THE POLLEN OF EPHEDRA

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THE ORIGIN OF THE GNETALES and their relationship to other fossil and living gymnosperms is a problem which is nearly as baffling as that of the origin of the flowering plants; and indeed the two problems have often been linked. On the study of the Gnetales, paleontology has contributed very little because of the extreme paucity of fossil remains (Pearson, 1929). Consequently any early fossil material of this group, and particularly of the most primitive member, *Ephedra*, may be regarded with great interest by students of plant evolution. The first reference to fossil remains of this gnetalian genus is found in *Die im Bernstein befindlichen organischen Reste der Vorwelt*, a description of the Oligocene Baltic Amber flora (Berendt and Göppert, 1845). In their study, twigs bearing ovuliferous structures were designated *Ephedrites johnianus*. A translation of their Latin description is as follows:

Stem jointed, joints cylindrical with longitudinal striations ending in an annular sheath.

Aments subglobose, single, composed of imbricated bracts, and elevated on the apex of thickened peduncles. The peduncles are verticillate, in the axis of the sheath and non-articulate.

As a result of Menge's subsequent discovery of a preserved male strobilus from the same flora and further study of Göppert and Menge's material, the close similarity between the fossil remains and modern *Ephedra* became apparent. For this reason the genus was redescribed as *Ephedra* (Göppert, 1853; Göppert and Menge, 1883).

Later workers have described *Ephedra* fragments from the Miocene of Germany and Switzerland (Unger, 1851, 1870), and the Miocene of France (Saporta, 1889, cited by Wodehouse, 1934) but there has been some dispute concerning the validity of these identifications. Heer (1855), in publishing a report of *Ephedrites sotzkianus* Unger in his *Flora Tertiaria Helvetiae*, conceded that there was a superficial similarity between these articulate, striated, fossil stems and those of *Casuarina*, an isolated, Australian genus of angiosperms. However, Schimper (1890) saw no similarity with the genus *Casuarina* but questioned all previous reports of the genus from the Tertiary on the grounds that they could belong to poorly preserved specimens of either *Equisetum* or the conifer *Callitris*.

As a result of this confusion it was not until the application of pollen analysis to older sediments that remains of *Ephedra* were uncontestably demonstrated in the Tertiary. Furthermore, with the discovery of *Ephedra* pollen by Wodehouse from the Green River Formation (1933), the past geographic distribution of the genus was broadened to include North America. Likewise, its geologic record was extended back to the Eocene.

Although Tertiary and Pleistocene records in the Western Hemisphere have become more complete with the discoveries of megascopic remains of *Ephedra* from the Florissant beds of Colorado (Wodehouse, 1934), the Pleistocene of California (Axelrod, 1937), the Pleistocene of Nevada and Arizona (Laudermilk and Munz, 1934, 1938), micropaleontological evidence has been surprisingly rare both in Europe and the United States. Thiergart (1940) reported the presence of fossil *Ephedra* pollen grains from Tertiary beds in Germany, Cookson (1956) has recorded them from Australian Tertiary sediments, and, as a result of recent pollen studies, it has been shown that *Ephedra* persisted as a late- and postglacial desert steppe plant in protected areas in Europe (Christensen, 1949, cited by Iversen, 1954; Lang, 1951; Iversen, 1954; Welten, 1957) as well as in South America (Auer, 1933) and the United States (Anderson, 1954).

In view of the facts that *Ephedra* possesses a high degree of structural specialization, and also that early Tertiary *Ephedra* exhibits pollen structures essentially comparable with that of modern species it is apparent that the genus or its close ancestral type had an extended pre-Tertiary history. An extension of this pre-Tertiary history has been found during an analysis of a series of cores from the Cretaceous Raritan and Magothy formations from east-central Long Island, New York. In these sediments a number of intact, as well as fragmented, pollen grains assignable to *Ephedra* were observed. This discovery extends the known fossil record of the genus in North America back to the lower Upper Cretaceous period.

The first part of this paper will deal with a description of the fossil grains found on Long Island; in the second part the results of a detailed survey of the pollen morphology of the living members of the genus will be presented with a view to interpreting the fossil forms and their phylogenetic significance.

FOSSIL EPHEDRA FROM CRETACEOUS SEDIMENTS OF LONG ISLAND

In the process of exploratory sub-surface geologic studies at the Brookhaven National Laboratory, two deep well cores were recovered from two borings approximately one mile apart. The cores extended from the surface Pleistocene drift through the Cretaceous and into the underlying bedrock. The cores were recovered nearly intact and represent an unusually complete section of the Cretaceous formations underlying eastern Long Island. One of us had the opportunity to sample both of these cores throughout, and this study comprises one aspect of an intensive micropaleontological study still in progress.[1]

The cores, designated Well No. 1 (S 6409) and Well No. 2 (S 6434) were drilled to a depth of 1,568 feet and 1,294 feet, respectively. In both

[1] Samples of the cores were made available in May 1950 by the Ground Waters Division of the U. S. Geological Survey and were transmitted through the courtesy of the Paleontology and Stratigraphy Branch of the Geologic Division of the U. S. Geological Survey.

cores, which were drilled through the Magothy and Raritan formations, the sediments recovered were all non-marine, Coastal Plain deposits, comprising variegated and lignitic clays, white, fine-grained and coarse arkosic sands, and gravels. Occasional lignite beds were dispersed throughout the section. The entire sequence rested on crystalline igneous rocks of presumed pre-Cambrian age.

The Magothy formation is regarded as of Upper Cretaceous age and has been correlated with the Austin chalk of the Gulf Coast region. Although it rests unconformably on the Raritan, rarely is the Magothy clearly differentiated from it. According to Spangler and Peterson (1950), the two formations are comparatively easy to differentiate in the field but insufficient contacts of the two have been found to map them satisfactorily. Data available from well logs are usually too uncritical and incomplete for stratigraphic purposes. The Raritan formation of New Jersey was considered by Spangler and Peterson (1950) as equivalent to those non-marine sediments in Delaware, Maryland and Virginia referred to as "Raritan," Patapsco, Arundel and Patuxent. This series, they believe, should be considered as a single unit and comprises both Upper and Lower Cretaceous beds. Furthermore, the beds called "Raritan" in Maryland-Delaware are only part of the sediments called Raritan in New Jersey. However, they point out that the contact of the Upper and Lower Cretaceous occurring within the Raritan formation in New Jersey has not been recognized in outcrop and sub-surface sediments have not been studied. This interpretation has been refuted by Dorf (1952) who, after reviewing the faunal and floral evidence, reaffirmed the assignment of the Raritan formation to the early Upper Cretaceous. Hence, in his view, the Potomac beds (Arundel, Patapsco and Patuxent) are pre-Raritan and assignable to the Lower Cretaceous. One of the purposes of this study was to examine the possibility of separating the Raritan from the Magothy on the basis of evidence from plant microfossils. Such a separation might render stratigraphic correlation possible in other parts of the Coastal Plain where the two formations are at present unsatisfactorily separable.

Small samples (1–2 gms.) taken at intervals along the length of both cores were prepared according to techniques modified from Erdtman (1943), Faegri and Iversen (1950). The material was first demineralized by a treatment of cold 50% HF for 24–48 hours, then boiled in 10% KOH in a water bath for six minutes, washed, and dehydrated with glacial acetic acid. The remaining cellulose was removed by acetylation for 1½ minutes at 100° C. By this sequence of chemical treatments such constituents as quartz and clay minerals, lignin and cellulose are removed and the cutinized and suberized pollen grains and spores are concentrated.

In our material, evidence for the existence of a species of *Ephedra* was provided by the presence of ridged pollen grains found at the 603–613 foot level of Well No. 2. To these grains, which could be related to modern forms of *Ephedra*, the designation "Type A" was given.[2]

[2] This terminology is based on a study of modern *Ephedra* and will be clarified in the second part of this paper.

A total of eight intact grains of Type A and a number of fragments of similar type were found. A list of the intact fossil grains and their measurements is shown in TABLE I.

The Type A grains are prolate, their shape class index [3] varies from 1.5 to 1.9, the average being 1.7. The polar axis measures 47–53 μ, the average being 49 μ; the equatorial diameter varies from 26–33 μ, the average being 29 μ.

TABLE I. **A list of the fossil grains and their measurements.**

Ephedra	LOCATION	SIZE	NUMBER OF RIDGES	S.C.I.*
A 1	45–85.5 (S1)	47 × 29 μ	5	1.6
A 2	45–85.5 (S1)	49 × 26 μ	6	1.9
A 3	39.8–88 (S3)	53 × 33 μ	6	1.6
A 4	27.5–88 (S2)	47 × 30 μ	6	1.5
A 5	41–97 (S2)	dia. 32 μ	6	
A 6	37.5–103(S1)	50 × 27 μ	6	1.8
A 7	40–87.5 (S1)	53 × 29 μ	6	1.9
A 8	42–95.5 (S1)	47 × 30 μ	6	1.5
Average		49 × 29 μ	6	1.7

* Shape class index.

Characteristic features of these pollen grains are the narrow, undulating ridges which extend meridionally from pole to pole. These ridges fuse at the poles so that there are actually three continuous, intersecting ridges circumscribing the grain.

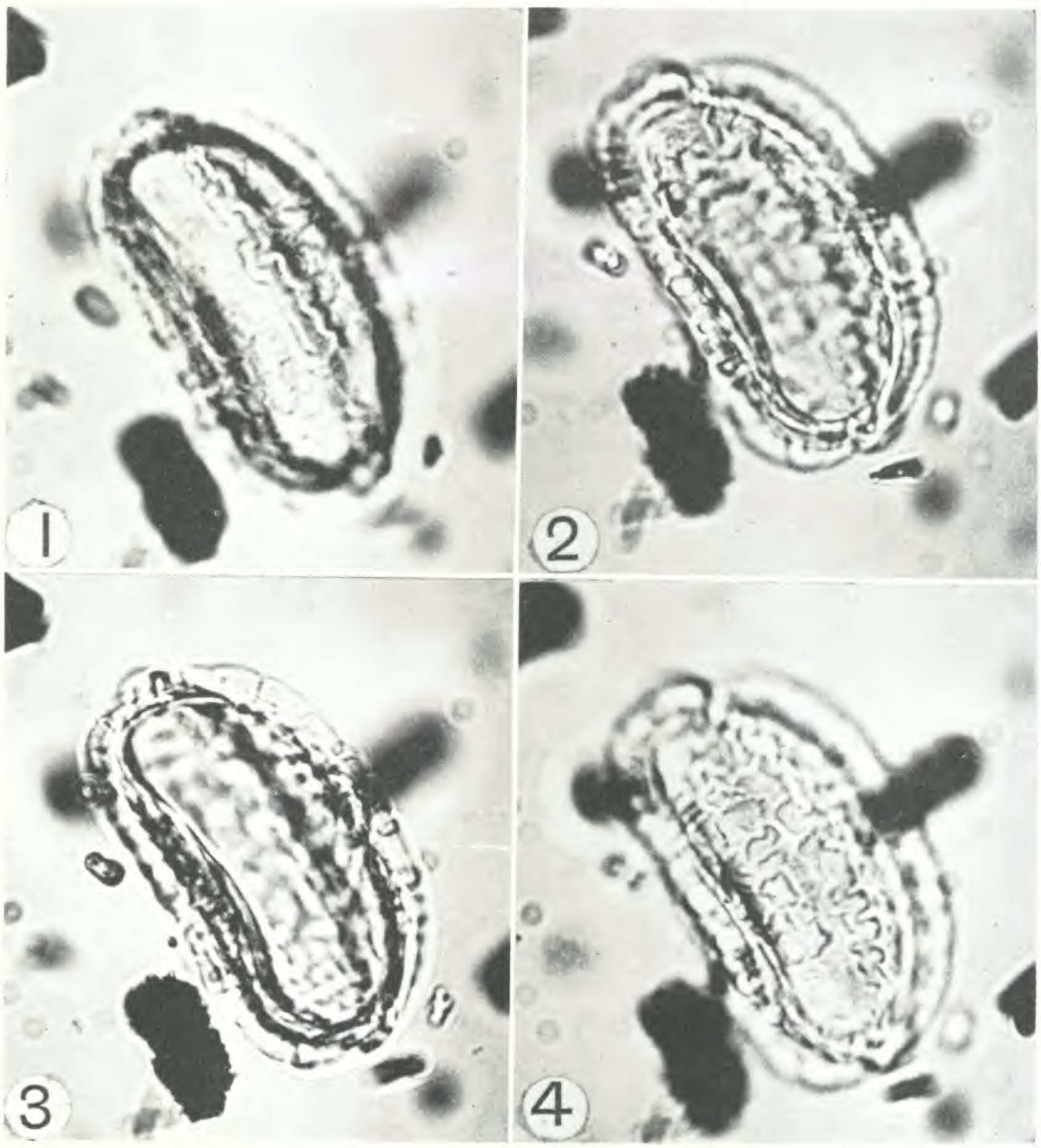
The exine is double and intectate. It consists of a thick endexine and a highly variable ektexine. In thickness the endexine is constant, averaging between 0.5 and 1 μ over the entire surface of the grain. However, the ektexine fluctuates considerably in thickness, averaging 0.5–1 μ along the region between the ridges and 3–4 μ at the central peak of the ridge at the equator. Furthermore, ridge height increases poleward to 4–5 μ as a result of the fusion of the ridges.

In surface view, the highly undulate wave-like pattern of the ridge is evident. The wave height measures 2–3 μ and the wave length averages 2–4 μ. In the majority of cases the ridges are continuous. However, in a few cases the ridges are composed of short, individual, angular undulations which overlap one another but are not fused. In width, the ridges average between 0.8 μ and 1.5 μ at the equator becoming thinner at the poles. With high magnification two slender, hyaline lines, averaging less than half a micron in width can be seen to run along the surface of each ridge bordering its edge. A central strip 0.2 μ wide, which remains dark, separates these two undulate and highly refractive borders. With changing focal levels a reversal of the light-dark relationship of the central strip and

[3] Shape class index is the ratio of the long axis to the short axis (Erdtman, 1943).

the bordering lines is produced, so that the central strip appears as a single hyaline line.

In optical section, the ridges appear to be composed of individual baculate projections which extend out from the grain at right angles to the endexine. However, these are not true baculae, which are defined by Faegri and Iversen (1950) as "radial projections with the height of the element greater than the greatest diameter of projection and the upper end of the element not thicker than the base." Rather, the projections represent profile views of the ridge which is seen optically sectioned at various angles as a consequence of its highly irregular form.



TEXT-FIGURE I. *Ephedra stapfii* Steeves & Barghoorn, n. sp. 1, High focus view of the undulating ridge. 2, Same grain at mid-focus, showing the outline of the distinct, thick endexine. 3, A view slightly beyond mid-focus showing the thickness as well as the baculate appearance of the ektexine in optical section. 4, High focus view of the reticulate sculpturing found on the surface of the exine between the ridge crests on the opposite side of the grain. (All × 1000.)

The grains as a whole appear slightly angular in polar aspect with the ridges forming the angles. In this view the ridges themselves appear rounded and slightly constricted at their bases.

The surface sculpturing of the grain is rugulate-reticulate with muri 0.8–1 μ wide and 0.5 μ high extending out from the ridge crest down the ridge flanks enclosing lumina 2–4 μ in diameter.

Ephedra stapfii, n. sp. TEXT-FIGURE I.

DIAGNOSIS: Grains prolate, the polar axis varying from 47 to 53 μ, averaging 49 μ; equatorial diameter varying from 26 to 33 μ, averaging 29 μ. Ridges 5 or 6, highly undulate, extending from pole to pole. Shape class index varying from 1.5 to 1.9, averaging 1.7.

LOCALITY: Brookhaven, Long Island, New York; U.S.G.S. Well No. 2, 603–613-foot level.

GEOLOGIC OCCURRENCE: Raritan formation, lower Upper Cretaceous.

MATERIAL: Eight intact pollen grains and a number of fragments.

HOLOTYPE: No. 56011, Palaeobotanical Collections, Harvard University.

POLLEN MORPHOLOGY OF MODERN SPECIES OF EPHEDRA

Stimulated by the discovery of ephedroid pollen of considerable geologic age, an intensive study was made of the pollen of existing species of *Ephedra* with a view to determining the possible phylogenetic significance of the fossils.

Modern *Ephedra* pollen was first described extensively by Wodehouse (1935), who recognized basic differences within the genus based on his work with *E. equisetina* and *E. foliata*. In his description of *E. equisetina* he states that the pollen is characterized by having "high few ridges 5–8 with their crests blade like and arching from end to end of the grain, and in each of the grooves between the ridges is a hyaline line which follows a serpentine course its full length." A description of *E. foliata* notes that "when the ridges are more numerous, 11 to 15, they are not so high and the hyaline lines in the grooves are absent or only represented by a faint streak." His descriptions of these two species represent a few of the many variations in form that characterize pollen of the genus. Although the grains are all similar in their possession of ridges, they differ in size, in shape, in number of furrows and ridges and in exine structure. Recently, Welten (1957) studied extensively the species of the Mediterranean and western Asian regions in order to identify pollen of *Ephedra* from northern and central European late- and postglacial sediments.

Although the taxonomic treatment of the genus is somewhat unsatisfactory, forty-three of the currently recognized forty-eight species of *Ephedra* were examined in the present study. A list of the species, as well as their geographic source, is given in TABLE II. In the course of the work it became apparent that the pollen of *Ephedra* falls into certain major morphological categories. These we have arbitrarily designated A, B, C, and D. The characteristics of the four designated pollen types will be considered in detail as illustrated by descriptions of individual species. It would be of much interest to examine the relationship of these divisions, based on pollen morphology with those based on other organs and parts of the plant. Although such information is not available on a wide range of species it would add to the phylogenetic significance of the fossil forms.

POLLEN TYPE A

The grains are perprolate to subprolate in shape, their shape class index varying from 1.1 to 2.6 but generally averaging 1.8. The grains are sculptured by an average of 5 to 9 heavy, hyaline, ektexinous ridges which extend meridionally from pole to pole. The least amount of variation is observed in *Ephedra sinica* where the ridge number ranges between 4 and 6 and averages 5.8. The greatest number is found in *E. pachyclada* and *E. funera*. In the former species the ridge number varies from 5 to 12 and averages 7.9, in the latter it ranges from 6 to 13 and averages 8.3. (See CHART II which is based on an average of 50 grains per species.)

In the polar view the grains are polygonal with the alternating ridges and deep concave furrows forming an angular outline. A narrow and serpentine colpus [4] is situated at the base of each furrow. In most cases the colpi are highly undulate. The undulation of the colpus may be either rounded or highly angular and the frequency of undulation may vary, as well as the degree. The colpus may divide forming lateral branches which extend up the ridge where they may occasionally divide again. In this manner the ektexine forms a reticulate pattern, such as that found in *E. distachya*. In a few cases, as in *E. clokeyi*, the colpus scarcely divides. Also, the width of the colpus may vary, as well as the depth to which it cuts into the ektexine.

The ridge itself may be relatively smooth or highly verrucate. The term "verrucate" in the manner in which it is used here may be open to question but it is chosen for the sake of simplicity. The true "verruca" has been defined as a sculpturing element in which "the greatest diameter of the radial projection is greater than the height of the element" (Faegri and Iversen, 1950). In *Ephedra* pollen, however, the ridge crest appears verrucate in optical section because of the cutting of the ektexine by the branching colpi which extend up the ridge. In all species possessing Type A pollen, except *E. sinica*, the ridges are triangular in shape in the polar aspect with bases which vary in width from 0.5 to 18 μ and central axes which range in height from 3 to 8 μ. As was recognized by Welten (1957), the ridge in this view is composed of an inner, central, hyaline core and a thin,

[4] Colpus (pl. colpi), germinating furrow, the area on the grain forming or surrounding the normal place of emergence of the pollen tube, with a length-breadth ratio higher than 2. The ektexine is reduced, even absent (Faegri and Iversen, 1950; Ingwersen, 1954). Although the terms furrow and colpus may be used interchangeably, in this case a distinction between the two will be made. The term "furrow" will be used to refer to the region between the ridges; the term "colpus" will be used to describe the thin, longitudinal, serpentine grooves located in the middle of the furrow area and formed by the absence of or the thinning of the ektexine.

TABLE II. **Species of Ephedra examined in this study.***

SPECIES	SOURCE	COLLECTION
Ephedra alata Dcne.	Algeria	*Bornmüller* (A)
E. altissima Desf. var. *mauritanica* Stapf	Morocco	*Balls 2487* (A)
E. americana Humb. & Bonpl. ex. Willd.	Bolivia	*Cardenas 3422* (GH)
E. andina Poepp. & Endl.	Chile	*Joffuel 2751* (GH)
E. antisyphilitica Berland	W. Texas	*E. Palmer 1292* (GH)
E. aspera Engelm. ex. S. Wats.	New Mexico	*Wright 1851* (GH)
E. bracteata Miers	Chile	*Jegons* (GH)
E. breana Phil.	Prov. Antofagasta, Chile	*Johnston 3613* (GH)
E. californica S. Wats.	San Diego Co., California	*Epling* (GH)
E. chilensis Miers	Valparaiso, Chile	*Goodspeed 4592* (GH)
E. clokeyi Cutler	Washington Co., Utah	*Gould 1526* (GH)
E. coryi Reed var. *viscida* Cutler	Rock Point, Arizona	*Cutler 2768* (GH)
E. distachya L.	Germany	*Flora Germanica Exsiccatae 7513* (GH)
E. equisetina Bge.	Turkestan	*Korshinsky, Herb. Inst. Bot. Ac. Sc. USSR 6384* (A)
E. foliata Boiss. & Kotschy ex. Boiss.	Punjab, India	*Parker 3304* (A)
E. foliata Boiss. var. *ciliata* (C.A.Mey.) Stapf		*Aitchison 537* (GH)
E. fragilis Desf.	Prov. Almeria, Spain	*Reverchon 611* (A)
E. fragilis Desf. var. *campylopoda* (C.A. Mey.) Stapf	Palaestine	*Bornmüller 1746* (A)
E. frustillata Miers	Rio Negro, Argentina	*Parodi 11858* (GH)
E. funera Cov. & Mort.	California	*Hitchcock 329* (GH)
E. gerardiana Wall.	Kashmir	*G. L. Webster 5830*
E. gracilis Phil.	Prov. Atacama, Chile	*Johnston 6208* (GH)
E. graeca C. A. Mey.	Morocco	*Baumier* (GH)
E. helvetica C. A. Mey.	Switzerland	*Reliquiae Mailleanae 7046* (GH)
E. intermedia Schrenk & C. A. Mey. var. *schrenkii* Stapf	Teheran	*Bornmüller* (A) det. *Florin*
E. major Host var. *procera* Aschers. & Graebn.	Talas Ala-Tau branch of the Tien-Shan Mountains in N. W. Kirghiz USSR.	*Herb. Hort.* (A) *Bot. Univ. Asiae Mediae*

* Pollen obtained from herbarium specimens in the herbarium of the Arnold Arboretum (A) and the Gray Herbarium (GH). The dried herbarium pollen grains were acetylized for one and one-half minutes in boiling water, washed in three changes of distilled water and mounted in glycerine jelly.

Species	Source	Collection
E. major Host var. *villarsii* Stapf	Amasya, Turkey	*Bornmüller 3544* (A)
E. monostachya L.	Saknain-Nor, Tibet	—— (A)
E. multiflora Phil. ex. Stapf	Argentina	*Johnston 6286* (GH)
E. nana Dusen	Patagonia	*Donat* 42 (GH)
E. nevadensis S. Wats.	New Mexico	*Tower* (GH)
E. ochreata Miers	Argentina	*Fisher 15* (GH)
E. pachyclada Boiss.	Afghanistan	*Aitchison 1122* (GH)
E. pedunculata Engelm. ex. S. Wats.	Mexico	*Stewart 2265* (GH)
E. peninsularis I. M. Johnston	Mexico	*Anthony 281* (GH)
E. regeliana Florin	Skardu, Baltistan	*G. L. Webster 5950*
E. rupestris Benth.	Bolivia	—— (GH)
E. sinica Stapf	Prov. Suiyuam, China	*Licewtak 13523* (A)
E. strobilacea Bge.	Turkmenistan, USSR	*Herb. Inst. Bot. Ac. Sc. USSR* (A)
E. triandra Tul.	Bolivia	*Fiebrig 2151* (GH)
E. trifurca Torr.	New Mexico	*Hortman 642* (GH)
E. torreyana S. Wats.	Rocky Mt. Region, Uinta Co., Utah	*Rollins 1719* (GH)
E. tweediana Fisch. & C. A. Mey.	Uruguay	—— *5683* (GH)
E. wraithiana I. M. Johnston	Chile	*Johnston 4705* (GH)
E. viridis Cov.	Mt. Pinos, Kunto, California	*Howell 3824* (GH)
E. vulgaris C. A. Mey.	Magnesia, Greece	*Aitchison 40* (GH)

outer, non-hyaline layer. The ridge peak is not pointed, but rounded, and averages 1.5 to 4 μ in width. The ridges tend to decrease slightly in height at the poles and the verrucae gradually disappear.

The exine is always double and may measure up to a maximum of 8 μ in thickness. It is composed of a relatively thin endexine which extends continuously and evenly around the grain, varying in thickness from 0.8 to 2 μ, and an ektexine which averages 1 to 2.5 μ in thickness in the furrow region and 3 to 6 μ along the central axis of the ridge. The ektexine is double. One component, the inner, hyaline layer forms the triangularly shaped central core of the ridge. This layer extends completely around the grain becoming thinnest at the colpi and accounts for the hyaline appearance of the colpi at some levels of focus. The thinner, outer layer is continuous or discontinuous, depending upon the depth of the colpi.

The group as a whole ranges in size along the polar axis from 51 μ, the average in *E. vulgaris*, to 69 μ, the average in *E. funera*, with considerable overlap between species. To a certain extent a distinction between species with large pollen and species with small pollen in the Type A group can be

CHART I

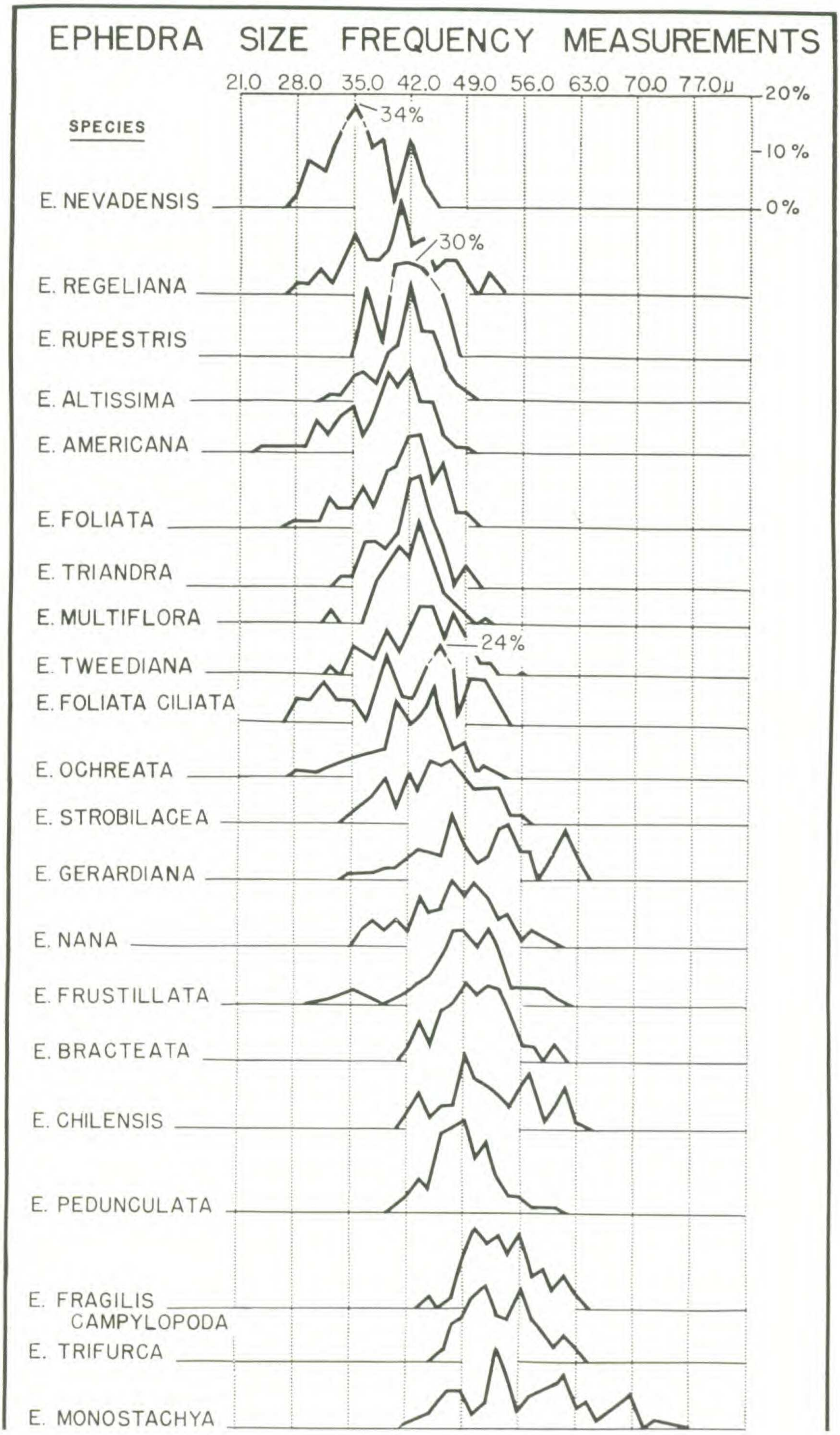
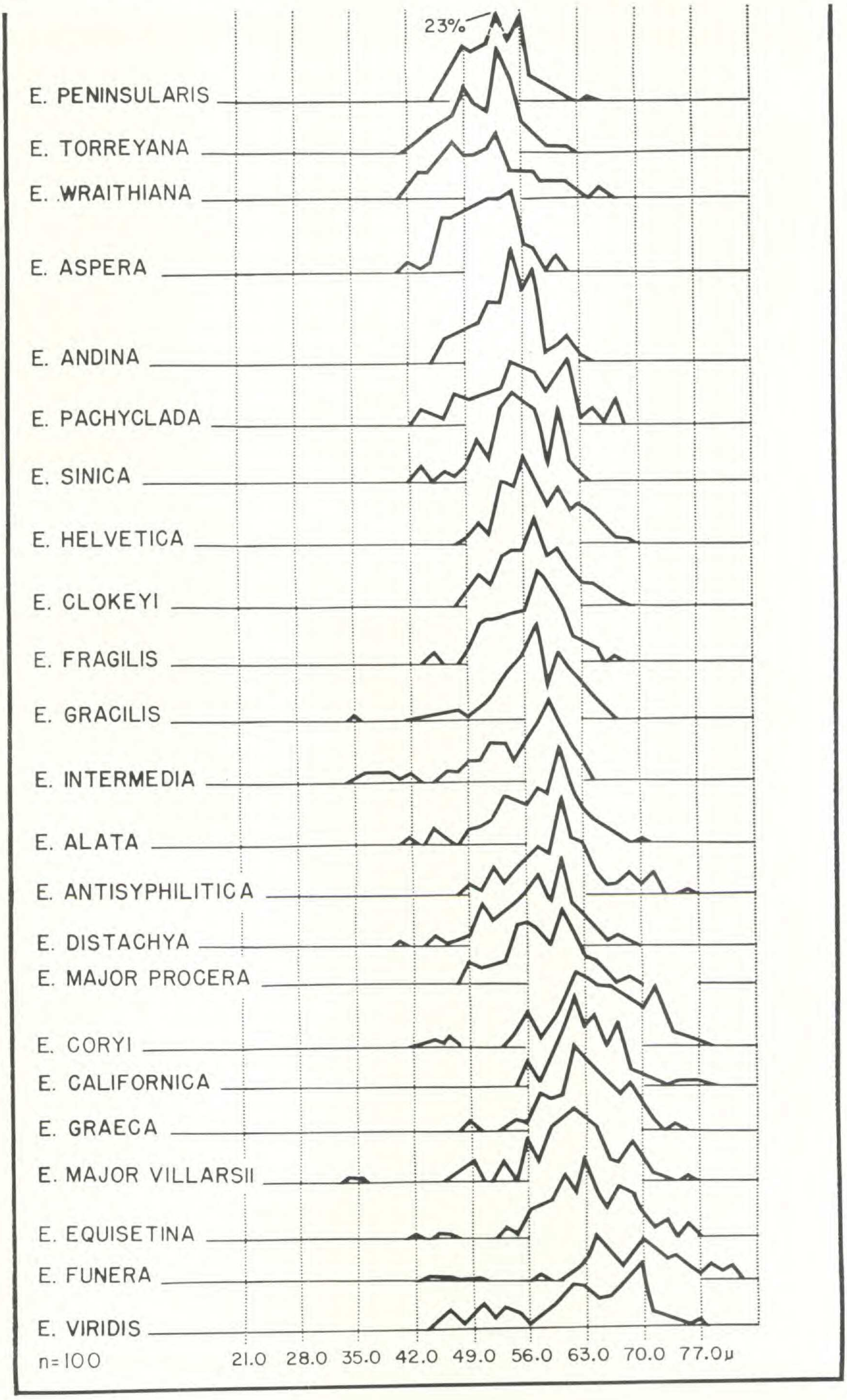

EPHEDRA SIZE FREQUENCY MEASUREMENTS
21.0 28.0 35.0 42.0 49.0 56.0 63.0 70.0 77.0μ
20%
10%
0%
SPECIES
34%
30%
24%
E. NEVADENSIS
E. REGELIANA
E. RUPESTRIS
E. ALTISSIMA
E. AMERICANA
E. FOLIATA
E. TRIANDRA
E. MULTIFLORA
E. TWEEDIANA
E. FOLIATA CILIATA
E. OCHREATA
E. STROBILACEA
E. GERARDIANA
E. NANA
E. FRUSTILLATA
E. BRACTEATA
E. CHILENSIS
E. PEDUNCULATA
E. FRAGILIS CAMPYLOPODA
E. TRIFURCA
E. MONOSTACHYA

CHART I (*Continued*)



made, although the variability in size within the species limits the taxonomic usefulness of this character (CHART I).

DESCRIPTION OF SPECIES OF TYPE A

Ephedra distachya L. PLATE I, *fig. 3*; PLATE II, *figs. 1, 2.*

Polar axis 56 μ (40–66.5 μ); equatorial diameter 30.5 μ (24–36 μ). Ridges 6.4 (4–9). Shape class index 1.8 (1.4–2.1); prolate.

Viewed in the equatorial plane, the grains are prolate, their shape class index averaging 1.8 and lying between 1.4 and 2.1, whereas in their polar aspect they are polygonal. The furrows are deep, with concave sides and narrow, serpentine colpi situated at their bases. The grains could be termed polycolpate, possessing 4–9 undulating colpi which extend between the poles. The undulations are acutely angular and occur every 2–6 μ. The colpi average 0.8 μ in width and are formed by a complete absence of ektexine in that region. The colpate condition (according to Wodehouse, 1935) permits harmomegathic contraction and expansion along the equatorial axis of the grain where the exine is thinnest or absent. The colpi are bordered by a verrucate ridge 5–6 μ high, the verrucae measuring 2–4 μ in length and 2–3 μ in width. In optical section the individual verrucae appear semicircular in shape with slightly flattened edges. The colpi merge but do not fuse at the poles, terminating just previous to it; the ridges fuse at the poles. At the equator the ridges average 5–7.5 μ in width at the base and 2.5–3 μ at the crest. Their height ranges from 5–6 μ at the equator to 1.5 μ at the poles.

The ektexine is variable in thickness, measuring 3–4 μ along the ridge peak at the equator, decreasing toward the poles where it is 1.5–2 μ, as well as toward the colpi where it is probably absent. The endexine is thinner than the ektexine, measuring 1 μ or less and is continuous. The structure of the exine is intectate. In surface view within the furrow a coarse, reticulate sculpturing of the ektexine is visible. However, this is an inverted reticulum in the sense that the exine is not divided into lumina by the presence of walls or muri but rather by thin, narrow indentations derived from short, lateral branches of the main, longitudinal colpus. This branching occurs only at the angles formed by the undulations of the colpus (Faegri and Iversen, 1950, use the term fossulate to describe an exine dissected in this manner). These lateral branches are set off 2.5–6.5 μ apart along the course of the main colpus, and may dichotomize again and continue up the ridge to the crest, deeply cutting the thick exine into angular, closely set verrucae.

Ephedra clokeyi Cutler

Polar axis 56 μ (47–68 μ); equatorial diameter 31 μ (27–41 μ). Ridges 7.2 (6–9). Shape class index 1.6 (1.4–2.1); prolate.

Similar to the *Ephedra distachya* type but differing in the possession of a markedly smoother exine, the ridge flanks of this species are not cut by branching, lateral colpi, which in the other species of the A type extend from the main colpus up the ridge to its crest. The ridge crest, however, is slightly crenulate. Moreover, the ridge is highly irregular with undulations measuring 8–12 μ in length and 2.5–3 μ in height. At the equator the ridges average 7 μ in width at the base and 2 μ at the crest; the colpi are narrow, straight or only slightly undulate and average 0.3 μ in depth.

Thickness of the ektexine at the ridge crest at the equator 2.5–3 μ, at the poles 2 μ, in the furrow area 0.8–1 μ; thickness of the endexine 1 μ.

Ephedra coryi Reed var. **viscida** Cutler

Polar axis 63 μ (43.5–76.5 μ); equatorial diameter 31 μ (28–42 μ). Ridges 6.9 (4–9). Shape class index 2.0 (1.5–2.6); prolate–perprolate.

Although similar to those of *Ephedra distachya* in general structure, the grains differ in the possession of a thicker exine and in the shallowness of the lateral branches of the colpi. The thickness of the ektexine varies from 4.5–6 μ at the center of the ridge at the equator and decreases to 3 μ at the poles; in the region of the furrow it measures 0.8–1 μ. The endexine averages 1.6 μ in thickness. Unlike those found in *E. distachya* the verrucae are semicircular in optical section, widely spaced and project well above the surface of the grain, averaging 4–6 μ in length. Often the ridge crest itself is undulant.

The colpi average 0.5 μ in width and follow a very slightly angular path to the poles. Lateral branching occurs every 4–6 μ; secondary branching seldom occurs. The depth to which these secondary branches cut into the ektexine along the ridge crest averages 0.5 μ. At the equator the ridges average 10–11 μ in width at the base and 2–3 μ at the crest.

Ephedra equisetina Bunge

Polar axis 56 μ (39–66.5 μ); equatorial diameter 30.5 μ (23–36 μ). Ridges 5.9 (4–8). Shape class index 1.9 (1.4–2.1); prolate.

The grains, more delicate than the preceding species, have thin exines composed of ektexines measuring 1.5 μ at the ridge crests at the equator and endexines averaging 0.8–1 μ in thickness. At the poles and in the furrow region the thickness of the ektexine diminishes to 1 μ. The colpi are narrow, shallow and angular in their undulations. Lateral branching is sporadic. When present, the branches are long and widely spaced, occurring every 6–7 μ; secondary branching is absent. At the equator the ridges average 10 μ in width at the base and 1.4–1.8 μ at the crest. In optical section the ektexine along the ridge crest is verrucate with the verrucae low and semicircular in outline. They average 3.5–5 μ in length.

Ephedra funera Cov. & Mort. PLATE II, *fig. 5.*

Polar axis 69 μ (43–81.8 μ); equatorial diameter 40 μ (36–45 μ). Ridges 8.3 (6–13). Shape class index 1.7 (1.5–1.9); prolate.

This species differs from the preceding in possessing pollen of larger size with smooth, non-verrucate ridges. However, in optical section the ridge crest may appear slightly irregular in outline. At the equator the ridges measure 8–10 μ in width at the base and 2.4–2.8 μ in width at the crest.

Although the colpi are straight, occasional angular undulations may occur. There is no evidence of lateral branching.

Thickness of ektexine at the ridge crest at the equator 2–3 μ, at the poles 1.5 μ, in the furrow region 1 μ; thickness of endexine 1.4 μ.

Ephedra gerardiana Wall.

Polar axis 52 μ (35–63 μ); equatorial diameter 25 μ (21–27 μ). Ridges 9.0 (8–11). Shape class index 2.0 (1.5–2.6); prolate–perprolate.

The grains are characterized by straight, wide-crested ridges which are slightly irregular in texture. In polar view they are triangular in shape, extending 2–3 μ in height, and measuring 5–8 μ in width along the base and 1.5 μ at the crest. The ridges may undulate at the equator, the undulations ceasing near the poles. The colpi may be straight or very slightly undulant with the undulations angular and set close together. Lateral branching may or may not occur. When it does occur the branches are extremely short and shallow; consequently the furrow area is psilate, although there is a slight evidence of verrucate sculpturing along the ridge crest.

Thickness of ektexine at the ridge crest at the equator 2–3 μ, at the poles 1.5 μ, in the furrow region 1 μ; thickness of endexine 0.8 μ.

Ephedra graeca C. A. Mey.

Polar axis 62 μ (49–72 μ); equatorial diameter 31 μ (25.5–34.5 μ). Ridges 6.5 (5–9). Shape class index 1.8 (1.6–2.6); prolate.

The exine is thicker than in *Ephedra distachya*, measuring 5 μ at the ridge axis at the equator and 2–3 μ at the poles. It decreases in thickness to 0.7–1 μ in the furrow region and appears to be absent over the colpi. The endexine is continuous and averages 0.8–1.5 μ in thickness. The colpi are narrow, averaging 0.8 μ in width, angular and undulate to the poles, branching every 5–7 μ. Secondary branching is lacking but the sides of the ridge are highly dissected by long, primary, lateral colpi. The verrucae along the ridge crest are not as prominent as in *E. coryi* nor as numerous as in *E. distachya*. In optical section their surface appears flat or only slightly rounded. They vary in length from 5 to 7 μ. The average width of the ridges at the equator varies from 10 μ at the base to 3.5 μ at the crest.

Ephedra helvetica C. A. Mey.

Polar axis 57 μ (43–67 μ); equatorial diameter 27 μ (21–33 μ). Ridges 6.9 (5–9). Shape class index 2.0 (1.6–2.5); prolate–perprolate.

The grains are coarser in appearance than those of *Ephedra distachya* and are so similar in structure to *E. graeca* that pollen of these species cannot be distinguished. The ektexine averages 4–5 μ in thickness at the ridge crest at the equator and 2 μ at the poles. It decreases to 1 μ in the furrow region. The endexine measures 1–1.5 μ. Individual verrucae average 7–8 μ in length.

Ephedra intermedia Schrenk & C. A. Mey.

Polar axis 54 μ (34–65 μ); equatorial diameter 25.5 μ (20–31 μ). Ridges 7.8 (6–10). Shape class index 1.9 (1.2–2.2); prolate–perprolate.

Although the verrucate ridge is composed of series of smaller, angular verrucae, set close together, measuring 2–3 μ in length, the grains appear coarser than those of *E. distachya* as a result of the thicker exine. At the equator the ridges average 6–7 μ in width at the ridge base and 3.5–4 μ at the apex; the width of the furrow area ranges between 5–5.5 μ. In optical section the ridge surface appears almost smooth because of the shallowness of the dissecting grooves. The colpi are thin, shallow and slightly angular in their undulation. Secondary branching does not occur.

Thickness of the ektexine at the ridge crest at the equator 4–5 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 1.5–1.8 μ.

Ephedra major Host var. **procera** Aschers. & Graebn.

Polar axis 56 μ (37–68 μ); equatorial diameter 23 μ (20–27 μ). Ridges 6.3 (5–8). Shape class index 2.3 (1.9–2.6); prolate–perprolate.

The ridge surface is verrucate. In optical section the verrucae are distinctly visible, slightly rounded and average 5–6 μ in length. At the equator the ridges average 8–10 μ in width at the base and 3 μ in width at the crest. The furrow region measures 5–8 μ in width. The colpi are thin, averaging 0.5 μ in width, extremely faint and slightly rounded in their undulations. Long, primary branches of the main colpi occur every 2–6 μ.

Thickness of the ektexine at the ridge crest at the equator 4 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 0.5–0.8 μ.

Ephedra major Host var. **villarsii** Stapf

Polar axis 59 μ (33–74 μ); equatorial diameter 27 μ (20–33 μ). Ridges 6.5 (5–8). Shape class index 1.9 (1.6–2.6); prolate.

These grains are similar to those of *E. equisetina* and *E. monostachya* in the possession of a characteristically thin exine which is composed of an ektexine measuring 0.8–1.4 μ in thickness along the ridge crest and an endexine averaging 0.5–0.8 μ. The thickness of the ektexine in the furrow region decreases to 0.5–0.8 μ. The colpi are narrow and shallow measuring 0.5 μ in depth, and slightly undulate to the poles. Sporadic lateral branching may occur. In some cases these may be cut off every 5.5–7 μ along the course of the main colpi. However, they seldom continue up the ridge surface to its crest. The delicacy of the grain is due to the absence of reticulation or to the extremely faint reticulation on the ridges. The ridges are slightly verrucate along the crest, with verrucae semicircular in outline. These average 2.8–3.5 μ in length and are low, ranging in height from 0.8 to 1 μ. At the equator the width of the ridges at the base is 9 μ and at the crest is 1 μ.

Ephedra monostachya L.

Polar axis 56 μ (42–75 μ); equatorial diameter 32 μ (22–39 μ). Ridges 7.3 (6–9). Shape class index 1.6 (1.3–1.8); prolate.

As in the case of *E. equisetina*, the grains are characterized by thin exines, with ektexines measuring 1.5–2 μ along the ridge crest and endexines measuring 0.5–0.8 μ in thickness. The ridges are delicate, and irregularly verrucate with the length of the individual verrucae varying from 4–8 μ. In optical section the verrucae average 1–1.4 μ in height along the ridge crest and the majority are gently domed along their protruding surface. Colpi are shallow, averaging 0.8 μ in depth, and slightly undulate with only occasional branching.

Ephedra pachyclada Boiss.

Polar axis 55 μ (43–68 μ); equatorial diameter 30 μ (27–36 μ). Ridges 7.9 (5–12). Shape class index 1.7 (1.1–1.9); prolate.

The grain is featured by an endexine which may be as thick as the ektexine. The colpi are narrow, shallow and acutely angular in surface view. Short, lateral branches occur every 2–3 μ at the apices of the angles. Secondary branching seldom occurs. As a result of the shallowness of the lateral branches of the colpus the verrucae are indistinct. They average 2–3 μ in length. In optical section their surfaces are slightly rounded. At the equator the ridges average 5.5–8 μ in width at the base and 3 μ in width at the crest.

Thickness of the ektexine at the ridge crest at the equator 2–3 μ, at the poles 1.5 μ, in the furrow region 1 μ; thickness of the endexine 1.6–2 μ.

Ephedra sinica Stapf PLATE I, *fig. 2*; PLATE III, *figs. 3–6*; PLATE IV, *figs. 5, 6.*

Polar axis 54 μ (42–62 μ); equatorial diameter 28 μ (25–31 μ). Ridges 5.8 (4–6). Shape class index 1.6 (1.4–1.8); prolate.

This species possesses the most highly ornamented pollen grains to be found in the genus. They are sculptured by four to six steep, undulating ridges which project sharply above the rounded contours of the grain. The ridge undulations are slightly rounded to angular and the wave of the undulation measures between 3 and 5 μ in length and 3 and 4 μ in height. Furthermore, small ektexinous ridges, or muri, 0.8–1 μ wide, extend out from the crest of the ridge into the inter-ridge area in a rugulate-reticulate sculpturing pattern enclosing lumina 2–4 μ in diameter.

Viewed in the equatorial plane, the grain is prolate to ellipsoidal, whereas in polar aspect the outline is polygonal with the ridges situated at the angles of bulging, convex sides. Also in polar view, it may be seen that the ridges are rounded, with an average diameter of 1.5 μ, a height of 4–5 μ and are slightly constricted at their bases.

Occasionally, evidence of a thin, slightly branched colpus at the base of the ridge can be seen. However, when present the colpus is indistinct.

The exine is double. The ektexine, at the center of the ridge at the equator varies from 4 to 5 μ in thickness, decreasing slightly toward the poles. In polar view, the ektexine abruptly thins, at the base of the ridge, ceasing altogether at the colpi. The endexine is 2–3 μ thick. In profile view, the ektexine appears to be composed of baculae 4 μ high and 2 μ wide. These are merely the optical sections of the undulating ridge.

Ephedra viridis Cov. PLATE IV, *figs. 1, 2.*

Polar axis 61 μ (44–77 μ); equatorial diameter 34 μ (30–39 μ). Ridges 7.1 (5–9). Shape class index 1.7 (1.5–1.9); prolate.

The grains are characterized by straight, thin-crested, smooth ridges. The main, longitudinal colpi are distinct, narrow and acutely angular. Short lateral branches occur every 2–3 μ and an occasional secondary branch may be found. In optical section, verrucae are evident but they are faint because of the shallowness of the lateral colpi and their surface outline is flattened. At the equator the ridges average 10–14 μ in width at the base and 3.5 μ at the crest.

Thickness of the ektexine at the ridge crest at the equator 3 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 1.5 μ.

Ephedra vulgaris C. A. Mey.

Polar axis 51 μ (49–57 μ); equatorial diameter 28 μ (25–31 μ). Ridges 7. Shape class index 1.7 (1.5–1.9); prolate.

The ridges are smooth, measuring at the equator 3 μ in width at the crest and 7–10 μ at the base. The colpi are thin grooves which branch occasionally but, as in the case of *Ephedra funera*, the lateral branches do not continue far up the ridge.

Thickness of the ektexine at the ridge crest at the equator 2–3 μ, at the poles 0.7 μ, in the furrow region 1 μ; thickness of the endexine 1 μ.

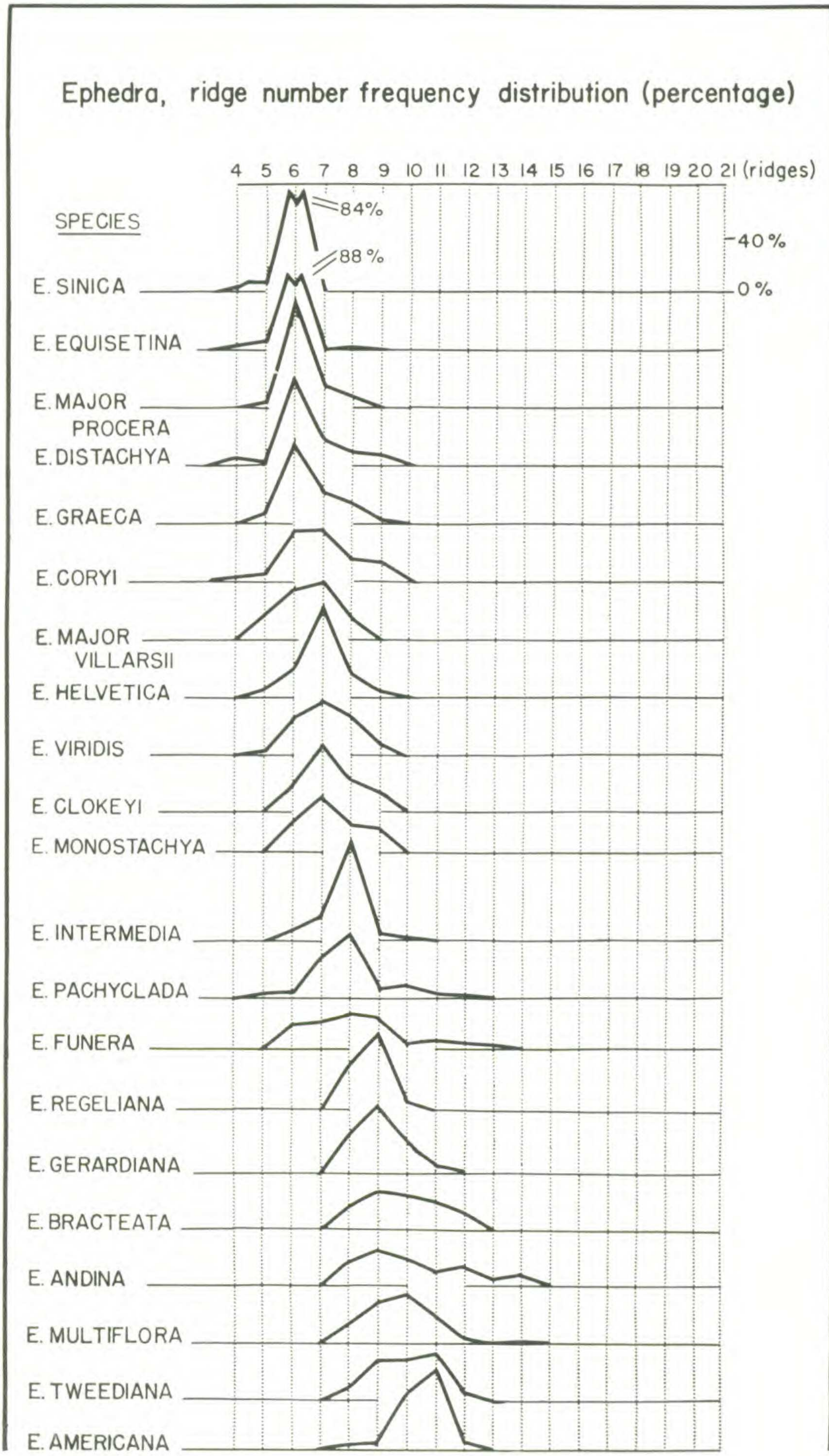
POLLEN TYPE B

This type is approximately of the same size as Type A. The majority of grains are basically polycolpate, although the colpus is often indistinct, and all are sculptured by ektexinous ridges extending meridionally across the grain merging with those from the opposite side.

However, the grains differ significantly from the preceding type in furrow and ridge characteristics. In Type B the ektexine is thickened irregularly to form extremely narrow, undulating, psilate ridges. When viewed in the equatorial plane the narrow ridges appear as highly refractive, smooth, serpentine lines extending the length of the grain. In some cases as in *Ephedra californica*, the undulations continue to the poles; in others, as *E. altissima*, the height of the ridge as well as the degree of undulation decreases at the poles.

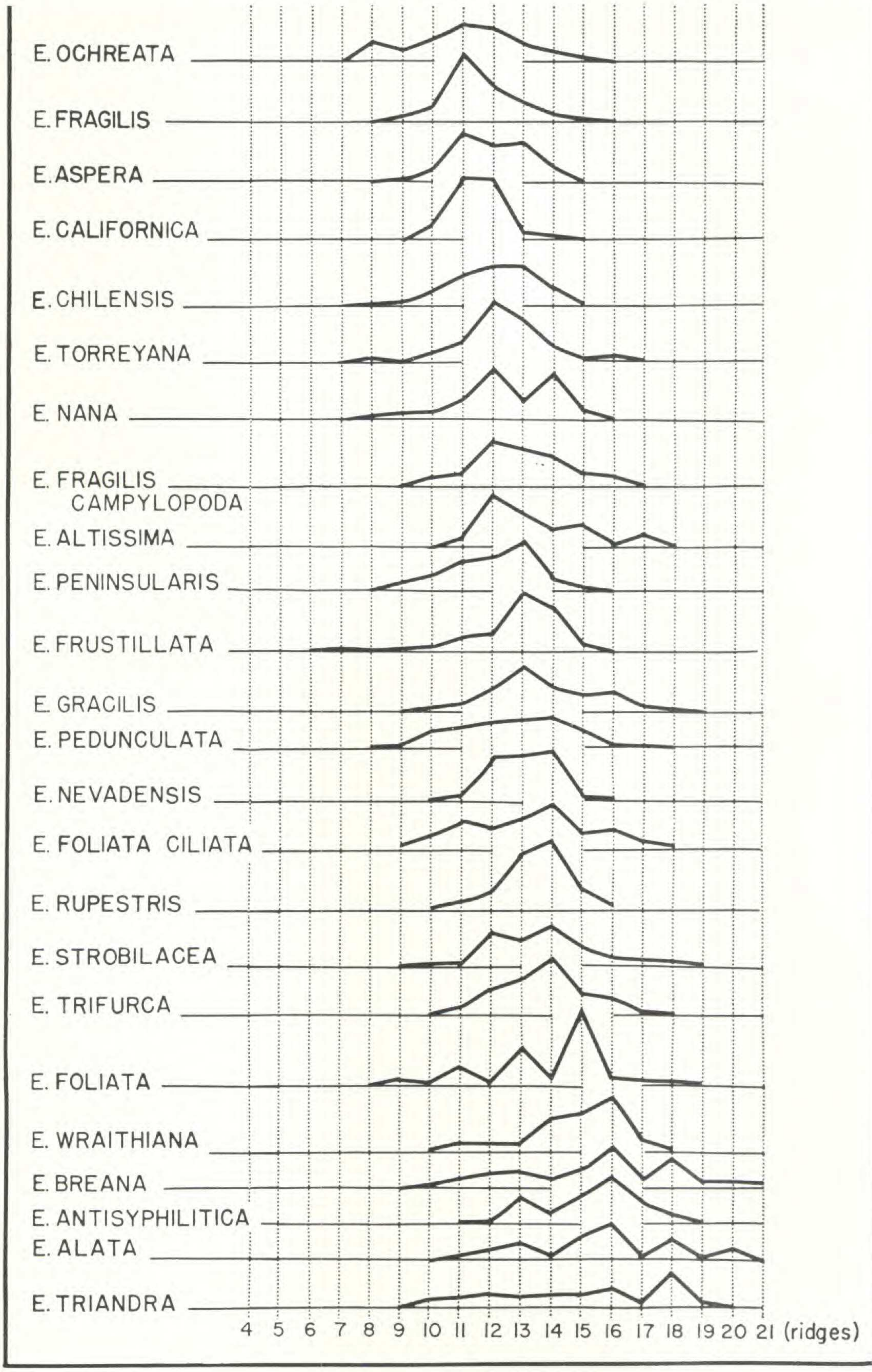
The number of ridges in Type B is generally more numerous than in Type A, ranging, on the average, from 10 to 13. The least amount of variation in our material occurs in *E. californica* where the number of ridges ranges from 10 to 14; the greatest amount of variability was observed in *E. pedunculata* where the ridge number ranges from 9 to 17 (CHART II). The high degree of variability within some species results

CHART II



Ephedra, ridge number frequency distribution (percentage)
4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 (ridges)
SPECIES
84%
88 %
40 %
0 %
E. SINICA
E. EQUISETINA
E. MAJOR PROCERA
E. DISTACHYA
E. GRAECA
E. CORYI
E. MAJOR VILLARSII
E. HELVETICA
E. VIRIDIS
E. CLOKEYI
E. MONOSTACHYA
E. INTERMEDIA
E. PACHYCLADA
E. FUNERA
E. REGELIANA
E. GERARDIANA
E. BRACTEATA
E. ANDINA
E. MULTIFLORA
E. TWEEDIANA
E. AMERICANA

CHART II (*Continued*)



in a few individual cases of overlapping values with respect to ridge number in Types A and B. This somewhat lessens the value of but does not preclude the use of this characteristic, in conjunction with others, as a means of separating the two groups. The high amount of intraspecific variation does, however, prevent the use of this characteristic alone in separating species within each group, or in distinguishing between groups.

The exine is distinctly double and is composed of a thin, continuous endexine and an ektexine which may be continuous or discontinuous. The ektexine is laid down in the form of ridges which in polar view are triangular in outline. In this aspect the highly refractive component of the ridge comprises the central core of the triangle which, according to Welton (1957), varies in shape depending upon species. This, in turn, is covered by the non-hyaline layer. Both of these different layers form the ektexinous ridge. In this respect the structure of the ridge is similar to that found in Type A as well as in Type C. The width of the base of the triangle may vary from 2 to 4 μ, decreasing at the top to a narrow peak of 0.5 to 1 μ; the height of the ridge may range from 2 to 3.5 μ. The ridges are not as massive as in the Type A group. Consequently, the grains appear more delicate, an appearance enhanced by the lack of verrucae along the ridge and the absence of reticulate sculpturing in the furrows.

In a few species colpi are absent.[5] When colpi are present they are located at the base of the furrow, extending unbranched their full length. Moreover, the distinctness of the colpi varies between species, depending upon whether the colpus is the result of a complete absence or merely a thinning of the ektexine. In *E. chilensis* the colpi are only occasionally discernible, whereas in *E. tweediana* well defined colpi can be observed.

DESCRIPTIONS OF SPECIES OF TYPE B

Ephedra altissima Desf.

Polar axis 40 μ (30–49 μ); equatorial diameter 23 μ (21–27 μ). Ridges 13.3 (11–17). Shape class index 1.6 (1.4–1.8); prolate.

The ridges undulate slightly in the equatorial region of the grain, gradually ceasing near the poles. In polar view the ridges measure 5–6 μ in width at the base and decrease to a peak 1–1.5 μ wide. The thickness or height of the ektexinous ridges averages 2–3 μ at the equator. The ridge undulations are variable in extent and may average 4–8 μ in length and 2–3 μ in width. A faint, unbranched, straight colpus is present at the base of each ridge.

Thickness of the ektexine in the furrow region 0.8 μ; thickness of the endexine 1 μ. At the poles the ektexine often projects 5–6 μ beyond the endexine.

Ephedra antisyphilitica Berland.

Polar axis 59 μ (42–59 μ); equatorial diameter 43 μ (33–49 μ). Ridges 15.3 (12–18). Shape class index 1.4 (1.2–1.8); prolate.

[5] For our definition of colpus as applied to *Ephedra* pollen see footnote 4.

This species possesses the largest pollen grains in the group. These may be further characterized by the presence of an extremely tenuous ektexine which easily becomes dissociated from the endexine. The ektexine may become free at one pole only, at both poles, or irregularly around the entire grain. The ektexine is irregularly thickened forming ridges which measure 2.5 μ in height at the equator. In the polar aspect they are triangular in shape and at the equator average 2.5–5 μ in width at the base and 0.7 μ at the crest. The ridges may be either highly undulate, slightly undulate or, in a few cases, almost straight. A slightly undulate, faint, unbranched colpus is present between each ridge. The thickness of the ektexine decreases to 0.5 μ in the furrow region. The endexine averages 1 μ in thickness.

Ephedra californica S. Wats. PLATE I, *fig. 5*; PLATE III, *figs. 1, 2.*

Polar axis 63 μ (53–77 μ); equatorial diameter 32 μ (21–40 μ). Ridges 11.5 (10–14). Shape class index 2.0 (1.5–2.5); prolate–perprolate.

The grains are characterized by ridges 6–7 μ apart that zigzag meridionally the length of the grain. In polar view, the ridges appear triangular with a base measuring 3–4 μ in width, decreasing to a thin crest of 0.5–1 μ. The serpentine ridge undulates sharply throughout its length. The ektexine is 2.4–3.2 μ thick at maximum at the equator, decreasing to 0.5–1 μ in the furrows. The endexine measures 1–1.6 μ. Slightly undulant colpi may be present. The type of undulation varies from tightly angular to widely spaced and semicircular. Occasional primary branches of the main colpi are evident.

Ephedra chilensis Miers PLATE IV, *fig. 3.*

Polar axis 52 μ (35–68 μ); equatorial diameter 30 μ (27–31 μ). Ridges 11.9 (8–14). Shape class index: 1.6 (1.3–1.8); prolate.

Among the Type B species, these grains are distinctive in the greater thickness of their exine. The ektexine averages 2–3 μ along the ridge crest; the endexine measures 1.5–2.8 μ. A thin, serpentine, straight colpus may be visible in each furrow. The ridges are undulant to a varying degree. At the equator they average 5–6 μ in width at the base and 0.5 μ at the crest.

Thickness of the ektexine at the furrow region 1–1.4 μ. As in some of the preceding grains, the ektexine at the poles may project as much as 5 μ beyond the endexine.

Ephedra fragilis Desf. var. **campylopoda** (C. A. Mey.) Stapf

Polar axis 56 μ (44–66 μ); equatorial diameter 30 μ (22.5–36 μ). Ridges 12.9 (10–16). Shape class index 1.8 (1.2–2.4); prolate–perprolate.

Although larger than most members of this group, the pollen grains of this species are smaller than those of *Ephedra californica* or *E. antisyphilitica.* The ridges are narrow at the crest, varying from 1–1.5 μ; wide at the base, the width averaging 2–3 μ; and measure 0.8–1 μ in height at the equator. The ridge crest is acutely undulate with undulations averaging

2.5–5 μ in length and 2.5 μ in width. However, the degree of undulation tends to diminish toward the poles. Indistinct, thread-like, straight colpi are present.

There is a strong tendency for the endexine and the ektexine to separate resulting in the shedding of the ektexine by the grain. This separation is evident at the poles where the ektexine becomes detached and projects out 3–5 μ beyond the endexine to form rectangular enclosures between the two exine layers.

Thickness of the ektexine at the ridge crest at the poles 0.5 μ, in the furrow region 0.5 μ; thickness of the endexine 0.5 μ.

Ephedra multiflora Phil. ex Stapf

Polar axis 41.5 μ (31.5–51 μ); equatorial diameter 24 μ (20–30 μ). Ridges 9.8 (8–14). Shape class index: 1.6 (1.1–2.0); prolate.

The grains are similar to those of *Ephedra tweediana* in their small size, and resemble *E. fragilis* var. *campylopoda* in a tendency to shed their ektexine. The ektexine is 2–3 μ thick at the ridge crest at the equator, often ballooning out 5–6 μ beyond the endexine at the poles. The ridges are featured by a few minor undulations measuring 6–7 μ in length and 3–3.5 μ in width. At the equator the ridges average 7 μ in width at the base and less than 1 μ at the crest. Distinct but thin, straight, unbranched colpi are present.

Thickness of the ektexine in the furrow region 0.8 μ; thickness of the endexine 0.8–1.2 μ.

Ephedra nevadensis S. Wats. PLATE IV, *fig. 7.*

Polar axis 35 μ (31.5–45 μ); equatorial diameter 22 μ (18–27 μ). Ridges 13.0 (11–15). Shape class index 1.6 (1.4–1.9); prolate.

Characteristic features of these grains are the closely undulate colpi which extend along the center of the furrows. The undulations are angular and occur every 2–2.5 μ.

The ridge crests are extremely thin and vary from straight to closely undulate with waves which range in length from 2–2.5 μ and in width from 1.4–1.8 μ. At the equator the ridges measure 3.5–5 μ in width at the base and 0.3–0.5 μ at the crest.

Thickness of the ektexine at the ridge crest at the equator 2.8 μ, at the poles 1.5 μ; thickness of the endexine 0.8 μ. The ridges project out a distance of 2.8 μ beyond the endexine at the poles.

Ephedra pedunculata Engelm. ex S. Wats.

Polar axis 48 μ (40–60 μ); equatorial diameter 29 μ (25–39 μ). Ridges 12.6 (9–17). Shape class index 1.6 (1.4–1.8); prolate.

The ektexine is thicker than the endexine, measuring 2.8 μ at the ridge crest at the equator and 2 μ at the poles. In polar view the ridge measures 3.5–7 μ in width at the base, decreasing to 0.7–0.1 μ at the crest. The colpi are indistinct, thin and slightly undulate. Ridge undulations are irregular in occurrence and measure 4–6 μ in length and 1.5–3.5 μ in width. The thickness of the endexine is 1.6 μ increasing to 2–2.5 μ at the poles.

Ephedra tweediana Fisch. & C. A. Mey.

Polar axis 42 μ (21–55 μ); equatorial diameter 25 μ (24–28 μ). Ridges 10 (8–12). Shape class index 1.7 (1.4–1.9); prolate.

The grains of this species are ornate with highly undulant ridges. At the poles the fused ridges abruptly project forming a circular process at each end of the grain. The ridges are high, projecting 5 μ at the equator. Their basal width at the equator varies from 4 to 12 μ; the crests average 0.5–1 μ. A distinct, straight colpus is present.

Thickness of the ektexine in the furrow region 2 μ; thickness of the endexine 1.5 μ.

POLLEN TYPE C

Although similar to Type B in many respects, the ridge structure in Type C is prevailingly different. The ridges are somewhat higher than in Type B, and usually straight. In some cases, however, there is a tendency for slight undulation in the ridge crest. Although in their most characteristic form the two types are readily separable, there is a tendency in some species for pollen grains to exhibit features of both the B and C types. Hence the Type B and Type C categories are not consistently separable as other than varying degrees of morphological expression. It might be argued that the two types should be merged as one, but in our opinion there is a preponderance of one or the other within a given species, and hence the concept has morphological validity. As will be shown later there is no difficulty in distinguishing the A types from the D types, nor is there in distinguishing the C from the D nor the A from the C types. In this respect we are dealing with a continuous spectrum of structural variation on which arbitrary limits are imposed.

DESCRIPTIONS OF SPECIES OF TYPE C

Ephedra americana Humb. & Bonpl. ex Willd. PLATE II, *figs. 6, 7.*

Polar axis 38 μ (27–49 μ); equatorial diameter 25 μ (21–30 μ). Ridges 10.5 (8–12). Shape class index 1.6 (1.2–1.8); prolate.

A conspicuous feature of these grains is the outbulging of the ektexine which may exceed 6 μ on one or both sides, or circumferentially around the complete grain freeing the two layers of the exine.

In those cases in which the ektexine is attached to the endexine, it measures 2–2.5 μ in thickness at the equator and slightly thicker (3 μ) at the poles. The average thickness of the endexine is 2 μ. With separation of the exine layers the whole grain expands. However, the furrowed ektexine is more flexible than the continuous endexine and expands to a greater degree, resulting in an ektexine "shell" measuring approximately 40 × 30 μ and an endexine "shell" whose average dimensions are 30 × 20 μ.

This disproportionate increase in diameter of the two wall layers of the grain effects a decrease in thickness of the ektexine and endexine proportionately. The average thickness of the ektexine in the mature grain is from 1 to 1.2 μ; whereas the thickness of the endexine remains slightly under 2 μ. Because of the variable nature of the ektexine, the outline of the grain in both polar and equatorial views is highly irregular, but the endexine appears regular in outline and prolate in shape. The ridge crests are narrow, averaging 1 μ in width at the equator and are spaced 4–5 μ apart. At the base of each furrow is a distinct, thread-like, unbranched colpus.

Ephedra andina Poepp. & Endl. PLATE IV, *fig. 4.*

Polar axis 53 μ (42–63 μ); equatorial diameter 27 μ (24–30 μ). Ridges 10.3 (8–14). Shape class index 1.8 (1.7–2.1); prolate.

These grains possess the characteristic, psilate ridges of Type C. At the equator they may measure as much as 4 μ in height. The base of the ridge averages 5 μ in width at the equator, and 0.5–0.8 μ at the crest. The majority of ridges are straight. A narrow, slightly undulating, unbranched colpus is visible at the base of each furrow. The ektexine is thicker than the endexine and averages 3 μ along the ridge crest, thinning to 1 μ in the furrow. The endexine averages between 2 μ and 2.5 μ in thickness. There is a slight projection of the ektexine at the poles.

Ephedra aspera Engelm. ex S. Wats. PLATE I, *fig. 1*; PLATE IV, *fig. 8.*

Polar axis 50 μ (42–59 μ); equatorial diameter 25 μ (22–27 μ). Ridges 11.9 (9–14). Shape class index 1.8 (1.5–2.2); prolate.

The ridges are thin and slight, rising 1.6–2.5 μ above the endexine at the equator, decreasing to 1 μ at the poles. At the equator they measure 4–5 μ in width at the base and 1 μ at the ridge crest. A conspicuous feature of the grains is the projection of the ektexine 3–4 μ beyond the endexine forming small, handle-like structures at both poles. A narrow, slightly undulating colpus is present at the base of each furrow.

Thickness of the ektexine in the furrow region 0.5 μ; thickness of the endexine 1.6 μ.

Ephedra bracteata Miers

Polar axis 50 μ (42–60 μ); equatorial diameter 29 μ (25–33 μ). Ridges 9.8 (8–12). Shape class index 1.6 (1.5–1.7); prolate.

In contrast to the thin, smooth condition of the ridges in *Ephedra aspera*, the ridges in *E. bracteata* are heavy, wide and slightly irregular in surface view. At the equator they measure 5–7 μ in width at the base and 2 μ in width at the ridge crest. The bases of the ridges are cut by an irregular, highly undulate colpus which occasionally branches.

Thickness of the ektexine at the ridge crest at the equator 3–3.5 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 3 μ.

Ephedra foliata Boiss. & Kotschy ex. Boiss.

Polar axis 44 μ (30–53 μ); equatorial diameter 28 μ (22–30 μ). Ridges 13.9 (9–18). Shape class index 1.6 (1.4–2.0); prolate.

The grains are featured by narrow, straight ridges, measuring 4–7 μ in width at the base at the equator and 0.5–1 μ at the crest. They extend 1.8–2.5 μ in height at the equator decreasing to 1.4 μ at the poles. The majority of the ridges are straight but a few undulating ones are present. A narrow, straight colpus is present at the base of each furrow.

Thickness of the ektexine in the furrow region 0.5 μ; thickness of the endexine 2 μ.

Ephedra foliata Boiss. var. **ciliata** (C. A. Mey.) Stapf

Polar axis 47 μ (44–54 μ); equatorial diameter 29 μ (25–36 μ). Ridges 13.2 (10–17). Shape class index 1.5 (1.1–1.7); prolate.

The ridges are narrow and straight, measuring 3.5 μ in height at the equator, decreasing to 2 μ at the poles. At the equator they average 3.5–4 μ in width at the base and 0.5 μ at the crest. Thin, thread-like colpi are present at the base of each furrow.

Thickness of the endexine 1.4 μ.

Ephedra fragilis Desf.

Polar axis 53 μ (44–63 μ); equatorial diameter 33 μ (28–51 μ). Ridges 11.5 (9–15). Shape class index 1.5 (1.3–1.7); prolate.

The grain appears almost spherical in equatorial view with projecting, ektexinous ridges at the poles. The ridges measure 1–1.5 μ in height at the equator and project a distance of 3–4 μ beyond the polar limits of the endexine.

With high magnification, the crest of the ridges exhibits tight undulations; under low power there is little evidence of this condition and the ridge crests appear straight. The ridge crests are thin, averaging 0.5 μ at the equator; the bases of the ridges are wider, averaging 5 μ at the equator and decreasing to 1.4 μ at the poles. A thin but distinct, slightly undulating colpus is present in each furrow.

Thickness of the ektexine in the furrow region 0.8 μ; thickness of the endexine 2 μ.

Ephedra frustillata Miers

Polar axis 48 μ (30–60 μ); equatorial diameter 30 μ (28–36 μ). Ridges 12.7 (7–15). Shape class index 1.5 (1.2–1.7); prolate.

These differ from some of the preceding grains in the larger size and in the absence of any tendency toward separation of the exine layers. In company with *Ephedra regeliana* and *E. ochreata* they possess a thin exine which measures 1.5 μ along the ridge crest at the equator, a thin endexine of 0.8 μ, and narrow, straight ridges.

Thickness of the ektexine at the ridge crest at the poles 1 μ, in the furrow region 0.5 μ.

Ephedra nana Dusen

Polar axis 46 μ (35–60 μ); equatorial diameter 27 μ (24–30 μ). Ridges 12.4 (8–15). Shape class index 1.6 (1.4–2.0); prolate.

The grains possess ridges of the Type C structure which are bordered at their bases by thin, tightly undulate or straight colpi. The ridges average 3.5–5 μ in width at the equator at the base and 0.5 μ at the crest.

Thickness of the ektexine along the ridge crest at the equator 2 μ, at the poles 0.7–1 μ; thickness of the endexine 1.5 μ. The ektexine projects 2.5–3 μ beyond the endexine at the poles.

Ephedra ochreata Miers

Polar axis 41 μ (27– 51 μ); equatorial diameter 22 μ (18–30 μ). Ridges 11.0 (8–15). Shape class index 1.7 (1.6–2.0); prolate.

The exine is thin, the ektexine measuring 0.8–1.4 μ in thickness along the ridge crest; the endexine as thick as the ektexine or slightly more so varying between 1 and 1.5 μ. In the furrow region the thickness of the ektexine decreases to 0.5 μ. A slight increase in thickness of the ektexine may or may not occur at the poles. At the equator the width of the ridges at the base averages 3.5–6 μ; that of the ridge crest is 0.7 μ. A tightly undulate to straight colpus is present at the base of each ridge. In optical section the ridge crest is minutely irregular in outline.

Sculpturing of the ektexine: slightly scabrate.

Ephedra peninsularis I. M. Johnston

Polar axis 52 μ (38–63 μ); equatorial diameter 30 μ (30–31 μ). Ridges 11.9 (9–15). Shape class index 1.6 (1.5–1.8); prolate.

The ridges are completely straight, averaging at the equator 5–8.5 μ in width at the base and 1–2 μ at the crest. Each furrow contains a distinct, thin, straight colpus. Although the surface of the ridge is psilate, the overall appearance of the grain is one of massiveness as a result of the thick exine.

Thickness of the ektexine at the ridge crest at the equator 3–4 μ, at the poles 4 μ, in the furrow region 1 μ; thickness of the endexine 1.6 μ.

Ephedra regeliana Florin

Polar axis 38 μ (28–51 μ); equatorial diameter 19 μ (16–21 μ). Ridges 8.7 (8–10). Shape class index 1.9 (1.6–2.0); prolate.

Distinctive because of size, this species, together with *E. americana*, possesses the smallest pollen grains of the group. However, the grains differ from those of *E. americana* in the possession of an ektexine which adheres closely to the endexine. The ridges are straight to slightly undulate, and measure 1–2 μ in height at the equator decreasing to 0.5–1 μ at the poles. At the equator they average 5–7 μ in width at the base and 1–1.2 μ at the crest. A slightly undulate colpus is present in each furrow.

Thickness of the ektexine in the furrow region 0.5 μ; thickness of the endexine 0.5 μ.

Ephedra torreyana S. Wats.

Polar axis 51 μ (38–61 μ); equatorial diameter 27 μ (25–30 μ). Ridges 12.3 (8–16). Shape class index 1.8 (1.5–2.0); prolate.

The exine is thin, composed of an ektexine measuring 1.6 μ in thickness along the ridge crest, and an endexine equally as thick as the ektexine, 1.6 μ. There is some tendency for the ektexine to project 2–3 μ beyond the polar limits of the grain. The ridges are straight and at the equator measure 0.8 μ in width at the crest and 4 μ through the base. Thin, unbranched straight or slightly undulant colpi are visible.

Ephedra wraithiana I. M. Johnston

Polar axis 50 μ (38–65 μ); equatorial diameter 26 μ (24–28 μ). Ridges 14.8 (11–17). Shape class index 1.6 (1.4–2.1); prolate.

The grains are similar in structure to the preceding species. They possess characteristic Type C ridges measuring 4.5–5 μ in width at the base at the equator, and 1 μ at the crest. Each furrow is featured by a thin, straight colpus. In optical section the ridges appear slightly irregular in outline.

POLLEN TYPE D

The grains of Type D are characterized by wide, low, gently rounded, ektexinous ridges which measure 2–3 μ in height and 3.5–9 μ in width. In polar view the ridges appear semicircular in outline, in contrast to the triangular outline of the ridges in the three preceding groups. The furrows which abruptly flank the ridges at their bases are narrow (1–3.5 μ), unbranched and straight. They are the result of extreme thinning of the ektexine. No colpi are present.

Within this group occurs the species which possesses the greatest number of ridges, *E. alata* (CHART II). Moreover, the average number for the group as a whole is greater than in Types B and C. Pollen grains of the D type are quite distinctive and readily separable from the other pollen types. However, within some species, possessing predominantly Type D grains, occasional grains of the B and C types occur. None of the seven species possessing D type grains shows the least tendency toward the A type.

DESCRIPTION OF SPECIES OF TYPE D

Ephedra alata Dcne.

Polar axis 57 μ (42–70 μ); equatorial diameter 35 μ (30–39 μ). Ridges 15.6 (11–20). Shape class index 1.6 (1.4–1.8); prolate.

These grains are characterized by large size as well as by a granulate texture of the ektexine ridges. The ridges are sculptured by minute granules approximately 0.5 μ in diameter scattered irregularly over the surface. They may be found in distinct clumps or widely separated. When the granules are widely spaced, there is some indication that the intervening space is slightly pitted. The width of the ridges at the base varies from 4–7 μ at the equator to 2–3.5 μ at the poles, while the furrows measure 1–2 μ in width continuously along their complete length to their abrupt termination near the poles. The furrows are somewhat irregular in shape, and in surface view the ektexine of the furrow appears slightly granulate. The degree of sculpturing in the floor of the furrows is much less than on the ridges; the granules are smaller and less numerous.

In most cases the endexine is thicker than the ektexine, and may measure as much as 2.5 μ in thickness. The ektexine measures 1–1.5 μ at the center of the ridges at the equator but may project as much as 4 μ beyond the polar limits of the grain.

Ephedra breana Phil. PLATE IV, *fig. 9.*

Polar axis: 44 μ (34–54 μ); equatorial diameter 32 μ (27–39 μ). Ridges: 15.2 (10–16). Shape class index 1.3 (1.1–1.6); prolate.

Similar to *Ephedra rupestris*, these pollen grains are small and very compact in appearance. There is no tendency for the ektexine to project at the poles, although the ektexine is a little thicker there than at the equator. The average width of the ridges at their base at the equator varies between 3.5 μ and 4.5 μ.

Thickness of the ektexine at the ridge crest at the equator 2–3 μ, at the poles 4 μ, in the furrow region 1 μ; thickness of the endexine 0.8–1.4 μ.

Ephedra gracilis Phil.

Polar axis 56 μ (35–65 μ); equatorial diameter 26 μ (24–31 μ). Ridges 13.5 (10–18). Shape class index 1.9 (1.7–2.3); prolate.

The grains possess an average of 13 low ridges which measure 4–7 μ in width at the equator decreasing to 2.5–3 μ at the poles. The furrows are narrow, 1–1.5 μ, and slightly irregular in outline. The exine is composed of a variably thickened ektexine which averages 3–3.5 μ in thickness, the height of the ridges at the equator, decreasing laterally to 1 μ at the furrow, and a continuous endexine which measures 1.5–2 μ in thickness. The ektexine does not project at the poles.

Ephedra rupestris Benth.

Polar axis 39 μ (37–45 μ); equatorial diameter 28 μ (27–31 μ). Ridges 13.5 (11–15). Shape class index 1.4 (1.2–1.6); prolate.

These grains are among the smallest of the type D group. The ektexine measures 2 μ at the central point of the ridge at the equator, but gradually thins laterally in the furrow, and increases poleward to 3.2 μ. The endexine measures 0.8–1.5 μ in thickness. The ektexine adheres closely to the endexine of the grain at the poles and there seems to be no tendency for separation. The basal width of the slightly rounded ridges at the equator is 8–9 μ decreasing to 6–7 μ at the poles. The ridges are separated by extremely straight, narrow, psilate furrows.

Ephedra strobilacea Bunge

Polar axis 44 μ (31–60 μ); equatorial diameter 26 μ (20–31 μ). Ridges 13.7 (10–18). Shape class index 1.6 (1.5–1.7); prolate.

The ridges are thin, averaging 3 μ at the equator. The thickness of the ektexine at the equator varies from 0.8 μ in the furrow region to 1.5–3 μ at the ridge crest. The endexine varies in thickness from 1–1.5 μ. The ektexine projects 4–4.5 μ beyond the endexine at the poles in a manner similar to the preceding species. An indistinct, threadlike, straight furrow is present.

Ephedra triandra Tul.

Polar axis 41 μ (32–49 μ); equatorial diameter 26 μ (24–28 μ). Ridges 15.0 (10–19). Shape class index 1.4 (1.3–1.7); prolate.

The pollen grains closely resemble those of *Ephedra rupestris*. The ridges are low, measuring 1.5 μ in height and 4–5 μ in width at the equator. Thickness of the ektexine at the ridge crest at the equator 1.5 μ, at the poles 1.5 μ, in the furrow region 0.5 μ; thickness of the endexine 1.5 μ. The ektexine projects 4 μ beyond the polar limits of the endexine.

Ephedra trifurca Torr. PLATE I, *fig. 4*; PLATE II, *figs. 3, 4*.

Polar axis 53 μ (39–63 μ); equatorial diameter 29 μ (28–30 μ). Ridges 13.7 (11–17). Shape class index 1.8 (1.5–2.1); prolate.

These grains possess the thinnest exine in the D type group. The thickness of the two exine layers at the equator averages between 1.8 and 2.4 μ, of which 0.8–1 μ is the thickness of the ektexine and 1–1.4 μ is the thickness of the endexine. However, the thickness of the ektexine increases to 2 μ at the poles. In addition, the ektexine ridges, after following the contour of the grain up to this point, project outward. As is characteristic of the Type D group the grains possess gently rounded, wide ridges 2.8–5 μ in width. These narrow to 2–3 μ at the poles. The ridges are separated by distinct, unbranched furrows which are slightly irregular in outline where they border the steep-sided ridges.

DISCUSSION

The system of pollen classification presented here is based primarily on the number and structure of ektexine ridges, the size and form of the intervening furrows and the presence or absence and structure of the "colpi."[6] On the basis of these features, *Ephedra* grains may be divided into four groups, here designated as Types A, B, C and D. Pollen Types A and D represent the two extremes in the genus while Types B and C tend to be intermediate in ridge number and other characteristics. Furthermore, pollen grains of Type B seem to be more closely related to Type A (as is also true of Type C) than to Type D. Type A pollen grains tend to predominate

[6] For definition of our use of the term colpus see explanatory footnote 4.

in a taxonomically coherent group of species and there is less variation in ridge number within this group than in the other three. Furthermore, since the *average* ridge number in this group of species does not overlap with the *average* ridge number in other groups, species possessing grains of Type A may often be determined on the basis of ridge number alone. This is not the case for species possessing the other types of pollen because of the extensive variation within each group of species and even within a single species. The three remaining groups of species are separated by the use of other characters of the ridges, such as height, steepness of slope and shape in polar view. To a considerable extent this classification system possesses practical value only in separating species featured predominantly by the A and D pollen types, respectively, and is of more limited value in grouping species under the B and C types. In this respect the concept of pollen types as we have employed it here, is morphological rather than taxonomic.

An effort was made, however, to determine whether any relationship or correlation exists between the different pollen types and the generally accepted taxonomic system. Pearson (1929), in discussing the taxonomy of *Ephedra*, points out that the general habit of the plant is of little value as a systematic character because in most species it is profoundly influenced by environment. As an example he cites *E. distachya* which may occur as a dwarf bush a few inches in height, or may develop into a shrub up to six feet in height. He emphasized that the remarkable degree of uniformity in the vegetative form and anatomical structure of the plant introduces difficulty in the way of separating and grouping the species. The present taxonomic system is one proposed by Stapf (1889) who based his monographic study of the genus on the characteristics of the bracts of the female inflorescence. His study, although extensive, did not include all presently known species of *Ephedra*. A more recent taxonomic revision of the North American species of the genus was presented by Cutler (1939) and some of the South American species were investigated by Hunziker (1949), but no attempt was made to revise the genus as a whole nor to consider the phylogenetic relationships of the American species with those of the old world. The system in use (Stapf, 1889) remains incomplete and there is still great need for a revision of the entire group. Stapf's system is presented here in an effort to determine whether the pollen groups recognized in the present study have any relation to his taxonomic groups within the genus.

Section I. ALATAE. Mature spike dry; bracts more or less indurated along the midrib, otherwise membranous, produced laterally into wing-like expansions.

1. Tropidolepides.[7] *E. alata* (D); *E. strobilacea* (D).
2. Habrolepides. *E. trifurca* (D); *E. torreyana* (C); *E. multiflora* (B).

[7] Designated as tribes by Stapf, these subdivisions of sections are not validly published (Article 5, International Code of Botanical Nomenclature 1956) and should be republished as either subsections or series. They are used here, however, for purposes of comparison.

Section II. ASARCA. Mature female spike dry; bracts slightly hardened, scarcely membranous-winged.

3. Asarca. *E. californica* (B); *E. aspera* (C).

Section III. EPHEDRA (Pseudobaccatae). Mature bracts of female spike often narrowly membranous-margined, at length becoming thick and fleshy.

4. Scandentes. *E. altissima* (B); *E. foliata* (C); *E. fragilis* (C); *E. fragilis* var. *campylopoda* (B).
5. Pachycladae. *E. pachyclada* (A); *E. intermedia* (A).
6. Leptocladae. *E. helvetica* (A); *E. distachya* (A); *E. monostachya* (A); *E. gerardiana* (A); *E. equisetina* (A); *E. sinica* (A); *E. regeliana* (A).
7. Antisyphiliticae. *E. nevadensis* (B); *E. antisyphilitica* (B); *E. americana* (C); *E. gracilis* (D); *E. tweediana* (B); *E. triandra* (D); *E. ochreata* (C).

It is apparent that our pollen classification scheme shows only partial agreement with Stapf's groups. In the case of the "Pachycladae" and "Leptocladae" of Section III the correlation is good, inasmuch as Type A pollen only occurs throughout the group. Moreover Type A pollen is restricted in occurrence to these two groups in the genus. In Section I, the "Habrolepides" possess intermediate (Types B and C) as well as Type D pollen; while Section II (Asarca) has only intermediate pollen (Types B and C); Section III (Ephedra) is characterized by the presence of all four groups. In the "Scandentes" the intermediate pollen types are found; while in the "Antisyphiliticae" both intermediate and Type D pollen are characteristic.

As a further comparison, the pollen types and the species of *Ephedra* in which they occur are arranged below by major geographical areas.

ASIA.

Type A: *E. equisetina*, *E. gerardiana*, *E. major* var. *procera*, *E. monostachya*, *E. pachyclada*, *E. sinica*.

Type B: None.

Type C: *E. foliata*, *E. regeliana*.

Type D: *E. strobilacea*.

MEDITERRANEAN REGION.

Type A: *E. distachya*, *E. graeca*, *E. helvetica*, *E. intermedia*, *E. major* var. *villarsii*, *E. vulgaris*.

Type B: *E. altissima*, *E. fragilis* var. *campylopoda*.

Type C: *E. foliata* var. *ciliata*, *E. fragilis*.

Type D: *E. alata*.

NORTH AMERICA.

Type A: *E. clokeyi*, *E. coryi* var. *viscida*, *E. funera*, *E. viridis*.

Type B: *E. antisyphilitica*, *E. californica*, *E. pedunculata*, *E. nevadensis*.

Type C: *E. aspera*, *E. nana*, *E. torreyana*, *E. peninsularis*.

Type D: *E. trifurca*.

SOUTH AMERICA.

Type A: None.

Type B: *E. chilensis*, *E. tweediana*, *E. multiflora*.

Type C: *E. americana*, *E. andina*, *E. bracteata*, *E. frustillata*, *E. ochreata*, *E. wraithiana*.

Type D: *E. breana*, *E. gracilis*, *E. rupestris*, *E. triandra*.

From the above material it will be noted that pollen type A is predominantly Asiatic and Mediterranean in range, with only four of the sixteen species possessing Type A occurring in the western hemisphere and all of these in the United States. In contrast to this, five of the seven species bearing Type D pollen occur in the western hemisphere, four being located in South America and one in the United States. Concerning the remaining two species, one, *E. alata*, is North African, the other, *E. strobilacea*, is Asiatic. Among the intermediate groups B and C seventeen of the twenty-four species are found in the western hemisphere.

Insofar as the authors are aware, the fossil *Ephedra* pollen from Long Island represents the first Cretaceous occurrence known from North America. The grains represent an extreme in one of the four morphological types which we propose as characterizing *Ephedra* pollen. Moreover the grains are morphologically indistinguishable from *Ephedra sinica*, an old world species of the Type A group.

Ephedra today is predominantly a warm desert-steppe plant restricted to both meteorologically and physiologically dry areas. In North America it extends from the southwestern desert areas of the United States eastward to Texas and south to Mexico. In South America it occurs from the drier parts of Ecuador through western Chile into Patagonia. In Europe it extends along the northern Mediterranean coast in Spain and France and extends north and east into Germany and Hungary. It also occurs along the north coast of Africa, and extends eastward through Afghanistan into western China. According to Gams (1952, cited by Iversen, 1954) it is indifferent to temperature but seems to require both climatic and edaphic dryness. For example, the typical localities of *E. distachya* are warm, but the same species is found in isolated, remote localities in Siberia north to the arctic circle and in the alpine zone in Tibet. This extreme adaptability possibly explains the presence of *Ephedra* in North America and Europe during late glacial time. Gams (1927) further states that it occurs in very dry and open pine woods. This is extremely interesting in view of the association of the fossil material from Long Island with abundant pollen assignable to the Coniferales and Cycadales.

Tchigouriaeva (1954) suggests that an ancestral form of *Ephedra* (*Ephedrites*) evolved by the Jurassic. This conclusion is based on the similarity between modern *E. foliata* pollen and Permo-Triassic remains of the Cordaitales. These Permian cordaitalian remains are ridged pollen grains bearing two bladders. By the Lower Triassic a progressive reduction in bladder development had occurred until the bladders were either vestigial or, in a few cases, completely absent. Tchigouriaeva reasoned, therefore, that by the Jurassic, pollen of the modern *Ephedra* type (without bladders) had probably evolved. It should be noted, however, that no such Jurassic remains have thus far been discovered. Pollen having gnetalian affinities, possessing a varying number of ridges and occasionally a furrow, as in *Welwitschia*, has been described from Cretaceous sediments in Nigeria and Venezuela (Kuyl et al., 1955). Tchigouriaeva's hypothesis is rendered more plausible, however, by the discovery of Cretaceous pollen of essentially modern structure as demonstrated in this paper. Doubtless future discoveries will bridge the gap between ancestral forms and true *Ephedra* pollen, and clarify more fully the evolutionary story of *Ephedra* in pre-Cretaceous time.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–5. Major morphological types characterizing *Ephedra* pollen grains. FIG. 1. *Ephedra aspera*, Type C. FIG. 2. *Ephedra sinica*, Type A. FIG. 3. *Ephedra distachya*, Type A. FIG. 4. *Ephedra trifurca*, Type D. FIG. 5. *Ephedra californica*, Type B. (All figures × 1200.)

PLATE II

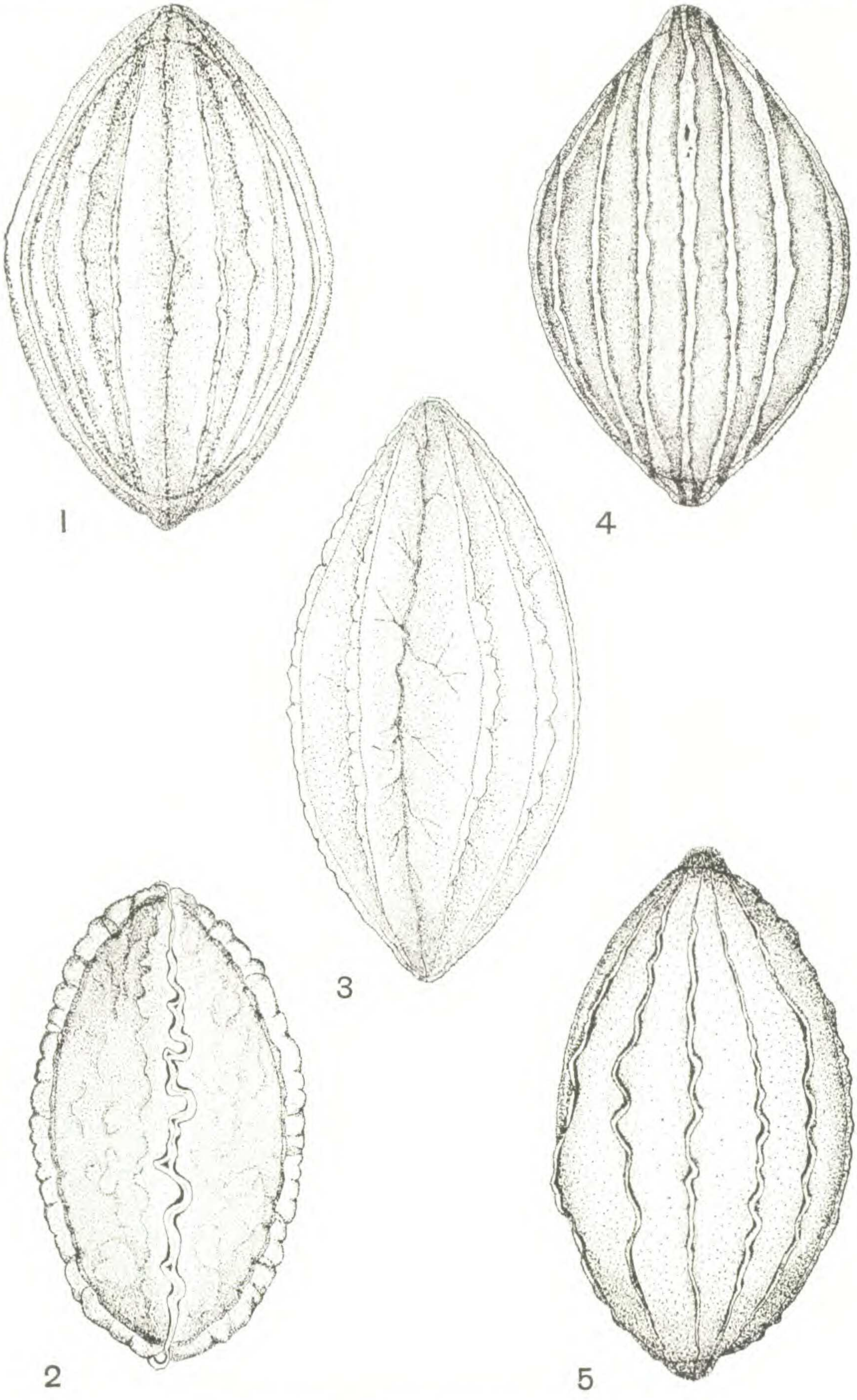
FIG. 1. Modern *Ephedra distachya*. View of the serpentine colpus. Note the primary and secondary branching. FIG. 2. Same grain at mid focus, showing the thickness of the exine in outline. Note also the dissection of the ektexinous ridge crests which are visible in optical section along both edges of the grain. This dissection is caused by branching lateral colpi. FIG. 3. Modern *Ephedra trifurca*. View at high focus of the wide, low, slightly scabrate ridges characteristic of Type D pollen. Note the bright, hyaline furrows. FIG. 4. Same grain at mid focus, showing the thickness of the ektexine. FIG. 5. Modern *Ephedra funera*. High focus view of the straight, slightly verrucate ridges. FIG. 6. Modern *Ephedra americana*. Mid focus view showing the projecting ektexine at the poles. FIG. 7. *E. americana*. A polar view of a similar grain. Note the high but fine, straight ridges and their junction at the poles. (All figures × 1000.)

PLATE III

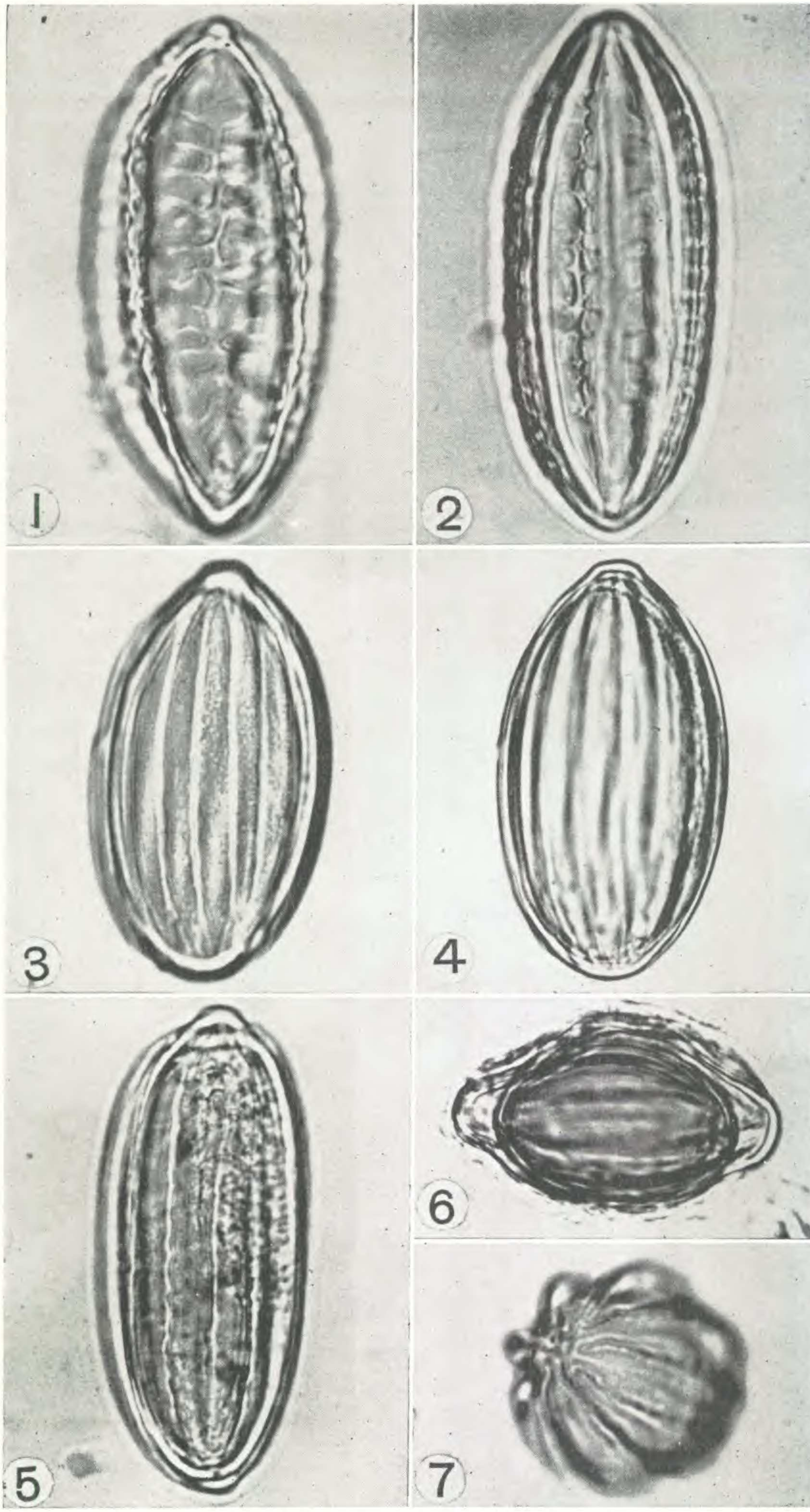
FIG. 1. *Ephedra californica*. High focus view of the narrow, undulating, hyaline ridges which characterize Type B pollen. FIG. 2. Same grain at mid-focus, showing the outline of the ridges along the edges of the grain. FIG. 3. *Ephedra sinica*. High focus view of the reticulation found along the surface of the exine between the ridge crests. FIG. 4. Same grain at mid-focus, showing the extent of the outline of the endexine. FIG. 5. The undulating ridge along the opposite side of the body is visible. FIG. 6. *E. sinica*. A smaller specimen in which the baculate condition of the ektexine is visible in optical section. (All figures × 1000.)

PLATE IV

FIG. 1. *Ephedra viridis*. High focus view of the angular, undulating colpus. FIG. 2. Same grain at higher focus. Note the smoothness of the ridge crest. FIG. 3. *Ephedra chilensis*. High focus view of the undulant ridge crest. FIG. 4. *Ephedra andina*. Typical Type C pollen grain. FIG. 5. *Ephedra sinica*. Polar view of mid focus showing the structure of the ridge. Note the continuous and evenly distributed endexine, the hyaline central core of each ridge and the thin outer tissue. FIG. 6. Same grain at high focus showing the junction of the ridges at the poles. FIG. 7. *Ephedra nevadensis*. High focus view of the tightly undulant ridge. FIG. 8. *Ephedra aspera*. High focus view of the characteristic straight ridges of Type C pollen grains. FIG. 9. *Ephedra breana*. High focus view of the low, gently domed ridges characteristic of Type D pollen grains. (All figures × 1000.)



Steeves & Barghoorn, Pollen of Ephedra



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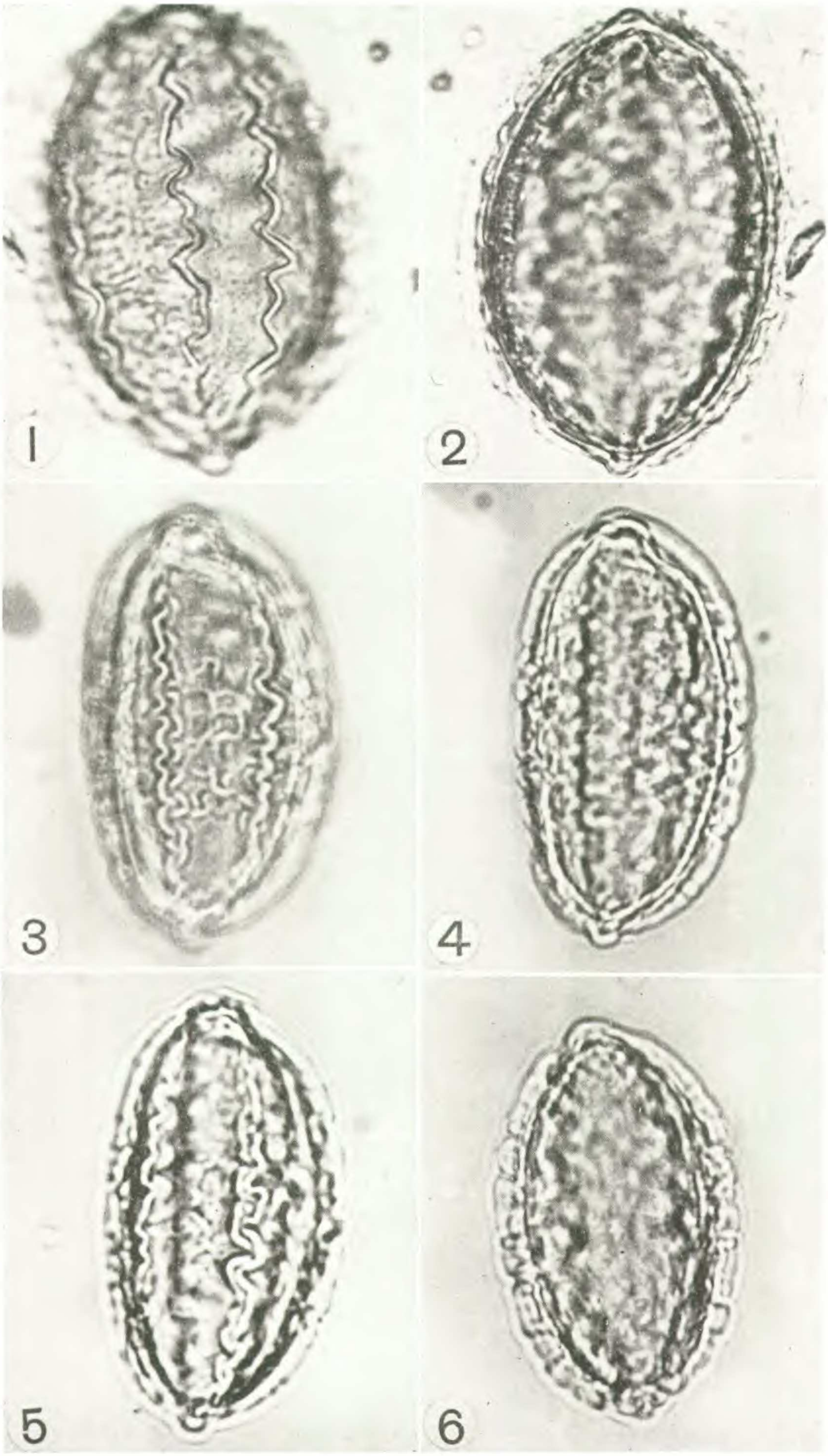
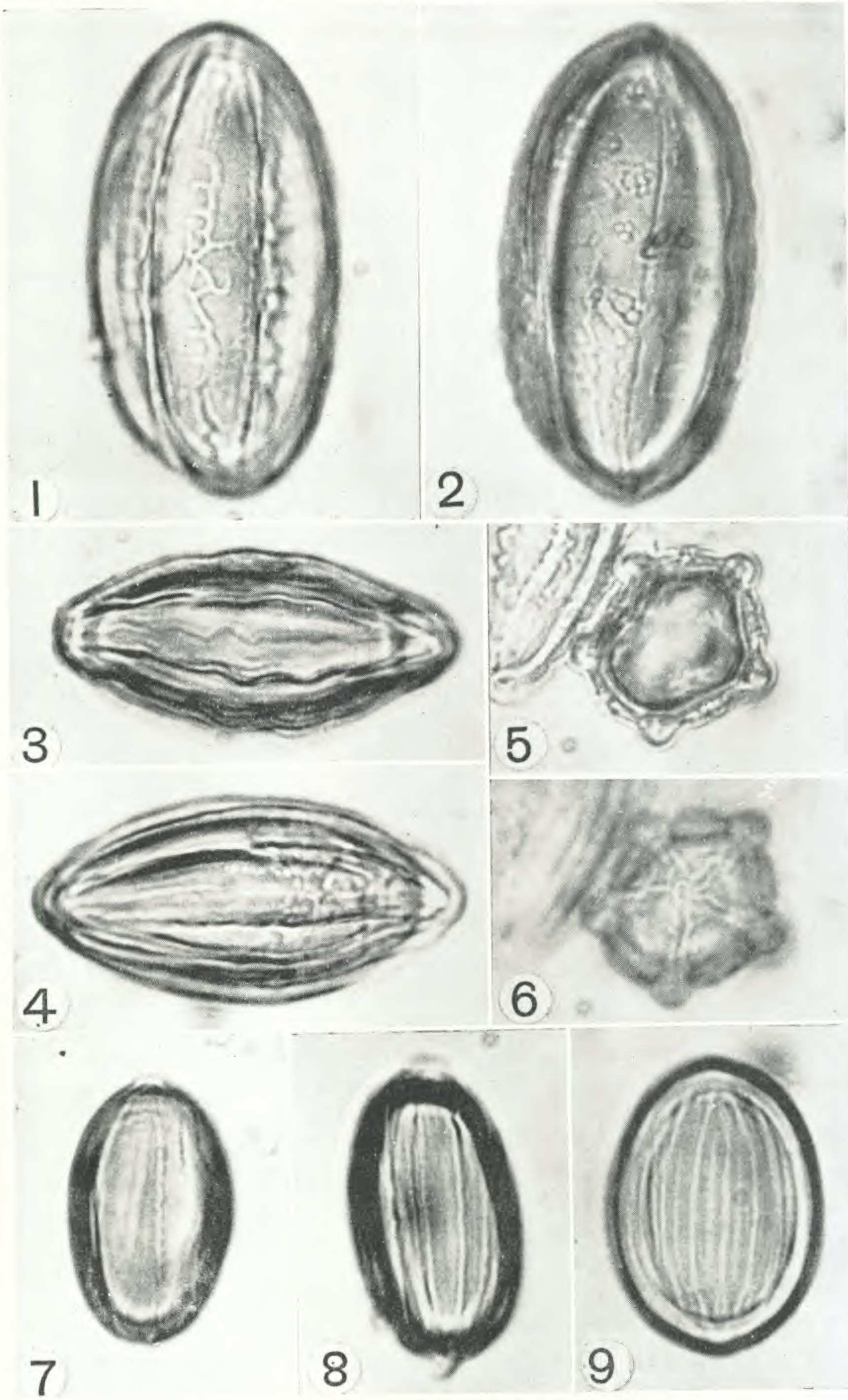


Steeves & Barghoorn, Pollen of Ephedra



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