The evolution of angiospermid pollen characteristics: conjectures and queries

G. Vasanthy, B. S. Venkatachala & S. A. J. Pocock

The origin and evolution of different exine layers of palynofossils is analysed in the light of accumulating ultrastructural data. Semi-diagrammatic illustrations based on the published TEM results of various exine types representing a cross section of extinct and extant plant groups are given for easy reference and comprehension. Some of the important palynological questions and issues discussed in the present work are: imprecise use, to describe the infra-tectum of pollen, of the flexible term "granular" that often leads to erroneous derivations and conclusions; ontogenetic differences between the apparently similar complexly alveolate columellate sexine types of gymnosperms and angiosperms respectively; independent evolution of columellar complexity in unrelated taxa: role of ubiquitous white lines in the exines of extinct and extant spores and pollen and adaptive rather than phylogenetic significance of sacci in progymnosperms, gymnosperms and angiosperms. Despite recognition of angiospermid pollen characteristics especially in tectally reticulate and columellate pollen of Triassic (Cornet, 1979, 1985, 1989; Pocock & Vasanthy, 1988; Pocock, Vasanthy & Venkatachala, 1988) the pre Cretaceous origin of angiosperm still remains an open question.

Key-words—Comparative analysis. Exine ultrastructure, Angiosperm evolution.

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सारौंश

आवृतबीजी परागकणों के लक्षणों का विकास : धारणायें एवं प्रश्न

जी० वासन्थी, बेंगलूर श्रीनिवासा वेंकटाचाला एवं एॅस० ए० जे० पोकोक

परासंरचनात्मक आँकड़ों के आधार पर अश्मित परागकणों की विभिन्न बाह्यचोल तहों का उद्भव एवं विकास विश्लेषित किया गया है। वर्तमान एवं विलुप्त पादप समूहों के विभिन्न प्रकार के बाह्यचोल की अनुप्रस्थ कांटों पर प्रकाशित पारगमन इलेक्ट्रॉन सूक्ष्मदर्शी के परिणामों पर आधारित अर्ध-चित्रित चित्र भी प्रस्तुत किये गये हैं। इस शोध-पत्र में विवेचित कुछ परागाणविक प्रश्न एवं विषय इस प्रकार हैं 'कणिकीय' शब्द, जिससे प्रायः त्रुटिपूर्ण व्याख्यायें एवं निष्कर्ष निकाले गये हैं, का अत्यन्त सीमित प्रयोग; क्रमशः अनावृतबीजीयों एवं आवृतबीजीयों के सदृश जटिल कूपिकीय/स्तंभिक सेक्साइनों के विभिन्न प्रकारों में उद्भवात्मक विभिन्नताएँ; असम्बद्ध वर्गकों में स्तंभी जटिलता का स्वतंत्र विकास; विलुप्त एवं वर्तमान परागकणों एवं बीजाणुओं के बाह्यचोल पर विद्यमान सर्वव्यापी सफेद रेखाओं की भूमिका तथा पूर्वअनावृतबीजी, अनावृतबीजी एवं आवृतबीजीयों 'कोष्ठकों' के जातिवृत्तीय महत्व के बजाय आनुकूलिक। त्रिसंधी कल्प (कॉर्नेट, 1979, 1985, 1989; पोकोक व वासन्थी, 1988; पोकोक, वासन्थी व वेंकटाचाला, 1988) के मुख्यतया स्तंभी एवं सततछदी जालिकावत् परागकणों में आवृतबीजी परागकणों के लक्षणों को मान्यता देने के बजाय आवृतबीजी पौधों का पूर्व-क्रीटेशी उद्भव अभी भी एक खुला प्रश्न है।

"POLLEN characters are subject to parallelism, convergence and possible reversal and the study of fine structural details of fossil pollen opens up possibilities of new sources of phylogenetic evidence" (Davis & Heywood, 1963). This paper is a follow-up of our recent contributions (Pocock & Vasanthy, 1988; Pocock, Vasanthy & Venkatachala, 1988; Vasanthy, Venkatachala & Pocock, 1988; Pocock, Vasanthy & Venkatachala, 1990) which emphasise the need for detailed palynological descriptions and critical analyses of exine characteristics of pre-Cretaceous palynofossils.

Light microscopic studies and SEM observations of various spore-pollen types have already amply discussed and hypothesised the evolution of germinal apertural types through ages. The objective of our present study was to trace the phylogenetic relationships with the aid of published

ultrastructural details of palynofossils from Palaeozoic through Cretaceous. For easy reference and comprehension we have included in this paper the semi-diagrammatic illustrations of 56 TEM pictures of exine types. Legends of these Text-figures include our comments, conjectures and queries chiefly pertaining to basic palynology, which may aid palynologists to appreciate the new dimensions of palyno-phylogeny.

From an analysis of ultrastructural data of palynofossil and pollen types we infer that : (i) the polyplicate pollen morphotypes of *Equisetosporites, Ephedripites, Ephedra* and *Spathiphyllum* (Araceae) are infrastructurally different, thus negating any phylogenetic relationship among them; (ii) pre-Cretaceous *Equisetosporites chinleanus* and *Cornetipollis reticulata* are columellate, like Cretaceous angiosperms (cf. Pocock & Vasanthy, 1988); (iii) prevalence of saccus in many non-angiospermous plant groups and in primitive angiosperm Lactoridaceae is not a good character to link angiosperms with gymnosperms; (iv) columellar complexity might have risen independently in extant Coniferae, Circumpolles, some Eocene fossils and many taxa of angiosperms; (v) the tripartite nexine of *Equisetosporites chinleanus* with lamellate inter-bedded, mid-zone may be representative of a transitional evolutionary stage, intermediate between lamellate gymnospermous and non-lamellate angiospermous nexine; and (vi) as myriads of exine-types have been imprecisely described as "granular" and "spongy", one ought to be very discreet while grouping these types to draw phylogenetic inferences.

GRANULAR INFRATECTUM : FACTS AND FALLACIES

In pollen morphological descriptions, the term granular is used in its broadest sense : to describe the sexinal or tectal surface sculpture (cf. Kremp, 1965, p. 61); the infra-tectal interstitial structure and sometimes even the nexine. Van Campo and Lugardon (1973) defined granular structure as sporopollenin organised into spherical grains, more or less densely distributed under the tectum and generally discernible under the electron microscope. The "synonyms" of granular infratectum—a network of rods of various size, poorly developed columellae, columellae formed of small granules, granular layer of endosexine and others—have been discussed in their informative review on granular exine.

"Granular" exines that occur both in gymnosperms and angiosperms, have been hypothetically derived from "atectate" exines (Doyle, Van Campo & Lugardon, 1975; Walker & Skvarla, 1975). Crane (1985; table 9) while reviewing the occurrence of granular exine in various plant groups (e.g. *Archaeopteris,* Corystospermales, Bennettitales, Gnetales and many angiosperms) accepted the hypothesis that granular pollen wall stratification is primitive within angiosperms (cf. Doyle, 1978).

Ultrastructure of "granular" types of exines in fossil and extant gymnospermous pollen has been the subject of many palynological papers. Foster and Price (1981) described the Permian palynofossil *Praecolpatites sinuosus* (Text-fig. 3 A) as "incipiently alveolate" and even compared its "cavitate" or "granular" exoexine to the "granular" exine of certain Magnoliaceae. Zavada (1984) considered the exine of *Praecolpatites* as a granular form. Should we then infer that the terms "granular" and "incipiently alveolate" are synonyms or equivalents? If so, the exine of Middle Jurassic Corystosperm *Pteruchus dubius* (Zavada & Crepet, 1985; Text-fig. 5 C) could be described as either granular or incipiently alveolate. The ultrastructure of another gymnospermid Mesozoic palynofossil *Eucommiidites* (Doyle *et al.,* 1975; Text-fig. 1 A) reveals an anastomosing granular infratectum (prelude to columellar evolution?). Although Zavada (1984) described the infratectum of bisaccate pollen of Triassic, Jurassic and Cretaceous as granular, the Cenomanian *Granabivesiculites* sp. cf. *G. inchoatus* and the Albian vestigial saccate pollen (Text-fig. 3 B, C) look complexly columelliform (anastomosing rods) rather than granular. Likewise the dispersed monosulcate pollen from the Cenomanian Dakota Formation (Zavada & Dilcher, 1988) are apparently columellar or distinctly columelloid (e.g. Text-fig. 5 D-F) but not granular.
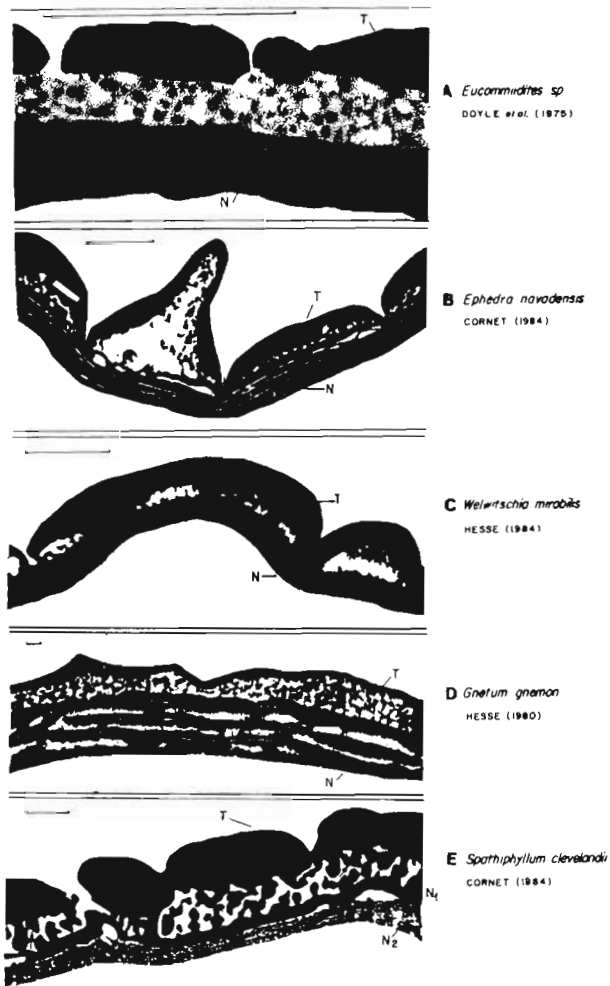
Amongst the extant gymnosperms, the exines of *Agathis alba* (Araucariaceae) and *Cupressus arizonica* (Cupressaceae) have granular ultrastructure (Van Campo & Lugardon, 1973). But in the latter (Text-fig. 3 D) the granular infratectum tends to be columelloid. Granular pollen development in *Cunninghamia lanceolata* (Taxodiaceae) has been investigated (Kurmann, 1988). The pollen wall of Gnetales is generally classified under granular type (Text-fig. 1 B, C, D). The inter-crestal infratectum of *Ephedra navadensis* (Cornet, 1985) and *E. distachya* (Van Campo & Lugardon, 1973) is columelloid unlike the granuliform infra-tectum of arched summit of the ridges. In *Welwitschia mirabilis* (Gullvag, 1966; Hesse, 1984), the interstitium is granulo-reticuloid (tending to be columelloid?). The infratectum of the

inter-spinular areas in *Gnetum* spp. (Gullvag, 1966; Zavada, 1984) tends to be columelloid unlike the crowded granules of the domed infra-spinular interstitium. Some of the aforementioned examples may be possibly or probably indicative of granulo-columellar transitional stages of infratectum in non-angiosperms.

The prevalence of granular exine in angiosperms (e.g. Juglandaceae, Betulaceae, Amborellaceae, Annonaceae, Canellaceae, Magnoliaceae) has been discussed by Crane (1985). Granulo-columellar layer is characteristic of the Lower Eocene Normapolles (Kedves & Stanley, 1976) and of the Eocene *Granotricolporites miniverrucatus* (Kedves, 1986). Superimposition of granules in columellae of *Mischogyne elliotianum*, Annonaceae (Le Thomas, 1980), secondarily granulate columellae in *Calliandra viscidula*,

Mimosoideae (Guinet & Barth, 1967), anastomosed granules orienting into columellae in *Vigna longifolia*, Papilinoideae (Horvat & Stainier, 1980) and the columellae secondarily reversing to granuliform infratectum accompanied by loss of footlayer in the Orchidaceae (Burns-Baloch & Hesse, 1988) are a few examples (Text-fig. 2) supportive of the hypothesis that granulo-columellar transition is a reversible and/or an atavistic trend.

In sum, the so-called granular infratectum is composed not only of spherical bodies (*sensu stricto*) but also of variously anastomosed patterns (*sensu lato*): incipiently alveolate, granulo-reticuloid, columelloid, imperfectly columellate, complexly columelliform and other transitional forms. In other words, the vague term "granular" has been commonly used to describe the exine types which differ from the typical alveolate columellate

A *Eucommiidites sp*
DOYLE et al. (1975)

B *Ephedra navadensis*
CORNET (1984)

C *Welwitschia mirabilis*
HESSE (1984)

D *Gnetum gnemon*
HESSE (1980)

E *Spathiphyllum clevelandii*
CORNET (1984)

← **Text-figure 1—A,** *Eucommiidites* sp., **Gymnosperm** *vs.* **Angiosperm affinity**. Aptian or Lower Albian? (Doyle *et al.*, 1975): Infra-tectal layer granular, spheroidal granules appear to be surficially apposed to the adjacent ones (prelude to the evolution of columella?), endexine laminated; **B,** *Ephedra navadensis,* **Gnetales** (Cornet, 1985): In the inter-crestal parts the thick tectum is not curved (cf. SEM by Ueno, 1978; pl. 46), it is linked with the lamellate nexine by columelliform structures (white arrows). Beneath the arched/domed/coniform tectum (cf. TEM pollen-sections of *Ephedra monosperma* by Gullvag, 1966, of *E. distachya* by Van Campo & Lugardon 1973 and of *E. californica* in Zavada, 1984) there is concentration of granules: few interlinked, the upper ones "hanging" from the tectal interior, lower ones dissociating from the nexinal boundary, and many crowded within the "cavus" (formed of tectal curvature during ontogeny?); **C,** *Welwitschia mirabilis,* **Gnetales** (Hesse, 1984): Beneath the thick tectum of ridges occurs the granulo-reticuloid interstitium; nexine lamellate (cf. TEM of *W. mirabilis* pollen by Gullvag, 1966); **D,** *Gnetum gnemon,* **Gnetales** (Hesse, 1980): Infra-tectum granulo-reticuloid; nexine lamellate (cf. TEM pollen-sections of *Gnetum gnemon, G. montanum* and *G. ula* by Gullvag, 1966, of *Gnetum* sp. by Zavada, 1984—wherein the "domed" infra-tectum of the medially-cut-spinules is infilled with interconnected granuloid structure and the inter-spinular area is narrow as the tectum is almost linked with the nexine by a row or two of granules); **E,** *Spathiphyllum clevelandii,* **Araceae** (Cornet, 1985): The anastomosing granulo-columellar infra-tectal structure is obviously complex.

"Granular" is an imprecise term. Is there any correlation between "granulo-reticuloid" and "granulo-columellar" structures and tectal curvature and ridging?
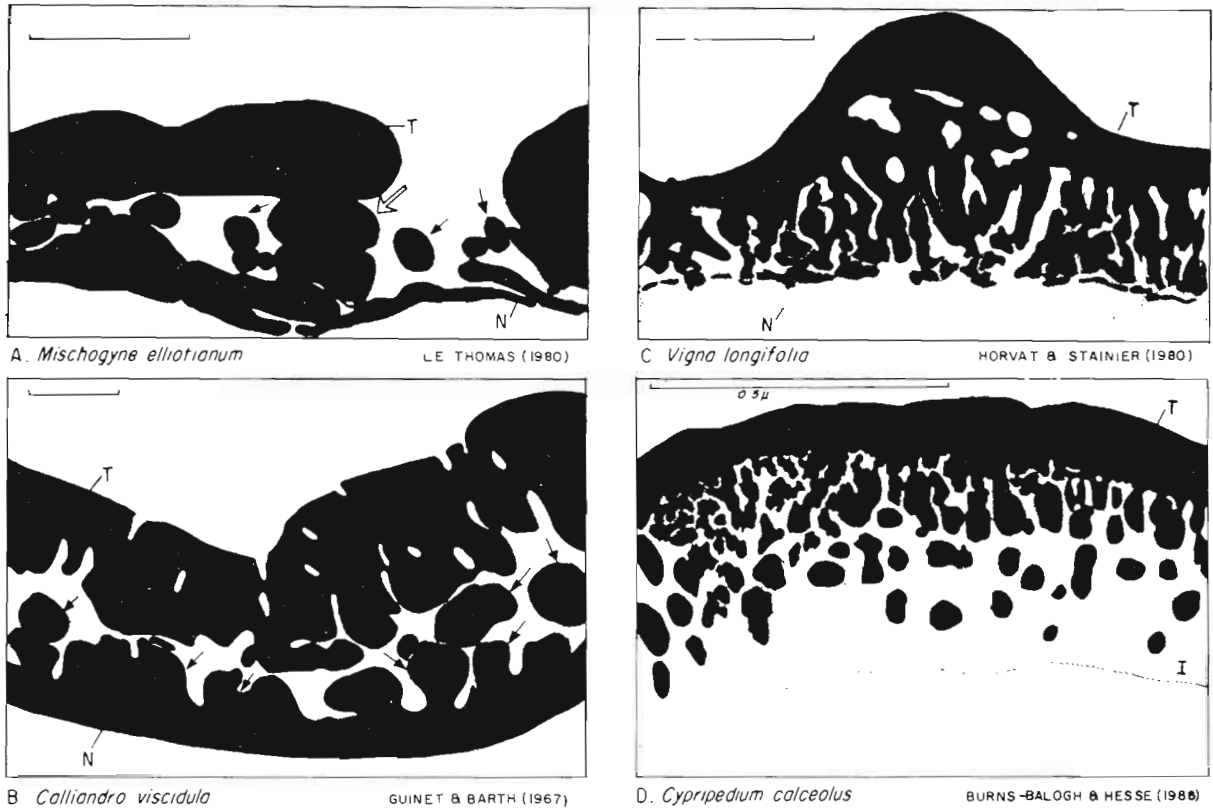
Abbreviations : **T** : tectum, faint tectum (Ueno, 1978) or the delimiting sexinal layer

N : footlayer (nexine-1) and endexine (nexine-2) either lamellate or non-lamellate.

C : columellae;

S : spine or spinules.

Scale lines : representing 1.0 micron unless otherwise specified.

Notes concerning Text-figures: All the figures are semi-diagrammatic transmission electron micrographs, published (except a few) in various works. Authors' names and years of publication are given against the taxa of all figures.

A. *Mischogyne elliotianum*   LE THOMAS (1980)

C *Vigna longifolia*   HORVAT & STAINIER (1980)

B *Calliandra viscidula*   GUINET & BARTH (1967)

D. *Cypripedium calceolus*   BURNS-BALOGH & HESSE (1988)

Text-figure 2—A, *Mischogyne elliotianum,* **Anonaceae** (Le Thomas, 1980): Infra-tectum with numerous free or agglomerated "granules" (short arrows) and coarse "columellar" elements (white arrow) formed of superimposition(?) of "granules"; **B,** *Calliandra viscidula,* **Mimosoideae** (Guinet & Barth, 1967): Section of distal face of a monad. The inner face of thick tectum is irregularly undulated, wavy or sinuous and the (granuliform?) columellae of unequal size (short arrows) are basally fused with the nexine; **C,** *Vigna longifolia,* **Papilionoideae** (Horvat & Stainier, 1980): The "granulated-orientated" ("grenu-orienté") and anastomosed infra-tectal type-intermediate between "*grenu non-orienté*" type and "*grenu-columellaire*" type, i.e., the "granules" upon fusion are oriented more perpendicularly to the pollen surface and less in other directions; **D,** *Cypripedium calceolus,* **Orchidaceae** (Burns-Baloch & Hesse, 1988): Beneath the tectum are the hanging columelliform "stalactite globules," i.e., the cross-sectioned remnants of columellae are sunken in the exintine (I), nexine absent (step toward fragmentation of columellae).

Granules ——→ Columellae (e.g. Annonaceae; Papilionoideae)
Columellae ——→ Granules (e.g. Mimosoideae; Orchidaceae)
Is granulo-columellar transition a reversible trend? (cf. Doyle, 1978).

exines (Text-figs 3, 4, 5, 9). In general, alveolar exines characterize the gymnosperm and columellar exines the angiosperms, but granular exines have been reported to occur in primitive and advanced taxa of both extant gymnosperms and angiosperms (Doyle *et al.,* 1975).
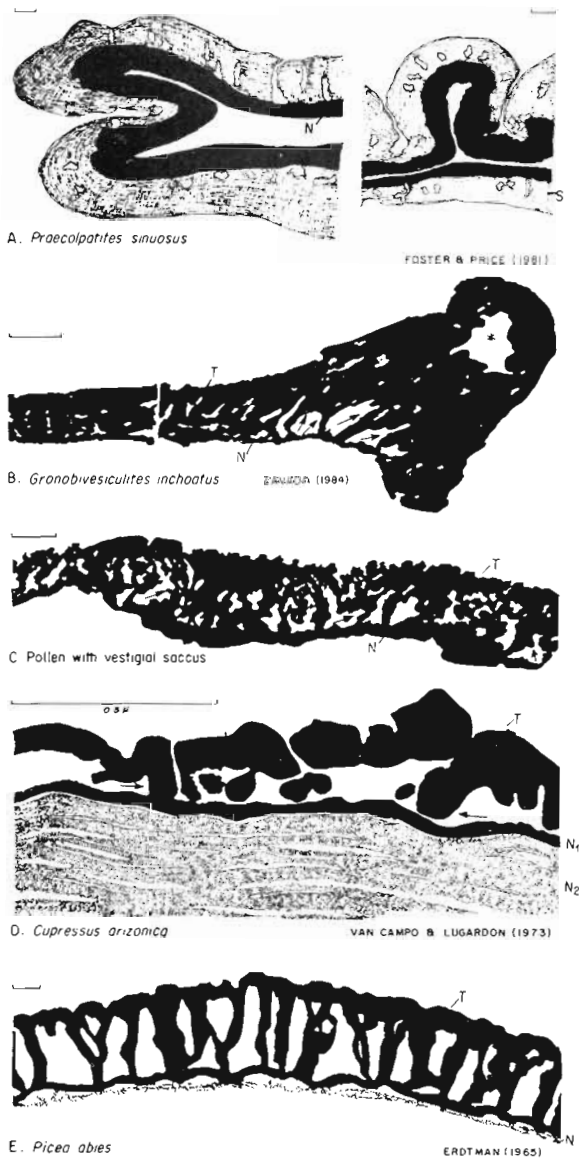
We thus conclude that knowledge of developmental patterns (comparative analysis of ontogeny) of all known granular exine types may throw light on their phylogenetic relationship and the evolutionary stages of angiospermid exine characters in the pre-Cretaceous palynofossils.

ARE COMPLEXLY ALVEOLATE AND COLUMELLATE EXINES ONTOGENETICALLY DIFFERENT?

Alveolar structure between the tectum and nexine consists of a more or less complex spongy or honeycomb-like system of alveolae (*L. alveolus* -a hollow) delimited by partitions attached at oblique or right angles to the inner surface of the tectum (Doyle *et al.,* 1975). The alveolar structures of gymnosperms are fundamentally different from the reticulate simple exine and the pseudoreticulate complex exines of angiosperms (Text-figs 3, 4, 7, 9) although some of these angiospermous and gymnospermous exines look "spongy" (another imprecise term like "granular"). Various alveolar types are broadly divided into cycad type in Cycadales, Medullosaceae and pinaceous type in Podocarpaceae and Pinaceae, Cordaites and saccate seed ferns.

The ultrastructure of multichambered or multitiered exines of pteridospermous pollen have been well-illustrated by Taylor (1971, 1973, 1978, 1980, 1982) and Kurmann and Taylor (1984) while

A. Praecolpatites sinuosus

FOSTER & PRICE (1981)

B. Granobivesiculites inchoatus   ZAVADA (1984)

C Pollen with vestigial saccus

D. Cupressus arizonica   VAN CAMPO & LUGARDON (1973)

E. Picea abies   ERDTMAN (1965)

Text-figure 3—A, Praecolpatites sinuosus, **Gymnospermid?** Permian (Foster & Price, 1981) An inner weakly laminated darker "intexine" (N) and an outer incipiently-alveolate "exoexine" enclosing cavities, **B,** Granabivesiculites inchoatus, **Gymnospermid?** Cenomanian (Zavada, 1984): Bisaccate pollen with "granular" (or complexly columelli-form or alveolate?) infra-tectal structure; saccus (*) resulting from a build-up of exinal material; **C,** Vestigial saccate pollen, Albian (Zavada, 1984): "Granular" (or complexly columelliform or alveolate?) infra-tectal structure; **D,** Cupressus arizonica, **Cupressaceae** (Van Campo & Lugardon, 1973): The infra-tectum is granulo-columellar(?) or tending to be columelliform (arrows)?, nexine lamellate; **E,** Picea abies, **Pinaceae-Abietoideae** (Erdtman, 1965): Complexly alveolate infra-tectum appearing like branched columellae; nexine lamellate.

Incipiently-alveolate (A), complexly-alveolate (E), "granular" or complexly alveolate/columelli-form (B&C), complexly-alveolate (E) and granulo-columelliform (D). Of these which is akin to the columellate exine?
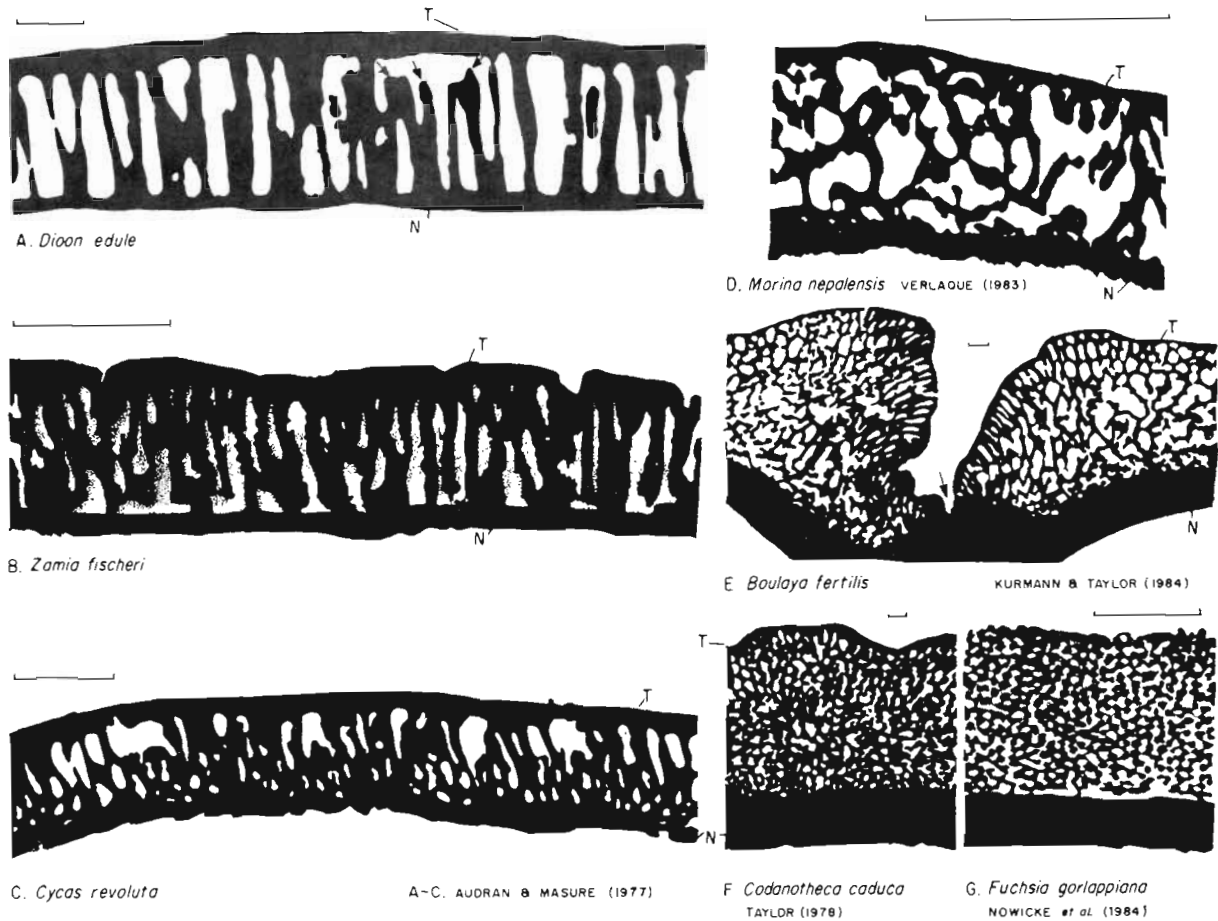
discussing their functional significance and adaptations These "alveolar" exine types are considered precursors to tubularly alveolate Cycadales. According to Zavada (1983) pollen wall development of cycads is identical with that of Pinus (Dickinson & Bell, 1970; Willemse, 1971) and Podocarpus (Vasil & Aldrich, 1973). Taylor (1982) even attempted to compare certain stages of pollen-wall development of Monoletes with those of Cycadales. Absence or scanty deposition of a primexine and limited secretory phase of tapetum during the free spore period differentiates the gymnospermous pollen ontogeny exemplified by Zamia (Zavada, 1983) from the angiosperm pollen ontogeny Whereas in the latter the gametophytically derived primexine or exine-template and an extremely active tapetum of free spore phase are the distinguishing characteristics.

Although it is tempting to compare the morphological peculiarities of complexly alveolate exines of Boulaya fertilis (Kurmann & Taylor, 1984) and Codonotheca caduca (Taylor, 1978; Text-fig. 4 E, F) with those of complexly columellate dicotyledonous Morina nepalensis, Morinaceae (Verlaque, 1983) and Fuchsia garlappiana, Onagraceae (Nowicke et al., 1984; Text-fig. 4 D, G), it is now clear that some ontogenetic or developmental differences have played important roles in the formation of complex sexine types. Hence we may infer that pollen ontogenetic dissimilarities are not supportive of any phylogenetic relationship among the morpholo-gically "similar" forms.

COLUMELLAR COMPLEXITIES IN UNRELATED TAXA : ATTRIBUTABLE TO INDEPENDENT EVOLUTION?

Ektexine in most angiosperms comprises radial, rod-like columnar "columellae" which are sandwiched between the outer tectal layer and the basal footlayer nexine-1 (Faegri & Iversen, 1975) The distally and basally branched columellar complex forms are believed to have been derived from simple columellae (Text-fig. 9). Columellar infratectal organization in angiospermous pollen is supposed to be the culmination of adaptive trends facilitating the conveyance of sporophytic substances (Heslop-Harrison, 1979) and the equalised distribution of bending stresses over the exine surface (Muller, 1979).

It is a widely accepted hypothesis that the occurrence of columellae is an exclusively angiospermous character. The reversible granular-columellar transition (cf. Doyle, 1978) and
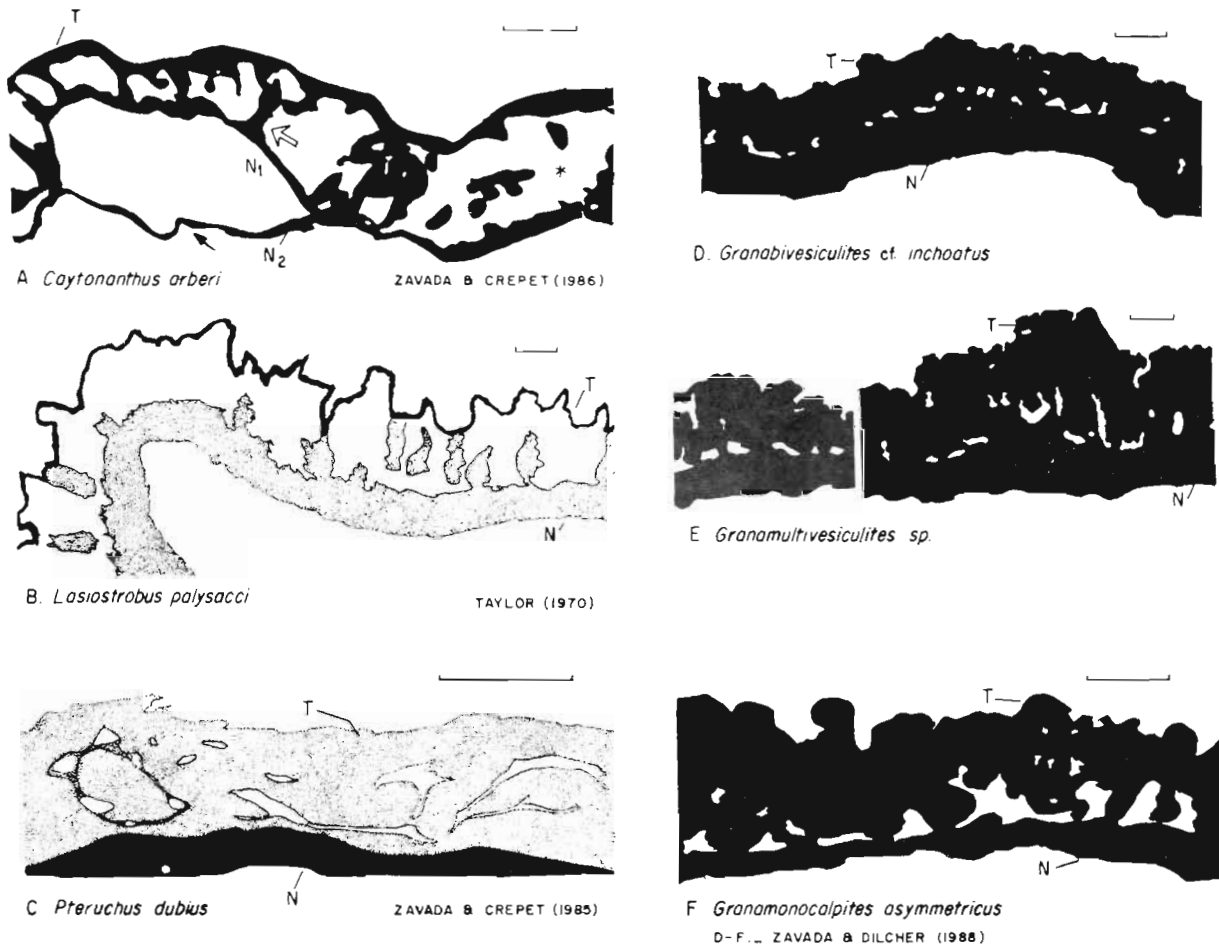
A. *Dioon edule*

B. *Zamia fischeri*

C. *Cycas revoluta*   A–C. AUDRAN & MASURE (1977)

D. *Morina nepalensis*   VERLAQUE (1983)

E. *Boulaya fertilis*   KURMANN & TAYLOR (1984)

F. *Codonotheca caduca*   TAYLOR (1978)

G. *Fuchsia garlappiana*   NOWICKE *et al.* (1984)

Text-figure 4—A, *Dioon edule*, **Cycadinae** (Audran & Masure, 1977): Exine section of lateral side; branched columellae like two dimensional view of septa or partitions of "alveolae"; B, *Zamia fischeri*, **Cycadinae** (Audran & Masure, 1977): Exine section of lateral side; very much branched columellae like two dimensional view of sectioned anastomosing septa of "alveolae"; C, *Cycas revoluta*, **Cycadinae** (Audran & Masure, 1977): Basally complexified "alveolar" infra-tectal structure of exine of prothallial pole. D, *Morina nepalensis*, **Morinaceae** (Verlaque, 1983): Sectioned portion of polar exine, infratectum "spongy" or complexly columellate resembling complex alveolar exine?; E, *Boulaya fertilis*, **Medullosales—Pteridosperms** (Kurmann & Taylor, 1984): An inner homogeneous nexine and an outer sculptured sexine composed of a series of anastomosing net work of muri of the interconnected chambers (apparently "spongy"), sexine diminishing over the proximal suture (arrow); F, *Codonotheca caduca*, **Monoletes-Pteridosperms** (Taylor, 1978): Multichambered sexine and non-lamellate nexine; G, *Fuchsia garlappiana*, **Onagraceae** (Nowicke *et al.*, 1984) The ektexine is not differentiated into tectum, columellae and foot layer units but consisting of a "spongy" or para-crystalline layer which is united with the endexine at numerous points along the ektexine-endexine surface (or complexly columelliform beneath the granulo rugulately sculptured tectum?).

Various grades of the alveolar complexity of Cycadinae pollen (e.g. A,B,C). The apparent similarity of the multichambered sexine of the Pteridosperms (e.g. E,F) with some complex sexine types of the Dicotyledons (e.g. D,G) is striking.

complexly anastomosing granulo-columellar structures in angiosperm exines have already been discussed Before considering the columellar complexity of angiosperms, it is necessary to discuss the columelloid structures and sexinal complexity in non-angiospermous palynofossils.

Although "granular" and alveolate types of exine are prevalent in living gymnosperms we may discern a small degree of granulo-columellar transition in *Cupressus arizonica*, Cupressaceae (Van Campo & Lugardon, 1973, Text-fig. 3 E). Columelloid structures of infratectum are apparent in the Cretaceous bisaccate *Granabivesiculites inchoatus*, rugulo-saccate *Granamultivesiculites* sp. (Zavada & Dilcher, 1988) as well as in Carboniferous *Lasiostrobus polysacci* (Taylor, 1970; Text-fig. 5). Sexinal complexity ("granular") is discernible in Cenomanian bisaccate *Granabivesiculites inchoatus* and a vestigially saccate pollen (Zavada, 1984; Text-fig. 3 B, C). The sexinal complexity of *Classopollis* and other Circumpolles bears some resemblance or analogous to the columellar complexity in some advanced taxa of dicotyledons (Pettitt & Chaloner, 1964, Burger, 1965, Pocock, Vasanthy &

A *Caytonanthus arberi*   ZAVADA & CREPET (1986)

B *Lasiostrobus polysacci*   TAYLOR (1970)

C *Pteruchus dubius*   ZAVADA & CREPET (1985)

D *Granabivesiculites* cf. *inchoatus*

E *Granamultivesiculites* sp.

F *Granamonocolpites asymmetricus*

D-F._ ZAVADA & DILCHER (1988)

Text-figure 5—A, *Caytonanthus arberi*, **Caytoniales-Pteridosperms**. Carboniferous Middle Pennsylvanian (Zavada & Crepet, 1986). Monosulcate, bisaccate; in the saccus region (*) inwardly directed stout partitions and rods beneath the tectum are separated from the basal layer, in the cappus region of corpus the infra-tectum (white arrow) is alveolar (apparently columellar in sectional view), in the sulcus region (curved arrow) there is no tectum nor infra-tectal layer; **B**, *Lasiostrobus polysacci*, **Gymnospermid?**. Carboniferous-Upper Pennsylvanian (Taylor, 1970). An exine of three distinct layers, thin tectum, and uniformly thick nexine are linked by vertically oriented "columellae" (non alveolar and saccate). **C**, *Pteruchus dubius*. **Corystospermales-Pteridosperms**. Middle Jurassic (Zavada & Crepet, 1985). Exine structure in the saccus region has two layers, the upper lightly staining layer encloses irregularly shaped processes separated by lacunae (non alveolate or incipiently alveolate granulate?) and the lower thin darker staining layer (N). **D**, *Granabivesiculites* cf. *inchoatus*. Monosulcate, bisaccate, exine structure of the proximal face: tectum thick, imperforate; infratectal layer thin "granular" (columellae?) and basal layer thick. **E**, *Granamultivesiculites* sp.: Monolete, with numerous small ruguloid sacci, exine structure of the proximal hemisphere; tectum thick, micro perforate, infra-tectal layer of irregular rods and columelliform structures and "granules" basal layer thick. **F**, *Granamonocolpites asymmetricus*: Monosulcate, asaccate, tectum thick, occasionally traversed by small perforations; infra tectal layer comprising small spherical or irregular shaped "granules" and "columellae" and a basal layer. **D—F**, Affinity? Cenomanian Cretaceous (Zavada & Dilcher, 1988)

Alveolate exine in Carboniferous Pteridosperms (A-bisaccate) non-alveolate (granuliform?); in Middle Jurassic Pteridosperms (C-Asaccate) and columellate (!) in Carboniferous gymnospermid palynomorph (B-polysaccate). D-F: Distinctly "columelloid" infratectum in Cenomanian pollen!

Venkatachala, 1990). Pocock *et al.* (1988) even surmised that if the evolution of complex feature is an intricate process resulting from simple forms, then could the sexine complexus of Circumpolles be regarded as culmination of structural evolution of Mesozoic Cheirolepidiaceae prior to their extinction during the Upper Cretaceous. This type of sexinal complexity in Circumpolles is not expressed in modern gymnosperm pollen (no regaining of lost character?).
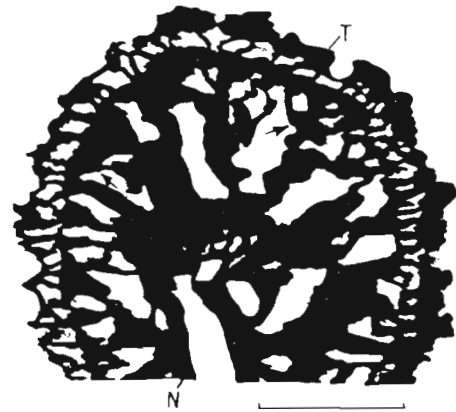
Sexinal complexity, usually involving columellar or granulo-columellar complexification, at times accompanied by tectal complexity (Vasanthy, 1978, 1985) has been encountered in unrelated taxa of angiosperms, for example, Alismataceae (Argue, 1976), Araceae (Trevisan, 1980; Cornet, 1985),
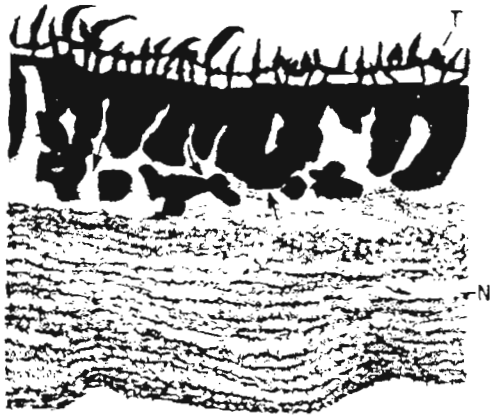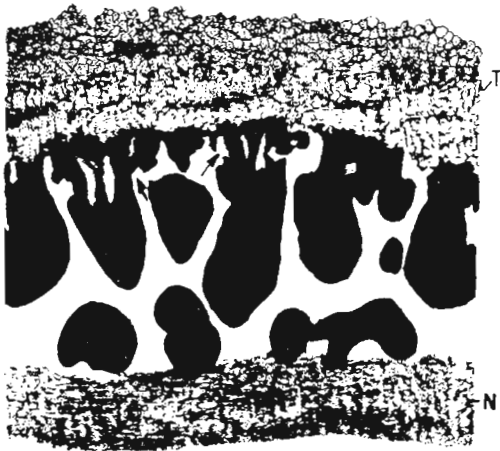
C. *Classopollis sp.*
TAYLOR & ALVIN (1984)

D. *Classoidites glandis*
MEDUS (1977)

B. *Classopollis harrisii*
MEDUS (unpubl.)

A *Classopollis classoides*
ROWLEY & SRIVASTAVA (1986)

Text-figure 6—A, *Classopollis classoides*, Oxfordian-Upper Jurassic (Rowley & Srivastava, 1986): Tectum thick (complex?), infra-tectal rods or complexly columellate structures(?) manifesting lateral adnation (arrows), nexine lamellate, **B,** *C. harrisii*, Rhaeto-Liassic; Triassic-Jurassic (Médus, unpubl.) **C,** *Classopollis* sp., Barremian-Lower Cretaceous (Taylor & Alvin, 1984): Tectum echinulate, complex enclosing inter-tectal rods (short arrows, infra-tectal columelloid elements showing small degree of adnation (arrows); nexine lamellate; **D,** *Classoidites glandis*, Turonian—Upper Cretaceous (Médus, 1977): The "columellae" beneath the tectal complex are distally ramified; nexine lamellate.

Are the infra-tectal complex structures of the extinct Circumpolles similar to the angiosperm columellae (Chaloner, 1976) or were these derived from the reduced muri of a subtectate alveolar system of *Triadispora* spp.? (Scheuring, 1976).

Juglandaceae (Stone *et al.*, 1979), Haloragaceae (Praglowski, 1970), Morinaceae (Verlaque, 1983), Asteraceae (Skvarla & Larson, 1965), Dipsacaceae (Text-fig. 9) and many others. Even some Eocene pollen manifest sexinal or rather columellar complexity: *Caryopollenites triangulus* and *Subtriporopollenites constans* subsp. *constans* (Kedves & Stanley, 1976; text-fig. G, I) and *Interporopollenites endotriangulus* (Kedves, 1986). Detailed pollen developmental studies, for example *Artemisia vulgaris*, Asteraceae by Rowley and Dahl, 1977, are required to draw conclusions on the evolution, distinctiveness and inter-relationship of complex sexines in various taxa. Wanting

ontogenetic data we may surmise that columellar complexity might have evolved independently in different plant groups and taxa.

DO THE "SACCI" IN PROGYMNOSPERMS, GYMNOSPERMS AND ANGIOSPERMS SIGNIFY ANY PHYLOGENETIC RELATIONSHIP?

A saccus is an exoexinal expression, often showing a separation of sexine from nexine ("eusaccate") and seldom with the attachment of the infrareticulum of saccus to the nexine of corpus ("protosaccate") Protosaccate type (*Triadispora bolchii, Protodisaccitrilete*, Scheuring, 1974) and various types of "eusaccate" forms (monosaccate *Felixipollenites* and *Sullisaccites* (Millay & Taylor,

1974, bisaccate *Pinus sylvestris* and *P. balfouriniana*, Willemse, 1971, Ting & Tseng, 1965 respectively) have been illustrated in Text-figure 7 Numerous forms of mono- or perisaccate, pseudo-saccate (*Rhabdosporites*), and bisaccate palynofossils have been elaborately illustrated and discussed by Millay and Taylor, 1970, 1974, 1976), Pant (1987) and Tiwari and Tripathi (1988). Crane (1985) tabulated the saccate spore-pollen bearing groups: Aneurophytalean progymnosperms, Carboniferous lycopods, Medullosan *Parasporites, Callistophyton, Glossopterids, Caytonia*, corystosperms and extant coniferae. The polysaccate condition in "non-alveolate" (columelloid?) palynofossil of Pennsylvanian Carboniferous *Lasiostrobus polysacci* is a unique phenomenon (Taylor, 1970). Zavada and
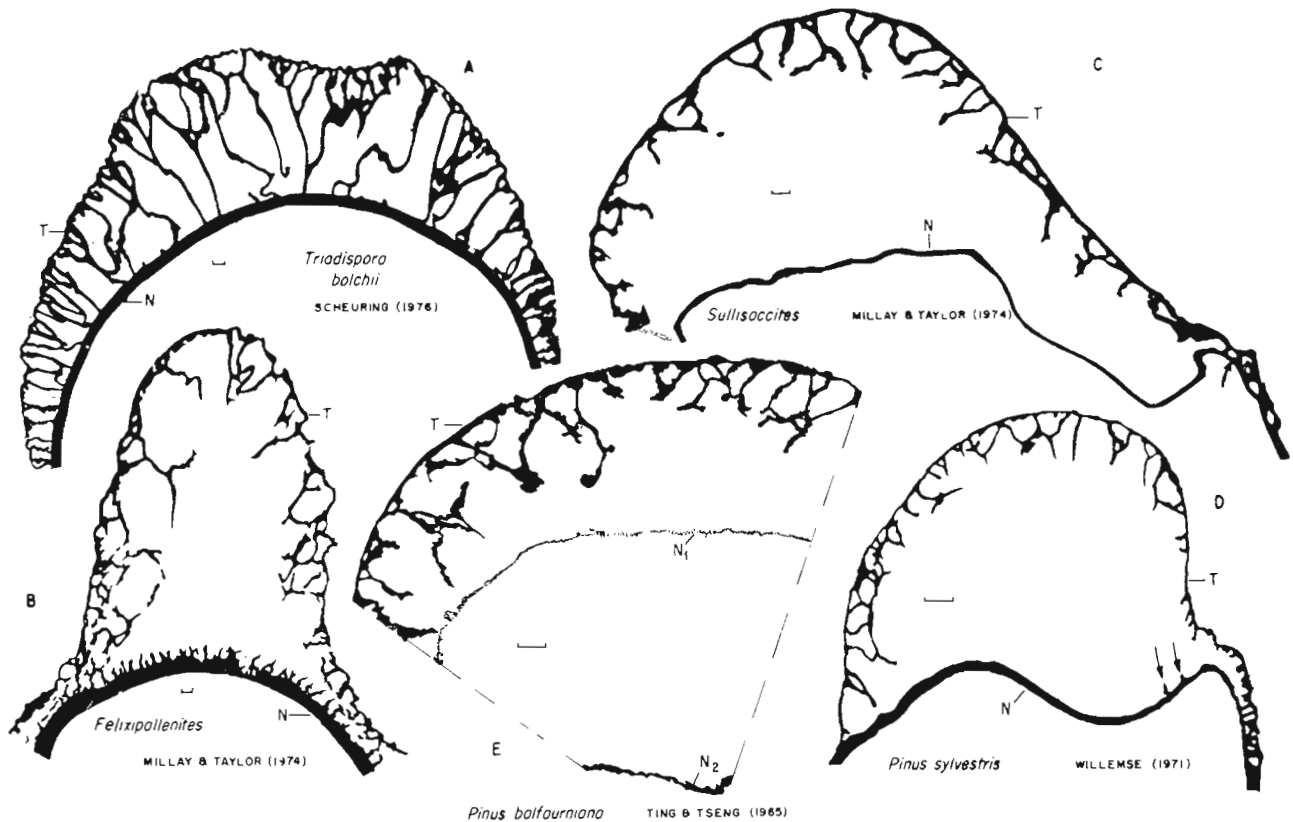

Text-figure 7—**A,** *Triadispora bolchii.* **Protodisaccitrileti,** Triassic (Scheuring, 1976): The infrasaccate "alveolar" system is divided into levels of different chamber size—the smallest underneath the tectum; all the elements of radially arranged infrastructure of the protosaccus reach the central body on the same sectional plane (i.e. apophysis-like structures near the central body); **B,** *Felixipollenites.* **Monosaccites,** Lower Pennsylvanian Carboniferous (Millay & Taylor, 1974): Laterally bulged infrasaccate alveolar system seemed to have broken away from the "apophyses" which are arising from the nexine; **C,** *Sullisaccites,* **Monosaccites,** Lower to lower-middle Pennsylvanian-Carboniferous (Millay & Taylor, 1974): Saccus intrareticulum is finer near region of distal saccus-corpus attachment (arrow) and saccus alveolae are dissociated from the saccus-floor within the lateral bulgings; **D,** *Pinus sylvestris.* **Pinaceae** (Willemse, 1971): In the saccus, the nexine is dissociated from the alveolar reticulation as in the lateral bulges of saccus in *Sullisaccites*: A few "apophyses" remnants (short arrows)?; **E,** *Pinus balfourniana,* **Pinaceae** (Ting & Tseng, 1965): Beneath the tectum are hanging the alveolar reticulation of the bladder, unlike in *Pinus sylvestris* there is a separation of nexine into two layers (N-1 and N-2).

Irrespetive of the differences (mono-or disaccate; proto-or eusaccate), the saccus infra-tectum both in the fossil and extant taxa is alveolate.

Dilcher (1988) have reported the ruguloid sacci on the distal surface of bisaccate Cenomanian *Clavabivesiculites* sp. (Aff.?). The epithet `` subsaccate'' (cavate, pouched, rugulosaccate, vesiculate, winged, cf. Kremp, 1965, p. 161) has been used by Erdtman (1952, fig. 208) to describe the separation of "stalactiform" columellae from nexine in pollen of *Grevillea pinnatifida*, Proteaceae. The "polysacci" of *Lasiostrobus* bear a small degree of resemblance to the verrucae of *Dorstenia erythrandra*, Moraceae and the sections of its

verrucae (Hoen & Punt, 1988) are partly comparable with radial sections of ridge-summits of *Ephedra navadensis* rather than that of *Lasiostrobus polysacci* (Text-figs 1 B, 8 E, F) Monosulcate pollen from the Albian-Cenomanian (e.g. *Granabivesiculites* sp. cf. *G. inchoatus*, *Clavabivesiculites* sp., Zavada & Dilcher, 1988) although flanged by two small sacci (non-alveolate but columelliform infratectum differing from proto and eusaccate intra-reticulate alveolar infratectum) are considered akin to the "saccate" tetrads of the Turonian *Lactoripollenites*
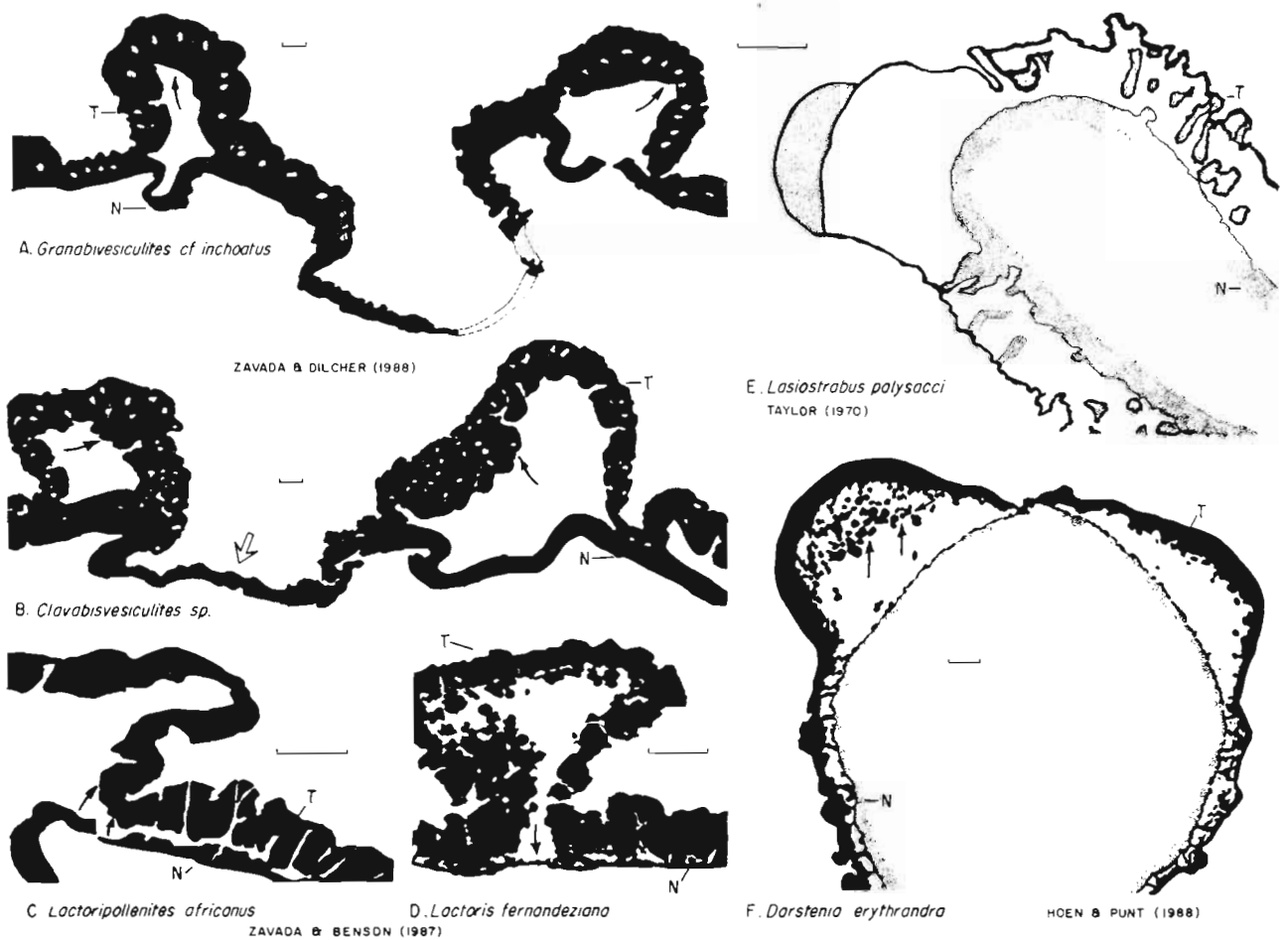
Text-figure 8—**A**, *Granabivesiculites* cf. *inchoatus*, Aff.?, Cenomanian-Cretaceous (Zavada & Dilcher, 1988): Monosulcate, bisaccate; the sulcus is flanged by two flange-like sacci; the sacci are formed by a separation of the tectum, infrastructural layer and part of the footlayer (arrows) from the rest of the nexine(N); **B**, *Clavabivesiculites* sp., Aff.?, Cenomanian-Cretaceous (Zavada & Dilcher, 1988): Two sacci and many small ruguloid sacci on the distal surface, in the flange like sacci on either side of the sulcus (white arrow) there is a separation of "granules"/columelloid structures (curved arrows) from the nexine; **C**, *Lactoripollenites africanus*, Turonian-Cretaceous (Zavada & Benson, 1987): Anasulcate, in tetrads, the "saccus" is formed by a separation of the sexine from the nexine (arrows); **D**, *Lactoris fernandeziana*, **Lactoridaceae** (Zavada & Benson, 1987): Tectum thick microperforate, nexine relatively thin and infra-tectum with columelliform structures; the conspicuous ridge or saccus adjacent to the aperture is formed by a separation of the sexine from the nexine (arrow); **E**, *Lasiostrobus polysacci*, **Gymnospermid?** Pennsylvanian-Carboniferous (Taylor, 1970): Exine stratification and distal thickened area of a "saccus", the tectum extends out from the body to form "sacci" often from the equatorial region, absence of columellae (!) in the saccal infra-structure; **F**, *Dorstenia erythrandra*, **Moraceae** (Hoen & Punt, 1989): Medial (left) and sub-medial sections of verrucae (partly "polysacci"-like?), note the crowded "granules" (short arrows) in the "caveate" infra-tectum of medially-cut verruca (cf. TEM of *Ephedra navadensis* in Text-fig. 1B)

Non-alveolate infratectal structure of "saccus"-types!
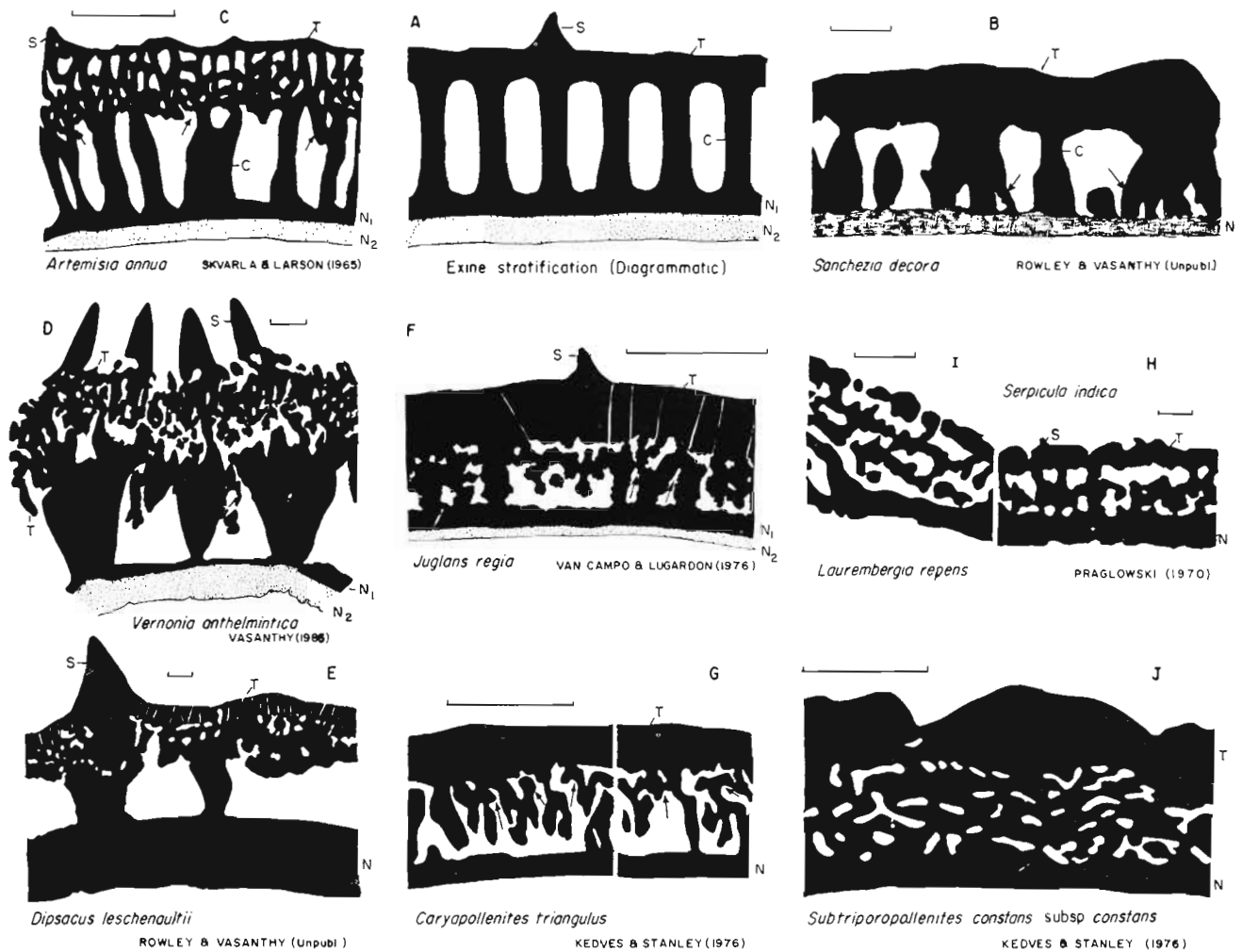
Text-figure 9—A, Exine stratification—Diagrammatic: A "typical" and simple exine form is composed of a tectal layer, an infra-tectal layer of unbranched simple columellae (*columellae simplicea*) which is supported by Nexine-1 (footlayer). The footlayer differs in stainability from the basal layer, Nexine-2, (endexine). Tectum may be perforate or imperforate and may bear sculptural elements (spines, verrucae, bacula, etc.); **B,** *Sanchezia decora,* **Trichanthereae-Acanthaceae** (Rowley & Vasanthy, unpubl.): The columellae (C) appear in radial section, basally branched (*columellae conjunctae?*); **C,** *Artemisia annua,* **Anthemideae-Asteraceae** (Skvarla & Larson, 1965): The columellae in radial section appear distally bifurcated (arrows) or branched ("*Columellae digitatae*"). The distal columellar "off-shoots" seem to intrude into the complex network of tectum; **D,** *Vernonia anthelmintica,* **Vernonieae-Asteraceae** (Vasanthy, 1985): Note the distally digitating columellar complex and the 'off-shoots" intruding into the downwardly descending tectal net; supratectal spines (S) are many; **E,** *Dipsacus leschenaultii,* **Dipsacaceae** (Rowley & Vasanthy, unpubl.): Note the distal complexity of infratectal columellar layer, micro-channelled tectum and the sunken base of tectal spine; **F,** *Juglans regia,* **Juglandaceae** (Van Campo & Lugardon, 1973): Tectum micro-channelled, spinulate; the "granulo-columellar" infra-tectum ("anastomosing rods") manifests distal complexity (arrows); **G,** *Caryopollenites triangulus,* Lower Eocene (Kedves & Stanley, 1976): A "granular"·columellar layer (or complexly anastomosing rods) resembles that of Juglandaceous pollen (Text-fig. F); **H,** *Serpicula indica* & **I** *Laurembergia repens,* **Haloragaceae** (Praglowski, 1970): Note the distal and proximal complexification of columellar layer; **J,** *Subtriporopollenites constans* subsp. *constans,* Lower Eocene (Kedves & Stanley, 1976)·cf. *Interporopollenites endotriangulus* (Kedves, 1986; pl.VI:1): Intergerminal exine; very rough tectum, a relatively thick granular-columellar layer (complexly anastomosed) and a thinner footlayer.

Did columellar complexity evolve independently in different groups and taxa?

africanus (Zavada & Taylor, 1986). The latter palynofossil is shown to bear some resemblance to the pollen tetrads of the primitive angiosperm *Lactoris fernandeziana* Phil. of Lactoridaceae. The conspicuous ridge adjacent to the aperture is formed by the separation of the footlayer (nexine) and the outer portion of the ektexine (sexine), forming a saccus (figs 2-6 in Zavada & Benson, 1987). However, the wavy tectal granular surface, and spheroidal stalactiform granular infratectum of "sacci" in *Lactoris fernandeziana* differ from tectal surface and columelloid saccus infratectum of

Lactoripollenites africanus (Text-fig. 8 C, D).

It may be inferred from these data that the exinal structural dissimilarity does not support the hypothetical evolution of sacci in the pollen tetrads of the Lactoridaceae from the sacci of gymnospermous monads.

THE ROLE OF WHITE-LINES IN THE EVOLUTION
OF SPORE-POLLEN EXINES

White-lines of the nexine layer have been primarily recognised as electron lucent ribbons of unit membrane dimension (50-60A) bound laterally by two dark zones. Reviews on various aspects of white-line-centered lamellations, by Rowley & Dahl (1977), Stone *et al.* (1979) and Guédès (1982) are pertinent to this discussion. While analysing the functional aspects of *Epilobium* endexine, Rowley

(1988) hypothesised that a single form of white-line was an image produced by a tubule not a lamella at all and these are visible during the fundamentally active state of endexine development (in dicotylendons?); white-lines are the junction planes between groups of tuft-units within the endexine and also between units of ectexinal processes and tuft-units of endexine. Published information relative to the occasional occurrence of erect or convolute lamellae rather than periclinal, in the developing ectexine is discussed by Guédès (1982). Linear orientation of ectexinal infratectal granules preceding columellar organization is attributable to the presence of radially oriented lamellae (Le Thomas & Lugardon, 1976).

The omnipresence of white-lines in bryophytic and pteridophytic spores as well as in pollen of gymnosperms, monocotyledons and dicotyledons (Text-fig. 10) is of both ontogenetic and
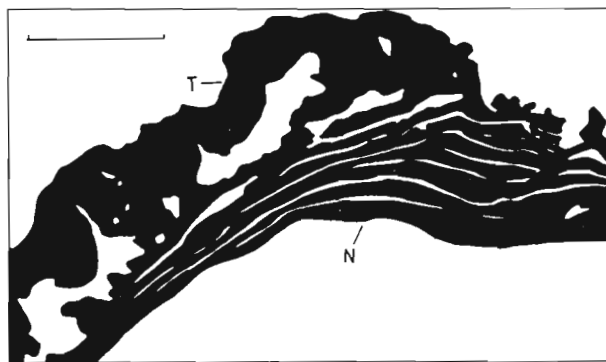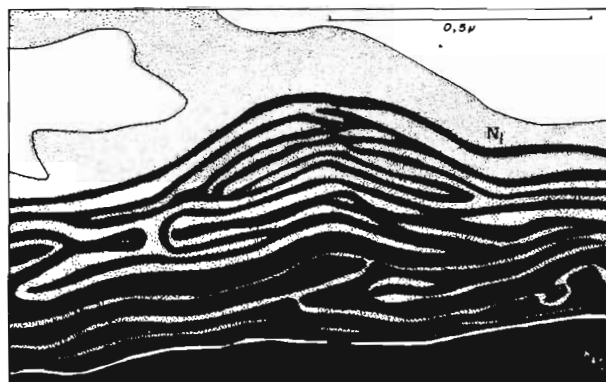

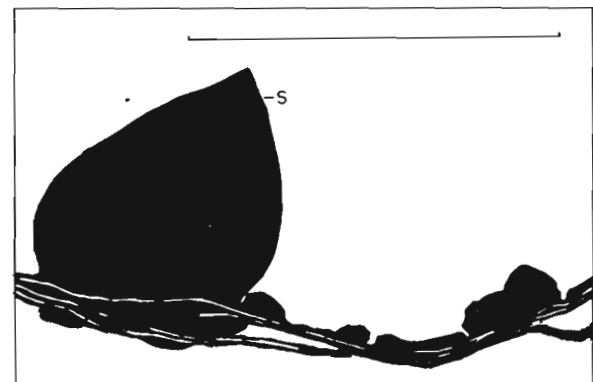A *Ginkgo biloba*   AUDRAN & MASURE (1978)
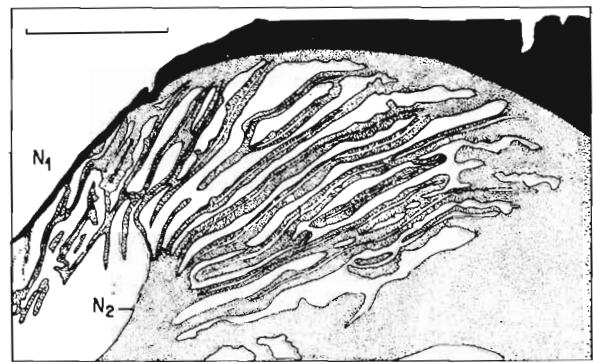
B - *Gerbera jamesonii*   SOUTHWORTH (1966)

D. *Equisetosporites chinleanus*   POCOCK & VASANTHY (1988)

C. *Heliconia nutans*   STONE *et al.* (1979)

Text-figure 10—A, *Ginkgo biloba*, **Ginkgoales** (Audran & Masure, 1978): Axial section of the edge of the furrow showing the large lamellated nexine; sexine tripartite enclosing a middle zone of irregular pits (columelloid layer?); **B**, *Gerbera jamesonii*, **Mutisieae-Asteraceae** (Southworth, 1966)· Lamellated Nexine (endexine) in a young stage (microspore period) of pollen grain; **C**, *Heliconia nutans*, **Heliconiaceae** (Stone *et al.*, 1979)· White-line formation prior to disappearance of the callose wall, segments of the initial white-lines probably develop beneath the spinule-precursors, the protosporopollenin from microspore layer down on a template of 4-5 white-lines (?); **D**, *Equisetosporites chinleanus*, **Proto-angiospermid**? Late Carnian-Triassic (Pocock & Vasanthy, 1988; pl IV)· Polyplicate or ridged pollen, tectum discontinuous in furrows; columellae simple, of variable orientation, nexine three layered with an intermediate lamellate, transitional layer of interstratified nexine-1 and nexine-2 (?).

Are the "white-lines" indispensable for (n)exine formation?

phylogenetic significance in exine evolution (Guédès, 1982; Kedves, 1986; Gabaraeva, 1987; Pocock, Vasanthy & Venkatachala, 1990). Stainability, chemical make-up and persistence vs disappearance of lamellae are some of the criteria generally used to differentiate the gymnospermous nexine from the angiospermous endexine.

The statement of Guédès (1982) that the primitive condition in angiosperm pollen is characterised by an exine with an endexine, probably laminated and continuous with an overlying ectexine sounds logical and helps in our interpretation of the tripartite nexine of the tectate, columellate pollen of *Equisetosporites chinleanus* Daugherty (Triassic). Although we have already discussed the peculiarity of its nexine (Pocock & Vasanthy, 1988; Pocock, Vasanthy & Venkatachala, 1988), we outline it again briefly, here its nexine peculiarity (Text-fig. 10 D): the unique nexine of *E. chinleanus* possesses a distinct, continuous but undulate, lamellate zone, apparently sandwiched between the non-lamellate parts of nexine-1 (footlayer) and nexine-2 (endexine). The lamellae (endexinal) and interlamellae (ectexinal?) of varying thickness (grading into "white-lines" and eventually becoming indistinguishable from the underlying endexine), are interstratified (transitional zone?). We may therefore infer that this tripartite nexine construction in a columellate-tectate exine could be representative of one stage in the exine evolution of proto-angiosperms.

CONCLUDING REMARKS

As greater importance had already been given to the apertural characters in the context of phylogeny and evolution, we are dealing with some of the extra-apertural pollen characteristics, in our present analysis of evolution of exines. Let us first consider the infra-tectal features which are generally believed to be of phylogenetic significance. The hypothetical precursors of incipiently columellate/alveolate exines are supposed to be the granular exines that should have resulted from the formation of cavities and their interlinkage (Walker & Skvarla, 1975; Walker & Walker, 1984) in primeval solid sporoderm or pollen-wall. According to Walker (1976) the columellar structure of cycads and saccate conifers represent divergent specializations *via* granular intermediates from homogeneous structure in the first gymnosperms. But his assumption on gymnosperm pollen evolution is wanting fossil evidence (cf. Doyle, 1976). It is relevant to quote Ehrendorfer (1976) here: "The prominent differences in chromosome patterns between various gymnosperm and angiosperm groups are clear expressions of different cytogenetic potentials and different phases of the evolutionary development of these groups. ... ... it appears that gymnosperms and angiosperms have followed different evolutionary strategies".

We have already discussed in this work the use of vague or ambiguous term "granular" in its broadest sense. Truly granular form (*sensu stricto*-does it exist?) ought to be a transitory or evolving character and progressive evolution of granuloid structure should have resulted in the formation of columelloid structure, simple to composite columellar infra-tectum and their derivatives. On the other hand, retrogressive evolution or secondary simplification of columellae has been supposed to have thrown back the granular infra-tectal character. As the granulo-columellar types occur in both gymnosperms and angiosperms (Zavada, 1984; Pocock & Vasanthy, 1988 and examples discussed in this work) the origin of angiospermid pollen characteristics cannot be easily elucidated from palynological data alone (Zavada, 1984). A hypothesis contradictory to the above view is that the "granular" exines in Magnoliidae represents survivals of a pre-columellar state linking angiosperm pollen with gymnosperm pollen (e.g. Foster & Price, 1981).

Stress-tensibility (Muller, 1979) and efficient conveyance of sporophytic substance (Heslop-Harrison, 1979) of columellar organization, an exclusively angiospermous character (Van Campo, 1971) and the evolution of angiospermy during the Cretaceous (e.g. Hughes, 1976; Doyle & Hickey, 1976) are points of great interest in palynology and palaeo-palynology. The significant lower Cretaceous pollen types *Clavatipollenites hughesii* Couper, *Asteropollis asteroides* Hedlund & Norris, *Stephanocolpites fredericksburgensis* Hedlund & Norris, *Retimonocolpites dividuus* Pierce and *Stellatopollis barghoornii* Doyle have well-developed columellae (Walker & Walker, 1984). Cornet (1979) first reported the angiosperm-like pollen with tectate, columellate wall structure from the Upper Triassic and Jurassic of the Newark Super Group (U.S.A.). His subsequent unpublished report (1985) on the Triassic pollen with angiosperm affinities is adequately illustrative (LM, SEM & TEM) of columellate exine types. Cornet's recent work (1989) on the Late Triassic angiosperm-like pollen from the Richmond rift basin of Virginia describes only the Crinopolles group consisting of six genera and eleven species of angiospermid sulcate pollen. Of these, *Dicropollis operculatus, Monocrinopollis doylei, M. microreticulatus, M. mulleri,*

Polycolpopollis magnificus, Tricrinopollis minutus and *T. olsenii* have dimorphic reticulum supported by columellae. Despite their close resemblance or morphological similarity to lower Cretaceous *Liliacidites* (Walker & Walker, 1984), Cornet (1989) was partly reluctant to attribute their affinity either to monocotyledons or to any angiosperms. This nebulous conclusion from Cornet, one of the staunch proponents of pre-Cretaceous angiosperm origin directs us to a logical analysis of views on angiospermid-pollen-characteristics: What do these three words mean? Could we equate the similarities or correspondences between angiosperm pollen and pre-Cretaceous pollen fossils to homologies or analogous convergences? Is not the combination of tectal reticulum and columellate infra-tectum a typical angiospermous character (cf. Van Campo, 1971)? However, Doyle (1978) remarked that the Triassic reticulate columellate monosulcate pollen reported by Cornet like the conifer *Classopollis* was indicative of the remarkable complexity of exine structure attained by the early Mesozoic seed plants, thus ruling out the conventional belief that earliest pollen should have the simplest structure. This statement is well-supported by the occurrence of columellar complexities in unrelated taxa (e.g. Text-figs 6, 9) and even in primitive families like Magnoliaceae (*Manglietia insignis* and *Magnolia acuminata*, Praglowski, 1973; fig. 1 b, c; fig. 7 g) and Annonaceae (*Uvariostrum pynaertii*, Le Thomas, 1980; Pl. 12, 3, 4) possess complexly granulo-columellate exine ultrastructure. Pocock and Vasanthy (1988) have inferred the angiospermic affinity on the basis of exine ultrastructure of two columellate upper Triassic palynomorphs: psilately banded *Equisetosporites chinleana* Daugherty and reticulately banded *Cornetipollis reticulata* Pocock & Vasanthy, 1988. Lacking data to bridge the gap between the Triassic "angiospermid" pollen and the Cretaceous angiosperm pollen types, may we conclude in accordance with Muller (1984) that the "angiospermid" pollen characters of Triassic were lost (due to extinction?) and reappeared in lower Cretaceous?

Alveolar complexity of Cycadinae and Pteridosperms in two dimensional view bear some resemblance to complex sexine types of dicotyledons (Text-fig. 4). It is intriguing to note the simplification of "alveolate" layer in *Boulaya fertilis*, Pteridosperms (Kurmann & Taylor, 1984, pl. 1, fig. 5) and that of columellate layer in *Artemisia vulgaris*, Asteraceae (Rowley & Dahl, 1977, pl. 23, fig. 3) over the apertural regions. Could we account for any exine substructural (e.g. Rowley *et al.*, 1981) similarity between these complexly alveolar and columellar sexine types?

Endexine evolution has been variously hypothesised by many palynologists (e.g. Guédès, 1982; Crane, 1985; Zavada & Dilcher, 1988; Cornet, 1989). Ubiquity of white-lines in exines of all plants either during development or their persistence after maturation is probably indicative of their significant role in (n)exine formation. The exine of *Equisetosporites chinleana* (Pocock & Vasanthy, 1988; pl. 4) distinguishes itself from most of the known types of exines by its tripartite nexine (Text-fig. 10 D) and inter-stratification or inter-bedding of nexine-1 and nexine-2 layers. According to Cornet (1989) the intermediate stage of nexinal development in *E. chinleana* is suggestive of progenesis: early or accelerated maturity of endexine.

Exinal inflation as an adaptation to pollen dispersal may have led to the formation of different types of sacci (e.g. Text-figs 7, 8). In other words, occurrence of sacci in spore-pollen bearing groups could be accounted rather for their functional significance (harmomegathic or pollen-export) than phylogenetic.

Having discussed some of the basic conjectures and queries relative to angiosperm ontogeny in the context of exine structural evolution, may we conclude our present work with the following quotation :

"We never stop investigating. We are never satisfied that we know enough to get by. Every question we answer leads on to another."
—Desmond Morris

ACKNOWLEDGEMENTS

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