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Eostangeria ruzinciniana (Zamiaceae) from the Middle Miocene of Bulgaria and its relationship to similar taxa of fossil *Eostangeria*, and extant *Chigua* and *Stangeria* (Cycadales)

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ABSTRACT. Characterisation of *Eostangeria ruzinciniana* (Palamarev, Petkova & Uzunova) Palamarev & Uzunova (Middle Miocene – Volhynian, Bulgaria) is augmented. The species is compared with morphologically similar cycads: *E. saxonica* Barthel (Eocene of Germany), *E. pseudopteris* Z. Kvaček & Manchester (Late Palaeocene and Eocene of western USA), and the extant *Chigua* D. Stevenson and *Stangeria* T. Moore. Leaf epidermal anatomy indicates that *E. ruzinciniana* is closely related to other members of *Eostangeria*, forming with them a natural unit. *Eostangeria* slightly differs from *Chigua* (Zamioideae) in the presence of short dark-staining cells in the lower epidermis, densely toothed margins, and in the case of *Eostangeria ruzinciniana* by obviously persistent, non-articulated leaflets. In morphological features of the leaflets, *Eostangeria* resembles *Stangeria* (Stangeriaceae); however, the latter decidedly differs in entirely cyclocytic stomata lacking ventral lignified lamellae, coarsely striated epidermis with strongly undulate anticlines and an absence of short dark-staining cells. A new subfamily Eostangerioideae is suggested to accommodate *Eostangeria* within Zamiaceae.

KEY WORDS: leaf anatomy, Cycads, Zamiaceae, Eostangerioideae, palaeoecology, Tertiary

INTRODUCTION

Discovery of every new taxon of fossil or recent cycads is of interest for deciphering evolution of this plant group. The cycads combine important morphological and anatomical features that help elucidate evolution and adaptations of the gymnosperms in general. In recent floras, the cycads are characterized by highly disjunct distribution ranges and pronounced endemism. The roots of these peculiarities have to be traced in the past history of this group.

The recognition of a new extinct species of the fossil genus *Eostangeria* in western North America (Kvaček & Manchester 1999) after *E. saxonica* (Barthel 1976) and *E. ruzinciniana* (Palamarev & Usunova 1992) in Europe and discovery of a new recent genus *Chigua* (Stevenson 1990) give a new stimulus for further comparative investigation of these cycads.

In this paper, we summarize the results from a reinvestigation of all samples of *Eostangeria ruzinciniana* (Palamarev, Petkova & Uzunova) Palamarev and Uzunova in detail and compare the species with the other extinct species of *Eostangeria* Barthel and representatives of the recent genera *Stangeria* T. Moore and *Chigua* D. Stevenson.

MATERIAL AND METHODS

The fossil samples of *Eostangeria ruzinciniana* (Palamarev, Petkova & Uzunova) Palamarev and Uzunova came from the Lower Sarmatian, i.e., Volhynian sediments (Middle Miocene) of the Krivodol Formation in northwestern Bulgaria near the village of Ružinci (coordinates lat. 43°40′ N, long. 23°20′ E). This site is the only place, where *E. ruzinciniana* has been recovered.

Fragments of pinnate leaves studied (samples No. 3517, 3518, 3615, 3657) are preserved in marly sandy shale as impressions with preserved cuticles. The slides with cuticular membranes (Nos 21, 28, 34, 39, 44a, 46, 60, 61 and 61a) were prepared from the sample No. 3518. The comparative material of recent cycads has been studied in the herbaria and on plants in cultivation (National Museum of Natural History, Washington, DC (USNM), New York Botanical Garden (NY), botanical gardens Berlin-Dahlem and Gainesville). Anatomical slides belong to the collections of the Department of Palaeobotany and Pollen Analysis of the Botanical Institute of Bulgarian Academy of Sciences (Nos 2627, 2628 2629, 2630, 2631, 2632, 2633) and Faculty of Science, Charles University, Prague. Leaf fragments for anatomical observation have been obtained from *Chigua restrepoi* (D. Stevenson 693, NY) and *C. bernalii* (Bernal, Galeano Restrepo 1189, USNM), the specimens of *Stangeria eriopus* came from the cultivated plants in the Botanical Garden Berlin-Dahlem (E. Palamarev 2604), and Gainesville, those of *Zamia* and *Ceratozamia* from the collection of Florida University (G. Schutzman, Gainesville).

The descriptions of morphological and anatomical characters follow the terminology of Pant and Nautiyal (1963) and Dilcher (1974).

Preparations of cuticular membranes were made by maceration in Schulze solution followed by clearing in 5% KOH or by treatment in 20% hydrogen peroxide. Most of the cuticular membranes have been stained in Sudan IV, or safranine.

COMPARATIVE MORPHOLOGICAL DATA OF LEAFLETS

FORM AND SIZE

Eostangeria, *Chigua* and *Stangeria* all possess fernlike leaves with a stout rachis and leaflets with pinnate venation (Fig. 1a-f). The leaflets are opposite to predominantly alternate. *Eostangeria ruzinciniana* has markedly spiral arrangement but in the other two fossil species of the genus *Eostangeria* the phyllotaxy is unknown. In the recent species *Stangeria eriopus* both types of the leaflet arrangement can be observed (Greguss 1968). The species of *Chigua* also have mixed arrangements, being spiral on the base of the rachis, almost opposite in the middle part of the rachis and opposite in the upper part (Stevenson 1990). These data show that the arrangement of leaflets lacks any taxonomic value.

According to the form of leaflets, we can recognize a range from lanceolate (*E. saxonica*, *E. ruzinciniana*, *Stangeria eriopus*, *Chigua restrepoi*) to the linear-lanceolate shape (*Chigua bernalii*) with the intermediate form (oblong-lanceolate) ocurring in *Eostangeria pseudopteris* and *Stangeria eriopus*. The leaflets show great size variation. The fossil species *E. saxonica* and *E. pseudopteris* have similar dimensions of the leaflets while *E. ruzinciniana* differs from them in its shorter and slender leaflets (about 60 mm long and 5–10 mm wide). The two species of the recent genus *Chigua* and *Stangeria eriopus* possess much larger leaflets than all the fossil taxa of *Eostangeria* (Tab. 1 and Fig. 1a, b).

ATTACHMENT

Leaflets of *Eostangeria ruzinciniana* are always fossilized together with the rachis (Pl. 1 figs 1–2, 4). This is an indication they may not be deciduous and the pinnate leaf has probably fallen completely. The other species of *Eostangeria* have been found always as detached leaflets, a possible evidence that they were articulate (as is the case in all Zamioideae incl. *Chigua*). The leaflets of *Stangeria* are not deciduous from the rachis.

VENATION

All species compared have more or less frequently dichotomizing secondary veins and the venation is basically pinnate craspedodromous and camptodromous. In some species, the veins terminate in the leaflet teeth but in *Eostangeria ruzinciniana*, *Chigua restrepoi* and *C. bernalii* the veins are faintly visible before entering the teeth or join the margin (Pl. 1 fig. 3). In *Eostangeria pseudopteris* (like in *Stangeria*), a peculiar looping (fusing) of two adjacent secondaries on the leaf margin was rarely observed (Kvaček & Manchester 1999).

In *Stangeria*, *Eostangeria*, and *Chigua restrepoi* the midrib reaches the leaflet apex, while in *C. bernalii*, it splits into individual veins within its course and loses its individuality before reaching the leaflet tip (Fig. 1a).

These species can be further differentiated into two groups according to the density and angle of divergence of the secondaries: a group with more than 15 pairs of secondaries and wide angles (50–75°) – *Eostangeria saxonica*, *E. pseudopteris* and *Stangeria eriopus*, and a group with only 10–15 pairs of veins and narrow angles (less than 50°) – *Eostangeria*

Table 1. Morphological features of the leaflets of *Eostangeria*, *Chigua* and *Stangeria*

Species	Form	Base	Apex	Margin	Midvein	Number and angle of secondaries	Termination of secondaries	Size (in cm)
Eostangeria saxonica Barthel	lanceolate	asymmetric cuneate sessile	acute	toothed irregularly along the whole leaflet length	prominent	more than 25 pairs, dichotomic 60–75°, alternate	±every third vein terminates in a tooth	12.0×1.6
E. ruzincianiana (Palamarev, Petkova & Uzunova) Palamarev & Uzunova	lanceolate	asymmetric cuneate-decurrent, sessile	acute	regularly toothed, the base entire	moderate	about 15 pairs dichotomic 40–50°, alternate	±every second vein terminates obscurely in a tooth	5.0–7.0×1.0–2.0
E. pseudopteris Z. Kvaček & Manchester	oblong- lanceolate	asymmetric cuneate sessile or short petiolulate	attenuate	irregularly toothed, the base entire	moderate	more than 25 paires, mostly simple 60–75°, opposite or alternate	±every second vein terminates obscurely in a tooth	11.0×2.0–3.0
Chigua restrepoi D. Stevenson	lanceolate to lanceolate-ovate	symmetric cuneate sessile	acute	irregularly toothed, the base entire	moderate weak	about 10–12 pairs, mostly simple 2–30°, alternate	most secondaries terminate obscurely in widely spaced teeth	15.0–25.0×3.0–5.0
C. bernalii D. Stevenson	linear- lanceolate	symmetric cuneate sessile	attenuate	irregularly toothed, the base entire	moderate, not reaching the apex	about 10–15 pairs, mostly simple 2–10°, alternate	most secondaries terminate obscurely in solitary teeth	30.0–35.0×1.0–1.5
Stangeria eriopus (Kunze) Baillon (incl. *S. paradoxa* T. Moore)	oblong-lanceolate	±asymmetric cuneate petiolulate to sessile or decurrent	attenuate	irregularly toothed or entire	moderate	more than 25 paires 55–70°, alternate	secondaries terminate in teeth or fuse with the margin	10.0–30.0×2.0–5.0

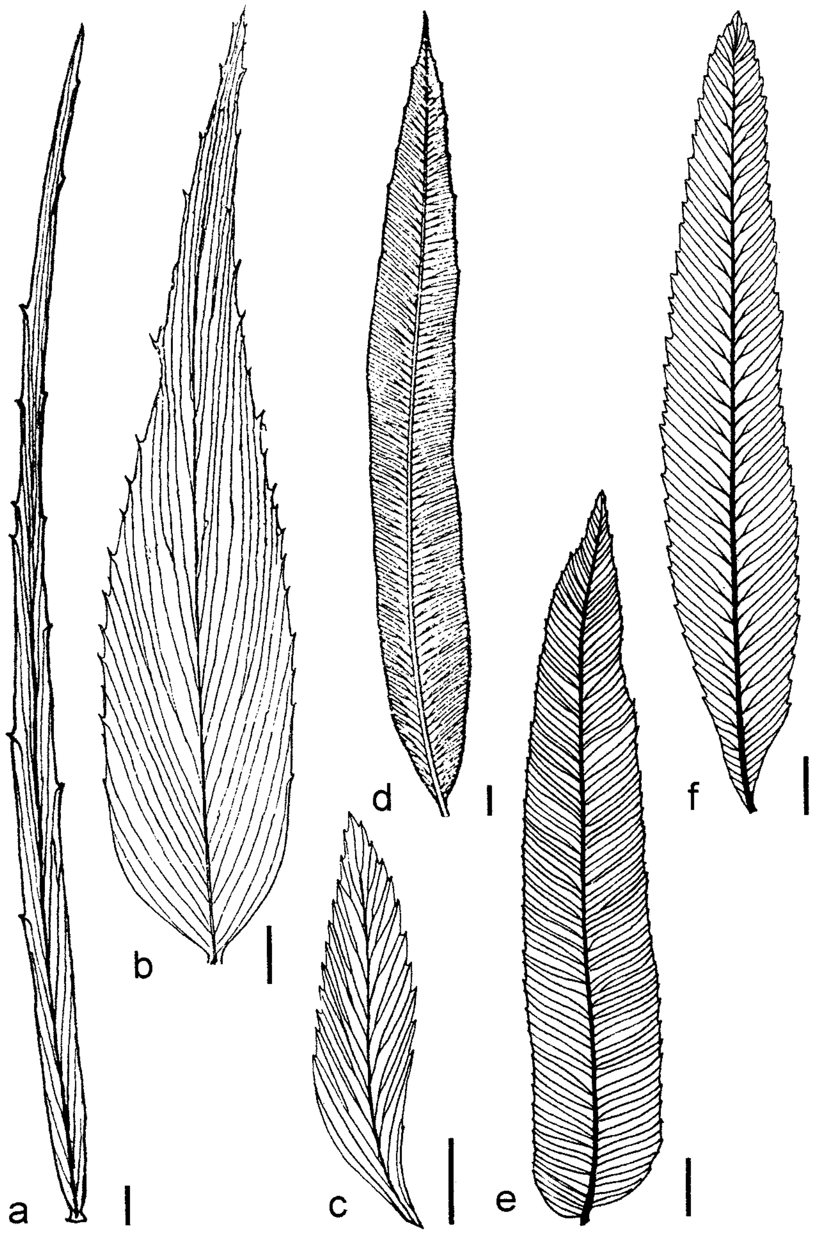

Fig. 1. Comparative leaflet morphology: **a** – *Chigua bernalii* D. Stevenson, extant, Colombia, **b** – *Ch. restrepoi* D. Stevenson, extant, Colombia, **c** – *Eostangeria ruzinciniana* (Palamarev et al.) Palamarev & Usunova, Middle Miocene, Bulgaria, **d** – *Stangeria eriopus* (Kunze) Baillon, extant, South Africa, **e** – *Eostangeria pseudopteris* Z. Kvaček & Manchester, Late Palaeocene-Eocene, USA, **f** – *Eostangeria saxonica* Barthel, Eocene, Germany (scale bar – 10 mm)

ruzinciniana, *Chigua restrepoi* and *C. bernalii* (Fig. 1).

OTHER GROSS MORPHOLOGICAL FEATURES

The leaflets of *Eostangeria pseudopteris* and *Stangeria eriopus* sometimes possess a short petiolule, otherwise they are sessile (subsessile), and in *Stangeria* even decurrent. All other species have sessile leaflets. In *Chigua* the leaflet base is conspicuously narrowed (Fig. 1a-b) like in many other Zamioideae, several veinlets enter the leaflet base besides the midrib (Pl. 1 fig. 5). In the species *Eostangeria ruzinciniana* and *Stangeria eriopus*, the basal portion of the leaflets is entire (or the whole leaflet is entire in some plants of *S. eriopus*); in other species of *Eostangeria* the leaflets are more or less dentate (Fig. 1a-f). Both species of *Chigua* are distinct by the entire margin of the leaflet base, and narrow, widely spaced teeth bent out from the margin (Pl. 1 fig. 6), like in some species of *Zamia*, e.g., *Z. muricata* Willd., *Z. cremnophila* Vovides, Schutzman & Dehgan

(Pl. 1 fig. 7). Of the recent genera of cycads, only *Stangeria, Chigua* and *Cycas* have a marked midvein in the leaflet, but in *Cycas* the leaflets or leaf segments are univeined, lacking secondary veins. The pinnate secondary venation of leaflets is shared by all species of *Eostangeria*, *Chigua* and *Stangeria*.

COMPARATIVE LEAF EPIDERMAL DATA

Table 2 summarises the epidermal features of taxonomic value. It shows that the three species of *Eostangeria* possess many traits in common. The upper epidermis consists of elongate cells with straight to slightly curved anticlinal walls and solitary short trigonal to elongate trapezoidal dark-staining cells scattered among them (Pl. 2). The nature of these cells is not certain but they may most probably represent thin-walled cells (in sense of Pant & Nautiyal 1963). When stained in Sudan IV or safranin the cuticular membrane of these cells in *E. ruzinciniana* (and also in other species of *Eostangeria*) takes the same colour as lignified lamellae of the stomata and subsidiary cells. Similar dark-staining cells can also be observed among ordinary cells in the lower epidermis. This feature readily differentiates the fossil species from some recent cycads, notably *Stangeria* (Tab. 2 and Bobrov 1962), where cells are hardly stained differentially because of high content of cellulose in the cell walls (cf. Pant & Nautiyal 1963). But in many Zamiaceae, thin-walled cells with an increased affinity for stains are common (e.g. Pl. 4 fig. 4). Stomata of *Eostangeria ruzinciniana* are distributed almost parallel to the secondary veins and only a few stomata are obliquely distributed (Pl. 2 fig. 5). The stomatal apparatus is monocyclic to amphicyclic. The species of *Eostangeria* differ in detailed form of subsidiary cells but all three species possess some stomata with one cell missing from the circle and sometimes include elongate trapezoidal dark-staining cells in the circle (Pl. 2 figs 3–5). Some differences have been observed in the epidermal structure of the individual species, e.g., in the arrangement of stomata and epidermal cells, peculiarities of the stomatal apparatus, trichome bases etc. but, as a whole, all three species of *Eostangeria* form a complex which can be accepted as a natural unit (genus).

The epidermal structure of *Stangeria eriopus* is markedly different not only from the fossil species of *Eostangeria* but also from all other recent cycads (see Bobrov 1962, Pant & Nautiyal 1963, Greguss 1968). The upper (adaxial) epidermis of *Stangeria eriopus* consists of elongate cells with deeply undulate walls and coarsely striated cuticle on the outer surface (Pl. 4 fig. 1). The cells of the lower epidermis are also with deeply undulate anticlinal walls (Pl. 4 fig. 2). The guard cells have a thickly cutinized inner stomatal rim (Pl. 4 fig. 3), and most importantly, the stomata are not sunken and lack ventral lignified lamellae. Such lamellae on the stomata are characteristic not only of the majority of the cycads but also of the conifers. Some primitive angiosperms have also lamellae on the stomata, but they are not lignified (Baranova 1972).

The distribution of stomata in *Stangeria* is chaotic and strongly resembles the distribution of the stomata in angiosperms. The stomatal apparatus is of the completely monocyclic (to amphicyclic) type. It is more appropriate to use Dilcher's (1974) classification for such stomatal types as for angiosperms and to call this type cyclocytic because it shows a well differentiated circle of subsidiary cells (Pl. 4 figs 2–3). This and other leaf epidermal features separate *Stangeria* from the other cycads, and support its placement in a different family – Stangeriaceae (Pilger) L.A.S. Johnson (Pant & Nautiyal 1963, Greguss 1968).

Both species of *Chigua* possess elongate straight-walled cells on the upper (adaxial) epidermis. Some of the epidermal cells in *C. bernalii* and the majority of them in *C. restrepoi* are darker, i.e., absorb intensively Sudan IV (Pl. 3). The epidermal cells in intercostal areas are shorter with straight to curved walls (more curved in *C. restrepoi*). Stomata in both species are monocyclic to amphicyclic. The subsidiary cells are 4–7 in number forming a circle. They absorb intensively Sudan IV and appear darker than ordinary epidermal cells after staining but their colour is different from that of lignified lamellae of the guard cells. Sometimes one polar subsidiary cell is missing and sometimes one subsidiary cell is longer, trapezoidal in form (Pl. 3 figs 3–5). Similar patterns and structures of stomata are widely distributed in *Zamia* (Pl. 3

Table 2. Comparison of epidermal features with taxonomical value between *Eostangeria*, *Chigua* and *Stangeria* (+ present, – lacking)

Species	Type of leaves	Adaxial cuticle			Abaxial cuticle							
		Epidermal cells	Dark-staining cells	Trichome base (µm)	Epidermal cells	Dark-staining cells	Stomatal topography	Stomatal type	Lignified lamellae	Subsidiary cells	Trichome base (µm)	Stomatal frequency (mm^2)
1	2	3	4	5	6	7	8	9	10	11	12	13
Eostangeria saxonica Barthel	hypostomatic	elongate acute to oblique ends straight to curved anticlines	short trigonal	+	elongate, irregularly polygonal, straight to slightly curved anticlines	short trigonal	randomly distributed in intercostal area	monocyclic rarely dicyclic, sometimes polar cells missing	+	2–7 irregularly polygonal, rounded, partly polar trigonal	20.0	–
E. ruzinciniana (Palamarev, Petkova & Uzunova) Palamarev & Uzunova	hypostomatic	elongate acute ends straight to slightly curved anticlines	short trigonal	20.0–30.0 10.0–20.0 ellipsoidal	elongate, shorter and irregularly polygonal between stomata straight to curved anticlines	short sometimes elongate, trigonal or trapezoidal	evenly distributed in intercostal area	monocyclic rarely dicyclic, sometimes polar cells missing	+	polygonal rounded polar cells elongate trapezoidal	12.0–17.0 5.0–10.0 ellipsoidal to rounded	67
E. pseudopteris Z. Kvaček & Manchester	amphistomatic	elongate acute ends slightly curved anticlines	short trigonal	+	polygonal, shortly elongate to isodiametric straight to curved anticlines	short trigonal	unevenly distributed in intercostal area	monocyclic	+	polygonal deltoidal trigonal	+	ca. 50
Chigua restrepoi D. Stevenson	amphistomatic	elongate rounded ends slightly curved anticlines	many of the ordinary epidermal cells darker than the others	15.0	elongate, curved anticlines	–	evenly distributed in intercostal area	monocyclic sometimes polar cells missing	+	irregularly polygonal, elongate, rounded	–	45
C. bernalii D. Stevenson	amphistomatic	elongate acute to rounded ends straight to curved anticlines	some of the epidermal cells darker than the others	20.0×15.0	elongate, shorter between stomata straight to slightly curved anticlines	–	in short rows in intercostal area	monocyclic sometimes polar cells missing	+	irregularly polygonal, elongate, rounded	15.0	66
Stangeria eriopus (Kunze) Baillon var. *schizodon* Moor (incl. *S. paradoxa* Moore)	hypostomatic	elongate, deeply U-shaped undulate anticlines coarse cuticular striations	–	15.0×12.0	elongate deeply U-shaped undulate anticlines	–	randomly distributed in intercostal area	monocyclic to dicyclic	–	elongate, narrower than epidermal cells with straight to shallow undulate anticlines	16.0	31

fig. 6, Pl. 4 fig. 5, see also Greguss 1968, Pls 166–182).

The comparison of the epidermal structure of *Chigua* and *Eostangeria ruzinciniana* (Pls 2–3) indicates many similarities between them, especially in the structure of the stomatal apparatus and some other features of the epidermis, like the distribution of the stomata, epidermal cells, trichome bases etc.

STRATIGRAPHIC DISTRIBUTION

The available palaeobotanical data document the three species of *Eostangeria* from the Upper Palaeocene (Fort Union Formation and possibly Wasatch Formation in USA) and Eocene (Clarno Formation in USA) – *Eostangeria pseudopteris*; Middle and Upper Eocene (Geiseltal and Boehlen Basins in Germany) – *E. saxonica*; and Middle Miocene, Lower Sarmatian (Ružinci-Krivodol Formation in Bulgaria) – *E. ruzinciniana*. These records indicate comparatively long stratigraphic range of the genus but with a long gap during the Oligocene and Lower Miocene.

PHYTOGEOGRAPHICAL AND ECOLOGICAL NOTES

In view of biodiversity of extant gymnosperms, the cycads, with about 130 species, are second only to the conifers. They occupy disjunct and strongly differentiated areas, typical of generic endemism: Central and South American; South and central African; south-eastern Asian-Australian-New Zealandian. Some of them are distributed on coastal areas of the continents. The cycads are elements of evergreen sclerophyllous forests or rain tropical forests but they also inhabit dry habitats (Jones 1993). This is one of the reasons for their xeromorphic appearance. In particular, the structure of the leaves is partly due to their weakly developed and relatively primitive (non reticulate) vascular system. Grushvitskyi and Chavchavadze (1978) observed that the plants which inhabit clearings in forests bear leaves with half the size leaflets and much thicker cuticle than those which grow under closed canopy.

Stangeria eriopus is a component of the coastal savanna forests (var. *katzer*i Rgl.) and the shrub community in more shaded habitats (var. *shizodon* T. Moore) in South Africa (Grushvitzkiy & Chavchavadze 1978). Both taxa show some morphological – anatomical differences and some authors treat them as separate species (Pant & Nautiyal 1963, Greguss 1968, Grushvitzkiy & Chavchavadze 1978).

Chigua restrepoi and *C. bernalii* are components of the understory of the tropical rain forest of Colombia and can be classified as mesohygrophytes (Stevenson 1990).

Eostangeria saxonica was a component of drier habitats in Eocene moors of the Geiseltal Basin, together with *Comptonia* and various representatives of Myrtaceae. Barthel (1976: 472) defines this ecological type of associated vegetation as “Trockene Waldmoore mit nur lokalen sumpfigen Senken und kleinen offenen Gewässern”.

Eostangeria ruzinciniana was a coastal element in plant communities that surrounded the Sarmatian sea during the Volhynian. This species presumably thrived in the understory of a Conifer-laurel forest on relatively open places. Palamarev et al. (1999) accepted it as an important element of the Badenian-Volhynian palaeofloristic cycle and of “Mischwald mesoxerophytische Zönosen”.

E. pseudopteris enters as an understory plant in the Mixed Mesophytic Forest of the Late Palaeocene of the western USA dominated by ancient broad-leaved deciduous Hamamelidaceae, Juglandaceae, Ulmaceae, Betulaceae, together with evergreen broad-leaved trees and palms (Graham 1999). Its individual occurrences, still under the study, are not yet fully characterized floristically. In the Nut Beds Eocene in Oregon, this species is associated with subtropical to paratropical forests dominated by Lauraceae, Juglandaceae, Platanaceae and palms with many lianas (e.g. Menispermaceae, Icacinaceae), but its exact ecological role is still not known. A *Dioon*-like cycad, a few conifers and some ferns are also represented in this flora (Manchester 1981, 1994).

CONCLUSIONS

This analysis of fossil and extant representatives of the genera *Eostangeria*, *Stangeria* and *Chigua* leads to the following more general conclusions.

Morphological and anatomical data corroborate an isolated position of the genus *Stangeria* from other fossil and recent cycads especially for its leaf anatomical structure (Tab. 2). This anatomical differentiation is most probably due to separation of Gondwana from Laurasia during the Mesozoic and isolation of *Stangeria* in South Africa.

A different process took place north of the equator. The Tethys and Paratethys basins in Holarctis were zones of active speciation. On this territory within the Tethys zone, the genus *Eostangeria* underwent speciation during the Palaeogene in two places: Central Europe (*E. saxonica*) and western North America (*E. pseudopteris*). The name *Eostangeria* is not very suitable because it presumes a close connection with the recent genus *Stangeria*, which is refuted in our study. Later on during the Oligocene and Miocene, a new round of speciation must have appeared leading to *Eostangeria ruzinciniana*, which survived in the Lower Sarmatian of southeastern Europe.

The discovery of the genus *Chigua* in tropical forests of Colombia, which is very similar morphologically and especially anatomically to *Eostangeria*, notably to *E. ruzinciniana*, stimulates questions concerning previous history of this lineage. One of the possible answers is that the origin of *Chigua* is a result of the evolution of the Madro-Tertiary geoflora (Axelrod 1975) or migrations from North America to South America during the late Tertiary.

Eostangeria ruzinciniana shows some general similarities (non-articulate leaflets, venation) with *Stangeria*, but in detailed leaf morphology and anatomy, this taxon greatly resembles *Chigua*, namely *C. restrepoi*. In our opinion, it should be treated as a Neogene derivative of the Palaeogene *Eostangeria saxonica*.

The fossil species *E. saxonica* and *E. pseudopteris* form a separate Palaeogene group resembling more closely *Stangeria* by its morphological features but differing decidedly from this genus in leaf anatomy. The recent species *Stangeria eriopus* has specific morphological, anatomical and ecological properties which make us to share the view of Johnson (1959), Greguss (1968), and others to accept it as a member of an independent family, namely Stangeriaceae.

The above analysis allows us to suggest that the fossil *Eostangeria* with all three species should be better accommodated within Zamiaceae in a new subfamily Eostangerioideae, in addition to Encephalartoideae D. Stevenson (1992) and Zamioideae.

Zamiaceae Horaninov

Eostangerioideae Z. Kvaček, Palamarev & Uzunova **subfam. nov.**

Type. *Eostangeria saxonica* Barthel

Diagnosis. In most leaf anatomical characters matching Zamioideae: scattered dark-staining cells in epidermal tissue, upper epidermal cells mostly elongated, stomata very slightly sunken, monocyclic to amphicyclic, with dark-staining subsidiary cells, interstitial strands between secondaries partly present; but different in leaflet morphology: venation strongly reminiscent on *Stangeria* in occasional looping of dense secondaries, densely dentate margin, and (? partly) non-articulate leaflets.

Monogeneric. *Eostangeria* Barthel 1976, Abh. Zentr. Geol. Inst. 26: 466.

Key to species

1. About 15 pairs of secondaries in a leaflet at angles of 40–50°, margin simple dentate . . . .
Eostangeria ruzinciniana (Palamarev, Petkova & Uzunova) Palamarev & Usunova 1992. Cour. Forschungsinst. Senckenberg, 147: 288.

1*. Over 25 pairs of secondaries in a leaflet at angles of more than 50° (usually 60–75°), margin irregularly (indistinctly double) dentate. 2

2. Secondaries mostly simple, percurrent, stomata typically with two, rarely more lateral subsidiary cells, leaflet width 20–30 mm . . . .
Eostangeria pseudopteris Z. Kvaček & Manchester 1999. Int. J. Plant Sci. 160: 622.

2*. Secondaries mostly forked, stomata typically with more lateral subsidiary cells, leaflet width 16 mm or less. . . . .
Eostangeria saxonica Barthel 1976. Abh. Zentr. Geol. Inst. 26: 466.

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PLATES

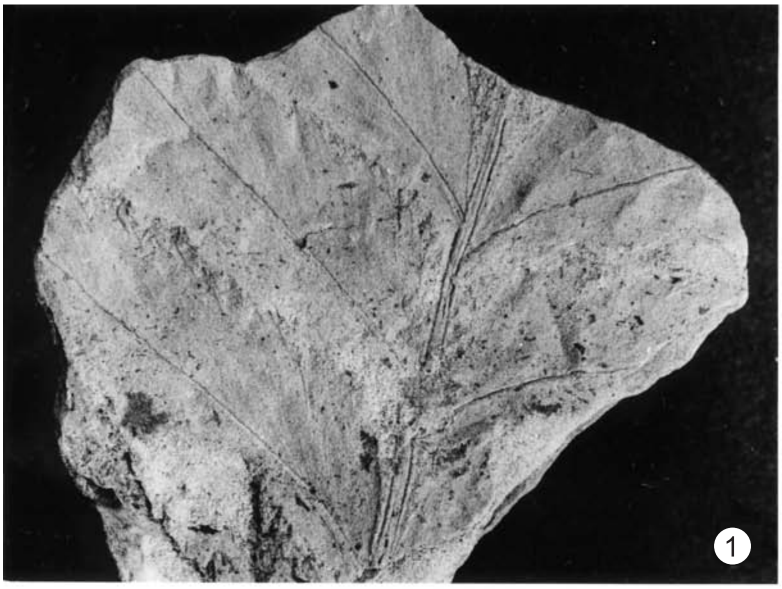
Plate 1

1–4. *Eostangeria ruzinciniana* (Palamarev, Petkova & Uzunova) Palamarev & Uzunova, Ruzinci, Sarmatian
  2. Fragmentary leaf fronds, No. 3617a, and No. 3615, × 2
  3. Detail of leaflet teeth and termination of secondary veins, No. 3517e, × 25
  4. Single leaflet, No. 3657, × 4

5. *Chigua bernalii* D. Stevenson, extant, Colombia (Bernal et al. 1189), leaflet base (note additional veinlets entering the lamina besides the midrib), × 10

6. *Chigua restrepoi* D. Stevenson, extant, Colombia (D. Stevenson 693), detailed marginal venation and teeth (note interstitial strands), × 10

7. *Zamia cremnophila* Vovides, Schutzman & Dehgan, extant, Tabasco, southern Mexico (Schutzman s.n.), detailed marginal venation and teeth, × 3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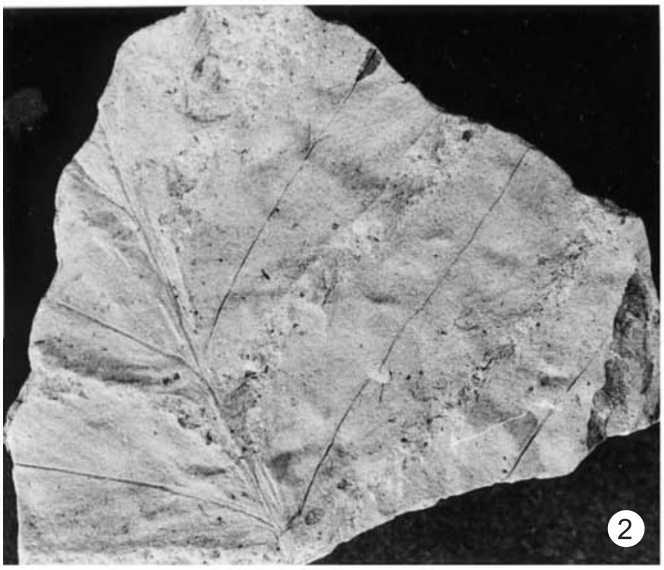
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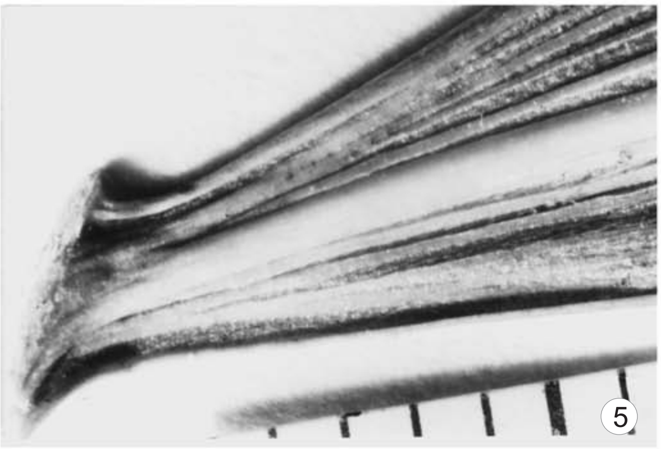
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Plate 2

1–5. *Eostangeria ruzinciniana* (Palamarev, Petkova & Uzunova) Palamarev & Uzunova
1. Adaxial cuticle with dark-staining cells and a trichome base, No. 3518, × 180
2. Adaxial cuticle, No. 3518, × 300
3. Abaxial cuticle with stomata and a trichome base, (in the circle of subsidiary cells one subsidiary cell is lacking), No. 3518, × 300
4. Abaxial cuticle with stomata and scattered short dark-staining cells, No. 3518, × 300
5. Abaxial cuticle near a costal area with stomata and scattered triangular dark-staining cells, No. 3518, × 300


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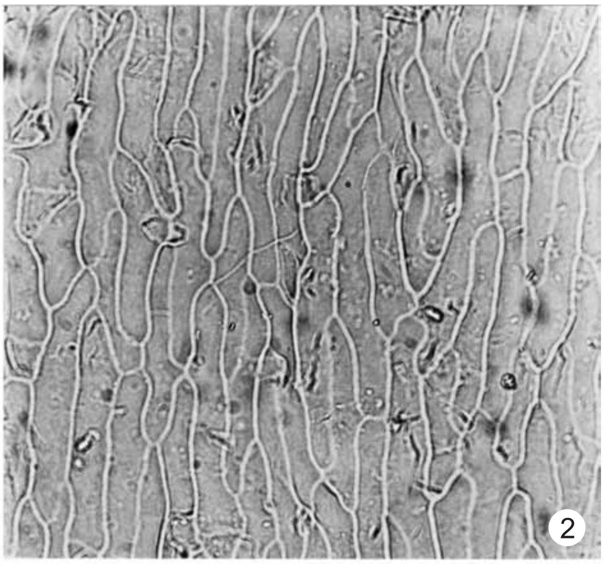
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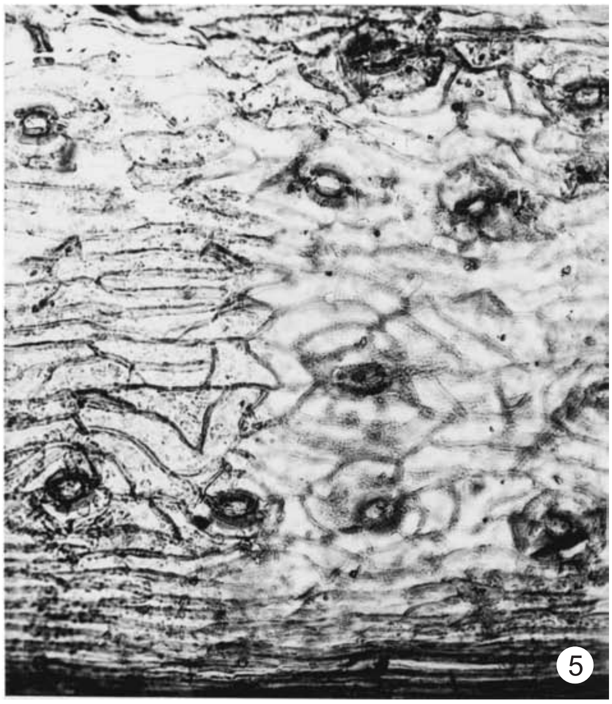
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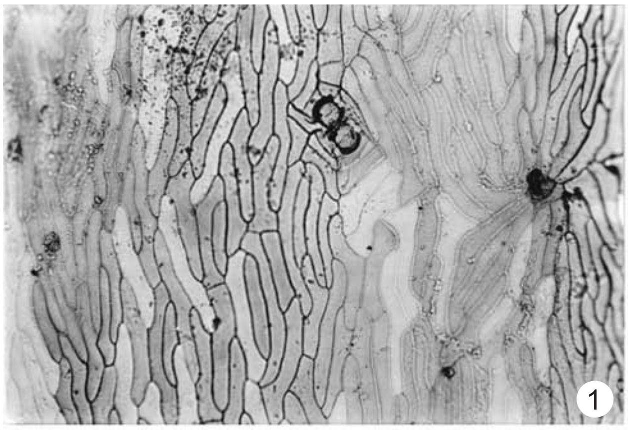
Plate 3

1–3. *Chigua restrepoi* D. Stevenson (D. Stevenson 693, Colombia)

1. Adaxial cuticle with stomata, a trichome base and many darker cells, x 100
2. Abaxial cuticle showing stomata with incomplete circles of partly long triangular subsidiary cells (one subsidiary cell lacking) and trichome bases, × 180
3. Details of stomata (cuticle not stained), × 300

4–5. *Chigua bernalii* D. Stevenson (R. Bernal, G. Galeano & D.L. Restrepo 1189, Colombia)

4. Adaxial cuticle with dark-staining cells and a stoma, × 100
5. Abaxial cuticle showing stomata with partly elongate triangular subsidiary cells (polar subsidiary cells mostly missing), and a trichome base, × 100
7. *Zamia soconuscensis* Schutzman, Vovides & Dehgan (B. Schutzman S-885, Chiapas), abaxial cuticle with stomata, × 200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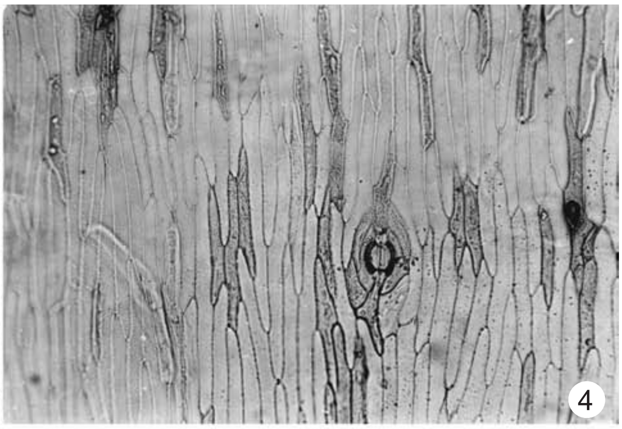
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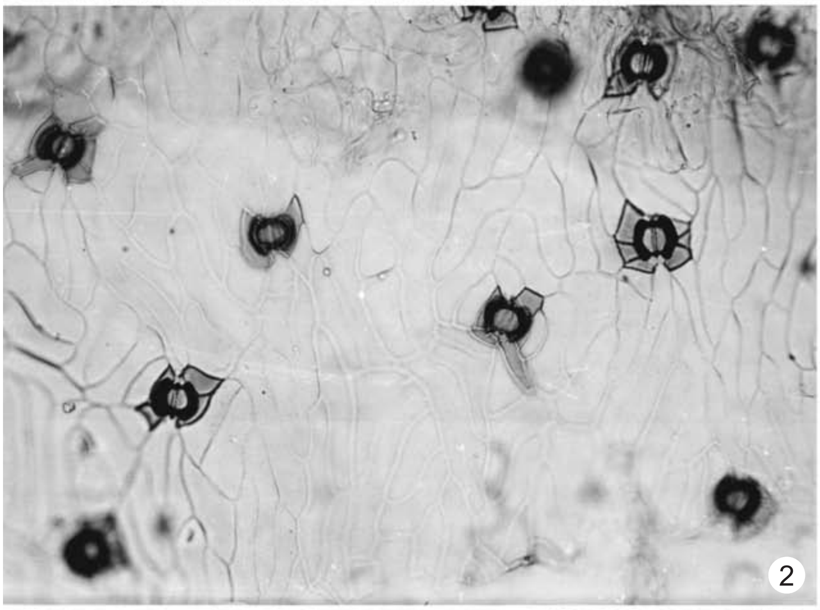
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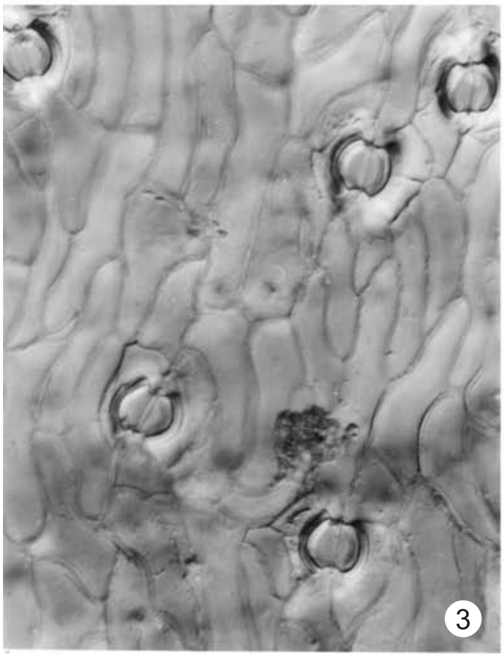
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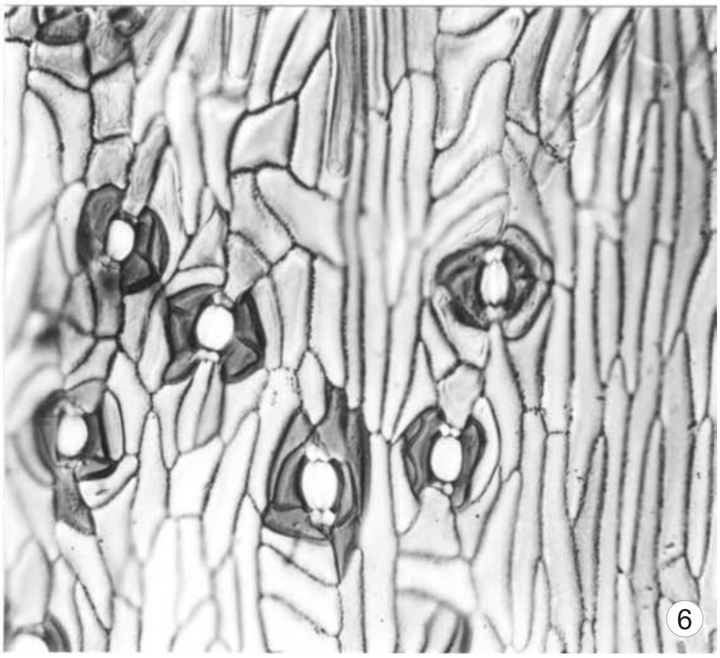
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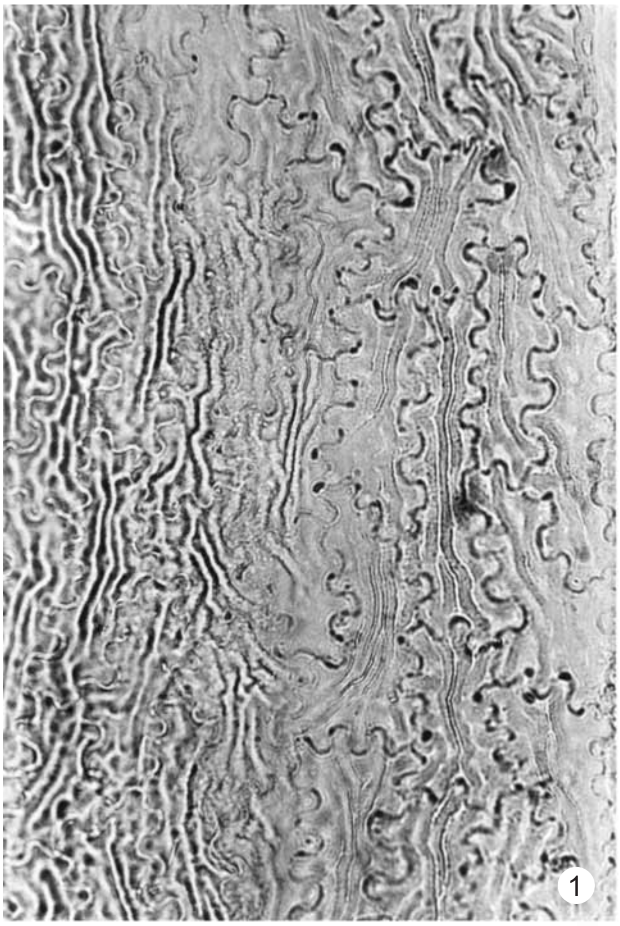
Plate 4

1–3. *Stangeria eriopus* (Kunze) Baillon (cult. Berlin-Dahlem)
  1. Adaxial cuticle showing outlines of cells and cuticle striation, × 300
  2. Abaxial cuticle showing epidermal cells with deeply undulate anticlines, and monocyclic (to amphicyclic) stomata with a well differentiated circle of subsidiary cells, × 180
  3. Abaxial cuticle showing striations and stomata with a strongly cutinized inner stomatal rim, × 300

4–5. *Zamia muricata* Willd. (B. Schutzman, s.n., Puerto Cabello, Venezuela)
  4. Adaxial cuticle with numerous darker cells, × 180
  5. Abaxial cuticle showing stomata with partly elongate triangular subsidiary cells (polar subsidiary cells often missing), × 180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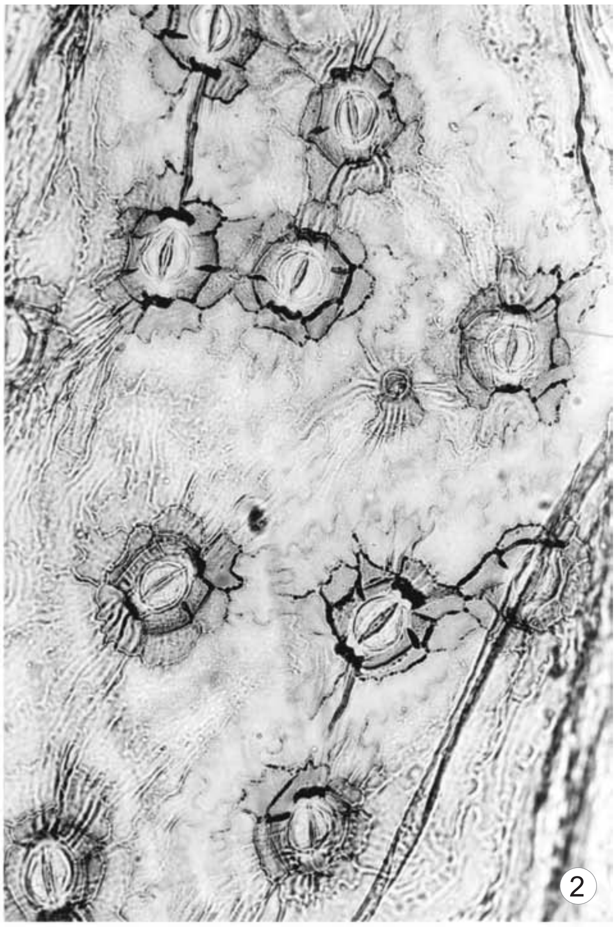
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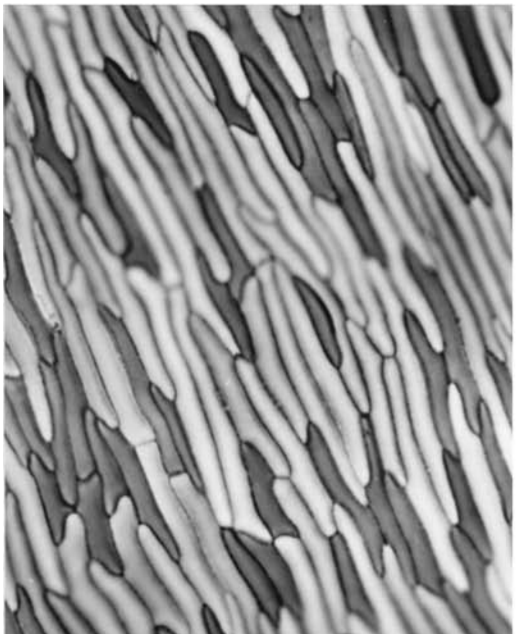
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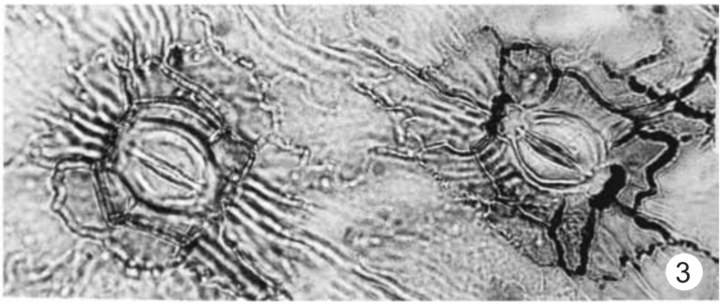
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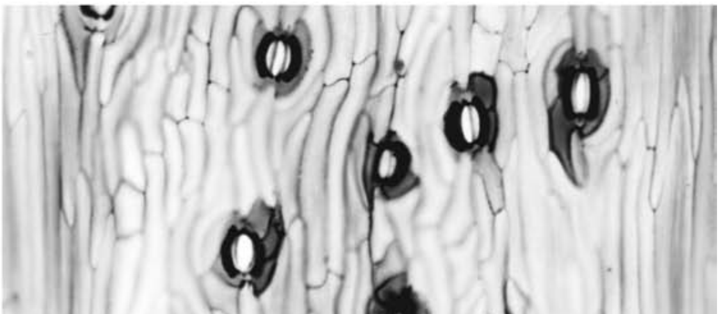
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