

Evolution of proangiosperms during Late Triassic: pre-Cretaceous pollen trends towards mono- and dicotyledonous taxa diversification

*G. Vasanthi, **B. Cornet and ***S.A.J. Pocock

**Institut Français, P.B. 33, Pondicherry-605 001, India*

***27 Tower Hill Ave., Red bank NJ., 07701, USA*

****R.R. 1 West Arrow Creek, Creston, B.C., Canada*

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The Late Triassic angiospermid palynomorphs (mostly from the Chinle Formation, Arizona and the Richmond basin, Virginia, USA), *Equisetosporites chinleanus* Daugh., *Cornetipollis reticulata* Pocock & Vasanthi and the *Crinopolles* group (Cornet, 1989) have pollen characteristics that provide clues to the existence of pre-Cretaceous proangiosperms. *Equisetosporites chinleanus* and *Cornetipollis reticulata* are inaperturate, banded, tectum discontinuous in furrows, columellate; bands are psilate and nexine 3-layered with an intermediate lamellate transitional layer in *Equisetosporites* whereas bands are scalariformly reticulate, and nexine is uni-/bi-layered, and non-lamellate in *Cornetipollis*. *Mono-*, *Di-*, *Tri-*, and *Zona-Crinopolles*: Proximally reticulate, distinctly columellate, distally foveoreticulate à foveolate-pitted, exhibiting diminution of columellae and footlayer. "Apertures" distal, (sub-) equatorial or distal or/and lateral. *Monocrinopolles*: monosulc(ul)ate (2 compound sulc(ul)i), pontopericulum narrow; *Dicrinopolles*: bisulc(ul)ate with wide detachable opericulum; *Tricrinopolles*: trisulc(ul)ate, sulc(ul)i independent, one distal sulcu(lu)s flanked by a pair of equatorial or lateral sulc(ul)i, ±parallel to the distal sulcus; *Zonacrinopolles anasulcatus*: zonal sulcu(lu)s dividing the grain into 2 subequatorial halves. *Pentecrinopolles traversei*: sculpture clavate, with 5 distal aperturoid thinnings, finely reticulate proximally between the clavae. *Polycolpopollis magnificus*: zonal sulc(ul)ate to spiraperturate, coarsely reticulate.

Columellae supported coarse/fine reticulum and scalariform reticulum in the *Crinopolles* group and *Cornetipollis* respectively are assertive of their angiospermid nature; uniformly thickened endexine in some taxa of the *Crinopolles* may be indicative of the less evolved nature of sulc(ul)ate apertures and also of a desiccation minimizing adaptation during the arid Triassic Period.

Key-words- Angiospermid palynomorphs, Late Triassic, Biodiversification.

The monosulcate to multiaperturoid character states of these palynomorphs had preceded the monosulcate → tricolpate → tricolporate → triporate evolutionary sequence of the Cretaceous. From the presence of columellae supported proximal reticulum, psilate tectum, proximo-distal luminal-foveoloid gradations (monocotyledonoid) and of endexine (dicotyledonoid) it is inferable that the *Crinopolles* types straddle both classes. The 3-layered nexine in *Equisetosporites* may be representative of an evolutionary stage of pollen-wall of pro-angiosperms.

INTRODUCTION

Dilcher (1984) remarked "Studies of fossils, their affinities, analysis of their characters in the context of related modern taxa including the establishment of

homologies will continue to be an important aspect of angiosperm palaeobotany". 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).

The Late Triassic angiospermid foveoreticulate to scalariformly reticulate pollen (Cornet, 1979a) differing from the psilate banded "*Equisetosporites*" has been named as *Cornetipollis reticulata* by Pocock and Vasanthi (1988), the specific epithet underscoring the angiospermous character. Cornet (1989) proposed 7 new genera for the Late Triassic angiosperm-like pollen from the Richmond rift basin of Virginia.

We are here dealing with the distinctively columellate Triassic palynomorphs: *Equisetosporites chinleanus* Daugh., *Cornetipollis reticulata* Pocock

& Vasanthi and the *Crinopolles* group (Cornet 1989). These pollen types may be representative of different levels of pollen characters (apertural and exinal evolution in angiosperms). But our attempts to find modern analogues for the Triassic angiospermid palynomorphs have resulted in matching certain characters of the Triassic pollen partly with those of the angiosperms (Table 2).

Contributions by Vasanthi and Pocock (1986), Pocock and Vasanthi (1988), Pocock *et al.* (1988), Cornet (1989), Vasanthi *et al.* (1990, 1991) and Cornet and Habib (1992) have addressed the difficult and long-standing question "How old are the angiosperms?". And in this paper on the Triassic angiospermid pollen we are re-evaluating this enduring question.

"Angiosperm Origins: Pre-Cretaceous vs Lower Cretaceous" is a much-debated subject of palaeobotanical interest. Defenders of Palaeozoic origin (Axelrod 1961) advocated that precursors to proto-angiosperms of Jurassic through Cretaceous were in existence by Permo-Triassic; those of Mesozoic origin (Axelrod 1970, Takhtajan 1969), postulated that angiosperms diverged from an ancestral alliance during the middle Mesozoic and those of Lower Cretaceous (Doyle 1969, Muller 1970) hypothesized on the bases of the then available fossil evidence that angiosperms were not present anywhere in the world before Barremian time and angiosperm fossil mostly leaves first become a regular component of fossil record during the late lower Cretaceous, approximately 100 million years ago.

Cornet's report (1979b) on the Late Triassic

monosulcate, tectally perforate, columellate angiospermid palynomorphs received immediately a favourable citation: "even under the light microscope, many of the grains described by Cornet show exine features that occur today only in angiosperms; coarsely reticulate sculpture resulting from large perforations in the tectum (are) supported by well-developed rods or columellae rather than granules or partitions of alveolae" (Doyle 1978). Doyle and Hotton (1991) remarked that the Late Triassic reticulate-columellate pollen type described by Cornet (1989) as the *Crinopolles* group is reminiscent of *Liliacidites* and approved of a relationship between the *Crinopolles* and angiosperms.

The objectives of this paper are to emphasize the angiospermid features observed in the selected angiospermid Triassic pollen types (occurrence of columellae supporting either the scalariformly reticulate or coarsely to finely reticulate or psilate tectum and the presence of endexine but unmodified under the "apertures" and to underscore the relationship between the angiosperm pollen and the selected Triassic angiospermid palynomorphs. Their angiospermid pollen characters may be representing the evolutionary stages in angiosperm pollen wall constitution.

MATERIAL AND METHOD

Palynomorphs included in this work were recovered from the late Triassic sediments of USA Outgroup locality VB4 of the Richmond Basin, Virginia (Cornet 1989); earliest Carnian to late middle Carnian or early late Triassic; Petrified Forest National Park, Chinle, Arizona, and Ciniza lakebeds, Chinle Formation, Western New Mexico.

PLATE 1 (SEM)

Equisetosporites chinleanus (from the Ciniza lakebeds, Chinle Formation, Western New Mexico, Late Carnian).

1. Obliquely oriented psilate bands; note the two points of convergence of bands in this view. x 1000.

Cornetipollis cf. *reticulata* (from Middle Carnian of the Richmond basin, Virginia, VB4, VA, USA).

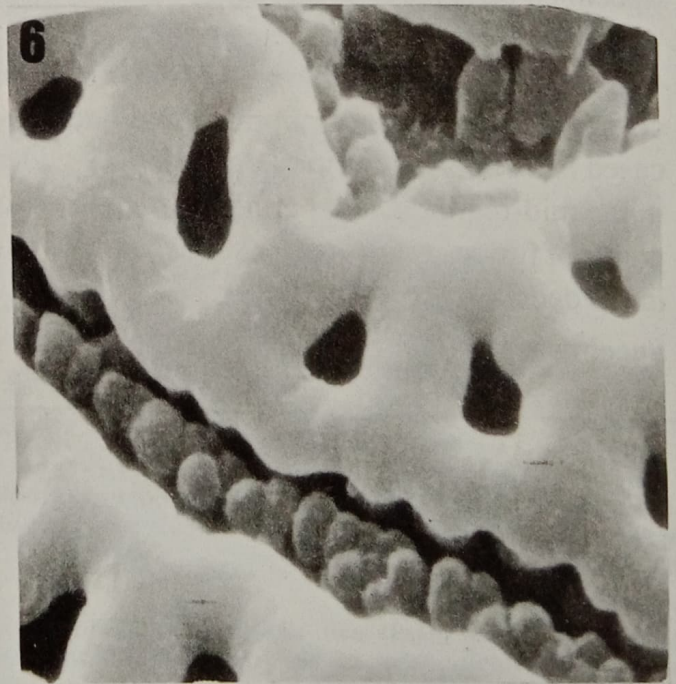
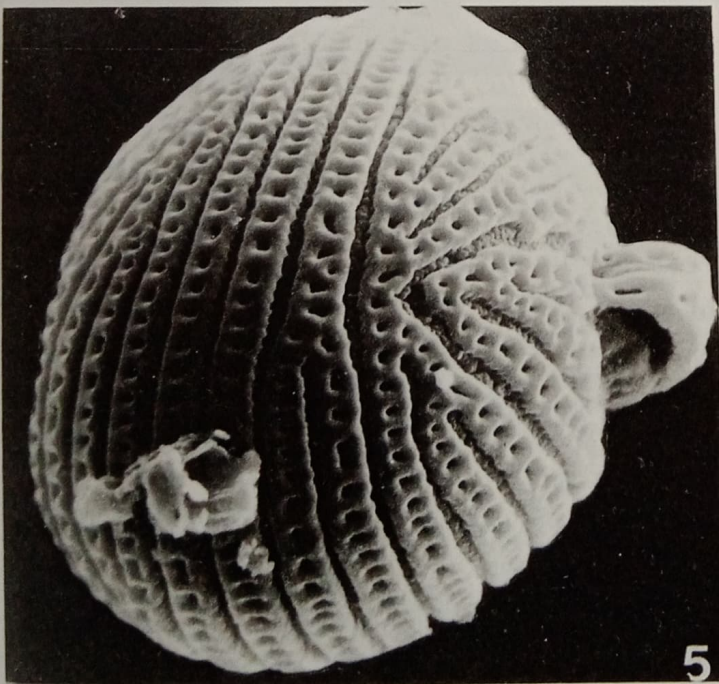
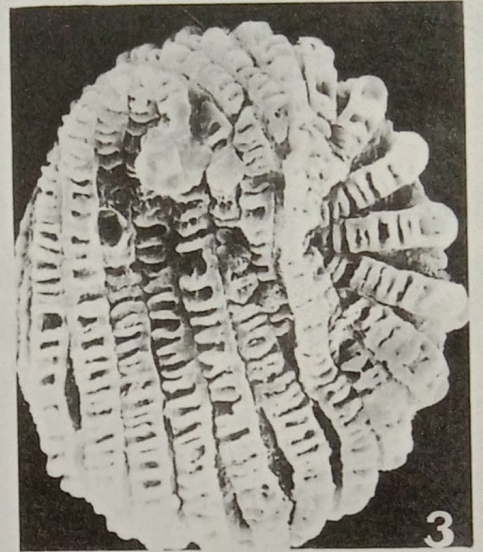
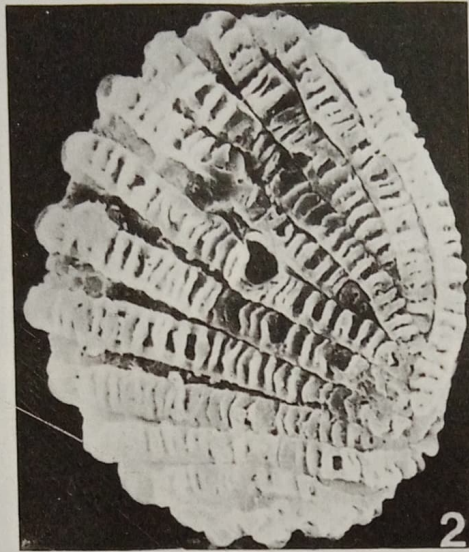
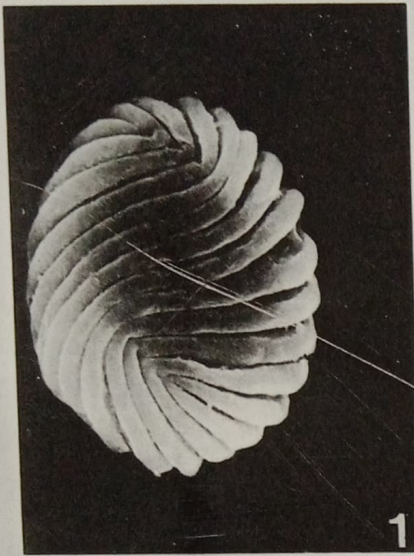
- 2-3. Two sides of a bilaterally and rotationally (<90°) symmetric grain (resembling medially sectioned half). x1025.
4. Enlargement of 2; the ladder-like (scalariform) mural pattern, a bifurcating ring (arrow) and the distal doming on medial convexity

of rung (double-headed arrow). x4100.

Sanchezia decora Leonard and Smith (Tribe Trichanthereae, Acanthaceae, from NY: New York Botanic garden Herbarium).

5. A rotationally symmetric grain; note the bifurcation of one of the three middle bands and the supra-oral flaps on the right side of the grain and the unusual presence of baculate elements (throw-back of a primitive character?) in the pseudocolpi. x1000.
6. Enlargement of 5; note the differences between the exine surface details of bands of *Cornetipollis* and *Sanchezia*. x7000.

1-4 by J.W. Walker and 5-6 by S.A.J. Pocock



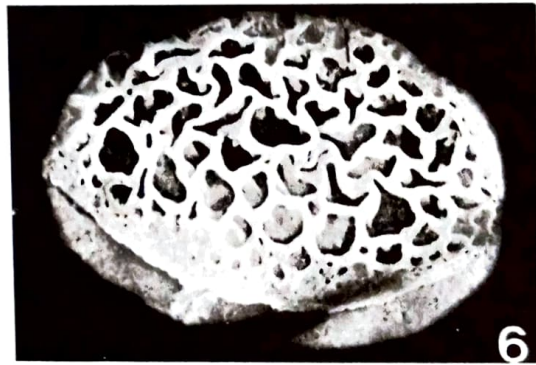
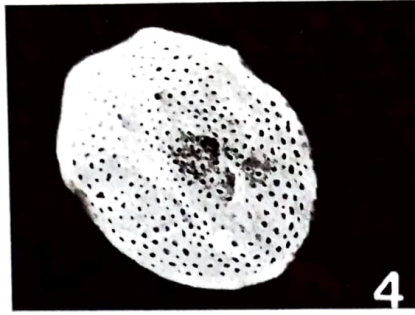
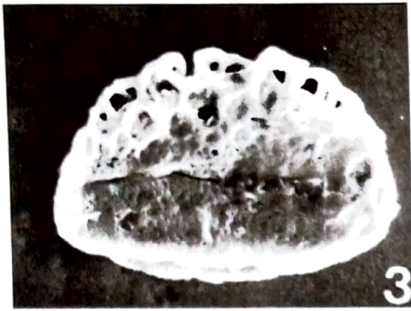
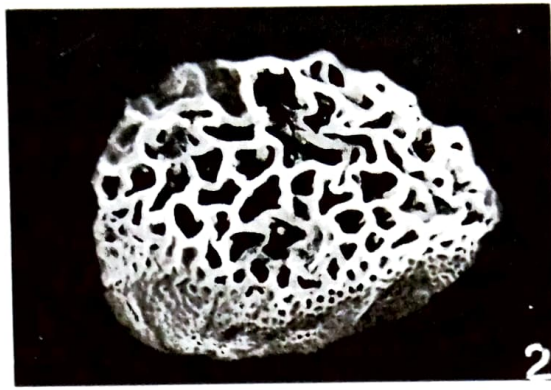
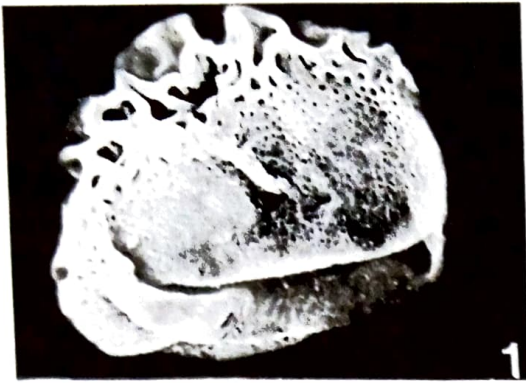


PLATE II

Palynomorph extraction methods and details of microscopic (LM, SEM and TEM) techniques and of lodgement of reference palynomorph slides, have been given in our earlier works (Pocock & Vasanthy 1988, Cornet 1989, Cornet & Habib 1992).

DESCRIPTION

Equisetosporites and *Cornetipollis*

Equisetosporites chinleanus Daugherty 1941

- 1) Specimen from the type locality (Petrified forest member, Chinle Formation, Arizona) late Carnian (Pocock & Vasanthy, 1988, Plates I, II, III). Ellipsoidal, 48(50.5)56x25(31)39 μm ; ellipsoidal; psilate, 9(15)18 ectexinal bands enveloping the smooth nexinal core.
- 2) Specimen from the Ciniza lakebeds, Chinle Formation, Western New Mexico, late Carnian (Pl. 1, fig. 1, Pl. 5, figs. 1 & 2).
- 3) Specimen from the Chinle Formation, Garyfield County, Utah, Western USA (Zavada 1992, Plate VI, 1, 2, dimensions 41 x 29 μm and Zavada 1984, Figures 8, 9).

Cornetipollis reticulata Pocock & Vasanthy, 1988

- 1) Specimen from the type locality (Petrified Forest member, Chinle formation, Arizona), late Carnian; ellipsoidal, 63 (77 \pm 8) 86 x 31 (45 \pm 7) 60 μm , comprising an almost smooth central body encased in a banded exterior, bands (14 \pm 1), wider in the mid-region, and tapering towards the two points of fusion, at times manifesting slight twisting (Pocock & Vasanthy 1988).
- 2) Specimens from Ciniza lake beds, Chinle Forma-

tion, Western New Mexico, late Carnian, ellipsoidal, 90x75 μm , 16-18 scalariformly reticulate bands (Cornet 1985).

- 3) Specimens from the palynoflorule VB4, early Carnian, the Richmond rift basin of Virginia, Newark Supergroup:
 - a. Spheroidal, D= 108.0 μm , 90° rotated, 10-11 scalariformly reticulate bands in each hemisphere (Cornet & Habib 1992).
 - b. Ellipsoidal, 90x75 μm , 10-11 scalariformly reticulate bands in each hemisphere with 3-4 middle bands (Plate 1, figs. 2-4, Plate 5, fig. 3).

Dimensions of lumina: Cornetipollis: 1.0-1.5 μm .

Columellar heights: Equisetosporites: 0.5-0.6 μm ; Cornetipollis: 0.5-1.0 μm .

Nexine: Equisetosporites: 3.0-4.0 μm (three layered); Cornetipollis: 3.0-3.5 μm uni- or bi-(?) layered.

Description of structure and sculpture of *Equisetosporites chinleanus* and *Cornetipollis reticulata* have been published by Pocock and Vasanthy (1988, Plate 5, figs. 1-3).

Crinopolles and *Polycolpopollis*

Specimens and holotypes (3 species of *Monocrinopollis*; *Dicrinopollis operculatus*, 2 species of *Pentecrinopollis*, *Zonacrinopollis anasulcatus* and *Polycolpopollis magnificus*) are from the outcrop locality VB4 of the Richmond rift basin, Virginia, USA (Cornet 1989). *Monocrinopollis microreticulatus* has been reported (Litwin 1985) from the upper Carnian Petrified Member of the Chinle Formation

PLATE 2 (SEM)

(The taxa belonging to the *Crinopolles* group are from earliest Carnian to late middle Carnian or early late Triassic), the Richmond basin of Virginia, USA)

Monocrinopollis doylei

1. Oblique lateral view (44x35 μm), showing transition from fine to coarse sculpture; one of the two sulc(ul)i and the pontopericulum are in view. x1000.
2. Oblique lateral view (48x35 μm), showing transition from coarse to finely graded reticulate sculpture.

Dicrinopollis operculatus

3. Oblique distal view (38x25 μm) showing operculum. x1000.

Monocrinopollis microreticulatus

4. Micro-reticulately patterned proximal (31x25 μm) side. x1000.
5. Oblique distal view (62x38 μm), showing median sulc(ul)us and one of the lateral sulc(ul)i. x1000.
6. Oblique proximal view (40x30 μm) showing one of the lateral sulc(ul)i. x1000.
7. Enlargement of the lateral side showing transition from fine to coarse reticulum.
8. Enlargement of foveoreticulate surface of the distal side. 1-2, 4-8 by J. W. Walker and 3 by R. R. Keith.

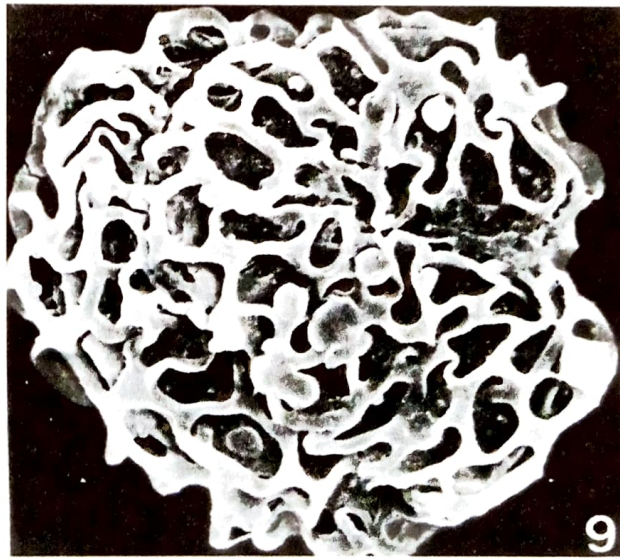
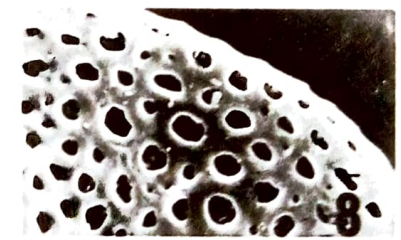
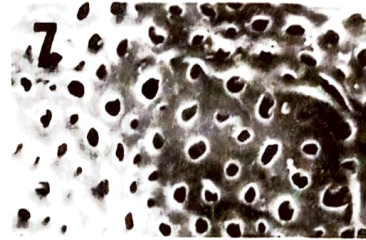
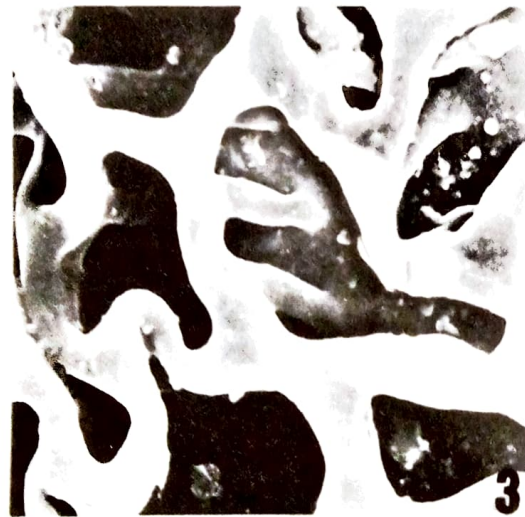
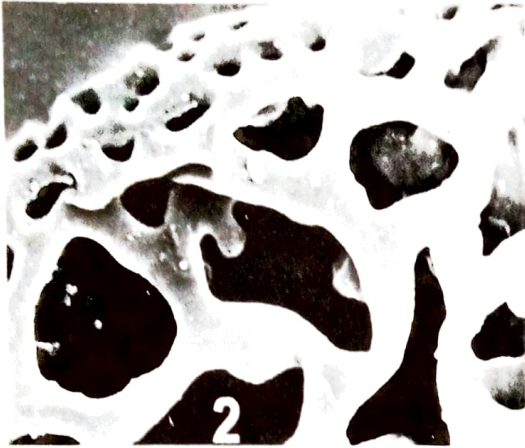
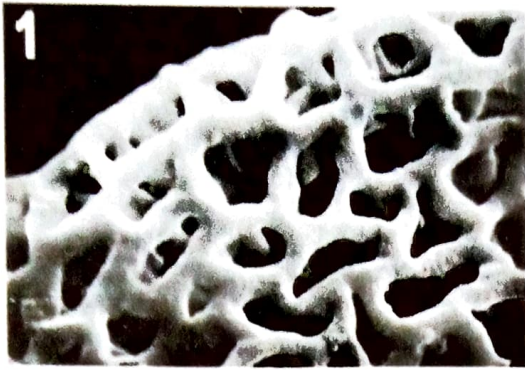


PLATE III

(*Tricrinopollis*) or finely pitted (*Monocrinopollis* and *Dicrinopollis*). The proximo-distal surface pattern in *Polycolpopollis* is coarsely reticulate. Muri of reticulum in all these taxa are psilate.

Dimensions of lumina: Monocrinopollis doylei: dimorphic, larger: 4.5-12.0 μm ; smaller: 0.8-2.0 μm ; *M. microreticulatus*: 0.4-0.6 μm ; *M. mulleri*: 1.5-6.0 μm ; *M. walkeri*: dimorphic, larger: 1.1-2.6 μm ; smaller: 0.4-0.5 μm , *Dicrinopollis operculatus*: 3.0-9.8 μm ; *Tricrinopollis olsenii*: heteromorphic reticulum, larger lumina 3.0-10.5 μm ; *Pentecrinopollis traversei*: <1.0 μm ; *Zonacrinopollis anasulcatus*: 4.5-7.5 μm and *Polycolpopollis magnificus*: 3.0-11.0 μm (maximum length of lumina).

Exine structure: Monocrinopollis spp.: 2-layered, with a well-developed footlayer proximally, ectexine thinner distally with footlayer discontinuous or missing, columellae reduced to granules and short rods under area with finer reticulum, endexine if present is thicker under distal aperture. *Monocrinopollis doylei*: 1.8-3.0 μm ; *M. microreticulatus*: 0.4-0.6 μm ; *M. mulleri*: 1.1-1.5 μm ; *M. walkeri*: 0.6-0.7 μm ; *Dicrinopollis operculatus*: ca 1.4 μm with a well-developed footlayer proximally, ectexine thinner distally, with a footlayer discontinuous or missing and columellae reduced or absent under area with finer reticulum, endexine present; *Tricrinopollis olsenii*: 2.0-3.0 μm , with a well-developed footlayer proximally, distal ectexine much thinner than proximal ectexine, footlayer 0.15-0.21 μm thick proximally, disappears equatorially and distally under finer reticulum, endexine present, continuous and noticeably thicker under sul(cu)li and where footlayer is absent (Plate 5: 6); *Pentecrinopollis traversei*: exine composed of a 1.0-1.5 μm thick nexine bearing large prominent clavae whose heads are joined by a delicate reticulum that abruptly becomes an imperforate tectum along the sides of furrows containing the sulculi

(Cornet 1989); *Zonacrinopollis anasulcatus*: exine 2-layered with a well-developed foot layer proximally, ectexine thinner distally with footlayer discontinuous or missing and columellae reduced or absent under area with fine reticulum, endexine not observed; ca. 3.0 μm and *Polycolpopollis magnificus*: 4.0-6.0 μm , nexine ca. 0.8-1.0 μm thick, apparently single-layered without an endexine, sexine thins at apertural margins as reticulum joins footlayer.

Heights of proximal columellae: Monocrinopollis doylei: 1.8-3.0 μm ; *M. microreticulatus*: 0.4-0.6 μm ; *M. mulleri*: 1.1-1.5 μm ; *M. walkeri*: 0.6-0.7 μm ; *Dicrinopollis operculatus*: ca 1.4 μm ; *Tricrinopollis olsenii*: 2.0-3.0 μm ; *Pentecrinopollis traversei*: <0.5 μm ; *Zonacrinopollis anasulcatus*: ca. 2.2 μm and *Polycolpopollis magnificus*: 4.0-6.0 μm .

Table 1 includes the dimensions of the selected pre-Cretaceous columellate angiospermid palynomorphs and their key characters for easy comprehension.

DISCUSSION

Inaperturate and banded Equisetosporites vs Cornetipollis

The Late Triassic psilate banded *Equisetosporites* is exo- and endo- morphologically different from the foveoreticulately and/or scalariformly banded *Cornetipollis* (Pl. 1, figs 1-4, Pl. 5, figs 1-3)

“Reticulately” banded *Cornetipollis reticulata* vs the pollen type of the tribe Trichanthereae (Acanthaceae)

Without reiterating discussions in Vasanthy and Pocock (1986) and Pocock and Vasanthy (1988), we briefly differentiate the former from the latter (Pl. 1, figs 2-6, Pl. 5, figs 3-4): besides the differences in

PLATE 4 (SEM)

Classopolis minor Pocock & Jansonius 1961

1. Distal view, poral membrane detached exposing the edges of endo-annulus; note the sub-equatorial furrow (white arrow). x3 600. (SEM by S.A.J. Pocock).

Classopolis harristii Muir & Van Kon. Middle-Jurassic: Rhaeto-Liassic.

2. Note the columellar complexity (C), faint lamellations within the nexine and the complex tectum (T). x13100 (by J. Medus).

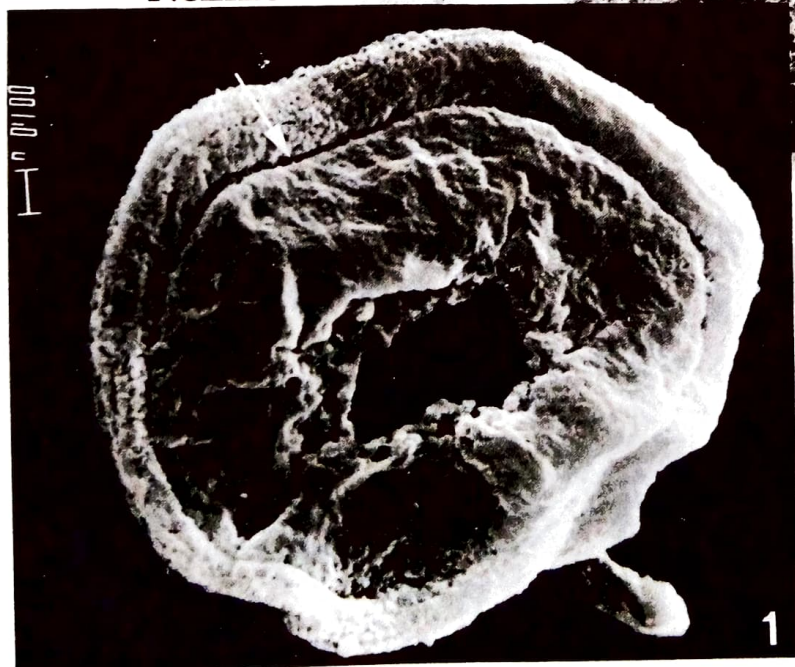


PLATE IV

Table 1. Key characters of the selected pre-Cretaceous columellate angiospermid palynomorphs

Taxa	Key characters			
	Daugherty (1941)	Dimension (lxb)	No. & type of apertures	Surface features
1. <i>Equisetosporites chinleanus</i> Pocock & Vasanthi (1988)		48-56x25-39 µm	9-18 furrows	psilate
1. <i>Cornetipollis reticulata</i> Cornet (1989)		63-86x31-60 µm	14-15 furrows	scalariformly reticulate
1. <i>Monocrinopollis</i>			1-distal compound sulculus,	proximo-distally finely or
a. <i>M. doylei</i>		36-51x29-45 µm	pontoperculum narrow	coarsely reticulate to
b. <i>M. microreticulatus</i>		27-35x21-27 µm		foveoreticulate or faintly
c. <i>M. mulleri</i>		36-49x25-40 µm		pitted
d. <i>M. walkeri</i>		24-38x16-35 µm		
2. <i>Dicrinopollis operculatus</i>		38-46x25-39 µm	2-lateral sulculi with a wide foveoloidate operculum	proximo-distally coarsely reticulate to foveoreticulate
3. <i>Tricrinopollis olsenii</i>		42-53x25-39 µm	1 distal + 2 lateral sulculi	proximo-distally coarsely reticulate to foveoreticulate
4. <i>Pentecrinopollis traversei</i>		66-88x42-55 µm	"5-plicae" or 5-sulculi	clavae on micro-reticulum
5. <i>Zonacrinopollis anasulcatus</i>		39-41x30-33 µm	zonasulculus	proximo-distally coarsely reticulate to foveoreticulate
6. <i>Polycolpopollis magnificus</i>		D: 69-90 µm	zonasulculus, spiraperturate	coarsely reticulate

dimensions, number of bands, tectal columellar distribution patterns, and the presence of baculoid sculptural elements (Pl. 1, figs 2-5), we underscore here the following exinal differences of significant diagnostic value: the columellae of *C. reticulata* are

short (<0.5 µm) and well-fused with the foot layer or unstructured nexine whereas the basally branched or "hollowed out" columellae (3.5-4.0 µm) of Trichanthereae type of pollen are superficially "attached" to the surface of endexine or nexine which

PLATE 5 (TEM)

Equisetosporites chinleanus, palynomorph from the Ciniza lakebeds, Chinle Formation, Western Mexico, late Carnian.

1. TEM section of Pl. 1, fig. 1 illustrating the juxtaposed layers of endexine bordered by their respective lamellate zones; note the periclinal lamellae darkly staining and interlamellae (weakly staining) are undulate, convoluted, looped and also humped (arrow). x21000.
2. Section through about half of a grain with rotated halves or hemisphere (<90° rotation of bands): a parallelly sliced band in the left side and five cross sectioned bands in the right: the inner faces of the opposing hemispheres are juxtaposed due to the flattening of the grain or its lateral compression. The thick tectum (T) hemispherical in cross section is supported by short columellae (C), mostly of inclined or oblique orientation arising from the non-lamellated footlayer. x4900.

Cornetipollis cf. *reticulata*, from the Middle Carnian of the Richmond basin (VB4), VA, USA.

3. A thin bilaterally compressed section of the palynomorph in Plate 1: 2 & 3 passing through the rotated furrows and bands (across lumina or foveolae, and marginal cross-walls or muri) exhibiting different planes of sectioning. x4250. Inset: Enlargement (x6000) of the upper right portion of the above section; note the

columellae (arrows) and conic and wedge-shaped sections of cross-walls interlinked by a thin tectal connection of part of marginal murus (short white arrow).

Sanchezia equatoriensis Leonard (Tribe Trichanthereae, Acanthaceae, from the NY Botanic Gardens Herbarium.

4. The basally bifurcated or hollowed (arrow) columellae (C) supporting the thick tectum (T) are superficially "attached" to the surface of endexine or nexine which encloses many small "gaps" and is lined by a few lamellae in the upper part. x27500.

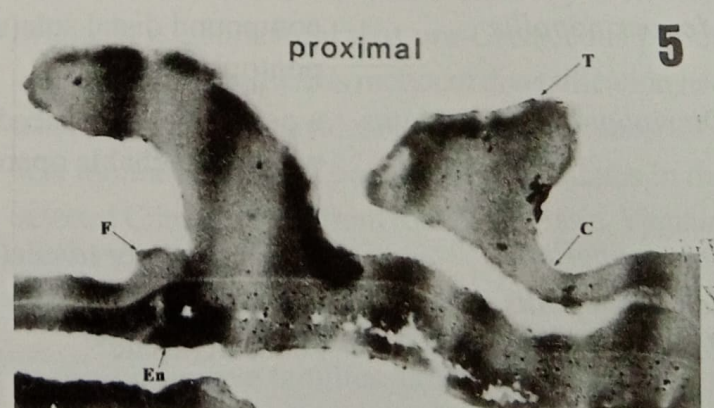
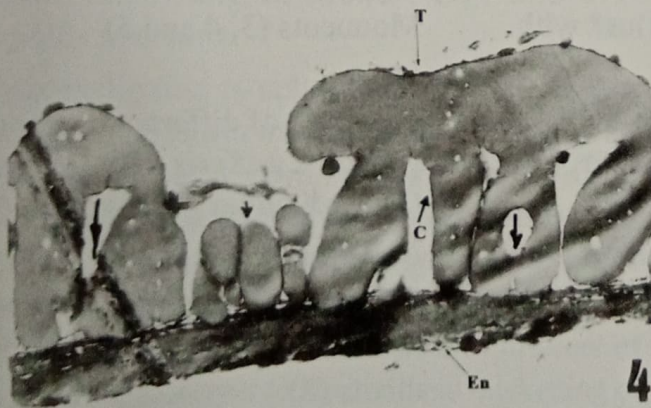
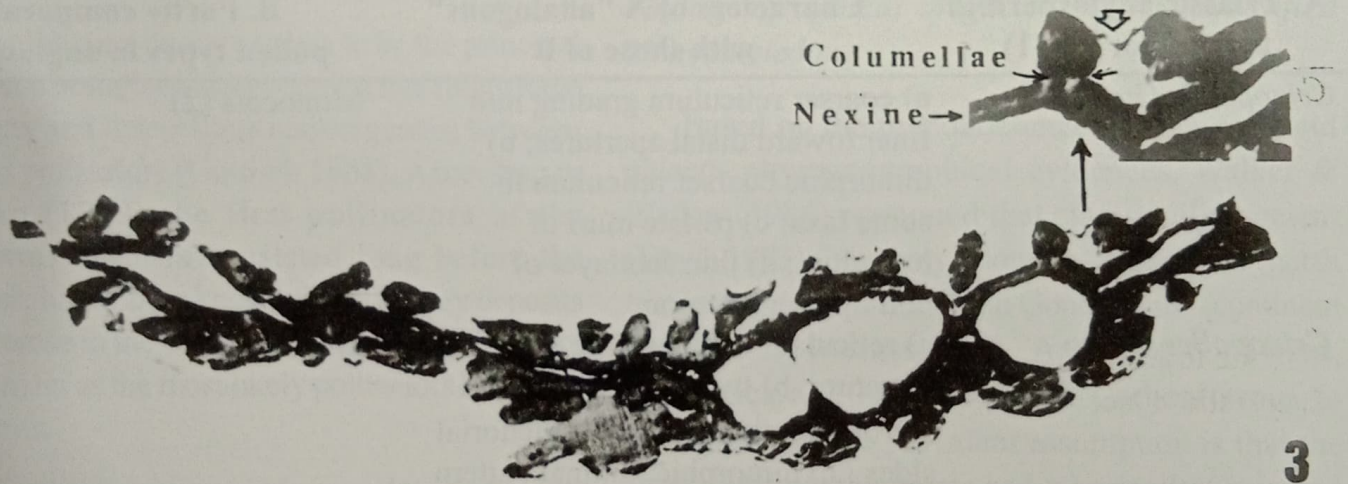
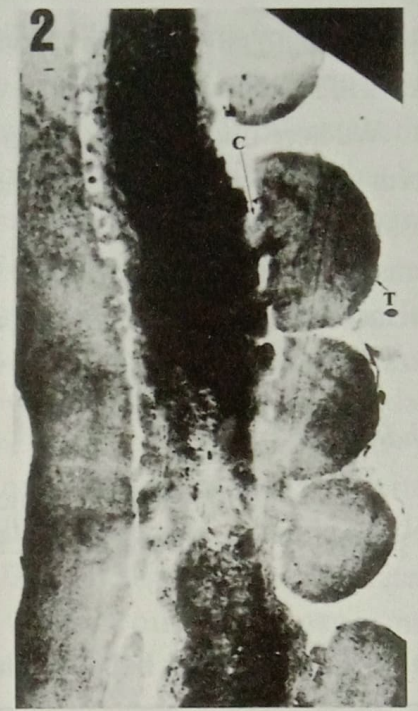
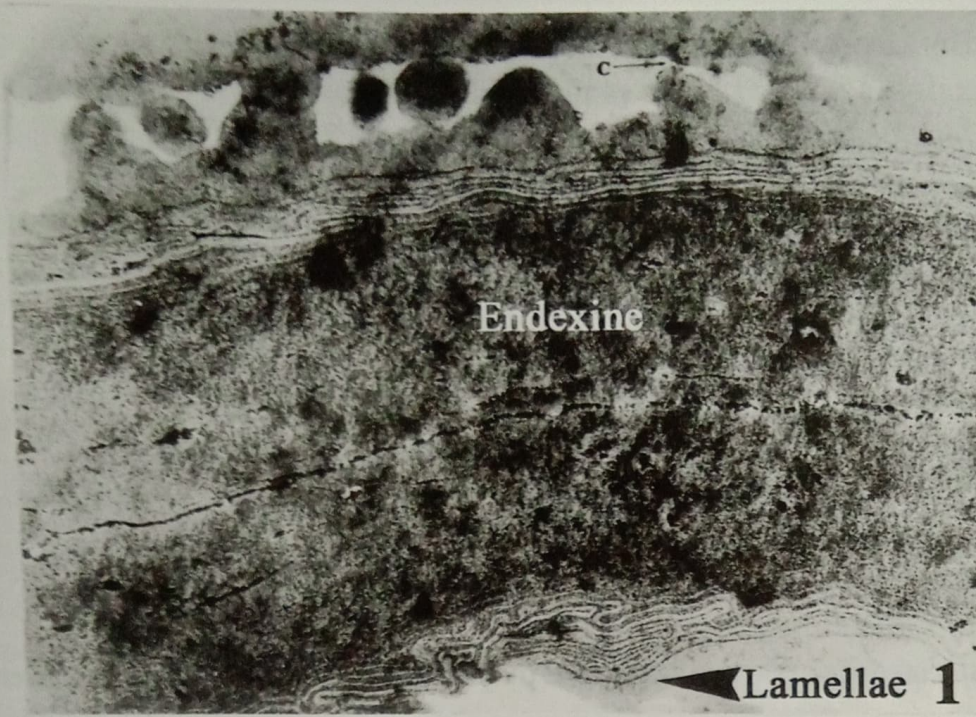
Monocrinopollis doylei

5. TEM enlargement of exine showing dark non-laminated endexine (En) with many small holes or "gaps" and a footlayer (F) on the proximal side; note the columellae (C) and the tectum (T) of coarsely reticulate proximal side. x27470

Tricrinopollis olsenii

6. TEM showing coarsely reticulate-columellate proximal side (on bottom and upper right) and foveolate distal side (upper left); note the darker endexine, and the ectosul(cu)lus (S). X4,690.

1-2 by A.V. Chadwick; 4 by J.R. Rowley. and 5-6 by J.W. Walker;



encloses many small "gaps" and lined by a few lamellae in the upper part (Pl.5, fig. 4).

We here underscore that foveoreticulate bands occur not only in extant Trichanthereae pollen and their fossil "look-a-likes" from the Late Triassic, Late Jurassic, Cretaceous and Tertiary but also in the Upper Cretaceous non-columellate spore *Costatafoveosporites foveolatus* Deak (Srivastava 1990).

Change of symmetry

Radial through rotated symmetry via torsion which is probably a non-adaptive character, has been

encountered in plant groups of different geological ages and evolutionary lineages: *Tornopollenites* complex and *Ephedripites* complex (Triassic through Tertiary), and recent taxa *Ephedra* spp. (Ephedraceae), *Holochlamys* (Araceae in Thanikaimoni 1969) and acanthaceous *Bravaisia*, *Sanchezia*, *Trichanthera* (Tribe Trichanthereae) and *Nilgirianthus* (Pocock & Vasanthy 1986 and references cited therein).

Columellae supported reticulate exine

Columellate infratectum and non-lamellate (non-gymno-spermous), unilayered nexine in combination

Table 2. Similarities between the selected Triassic angiospermid palynomorphs and angiosperm pollen

A. Triassic angiospermid palynomorphs (1)	Characters of A "analogous" with those of B	B. Partly comparable pollen types in angiosperms
<i>Crinopolles</i> Group	a) coarser reticulum grading into finer toward distal apertures; b) dimorphic coarser reticulum in some taxa; c) psilate muri of reticulum; d) thin footlayer of non-apertural region	Monocots (2)
<i>Crinopolles</i> Group	a) reticulate - columellate exine structure; b) two or more sulc(ul)i* or furrows on the distal and equatorial sides ; c) dimorphic luminal pattern	Liliaceae (2)
<i>Monocrinopollis</i>	compound distal sulc(ul)us* with pontoperculum	Monocots (3, 4 and 5)
<i>Dicrinopollis operculatus</i>	a pair of widely spaced sulc(ul)i* with a detachable operculum	a number of different monocot genera, e.g. <i>Xyris</i> - Xyridaceae (3); <i>Polianthes</i> - Agavaceae (6)
<i>Tricrinopollis</i>	tricolpoidate or trisulc(ul)ate*	<i>Nelumbo</i> - Nymphotoideae (7)
<i>Zonacrinopollis</i>	occasional union of eq sulc(ul)i* .	<i>Nelumbo</i> - Nymphotoideae (7)
<i>Zonacrinopollis</i>	zonasulc(ul)ate*	Monocots (3) and primitive dicots (8)
<i>P. traversei</i>	large size and finely reticulate exine	insect pollinated angiosperms (1)
<i>Polycolpopollis magnificus</i>	ring sulc(ul)ate* or spiroaperturate	Scrophulariaceae, Berberidaceae, and Acanthaceae (a)

* Sulcooidate apertures of the Triassic *Crinopolles* group are partly similar to the sulcate apertures of angiosperms.

(1) Comet, 1989; (2) Walker and Walker, 1984; (3) Thanikaimoni, 1969; (4) Chanda and Ghosh, 1976; (5) Chandæt al., 1978; (6) Alvarez and Köhler, 1989; (7) Kuprianova, 1979; (8) Walker, 1976; and (9) Furness, 1985.

with a foveo-reticulate to scalariformly reticulate tectum in *Cornetipollis reticulata* strongly impart an angiospermid semblance, despite the lack of distinctive germinal aperture in the nexine. It is generalised that the earliest unequivocal angiosperm pollen grains from the Lower Cretaceous (Barremian-Aptian) have reticulate sculpturing with tectate-columellate wall structure (Zavada 1984). Zavada hypothesized that in angiosperm pollen the reticulate sculpturing is indicative of sporophytic self-incompatibility (SSI) while imperforate and microperforate exine sculpturing is indicative of gametophytic self-incompatibility (GSI). Applying the same criteria, could we infer that the Late Triassic *Cornetipollis* and *Crinopolles* were sporophytically self-incompatible?

Pollinators of pre-Cretaceous Period

The pollination process seems to be the principal driving force in angiosperm evolution that might have led to many and marvellous convergences between plants and pollinators (Gottlieb 1968). According to Takhtajan (1969) the first pollinators of the angiosperms must have existed long before the Cretaceous; honey bees known from Tertiary deposits probably arose in the Cretaceous period and therefore beetles remain as the most likely pollinators of extinct angiosperms.

Endexine thickening in Mono-, Di-, and Tri-Crinopolles structure:

Proximal exine is columellate with a thicker footlayer in *Monocrinopollis*, *Dicrinopollis*, *Tricrinopollis*, and *Zonacrinopollis*; distally columellae are much reduced to granules or short rods and footlayer is absent. Endexine is thickened under aperture(s) (e.g. *Tricrinopollis olsenii* in Pl.5, fig. 5) in the three aforementioned taxa. Diminution of columellae and footlayer (ectexinal) and thickening of endexine at the furrows may be functionally semi-harmogathic or desiccation minimising adaptation protecting the pollen cytoplasm (Heslop-Harrison 1979) under the arid climatic condition of the Triassic.

Evolution of columellae

If the columellae are the exclusive features of

angiosperms, then how to account for columellar and tectal complexity in Mesozoic coniferalean Circumpolles? (Plate 4, fig. 2). Pre-Cretaceous *Classopollis* has a columellate infrastructure but has an unusual apertural arrangement and the exinal elaborations (Pocock *et al.* 1990).

The angiosperm-like pre-Cretaceous pollen *Cornetipollis* is tectate-columellate with a thin foot layer and lacks a sulcus but with multiaperturoidate grooves. The hypothetical view on the primitivity of angiospermic exine columellae is not only supported by their presence in the Cretaceous angiosperm pollen (Doyle & Hickey 1976) but also in these reticulately sculptured pre-Cretaceous angiospermid palynomorphs.

Phytogeographical origin of earlier diversified Monocotyledons

Based on the preponderance of both neo- and palaeo- phytogeographical evidences, Walker & Walker (1986) presumed that cladistically ancient (Doyle 1973) monocotyledons had a laurasian (north temperate) origin rather than Gondwanian (continent connecting India with S. America, S. Africa, Antarctica and Australia from Carboniferous to Jurassic). But the prevalent assumption is that the monocots like the dicots had a basically Gonwana origin. It is conjectural that pre-Cretaceous pollen exhibiting trends towards monocot diversification had a laurasian origin as evidenced from the presence of a few monocotyledonid pollen character states in the selected *Crinopolles* taxa from Richmond Basin, Virginia, USA (Table 2).

The tectate-columellate wall structure is observed in most primitive families and orders of monocots. Endexine is very rare in monocots and when present is different from the endexine observed in dicots (Zavada 1983). That the endexine in the *Crinopolles* (Pl.5, figs 5,6) is dicotyledonid rather than monocotyledonid is conjectural. So the pollen types of the *Crinopolles* group seem to straddle both the mono- and di- cotyledonous classes.

Aperture evolution

The hypothetically most primitive monosulcate pollen characterises Magnoliales, some other primitive dicots, the majority of monocots and many gymnosperms including *Bennettitales*, cycads, *Welwitschia*, and *Ginkgo*. The monosulcoid to multiaperturoid (Table 1) character states of these palynomorphs appear to have preceded the monosulcate → tricolpate → tricolporate aperture evolution of the Cretaceous.

Pseudoapertures or harmomegathic furrows in *Cornetipollis* and *Equisetosporites* and sulcoidate apertures of *Crinopolles* lacking localised germinal pore with or without endexinal thickening had probably provided exits by flexure for pollen tube.

Triassic *Crinopolles*, upper Albian *Liliacidites* and extant *Lilium* pollen: Dissimilarities

Comparative exine structural analysis of Late *Tricrinopollis* and *Monocrinopollis* (Pl. 5, figs. 5 & 6) differ from *Liliacidites* (TEM in Walker & Walker, 1984) and *Lilium longiflorum* (Baldi *et al.*, 1987) not only by their tall columellae and considerably thicker tectum but also by the presence of a thick endexine or nexine-2. Presence of endexine is not typical of monocotyledons

Inferences

1. Striations-like-apertures underlined by unmodified endexine and/or nexine are indicative of pollen-wall protective strategy (desiccation minimizing) for pollen protoplasm during anther-stigma transits in the arid climate of the Triassic.
2. Three layered nexine in *Equisetosporites* may be representative of an evolutionary stage in nexine evolution (Guèdes 1982; Vasanthy *et al.* 1990).
3. Proximo-distally reticulate to foveo-reticulate exine in *Crinopolles* group is apparently monocotyledonoid.
4. Reticulate-columellate exines in *Cornetipollis* and *Crinopolles* group are assertive of their angiospermic nature.
5. The *Crinopolles* types seem to straddle both monocots and dicots.

6. The Late Triassic angiosperm precursor (relatively "fragile") plants which produced *Equisetosporites*, *Cornetipollis* and *Crinopolles* might have been probably non-fossilized due to the aridity-induced degradation of organic matters of vegetative and reproductive parts except exines formed of one of the hardest organic compound (the carotenoid "sporopollenin").

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