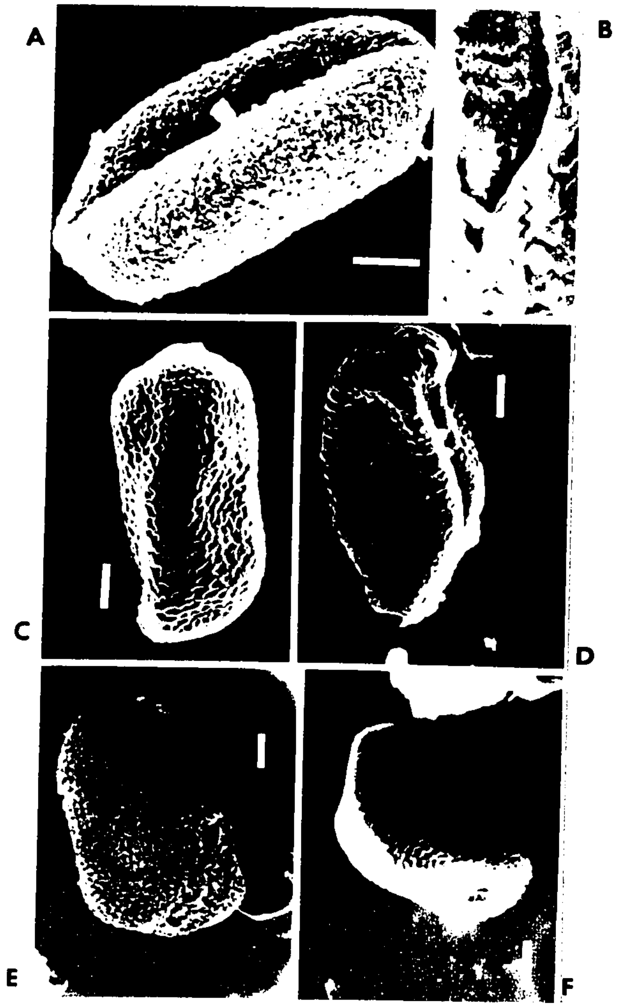
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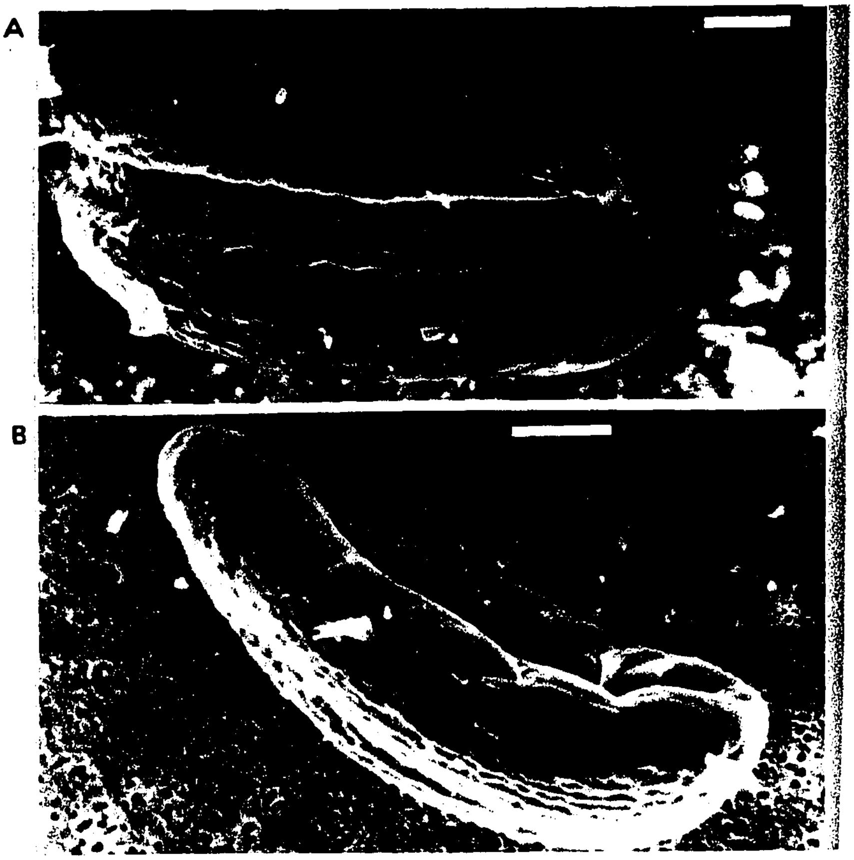
Fig. 21: Pollen of Cephalostemon angustatus (Harley et al, 25449); a) equatorial view with zonisulcate aperture; b) polar view, bar= 10 um.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Chapter 4

Stomata Types

Stomata are minute openings of epidermal origin, usually elliptical and bordered by a pair of guard cells and the stomatal aperture between them (Metcalfe & Chalk, 1979). They can be found in organs such as stems, petals, ovaries, stamens etc., but they are most common in leaves. The epidermal cells next to the guard cells may or may not be morphologically distinctive; if different then they are known as subsidiary cells (Mauseth, 1988). Baranova (1987) mentioned that three historical approaches have prevailed in stomata classification, the morphological, the ontogenetical and a combination of both. In the morphological classification it is important to know whether the cells that surrounded the mature stomata are ordinary epidermal cells or subsidiary cells that may differ in number, form, and arrangement (Metcalfe & Chalk, 1979). According to Rasmunssen (1981) the ontogenetical classification includes several patterns that relates the cell lineage and the cell position during development. The structure or morphology of the mature stomatal complex provides a character of a certain taxonomic importance.

Previous studies described the stomata in Rapateaceae as paracytic and being

restricted to the abaxial side of the blade (Carlquist, 1969). The term paracytic refers to restricted to the abaxial side of the blade (Carlquist, 1969). The term paracytic refers to those stomata that are accompanied by one or more subsidiary cells parallel to the long axis of the pore and guard cells (Metcalfe & Chalk, 1979).

In order to verify Carlquist's definition and to analyze if there whether any morphological differences at the generic level, a SEM (Scanning Electron Microscopy) survey was undertaken for mature stomata of the subfamilies Saxofridericioideae and Rapateoideae and the family Thurniaceae. Our approach was mainly descriptive) Samples were taken from spirit collections or from herbarium specimens, critical point dried and gold coated in preparation for SEM. The most common variations observed at the generic level are shape and size of the guard cells, length and width of the pore and ornamentation in the subsidiary cells.

The standard deviation is larger for length than for width in four out of eight species (Table 4). It can be seen in Figs. 22b and 23c the subsidiary cells are relatively close to the guard cells in Saxofridericia inermis and Amphyphyllum schombgurgkii, and it can also be seen in Figs. 22d and 23d that their distribution in the epidermis is not regular.

In Kunhardtia rhodantha the subsidiary cells are more isolated from the guard cells than they are in Saxofridericia inermis and Amphyphyllum schomburgkii (Fig. 22a). The distribution of the stomata in the epidermis is in rows (Fig. 22c). In the subfamily Rapateoideae the species Cephalostemon affinis and Duckea flava have long stomata whereas Maschalocephalos dinklangei has much shorter stomata. In the Rapateoideae both length and width of the pore are more variable than in the Saxofridericioideae.

In Rapatea sp. nov. the stomata are as usual, distributed in rows but the guard cells show ridges in a unusual configuration. Epicuticular waxes like granules are reported for the first time in Rapatea sp. nov. (Fig. 24). The West-African species Maschalocephalos dinklangei have long and narrow stomata and the epicuticular waxes are scaly (Fig. 25a). Spathanthus unilateralis shows a thickening near the pore and the same feature is also reported in Cephalostemon affinis (Fig. 23b, 24c). In the Thurniaceae, Thurnia sphaerocephala exhibits stomata that are quite narrow (Fig. 25b). They are not in rows (Fig. 25c) and are paracityc as in Rapateaceae. In both cases, the data support the previous descriptions of the stomata types in Rapateaceae and Thurniacea, however the tetracytic type reported in Thurniaceae by Cutler (1965) was not found.

Preliminary Statistical Analysis of the Stomatal Measurements of Width and

Length of the Pore in Rapateaceae and Thurniaceae

I called this analysis preliminary because the sample size is small. Table 4 shows the mean and the standard deviation (in parenthesis) of five measurements done on the stomata of Rapateaceae and Thurniaceae from scanning electron micrographs. Variables measured were length and width of the pore in um (microns). Five measurements of length and width were done for each species in the stomata of eight genera of Rapateaceae and one of the Thurniaceae. Due to the scarcity of leaf material measurements of the stomata in the genus Maschalocephalus could not be replicated. The rationale in this analysis was to observe variations in stomatal length and width at the generic level that could justify or contradict Maguire's (1958) hypothesis on the systematics of Rapateaceae.

In Table 4 we can observe that mean variations of stomatal lengths are larger in Duckea flava 55.74 um (.811), Cephalostemon affinis 39.5 um (.925) and Rapatea sp. nov. 32.92 um (.807), all members of the subfamily Rapateoideae. Whereas the same variable in members of the subfamily Saxofridericioideae are more uniform, Saxofridericia aculeata 35.7 um (2.387), Marahuacea schomburgkii 34.80 um (1.144) and Kunhardtia rhodantha 34.12 um (.729). A similar trend is true for the stomatal width with few deviations.

An ANOVA (Analysis of Variance) was done in order to analyze the variability of the width and length of the stomata among taxa and its possible taxonomic value. Fisher's factorial analysis for pair of taxa among the subfamilies Saxofridericioideae and Rapateoideae of the Rapateaceae and the genus Thurnia in the Thurniaceae is reported in Tables 4 and 5 for the first time. Table 5 shows the multiple comparisons for Stomatal length pairs. When the p-value is significant, it can be assumed that the measurements of stomatal length or width are different among pairs. In some cases that significance correlates with taxonomic differences, but in other occasions it does not.

In analyzing Table 5, we observed that the pair Saxofridericia-Kunhardtia, (Saxofridericioideae), are placed in different tribes corresponding to their difference in stomatal length (p=0.0331) agrees. The pair Saxofridericia-Marahuacea belongs to the same subfamily and its p-value (0.0901) shows that there are no significant differences and this is in accordance with their taxonomic relationship. When comparing the p-value of the pairs Saxofridericia- Rapatea (0.0004), Saxofridericia-Cephalostemon (0.0001), Saxofridericia-Spathanthus (0.0024), Saxofrideicia-Duckea (0.0001) and Saxofridericia-Thurnia (0.0001) we conclude that the p-values are significantly different, this is in accordance with the taxonomic position of these pairs. The genera Rapatea, Cephalostemon, Spathanthus and Duckea belong to the subfamily Rapateoideae and the genus Thurnia belongs to the family Thurniaceae. The genus Marahuacea belongs to the Saxofridericioideae, and it shows differences with members of the Rapateoideae such as Rapatea (0.0375), Cephalostemon (0.0001), Duckea (0.0001) and Thurnia (0.0001) but not with Spathanthus (0.1309). The genus Kunhardtia, belongs to the Saxofridericioideaea (tribe Schoenocephalieae) and showed differences with some members of the Rapateoideae such as Cephalostemon (0.0001), Duckea (0.0001), and Thurnia in the Thurniaceae (0.0001). However differences were not significant when comparing Kunhardtia with other members of the same subfamily such as Rapatea (0.1005), and Spathanthus (0.2922). The p-values of the majority of the members of the subfamily Rapateoideae are significantly different (except for Rapatea-Spathanthus with p=0.5396). In all cases differences between pairs of members of the Rapateaceae and Thurnia (Thurniaceae) were always significant.

Table 6 summarizes the Multiple comparisons of stomatal width in pairs of taxa that belong to the Saxofridericioideae, Rapateoideae and the genus Thurnia in the Thurniaceae. The p-value of the pair Saxofridericia-Marahuacea is not significant (0.0901) the same was reported when comparing differences in stomatal length. With few exceptions, the remaining taxa showed significant differences in stomatal width. The exceptions are Marahuacea-Kunhardtia (0.6351), Marahuacea-Spathanthus ((0.1309), Kunhardtia-Rapatea (0.1005), Kunhardtia-Spathanthus (0.2922), Rapatea-Spathanthus (0.5396). These values do not correlate with taxonomic differences among taxa. In all cases the p-values of the Rapateaceae were significantly different when compare with those of Thurnia.

Differences in the means of stomatal length and width measurements among Rapateaceae and Thurniaceae are presented in Figs. 26a, and 26b. Variations in the means of stomatal lengths are more evident in Duckea flava, Cephalostemon affinis (Rapateaceae) and Thurnia sphaerocephala (Thurniaceae), the remaining taxa's means are approximately within the same range of values (Fig. 26b). Variations in the mean of stomatal width among taxa, show a more variable pattern, and here Duckea flava also has the greater variation (Fig. 26a). The West-African genus Maschalocephalus was not included as we were unable to obtain enough stomatal measurements.

We conclude that our preliminary statistical analyses do not help to resolve clear taxonomic differences or affinities between groups, probably because the sample size was too small or, the characters used –stomatal length and width- are not very informative.

Fig. 22: Stomata types: a) Kunhardtia rhodantha (Colella s/n) single stomata, bar= 5 um; b) Saxofridericia duidae (Colella, 2206) single stomata, bar= 5 um; c) Kunhardtia rhodantha epidermis detail, bar= 10 um; d) Saxofridericia inermis epidermis detail, bar= 10 um.

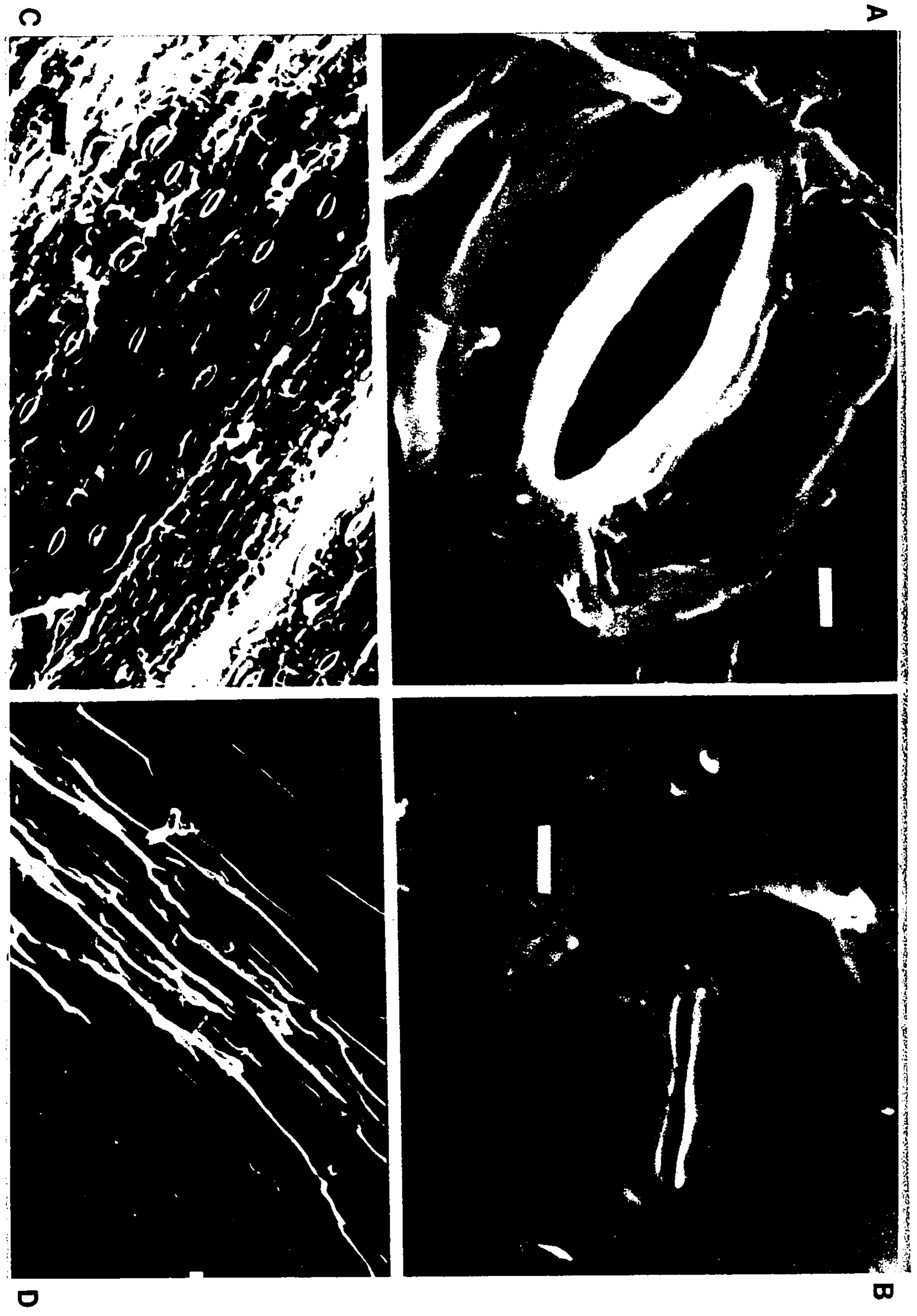
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Fig. 23: Stomata types: a) Cephalostemon affinis (Colella et al 2069) epidermal view, bar= 5 um; b) C. affinis detail of individual stomata, bar= 50 um; c) Amphyphyllum schomburgkii (Steyermark, 58.249) detail of individual stomata, bar=5 um; d) A. schomburgkii epidermal view, bar= 50 um.


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C

Fig. 24: Stomata types: a) Rapatea sp. nov. (Daly, s/n), 25um; b) Rapatea sp. nov. (Daly, s/n) epidermal view 50um; c) Spathanthus unilateralis (Colella, 2091) 5um; d) Duckea flava (Colella, 2090) 10um.

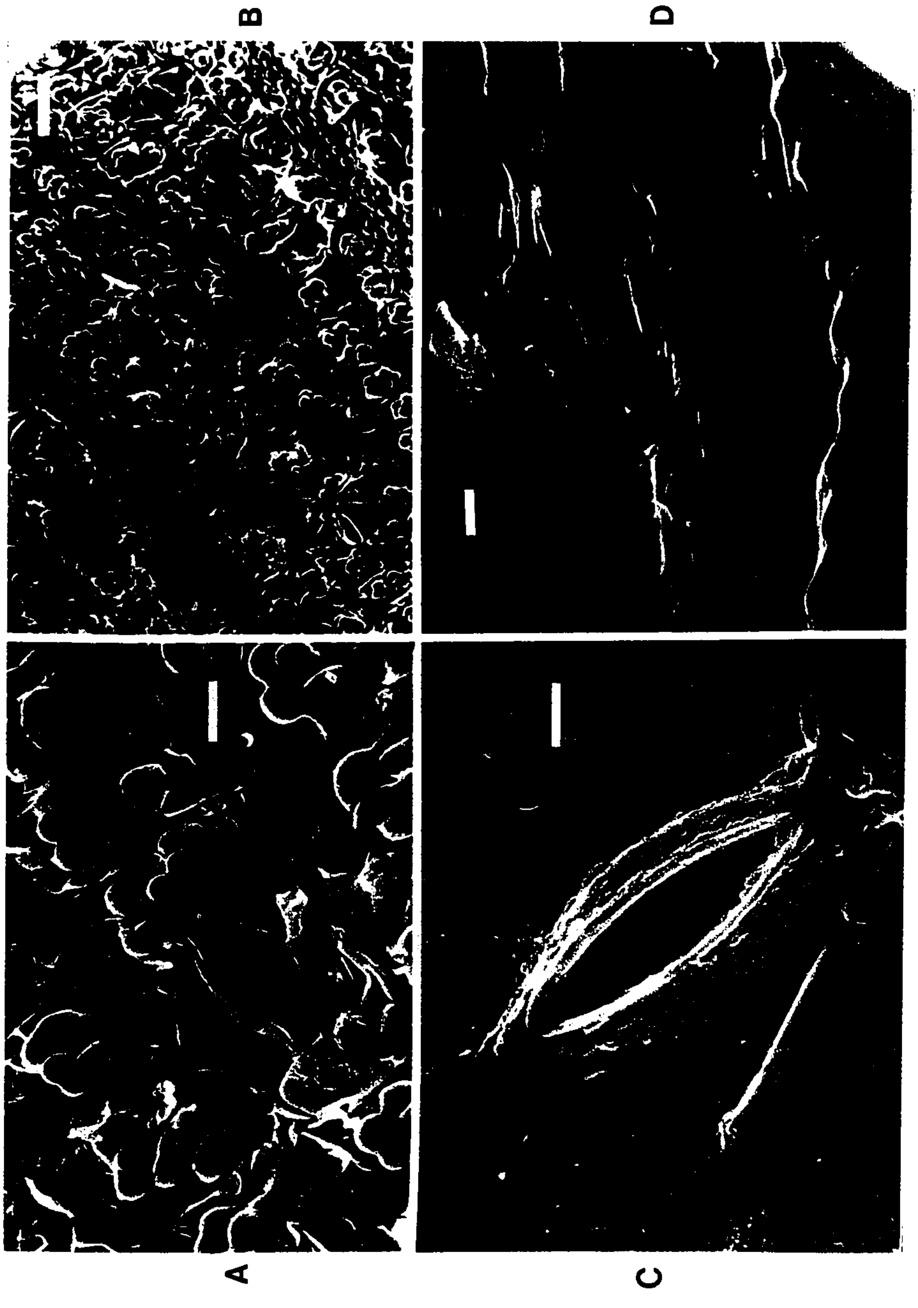
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Fig. 25: Stomata type: a) Maschalocephalus dinklagei (Adams, 469) single stomata showing epicuticular waxes, bar= 5um; b) Thurnia sphaerocephala single stomata (Colella & Morales, 1250) bar= 5 um; c) T. sphaerocephala, bar= 10 um.


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Fig. 26: Mean of a) Stomatal width and b) Stomatal length. Bars= standard error

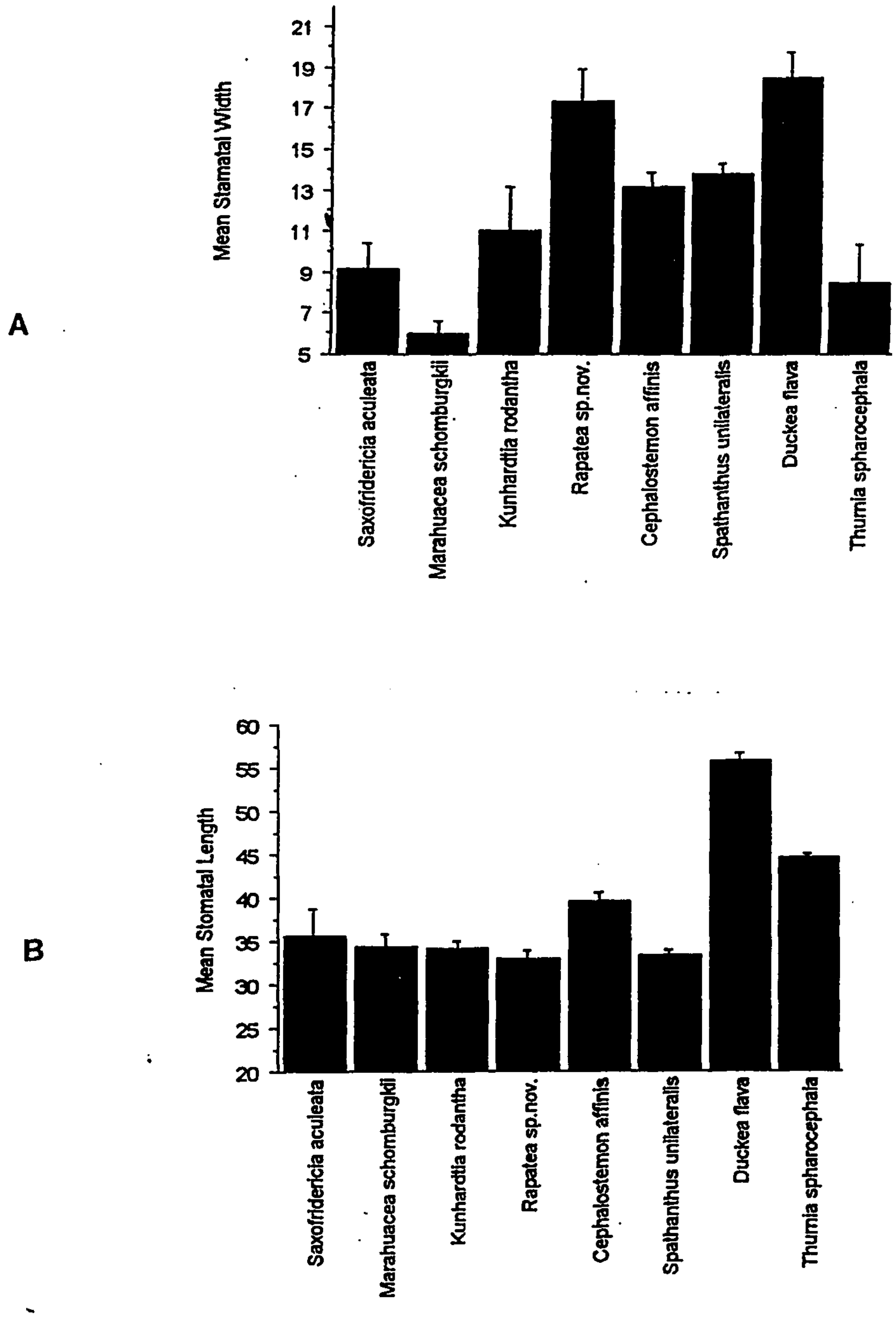

Table 4: Stomatal length and width means. Standard deviation in parenthesis.

Taxa	Stomatal Length	Stomatal Width
Saxofridericia aculeata	35.7 (2.387)	9.12 (1.035)
Marahuacea schomburgkii	34.80 (1.144)	5.94 (.546)
Kunhardtia rodantha	34.12 (.729)	10.98 (1.733)
Rapatea sp.nov.	32.92 (.807)	17.3 (1.273)
Cephalostemon affinis	39.5 (.925)	13.18 (.559)
Spathanthus unilateralis	33.36 (.472)	13.78 (.449)
Duckea flava	55.74 (.811)	18.48 (1.013)
Thurnia sphaerocephala	44.62 (.377)	8.42 (1.53)

Table 4: Stomatal length and width means of five measurements by species (in um). Standard Deviation in parenthesis

Tables 5 and 6: Multiple comparisons for stomatal length and width

Taxa	Mean differences	P-Value
Saxofridericia-Marahuacea	1.240	0.0901
Saxofridericia-Kunhardtia	1.580	0.0331 (s)
Saxofridericia-Rapatea	2.780	0.0004 (s)
Saxofridericia-Cephalostemon	-3.800	0.0001 (s)
Saxofridericia-Spathanthus	2.340	0.0024 (s)
Saxofridericia-Duckea	-20.04	0.0001 (s)
Saxofridericia-*Thurnia*	-8.920	0.0001 (s)
Marahuacea-Kunhardtia	0.340	0.6351
Marahuacea-Rapatea	1.540	0.0375 (s)
Marahuacea-Cephalostemon	-5.04	0.0001 (s)
Marahuacea-Spathanthus	1.100	0.1309
Marahuacea-Duckea	-21.280	0.0001 (s)
Marahuacea-Thurnia	-10.160	0.0001 (s)
Kunhardtia-Rapatea	1.200	0.1005
Kunhardtia-Cephalostemon	-5.380	0.0001 (s)
Kunhardtia-Spathanthus	0.760	0.2922
Kunhardtia-Duckea	-21.620	0.0001 (s)
Kunhardtia-Thurnia	-10.50	0.0001 (s)
Rapatea-Cephalostemon	-6.580	0.0001 (s)
Rapatea-Spathanthus	-0.440	0.5396
Rapatea-Duckea	-22.820	0.0001 (s)
Rapatea-Thurnia	-11.700	0.0001 (s)
Cephalostemon-Spathanthus	6.140	0.0001 (s)
Cephalostemon-Duckea	-16.240	0.0001 (s)
Cephalostemon-Thurnia	-5.120	0.0001 (s)
Spathanthus-Duckea	-22.380	0.0001 (s)
Spathanthus-Thurnia	-11.260	0.0001 (s)
Duckea-Thurnia	11.120	0.0001 (s)

Table 5: Multiple comparisons for Stomatal length among taxa. Significance level: 5%.

Taxa	Mean differences	P-Value
Saxofridericia-Marahuacea	3.180	0.0001 (s)
Saxofridericia-Kunhardtia	-1.860	0.0125 (s)
Saxofridericia-Rapatea	-8.180	0.0001 (s)
Saxofridericia-Cephalostemon	-4.060	0.0001 (s)
Saxofridericia-Spathanthus	-4.660	0.0024 (s)
Saxofridericia-Duckea	-9.360	0.0001 (s)
Saxofridericia-Thurnia	0.700	0.3266
Marahuacea-Kunhardtia	-5.040	0.0001 (s)
Marahuacea-Rapatea	-11.360	0.0001 (s)
Marahuacea-Cephalostemon	-7.240	0.0001 (s)
Marahuacea-Spathanthus	-7.840	0.0001 (s)
Marahuacea-Duckea	-12.540	0.0001 (s)
Marahuacea-Thurnia	-2.480	0.0013 (s)
Kunhardtia-Rapatea	-6.320	0.1005
Kunhardtia-Cephalostemon	-2.200	0.0037 (s)
Kunhardtia-Spathanthus	-7.500	0.0001 (s)
Kunhardtia-Duckea	-21.620	0.0001 (s)
Kunhardtia-Thurnia	2.560	0.0009 (s)
Rapatea-Cephalostemon	4.120	0.0001 (s)
Rapatea-Spathanthus	3.520	0.5396
Rapatea-Duckea	-1.180	0.1028
Rapatea-Thurnia	8.800	0.0001 (s)
Cephalostemon-Spathanthus	0.600	0.3995
Cephalostemon-Duckea	-5300	0.0001 (s)
Cephalostemon-Thurnia	-4.760	0.0001 (s)
Spathanthus-Duckea	-4.700	0.0001 (s)
Spathanthus-Thurnia	5.360	0.0001 (s)
Duckea-Thurnia	10.060	0.0001 (s)

Table 6: Multiple cpmparisons for Stomatal width among taxa. Significance level: 5%.

Chapter 5

Floral Morphology and Reproductive Biology

The history and uses of embryology goes back to Theophrastus who mentioned the pollination of the date plant for the first time. For a long period of time the topic on plant's sexuality was forgotten. It was Giovanni Amici (1824) who discovered pollen tube growth. But many debates arouse between Schleiden (1837) and Amici in relation to the identity of the female gametophyte as Schleiden thought that the female gametophyte was related to the pollen tube. It was Wilhem Hofmeister (1867) who discovered that the embryo sac originated from a preexisting cell in the embryo sac and not from the pollen tube. By the end of the 19th century, plant scientists knew most of the basic factors, about reproduction in flowering plants, and embryology became an established discipline.

In 1920, Schnarf published his seminal work on embryology under the title of " Vergleinchende Embryologie der Angiosperm" in which he described many original processes as well as synthesized the contribution of other contemporary embryologists. Since then, there have been significant advances in our knowledge of embryology brought about by the improvement in microscopy and the advancement of new techniques.

Many important embryologists of this century have work on the systematic relationships of Angiosperms (Maheshwari, 1950, 1963; Davis 1966; Palser 1957). Their contributions help to elucidate and identify many systematic affinities at the family, generic and ordinal level. The examination of embryological characters of taxonomic importance has been of tremendous help towards the solution of complex systematic relationships. These embryological characters are related with the behavior of male and female gametophytes before and after fertilization. The features and data presented in this research are derived from the experiences of previous embryologists (Maheshwari, 1950, 1953; Bhojwani & Bhatnagar, 1983) and the application of embryological data to taxonomy. Tables 5, and 6, summarize the characters most commonly analyzed in both male and female gametophytes.

Previous Embryological studies in Rapateaceae and Thurniaceae

Venturelli & Bouman (1984) and Tiemann (1983) published descriptions on the embryology of the family Rapateaceae. Tiemann surveyed many genera and the genus Abolboda in the Xyridaceae, her studies had a broader scope and she compared the characteristics and behavior of the male and female gametophytes within the two subfamilies of the Rapateaceae and among the orders Commelinales and Cyperales. The contribution of Bouman and Venturelli concentrated more on the embryology of the subfamily Rapateoideae, however they surveyed the seed morphology of many genera. Based on the mentioned previous works, this research concentrated on the study and description of embryological data in those genera of Rapateaceae that were not studied before. The systematic position of the family Thurniaceae is not clear yet, however new embryological data was generated in order to solve potential interfamilial affinities within the order Commelinales or Juncales.

Tables 7 and 8: Female and male features before and after fertilization has occurred.

Female Features before and after fertilization
Zonation in ovule primordium
Integument initiation
Number of archesporial cells
Position of ovule
Nature of nucellus
Composition of basal nucellus
Form of megaspore tetrads
Formation of mycropile
Width of the outer integument
Width of the inner integument
Special features in the integuments (depositions, topology)
Tannins and starch in the integument
Embryo sac formation
Morphology of egg apparatus
Behavior of antipodal cells
Fate of the basal nucellus
Shape of the ovule

Table 7: Female features before and after fertilization

Male features before and after fertilization
Androecial initiation (number of whorls)
Anther wall development (Basic or Monocot type)
Number of middle layers
Number of nuclei in the tapetum cells
Form of pollen
Tapetum type (secretory or a secretory variant)
Distribution of starch, tannins, and silica bodies
Secondary thickening of endothecium
Anther attachment
Anther wall composition at anthesis
Anther position during anthesis (exserted or inserted)
Anther morphology near maturity
Anther cross section, configuration of sporangia and connective
Anther appendages
Dehiscence, number and type of pores

Table 8: Male features before and after fertilization

I) Floral Morphology and Reproductive Biology

A) Rapateaceae

The two subfamilies Saxofridericioideae and Rapateoideae feature similar floral morphology and floral formula but the size of the hermaphroditic flowers fluctuates from 1 to 6 cm. The largest flowers are in the Saxofridericioideae. In both subfamilies, the inflorescence are quite complex, made of spikelets with terminal flowers and a variable number of infertile coriaceous bracts. The terminal flower has two perianth whorls.

The outer whorl consists of three coriaceous sepals alternating with the next whorl of three petals. The number of stamens equals six, and they are in two series of three; the outer series is opposite to the petals whereas the inner series alternates with the petals. The anthers are basifixed, saggitate, and four or sometimes two locular. Anther dehiscence is by means of two, four or less often one pore. In a few taxa the dehiscence is by small intermediate lateral slits. The variation in anther dehiscence appears to be a character that has many states, and the transformation series may be better understood with further research.

In many instances insects or birds (hummingbirds) pollinate the Rapateaceae; the presence of poricidal anthers or a homologous modification of the pores strongly suggests the "Buzz pollination syndrome" (Vogel, 1981). This syndrome is very common in other poricidal families such as Solanaceae and Ericaceae. Reported insects that pollinate Stegolepis sps. vibrate their wings to facilitate the expulsion of the pollen to the outside.

The degree of stamen adnation to the petals is variable; thus, in Saxofridericia the anthers are fused at the base, whereas in Monotrema the anthers are free. In the majority of the cases, the flowers are actinomorphic but slightly zygomorphic in the bird pollinated group (Kunhardtia). The sepals are free in most of the cases; in some taxa, however the stamens are fused at the base, forming a continuous ring (Subfamily Rapateoiodeae). The fruit is always a septicidal capsule.

A1) Subfamily Saxofridericioideae

Tribe Saxofridericieae

The genus *Stegolepis* Klotzsch ex Kornicke

The genus Stegolepis has about 30 species and it occurs in Venezuela, Brazil, Colombia and Guyana. The plants can be terrestrial, saxicole or epiphytic.

Reduction in the number of heads and spathaceous bracts (lacking or vestigial) is a unique feature in this genus and the sepals and the petals are oftentimes fused at the base. The six stamens can be free or connate at the base, and the same pattern of conation is reported in the corolla. Anther dehiscence is poricidal. In the majority of the cases the flowers are yellow (white in a few taxa), and pollination syndrome is entomophylous. Several pollinators are frequent visitors, namely the Apidae, Apis melifera var. scutellata Lat., Bombus atratus Franklin, B. pullatus Franklin, and B. volucelloides Gridobo; these were among the most frequent visitors. Less frequent visitations were observed in individuals of the Hesperidae such as Panoquia bola Bell, Halictidae (Pseudodagochloropsis sp.), and Antophoridae (Xylocopa sp.).

All the embryological features analyzed in the Rapateceae and Thurniaceae are given on Tables 7 and 8. These embryological patterns may occur before or after fertilization.

The embryology of Stegolepis guianensis Klotzsch ex Kornicke was already studied by Tiemann (1985). She reported that (1) the embryo sac formation is of Monosporic, (2) tapetum is secretory, and (3) anther wall formation is of the monocotyledon type. Davis (1966; Mashewari, 1957) assumed that general embryological features have little variation among species of the same genera.

Based on that assumption studies were made on other floral features of two endemics taxa from the Venezuelan Tepuis: Stegolepis squarrosa Maguire and S. cardonae Maguire. The pistil of these two species is tricarpellate, hollow and umbranched (Figs. 27d, 28a); it has several ovules per locule and the stigma surface is more likely of the "wet type". Placentation is axial. Transmitting tissue is present along the stigma and pistil, and in the inner side of the locules. The cytoplasm of cells of the transmitting tissue is dense which may suggest that these cells are secretory in nature.

The stigma is covered by small cillia-type of cells most likely related with the pollen entry and incompatibility mechanisms (Fig. 27d). The cells of the young pistil epidermis are filled with a tannin-like substance. In later stages, these cells elongate in the radial plane, and a cuticle develops on the tangential walls (Figs. 28a, b). Below the cuticle a deposition of tannins is often common. At maturity small spherical silica bodies are present in the pistil epidermis.

Megasporangium and Megasporogenesis

The ovules of Stegolepis cardonae and S. squarrosa are anatropous, bitegmic and crassinucelate. The inner integument is two cell layers thick, and some radial elongation occurs towards the micropyle in both layers (Fig. 27c). The outer integument is approximately six cell layers thick, and elongation in the radial plane of the outer layer is more evident towards the mycropile. In S. cardonae, the cells of the outer layer of the outer integument have slightly lignified cell walls in both the tangential and radial plane. Cell growth in the remaining layers is mostly periclinal (Fig. 27c). The two integuments form the micropyle. The outer integument overgrows when mature forming an appendage-like structure that it will be interesting to follow in later developmental stages. A U-pattern in the cells of the outer layer of the outer integument is present in the genus Stegolepis and Amphiphyllum.

When the embryo sac reaches maturity, an obturator and an hypostase are more evident. The raphal vascular bundle enters the nucellus and has some degree of continuity with the hypostase (Fig. 27b).

Microsporangium and Microsporogenesis

The anther wall development was not investigated because the general pattern may not vary greatly among individuals of the same genus. Instead the developmental morphology of the anthers was analyzed.

The tapetum is of the secretory type in Stegolepis cardonae and S. squarrosa. The tapetal cells migrate towards the anther locule to nurture the young pollen grains, the integrety of its cell membrane remains intact, and no cytoplasm is free. Ubish bodies are common during pollen wall deposition. The tapetum is binucleate in Stegolepis cardonae (a common feature to all Rapateaceae), and becomes binucleate when the callose wall is being deposited around the young spores.

Anther Development

The anthers of Stegolepis cardonae are shown before anthesis in Figs. 29a, b, c. The anther appendage disintegrates before the pollen is release, and the whole unit is covered by mucilage in all occasions. Tieman (1985) reported that the pollen dehiscence of Stegolepis guianensis is by two terminal pores, this is in agreement with our results (Fig. 29d). However, in her diagrams the anther did show smaller appendages in earlier stages than Stegolepis cardonae. This dehiscence pattern is confirmed by anatomical data. Thus, at maturity the anthers showed four locules in the middle portion and only two in the basal and apical area (Figs. 30a, b).

At maturity the endothecium is multilayered (up to three layers), and consists of cells with little cytoplasm and thickened walls in all planes (Fig. 30c). This in contradiction with the general U-type endothecium reported previously for most Rapateaceae (Tieman, 1985; Gerenday & French, 1988). A multilayered endothecium is a common feature among monocots. The epidermal pattern of the a anthers is very interesting in the entire family because it consists of cells filled mostly with tannins and less often silica bodies and starch; its texture is often coarse. The external appearance of the anther epidermis is papillate (Tieman, 1985). The same papillate pattern is found in Stegolepis cardonae and S. squarrosa

(Figs. 30c, d). A continuous ornamented cuticule covers the tangential walls of the epidermis. The above species have saggitate anthers and their attachment is basifixed (Fig. 29a) Pollen grain is shed in the bicellular stage in S. cardonae.

Fig. 27: Placentation and ovule detail of <u>Stegolepis</u> <u>cardonae</u> (Pruski, 3689): a) pistil showing placentation and tannins in the parenchyma (100x); b) raphal bundle ending at the chalazal side (100x); c) outer layer of the outer integument showing U-pattern in the tangential walls (200x); d) stigma showing minute cillia (6 um).

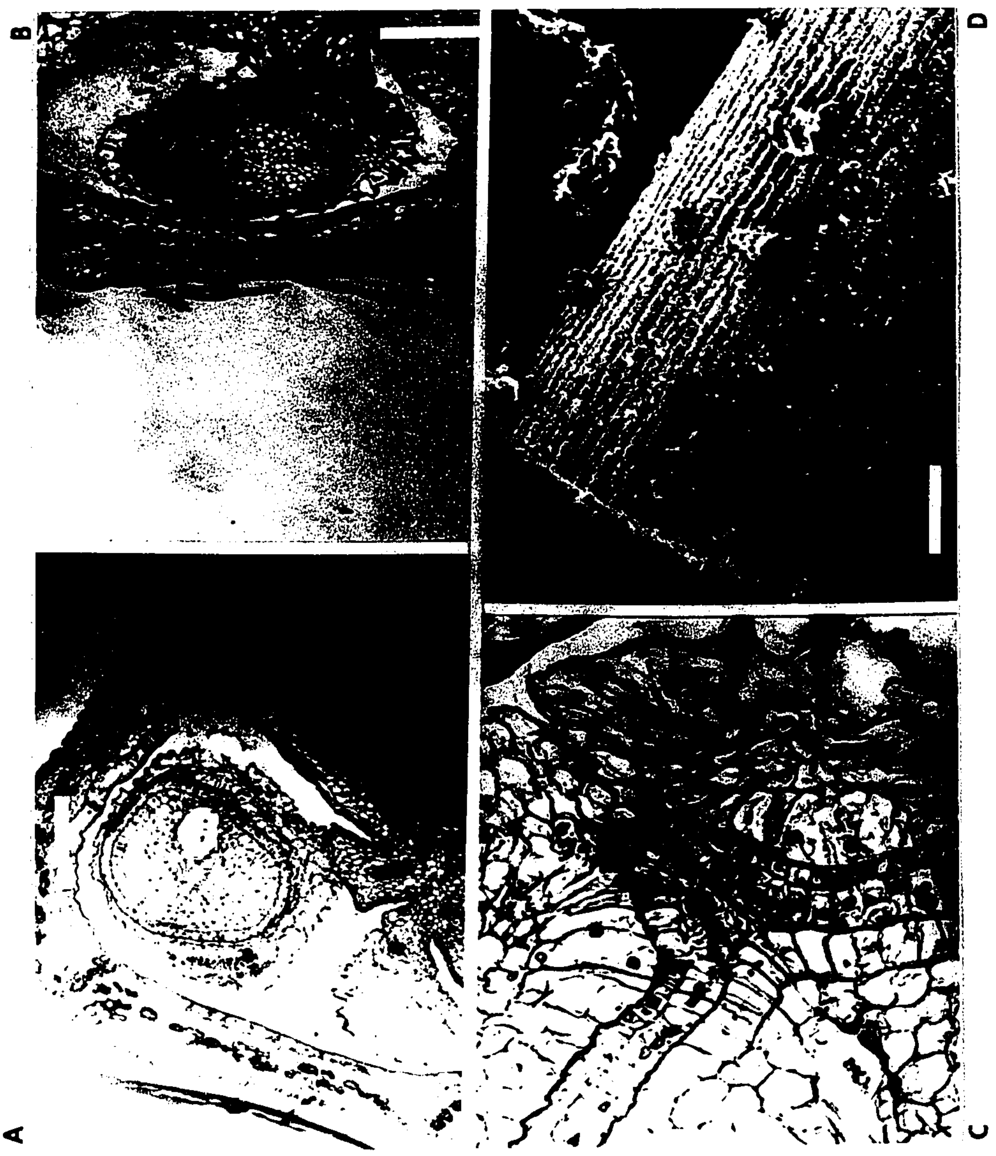
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Fig. 28: Pistil anatomy of Stegolepis cardonae (Pruski, 3689): a) young carpel epidermis filled with tannins (100x); b) mature epidermis with radially elongated cells filled with tannins and silica bodies (200x).

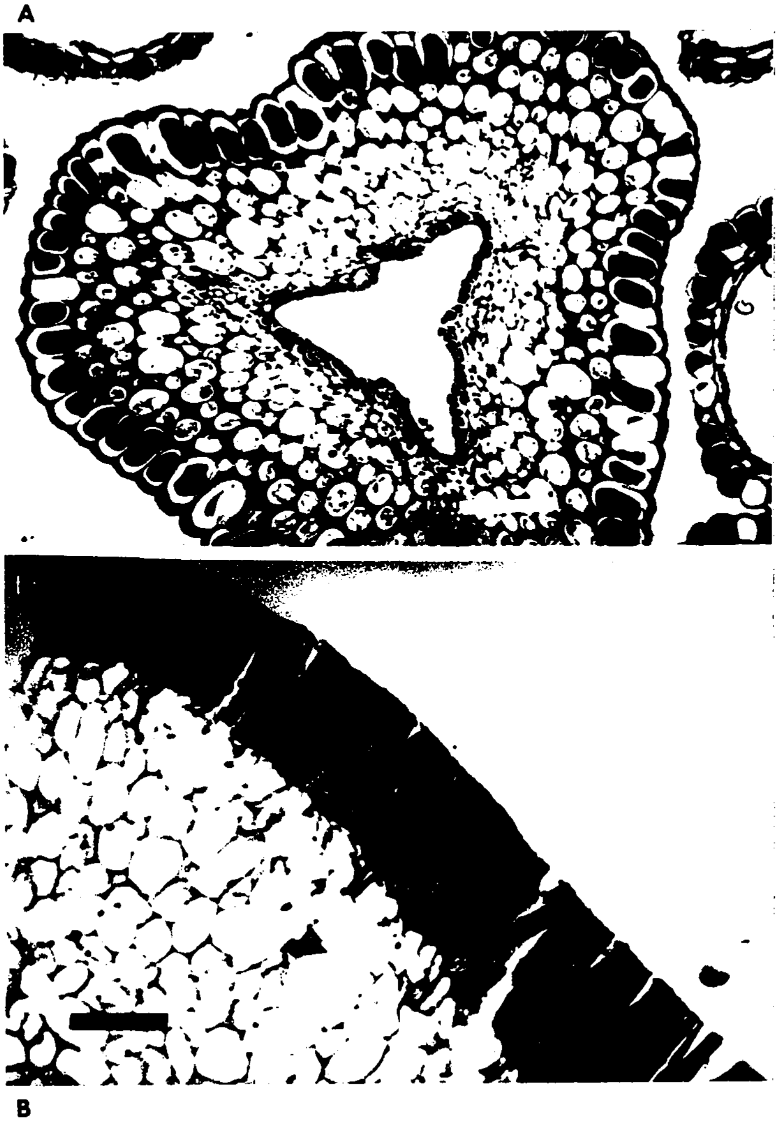
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Fig. 29: Anther development of Stegolepis squarrosa (Boom, 9372); a) close mature anther (7 um); b) detail of dehiscence pore, ventral side (5 um); c) anther appendage, lateral view (5 um); d) mature open pore (8 um).

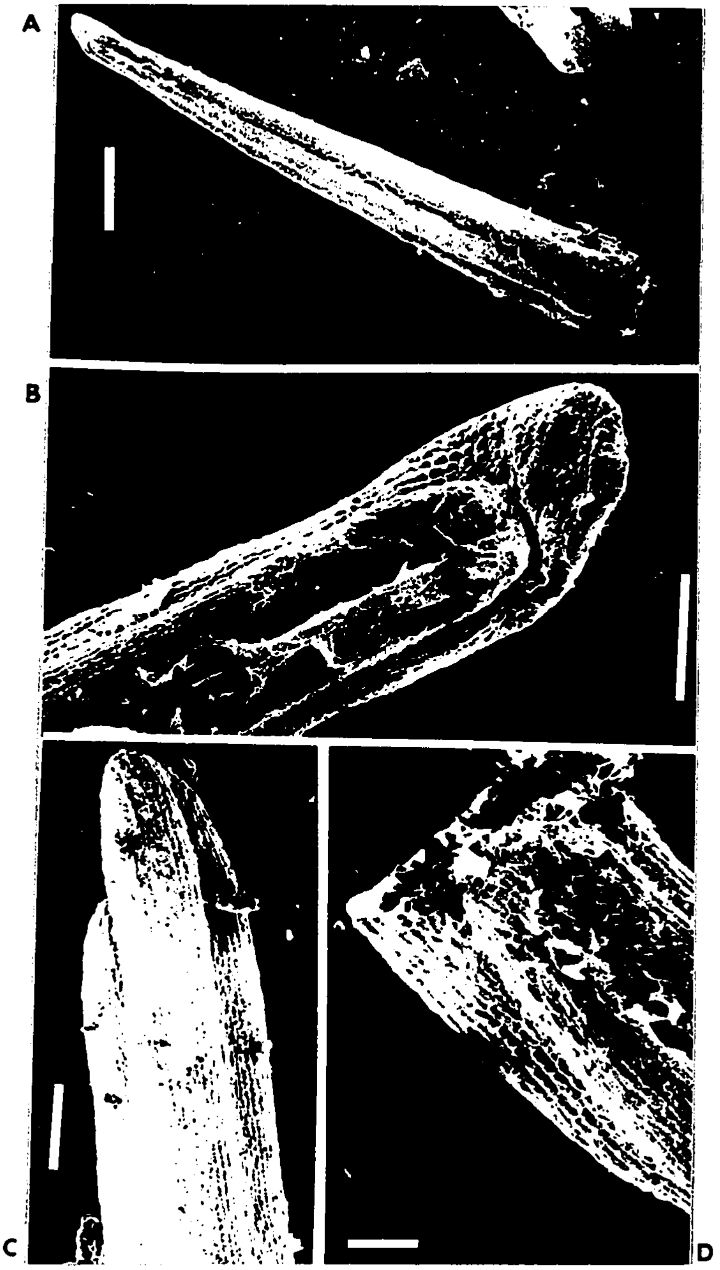
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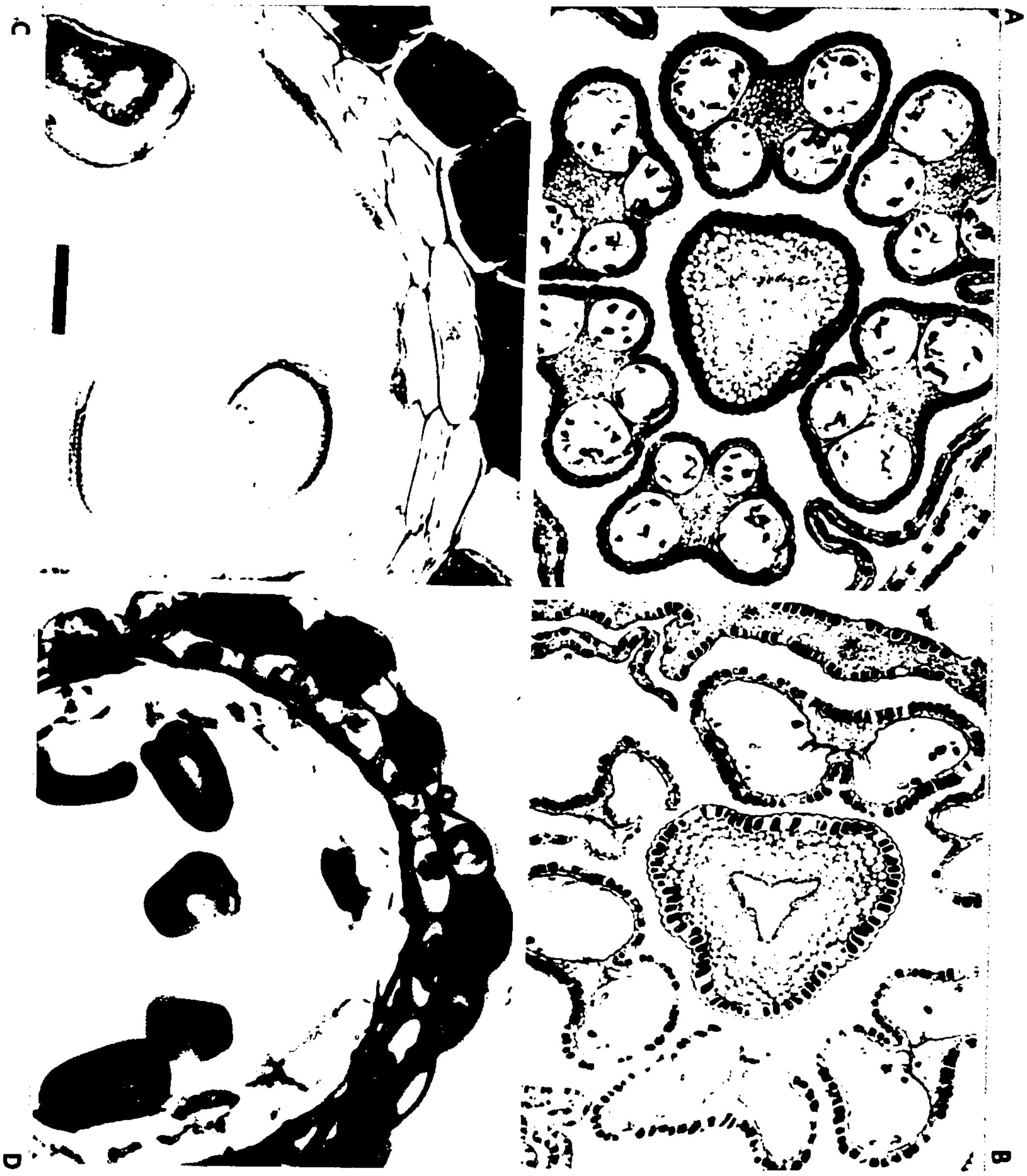
Fig. 30: Flower development in Stegolepis cardonae (Pruski, 3689); a) mid-anther portion (100x); b) basal portion showing two locules (100x); c) detail of epidermis, endothecial thickenings and mature pollen (200x); d) mature pollen grain and Ubish bodies (200x).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The genus Amphiphyllum Gleason

The genus Amphiphyllum Gleason has two species, A. rigidum Gleason and A. schomburgkii Maguire; both taxa are geographicaly restricted to the Duida-Marahuaca mountain complex in the Venezuelan amazon. The inflorescences are heads flattened towards their sides, and they carry not more than six spikelets per head. The spathaceous bracts are valvate, coriaceous, connate at their base, and they cover most of the spikelets without enclosing them. The flowers are dark yellow or orange. The genus Amphiphyllum is poorly known due to its scarcity and remoteness. No studies in its floral morphology or embryology have been done previously; this is the first report on the embryology of Amphiphyllum schomburgkii.

The spikelets consist of numerous coriaceous bracts arranged in spirals. The sepals in number of three are free, exsert, membranaceous at the base, and coriaceous in the apex. The prefloration is imbricate (Figs. 30a, b). The three petals are membranaceous, and connate at their base forming a short tube. The six saggitate anthers are adnnate to the corolla tube, and their filaments are flat, wide, and membranaceous. The anthers open by two subapical-lateral terminal pores.

The pistil is tricarpelate (Fig. 31c), with numerous ovules per locule, the placentation is in some cases incompletely axial. The mature pistil epidermal cells are radially elongated, with abundant silica bodies, and a cuticular deposition. These epidermal cells are more lignified in their tangential walls (Fig. 31d). The cortex of the pistil is filled with abundant tannin globules. The same secretory hairs (mucilage secretion) that appear in the vegetative organs are also common in the pistil locules. The stigma is simple with inconspicuous cillia, and the style is hollow. The transmitting tissue covers the inner side of the stigma and the locules. The cells of the transmitting tissue are located in the inner epidermis of the locules (Fig. 32a), and they are of the secretory type. These cells have a large nucleus and a dense cytoplasm; their tangential walls have an unknown deposition. The outer epidermis of the stigma is filled with tannin globules. Some flowers showed aborted ovules and poorly developed placentas. Schizogenic spaces are common in the basal region of the pistil cortex; the schizogenic spaces are probably related with the presence of secretion (Fig. 32b).

The ovule

The ovules are anatropous, bitegmic, crassinucellate, and with an obturator (Figs. 32a, 33c). In the young ovule, the primary parietal cell divides anticlinally (Figs. 33a, b, d) and its derivative cells occasionally divide giving rise to a parietal layer that remains until fertilization. The mature ovule has an obturator and a conspicuous hypostase. A undeveloped or vestigial arile or seed appendage is present. When mature, the inner integument consists of two layers and the outer integument consists of six layers; elongation of the outer layer of the outer integument is more evident towards the micropyle (Fig 33b,d). Tannin globules are present in the middle layers of the outer integument and cell growth in the intermediate layers is mostly periclinal. The outer layer of the outer integument presents cells with a U-pattern (Fig. 32d), a shared feature with the genus Stegolepis. The micropyle is formed by the two integuments.

Megagametogenesis

The embryo sac type remains still unknown due to the lack of proper ontogenetic stages. However, in Figs. 32c, d, and 33d, the mature embryo sac shows the synergids, the egg cell and the polar nuclei. The polar nuclei remain unfused but in other Rapateaceous genera they certainly fused before fertilization, a fact that has been previously reported in selected taxa of the family (Tiemann, 1985; Venturelli & Bouman, 1988). The antipodals are probably ephimerous. The synergids are rather small and ovoid (Fig. 32c). The chalaza side is slightly vacuolated, and the filiformis apparatus is not well developed.

Microsporangium and Microsporogenesis

Due to the lack of very young flowers, the anther wall development could not be studied however other morphological features such as male gametophyte and anther morphology were studied. The anthers open by a terminal confluent pore, they are tetrasporangiate, and the epidermis is filled with tannins during early stages of development (Figs. 34b, d). In the young anther, the tapetum is binucleate and the young pollen is surrounded by callose. The tapetum is of the secretory type. Although some movement of tapetal cells towards the locule occurred, the tapetal cells kept their cytoplasmic integrity (Fig. 34b). A cuticular deposition in the anther epidermis is very common at the callose stage. At maturity, the 4-lobed anther has a distinct morphology depending on the region of the anther. Thus, near its tip the locules are smaller and separated by broader connective tissue; at this stage, the pollen is mature and the tapetum is degenerating (Fig. 34c). The upper locules are smaller than basal, and the typical saggitation of this portion can be seen in Fig. 34d. The epiderrmis is of the papillate type, and a central vascular bundle can be distinguished. Endothecial thickenning are present, and the mature pollen is shed at the bi-cellular stage. The young male gametophyte is vacuolated, and its cytoplasm is dense (Fig. 33e). The generative cell is larger then the vegetative one (Fig. 33e) and it is located near the cell membrane. The vegetaive cell has two nucleoli. Ubisch bodies are more evident during the second meiosis. In the flowers of Amphiphyllum shomburgkii, the anthers develop before the pistil; thus, when the pollen is at the one-celled stage, after the second meiosis, the ovule is still at the archesporial stage.

Fig. 31: Flower morphology of Amphyphyllum schomburgkii (Maguire et al, 65564); a) prefloration (100x); b) stamen development (100x); c) trilocular pistil (100x); d) detail of young epidermis (200x).

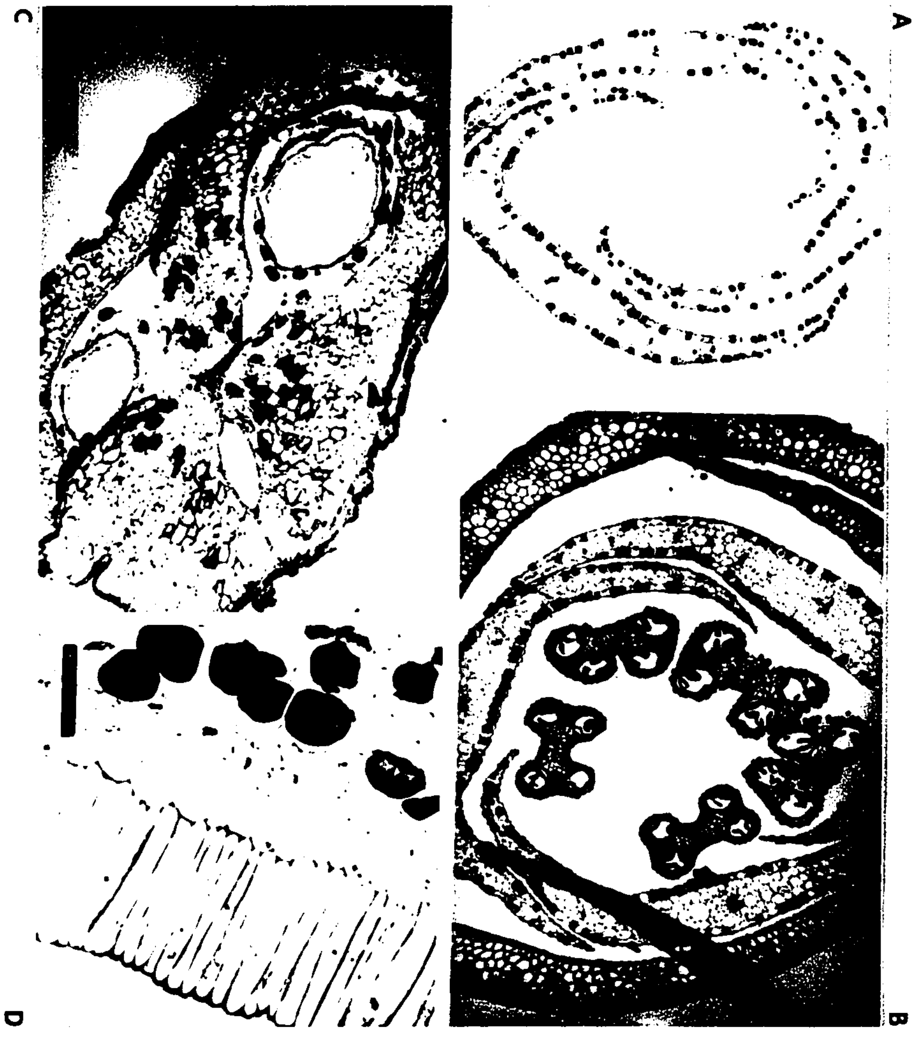
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Fig.32: Ovule development in Amphymphyllum schomburgkii (Steyermark, 58249); a) tannins in the outer integument showing secretory cells on the inner epidermis of the locule (100x); b) after fertilization, hypostase and tannins in the outer integument (100x); c) synergids (200x); d) u-pattern in the cells of the outer layer of the outer integument (200x).

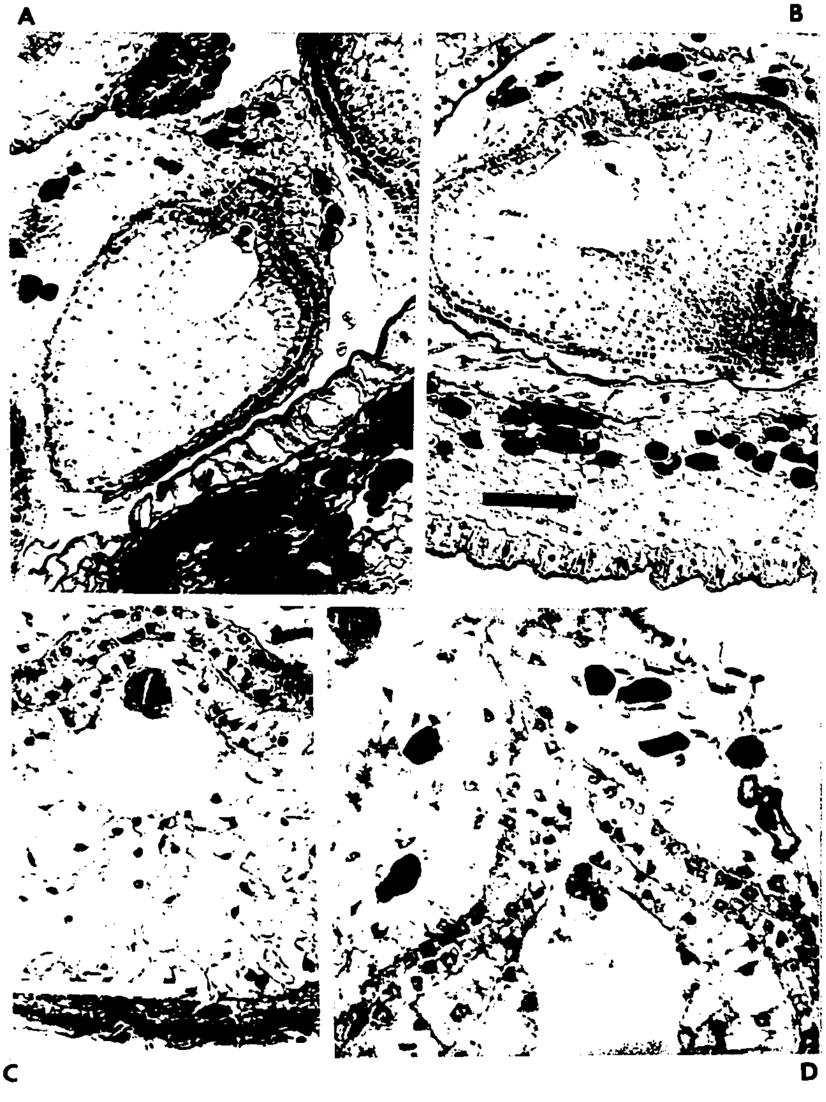
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Fig. 33: Ovule and pollen morphology of Amphyphyllum schomburgkii (Steryermark, 58249); a and b archesporial cell (3,3 um); c) mature ovule showing obturator; d) mature embryo sac (2 um); e) mature male gametophyte (7 um).

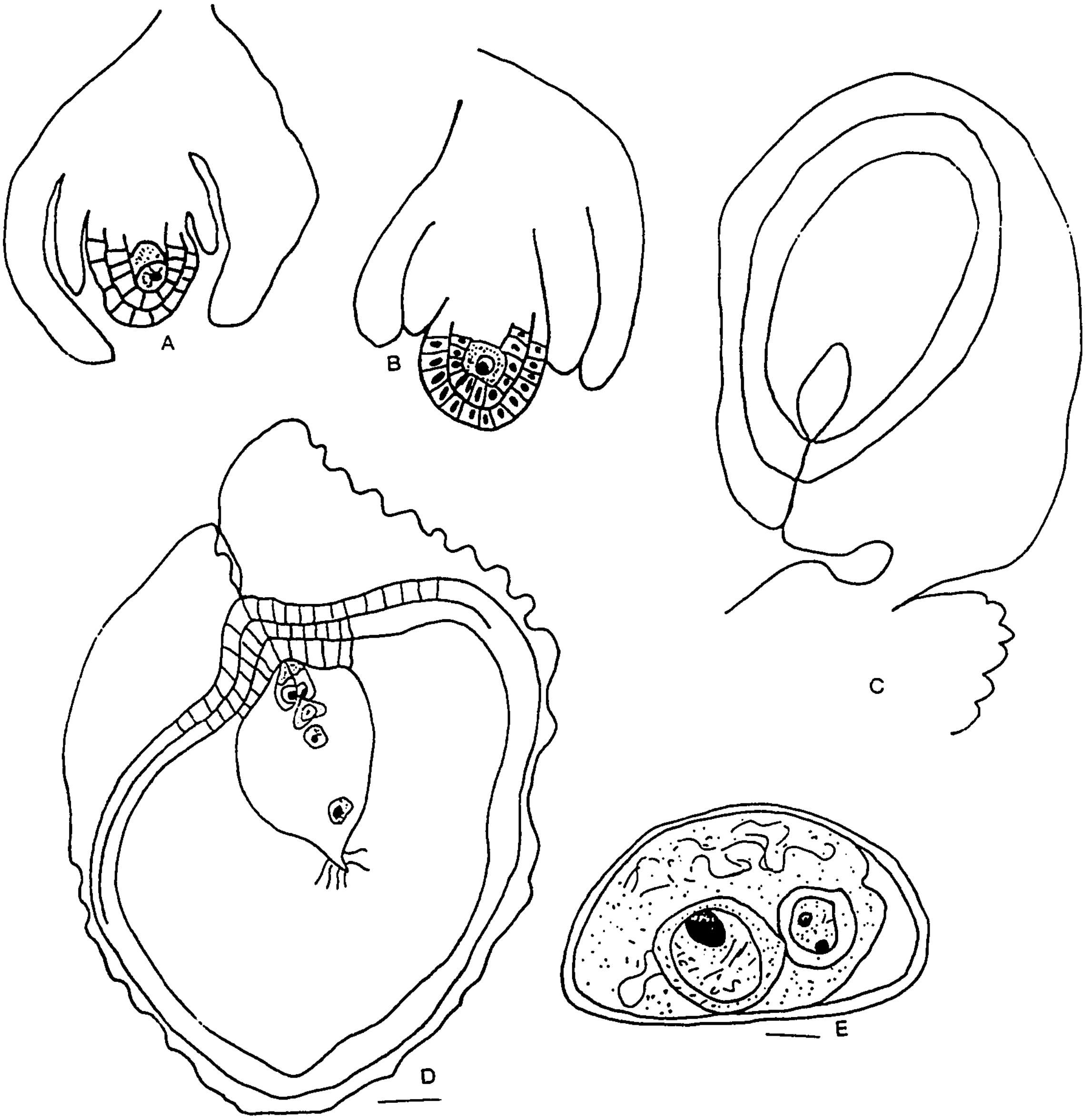
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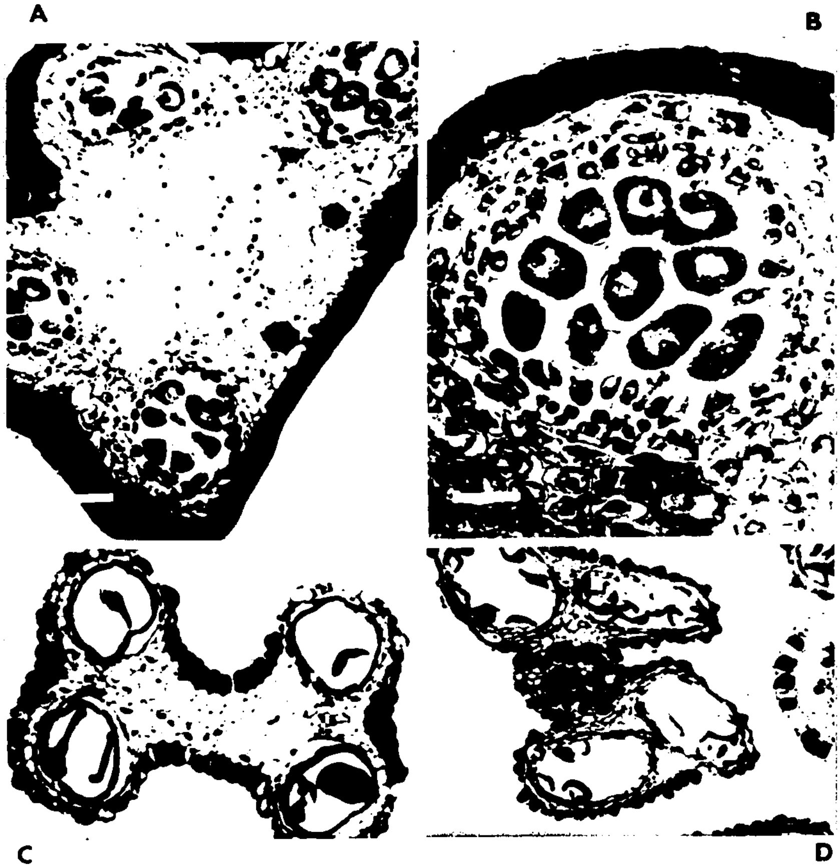
Fig. 34: Anther development of Amphyllum schomburgkii (Stermark, 58249); young pollen surrounded by callose (200x); b) young pollen detail 200x) c) upper region of anther (100x); d) mid region of anther with papillate epidermis (100x).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The Genus *Saxofridericia* Rob. Schon.

The genus Saxofridericia, occurs in Venezuela, Brazil, the Guianas, and Colombia. The inflorescence is a globose head made of numerous spikelets, subtended by two spathaceous bracts, whose margins are usually connate. These bracts are often saccate and cover the entire inflorescence until post-anthesis. In most of the cases, the mature spikelet penetrates the spathaceous bracts before the flower opens. Pollination takes place afterwards. Abundant mucilage is common in the inflorescence of all Saxofridericia; the number of floral parts remains the same for the entire family. The flowers are yellow, or light orange, the sepals are free, and the petals are connate in a short tube at their base. The stamens are adnate to the corolla tube. The anthers open by two pores and they are tetrasporangiate. The anther apex has a small appendage.

The pistil of Saxofridericia duidae Maguire, is trilocular, umbranched, and with a cilliate stigma. There are several ovules per locule. Placentation is incompletely axial. It appears that few ovules reach maturity and the percentage of aborted ovules in many flowers of the Duida mountain population is notorious.

Tieman (1985) discussed some aspects of the embryology of Saxofridericia aculeata Kornicke, and S. regalis Schomburgk. She reported that the ovules were anatropous, crassinucellate and bitegmic. Obturators are common; the tapetum is of the secretory type, and their cells are binucleate. Embryo sac development is monosporic. The pollen is shed in the bicellular stage.

Some embryological features of the ovules of S. duidae Mag., a species endemic of the Amazonian Mountain "Cerro Duida" (Venezuela) were studied. In this species the ovules are anatropous, bitegmic and crassinucellate. In Fig. 35a early stages of ovule development are shown, the two integuments are of dermal origin. The outer integument differentiates early and in subsequent stages, is three layers thick (Fig. 35b). The young inner integument has two layers, and remains with the same number of layers at maturity. The anatropous curvature is visible when the two integuments are already differentiated (Fig. 35b). No further studies were done.

Fig. 35: Ovule development in Saxofridericia duidae (Colella, 2206); a) young ovule showing outer integument (200x); b) development of inner integument (200x).


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B

Tribe Schoenocephalieae

Maguire (1958) formed the Schoenocephalieae by putting together the genera Kunhardtia, Guacamaya, and Shoenocephalium. The geographic distribution of the tribe is restricted to the Amazonian (Rio Negro drainage) lowlands of Venezuela and Colombia. In some cases the genus Kunhardtia reaches the top of some tepuis. The three genera share a number of floral, embryological, and morphological characters; members of the genus Schoenocephalium show some hybridization. However, the three genera differ in pollination biology, ecological preferences, and floral and vegetative morphology. Schoenocephalium teretifolium Mag., is the only member of the tribe with cylindrical or terete leaves and semi-close sheath. The embryology of the members of the Schoenocephalieae is virtually unknown and the present study is the first report on that topic.

In general the inflorescences in the tribe Schoenocephalieae are racemose and the spathaceous bracts are usually free however, the spathaceous bracts remain connate after anthesis in the genus Guacamaya Maguire. The flowers of Guacamaya penetrate the connate sacciform spathaceous bracts as in Saxofridericia sps. The genus Kunhardtia Mag. can be distinguished by the size of its flowers, which are the largest in the entire family. The flowers are zygomorphic with light pink exserted corollae.

Three pollination syndromes are apparent in the tribe Schoenocephalieae: 1) partial cleistogamy observed in Guacamaya and Schoenocephalium, 2) ornitophylly common in Kunhardtia, and 3) entomophyly (as playing a minor roll). The presence of nectaries at the base of the pistil occurring in large pink tube-like corollas is correlated with ornitophylly in Kunhardtia. Berry (pers. commn.) surveyed the pollination biology of Kunhardtia radiata and he noticed that hummingbirds were the common visitors. He also observed an abundant secretion of nectar at the base of the corolla. Later on, Berry (pers. commn.) provided flowers of Kunhardtia radiata Maguire for embryological studies and the anatomical evidence of pistil nectaries was determined. Venturelli & Bouman (1985) and Tiemann (1983) reported floral nectaries in Spathanthus unilaterlais and Rapatea sps. but they did not describe them nor did they showed their anatomical structure.

The remaining cleistogamous genera -Guacamaya and Schoenocephalium- have colorful flowers ranging from pink to bright red and smaller nectaries; in some cases the flowers still secrete nectar (Berry, pers. comm.). This may indicate that ornitophylly is the plesiomorphic character for the entire tribe. Partial cleistogamy in Guacamaya sps. and Schoenocephalium sps. can be interpreted as an adaptation to habitats where the availability of pollinators fluctuates or the plants are in the process of adaptation to local pollinators. Self-pollination guarantees the completion of the reproductive cycle and the production of seeds without the participation of any insect. Partial cleistogamy has also been reported in Mayaca fluviatilis Aublet (Venturelli and Bauman, 1983) another member of the order Commelinales.

The genus ***Kunhardtia*** Maguire

The genus Kunhardtia consists of two species K. rhodantha Maguire and K. radiata Maguire. The two species differ in habitat preference, size and shape of the inflorescence. As an adaptation to ornitophyly the flowers are slightly zygomorphic in both cases. K. rhodantha has smaller flowers and has being collected at altitudes between 600-1500 mts whereas K. radiata with bigger flowers occurs at lower altitudes. Both species were surveyed but early stages were insufficient in K. radiata. In both cases the inflorescences are globose and with numerous spikelets (ca. 20-50); those located near the base become reflexed at maturity. The spiklets have several whorls of gradate bracts arranged in spirals; three sepals are free and three petals are connate at their base. The filaments are adnate to the lower portion of the corolla (Fig. 35d) and the stamens dehisce by two terminal pores.

The ovary is a compound pistil with three locules and incompletely axial placentation; there are many ovules per locule (Figs. 36b,c, and 37a). Prefloration is imbricate and the petals are three cell layers thick (Fig. 37b). Oftentimes the epidermal cells of the petals accumulate tannins and other unknown pigments (Figs. 37b,d). The parenchyma of the pistil has some globules of tannins; pistil nectaries are located in the interlocular region near the base (Fig. 37a, c). At maturity these nectaries secrete abundant nectar that moves by diffusion towards the outside and remain at the base of the petals. The style is hollow and transmitting tissue was observed only in the inner side of the stigma. The style surface is sculptured and the stigma shows short hairs or papillae (Fig. 36a). The epidermal cells of the mature pistil are elongate in the radial plane with tangential lignified cell walls and silica bodies. Fig. 36d shows young flower with the perianth remove, in later stages the stigma bends and it is always larger than the stamens. A cross section of the young pistil shows the placental primordia and the three locules

(Fig.38c).

The ovule

No embryological differences were noticed when comparing equivalent ontogenetic stages in the two species of Kunhardtia. Early stages of megasporogenesis were analyzed in K. rhodantha. The ovules are dizonate, anatropous, bitegmic and crassinucellate. Ovule maturation inside the pistil is acropetal and some ovule primordia can be seen near the apex of the ovary (Fig. 36c). The micropyle is bend and more evident during the early stages of fertilization (Fig. 38b). At this point the shape of the ovule is nearly prismatic; this is the common shape of the mature seeds. The micropyle is of the zigzag type and is formed by two integuments. The inner integument consists of two layers. Prior fertilization, the cells of the outer layer of the inner integument elongate in the radial plane. The outer integument consists of approximately fourteen layers. Cell growth in the intermediate layers is mostly periclinal.

In the young ovule, the primary parietal cell divides anticlinally and their derivative cells occasionally divide giving rise to a parietal layer that in some cases remains after fertilization. During embryo sac formation, some degree of lignification is present in the tangential walls of the cells of the inner integument. A well-developed hypostase persists after fertilization. The ovule vascular strands ends at the chalazal side.

Megasporogenesis and Megagametogenesis

The archesporial cell undergoes meiosis an gives rise to a linear tetrad of megaspores, of this only the chalazal megaspore survives and the three remaining degenerate (Fig. 39a). This pattern of spore development conforms the monosporic type and it is always present in the Rapateaceae studied before (Tiemann, 1983; Bouman & Venturelli, 1985). Soon after the degeneration of the three spores (Figs. 39a, b) two vacuoles appear near the nucleus of the functional megaspore. The embryo sac enlarges considerable during ontogeny and in successive stages its diameter doubles the initial size. The embryo sac formation follows the Polygonum type. At maturity the synergids and the egg cell are ovoid and their nucleus face the chalaza. The polar nuclei fused before fertilization and the three antipodals are ephemeral. The epidermal cells of the nucellus undergo radial elongation at maturity; a cavity or "pocket" is visible at the chalazal side before the polar nuclei fused. The egg apparatus is shown in Figs. 39c, d, e, before fertilization has taken place, remnants of cytoplasm surround them.

Microsporangium and Microsporogenesis

The six-saggitate anthers develop in two series of three (Figs. 40a,c). The young anther consists of four lobes and one central vascular bundle. The anthers are tetrasporangiate with a connective tissue that is broader towards the median portion of the mature anther. The anther dehisces by means of two terminal pores (Fig.41d). A group of hypodermal archesporials differianted in each lobe, each archesporial cell undergoes a periclinal division-giving rise to a primary parietal cell and a primary sporogenous cell. The primary parietal cell divides periclinally giving rise to a secondary parietal cell. The outer and inner secondary parietal layers divide periclinally and form the endothecium, two middle layers and the tapetum (Fig. 40d). This type of anther wall development is in agreement with the Basic type. At maturity, the middle layers disintegrate. The sporogenous cells are larger than the surrounding cells, their nucleus are conspicuous and dense but cytoplasm is less dense; these cells never develop vacuoles. Some areas of the tapetum and middle layers originated from the connective tissue. The same type of anther wall ontogeny was reported in

Cephalostemon ridelianus Kornicke and in Spathanthus unilateralis (Rudge) Desv. by Venturelli & Bouman, (1985). However, Tiemann (1983) reports a Monocotyledonous type of anther wall development in the same genera. In order to elucidate proper anther wall development very young stages are needed; lack of these developmental stages may lead to equivocal conclusions. The tapetum is of the secretory type and in early stages of pollen development the orbicules or Ubisch bodies are evident. When the pollen is mature the cells of the tapetum may degenerate or sometimes migrate towards the inner side of the locule near the pollen grains. The shape of the anthers changes with age and position. Thus, a young anther is wider towards its base (Fig. 40a) and narrows near the apex.

Anther Development

Young anthers have a smooth patterned epidermis, and there is no appendage (Figs. 41a, b). The base of the anther is wider than its apex. At maturity the papillate cells of the epidermis differentiated given its peculiar texture. Two terminal pores open through the abscission zone (Figs. 41c, d).

Fig. 36: Pistil and ovules of Kunhardtia rhodantha (Berry, 4808); a) papillate stigma; b) ovules showing mycropile; c) young undifferentiated ovules; d) young flower, perianth removed (bar= 5 um).


A
B
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D

Fig. 37: Pistil and petals of Kunhardtia rhodantha (Berry, 4808); a) placentation detail (100x); b) prefloration and hollow style (100x); c) schizogenic secretory spaces (100x); d) epidermis with tannins (200x).

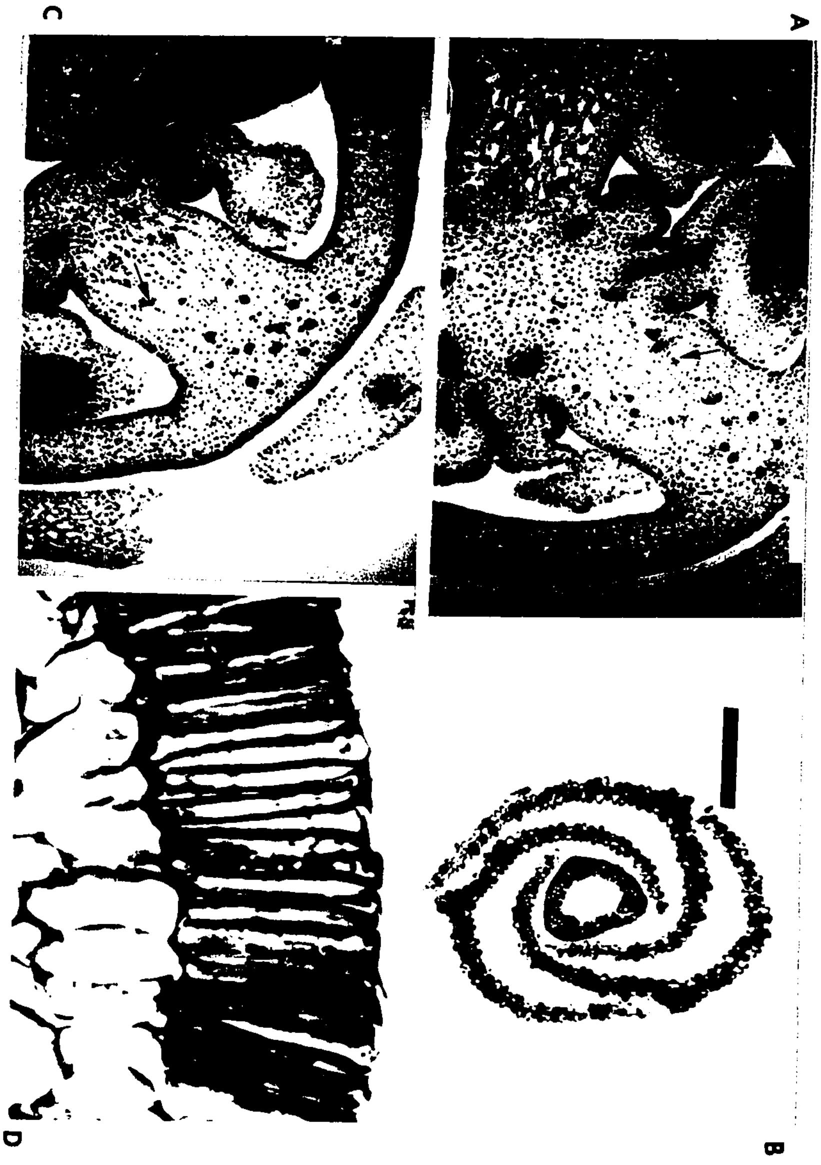
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Fig. 38: Ovule and pistil development of Kunhardtia rhodantha (Berry, 4808); a) megaspores surrounded by calose (200x); b) mycropile detail (100x) c) ovule primordia (100x); d) synergids and egg cells (200x).


A
B
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Fig. 39: Ovule development in Kunhardtia rhodantha (Berry, 4808): a) degenerating megaspores (0.7 um); b) functional megaspore on the chalazal side (0.7 um); c) two antipodals and egg apparatus(8,8 um); d) two synergids, egg, and polar nuclei (8,8 um); e) egg apparatus (0.2 um).

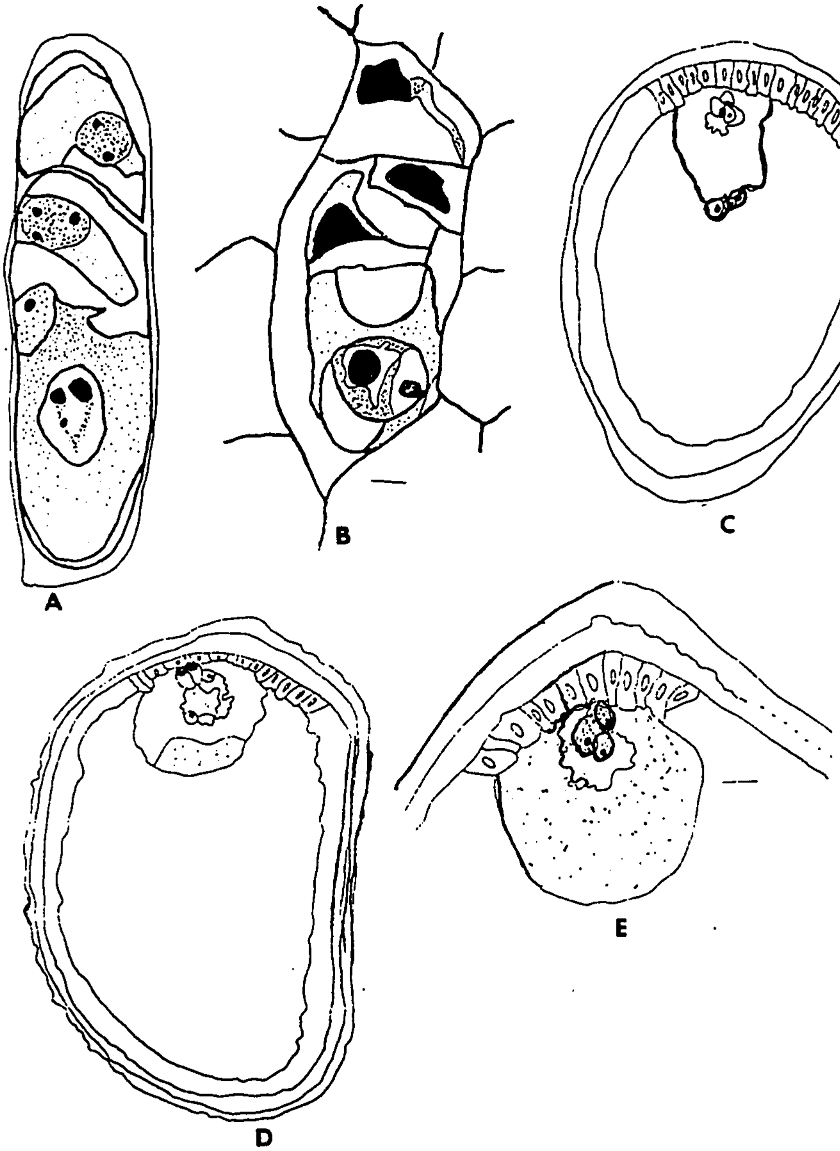
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Fig. 40: Anther morphology of Kunhardtia rhodantha (Berry 4808); a) young anthers at their base (100x); b) young anther near tip (100x); c) mature anther showing papillate epidermis (100x); d) detail of Pollen Mother cells and microsporangium layers (200x).

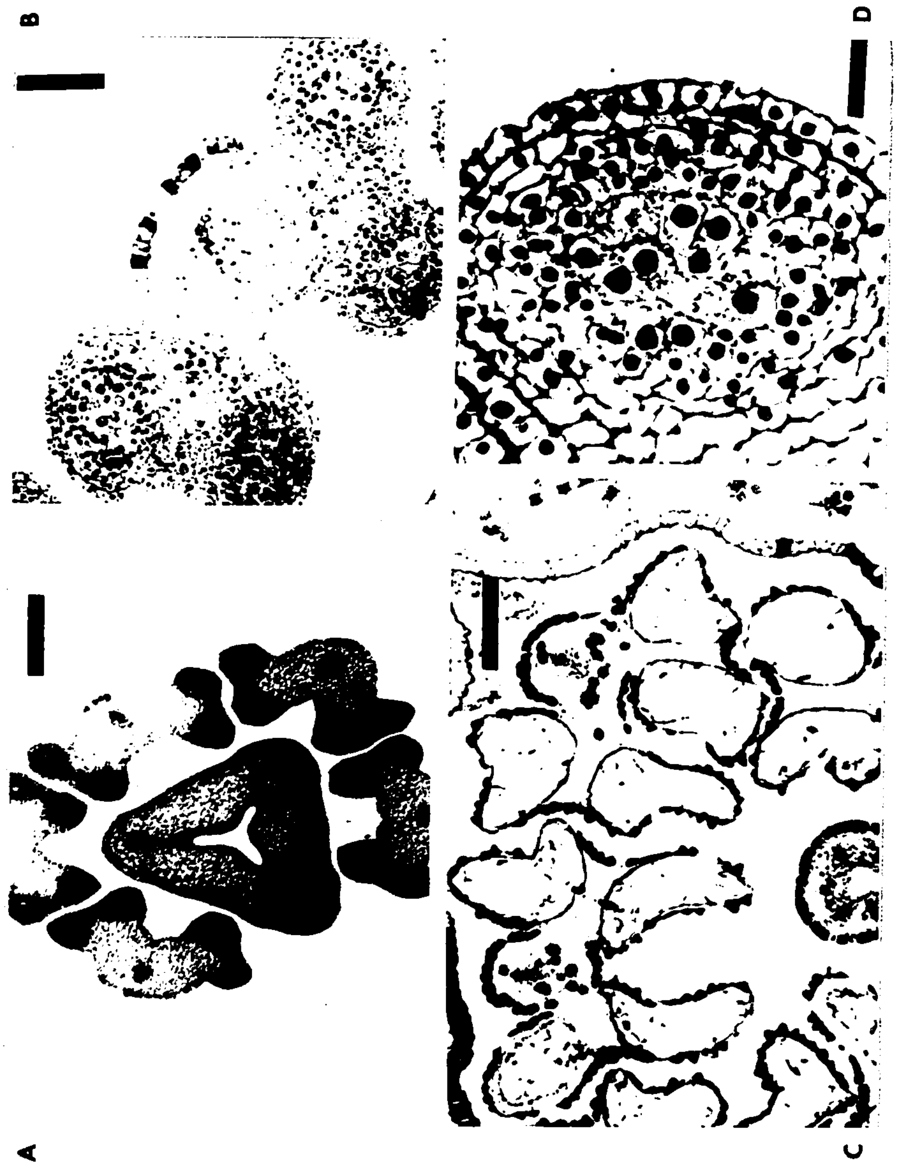
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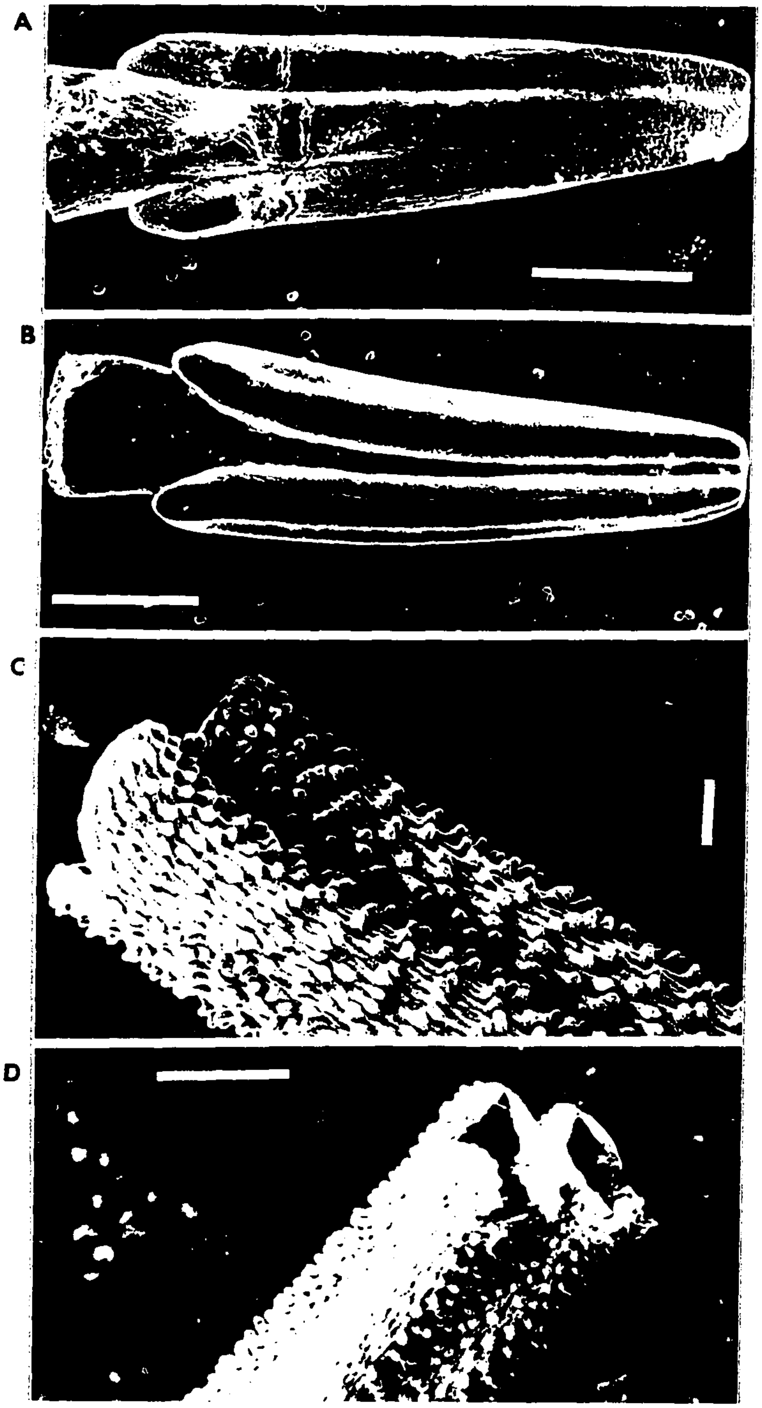
Fig. 41: Anther morphology of Kunhardtia rhodantha (Berry, 4808); a) dorsal view of young anther; b) ventral view; c) dorsal mature pore; d) ventral mature pore (bar= 5 um).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The genus *Schoenocephalium* Seubert

The genus Schoenocephalium has five species distributed mostly in the Venezuelan and Colombian Rio Negro region (Amazonian Hylaea). Some species occur in the Vaupes (S. schultesii Mag.) or in the Casiquiare-Pacimoni Upper Orinoco vicinities and tributaries. Usually they grow on white sand savannas, banas and caatingas that may be flooded sometime during the year. It was possible to collect material of only two species, Schoenocephalium teretifolium Mag. and S. coriaceum Mag.

An interesting feature in Schoenocephalium teretifolium is the changes of flower colors during inflorescence ontogeny. In early stages the bracts of the spikelets remain white, when the flowers are near maturity the lower portion of the bracts of the spikelets changes to pink or red and the bracts of the top of the spikelet remain white. When the inflorescence is fully mature and reaches about 3-5 cm in width all of the spikelets are coral red. In the globose inflorescence the basal spikelets develop before than the apical spikelets these is a common feature in some Rapateaceae. The number of spikelets per inflorescence is variable but usually between 15-25. The spikelet consists of a series of gradate, coriaceous bracts spirally arranged. The apical bracteols of the spikelet are larger than the basal ones.

The three sepals are free and the three petals are connate at their base. The two spathaceous bracts are caducifolius in some cases, short, membranaceous and green. The fact that the genus is partially cleistogamous posses an interesting question about the meaning of the color changes in the spikelets; few pollinators were observed and the flowers seldom are fully open. Prefloration is imbricate and tannins accumulate in the abaxial and adaxial epidermis of the sepals and petals. The ovary is a compound pistil with three locules, placentation is axial and there are a few ovules per locule (Fig. 42a). The parenchyma of the pistil accumulates tannins and the nectaries are located in the basal portion at the interlocular region as in Kunhardtia; the schizogenenic cavities are smaller and less conspicuous. The style is hollow and the transmitting tissue is inconspicuous in the locular region. The pistil epidermis does not show the typical radial elongation that is common in the remaining members of the tribe; instead, their cells have the cytoplasm filled with tannins and in the upper region of the pistil the cells accumulated silica bodies (Figs. 43b, c). The stigma ends on a tuff of unicellular secretory long hairs (Fig. 43a). Its epidermis is sculptured and has a waxy deposition.

The ovule

The ovules are anatropous, cras inucellate, bitegmic, and probably dizonate. The two integuments form the micropyle and it is slightly oblique. The inner integument is of dermal origin. The origin of the outer integument could not be discerned. The ovules of S. teretifolium remain straight during early ontogeny (Fig. 42a). The young archesporial cell differentiates very early. The shape of the mature ovule is obovate.

The inner integument consists of two layers and towards the micropyle some periclinal division may add one more layer. The cells of the outer layer of the inner integument elongate near the mycropile and slightly in the radial plane. The outer integument is multilayered and consists of twelve cell layers. Cell growth in the intermediate layers is mostly periclinal. There is some degree of lignification in the tangential walls of the cells of the outer layer of the outer integument. These cells showed a "wavy" pattern and they accumulate tannins towards the chalazal side (Fig. 42c).

A contrasting feature for the entire subfamily is that the outer integument leaves an empty space that is located near the chalaza in the concave side of the ovule (Fig. 42c). The vascular strands end in the chalaza and well develop hypostase remains after fertilization.

Megasporogenesis and Megagametogenesis

The archesporial cell undergoes meiosis and gives rise to a linear tetrad of megaspores, of these, only the chalazal megaspore survives and the three remaining degenerate (Fig. 42e). During megasporogenesis a noticeable callose deposition envelops the young meyocites. A hypostase is visible at this stage (Fig. 42d). This pattern of spore development is in accordance with the monosporic type, which has been reported in many Rapateaceae (Tiemann, 1984; Venturelli & Boumann, 1988). The embryo sac enlarges during ontogeny and its development follows the **Polygonum** type. The primary parietal layer of the young ovule divides anticlinaly and their derivatives cells, occasionally divide and give rise to a parietal layer that in may remain after fertilization (Fig. 44b).

The most important stages of embryo development can be seen in Fig. 44. The first mitotic division of the megaspore produces two nuclei that migrate towards opposite sides (Fig. 44a), a second mitotic division duplicates the number of nuclei (Fig. 44b). At the end of the third mitosis and before fertilization has taken place, the three antipodals remain in the chalazal side; one of the polar nuclei migrates and fuses with the micropilar polar nuclei.

At maturity the antipodals disappear and the synergids are spherical, the egg cell is slightly elliptical (Fig. 44d). The cells of the hypostase are strongly lignified at this stage. At maturity the cells of the nucellar epidermis elongate in the radial plane. An appendage is visible when the outer integument elongates; at this stage, both integuments accumulate tannins and a group of cells located in the base of the chalaza are lignified.

Microsporangium and Microsporogenesis

The six saggitate anthers develop in two series of three (Fig. 45c), both series are opposite to the petals. Early stages in floral development are needed in order to establish proper stamens inception. The anthers are tetrasporangiate and the connective tissue is broader towards its middle portion. A young anther consists of four lobes and some connective tissue filled with tannins. The pollen mother cells are visible in early stages (Fig. 45a). When the anther is young, the filament is very short and the connective is less massive than in Kunhardtia spp. In Fig. 46, the young anthers can be seen in lateral, abaxial and adaxial view.

The four pores are undifferentiated and the epidermis is already sculpture and filled with tannins. When mature the anther dehiscences by four apical pores (cruciform). In the young anther the primary parietal cell divides periclinally giving rise to a secondary parietal cell. The outer and inner secondary parietal layers divide periclinally; the inner secondary parietal layer divides once more giving rise to the tapetal layer. The outer layer gives rise to the endothecium and middle layer (Figs. 44e, f, and 45e). This type of anther wall development is the Basic type and I reported it in Kundhardtia rodantha. The same anther wall formation has been reported in Rapateaceae by Venturelli & Boumann, (1988).

The tapetum is binucleate and secretory. By the time the pollen mother cells reach the first meiosis the tapetum cells remain attached to the wall of the locules, later on the young sporocytes are surrounded by callose (Fig. 45c). During the second meiosis, the tapetal cells move towards the young spores but the cellular integrity of the tapetal cells remains intact; the deposition of callose still envelopes the developing pollen grain (Fig. 45f). The same occurs with the tapetal cells of Kunhardtia; microsporogenesis is simultaneous.

The epidermis cells of the young and mature anther have their cytoplasm filled with tannins. The typical papillate epidermal pattern reported for the other genera is present also in Schoenocephalium. The mature anther has a central vascular bundle with less connective tissue above the median portion (Figs. 45a,d).

Fig. 42: Ovule development and detail of pistil in Schoenocephalium teretifolium (Colella, 2123); a) pistil showing ovules (100x); b) young ovule showing archesporial (200x); c) ovule detail showing micropile detail (200x); d) linear megaspores (200x); e) chalazal functional megaspore (400x).


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Fig. 43: Pistil morphology of Shoenocephalium teretifolium (Colella, et al 2123); a) detail of papillate stigma (10um); b) epidermis near base with tannins (100x); c) epidermis near top showing transmitting tissue (100x); d) epidermis showing silica bodies (100x).

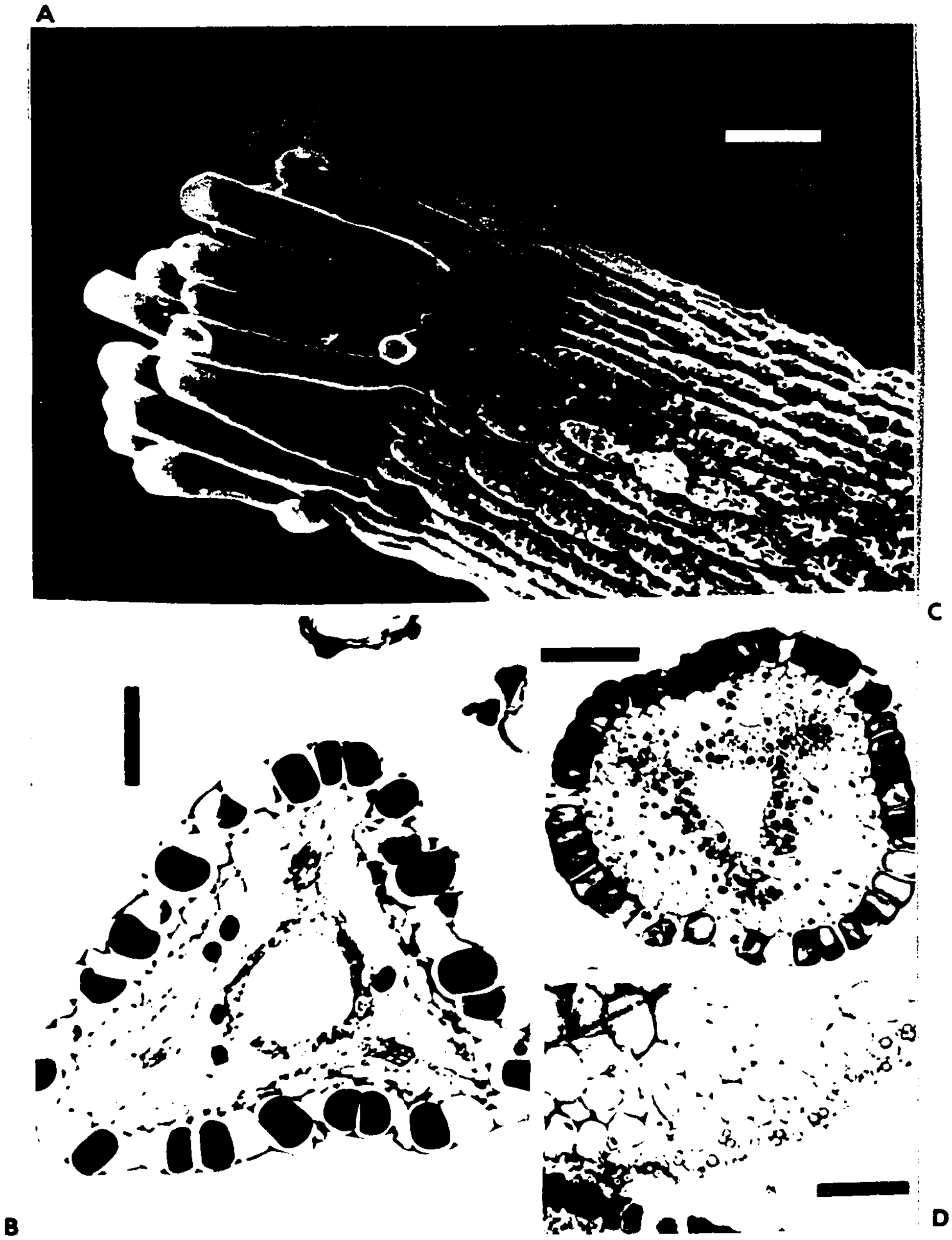
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Fig. 44: Anther and ovule development of Schoenocephalium teretifolium (Colella et al, 2123); two-celled stage (7 um); b) 4-celled stage (18 um); c) inmature eight-celled embryo sac (3,3 um); d) egg apparatus and polar nuclei (3,3 um); e) young anther showing primary parietal layer, secondary parietal layer and Pollen Mother Cells (18 um); f) young anther showing middle layer (18 um).

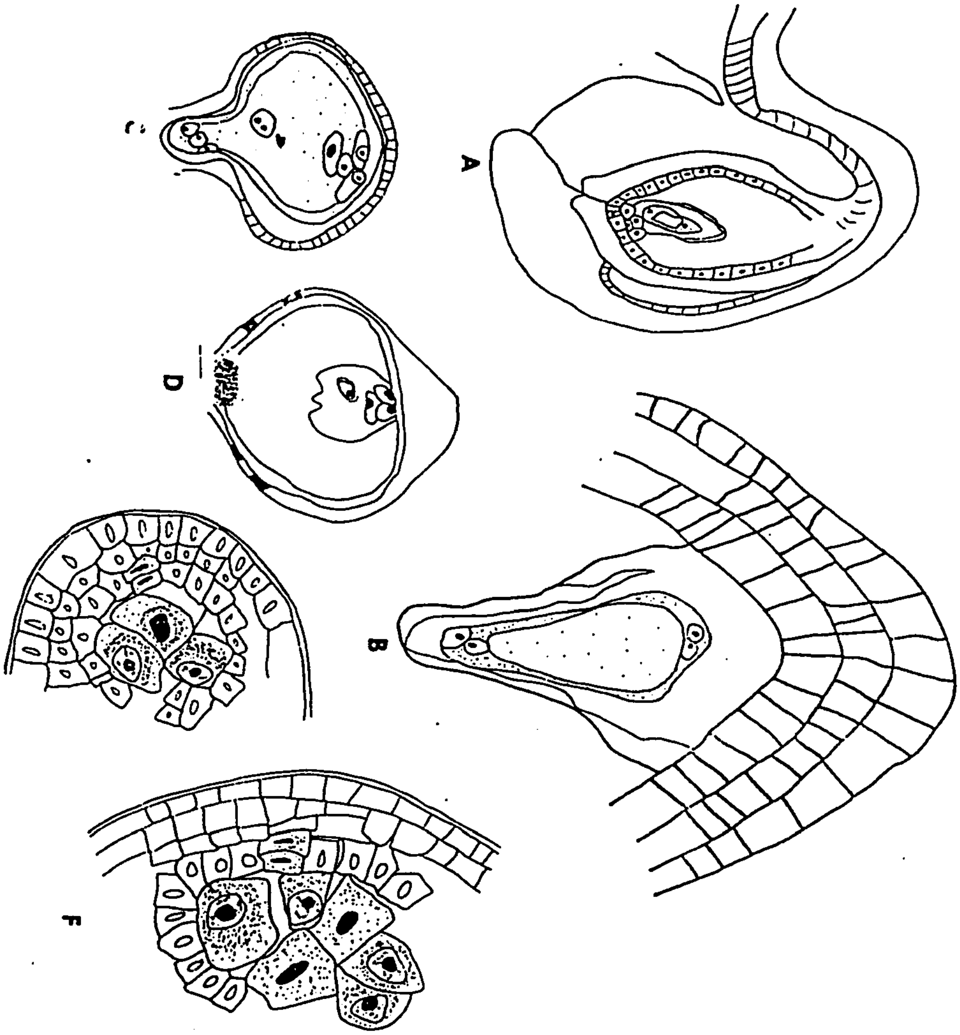
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Fig. 45: Anther development in Schoenocephalium teretifolium (Colella et al 2123); a) young anther showing sporocytes (100x); b) mature anther near base (100x); c) anthers in flower (100x); d) young anthers near base (100x); e) tapetum (200x); degenerating tapetum and tetrads (200x)

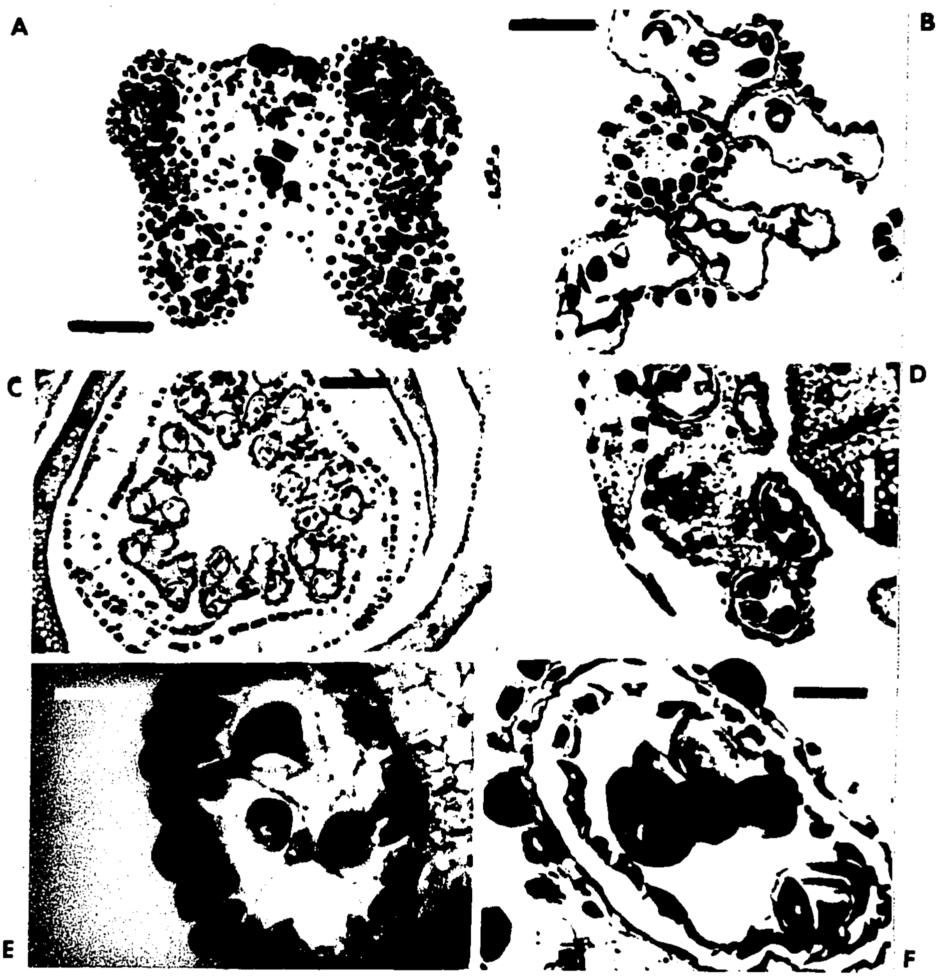
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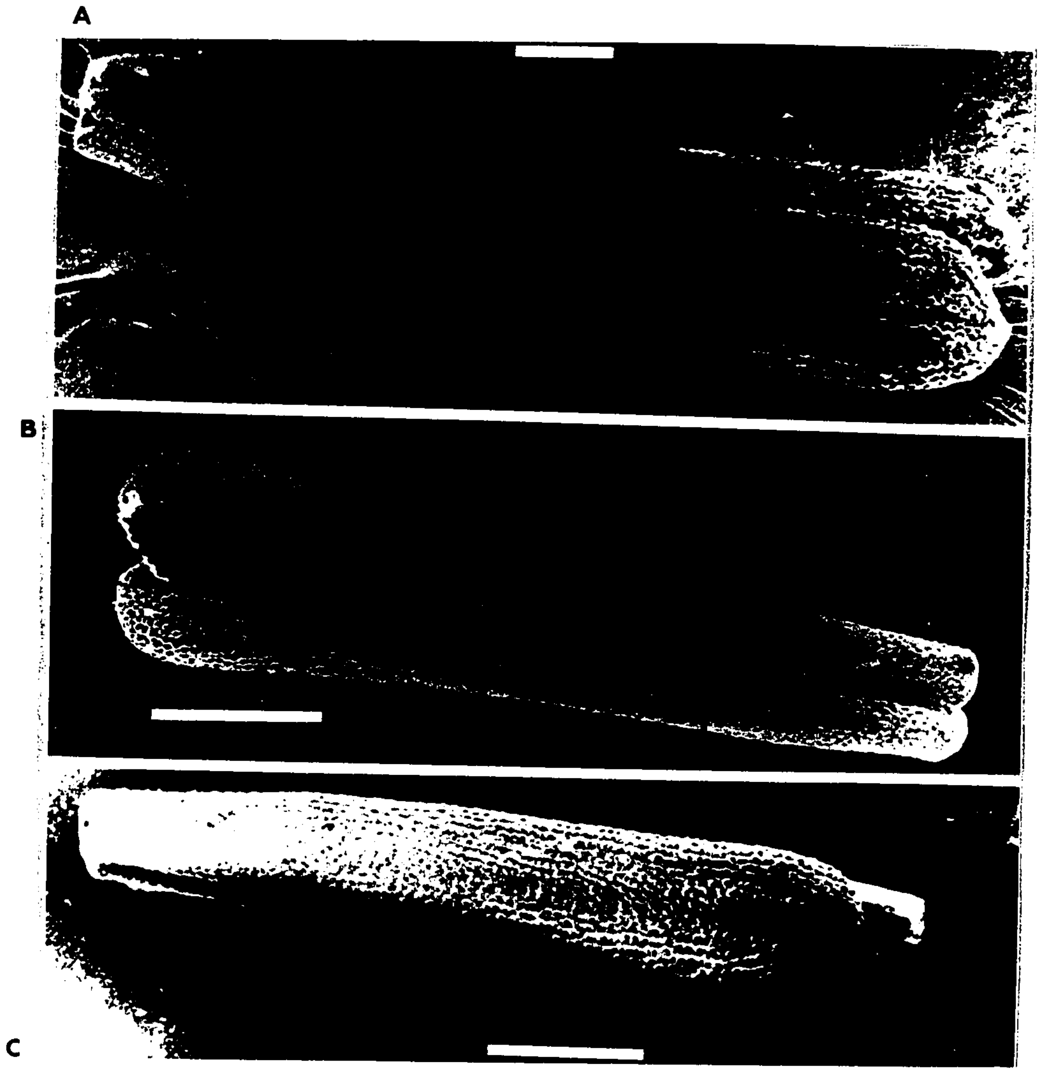
Fig. 46: Young anthers of Schoenocephalium teretifolium (Colella et al, 2123); a) ventral side and immature aperture (5um); b) ventral side (5 um); c) lateral view (5 um).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The genus Guacamaya Maguire

Guacamaya is the name that the natives give to the parrots (Ara spp.) in Venezuela. This was the name chosen by the late Dr. B. Maguire in recalling the beautiful colors of the bird in the flowers of this spectacular plant. It is a monotypic genus with only one representative, Guacamaya superba Maguire, which grows in the white sand savannas and open caatingas of the Rio Negro-Guainia region in the Venezuelan and Colombian amazon. The plant forms clusters of individuals that are pseudodichotomous and locally abundant. The inflorescence are subconical pseudanthia with clusters of numerous spikelets (c.a. 40-50) spirally arranged. The two spathaceous bracts remain connate and the developing spikelets penetrate the bracts before anthesis as in Saxofridericia spp.

The bracts of the spikelets are red or pink salmon and the petals are whitish. Floral changes in color ranges, from whitish at earlier stages to red at maturity. In the inflorescence, the proximal spikelets have the tendency to become reflexed near maturity, a feature shared with Kunhardtia and Schoenocephalium. In the inflorescence, the basal spikelets develop before the apical ones as in most of the Rapateaceous genera. The spikelet consists of a series of coriaceous bracts spirally arranged and gradated. Thus, the basal bracts of the spikelet are always larger than the apical ones. The three sepals are free and the three petals are connate at their base. The corolla is included in the sepals during anthesis; this behavior is usually correlated with cleistogamy. However, Berry (pers. comm.) observed hummingbirds visiting and feeding from the unopened flowers of Guacamaya. Prefloration is imbricate, and tannins accumulate in the abaxial and adaxial epidermis of the sepals and petals (Fig. 49a).

The ovary is a compound pistil with three locules. Prefloration is imbricate, and the placentation is axial; there are a few ovules per locule (Fig. 47a). The cortex of the pistil does not accumulate tannins, and the inconspicuous schizogenic nectaries (gynoecial nectaries) are located in the interlocular region. Nectar secretion occurs at the base of the petals while the flowers are almost unopened. The style is hollow, and the transmitting tissue is of the secretory type in the locular region as in Amphiphyllum. When mature, the pistil epidermal cells elongate in the radial plane; the tangential and radial walls of those cells show a certain degree of lignification and silica bodies are abundant here. (Fig. 47d). The stigma ends on a "tuff" of hairs (ciliate stigma), and is most likely of the wet type.

The Ovule

The ovules are anatropous, crassinucellate, and bitegmic. The two integuments form the micropyle and this is of the zigzag type (Fig. 47c). The shape of the mature ovule is obovate. The inner integument consists of two layers, but some periclinal division may add one more layer towards the mycropile. When mature the cells of the outer layer of the inner integument elongate slightly in the radial plane; this is particularly notorious near the micropyle. The outer integument is multilayered and consists of at least nine layers of cells. Cell growth in the intermediate layers is mostly periclinal. There is some degree of lignification in the tangential walls of the cells of the outer layer of the outer integument. These cells show a "wavy" pattern only in the micropylar region. The vascular strands end in the chalaza, and a well-developed hypostase remains after fertilization has occurred (Figs. 47a, b). The outer integument is smaller on the concave side of the ovule and this asymmetry accounts for the zigzag pattern of the micropyle.

Megasporangium and Megasporogenesis

The archesporial cell undergoes meiosis and gives rise to a linear tetrad of megaspores. The chalazal megaspore or the one above the chalazal survives and the three remaining megaspores degenerate (Fig. 50a). During megasporogenesis, a noticeable callose deposition is visible towards the chalazal side; this envelops the young megaspores. A hypostase is visible at this stage (Fig. 49b). This pattern of spore development is in accordance with the monosporic type, and it has been reported in most of the members of the Rapateaceae (Tiemann, 1984; Venturelli & Boumann, 1988). In the young ovule the primary parietal layer divides anticlinaly, and its derivative cells occasionally divide, giving rise to a parietal layer that in some cases remains after fertilization (Fig. 51a).

The most important stages of embryo sac development can be seen in Figs. 50b, d, 51a,and b. The first mitotic division of the megaspore produces two nuclei that migrate towards opposite sides and, a second mitotic division duplicates the number of nuclei. At the end of the third mitosis, the three antipodals remain on the chalazal side. Before fertilization has occur, the polar nuclei migrate and fused with the micropylar nuclei. At maturity, the antipodals disappear; the egg cell is slightly elliptical. At this stage, the cells of the hypostase are strongly lignified. The integuments accumulate tannins.

At maturity, the cells of the nucellar epidermis elongate in the radial plane and the cells located in the chalaza are lignified (hypostase).

Microsporangium and Microsporogenesis

The six-saggitate anthers develop in two series of three (Fig. 52a); both series seem to be opposite to the petals, but more stages, in particular during early development, are needed in order to elucidate stamen inception during floral ontogeny. The anthers are tetrasporangiate, and the connective tissue is broader towards its middle portion. A young anther consists of four lobes and some connective tissue filled with tannins. The pollen mother cells and the anther walls are visible at this stage (Figs. 52a, b). When the anther is young, the filament is very short and the connective tissue is less massive than in Kunhardtia spp. At maturity, the anther opens by two pores.

In the young anthers, the pores are undifferentiated, and the epidermis is already sculptured and filled with tannins. The primary parietal cell divides periclinally giving rise to a secondary parietal cell. The outer and inner secondary parietal layers divide periclinally. The inner secondary parietal layer divides once more, giving rise to the tapetal layer, and the outer layer gives rise to the endothecium an a middle layer (Figs. 51d, c, 52b). This type of anther wall development is probably in agreement with the Basic type pattern of anther wall formation, reported also in another member of the Tribe Schoenocephalieae (Kunhardtia spp.) and in other Rapateaceous genera by Venturelli & Boumann, (1988).

The tapetum is of the secretory type and its cells are binuclear. It shows an interesting behavior, by the time the pollen mother cells reach the first meiosis, the tapetum remains attached to the wall of the locules and the young sporocytes are surrounded by callose (Fig. 52e). Microsporogenesis is simultaneous (Fig. 52f).

The cells of the epidermis of the young and mature anther have their cytoplasm filled with tannins. The typical epidermal pattern reported for the other genera is present also in Guacamaya. The papillae of the epidermis in the mature anther are bigger than in the young anther. The mature anther is characterized by a central vascular bundle; connective tissue is less massive above the median portion than in the basal portion (Figs. 52d, e).

Endosperm and young seed

The endosperm formation is nuclear. After the fusion of the polar nuclei with the remaining sperm cell, mitotic divisions take place and form a ribbon-like coenocyte located at the chalazal side (Figs. 48a, c) whose number of nucleoli varies. The mature seed shows the jigsaw pattern and labyrinth structure of the exotegm cells during seed development, a feature share with Cephalostemon, and Rapatea reprted previously by Venturelli and Bouman (1988) and Tieman (1985).

Fig. 47: Guacamaya superba (Colella et Morales, 1275); a) cross section of pistil (100x); b) young ovule showing vascular supply (100x); c) zig-zag mycropyle (100x); d) pistl epidermis with silica bodies (200x).

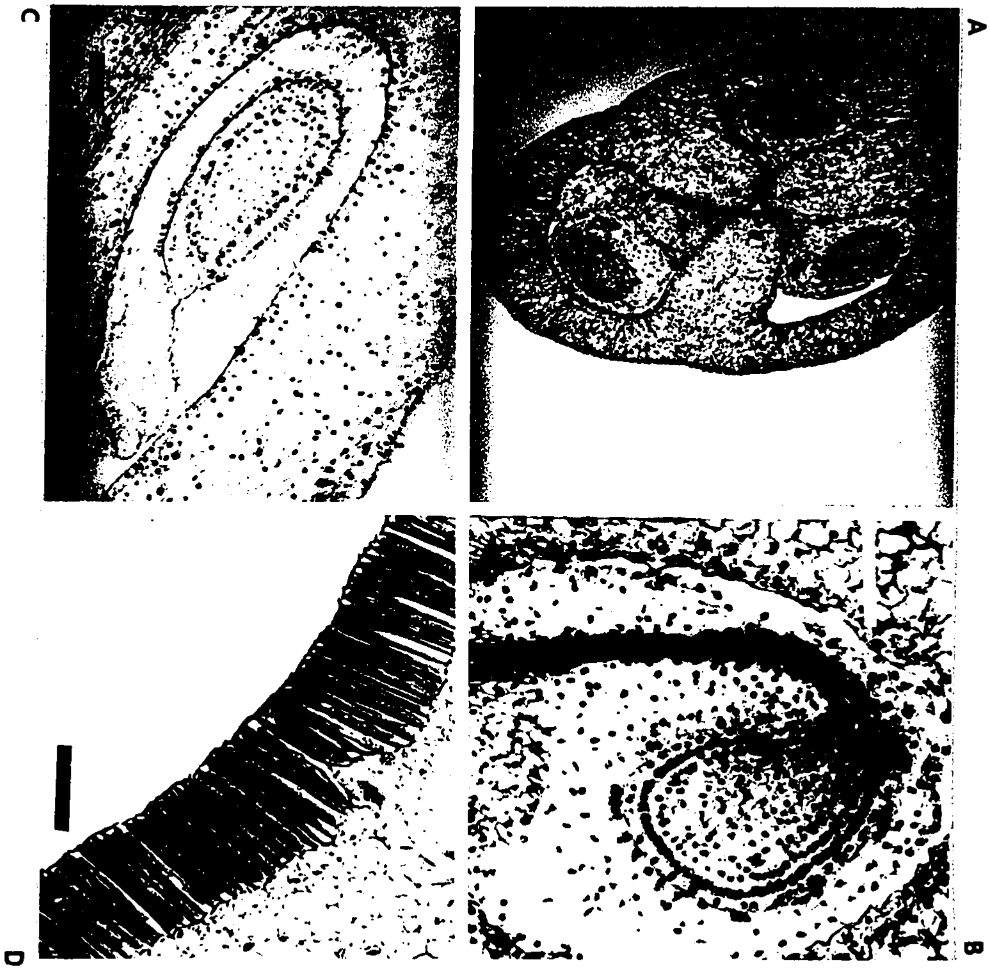
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Fig. 48: Ovules of Guacamaya superba (Colella et Morales, 1275); a) fertilize ovule with inmature endosperm (100x); b) ovule showing hypostase (100x); c) endosperm detail (400x); d) zig-zag seed coat pattern (200x).

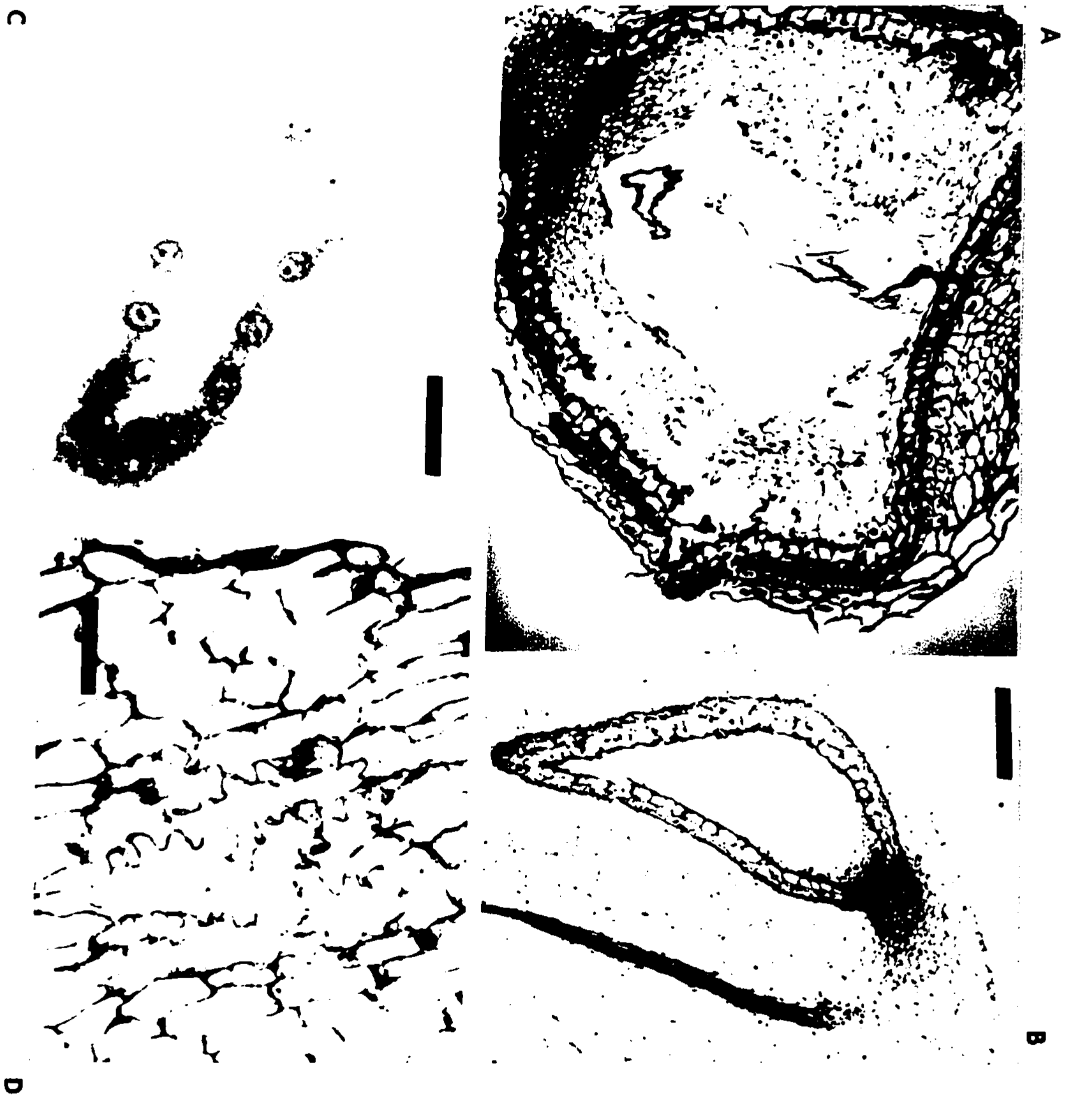
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Fig. 49: Guacamaya superba (Colella, 1275); a) prefloration (100x); b) ovule detail (200x).

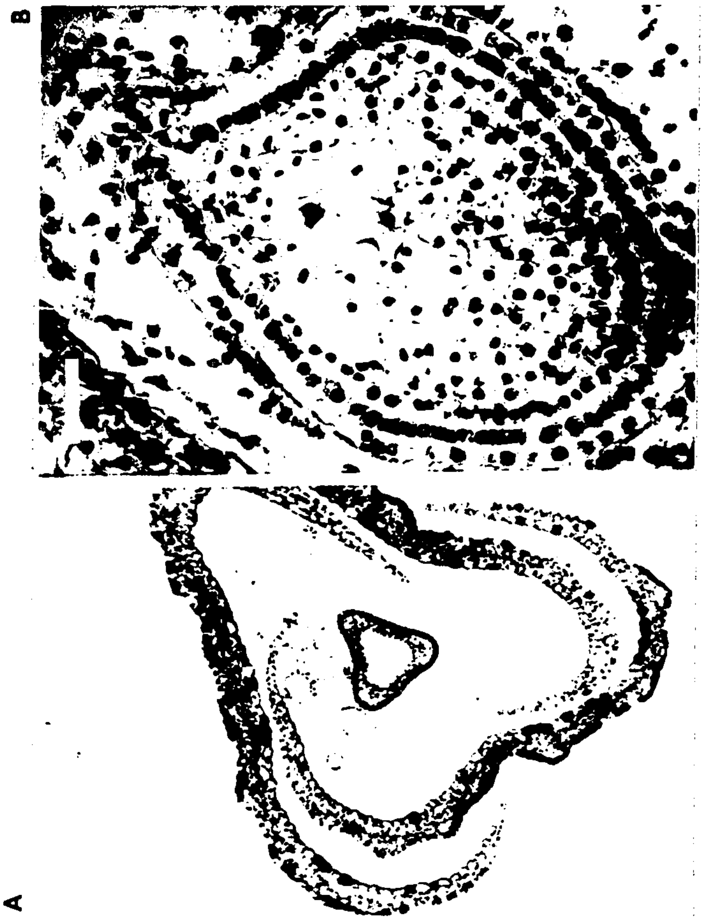
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Fig. 50: Embryo sac development of Guacamaya superba (Colella et Morales, 1275); a) degenerating spores (400x); b) dyad stage (100x); detail of dyad stage (1000x); d) tetrads (1000x).

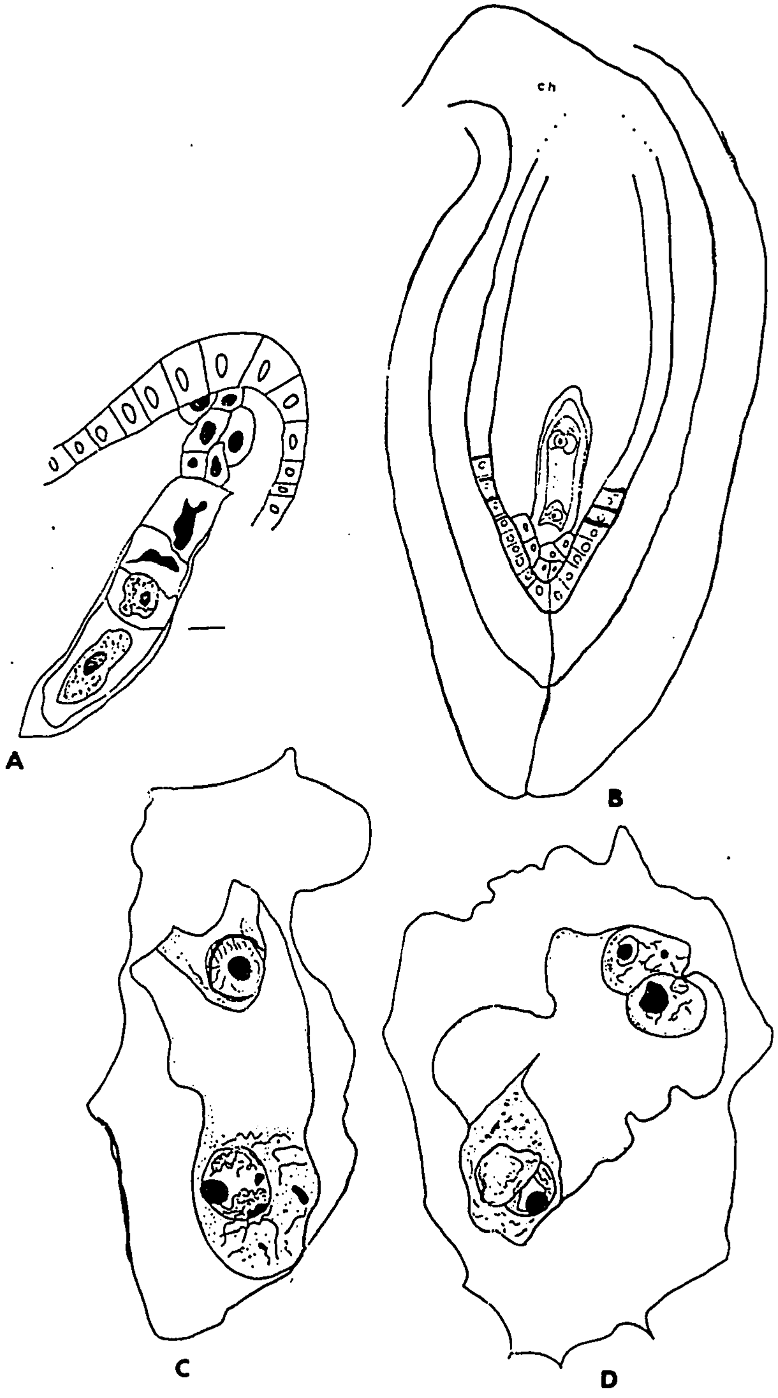
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Fig. 51: Anther and ovule development of Guacamaya superba (Colella & Morales, 1275); a) 6-nuclei stage (3,3 um); b) 8-celled embryo sac (8 um); c) young anther (8,8 um); d) pollen tetrads and tapetum (2 um); e) mature pollen grain (1,8 um); f) flower prefloration (20 um).

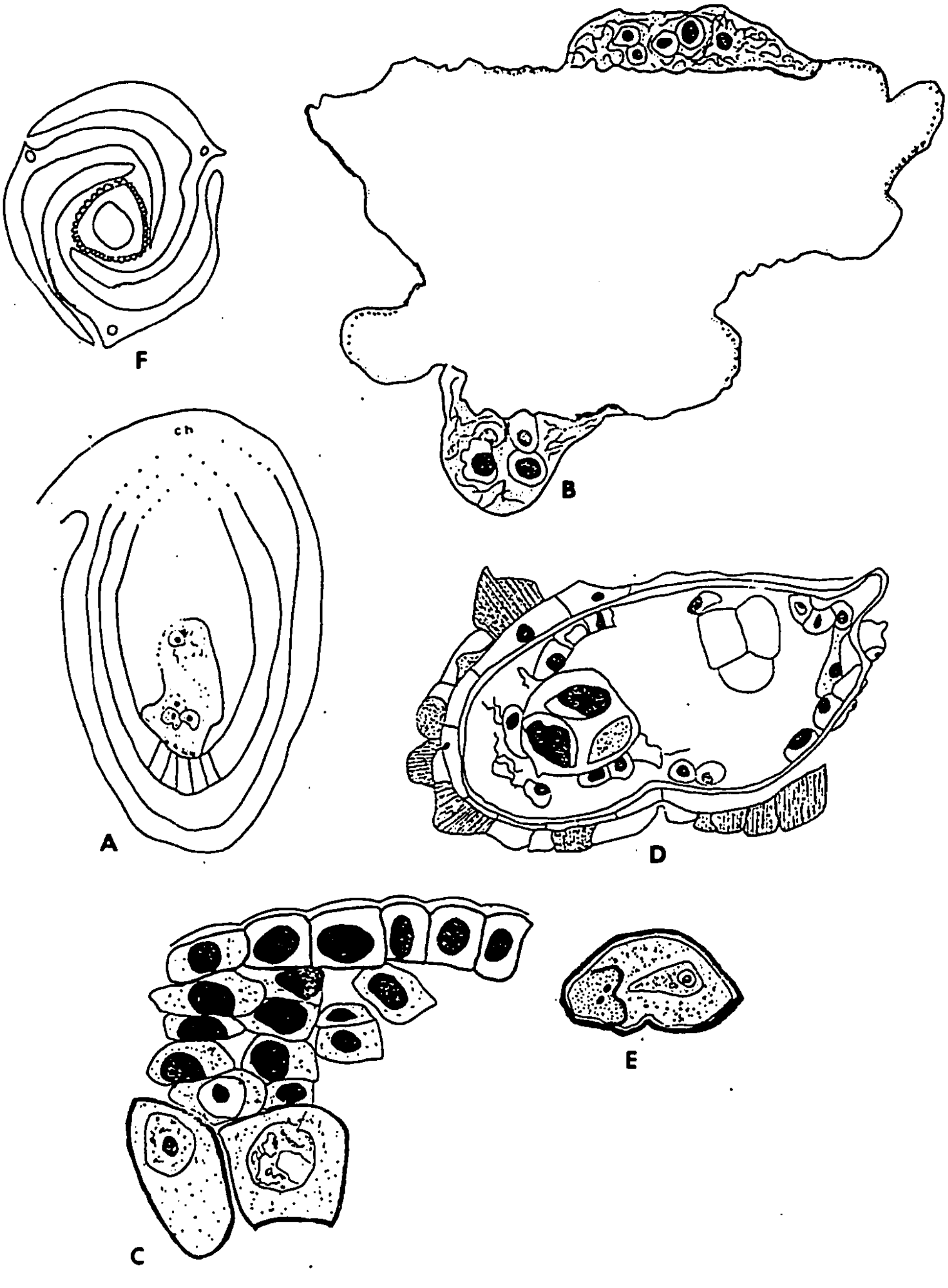
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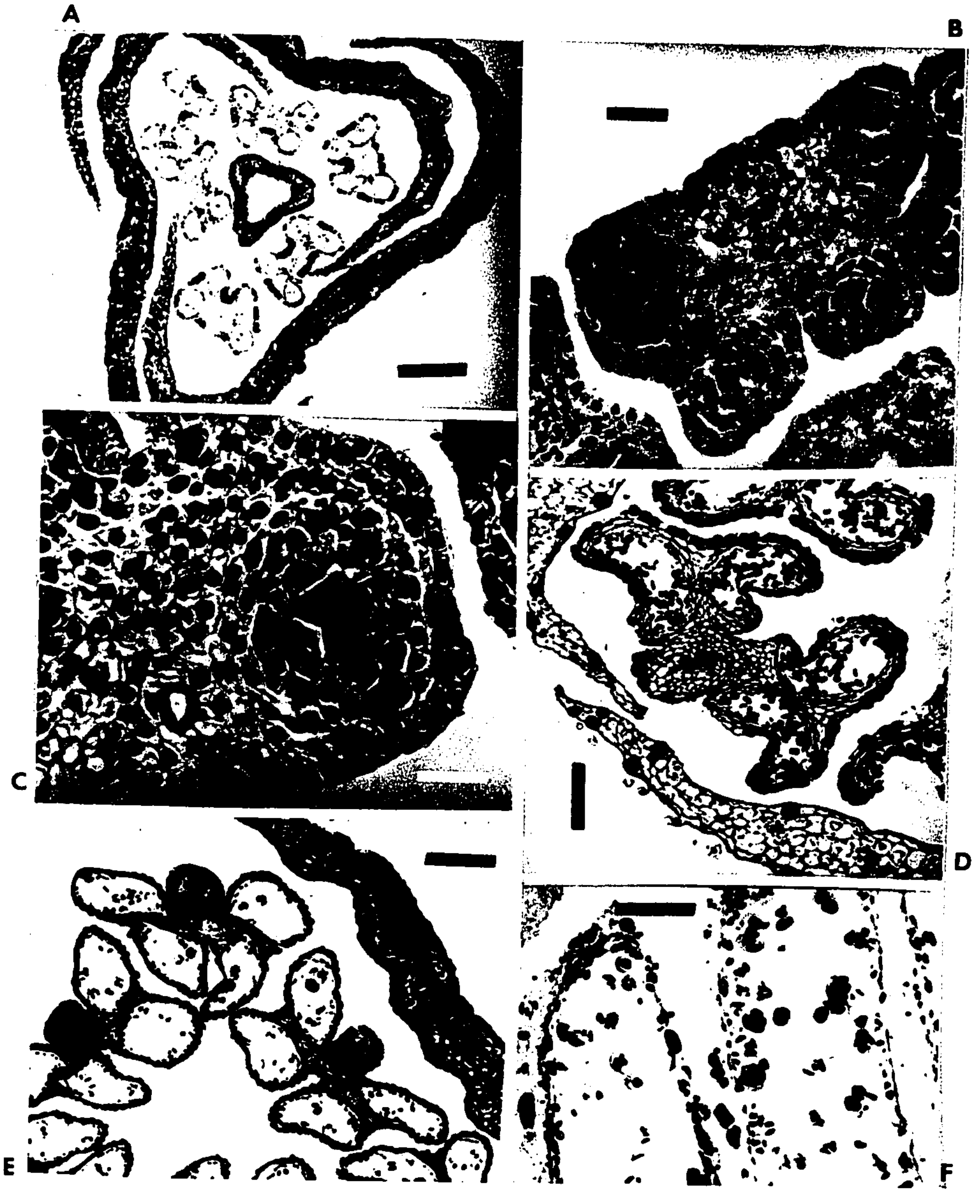
Fig. 52: Guacamaya superba (Colella & Morales, 1275); Anther development: a) anthers at its base (100 x); b) young anther showing Pollen Mother Cells (200x); c) detail of anther wall (400x); d) mature anther (100x); e) mature anther near the tip (100x); f) tetrads with callose (200x).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A2) Subfamily Rapateoideae

The subfamily Rapateoideae consists of the tribes Rapateeae and Monotremeae. The Rapateeae consists of four genera: Rapatea, Cephalostemon, Duckea and Spathanthus. The genus Rapatea has an ample niche and it can be found on Tepui summits or in the lowlands where it is quite diverse. The remaining genera with a narrow distribution and more local endemics had reach a notorious diversity in the white sand savannas, shrubby vegetation or campos of the Guianan shield, the Amazon and Brazil. The tribe Monotremeae consists of four genera: Monotrema, Potarophytum, Windsorina, and the only extra-American member of the Rapateaceae, the west-African genus Maschalocephalus. As is the case with some other tribes, it is interesting to notice that the degree of local endemism in the Monotremae is quite high, thus Windsorina and Potarophyton have been collected only in the Potaro River in Guiana. However, Monotrema with a wider distribution occurs mainly in sandy, periodically wet shrubby savannas of the upper Orinoco River, Rio Negro, Caquetá (Colombia) and Brazil.

Maguire (1958) distinguished the subfamily Rapateoideae from the subfamily Saxofridericioideae by the presence of carpels with one ovule per locule, placentation basal or subaxile, and seds obate or oblongue. Embryological differences among the two subfamilies will be discussed.

Tribe Rapateeae

The genus *Cephalostemon* Rob. Schomburgk

The genus Cephalostemon Rob. Schomburgk, consisting of an assemblage of probably five species is located in open white sand savannas of Venezuela and Bolivia, and in marshy campos in Matto Grosso and Minais Gerais. A major criterion for species delimitation has been based on morphological variations of the spikelets bracts and geographical distribution (Körnicke, 1873; Maguire, 1958). The majority of the species are small colonial herbs with underground rhizome and grassy leaves; in exceptional cases they may reach up to 1 Mt tall as in Cephalostemon ridelianus Könicke. The inflorescence consists of a relatively small (2-3 cm in diameter) head with two to eight spikelets. The two spathaceous bracts located at the base of the head are lanceolate and short. The scape is encircling by a closed sheath that covers about 25 % of the total length and ends on a rudimentary bifacial leaf.

As in all Rapateaceae, the flowers have three coriaceous sepals that are membranaceous at the base and three fragile petals. The three sepals and the petals are basally connate the six stamens are adnate to the corolla tube. The anthers are tetrasporangiate (Figs. 53a, d) and dehisce by a subapical confluent pore. In a detail of an immature spikelet shown in Fig. 53b, the young anthers differentiated early and the carpel show the ovule primordia (Fig. 53c). Glandular hairs are associated with mucilage secretion in the leaves, stems or floral parts in almost the entire Rapateaceae. In Cephalostemon affinis they are also located in the axile of the spikelets bracts (Figs. 54a, b, c, d), or at the base of the anthers.

Tiemann (1985) and Venturelli & Boumann (1988) studied the embryology of Cephalostemon ridelianus Körnicke and Cephalostemon angustatus Malme. Previous reports on the anther wall formation are contradictory: Tiemann (1985) concluded that it is of the monocotyledonous type whereas Venturelli & Boumann (1988) recorded it as basic type. The matter was not resolved because only stages of young anthers of Cephalostemon affinis (Figs. 53d, 55a) were sectioned and examined. Cytokinesis is simultaneous and the tapetum is glandular and binucleate; after meiosis the young spores are arranged in tetrahedral tetrads. The mature single pollen is shed in the two-cellular stage. The ovule is anatropous, bitegmic and crassinucelar, embryo sac formation follows the **Polygonum** type.

Cytology

Reports on chromosome numbers in Rapateaceae are insufficient and mostly concentrated on the subfamily Rapateoideae (Spathanthus sp. and Maschalocephalus sp.). In an attempt to study the cytology and chromosome numbers of Cephalostemon affinis, young anthers were fixed in New Commers solution, smashed and gently heated in diluted acetic acid and further stained with an alcoholic acetocarmine solution. This technique rendered no permanent slides. Tiemann (1985) reported that the chromosome number in Spathanthus bicolor was 2n=52, Mangenot & Mangenot (1958) showed that the chromosome number in Maschalocephalos dinklagei was 2n=22. From studies reported here on the chromosome number of Cephalostemon affinis it is concluded that it has a 2n= 52 as in Spathanthus unilateralis. Although more research is needed this preliminary cytological data will add some support in the actual tribal placement of the genus Cephalostemon. Primary and secondary parietal layers and pollen mother cells are present in a cross section of a young anther (Figs. 53d, 55a). In a detail of the pollen mother cells right before meiosis the nucleolus stained darker (Figs. 55a, b). Some phases of the successive meiosis were recorded, and Figs. 55d, e, and f, show early prophase, prophase I, Anaphase II and the pollen tetrads. At the end of meiosis I the tapetal cells become binucleate. Microsporogenesis is simultaneous and the microspores are tetrahedral.

The genus ***Rapatea*** Aublet

With a broader geographical distribution, the genus Rapatea can be found in Trinidad, Venezuela, Ecuador, Perú, Colombia, Brazil Bolivia, and the Guianas. It is perhaps the second in number after the genus Stegolepis. The size of the individuals is variable and taxa such as Rapatea pychnocephala may reach up to 10 cm or Rapatea paludosa and R. ulei may be up to 1,5 mt tall. They are colonial rhizomatous herbs with a strong preference for riverine or waterlogged habitats. In general, they like shadowy places more than open savannas. The inflorescence is a head with many spikelets concentrated mostly in the median plane, the spikelets bracts gradate in size and the longest are at the base. In general, the two spathaceous bracts may undergrowth the inflorescence or fused to it in both sides as in Rapatea xiphoides Sandwith and R. membranacea Maguire.

Flowers of Rapatea longipes and R. paludosa Aublet were fixed in FAA for 24 hours, then transferred to alcohol 70% for anatomical or SEM studies. Phase contrast and Normanski microscopy required that dissected young ovules were cleared with Herr's solution (Rudal, 1985) for 24 hours up to one week. Some diagrams were performed with the aid of camera lucida. The flowers of Rapatea longipes Spruce ex Kornicke and R. paludosa have three sepals fused at the base and three membranaceous petals basally connate. The six anthers are adnate to the corolla tube, three opposing the petals and three alternating with them. The young spikelets have numerous secretory hairs in the axile of the bracts (as in Cephalostemon sp.), but at this stage the pistil is not yet fully differentiated (Fig. 56a). Silica bodies are abundant in the epidermis of the mature pistil (Fig. 56b). The spikelet diagram on Fig. 57a, shows the pistil is less developed when the petals and the stamens are at the primordial stage. The lines that may anticipated the future abscission zones in the fruit could be noticed in a cross section of a mature pistil (Fig. 57b, arrows). The tricarpelate pistil has one ovule per locule and axilar placentation (Fig. 57b). In a longitudinal section of a mature carpel some of the ovules, have the integuments removed as to show the nucellus. (Fig. 58a); in a cross section, the triclocular pistil holds no more than three ovules per locule. A reduction in the number of ovules per locule in the Rapateoideae is associated with an increased in ovule size (Fig. 58c). The family Rapateaceae is enantyostilic due to differences in stigma morphology among the two subfamilies. In Rapatea longipes the stigma narrows and bends towards the apex (Fig. 58b) as it is the case with many other species of Rapatea.. This is a feature that has been associated with the "Buzz pollination syndrome" in Haemodoraceae (Sympson, 1985), Pontederiaceae (Barret, 1989), and in some

Rapateaceae such as Duckea spp. and Monotrema spp. (pers. obsv; Vogel, 1981). No records on stigma morphology and its taxonomic significance among members of the two subfamilies were reported before in previous publications. The stigma in the Saxofridericioideae is straight, open and ending on a tuff of glandular hairs of variable size. Whereas the tendency in the Rapateoideae is to have a narrow pointed partially closed and bends stigma without glandular hairs.

Megasporangium and Megasporogenesis

Tiemann (1985) studied the embryology of selected species of Rapatea (R. paludosa Aublet, R. rugulosa Maguire, R. friderici-angusti Schomburgk and R. xiphoides Sandwith) however, she did not analyzed R. longipes. The ovules of Rapatea longipes are anatropous, bitegmic and crassinucelate (Figs. 59a, b, and c), the raphe here becomes visible (Fig. 58d). The outer integument consists of up to 10 layers whereas the inner integument consists only of two (Figs. 59a, c). In the young ovule the primary parietal cell divides anticlinally and its derivatives cells occasionally divide giving rise to a parietal layer that remains until fertilization. The archesporial cell is often located several cell layers below the nucelus (Fig. 59b).

Of the four megaspores, the basal one will give rise to the mature embryo sac (Fig. 60b). Tiemann (1985) concluded that the embryo sac formation in all Rapatea studied was of the **Polygonum** type. The data reported here is in agreement with her conclusions. The inner integument forms the micropyle, and the filiformis apparatus is evident before fertilization takes place (Fig. 60a). The antipodals remained at the chalazal end and are probably ephemeral.

Microsporangium and Microsporogenesis

The morphology of the basifix saggitate anthers in the entire genus Rapatea is characterized by the presence of an apical appendage, which is ontogenetically related to the anther tissue, and is not part of the connective tissue. A study on anther development and dehiscence mechanism of the anthers of R. longipes is offered in Fig. 61a. The young anthers are shown in an abaxial and adaxial view. A distinctive furrow in the appendage can be seen on adaxial view, this furrow participates in the opening mechanisms by separating the two halves of the appendage and leaving one single space or pore for the pollen liberation (Fig. 61c). A cross section of the anthers near the top, shows two sporangia only, further up the sporangia disappear and a layer of long endothecial cells is located underneath the anther epidermis (Figs. 56d, e). Tiemann

(1985) reported the same in R. paludosa by Tiemann (1985). Anther epidermis is filled with tannins (in some cases with silica bodies) since early anther differentiation. This ornamented cuticle and epidermis may have an adaptative value in the "Buzz pollination" syndrome since the insects probably attached to the anther, make it vibrate and expulse the pollen at pace with their own wing vibrations.

The tapetal cells become binuclealte right before pollen maturation, and at this stage the tetrads are still enveloped by a callose deposition (Figs. 56c, f). After the release from the tetrad, the pollen grain is still mononucleate, later one it divides by mitosis and the generative cell migrates towards the walls near aperture (Figs. 60c, d), the vegetative cells may have two nucleoli. The mature spore is shed in the bicellular stage. Anther epidermis is presented in Fig. 60.

The genus ***Duckea*** Maguire

The genus Duckea (Link) Maguire consists of five species distributed mostly in the Rio Negro region (Venezuela), and less often in Colombia and Brazil. The ecological preferences of this genus are somehow similar to that of Cephalostemon, growing in many cases in wet sandy soils of savannas, campos and caatingas or in temporarily waterlogged open savannas or forests. The size of the individuals varies from 90 cm up to 1.5 mt tall; they often resemble sedges. Leaf morphology is quite variable, thus some species show linear leaves as in Duckea cyperaceoidea (Ducke) Maguire, while others may have cylindrical leaves as in Duckea junciformis Maguire. Apparently, the majority of the species are rhizomatous and form colonies of no more than 5 individuals. The spathaceous bracts tend to be longer than the inflorescence, and in many examples, the old inflorescences can be elongated in the median plane. Floral development follows the same pattern of the remaining Rapateaceous taxa: the oldest spikelets opening at the base and the youngest at the apex. However, when the head is fully mature the young spikelets show an arrested development, and quite often the inflorescence apex has several aborted young spikelets.

The inflorescences are in general globose or subglobose heads made of rather small and sessile spikelets. The spikelets show numerous coriaceous and gradate bracts with a terminal flower (Fig. 63b) that is usually yellow; some species are multiscapose. The sepals are slightly coriaceous, sometimes white, lanceolate, and connate at their base. The three petals alternate with the three sepals, and are basally fused. The anthers are adnate to the corolla tube (Fig. 63b), with the outermost whorl of three stamens facing the sepals and the innermost whorl of stamens in front of the petals (Fig. 63b). A major criteria for species delimitation has been the spikelet bracts and inflorescence morphology, this characters are sometimes of little help, and it may be possible that the five species merge into two or three in the near future. Prefloration is imbricate (Fig. 63d).

The floral morphology and embryology of some genera of the tribe Rapateeae has been studied by Tiemann (1985), and Venturelli & Boumann (1988) they described the genera Rapatea, Spathanthus, and Cephalostemon with the only exception of the genus Duckea. In the hope that better understanding could be obtained of the tribal and generic relationships within the subfamily Rapateoideae, a study of the floral morphology and embryology of Duckea flava (Link) Maguire and D. junciformis Maguire was undertaken. Flowers and entire plants were collected and fixed in FAA or FPA for 24 hours, then transfer to alcohol 70% for anatomical and SEM studies. Some diagrams were performed with the aid of camera lucida.

The pistil of D. flava has one ovule per locule, and is trilocular (Fig. 62h). Placentation is basal and the ovules here are probably one of the largest (Monotrema spp. has also big ovules) in the entire family. The stigma is glabrous, bend towards its end and punctiform (Figs. 64a, b), a common characteristic of many Rapateoideae. The pistil epidermis showed rounded silica bodies concentrated towards the surface. In the

Casiquiare populations, the ovules of Duckea flava were parasitated by puppae of a small-unidentified wasp. The invasion occurs in one of the three locules, and renders infertile fruits in many occasions as larvae uses the young growing ovule for food, and occupies most of the space while growing faster than the remaining healthy ovules.

Infected pistils showed a tiny punctiform scar probably linked to wasp ovoposition, the larvae are usually located at the chalazal or micropilar end. This parasite-host relationship may play an important role in the population dynamics of this particular species. It would be interesting to determine whether the remaining species of Monotrema face the same ecological constrain.

Megasporangium and Megasporogenesis

The ovules are anatropous, bitegmic and crassinucleate, with an outer integument consisting of approximately ten layers and an inner integument that is two layers thick. The two integuments form the micropyle, and the outer integument is of dermal origin. (Figs. 65a, b, c, and d). In the young ovule the primary parietal cell divides anticlinally and its derivatives give rise to some parietal tissue that remains after fertilization. Several archesporials develop at the same time below the nucellar epidermis but only one develops into a functional megaspore. When the embryo sac reaches maturity an obturator and an hypostase are visible. Further growth at the chalazal side may be interpreted as vestigial or as a precursor of a chalazal appendage (present in Cephalostemon). Tannins are very common in the integuments or nucellus of the subfamily Saxofridericioideae but are lacking in Duckea, instead compound starch bodies are taking their place, and they are often located in the chalazal end.

After meiosis has occurred in the megasporangium, the basal megaspore will give rise to the female gametophyte, the remaining three megaspores will degenerate (Figs. 62c). This type of embryo sac development is in accordance with the Polygonum type (monosporic type), as reported in all Rapateaceae previously studied (Colella, in press; Venturelli & Bouman, 1988; Tiemann, 1985). When the functional megaspore is mature, an evident deposition of callose takes place towards the chalazal side as is expected for monosporic embryo sacs (Fig. 65c). The two and four nucleate stages are not depicted here, however the eight-nucleate stage is discussed. At the end of the last mitosis a large vacuole continues to pull the nuclei in opposite directions but (Figs. 62e, f, g) none of the nuclei have a definite place and shape as they changed constantly until the embryo sac matures.

At this stage the synergids are visible (Figs. 62g, 65d), ovoid and vacuolated, the egg cell lies right below them, apparently the polar nuclei fused before fertilization. The antipodals are not visible at this stage and they may degenerate before fertilization.

Microsporangium and Microsporogenesis

The anther wall development was not investigated in detail because the spirit collection was poor for very early stages, instead the ontogeny of the anthers was studied. A more detailed description on the morphology and development of the microsporangium of Duckea flava was provided for the first time. The anthers are saggitate, tetrasporangiate, basifix and dehisce by means of an apical pore consisting of sporangial tissue (Fig. 62). A young anther has four lobes and some connective tissue, which is broader towards its base moreover its epidermis is filled with tannins as in all Rapateaceae. In young anthers, the filament is inconspicuous and the pollen grain remains near the future pore (Fig. 66c). Furthermore, as the anther maturation proceeds an appendage develops above the apical pore, (Fig. 66d). Such a structure plays an important role in anther dehiscence. The endothecial thickenings are mostly cellulosic depositions in the walls of the cells located just below the anther epidermis. It is believed that through this layer the anther dehisce and set the pollen free (Masheways, 1955), the pattern of this thickenings can vary among families or genera, and in many examples they have taxonomic value. Contrary to present though (Mashewary, 1955; Davis, 1964), some poricidal taxa do have endothecial thickenings near the pore, a fact that has been widely reported by Fisher and Gerenday (1983) in Rapateaceae and many others families. A cross section of the anther near the appendage of Duckea flava shows a continuous ring of endothecial thickenings below the epidermis (Fig. 62j).

Different developmental stages in the anthers of Duckea flava were recorded, the young microsporangium is seen in abaxial and lateral view where the appendage overgrows the sporangium, and at this stage the inmature pore is visible (adaxial side). Once the anther reaches maturity the pore is fully open.

A cross section of a young anther of Duckea flava shows the pollen mother cells, the undifferentiated tapetum and endothecium, and three sterile middle layers. The tapetum is binucleate and secretory, in later stages it begins to disintegrate but the Ubisch bodies are still visible at that time when the mature pollen has already separated from the tetrad. Microsporogenesis is simultaneous. The mature anther epidermis is filled with tannins, and shows the same type of pattern as in all Rapateaceae. The pollen is shed in the bicellular stage.

Tribe Monotremeae

The genus *Monotrema* Kornicke

The genus Monotrema Kornicke consists of 5-6 species, that are distributed mostly in Colombia, Venezuela, and Brazil specifically in the Rio Negro, Orinoco, Guania, and Casiquiare regions. The plants grow very well on seasonal flooded sandy savannas, caatingas, and shrublands. The four genera of the tribe Monotremae are: Potarophyton, Monotrema, Maschalocephalos and Windsorina, show differences in inflorescence construction, anatomy, embryology, local endemism, and geographic distribution in relation to the remaining Rapateaceae. Moreover, these differences raised many interesting questions about the speciation events that have been taken place in the tribe Monotremeae. The phylogenetic analysis that will be discussed later will help to raise many important questions about the speciation and branching patterns that occur within the entire family Rapateaceae especially in relation to its neighboring families, and its placement in the order Commelinales.

The species of the genus Monotrema are plants ranging from 60-90 cm tall, living in almost open sandy habitats and forming colonies of a few members. The plants bear distichous leaves (linear or graminose depending on the species), with axilary peduncles ending in a small subglobose inflorescence compose of several spikelets. The prophylls and other bracts of different sizes are located at the base of the spikelets but the spathaceous bracts that subtend the inflorescence vary in number, shape and size depending on the species. Thus, Monotrema xyridoides Gleason has small spataceous bracts (0,3-0,6 cm) that do not surpass the inflorescence, whereas Monotrema bractetaum Maguire has bigger ones (2-4 cm) that exceed the heads. Maguire (1958) reported that some of the basal spikelets tend to be infertile. However, they follow the same pattern of maturation as in the remaining genera of the family; the mature basal spikelets open first and the younger at the top will open later, sometimes a few of them may show an occasional arrested development.

The size of the population in the wild is often quite small, but the different species may yet actively interbreed as is perceived by the number of existing natural hybrids or ill-defined species. This in turn may influence the real number of species within the genus however more extensive fieldwork and taxonomic research will hopefully cast more clues on this topic.

Fertile plants of Monotrema aemulans were collected and fixed in FAA or FPA for 24 hours and then transferred to alcohol 70 % for anatomical and SEM studies. Drawings and diagrams were performed with the aid of camera lucida. The flowers have three coriaceous sepals alternating with tree membranaceous petals. The trilocular pistil bears one ovule per locule but sometimes two may be present, placentation is basal and the style is also hollow; silica bodies are present in the carpel epidermis. The flower has three coriaceous sepals, alternating with three petals, and six stamens in two series of three. The outermost whorl alternates with the sepals, and the innermost is oppose to the petals; the stamens are free, and the prefloration is imbricate. The seeds have a chalazal appendage. The main features in species delimitation are shape of the head, size of the spathaceous bracts, and size of the spikelet bracts (Maguire, 1958). The flower has three coriaceous sepals, alternating with three membranaceous petals.

Megasporangium and Megagametogenesis

The ovules are anatropous, crassinucelate, and bitegmic with some parietal (hypodermal tissue) tissue persisting after fertilization (Fig. 67f). The two integuments form the micropyle, and the inner integument is also of dermal origin. The outer integument consists of eight to ten layers, and the inner integument has two layers. The above mentioned ovular features are in accordance with that of the remaining Rapateaceae. The archesporial cell undergoes meiosis and gives rise to a tetrad of megaspores, of this the chalazal megaspore survives and the remaining degenerate however, occasionally the third megaspore gives rise to the embryo sac (Fig. 67). This type of embryo sac formation is in accordance with the monosporic type. The surviving megaspore will give rise to the embryo sac. During megasporogenesis, a thick deposit of callose covers half of the megasporangium and at the end of meiosis is more abundant towards the chalazal side. The embryo sac begins elongating at the bicellular stage, and a central vacuole is formed at the commencement of the first meiosis. The size of the vacuole and that of the embryo sac increases towards the third and fourth mitosis, when it reaches its bigger size (Figs. 67c, d, e, and f). Towards the eight-nuclei stage the cytoplasm of the megagametophyte is denser, and the cells migrate to its definite position before fertilization. The two synergids are obovate, and the egg cell lies bellow them. The antipodals, in number of three remain at the chalalazal side and disintegrate after fertilization. The polar nuclei fuse before fertilization takes place. Both integuments form the micropyle. Silica bodies and tannins are present in the carpel epidermis. There are secretory hairs at the base of the ovary. The outer integuments are ten cell layers thick, and the inner integuments are two cell layers thick.

Microsporangium and Microsporogenesis

The six-saggitate anthers dehisce by means of an apical pore, they are tetrasporangiate at the base, but near the pore the sporangia are fused. The anthers have appendages. A group of hypodermal archesporials is formed in the young anther (Fig. 69d) they divide to form a primary parietal layer that divides again to give raise to a second parietal layer. This layer divides again, and the inner secondary parietal layer gives rise to the tapetum, whereas the outer parietal layer gives rise to the endothecium, and middle layers (Figs. 68a, b). This anther wall development is in accordance with the Basic type. Ultimately the mature anther consists of elongated epidermal cells filled with tannins, the endothecium, four middle layers, the tapetum, and the pollen mother cells (Fig. 69a). The microspore mother cells undergo simultaneous meiosis resulting in tetrahedral or decussate tetrads (Figs. 68c, 69b). At this stage, a layer of callose covers the spores, and the cytoplasm of the tapetal cells becomes denser. In later stages, when the spores separate the tapetal cells disintegrate (Fig. 69c). The pollen is shed at the bicellular stage. The tapetal cells are binucleate when mature.

Seed and Embryo

After fertilization has taken place, a number of endosperm nuclei migrate towards the chalaza side, and form a ribbon like group of nuclei. Endosperm development is nuclear. As embryogenesis progresses, more endospermal cells are added until the seed cavity is filled with it, as they differentiate, the endosperm cells are filled with starch. The undifferentiated embryo lies at the micropylar side (Fig. 70d). The seeds are ellipsoidal, white, and with a chalazal appendage. The testa is multilayered and its outer and middle parenchymatous layers are compressed at maturity (Figs. 70a, c, d), Venturelli & Bouman reported the same. In the endotesta, the cells have a “U” pattern due to a deposition on the lower tangential cell walls (Fig. 70c). Towards the endosperm layer, a layer of cells with abundant tannin depositions surrounds the “U” cells. This pattern is present in some members of the tribe Rapateeae: Cephalostemon, Duckea, Spathanthus, Rapatea, and in Potarophyton of the tribe Monotremae, and seems to be absent in the Saxofridericioideae.

The “U” pattern present in the seeds of the Rapateoideae is another morphological character that justifies the taxonomic affinities among the different genera in this subfamily.

Fig. 53: Cephalostemon affinis young spikelets (Colella et al, 2069); a) anthers (100x); b) flower detail (100x); c) ovule primordia 100x); d) young anther (200x).

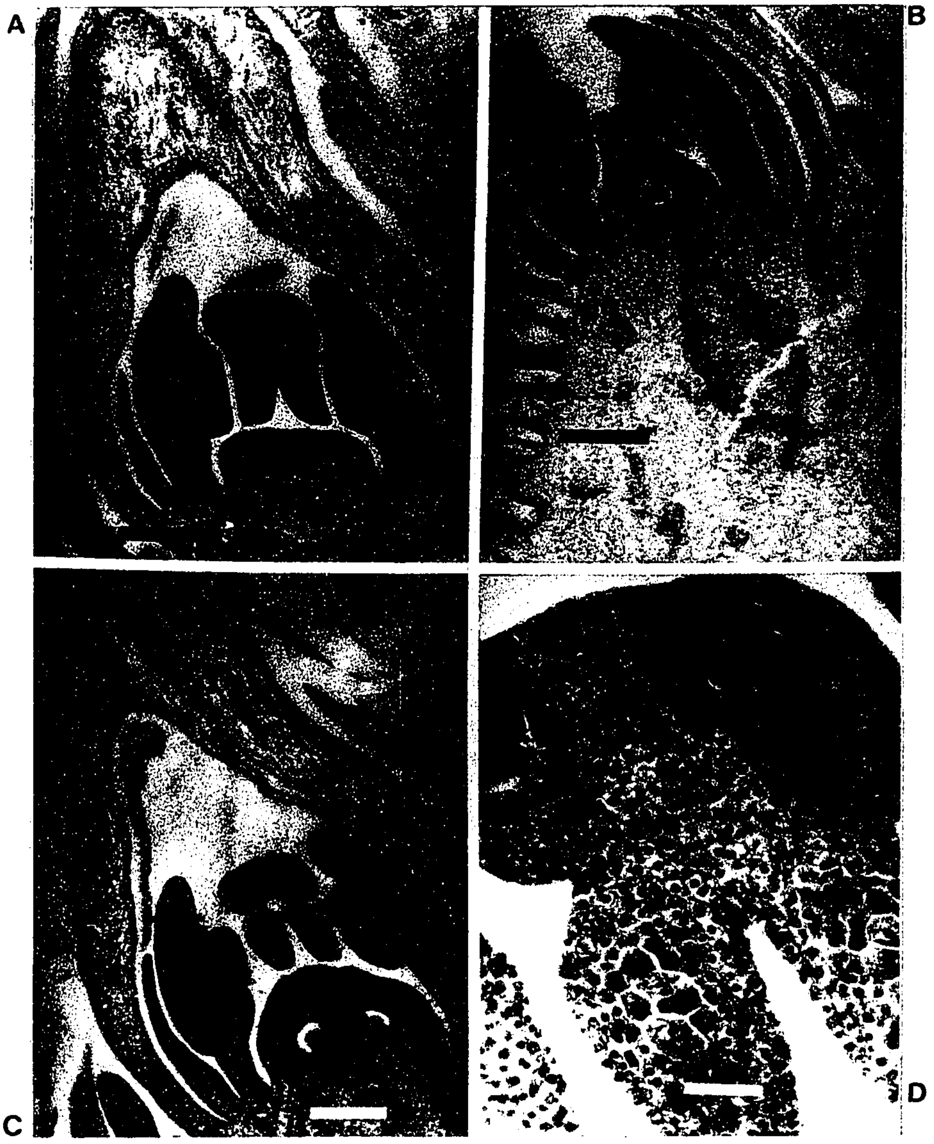
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Fig. 54: Cephalostemon affinis (Colella et al, 2069) secretory hairs: a) on the axile of spikelets(100x); b) detail of the hairs in a (100x); c) glandular hair on the anthers (200x); d) same as c (400x).


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Fig. 55: Cephalostemon affinis cytology (Colella et al 2069); a) anther locule (200x); b) pollen mother cells (400x); c) binucleate tapetum (1000x); d) prophase I (1000x); e) anaphase II (1000x); f) late anaphase (1000x).

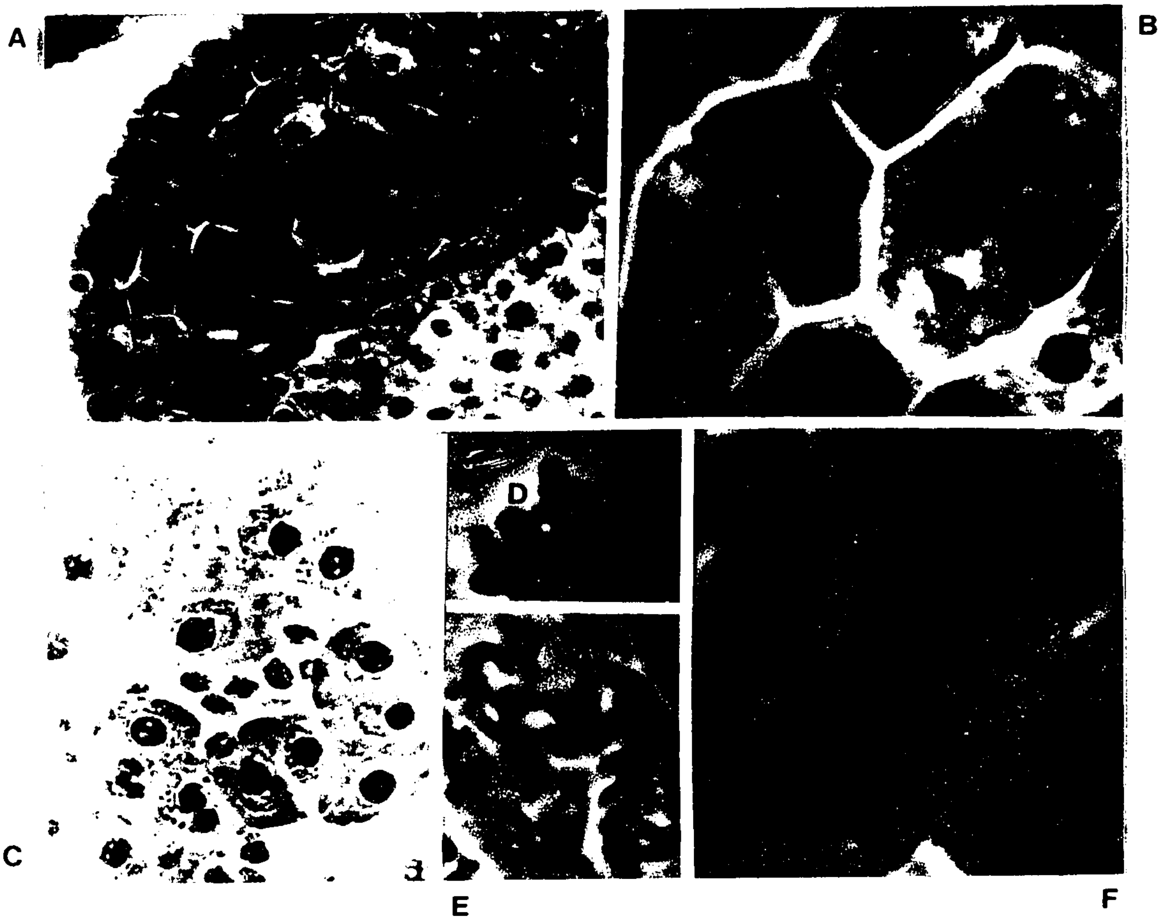
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Fig. 56: Rapatea longipes (Colella et al, 1774) young spikelet (100x); b) epidermis with silica bodies (400x); c) tapetal cell (1000x); d) anther near pore (100x); e) anther above pore (200x); pollen tetrads (1000x).

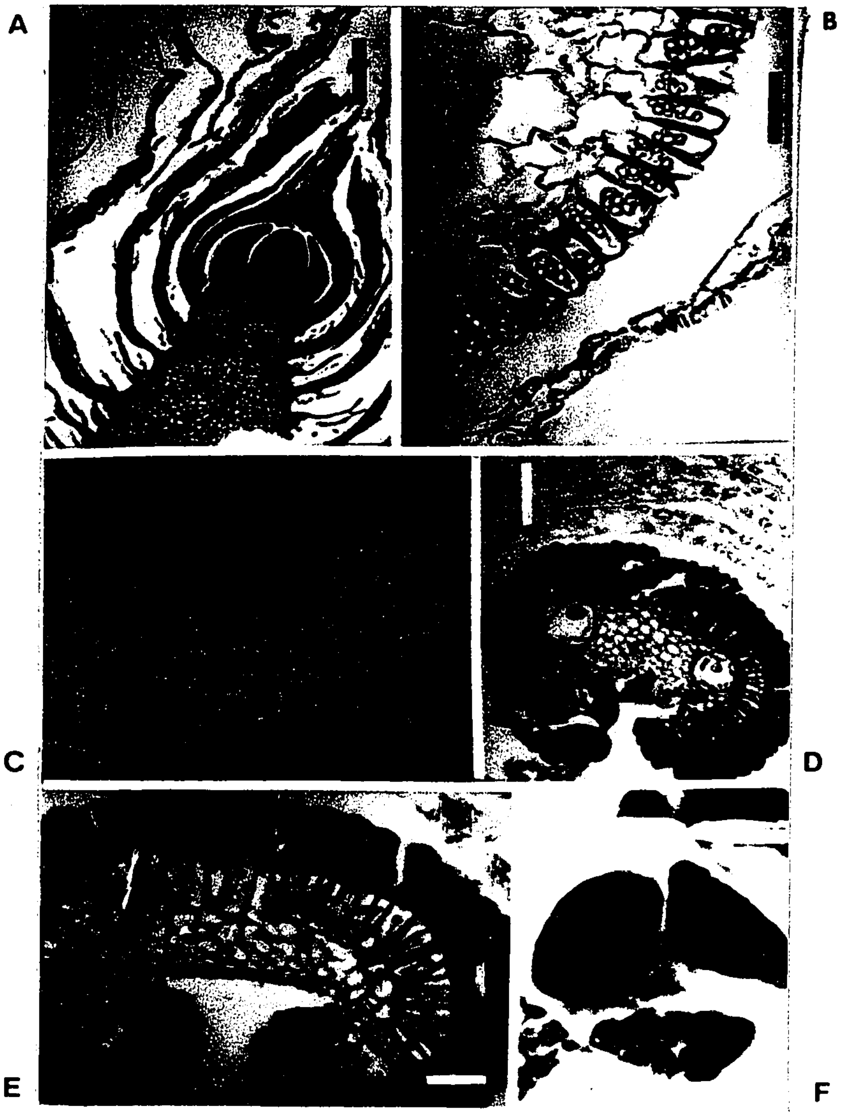
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Fig. 57: Rapatea longipes (Colella, 1774) flower detail: a) young spikelet (20 um); b) cross section of pistil showing future abscision zones (20 um).

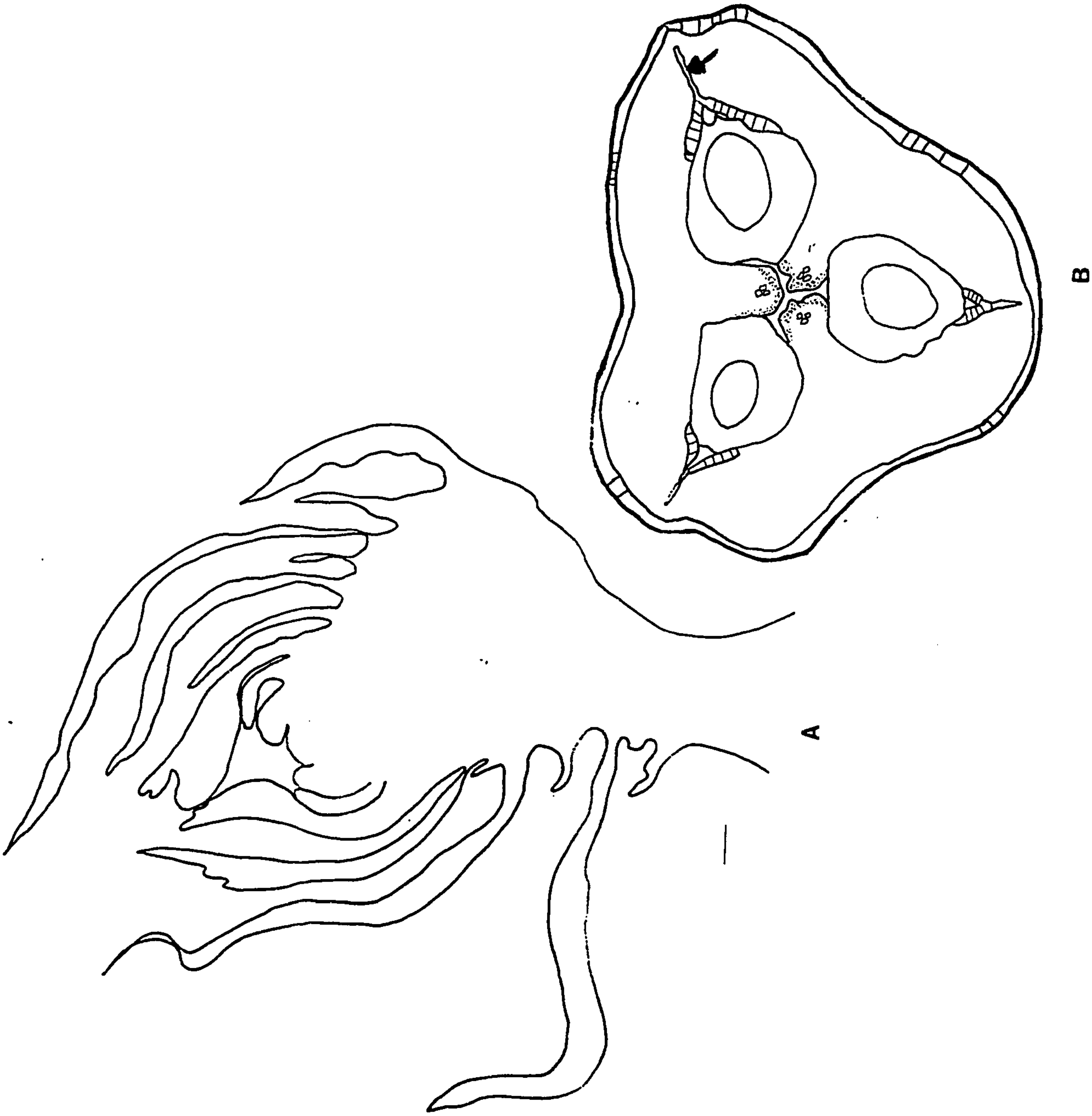
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Fig. 58: Rapatea longipes (Colella, 1774) flower: a) ovules with outer integument removed (5 um); b) detail of stigma (30 um); c)mature ovules (5um); d) mature ovule showing micropyle (200x).

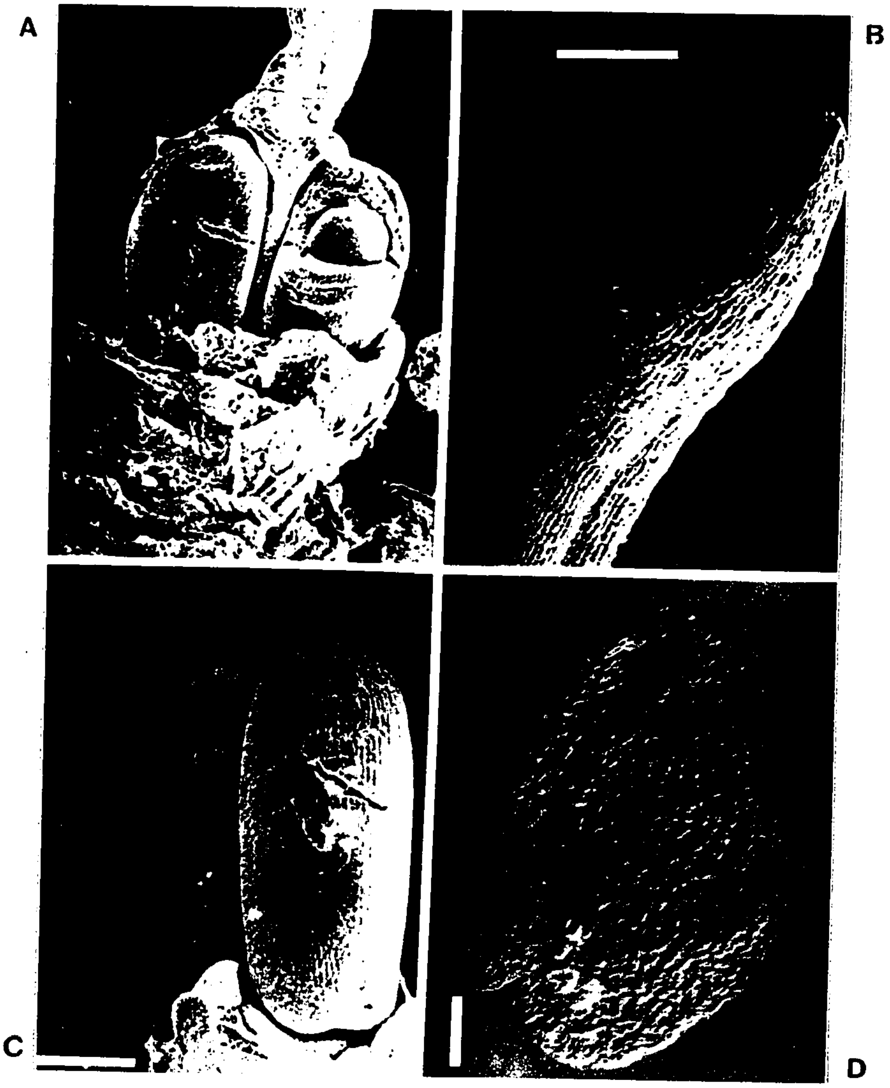
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Fig. 59: Rapatea longipes (Colella, 1774) ovules and pistil: a) young ovule showing two integuments (100x); b) archesporial and nucellus (400x); d) detail of megaspore (100x); d) style opening (100x).

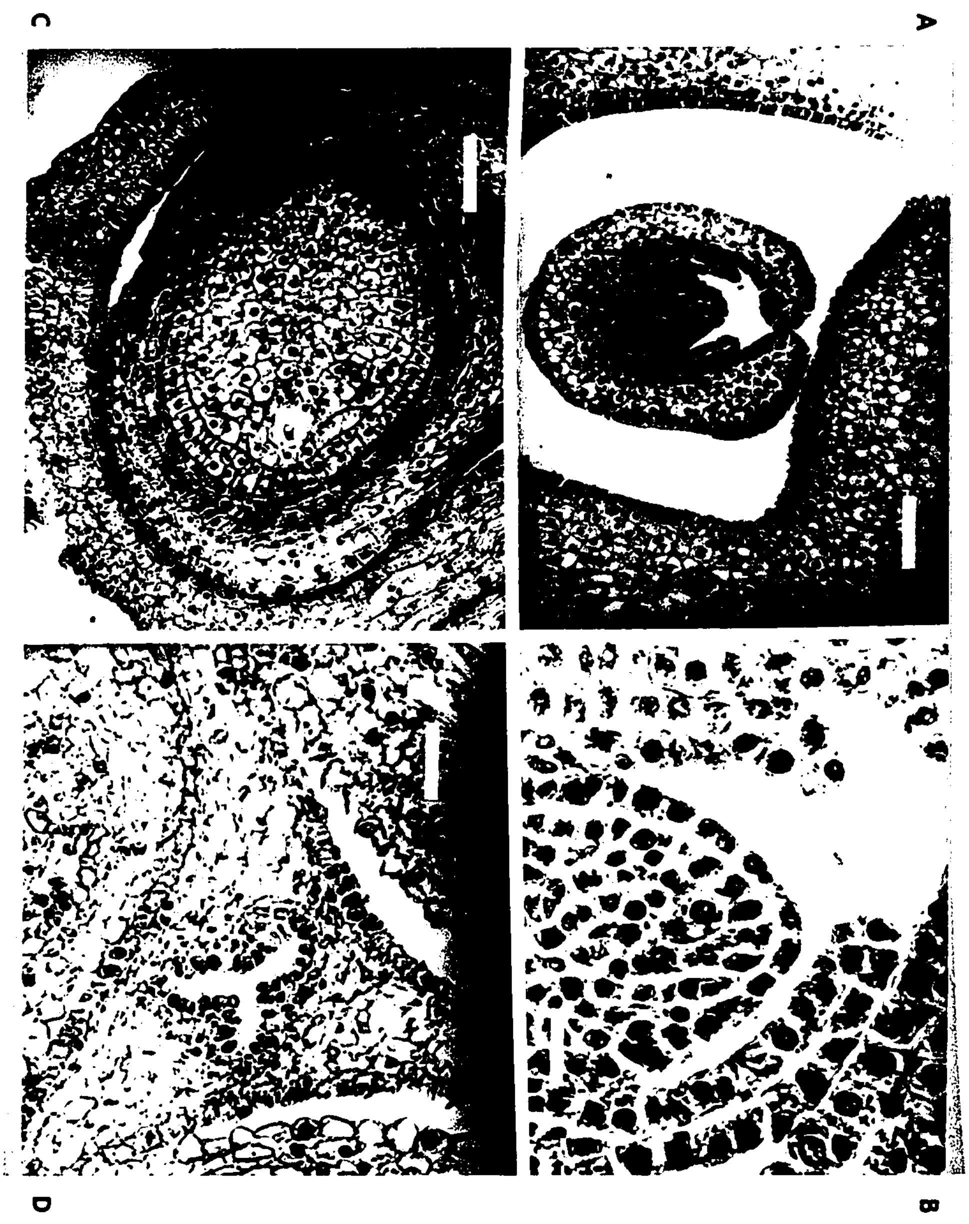
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Fig. 60: Rapatea longipes (Colella, 1774) ovule, anther and pollen: a) young ovule showing archesporial and parietal tissue (3,3 um); b)mature ovule showing degenerating synergids (2 um); c) young pollen in unicellular stage (1,8 um); d) bicellular pollen grain (7 um); e) anther epidermis (400x).

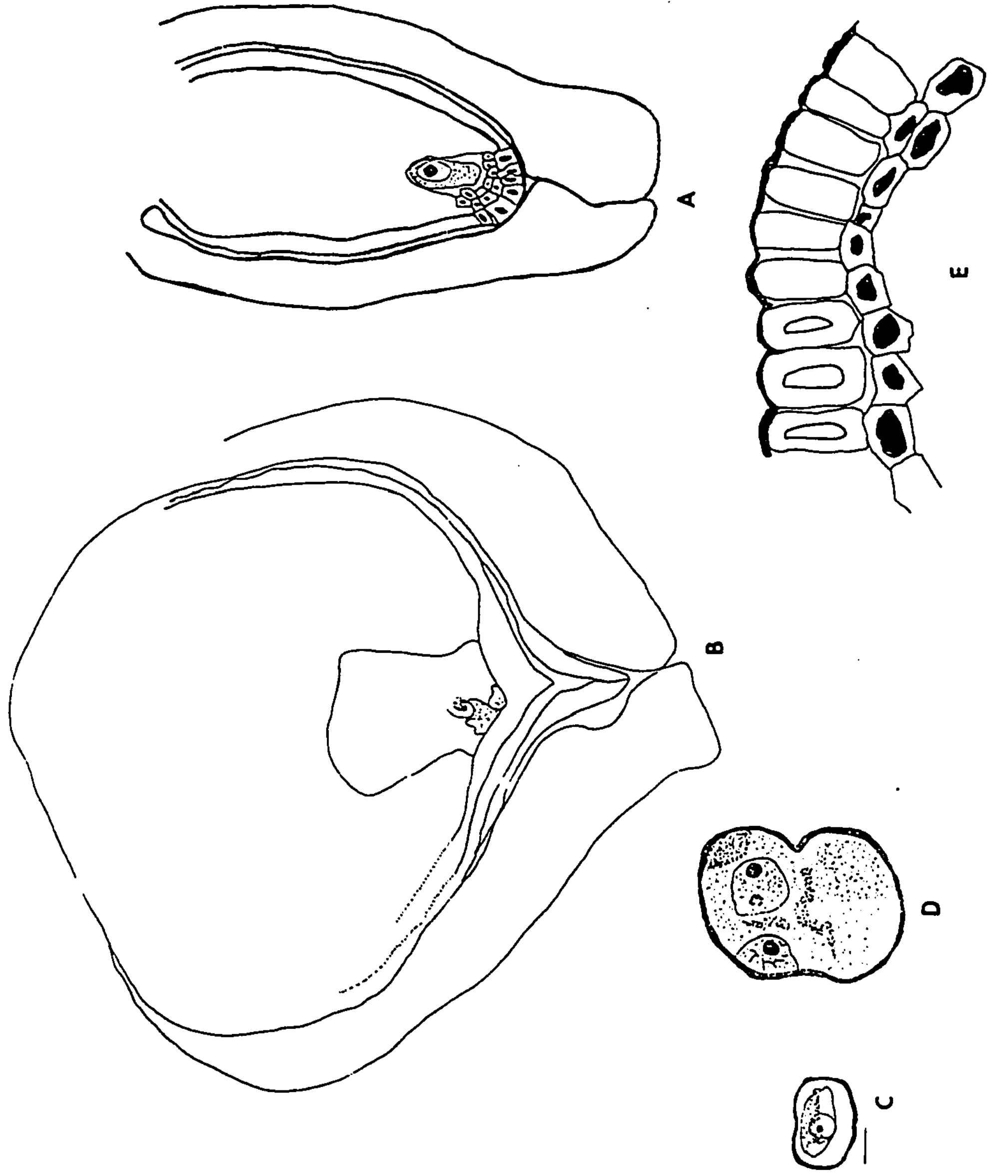
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Fig. 61: Rapatea longipes (M. Colella, 1774) anther morphology: a) young anther dorsal view (5um); b) young anther ventral view;c) mature pore and appendage (10 um).


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Fig. 62: Duckea flava (Colella et al 2068); a) young ovule (bar=3um); b) anther wall detail; c) degenerating megaspores; d) megaspore mother cell; e and f eight-celled; g) mature embryo sac; h) cross section of the ovary; i) outer integument formation; j) mature anther showing endothecial thickenings; k) young anther development.

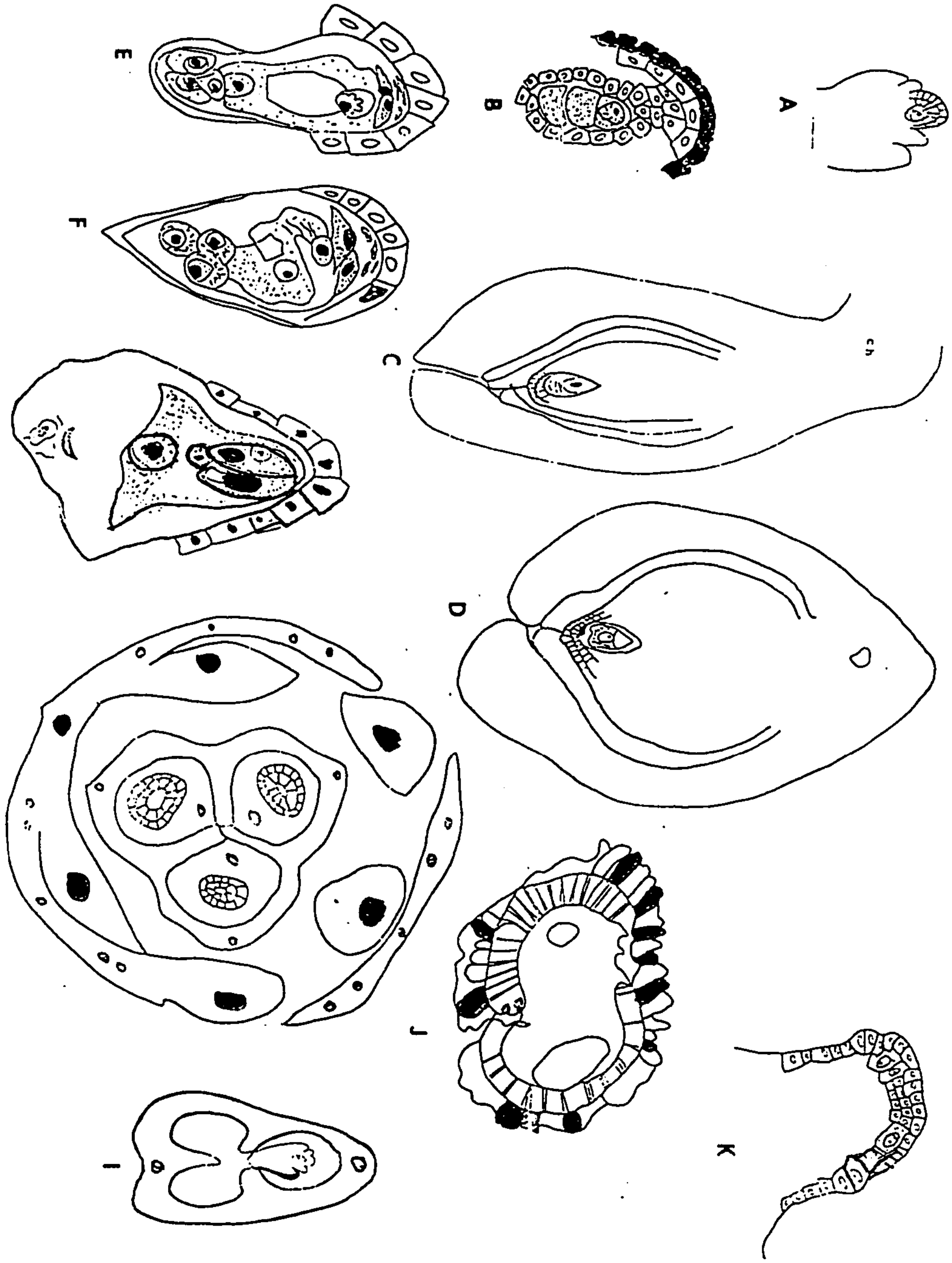
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Fig. 63: Duckea flava (Colella et al 2068); a) young flower (perianth removed); b) detail of spikelet and outer sepals and inner sepals; c) cross section of young spikelet showing stamens inception; d) cross section of young spikelet showing the sepals and the bracts, bar=1cm.

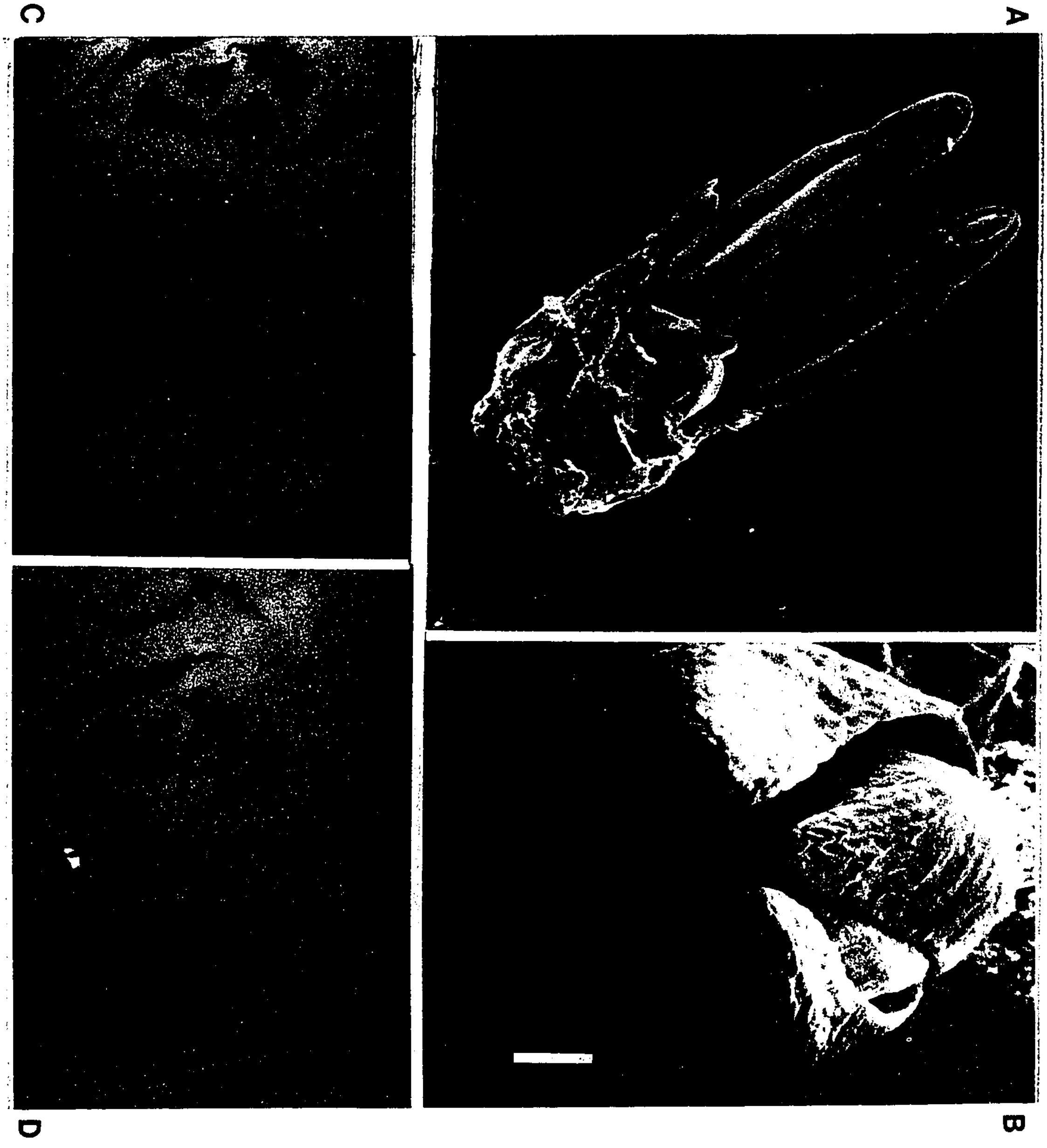
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Fig. 64: Duckea flava (Colella et al 2068) stigma and ovary detail: a) Stigmatic opening bar= 5 um); c) style and stigma (bar= 25 um).

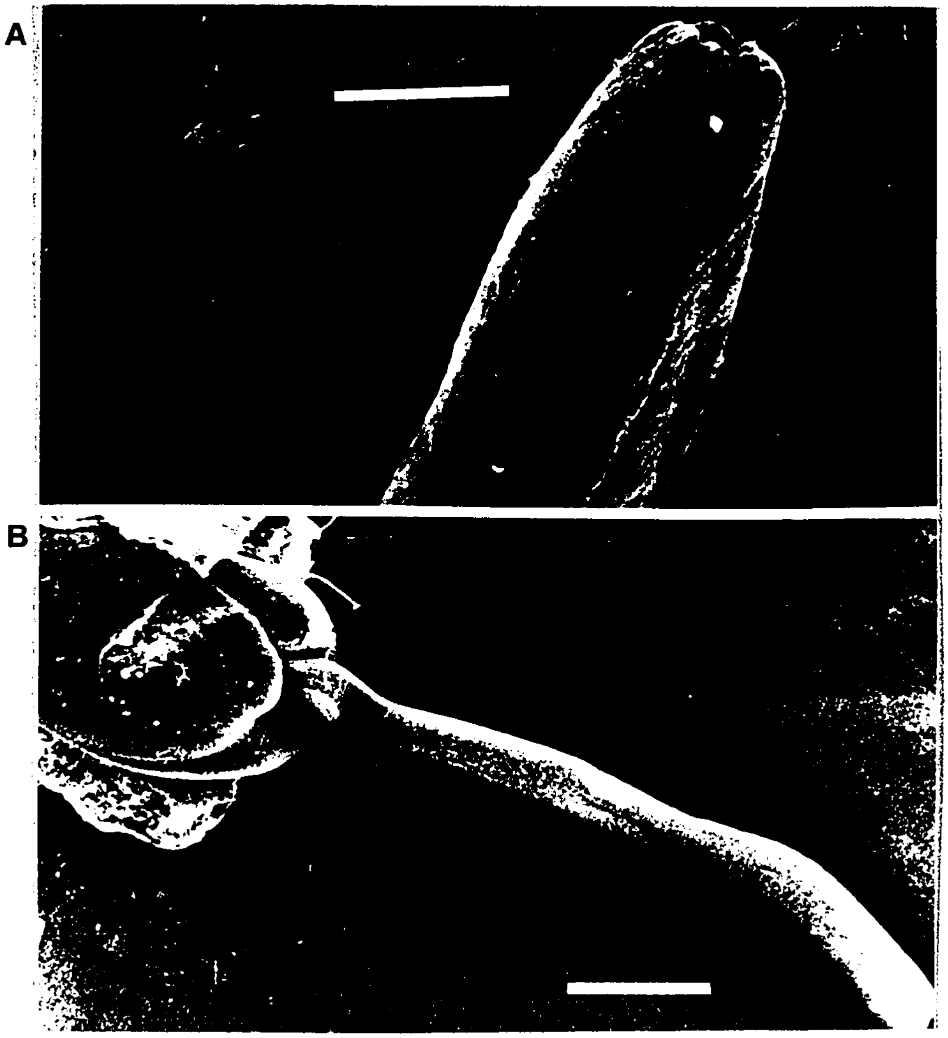
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Fig. 65: Duckea flava (Colella et al, 2068); ovule and embryo sac development: a) young ovule (100x); b) ovule showing two integuments (100x); c) degenerating megaspore (200x); d) mature embryo sac (200x)

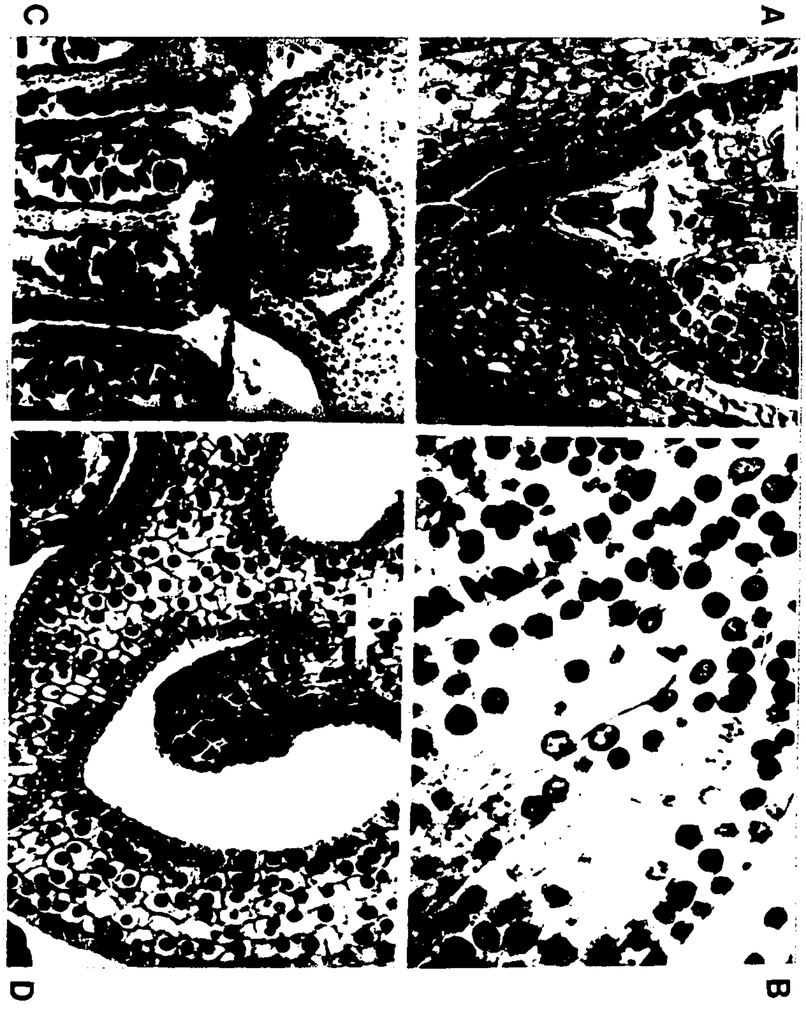
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Fig. 66: Duckea flava (Colella et al, 2068); anther development: a) young anther lateral view; b) ventral view (bar= 5 um); c) detail of the anther pore (bar 10 um); d) mature anther showing pore; e) dorsal view of young anther.

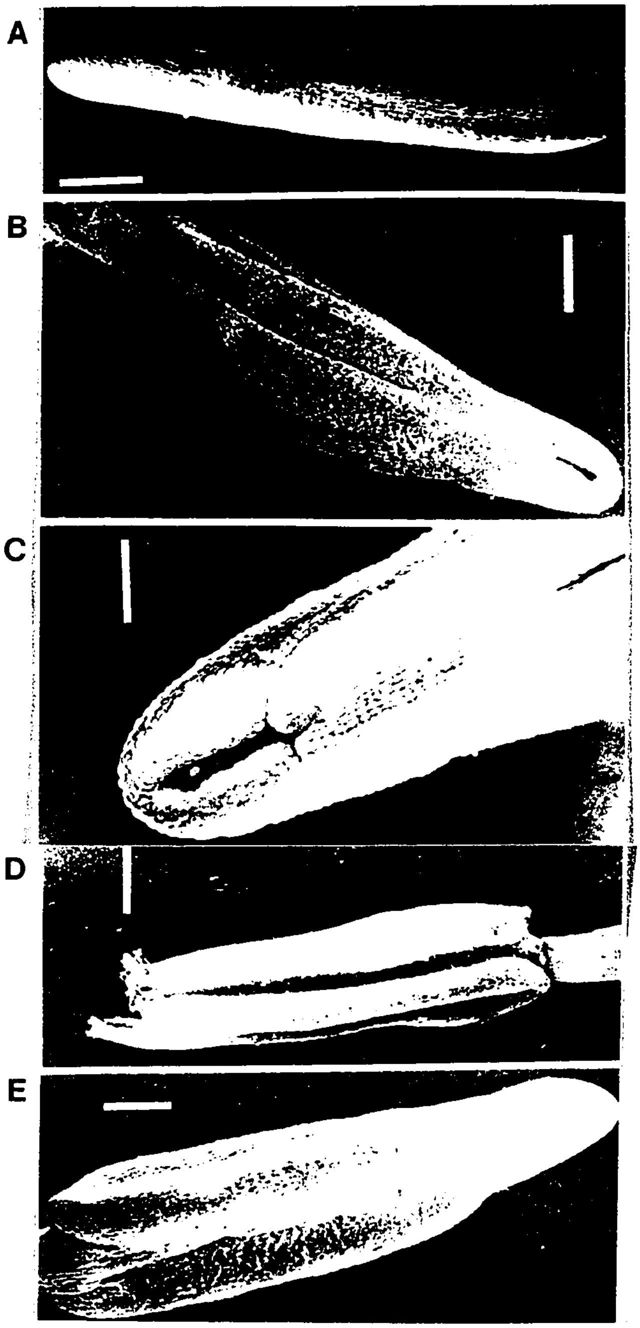
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Fig. 67: Monotrema aemulans (Colella et Morales, 1276);embryo sac development: a) young megaspore (bar= 20 um); b) degenerating megaspore (bar= 40 um); c,d,e,f megasporegenis of a monosporic embryo sac (bar= 30 um).

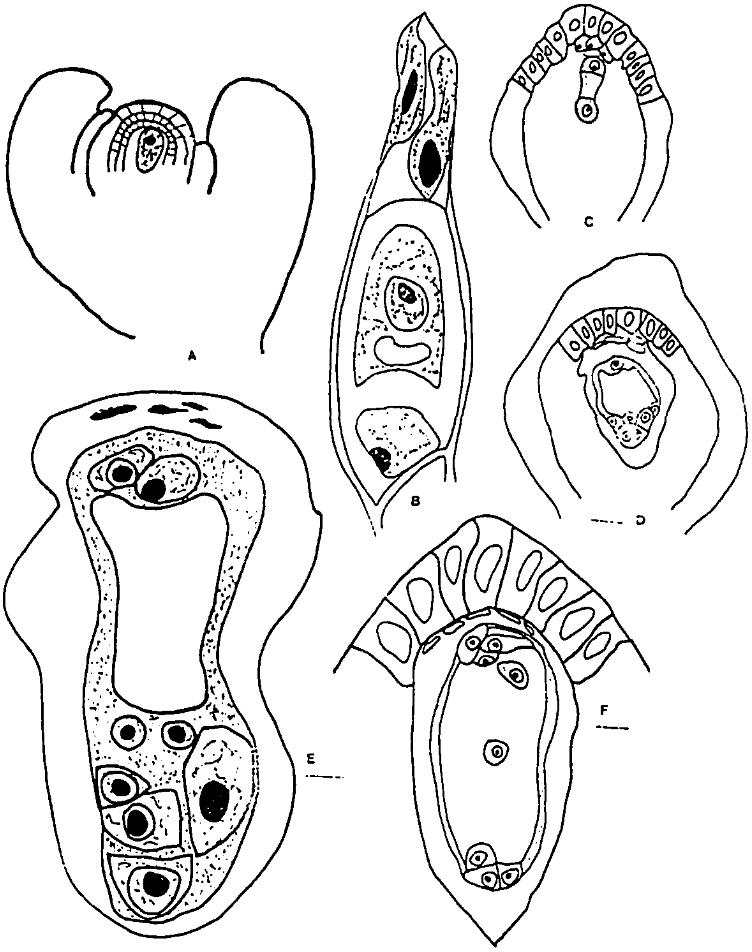
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Fig. 68: Anther development of Monotrema aemulans (Colella et Morales, 1276): a and b, parietal layer and sporocytes (bar= 0.7 um); c) young tetrads (bar=3.3 um); d) mature anther (bar= 20 um).

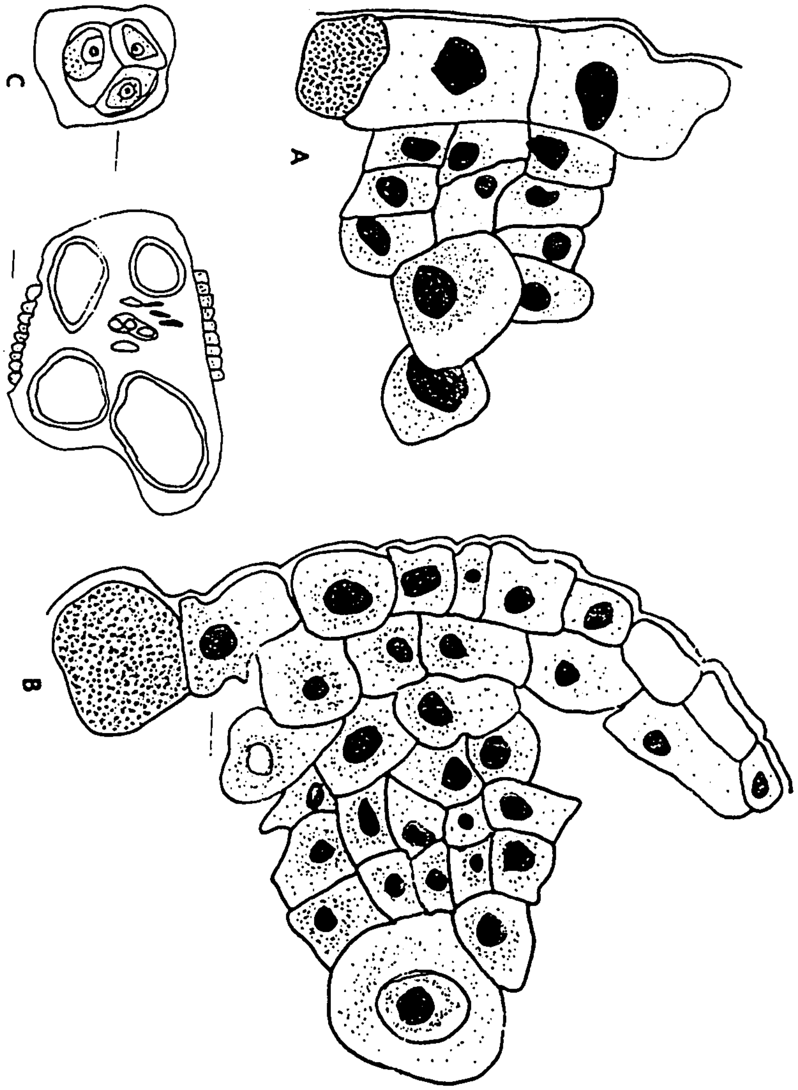
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Fig. 69: Anther morphology of Monotrema aemulans (Colella et Morales, 1276); a) pollen mother cells (200x); b) young microsporangia (100x); c) mature microsporangia; d) mature anther detail (100x)

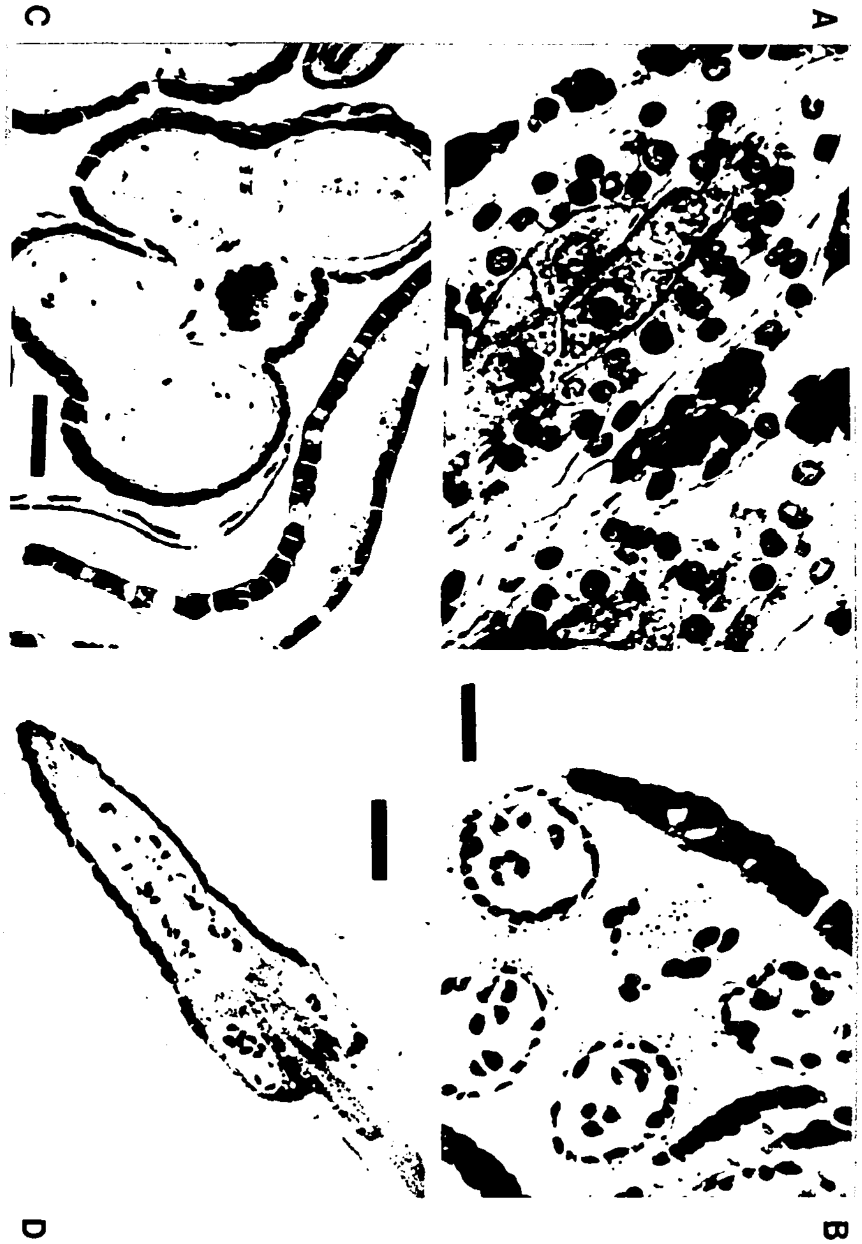
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Fig. 70: Seed coat and embryo of Monotrema aemulans (Colella et Morales, 1276; a) endosperm (100x); b) immature embryo (200x); c) detail of exotesta and "U" cells (200x); c) endotesta (200x).


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II) Results on the Floral Morphology and Reproductive Biology of Thurniaceae

The flowers of the genus Thurnia, are hermaphroditic, and about 1 cm long when mature. The perianth consists of two series of three distinct tepals (Fig. 71c). The inner and outer tepals are sepaloid, and they have brown spots. The outer and inner series of the six stamens develop in the same way as the tepals, (Fig. 71) and they are opposite to them. The ovary is a compound pistil with three locules, placentation is basal, and usually there are one or few ovules per locule (Fig. 72b).

The anthers and the style show the typical adaptation to wind pollination: thin, long, and motile filaments with a papillose stigma surface. The anthers are tetrasporangiate (Fig. 73d), dithecal, and opening by lateral silts. Endothecial thickenings are of the helical type. The pollen is dispersed in tetrads (Fig. 15a), and their proximal faces (Fig. 15c) unite the grains. The sculpturing pattern of the exine is scabrate-verrucate, the monads opening is monoporate. The floral and pollen morphology of Thurniaceae resembles that of the Juncaceous genera Luzula and Juncus.

For this study a spirit material of the two species of Thurniaceae that occur in the Venezuelan Hylaea: Thurnia polycephala and Thurnia spaerocephala was examined. Unfortunately only very young stages or young seeds were available so previous unanswered embrylogical questions such as embryo sac formation, tapetum type and endosperm formation remain unknown. However we were able to analyze some embryological processes not described before such as anther wall formation, nucella type, integuments number and origin, micropyle formation, endothecial thickenings and seed anatomy.

The ovule

The ovules are anatropous and bitegmic. The ovule primordia is visible when the anthers have not fully differentiated (Fig. 72a). The ovule shows the initial curvature when the pollen mother cells are visible (Figs. 72b). The primary parietal cell divides in two giving raises to a parietal cell and an archesporial cell, this is in accordance with the crassinucellate type. The initiation of the two integuments is dermal (Figs. 72c, d). When mature, the outer and inner integuments consist of four layers each one. An hypostase is visible. A young embryo of about 10-12 cells is shown in Fig. 74a, b. The undeveloped embryo is located near the chalazal side, surrounded by endosperm cells filled with starch and tannin globules. The embryogeny could not be determined.

Anther wall development

The young anthers show differentiation into four lobes (Fig. 73d). A continuous meristematic process gives raise to several anther layers. Thus, the primary parietal layer divides periclinally and produces a secondary parietal layer (Fig. 73c). Periclinal divisions in this layer will give rise to the endothecium, middle layer and tapetum (Fig. 73d). This pattern is in accordance with the Monocotyledoneous type of anther wall development. The tapetum is probably secretory but more stages are needed. Ubisch bodies are visible after the second meiotic division in the young pollen grain.

Seed morphology

The seeds are lanceolate but wider towards its center, tegmic and albuminous. Oftentimes, the testa bears many prickles or hooks that sometimes are filled with tannins (Figs. 75a, c). The seed shows two types of appendages, the micropylar (which is the smaller), and the chalazal one. The ontogeny of the micropylar appendage is related with radial elongation of the cells of the outer integument, whereas the chalazal appendage has probably a double origin. One side is an outgrow of the chalazal end, and the in other side some raphal tissue contributes to its lateral growth (Figs. 73a, b). The seed morphology resembles that of the Juncaceous genera Luzula and Juncus.

The chalazal appendage is referred as an elaiosome (seed appendage related with ant dispersal) in some Juncaceae but no oil bodies or secretory tissue in the chalazal appendage of the Thurniaceae was observed. Seed dispersal by ants is probably unlikely. More morphological and cytological evidence for the seed appendages is needed before any homology between Juncaceae and Thurniaceae seeds can be established.

Seed anatomy

Both integuments compose the seed coat the outer integument develops some sclerenchyma tissue. Several prickles or appendages filled with tannin are also common in the exotest. The mesotest and endotest consists of colorless schlerenchyma cells. The tegmen consists of two layers but the size, shape, and content varies. The outer layer of the inner integument has cells filled with tannins. The inner layer of the inner integument shows a continuous cuticle and its cells are radially elongated (Fig. 75).

The endosperm has small cells filled with starch. A remnant of the nucellus or perisperm, shows unequal thickness and encircles the endosperm (Figs. 75a, b). The most accepted definition of perispem is related with its physiology. This tissue is a

nutrient storage tissue that eventually will transfer nutrients (proteins, starch, oil) to the developing endosperm. In this study it was not possible to perform any cytochemical test in the perisperm.

A question arises in relation to seed dispersal: does fish, ants or water disperse the seeds? The seeds show anatomical adaptation (such as hooked appendages) to zoochory but the Thurniaceae are mostly aquatic plants, and in some cases hairs are related with hydrochory but only if the hairs are filled with air. Some of the Thurniaceous seeds are colorless and they maybe filled with air. In Figs. 76, and 77 the seed appendages of the seed and the spines are shown.

Less importance to autochory is given because the mechanism by which the capsule opens does not seem to be strong enough to separate the seeds from the fruit, and to expel them. More field observations will help to elucidate the seed dispersal mechanisms.

Fig. 71: Inflorescence and flower detail of Thurnia sphaerocephala (Colella et Morales, 1250). a and b shows a detail of the outer tepals; c and d show stamens inception and pistil; e) above pistil

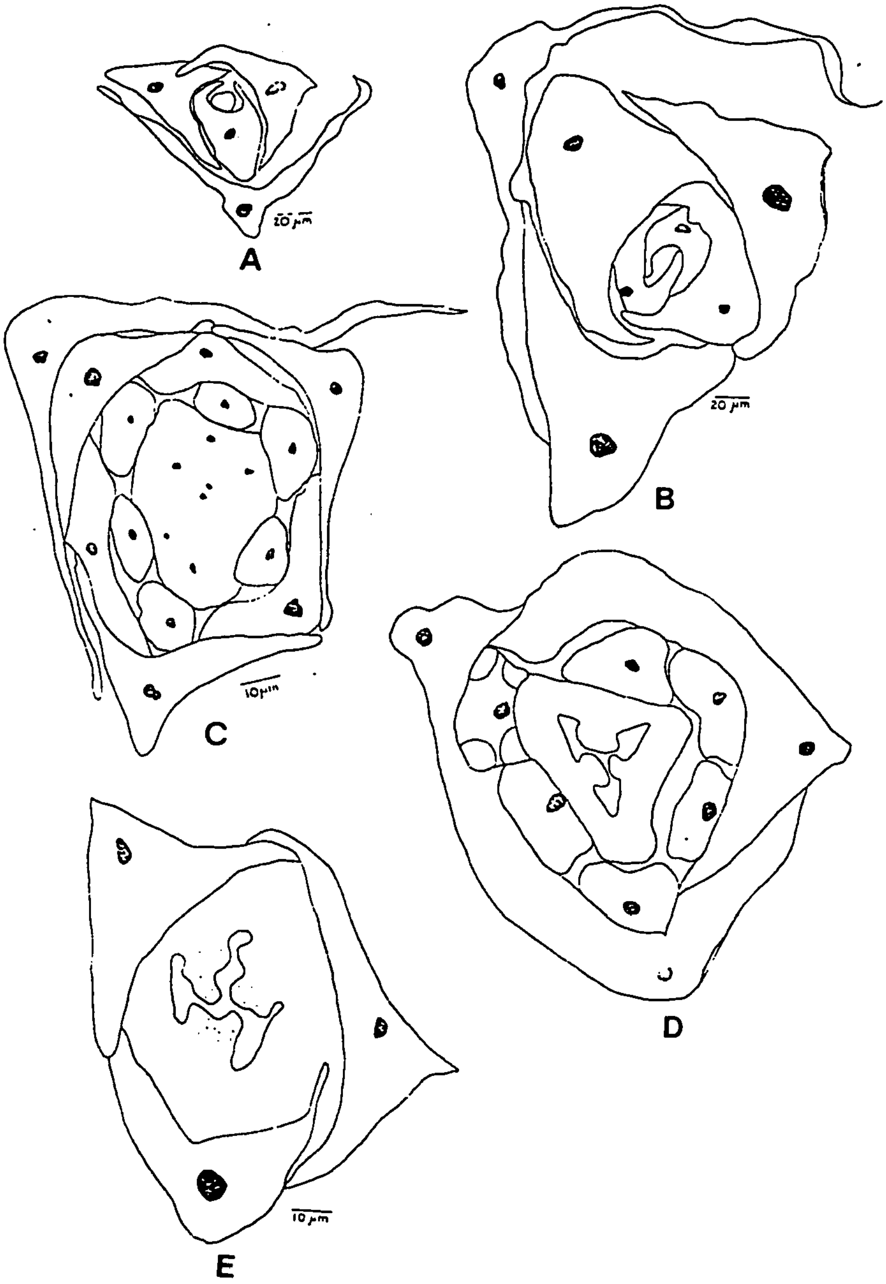
20 µm
A
20 µm
B
10 µm
C
D
10 µm
E

Fig. 72: Ovule morphology of Thurnia sphaerocephala (Colella et Morales, 1250); a) detail of megaspore (bar= 400x); b) detail of ovule showing integuments (bar=200x) c) detail of flower showing ovule (bar= 100x); d) young flower showing pistil (bar=100x).


A
B
C
D

Fig. 73: Seed and anther development of Thurnia sphaerocephala (Colella et Morales, 1250); a) phase contrast of seeds showing appendages (100x); b) detail of seed vasculature (100x); c) detail of young anther (200x); d) detail of pollen mother cells (400x).

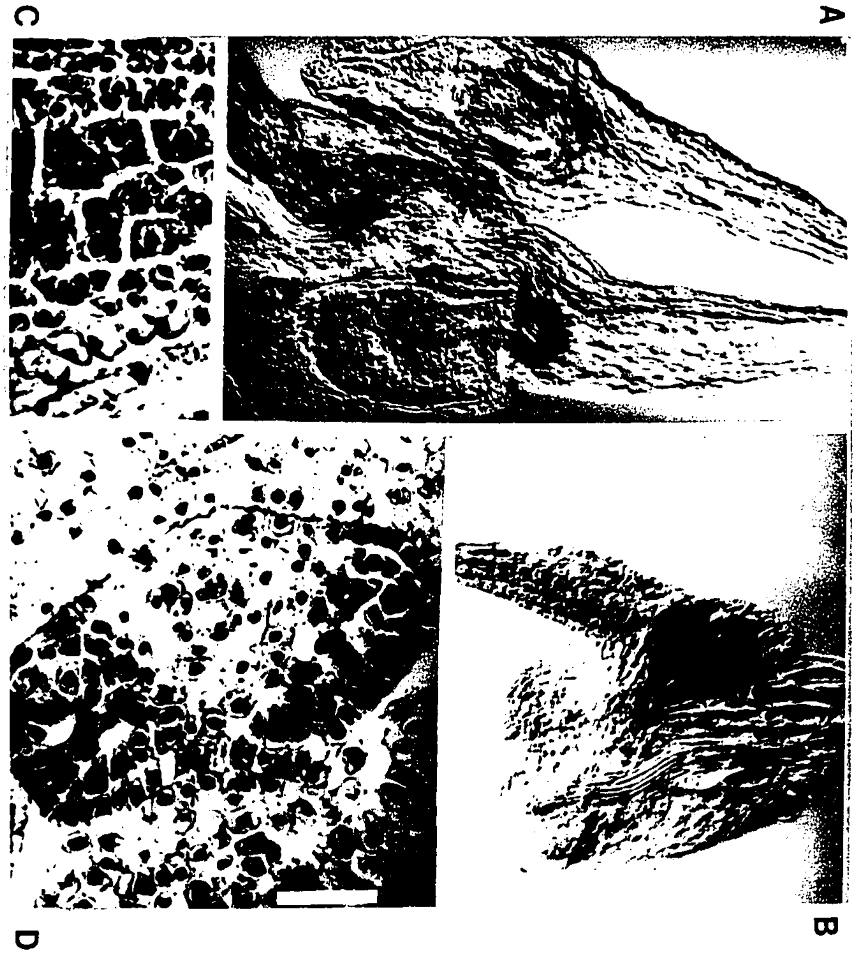
A
B
C
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Fig. 74: Embryo of Thurnia sphaerocephala (Colella et Morales, 1250); a) immature embryo on the micropylar end (100x); b) twelve-cell stage (bar=400x).

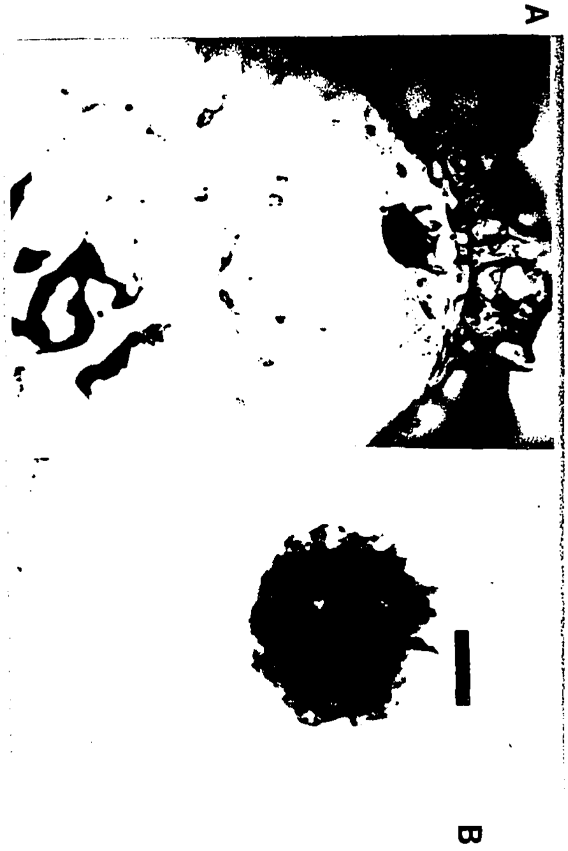

A
B

Fig. 75: Seed anatomy of Thurnia sphaerocephala (Colella et Morales, 1250); a) perisperm and chalazal appendages; b) endosperm; c) testa and tegmen; d) globular tannins and prickles; e) micropyle appendage, bar= 400x.

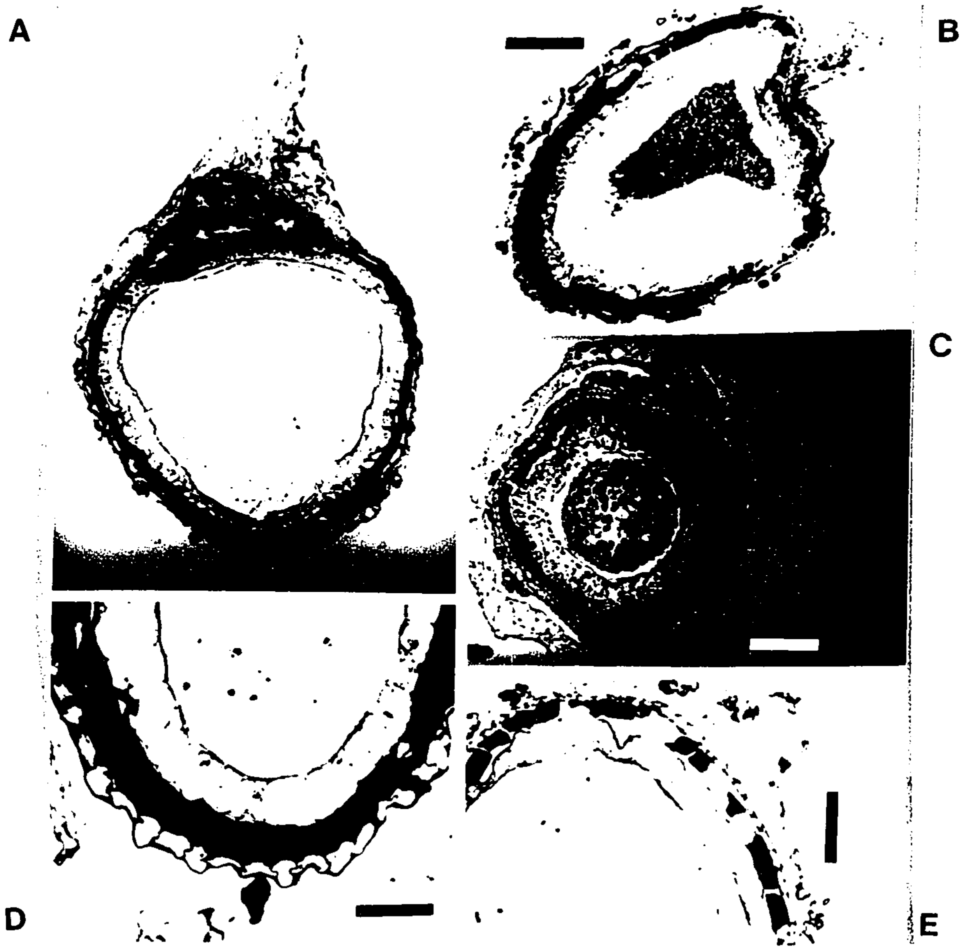
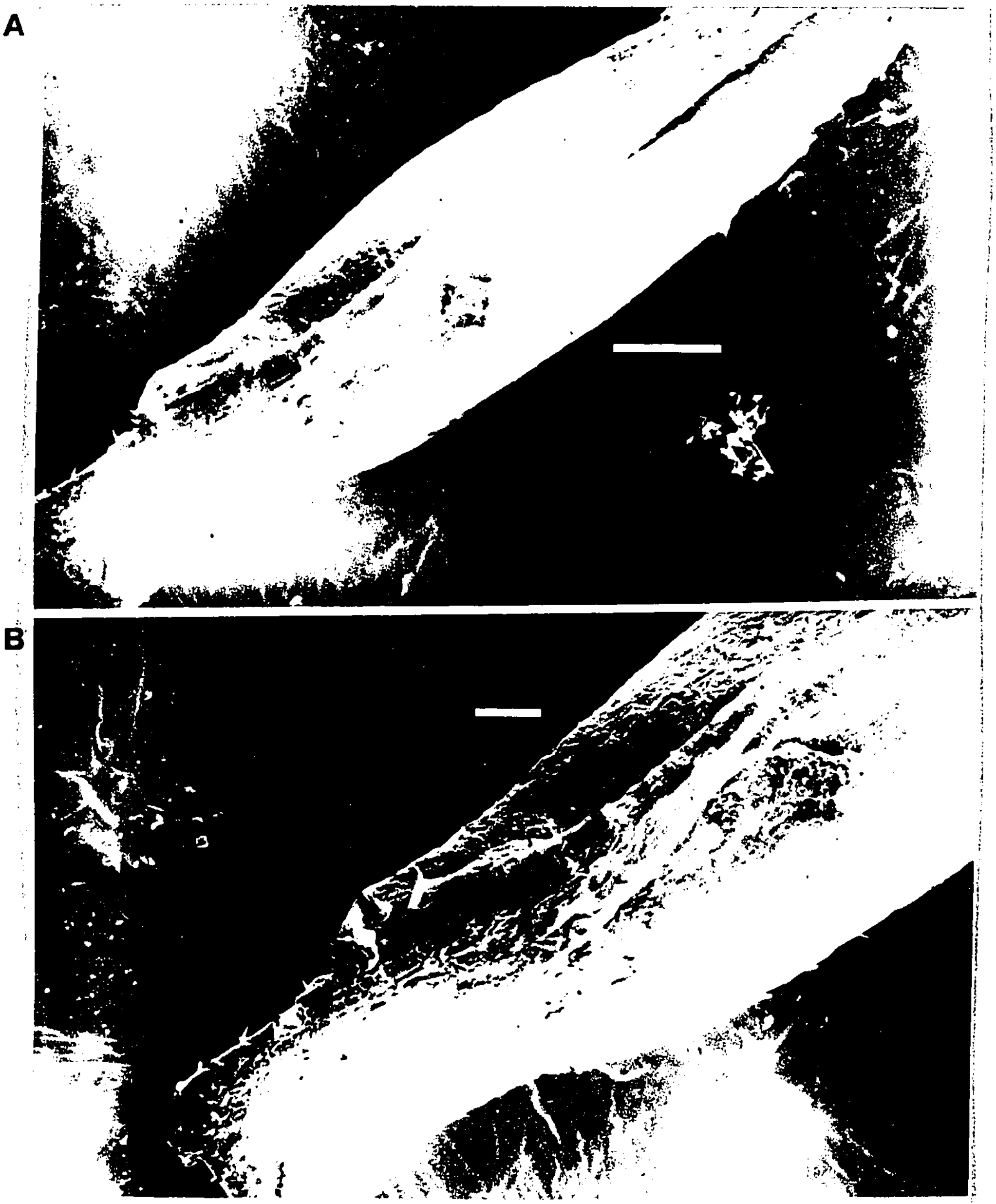

A
B
C
D
E

Fig. 76: SEM of the seed of Thurnia sphaerocephala (Colella et Morales, 1250) detail of the prickles, bar= 250 um.

Fig. 77: Seeds of Thurnia polycephala (Colella et Morales, 1250); a) micropilar and chalazal appendage, bar= 250um; b) detail of chalazal appendage and prickles, bar= 78 um.


A
B

Chapter 6

Cladistic Analysis

There is often a gap between theoreticians who discuss the nature of species and taxonomists working on a given group of organisms. Relationships considering homology among taxa at different levels have been elucidated to a certain extent with the aid of molecular and morphological analysis of their phylogenies. A parsimony criterion, such as the minimum number of character state changes along the branches of a cladistics tree, might be used for choosing the ancestral state at each node for each character. The presence of primitive or plesiomorphic characters is recorded, and the recent evolutionary novelties are referred as synapomorphies. An outgroup analysis gives insight into the relationships that may exist between the characters present in the taxa that are under scrutiny, and the assumed less evolved outgroup.

Stevenson and Laconte (1995) published a cladistic analysis of the monocots, and suggested that the family Commelinaceae is the sister group of the Rapateaceae. I used the same hypothesis in this study and analyzed a total of 63 characters from the five following families: Commelinaceae, Eriocaulaceae, Abolbodaceae, Rapateaceae and the genera Mayaca and Xyris (Xyridaceae sensu lato). The consensus tree of the phylogenetic analysis of the Rapateaceae was obtained based on the 63 characters previously mentioned (Tables 9 and 10). The Consistency Index CI=63, and the Retention Index RI=76. These data were analyzed using the softwares MacClade 3.01 (Madison & Madison), and PAUP 3.1.1 (Swofford, 1993) for MacIntosh.

Character Analysis

We were testing the hypothesis that the Commelinaceae are the outgroup of Rapateaceae, that the Rapateaceae are a monophyletic group, and that the classical Xyridaceae can be split into two different families: the Abolbodaceae with the genera Abolboda, Orectanthe, Aratitiyopea and Achlyphila, and Xyridaceae sensu stricto with Mayaca and Xyris as the only genera of that family. We also tested the proposed classification done by Maguire (1958) in which he mentioned that the Rapateaceae could be divided into two subfamilies Saxofridericioideae and

Rapateoideae, and four tribes Saxofridericieae, Schoenocephalieae, Rapateeae, and Monotremeae.

We studied the following families and genera of the Commelinales (Dahlgren et. al, 1988): Commelinaceae, Eriocaulaceae, and Rapateaceae. We analyzed the Abolbodaceae as a separated family from the Xyridaceae, and within the Xyridaceae we included the genera Xyris and Mayaca. The first column of Table 10 lists all the families and genera studied with detail in the present analysis, the following columns include character type and number. Table 9 shows the polarity of each of the characters discussed in Table 10.

The purpose of a character analysis is manifold. Character analysis does help to establish the selection of characters that are relevant in a phylogenetic study; it implies the definition of the character states, and the assessment of the homology of these characters and character states. It also helps to establish the assessment of the polarity of character states based on outgroup analysis. We will discuss each of the 63 characters and their states considered by the author to be important in understanding the relationships of the family Rapateaceae within the order Commelinales. The same analysis was also used to solve intrafamilial relationships.

Characters

Character 1 refers to the position of the lateral roots in relation to the xylem or phloem poles; they can be opposite to the xylem, opposite to the phloem. In our present analysis, state 0 is when they are opposite to the xylem poles a condition found in the outgroup Commelinaceae and in Rapateaceae. They are opposite to the phloem poles in Eriocaulaceae, Abolbodaceae, Mayaca, and Xyris.

Character 2 refers to plant phyllotaxis or leaf arrangement. This character has two character states, ranked and spiral; the family Commelinaceae shows both conditions; in Rapateaceae the genera Saxofridericia, Potarophyton, and Rapatea share this features with the Commelinaceae, the remaining Rapateaceous genera coded for spiral phyllotaxis. The same spiral phyllotaxis is present in Eriocaulaceae, Abolbodaceae, Mayaca, and Xyris.

Character 3 refers to leaf type, and it has been coded as simple (petiole and/or blade), ensiform (sword like), and terete (cylindrical). This character and its states seem to be complex and to repeat in some families. Thus, the leaves of Commelinaceae are always simple, in Eriocaulaceae they are either simple or terete. The leaves in Mayaca are simple. In Xyris they are always ensiform, as in the majority of the Rapateaceae. Abolbodaceae shares with Commelinaceae the simple leaves. The genera Shoenocephalium and Duckea have species with either ensiform or terete leaves.

Character 4 refers to the way the leaves fold in the buds and has been coded as adplicate, supervolute and conduplicate. The young leaves of Commelinaceae can be supervolute or conduplicate; the young leaves in Rapateaceae and Xyris are all conduplicate, sharing this character with some Commelinaceae. The leaves of Eriocaulaceae, Mayaca and some Abolbodaceae are adplicate; the remaining Abolbodaceae are conduplicate.

Character 5 refers to whether the leaves are differentiated into blade and sheath. This character has two states, differentiated or undifferentiated. Undifferentiated plants do not show sheaths. All Rapateaceae, Commelinaceae and Xyris have leaves that are differentiated whereas

Eriocaulaceae, Mayaca and Abolbodaceae have leaves that are undifferentiated.

Character 6 refers to the presence or absence of a leaf petiole. It is absent in Eriocaulaceae, Abolbodaceae, Mayaca and Xyris. Both conditions are present in some Commelinaceae and few Rapateaceae.

Character 7 refers to the morphology of the sheath that can be closed, partially open, or open. The Commelinaceae have close sheaths. The remaining families have open sheaths; however Duckea and Schoenocephalium in the Rapateaceae have both open or partially open sheaths.

Character 8 refer to the absence or presence of pubescence; ***Character 9*** refers to the absence or presence of glandular hairs. The hairs are present and glandular in all families, with the exception of the Abolbodaceae.

Character 10 refers to the absence or presence of hairs weather they are glandular or not on the leaf axils. They are absent in Commelinaceae and Abolbodaceae. They are present in the remaining families.

Character 11 refers to the absence of epicuticular waxes or to the presence of a particular pattern of epicuticular waxy depositions on the leaves known as ***Strelitzia***-type. The epicuticular waxes are absent in Commelinaceae, Eriocaulaceae, Abolbodaceae, Mayaca, Xyris. ***Strelitzia***-type waxes are present in Rapateaceae.

Character 12 refers to the absence or presence of air canals in the roots; when present the air canals can be randomly located, or of the septate type. They are absent in Commelinaceae and in some Eriocaulaceae. They are septate in some Eriocaulaceae and in Mayaca. They are randomly located in the entire Rapateaceae and in some Eriocaulaceae. The Eriocaulaceae shows all the character states; this appears to be an adaptation to all the various habitats they occupy.

Character 13 refers to the absence or presence of auricles, an outgrowth of the sheath, located on both sides of the apical area. The auricles are absent in all families with the exception of Stegolepis, Phelpsiella, and Amphiphyllum of the Rapateaceae.

Character 14 refers to the absence or presence of silica bodies. They are present in Commelinaceae and Rapateaceae. They are absent in the remaining families.

Character 15 refers to the aestivation or pre-formation of the young flower petals in the flower bud. This can be imbricate or valvate. The Commelinaceae have flowers that have either one state or the other;

Rapateaceaous flowers are all imbricate. The remaining families have flowers that are all valvate when young.

Character 16 refers to the patterns of anther dehiscence. This is a complex character with four states: the opening can be longitudinal, through one pore, or through two pores or through four pores. The opening of the anthers of the Commelinaceae is longitudinal or by means of one pore. Eriocaulaceaous anthers open longitudinally; the same is true in Xyris and Abolbodaceae. The anthers of Mayaca dehisce by one pore. Variations on the poricidal dehiscence type are common in Rapateaceae; thus, Guacamaya, Kunhardtia, Epydros and Phelsiella anthers dehisce by means of two pores, whereas Schoenocephalium anthers have four pores; the remaining genera have only one pore.

Character 17 refers to anther dehiscence orientation or to where in the anther the pollen is directed. This orientation has four states: introse, extrose, latrose and poricidal. The anthers in Commelinaceae present all four states, whereas in Eriocaulaceae they are always introse. Mayaca shares with Rapateaceae the poricidal condition. The anthers of Xyris and Abolbodaceae are latrose.

Character 18 refers to anther attachment, which can be basifixed and dorsifixed. The anthers of Rapateaceae, Mayaca and Xyris are all basifixed. The families Commelinaceae and Eriocaulaceae have anthers with either attachment; the anthers in Abolbodaceae are dorsifixed.

Character 19 refers to the absence or presence of anther appendages, which are anther outgrowths that may have different origins. They are absent in Commelinaceae, Eriocaulaceae, Abolbodaceae Xyris, and Mayaca. The anthers in Rapateaceae may or may not have anther appendages, however the presence of anther appendages is more common in the subfamily Rapateoideae; data for Windsorina is unknown.

Character 20 refers to the type of anther wall, this is related to the patterns of development of the different anther wall layers during anther ontogeny. Two types are discussed here: the monocot type, and the basic type. The anther wall development of all Rapateaceae studied is of the basic type, however four genera remain unknown. The anther wall formation in the remaining families is of the monocot type.

Character 21 refers to the type of microsporogenesis or the pattern of formation of the microspores which gives rise to the pollen. It can be successive or simultaneous. Microsporogenesis is simultaneous in most of the Rapateaceae, however in four genera this process is still unknown. Microsporogenesis in the remaining families is successive.

Character 22 refers to the number of nuclei in the tapetal cells, which can be uninucleate or binucleate. The tapetal cells of Commelinaceae and Mayaca, are uninucleate. The tapetal cells in the family Eriocaulaceae and in the genus Xyris have either conditions. In all the Rapateaceae studied within the past 15 years by Venturelli and Bouman(1988), and Tieman (1985) the tapetal cells are always binucleate. In the genus Abolboda, the tapetal cells are always binucleate.

Character 23 refers to the endothecial thickenings commonly present in the outermost layers of the anther wall. They can be spiral, girdle-like or absent. They are of the spiral type in all the Rapateaceae studied. They are girdle-like in Commelinaceae, Eriocaulaceae, and Abolbodaceae. They are absent in Mayaca and Xyris. This is one among many other important synapomorphies that give support to the hypothesis of the placement of Mayaca and Xyris together in one family.

Character 24 refers to the absence or presence of the exothecium, a layer of thickened anther walls located below the epidermis. It is present only in

Xyris and Mayaca, the remaining families do not have exothecium. This is another important synapormophy between Mayaca and Xyris.

Character 25 refers to the pollen apertures in the pollen grains. It has four states: sulcate, inaperturate, spiraperturate and trichotomosulcate.

The majority of the Rapateaceae are monosulcate, zonisulcate, with the exception of Schoenocephalium whose spores are sometimes trichotomosulcate. The spores of Commelinaceae, Mayaca and Xyris are also monosulcate. The spores of the Abolbodaceae are inaperturate, and the pollen aperture in Eriocaulaceae is spiraperturate, a very uncommon type in monocots.

Character 26 refers to the patterns of pollen sculpturing in the outermost layer of the pollen grain. This is a complex character with six states: reticulate, echinate, psilate, scabrate, striate, and foveolate. The spores in the Commelinaceae have most of the states, with the exception of the echinate sculpturing which is only present in Eriocaulaceae and Abolbodaceae. The sculpturing in the spores of the Rapateaceae, Mayaca and Xyris is reticulate.

Character 27 refers to the presence of a hypostase, a thickened tissue present in the chalazal side of the ovule. It can be present or absent. It is present in Rapateaceae, Commelinaceae, Abolbodaceae, Mayaca, and Xyris; it is absent in Eriocaulaceae.

Character 28 refers to the presence of pseudanthia or complex flower aggregations. They are absent in Commelinaceae, Mayaca, Xyris, Mashalocephalus and Windsorina. They are present in Eriocaulaceae, Abolbodaceae and the remaining genera of the Rapateaceae.

Character 29 refers to the behavior of the antipodals, the gametophytic cells located at the chalazal side. They can be ephemeral or persistent. The antipodals are ephemeral in all the families with the exception of the Commelinaceae where they can be both ephemeral and persistent.

Character 30 refers to the proliferation of the antipodals at the chalazal end. This is to say that successive mitosis takes place on these cells. The proliferation can be either absent or present. They proliferate up to a higher number (up to 40) in two genera only of the Rapateaceae already studied; these are Potarophyton and Mashalocephalus. The antipodals of the remaining families and genera do not proliferate as much.

Character 31 refers to absence or presence of gynoecial nectaries. They are only present in three genera of the Rapateaceae: Schoenocephalium, Kunhardtia and Guacamaya, which are located below the gynoecium. This synapormophy is share only by these three members of the tribe Shoenocephalieae.

Character 32 refers to the ovule types, they can be anatropous, campylotropous-amphitropous and orthotropous. The Commelinaceae present all the states, with the higher diversity of ovule types in the entire order. The ovules of the Eriocaulaceae, Mayaca, and Xyris are all orthotropous. The ovules of the Rapateaceae and Abolbodaceae are anatropous in the genera already studied.

Character 33 refers to the presence of tannins in the ovules. Tannins are only present in Cartonema spicatum of the Commelinaceae and in some genera of the Rapateaceae such as: Guacamaya, Kunhardtia, Schoenocephalium, Stegolepis, Amphiphyllum, Potarophyton, Monotrema, Spathanthus, and Cephalostemon. They are absent in the remaining families and genera.

Character 34 refers to the type of nucellus, which can be crassinucellate with few cells or with many cells, or it can be tenuinucellate. The nucellus of the Commelinaceae is crassinucellate but with few cells, whereas in the Rapateaceae studied the nucellus is crassinucellate with many cells. The nucellus in Eriocaulaceae, Mayaca, and Xyris is tenuinucellate.

Character 35 refers to the number of ovules per locule; the states are several or one ovule per locule. There is a notable reduction in the number of ovules per locule -one ovule per locule- in the subfamily Rapateoideae of the Rapateaceae. The remaining taxa have several ovules per locule.

Character 36 refers to absence or presence of arils of different origin in the ovule. They are only present in Duckea of the Rapateaceae.

Character 37 refers to the shape of the seeds; this character has several states: prismatic, ellipsoidal, pyramidal and sub-pyramidal. The shape of the seeds shows interesting differences in Rapateaceae. Maguire (1958) used this character as an important criterion for separating the two subfamilies of the Rapateaceae. The seeds are prismatic in Guacamaya, Amphiphyllum and Stegolepis; they are sub-pyramidal in Kunhardtia, Epydros, Phelpsiella and Schoenocephalium; they are pyramidal in Saxofridericia; they are mostly ellipsoidal in the entire Rapateoideae. The seed shape of the remaining taxa is ellipsoidal.

Character 38 refers to the absence or presence of seed appendages in the seeds. These outgrowths can have more than one origin. The family Abolbodaceae and the subfamily Rapateoideae have members whose seeds may be appendiculate or not. The seeds of the remaining taxa do not have seed appendages.

Character 39 refers to the type or shape of the seed appendages when present. It has three stages: absent, applanate and mitriform. The Abolbodaceae has seeds without appendages or when present they are applanate as in Orectanthe. They are applanate in the Rapateoideae, with the exception of Cephalostemon whose seed appendage is mitriform. The remaining taxa do not have seeds with appendages.

Character 40 refers to the absence or presence of striate seeds, a particular pattern or sculpturing on the seed coat. Seeds of the Commelinaceae and Rapateaceae have either both conditions. Eriocaulaceae, Xyris and Abolbodaceae have striate seeds; the seeds of Mayaca are not striate.

Character 41 refers to the presence or absence of peduncular bracts. They are always present in Eriocaulaceae and Rapateaceae. Both conditions are present in Abolbodaceae. The peduncular bracts are absent in the remaining taxa.

Character 42 refers to the absence or presence of spathaceous bracts. They are always present in Commelinaceae and Rapateaceae, this character can be interpreted as a plesiomorphy between these two families, as the

Commelinaceae are the out-group of the entire Commelinales. The spathaceous bracts are absent in the remaining taxa.

Character 43 refers to the absence or presence of oil in the endosperm of the seed. It is absent in Mayaca and in Commelinaceae. It is present in Eriocaulaceae, Xyris and Abolbodaceae. Oil in the endosperm of the Rapateaceae has been reported only in three Monotremeae genera: Monotrema, Mashalocephalus, and Potarophyton. The oil is absent from the endosperm of the seeds of the remaining genera.

Character 44 refers to the placentation type. It has four states: axile, parietal, basal, and apical. The placentation in the Commelinaceae and Abolbodaceae is axile, as in many genera of Rapateaceae, however the placentation in Rapatea, Maschalocephalus, and Potarophyton is basal. The placentation in Eriocaulaceae is basal. The placentation in Mayaca and Xyris is parietal.

Character 45 refers to the absence, presence and partially presence of cleistogamous flowers. The flowers of Mayaca are partially cleistogamous, whereas Guacamaya and Schoenocephalium flowers are cleistogamous. The flowers of the remaining taxa open regularly during anthesis.

Character 46 refers to the type of pollinators; it has three states: insects, birds, none. Commelinaceae, Mayaca, Xyris, are pollinated by insects. Insects and birds are the pollinators of the flowers of Abolbodaceae; the same pollination syndrome occurs in Rapateaceae, which are mostly entomophilous, with the exception of the bird-pollinated Kunhardtia.

Character 47 refers to the absence or presence of "buzz pollination", more common in flowers with poricidal anthers. It is present in Mayaca, and in all Rapateaceae. It is absent in the remaining taxa.

Character 48 refers to the absence or presence of the embryostega, a seed lid that can be derived from the outer or inner integument. It is derived from the outer integument in Commelinaceae. It is derived from the inner integument in Xyris, Mayaca and Abolbodaceae. It is absent in Eriocaulaceae and Rapateaceae.

Character 49 refers to the type of inflorescences; it has four states: solitary flowers, cymose, head and spike. The Commelinaceae have cymose inflorescences. The Eriocaulaceae have heads. The aquatic Mayaca has solitary flowers, and Abolbodaceae, and Xyris have spikes. The inflorescences of the majority of Rapateaceae are heads, with the exception of the genera Windsorina, Stegolepis and Mashalocephalus.

Character 50 refers to the type of stigma, which can be simple, trilobed or separate. It is simple in Commelinaceae, Mayaca and Rapateaceae. It is separated in Eriocaulaceae and Xyris. It is trilobed in Abolbodaceae.

Character 51 refers to the absence or presence of persistent epidermis in the nucellus. It is persistent in Commelinaceae, Eriocaulaceae, and Rapateaceae. The persistent epidermis is absent in Mayaca and Xyris; both conditions are present in the Abolbodaceae.

Character 52 refers to the absence or presence and number of inflorescences units; it has four states: very reduced, 3-5, 5-7, and many inflorescence units. The Commelinaceae have flowers with units ranging from 3-5, 5-7 and many units per inflorescence. Eriocaulaceae, Mayaca, Xyris and Abolbodaceae have inflorescences with very reduced units. In Rapateaceae the character is quite variable as in Commelinaceae, some genera have flowers with 5-7 units, reduced or many. It is interesting to notice that the flowers of the genus Stegolepis of the Rapateaceae show all the states of this character.

Character 53 refers to the absence or presence of connation in the petals. They are only connate in some Rapateaceae; the remaining taxa have free petals.

Character 54 refers to the absence and presence of the inflorescence peduncle; when present it can be terminal or lateral. It is terminal in Commelinaceae, Abolbodaceae and in the Schoenocephalieae, Guacamaya, Kunhardtia, and Schoenocephalium of the Rapateaceae. It is absent in Mayaca, and it is lateral in Xyris and the remaining genera of the Rapateaceae.

Character 55 refers to the number of anther locules, it has two states: two locules per anther, or four locules per anther. Two-locular anthers occur only in Epydros and Phelpsiella of the Rapateaceae. The remaining taxa are tetrasporangiate.

Character 56 refers to the absence or presence of migratory tapetal cells. There are migratory tapetal cells in Guacamaya, Kunhardtia, Schoenocephalium and Monotrema of the Rapateaceae. The tapetal cells of the remaining taxa do not migrate inside the anther locule.

Character 57 refers to the degree of fusion of the filaments, and they can be free or adnate. The filaments are free in Commelinaceae, Mayaca, and Abolbodaceae. They are fused in Eriocaulaceae and Xyris. Both states are present in Rapateaceae, where the adnate condition is more prevalent in the subfamily Saxofridericioideae.

Character 58 refers to the topological pattern of the endothecium, it can be absent, in the entire anther, or in the upper half. It is absent in Mayaca and Xyris. It is located in the entire locule in Commelinaceae, Eriocaulaceae and Abolbodaceae. It is located in the upper half of the anther in the subfamily Rapateoideae, and it is located in the entire anther locule in the subfamily Saxofridericioideae.

Character 59 refers to the thickening subtype of the endothecium. It can be reticulate, annular, helical and girdle. The Commelinaceae, Eriocaulaceae, and Abolbodaceae have endothecial thickenings of the girdle type. It does not apply to Mayaca and Xyris as they do not have endothecium. Guacamaya, Kunhardtia and Schoenocephalium have thickenings of the annular type; the remaining genera have reticular or helical thickenings.

Character 60 refers to the shape of the spikelet. It can be non-reflexed, weakly reflexed, and strongly reflexed. It does not apply to Commelinaceae and Mayaca as they do not have spikelets. They are reflexed in Guacamaya and Schoenocephalium, they are weakly reflexed in Kunhardtia, Stegolepis and Saxofridericia. They are non-reflexed in the remaining taxa.

Character 61 refers to the type of capsule, which can be either non-explosive or explosive. They are non-explosive in the majority of the taxa, with the exception of the Abolbodaceae, where the two characters are present in the fruits.

Character 62 refers to the absence or presence of stigmatic hairs. They are present in all Saxofridericioideae. They are absent in the remaining taxa.

Character 63 refers to the type of spikelet pedicel, which can be ovate or lanceolate. It is lanceolate in the Monotremeae genera Potarophyton, Monotrema and Maschalocephalus; it is ovate in the remaining genera. This character does not apply to those taxa with regular non-spicate flowers such as Commelinaceae, Eriocaulaceae, Mayaca, Xyris and Abolbodaceae.

Discussion

The family Rapateaceae are a monophyletic group, (Fig. 78, node M) defined by a series of synapomorphies that are unequivocally present here. The phylogenetic analysis of the distribution of these unique characters also has helped in resolving familial and sub-familial relationships in the in-group. Based upon the cladistic analysis we will discuss those characters that set the Rapateaceae apart as a separate family from the remaining Commelinales families; we will analyzed those other characters that the Rapateaceae share with the remaining Commelinales. Later on we will discuss the phylogenetic relationships, and placement of the Commelinaceae, Eriocaulaceae, Abolbodaceae, Rapateaceae, Mayaca and Xyris in Fig. 78. The overall tree was rooted at the Commelinaceae based on assumptions of polarity characters.

We will discuss the most important synapomorphies found only in Rapateaceae. These synapormophies are found among the vegetative, embryological, inflorescence, and floral characters.

Vegetative characters: The Rapateaceae have leaves that are in the majority of the cases ensiform and, less often, terete such as in Shoenocephalium and Duckea (character # 3). What makes this character unique for Rapateaceae is the combination of having leaves either ensiform or terete. These characters are present in the Commelinales, and Eriocaulaceae shows terete or simple leaves whereas Xyris leaves are always ensiform. However, no other family has both characteristics. The

Rapateaceae have sheaths than can be open and partially open (character # 7); epicuticular waxes are of the ***Strelitzia***-type (character # 11). The sheaths have auricles (character # 13).

Floral characters: The petals in Rapateaceae are connate or free (character # 53), the aestivation of the flowers is always imbricate whereas in the remaining families the aestivation is always valvate (character # 15). The filaments can be free or fused to the corolla tube (character # 57). The pattern of anther dehiscence is quite complex; it can be poricidal by means of one, two, or four pores (character # 16); the anthers of Commelinaceae and Mayaca have only one pore. The anthers of Rapateaceae may be appendiculate or not (character # 19). The pollination syndromes can be entomophylous (the most common one), ornithophylous, and anemophylous (character # 46). The ornitophylous syndrome is an autoapomorphy of the Schoenocephalieae. Cleistogamous flowers are also an autoapomorphy of the subfamily Saxofridericioideae, tribe Schoenocephalieae. Stigmatic hairs are only present in the Saxofridericioideae (character # 62).

Embryological characters: In Rapateaceae, microsporogenesis is simultaneous (character # 21), and the tapetal cells are always binucleate (character # 22); the tapetal cells are of the migratory type in Shoenocephalieae; endothecial thickenings are of the spiral type in all Rapats (character # 23). Anther wall formation is of the Basic type. The pollen can be monosulcate, dizonate or trichotomosulcate as in Shoenocephalium (character # 25). The antipodals proliferate up to 40 only in Rapateaceae (character # 30). Gynoecial nectaries were always thought to be absent in Commelinales, however this is the first report on the presence of gynoecial nectaries (character # 31) in the tribe Schoenocephalieae. The nucellus of the ovule in Rapateaceae is crasinucellate with many cells (character # 34) whereas the nucellus of the other crasinucellate type of ovules in the Commelinales has few cells. The ovary of Rapateaceae can have one to many ovules per locule (character # 35), and the seeds can be arilate as in Duckea (character # 36). The shape of the seeds can be ellipsoidal, pyramidal, sub-pyramidal and prismatic (character # 37). The seeds may have appendages of the mitriform or applanate type (character # 39). The placentation in Rapats can be axile or basal (character # 44). The flowers in many

Schoenocephalieae are cleistogamous (character # 45) although some birds have visited these flowers (Berry pers. com.).

Inflorescences characters: The Rapateaceae have inflorescences that are heads of spikelets, and if reduced in size or number, can be monopodial or sympodial (character # 49); the number of inflorescence units goes from a very reduced number up to seven (character # 52). The inflorescence peduncle can be terminal or lateral (character # 54). The spikelets can be reflexed or weakly reflexed (character # 60). The spikelet pedicel can be ovate or lanceolate (character # 63).

Comparison among Subfamilies and Tribes of Rapateaceae

We found a distinctive number of synapomorphies in the subfamilies Saxofridericioideae and Rapateoideae of the Rapateaceae that supports Maguire's subdivision of the Rapateaceae into two subfamilies. Tribal and generic status requires further reassessment, as more data has being obtained, especially at the embryological, palynological and molecular level. From the cladogram (Fig. 78, node A) we can observe that, the subfamily Saxofridericioideae can be defined by the presence of ovaries with axile placentation and many ovules per locule; stigma ciliate, ovary with gynoecial nectaries; entomophylous, and ornitophylous pollination syndrome. The flowers may be cleistogamous; there are numerous inflorescence units, with monopodial inflorescences, that can have terminal or lateral peduncles. The pollen is mostly monosulcate, rarely trichotomosulcate. The filaments are adnate to the corolla tube; endothecium present in the upper part of the anther, endothecial thickenings of the helical type and seeds that are prismatic, pyramidal and sub-pyramidal.

Autoapomorphies present only in the tribe Schoenocephalieae (Fig. 78, node B) are: gynoecial nectaries in all the three genera, bird-pollinated flowers in Kunhardtia, and cleistogamous flowers in Schoenocephalium and Guacamaya. The pollen is monosulcate, however, it has being reported trichotomosulacate in Shoenocephalium. The inflorescences are terminal. Synapomorphies present in the tribe Saxofridericieae (Fig. 78, node C) are epiphytic habitat in Epydros, and few Stegolepis; leaves with spines in Saxofridericia, auricles present in Amphiphyllum, Phelpsiella and Stegolepis. Inflorescences that sometimes have very reduced units. The anthers may have two or four locules; anthers dehisce by means of one, two or four pores. A better picture of this tribe will be obtained when the embryological data of the genera Phelpsiella and Epydros, will be known. Embryological data for Amphyphillum is still incomplete.

Synapomorphies of the subfamily Rapateoideae (Fig. 78, node D) are ovaries with one ovule per locule, placentation that is mostly basal. And the antipodals proliferate. Anthers that may be appendiculate; the seeds are ellipsoidal-ovoid, and they can be appendiculate as in Cephalostemon or arilate as in Duckea. The pollen is monosulcate, and zonisulcate in Rapatea. The anthers can be free from the corolla tube; endothecium throughout the anther. The stigma is always punctiform; the inflorescences may have reduced heads, or in a few cases they are sympodial with a sessile peduncle in Mashalocephalus. The inflorescences peduncle is lateral. Oil in the endosperm. Embryological data for the genus Windsorina is unknown.

The synapomorphies share by the members of the tribe Rapateeae (Fig. 78, node D) is monosulcate or zonisulcate pollen as in Rapatea. Filaments adnate to the corolla tube as in Duckea. The inflorescences are heads, with numerous units; seeds with arils as in Duckea or with mitriform appendages as in Cephalostemon. The seeds are mostly striate, or smooth as in Spathanthus. The synapomorphies share by the tribe Monotremeae (Fig. 78, node E) are petals connate in many cases, or free as in Windsorina. Inflorescences units from many to reduced or sympodial as in Windsorina and Maschalocepahlus, spikelet pedicel lanceolate in Potarophytum, Windsorina and Maschalocephalus; proliferating antipodals in Potarophytum and Mashalocephalus.Oil in the endosperm. Inflorescence peduncle sessile in Mashalocephalus.

Relationships at the Generic Level

In conclusion, the genera belonging to the subfamily Saxofridericioideae, share enough number of characters to support this clade (Fig. 78, node A). However, members of the Schoenocephalieae have shown several autoapomorphies, not present in the remaining genera of the subfamily. The cladistic analysis obtained (Fig. 78) for the subfamily Saxofridericioideae, is in accordance to Maguire (1958), however missing embryological data in the genera *Epydros*, *Phelpsiella*, and partially in *Amphiphyllum* may account for the lack of a better resolution in the Saxofridericieae clade.

According to our results and previous publications (Steyermark, 1985) the genera *Cephalostemon* and *Duckea* should be placed together under the oldest genus, which is *Cephalostemon* Rob. Schomburgk, 1845. Maguire published the new genus *Duckea*, in 1958 as a combination of species belonging to different genera and families such as the genera *Cephalostemon*, *Monotrema* and *Rapatea* of he Rapateaceae, and to the genus *Dichromena* of the family Cyperaceae. Maguire in 1958 described *Duckea junciformis* as a new species belonging to the recently created *Duckea*. More intensive collections that provided a larger number of specimens were needed in order to realize the similarities of these two genera. Although they have similar floral structure, seed structure and sculpturing, and ovular morphology, variations always occur in the shape of the spikelets bracts; in *Cephalostemon* they are of the bristle type, whereas in *Duckea* they are lanceolate. The seeds of *Duckea* still need more studies. Kubitzki (1998) acknowledge some of the previous mentioned similarities and he placed the two genera under *Cephalostemon*.

The Monotremeae clade is well resolve, and although the embryological and morphological features of the four genera agree to a certain extent, there are some variations in pollination syndrome, and inflorescence and floral construction. Embryological and morphological data in Windsorina will help to give a better resolution to this clade. Evidence of proliferating antipodals was not found in Monotrema. The four genera have appendiculate seeds.

Comparison of Rapatecaeae with other Commelinales

The Rapateaceae share a number of plesiomorphic characters with the Commelinaceae (Fig. 78, node O), which gives support to the outgroup in the present analysis, these characters are: spiral or rank phyllotaxis, conduplicate ptyxis, leaf differentiated into petiole and blade, the petiole sometimes absent. Silica bodies present, however, they have been reported only in the genus Cartonema of the Commelinaceae. The anther dehiscence is poricidal; anther attachment is basifix, the anthers have four locules; the filaments are free from the corolla tube. Endothecium present thorough the anther. The pollen is sulcate, with reticulate exine. The placentation is sometimes axial; the pistil may have many ovules per locule, the ovules are anatropous, with tannins; the female gametophyte has ephemeral antipodals. The stigma is simple; non-pubescent; the seeds are ellipsoidal, and striate. The inflorescences are cymose, with spathaceous bracts, and with many or few inflorescence units per inflorescence. The inflorescence peduncle is terminal. The fruits are capsules of the non-explosive type.

The Rapateaceace share with the Eriocaulaceae (Fig. 78, node L) the following features: Spiral phyllotaxis, with leaf petiole that may be absent, with open leaf sheaths, with axilar hairs. The air canals in the roots are of the random type. The stigmatic hairs are absent. Placentation can be basal, and there are many ovules per locule; the antipodals are ephemeral. The endosperm has oil as a reserve substance. The petals are free from the corolla tube. The seeds can be ellipsoidal, and striate. The anther attachments can be basifix, the cells of the tapetum may be binucleate; The anthers are tetrasporangiate. The filaments are adnate to the corolla tube. The endothecium occupies the entire anther. The almost always-pedunculate inflorescences are terminal heads. The seeds are capsules of the non-explosive type.

The Rapateaceae share with the genus Mayaca (Fig. 78, node L2) a number of features such as: spiral phyllotaxis, whose leaves have no petiole; glandular hairs are also present in the leaf axils. The petals are connate; the stigma is simple. There are many ovules per locule, the ovules have an hypostase. The anthers are tetrasporangiate, with poricidal dehiscence by mean of one terminals pore; the pollen is reticulate, and monosulcate. The filaments are adnate to the corolla tube. The flowers are partially cleistogamous, and they exhibit "buzz pollination", The seeds are ellipsoidal. The fruits are capsules of the non-explosive type.

The Rapateaceae share with the genus Xyris (Fig. 78, node L2) the following features: Phyllotaxis of the spiral type, differentiated and ensiform leaves, with open leaf sheaths. Glandular hairs present, and located in the axils of the leaves. The air canals in the root are randomly distributed. The petals are connate. There are many ovules per locules; an hypostase is present. The anthers are tetrasporangiate. The pollen is monosulcate, and the tapetum is binucleate. The elliptical seeds are of the striate type. The endosperm has oil as reserve substance.

The Rapateaceae share with the family Abolbodaceae (Fig. 78, node L3) the following features: Spiral phyllotaxis, and conduplicate ptyxis. The leaf petiole is absent, and the leaf sheath is open. The air canals are randomly located in the roots. The petals are free, and the anthers are tetrasporangiate, with basifix attachment, the filaments may be free. The endothecium occupies the entire anther locule; the tapetum is binucleate. Stigmatic hairs are absent. The pistil has many ovules per locule, with axial placentation and anatropous ovules. An hypostase is present. The inflorescences are pseudanthial, with reduced inflorescence units; the floral peduncle carries peduncular bracts. The seeds are oftentimes striate, sometimes with applanate appendages. The endosperm has oil as a reserve substance. Birds pollinate the flowers; the fruit is a capsule of the non-explosive type. Embryological data for Orectanthe, Achlyphila and Aratitiyopea is missing; more detailed palynological studies are needed.

Affinities between Mayaca and Xyris

Excluded from the traditional Mayacaceae and Xyridaceae **sensu stricto**, the genera Mayaca and Xyris (Fig. 78, node L) share a number of synapormophies unequivocally present here, that can be used to give support to the hypothesis of a separate family. As it was mentioned earlier, the hypothesis is that the Xyridaceae could be split into Abolbodaceae and Xyridaceae **sensu lato,** with Mayaca and Xyris as its only genera. The following unequivocally embryological characters share by Mayaca and Xyris are orthotropous ovules, and parietal placentation. Absence of an endothecium, instead an exothecium takes its placed. There is also an embryostega or seed stopper, however this character is also present in Abolboda.

The remaining characters are share also by Mayaca and Xyris, but they may also be present in other Commelinales, including the outgroup. The lateral roots are opposite to the phloem poles, the phyllotaxis is spiral, and the leaves of both genera lack petiole. Pubescent is present, and of the glandular type; it can be located in the axils of the leaves. The aestivation of the flowers is valvate, and the petals are free; the pistil has many ovules per locule; the stigmatic hairs are absent. An hypostase is present. The anthers are tetrasporangiate, with dorsifixed attachments; the anther wall is of the monocot type, and microsporogenesis is successive. The pollen is monosulcate. The seeds are ellipsoidal. The number of flowers or inflorescence units is reduced or the flowers are single as in Mayaca. Seeds ellipsoidal, in capsules of the non-explosive type.

Fig. 78: Cladogram of Commelinales showing generic resolution in the Rapateaceae.

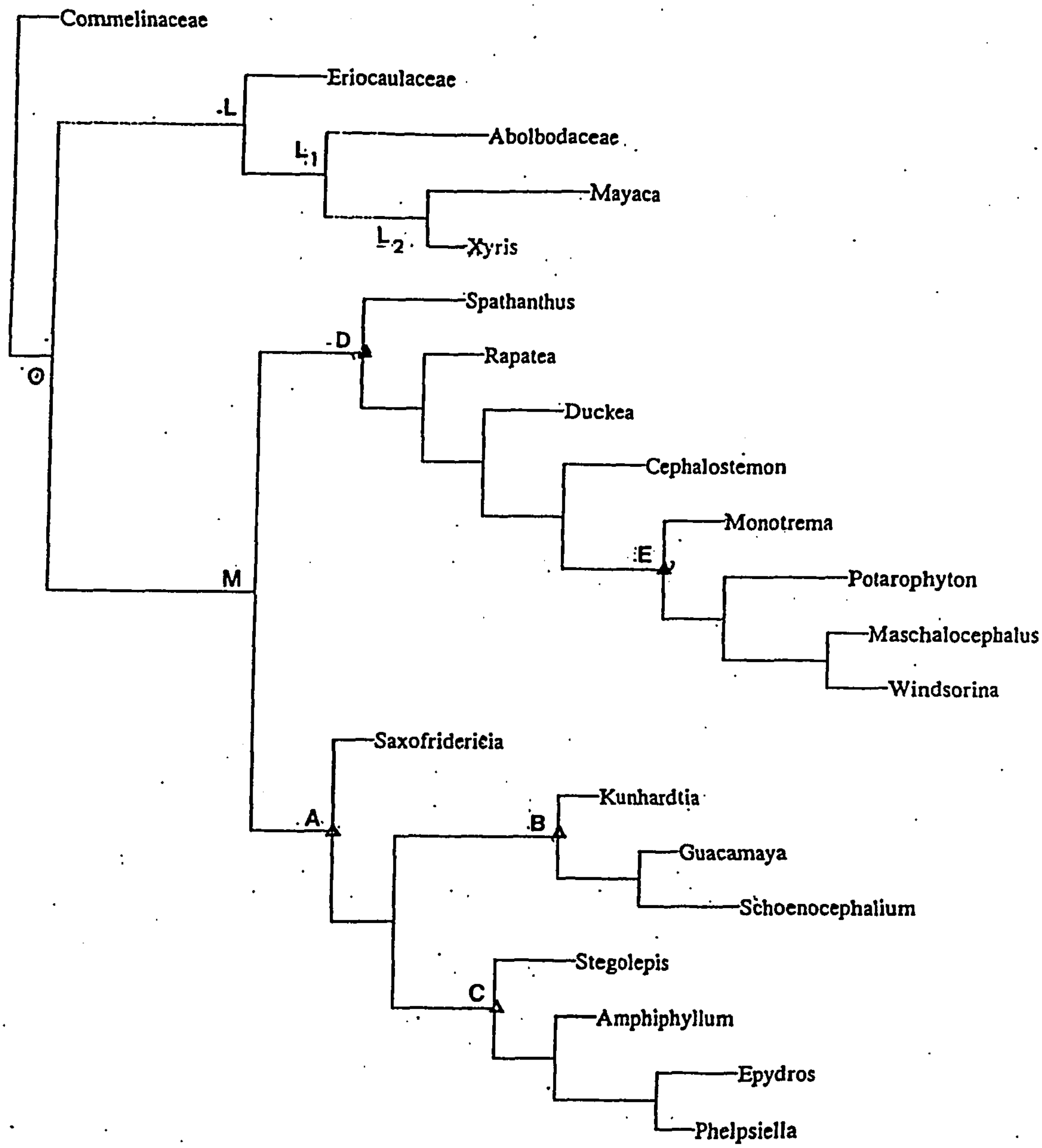

Commelinaceae
Eriocaulaceae
L
Abolbodaceae
L1
Mayaca
L2
Xyris
Spathanthus
D
Rapatea
O
Duckea
Cephalostemon
Monotrema
E
M
Potarophyton
Maschalocephalus
Windsorina
Saxofridericia
Kunhardtia
A
B
Guacamaya
Schoenocephalium
Stegolepis
C
Amphiphyllum
Epydros
Phelpsiella

Table 9

Character States Coding

1.) Lateral roots
    0: opposite to the xylem
    1: opposite to the phloem
2.) Phyllotaxys
    0: spiral
    1: ranked
3.) Leaf type
    0: simple
    1: ensiform
    2: terete
4.) Ptyxis
    0: adplicate
    1: supervolute
    2: conduplicate
5.) Leaf
    0: differentiated
    1: undifferentiated
6.) Leaf petiole
    0: absent
    1: present
7.) Leaf sheath
    0: closed
    1: partially open
    2: open
8.) Pubescence
    0: absent
    1: present
9.) Glandular hairs
    0: absent
    1: present

10.) Leaf axil hairs
  - 0: absent
  - 1: present

11.) Epicuticular waxes
  - 0: absent
  - 1: **Strelitzia**-type

12.) Air canals
  - 0: absent
  - 1: random
  - 2) septate

13.) Auricles
  - 0: absent
  - 1: present

14.) Silica bodies
  - 0: absent
  - 1: present

15.) Aestivation
  - 0: imbricate
  - 1: valvate

16.) Anther dehiscence
  - 0: longitudinal
  - 1: one pore
  - 2: two pores
  - 3: four pores

17.) Anther dehiscence orientation
  - 0: introse
  - 1: extrose
  - 2: latrose
  - 3: poricidal

18.) Anther attachment
  - 0: basifixed
  - 1: dorsifixed

19.) Anther appendages
  - 0: absent
  - 1: present

20.) Anther wall
  - 0: monocot type
  - 1: basic type

21.) Microsporogenesis
  - 0: successive

    1: simultaneous
22.) Tapetum nuclei
    0: uninucleate
    1: binucleate
23.) Endothecial thickenings
    0: spiral
    1: girdle-like
    2: absent
24.) Exothecium
    0: absent
    1: present
25.) Pollen apertures
    0: sulcate
    1: inaperturate
    2: spiraperturate
    3: trichotomosulcate
26.) Pollen sculpturing
    0: reticulate
    1: echinate
    2: psilate
    3: scabrate
    4: striate
    5: foveolate
27.) Hypostase
    0: present
    1: absent
28.) Pseudanthia
    0: absent
    1: present
29.) Antipodals
    0: ephemeral
    1: persistent
30.) Proliferated antipodals
    0: absent
    1: present
31.) Gynoecial nectaries
    0: absent
    1: present
32.) Ovule type
    0: anatropous

  1: campylotropous-amphitropous
  2: orthotropous
33.) Tannins in ovules
  0: absent
  1: present
34.) Nucellus # 1
  0: crasinucellate-few
  1: crasinucellate-many
  2: tenuinucellate
35.) Number of ovules
  0: several
  1: one
36.) Arils
  0: absent
  1: present
37.) Seed shape
  0: prismatic
  1: ellipsoidal
  2: pyramidal
  3: sub-pyramidal
38.) Seed appendages
  0: absent
  1: present
39.) Appendage type
  0: absent
  1: applanate
  2: mitriform
40.) Seeds striate
  0: absent
  1: present
41.) Peduncular bracts
  0: present
  1: absent
42.) Spathaceous bracts
  0: absent
  1: present
43.) Oil in endosperm
  0: absent
  1: present
44.) Placentation

0: axile
1: parietal
2: basal
3: apical
45.) Cleistogamy
0: absent
1: present
2: partial
46.) Pollinators
0: insects
1: birds
2: none
47.) Buzz pollination
0: absent
1: present
48.) Embryostega
0: absent
1: outer integument
2: inner integument
49.) Inflorescences
0: solitary flower
1: cymose
2: head
3: spike
50.) Stigma
0: simple
1: trilobed
2: separate
51.) Persistent epidermis
0: absent
1: present
52.) Inflorescence units
0: reduced
1: 3-5
2: 5-7
3: many
53.) Connate petals
0: absent
1: present
54.) Inflorescence peduncle

  - 0: absent
  - 1: terminal
  - 2: lateral

55.) Anther locules
  - 0: four
  - 1: two

56.) Migratory tapetum nuclei
  - 0: absent
  - 1: present

57.) Fusion in filaments
  - 0: free
  - 1: adnate

58.) Endothecium pattern
  - 0: absent
  - 1: throughout
  - 2: upper half

59.) Thickening subtype
  - 0: reticulate
  - 1: annular
  - 2: helical
  - 3: girdle

60.) Spikelet shape
  - 0: non-reflexed
  - 1: weakly reflexed
  - 2: strongly reflexed

61.) Capsule
  - 0: non-explosive
  - 1: explosive

62.) Stigmatic hairs
  - 0: absent
  - 1: present

63.) Spikelet pedicel
  - 0: ovate
  - 1: lanceolate

Table 10: Data Matrix for the Cladistic Analysis of Rapateaceae

Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Characht.	Late. rot.	Phyllot.	Leaf type	Ptyxis	Leaf	leaf pet.	Leaf.sht.	Pubesc.
Commel.	0	0/1	0	1/ 2	0	0/1	0	1
Eriocaul.	1	0	0/2	0	1	0	2	1
Mayaca	1	0	0	0	1	0	2	1
Xyris	1	0	1	2	0	0	2	1
Abolboda.	1	0	0	0/2	1	0	2	0
Guacama.	0	0	1	2	0	0	2	1
Kunhardt.	0	0	1	2	0	0	2	1
Schoenoc.	0	0	1/ 2	2	0	0/1	2/1	1
Saxofrid.	0	0/1	1	2	0	0	2	1
Stegolep.	0	0	1	2	0	0	2	1
Epydros	0	0	1	2	0	0	2	1
Phelpsie.	0	0	1	2	0	0	2	1
Amphiph.	0	0	1	2	0	0	2	1
Rapatea	0	0/1	1	2	0	0/1	2	1
Potaroph.	0	0/1	1	2	0	0/1	2	1
Maschalo.	0	0	1	2	0	0	2	1
Monotre.	0	0	1	2	0	0	2/1	1
Spathant.	0	0	1	2	0	0	2	1
Cephalos.	0	0	1	2	0	0	2	1
Duckea	0	0	1/ 2	2	0	0	1	1
Windsor.	0	0	1	2	0	0	2	1

Taxa	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Characht.	Glandul.	Leaf axil	Epicutic.	Air canals	auricle	Si bodies	Aestivac.	Anther dehisce.
Commel.	1	0	0	0	0	1	0/1	0/1
Eriocaul.	1	1	0	0/1/2	0	0	1	0
Mayaca	1	1	0	2	0	0	1	1
Xyris	1	1	0	1	0	0	1	0
Abolboda.	0	0	0	1	0	0	1	0
Guacama.	1	1	1	1	0	1	0	2
Kunhardt.	1	1	1	1	0	1	0	2
Schoenoc.	1	1	1	1	0	1	0	3
Saxofrid.	1	1	1	1	0	1	0	1
Stegolep.	1	1	1	1	1	1	0	1
Epydros	1	1	1	1	0	1	0	2
Phelpsie.	1	1	1	1	1	1	0	2
Amphiph.	1	1	1	1	1	1	0	1
Rapatea	1	1	1	1	0	1	0	1
Potaroph.	1	1	1	1	0	1	0	1
Maschalo.	1	1	1	1	0	1	0	1
Monotre.	1	1	1	1	0	1	0	1
Spathant.	1	1	1	1	0	1	0	1
Cephalos.	1	1	1	1	0	1	0	1
Duckea	1	1	1	1	0	1	0	1
Windsor.	1	1	1	1	0	1	0	1

Taxa	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Characht.	Anth.de.	Anth.att.	Anth.app.	Anth.wall	Micros.	Tapetu.	Endothec.	Exothec.
Commel.	0/1/2/3	0/1	0	0	0	0	1	0
Eriocaul.	0	0/1	0	0	0	0/1	1	0
Mayaca	3	0	0	0	0	0	2	1
Xyris	2	0	0	0	0	0/1	2	1
Abolboda.	2	1	0	0	0	1	1	0
Guacama.	3	1	0	1	1	1	0	0
Kunhardt.	3	1	0	1	1	1	0	0
Schoenoc.	3	1	0	1	1	1	0	0
Saxofrid.	3	1	0	1	1	1	0	0
Stegolep.	3	1	0	1	1	1	0	0
Epydros	3	1	1	?	?	?	0	0
Phelpsie.	3	1	1	?	?	?	0	0
Amphiph.	3	1	0	?	1	1	0	0
Rapatea	3	1	1	1	1	1	0	0
Potaroph.	3	1	1	1	1	1	0	0
Maschalo.	3	1	1	1	1	1	0	0
Monotre.	3	1	1	1	1	1	0	0
Spathant.	3	1	1	1	1	1	0	0
Cephalos.	3	1	1	1	1	1	0	0
Duckea	3	1	1	1	1	1	0	0
Windsor.	3	1	1	?	?	?	0	0

Taxa	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Characht.	Pollen appertur.	Pollen sculptur.	Hyposta.	Pseudant.	Antipod.	Prolife.	Gynoeci.	Ovule type
Commel.	0	0/2/3/4/5	0	0	0/1	0	0	0/1/2
Eriocaul.	2	1	1	1	0	0	0	2
Mayaca	0	0	0	0	0	0	0	2
Xyris	0	0	0	0	0	0	0	2
Abolboda.	1	1	0	1	0	0	0	0
Guacama.	0	0	0	1	0	0	1	0
Kunhardt.	0	0	0	1	0	0	1	0
Schoenoc.	0/3	0	0	1	0	0	1	0
Saxofrid.	0	0	0	1	0	0	0	0
Stegolep.	0	0	0	1	0	0	0	0
Epydros	0	0	?	1	?	?	0	0
Phelpsie.	0	0	?	1	?	?	0	0
Amphiph.	0	0	0	1	0	?	0	0
Rapatea	0	0	0	1	0	0	0	0
Potaroph.	0	0	0	1	0	0	0	0
Maschalo.	0	0	0	0	0	0	0	0
Monotre.	0	0	0	1	0	0	0	0
Spathant.	0	0	0	1	0	0	0	0
Cephalos.	0	0	0	1	0	0	0	0
Duckea	0	0	0	1	0	0	0	0
Windsor.	0	0	?	0	?	?	0	0

Taxa	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Characht.	Integum.	Tannins	Nucell.1	# ovules	Arils	Seed shape	Seed app.	Append.
Commel.	?	0	0	0	0	5	0	0
Eriocaul.	?	0	2	0	0	5	0	0
Mayaca	?	0	2	0	0	5	0	0
Xyris	?	0	2	0	0	5	0	0
Abolboda.	?	0	2	0	0	5	0/1	0/1
Guacama.	?	1	1	0	0	0	0	0
Kunhardt.	?	1	1	0	0	3	0	0
Schoenoc.	?	1	1	0	0	3	0	0
Saxofrid.	?	0	0	0	0	4	0	0
Stegolep.	?	1	1	0	0	0	0	0
Epydros	?	?	?	0	0	4	0	0
Phelpsie.	?	?	?	0	0	0	0	0
Amphiph.	?	?	?	0	0	?	0	0
Rapatea	?	0	0	1	0	1	0	0
Potaroph.	?	1	0	1	0	1	1	1
Maschalo.	?	0	0	1	0	1	1	1
Monotre.	?	1	0	1	0	1	1	1
Spathant.	?	1	1	1	0	5	0	0
Cephalos.	?	1	0	1	0	5	1	2
Duckea	?	0	0	1	1	5	0	0
Windsor.	?	?	?	1	0	1	1	1

Taxa	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Characht.	Ped.brt.	Spath.brt.	Oil in endosp.	Placen.	Cleist.	Pollinat.	Buzz pol.	Embst.
Commel.	0	1	0	0	0	0	0	1
Eriocaul.	1	0	1	2/3	0	0/2	0	0
Mayaca	0	0	0	1	2	0	1	2
Xyris	0	0	1	1	0	0	0	2
Abolboda.	0/1	0	1	0	0	0/1	0	2
Guacama.	1	1	0	0	1	2	1	0
Kunhardt.	1	1	0	0	0	1	1	0
Schoenoc.	1	1	0	0	1	2	1	0
Saxofrid.	1	1	0	0	0	0	1	0
Stegolep.	1	1	0	0	0	0	1	0
Epydros	1	1	?	0	0	0	1	?
Phelpsie.	1	1	?	0	0	0	1	?
Amphiph.	1	1	?	0	0	0	1	0
Rapatea	1	1	0	0	0	0	1	0
Potaroph.	1	1	1	1	0	0	1	0
Maschalo.	1	1	1	1	0	0	1	0
Monotre.	1	1	1	1	0	0	1	0
Spathant.	1	1	0	0	0	0	1	0
Cephalos.	1	1	0	0	0	0	1	0
Duckea	1	1	0	0	0	0	1	0
Windsor.	1	1	?	0	0	0	1	?

Taxa	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**
Characht.	Inflo.	Stigma	Persist.	Inf.unit	Cont.sp.	Inf.ped.	Ant.loc.	Migrat.
Commel.	1	0	0	1/3/2	0	1	0	0
Eriocaul.	2	2	0	0	0	1	0	0
Mayaca	0	0	1	0	0	0	0	0
Xyris	3	2	1	0	0	2	0	0
Abolboda.	3	1	0/1	0	0	1	0	0
Guacama.	2	0	0	3	0	1	0	1
Kunhardt.	2	0	0	3	0	1	0	1
Schoenoc.	2	0	0	3	0	1	0	1
Saxofrid.	2	0	0	3	0	2	0	0
Stegolep.	2	0	0	0/2/3	0	2	0	0
Epydros	2	0	0	1	1	?	1	?
Phelpsie.	2	0	0	1	1	?	1	?
Amphiph.	2	0	0	2	0	?	0	0
Rapatea	2	0	0	3	1	2	0	0
Potaroph.	2	0	0	3	1	?	0	0
Maschalo.	1	0	0	1	1	2	0	0
Monotre.	2	0	0	1	1	2	0	1
Spathant.	2	0	0	3	0	2	0	0
Cephalos.	2	0	0	1	0	2	0	0
Duckea	2	0	0	1	1	2	0	0
Windsor.	1	0	0	1	0	2	0	?

Taxa	**57**	**58**	**59**	**60**	**61**	**62**	**63**
Characht.	Adnat.fil.	Endothec.	Thickeni.	Spk.sh.	Capsule	Stig.hair	Spk.ped.
Commel.	0	1	3.	-	0	0	-
Eriocaul.	1	1	3	0	0	0	-
Mayaca	0	0	-	-	0	0	-
Xyris	1	0	-	0	0	0	0
Abolboda.	0	1	3	0	0/1	0	0
Guacama.	1	2	1	2	0	1	0
Kunhardt.	1	2	1	1	0	1	0
Schoenoc.	1	2	1	2	0	1	0
Saxofrid.	1	2	0	1	0	1	0
Stegolep.	1	2	0	0	0	1	0
Epydros	1	?	?	0	?	1	0
Phelpsie.	1	?	?	0	?	1	0
Amphiph.	1	2	0	0	0	1	0
Rapatea	0	1	2	0	0	0	0
Potaroph.	?	1	0	0	0	0	1
Maschalo.	0	1	0	0	0	0	1
Monotre.	0	1	0	0	0	0	1
Spathant	0	1	2	0	0	0	0
Cephalos.	0	1	2	0	0	0	0
Duckea	1	1	2	0	0	0	0
Windsor.	0	1	?	0	0	0	0

Appendix 1: Taxa and collector (s) number (s) used in this research

Appendix:

The following is a list of the field collection numbers or herbarium collections used in the present research. Herbarium specimens were taken from The New York Botanical Garden herbarium. The field collections of the author cited in this appendix have been deposited in Venezuela at the Herbario de la Universidad Ezequiel Zamora, Edo. Portuguesa (PORT) and at The New York Botanical Garden (NY) USA.

Taxa	Collector(s) and number(s)
Family: **Xyridaceae sensu lato:**	
Xyris lacerata Pohl ex Seub.	M. Colella, et al, 1224, 1269
Xyris involucrata Malme	M. Colella et al, 2121
Family: **Abolbodaceae**	
Abolboda pulchella H. et B.	M. Colella, et al, 1241
Abolboda sprucei Malme	M. Colella & V. Morales, 1271

Taxa	**Collector(s) and number(s)**
__Family:__ **Thurniaceae**	
Thurnia sphaerocephala Hook.f.	M. Colella & V. Morales, 1250
__Family:__ **Rapateaceae**	
Rapatea paludosa Aublet	M. Colella, 1272
Guacamaya superba Maguire	M. Colella, 1275
Monotrema aemulans Kornicke	M. Colella et al, 1276
Duckea cyperaceoidea (Ducke)Mag.	M. Colella, 1277
Rapatea longipes Spruce ex Kornicke	M. Colella, 1774
Schoenocephalium cucullatum Mag.	M. Colella, 1769, 1623
Schoenocephalium tertifolium	M. Colella et al, 2123
Stegolepis cardonae Maguire	Pruski J., 3689
Spathanthus unilateralis (Rudge) Desv.	M. Colella, 2091, 1744, 2091
Stegolepis squarrosa Maguire	B. Boom, 9372
Duckea flava (Link) Maguire	M. Colella et al, 2068, 2090
Duckea squarrosa (Willd ex Link) Mag.	M. Colella, 2069

Taxa	**Collector(s) and number(s)**
Cephalostemon angustatus Malme	Harley et al, 25449
Cephalostemon affinis Kornicke	M. Colella et al, 2069
Monotrema xyridoides Gleason	M. Pires 14999 (Herbarium especimen)
Monotrema aemulans Kornicke	O. Huber, 3383 (Herbarium specimen)
Monotrema aemulans Kornicke	Colella, M., Morales V., 1276
Kunhardtia rhodantha Maguire	P. Berry, 4808; M. Colella s/n
Rapatea paludosa Aublet	Colella, M. , Morales, V., 1272
Guacamaya superba Maguire	Colella, M., Morales, V., 1275
Saxofridericia duidae Maguire	M. Colella, 2206
Amphiphyllum schomburgkii Gleason	J. Steyermark, 58.249

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