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THE PORE NUMBER OF PERIPORATE POLLEN WITH SPECIAL REFERENCES TO *CHENOPODIUM*

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SUMMARY

The number of pores on isometric, periporate pollen can be estimated from two measurements (*1*) the distance between centers of two adjacent pores (chord) (C) and (*2*) the diameter of the grain (D). Considerations of spherical geometry indicate the C/D ratios bear a uniform, non-linear relationship to the pore number.

Chord to diameter ratios were determined for 74 collections of 35 species of *Chenopodium* by measuring a single chord and diameter on each of 50 grains of a collection. The means of the collections were compared, and, in general, the means of collections of the same species, or of closely related species, were similar indicating that the C/D ratio is a character of taxonomic significance. The application of C/D ratios to the identification of fossil pollen is discussed.

INTRODUCTION

The number of pores on periporate pollen has been used as a diagnostic character for taxonomic and pollen analytical purposes in the Caryophyllaceae and Plantaginaceae (FAEGRI and IVERSEN, 1964) and Chenopodiaceae (MONOSZON, 1952). FAEGRI and IVERSEN (1964) recommend making a pencil sketch when counting the pores, while MONOSZON (1952) counts the pores on the upper hemisphere of a grain and multiplies by two. We propose here a method of estimating the pore number by means of the ratio of two measurements, the chord or distance between centers of adjacent pores (C) and the diameter of the grain (D) (Fig.1). The chord to diameter ratio (C/D) bears a uniform, nonlinear relationship to the pore number. In the application of the C/D ratio it is assumed that the pollen are spherical and that the pores are evenly spaced, i.e., the pollen is isometric (WODEHOUSE, 1935).

In a survey of the pollen of the Chenopodiaceae, *Chenopodium* showed

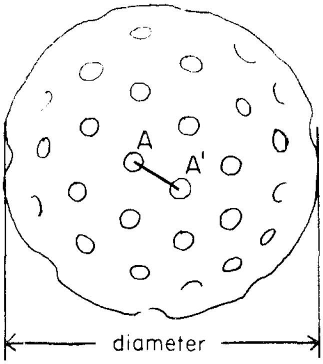

Fig.1. Upper hemisphere of an isometric periporate pollen grain showing the chord C(A–A in this figure) and diameter (D); the C/D ratio is 0.173.

an interesting variation in pore number between species and was selected to explore the possibilities of C/D ratios as a taxonomic character. The nomenclature for this genus follows WAHL (1954), except that *C. pratericola* RYDB. of that treatment is more properly called *C. desiccatum* A. NELSON (H. A. Wahl, personal communication, 1965).

MATERIALS AND METHODS

Slides of acetolized pollen were made from plant collections identified or annotated by H. A. Wahl. The pollen were stained with safranin and mounted in silicone oil. Duplicate slides, whose labels contain herbarium sheet information, were deposited at the Limnological Research Center of the University of Minnesota. All collections were of plants grown in the U.S.A. or Canada, except *C. vulvaria* T133 (Iraq), *C. polyspermum* T130, J15 (Europe), *C. serotinum* T138 (Austria), *C. hybridum* T160 (Germany), *C. multifidum* J45 (Australia) and *C. aristatum* J11 (China).

Measurements were made with an ocular screw micrometer in conjunction with an oil immersion lens. In practice, the chord was measured from the edge of a pore to the corresponding edge of an adjacent pore. In each collection, a single C/D ratio was determined for each of 50 grains. In addition, 10 C/D ratios (10 chords, 1 diameter) were determined on each of two grains from each collection. Although not reported here, pore diameters were also measured for the purpose of determining pore areas of pollen of various species.

RESULTS

Altogether 74 collections of 35 species of *Chenopodium* were measured. The species are arranged in Table I within their nine sections according to decreasing mean C/D values. The mean values may be cautiously interpreted as indicating a range of pore numbers between species of 36–150 (see discussion by Swanson on p.116).

The C/D values for a collection approximate a normal distribution. Where a species is represented by more than one collection, the means usually are within plus or minus one standard deviation of the other collections of the species (Fig.2, 3).

Species with many pores (low mean C/D ratio) tend to have larger pollen than species with few pores, but this relationship does not hold for individual grains within a collection.

Preliminary calculations indicate about 18% of the pollen wall is occupied by pores, the number of pores present and size of grain notwithstanding.

DISCUSSION

The sources of variation of C/D values within a collection are due to measuring errors in the microscopy and lack of strict isometry in the grain, as well as natural variation in pore number. Instrument error is estimated at 1–2%. A projection error exists whereby a chord may be measured that is not parallel to the plane of the ocular micrometer, and this results in a low value of perhaps 5%. As a practical matter, the grains are not perfectly spherical, and diameter measurements on a single grain may vary 5–10%. Another source of variation, due to lack of isometry, is the theoretical packing effect, whereby pores cannot be equidistantly spaced on the pollen wall (see p.116) thus giving an estimated variation of 3–5% for chord measurements. It follows that in a single C/D ratio there can be a maximum error of plus or minus 25%. That this variation is only rarely observed is, at least partly, due to the cancellation of errors for only the projection error operates in one direction. The variation of chord measurements is important as shown by the broad standard deviations of the 10 C/D values of single grains.

Taxonomic implications

The usefulness of C/D ratios and implied pore numbers as a taxonomic character rests upon their constancy within collections of well-defined species and similarity between closely related species. For comparison purposes, the mean value of the 50 C/D ratios per collection will be used (Table I).

Section Roubieva

The two collections of *C. multifidum*, a South American species, had similar C/D values of 0.185 and 0.178.

TABLE I

SUMMARY OF CHORD TO DIAMETER RATIOS FOR *Chenopodium* POLLEN

Section	*Species*	*Collection*	*Mean ± 1 standard deviation of single chord and diameter measurements for 50 grains*	*Mean ± 1 standard deviation for C/D ratios derived from 10 chord and 1 diameter measurement on each of 2 grains*	
				grain 1	*grain 2*
Roubieva	*C. multifidum*	L2502	0.185±.023	0.208±.021	0.201±.027
		J 45	0.178±.019	0.176±.018	0.174±.013
Orthospermum	*C. pumilio*	J 24	0.312±.035	0.289±.037	0.331±.029
		T119	0.293±.020	0.284±.020	0.316±.029
		J 40	0.289±.036	0.279±.048	0.268±.030
Botryoides	*C. graveolens neomexicanum*	T148	0.309±.029	0.266±.012	0.289±.029
	C. aristatum	J 11	0.288±.028	0.287±.017	0.304±.051
	C. botrys	T127	0.205±.028	0.183±.026	0.194±.014
		J 31	0.205±.028	0.174±.017	0.184±.021
		J 36	0.203±.023	0.201±.031	0.205±.030
Ambrina	*C. ambrosioides*	T48	0.172±.020	0.160±.017	0.155±.014
		J 33	0.164±.020	0.155±.016	0.166±.019
		J 26	0.159±.020	0.164±.015	0.157±.014
		T150	0.155±.018	0.163±.012	0.154±.015
Agathophyton	*C. californicum*	T122	0.202±.022	0.216±.013	0.216±.016
Eublitum	*C. capitatum*	T124	0.258±.029	0.264±.017	0.260±.027
	C. overi	T126	0.231±.019	0.231±.037	0.218±.010
Degenia	*C. macrospermum*	T128	0.288±.020	0.236±.013	0.218±.017
Pseudoblitum	*C. glaucum glaucum*	T118	0.254±.018	0.265±.026	0.224±.017
	C. rubrum	T2	0.210±.024	0.213±.019	0.217±.012
		T158	0.207±.024	0.200±.013	0.221±.019
Chenopodia	*C. polyspermum*	T130	0.314±.030	0.292±.047	0.328±.023
		J 15	0.312±.037	0.331±.040	0.298±.037
	C. vulvaria	T133	0.265±.023	0.264±.021	0.264±.021
	C. nevadense	T136	0.257±.028	0.248±.012	0.249±.016
	C. standleyanum	J 43	0.256±.030	0.251±.025	0.252±.031
		T131	0.253±.022	0.267±.015	0.254±.011
	C. neomexicanum	T144	0.253±.029	0.292±.032	0.254±.026
	C. fremontii	J 9	0.261±.022	0.286±.042	0.266±0.20
		T140	0.249±.019	0.274±.012	0.267±.010
	C. atrovirens	J 10	0.245±.016	0.250±.028	0.253±.017
		T152	0.244±.021	0.245±.020	0.252±.013
	C. incanum	T142	0.242±.024	0.257±.015	0.239±.015
	C. desiccatum leptophylloides	J 19	0.254±.026	0.238±.040	0.232±.037
		J 44	0.249±.023	0.266±.021	0.224±.019
		T64	0.230±.023	0.230±.028	0.244±.016

TABLE I *(continued)*

Section	*Species*	*Collection*	*Mean ± 1 standard deviation of single chord and diameter measurements for 50 grains*	*Mean ± 1 standard deviation for C/D ratios derived from 10 chord and 1 diameter measurement on each of 2 grains*	
				grain 1	*grain 2*
Chenopodia *(continued)*					
	C. murale	T78	0.248±.022	0.254±.026	0.233±.020
		J 35	0.243±.029	0.226±.034	0.246±.020
		J 20	0.213±.016	0.203±.021	0.228±.017
	C. leptophyllum	T7	0.234±.021	0.242±.024	0.231±.017
	C. serotinum	T138	0.233±.022	0.243±.018	0.239±.021
		J 23	0.227±.025	0.239±.033	0.212±.019
	C. cycloides	T151	0.232±.020	0.244±.021	0.242±.026
	C. foggii	J 12	0.245±.024	0.207±.012	0.225±.023
		J 22	0.225±.030	0.207±.027	0.225±0.31
	C. hybridum	T160	0.216±.026	0.206±.017	0.222±.019
	C. gigantospermum	T72	0.215±.022	0.189±.017	0.224±.017
	C. strictum strictum	J 29	0.223±.022	0.204±.012	0.217±.017
	C.s. glaucophyllum	J 52	0.211±.021	0.212±.017	0.207±.017
	C.s. glaucophyllum	T132	0.210±.018	0.217±.025	0.200±.017
	C.s. glaucophyllum	J 51	0.201±.018	0.194±.018	0.209±.018
	C.s. strictum	J 53	0.191±.017	0.195±.017	0.188±.018
	C.s. glaucophyllum	J 34	0.189±.017	0.192±.015	0.217±.019
	C. berlandieri zschackei	J 50	0.210±.021	0.215±.012	0.194±.017
	C.b. zschackei	J 49	0.199±.016	0.189±.022	0.187±.014
	C.b. boscianum	J 28	0.198±.023	0.209±.018	0.198±.022
	C.b. sinuata	J 41	0.196±.022	0.180±.022	0.209±.022
		T52	0.187±.016	0.196±.023	0.191±.018
	C. bushianum	T135	0.196±.019	0.200±.010	0.200±.012
		J 32	0.187±.016	0.200±.022	0.194±.013
		J 46	0.186±.019	0.191±.022	0.185±.013
	C. macrocalycium	J 13	0.193±.020	0.183±.025	0.183±.016
		J 42	0.190±.017	0.179±.015	0.188±.010
		J 27	0.190±.019	0.181±.020	0.183±.021
	C. opulifolium	T129	0.188±.017	0.204±.016	0.215±.021
	C. album	T137	0.204±.018	0.214±.022	0.207±.022
	C.a. album	J 39	0.193±.020	0.215±.022	0.196±.014
	C.a. lanceolatum	J 18	0.175±.017	0.190±.024	0.183±.019
		J 37	0.173±.019	0.169±.020	0.170±.012
	C. missouriense	T143	0.183±.014	0.195±.019	0.197±.018
		J 30	0.175±.020	0.166±.024	0.185±.023
		J 48	0.171±.014	0.172±.019	0.158±.013
		J 47	0.170±.018	0.153±.018	0.152±.013
		J 38	0.158±.018	0.161±.010	0.154±.017

Section Orthospermum

The three collections of *C. pumilio*, an Australian species, had consistantly high values of 0.312, 0.293 and 0.289. Only three other species had such high values, namely, *C. graveolens* and *C. aristatum* in section Botryoides and *C. polyspermum* in section Chenopodia.

Section Botryoides

Single collections of *C. graveolens* (0.309) and *C. aristatum* (0.288) had high values, in contrast to the three collections of C. *botrys* (0.205, 0.205, 0.203) (Fig.2). Thus the C/D values support the grouping of the former two species and clearly separate them from the latter.

Section Ambrina

Four collections of *C. ambrosioides*, a tropical American species, showed very low but varying means (0.172, 0.164, 0.159, 0.155); the variations may be related to the complexity of the species (WAHL, 1954).

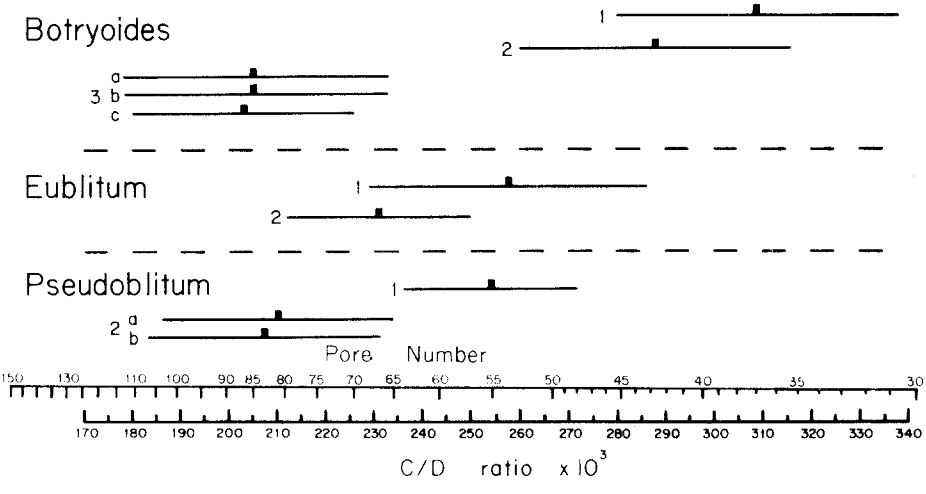

Fig.2. Means (±1 standard deviation) of chord to diameter ratios in seven species of *Chenopodium*, sections Botryoides, Eublitum and Pseudoblitum. A single C/D ratio was calculated for each of 50 pollen of a collection. In Botryoides: *1* = *C. graveolens* T148, *2* = *C. aristatum* J11, *3* = *C. botrys* (*a* = T127, *b* = J31, *c* = J36); Eublitum: *1* = *C. capitatum* T124, *2* = *C. overi* T126; Pseudoblitum: *1* = *C. glaucum* T118, *2* = *C. rubrum* (*a* = T2, *b* = T158).

Section Agathophyton

A single collection of *C. californicum*, a species confined to California, had a medium C/D value of 0.202.

Section Eublitum

Single collections of *C. capitatum* (0.258) and *C. overi* (0.231) had roughly similar C/D values (Fig.2) which supports WAHL's (1954) suggestion that these species of western and northern U.S.A. and Canada may not be specifically separable.

Section Degenia

A single collection of *C. macrospermum* had a C/D value of 0.228.

Section Pseudoblitum

A single collection of *C. glaucum*, a western U.S.A. and Canadian species, had a distinctly higher value (0.254) than two collections of *C. rubrum* (0.210, 0.207) (Fig.2). This supports WAHL's (1954) doubt about the relationship of the two species within the section.

Section Chenopodia

This section contains most of the species examined, and there is a wide range of mean values between species ranging from *C. polyspermum* with very high values (0.314, 0.312) to very low values in *C. missouriense* (0.183, 0.175, 0.171, 0.170, 0.158).

In this section, WAHL (1954) recognizes 22 species as native to the U.S.A. Sixteen species are primarily distributed west of the Mississippi River, and five are eastern; one species is cosmopolitan. The western species are usually characterized by leaves that are entire, sometimes fleshy, with a linear, lanceolate or triangular shape, while the eastern species usually have leaves that are toothed and ovate.

Eight of the nine western species examined had mean C/D ratios of more than 0.220, while three of the five eastern species had lower values (Fig.3). Both the eastern species with relatively high mean C/D ratios were probably derived from western species. The eastern *C. standleyanum* resembles a complex of western species typified by *C. fremontii* in having thin leaves and fruits maturing successively and largely exposed at maturity; *C. standleyanum* differs in having primary leaves serrate margined. WAHL (1954) suggests that it is an offshoot of western progenitors. Similarly, he regards *C. foggii* as an eastern relative of the widely

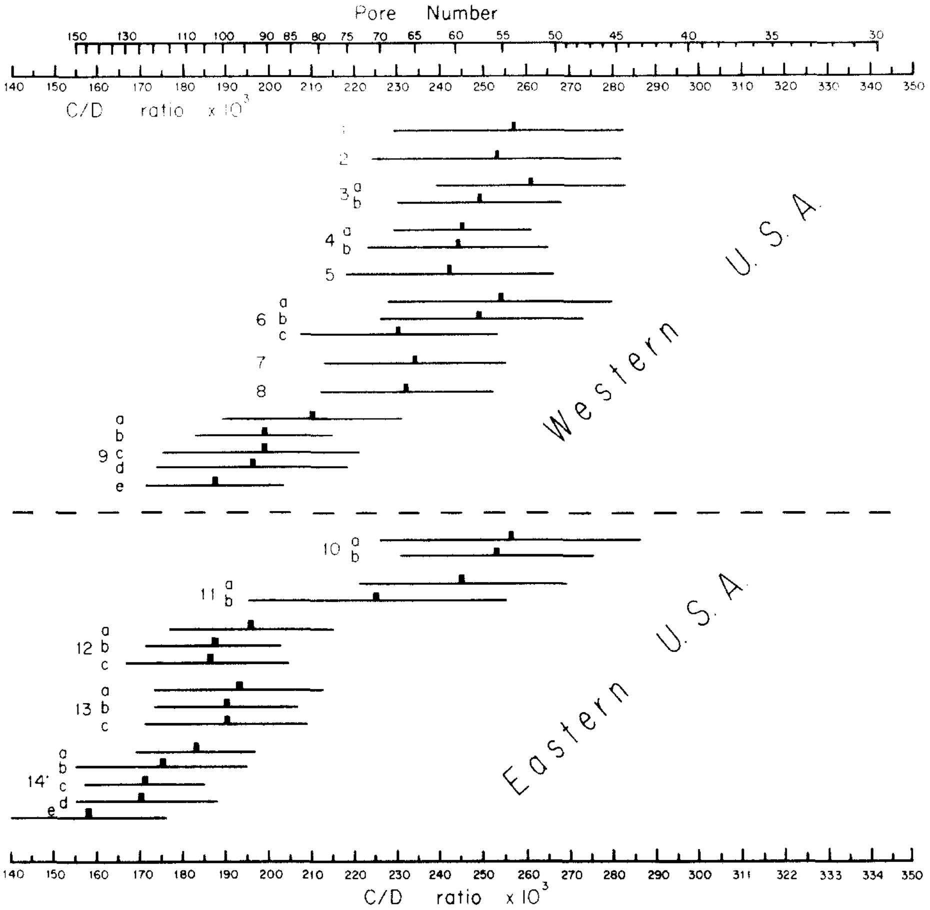

Fig.3. Means (± 1 standard deviation) of chord to diameter ratios in fourteen species of *Chenopodium*, section Chenopodia. A single C/D ratio was calculated for each of 50 pollen of a collection. Species *1* = *C. nevadense* T136, *2* = *C. neomexicanum* T144, *3* = *C. fremontii* (*a* = J9, *b* = T140), *4* = *C. atrovirens* (*a* = J10, *b* = T152), *5* = *C. incanum* T142, *6* = *C. desiccatum* (*a* = J19, *b* = J44, *c* = T64), *7* = *C. leptophyllum* T7, *8* = *C. cycloides* T151, *9* = *C. berlandieri* (*a* = J50, *b* = J49, *c* = J28, *d* = J41, *e* = J52), *10* = *C. standleyanum* (*a* = J43, *b* = T131), *11* = *C. foggii* (*a* = J12, *b* = J22), *12* = *C. bushianum* (*a* = T135, *b* = J32, *c* = J36), *13* = *C. macrocalycium* (*a* = J13, *b* = J42, *c* = J27), *14* = *C. missouriense* (*a* = T143, *b* = J30, *c* = J48, *d* = J47, *e* = J38).

distributed, western *C. desiccatum*, an opinion supported by similar C/D ratios for this pair of species.

Chenopodium berlandieri is a western species having a reticulate pericarp, a character that relates it to the eastern *C. bushianum* and *C. macrocalycium*. The five collections of *C. berlandieri* have a range of means of C/D ratios between 0.187 and 0.210; the means of three collections each of the two eastern relatives essentially fall within this range, further supporting their relationship. WAHL

(1954) states that the reticulate-seeded *C. berlandieri* complex had its center of speciation in Central and South America, a separate center from the western U.S.A. species with their higher C/D ratios.

The relationship of *C. missouriense* to other native U.S.A. species is uncertain, although it can hybridize with the introduced *C. album* (H.A. Wahl, personal communication, 1965) with whose ranges of mean C/D ratios it overlaps.

Chenopodium gigantospermum is a North American species of cosmopolitan distribution. The mean C/D value of a single collection (0.215) is intermediate between eastern and western U.S.A. species, but it is essentially identical with the closely related Eurasian *C. hybridum* (0.216).

Another European species, *C. polyspermum*, has an uncertain relationship with other species in the section, although WAHL (1954) associates it with *C. vulvaria*. The mean C/D ratios of *C. polyspermum* (0.314, 0.315) are the highest and *C. vulvaria* (0.265) the second highest of the 23 species of this section that were examined, thus confirming an opinion based on traditional taxonomic criteria.

The chord to diameter ratios appear to be a conservative taxonomic character that tie together closely related groups of species. They appear to be more conservative than some leaf and seed characters. The ratio data suggest that sections Botryoides, Agathophyton and Chenopodia may contain species that are not closely related. An evolutionary trend in pollen pore number cannot be postulated from the data presented here.

In the field of pollen analysis, C/D ratios may be used along with other pollen morphological characters to aid in the identification of fossil Chenopodiaceae pollen. The C/D ratio can best be applied where abundant, well-preserved pollen is present in the sediment sample and where the available fossil flora is limited or partly known through fossil seeds.

THE C/D RATIO AND PORE NUMBER

The model

We propose the following mathematical idealization for the distribution of pore sites on the surface of a pollen grain: a sphere of diameter D is populated with N equidistant points corresponding to the centers of the pore areas such that the great-circle arcs joining each point to its nearest neighbors partition the surface into F equilateral triangles of equal area, W. On the basis of this model, it is possible to calculate the number of pore sites, given the ratio of the chord length joining two adjacent pore centers to the diameter of the grain.

Derivation of the pore-number formula

Denoting the equilateral spherical triangle as T, we define the following quantities (see Fig.4):

a = the side of T (expressed in radians),
A = the internal angle of T (radians),
C = the length of the chord joining two verticies of T,
R = the radius of the sphere and
E = the spherical excess of T.

An expression of F is obtained as follows. The area of T is given by: $W = \mathrm{ER}^2$* and since F identical triangles occupy the total surface area of the sphere, $4\pi\mathrm{R}^2$, we have:

$$\mathrm{E} = 4\pi/F$$

Substituting this expression for the spherical excess into L'Huilier's formula and solving for F we obtain:

$$F = \pi/\tan^{-1}[\tan(3a/4)\tan^3(a/4)] \qquad (1)$$

Next, an expression for the total number of boundary lines, B, is obtained. Since there are 2π radians about a point on a spherical surface, the number of triangles, B′, which can have a common vertex, is $2\pi/\mathrm{A}$. A can be expressed in terms of a (using the law of cosines) and so we have for B′:

$$\mathrm{B}' = 2\pi/\cos^{-1}[(1-\cos(a))/\sin(a)\tan(a)] \qquad (2)$$

Since the number of boundary lines radiating from a given point is exactly equal to the number of triangles having that point as a common vertex, the total number of boundary lines on the sphere will be:

$$\mathrm{B} = (\tfrac{1}{2})N\,\mathrm{B}' \qquad (3)$$

where the factor of one half appears because each boundary line has two points associated with it.

A sphere, whose surface has been partitioned into a finite number of spherical polygons, can be regarded as the topological equivalent of a polyhedron with faces corresponding to the regions of the sphere. Thus Euler's rule for the polyhedra also can be applied to the regions of the partitioned sphere. Euler's rule is: $N = \mathrm{B} + 2 - F$; where F is the number of regions, N is the number of verticies, here the number of points to be determined, and B the number of boundaries between regions. Substitution of eq.3 into Euler's rule yields:

$$N = 2(F-2)/(\mathrm{B}'-2) \qquad (4)$$

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* This relation from solid geometry, L'Huilier's formula and the law of cosines which follow, may be found in DONNAY (1945).

TABLE II

RELATION OF CHORD TO DIAMETER RATIOS TO THE NUMBER OF PORES ON ISOMETRIC PERIPORATE POLLEN

Chord to diameter ratio		*Number of pores*	*Chord to diameter ratio*		*Number of pores*	*Chord to diameter ratio*		*Number of pores*
from	*to*		*from*	*to*		*from*	*to*	
0.7071	0.6730	6	0.2579	0.2556	54	0.1881	0.1873	102
0.6729	0.6379	7	0.2555	0.2534	55	0.1872	0.1864	103
0.6378	0.6069	8	0.2533	0.2512	56	0.1863	0.1855	104
0.6068	0.5796	9	0.2511	0.2490	57	0.1854	0.1846	105
0.5795	0.5553	10	0.2489	0.2469	58	0.1845	0.1838	106
0.5552	0.5337	11	0.2468	0.2449	59	0.1837	0.1829	107
0.5336	0.5144	12	0.2448	0.2429	60	0.1828	0.1821	108
0.5143	0.4969	13	0.2428	0.2409	61	0.1820	0.1812	109
0.4968	0.4810	14	0.2408	0.2390	62	0.1811	0.1804	110
0.4809	0.4666	15	0.2389	0.2372	63	0.1803	0.1796	111
0.4665	0.4533	16	0.2371	0.2353	64	0.1795	0.1788	112
0.4532	0.4411	17	0.2352	0.2336	65	0.1787	0.1781	113
0.4410	0.4299	18	0.2335	0.2318	66	0.1780	0.1773	114
0.4298	0.4194	19	0.2317	0.2301	67	0.1772	0.1765	115
0.4193	0.4097	20	0.2300	0.2285	68	0.1764	0.1758	116
0.4096	0.4006	21	0.2284	0.2269	69	0.1757	0.1750	117
0.4005	0.3920	22	0.2268	0.2253	70	0.1749	0.1743	118
0.3919	0.3840	23	0.2252	0.2237	71	0.1742	0.1736	119
0.3839	0.3765	24	0.2236	0.2222	72	0.1735	0.1729	120
0.3764	0.3694	25	0.2221	0.2207	73	0.1728	0.1721	121
0.3693	0.3626	26	0.2206	0.2192	74	0.1720	0.1714	122
0.3625	0.3563	27	0.2191	0.2178	75	0.1713	0.1708	123
0.3562	0.3502	28	0.2177	0.2164	76	0.1707	0.1701	124
0.3501	0.3445	29	0.2163	0.2150	77	0.1700	0.1694	125
0.3444	0.3390	30	0.2149	0.2136	78	0.1693	0.1687	126
0.3389	0.3338	31	0.2135	0.2123	79	0.1686	0.1681	127
0.3337	0.3288	32	0.2122	0.2110	80	0.1680	0.1674	128
0.3287	0.3240	33	0.2109	0.2097	81	0.1673	0.1668	129
0.3239	0.3194	34	0.2096	0.2085	82	0.1667	0.1662	130
0.3193	0.3150	35	0.2084	0.2072	83	0.1661	0.1655	131
0.3149	0.3108	36	0.2071	0.2060	84	0.1654	0.1649	132
0.3107	0.3068	37	0.2059	0.2048	85	0.1648	0.1643	133
0.3067	0.3029	38	0.2047	0.2037	86	0.1642	0.1637	134
0.3028	0.2991	39	0.2036	0.2025	87	0.1636	0.1631	135
0.2990	0.2955	40	0.2024	0.2014	88	0.1630	0.1625	136
0.2954	0.2920	41	0.2013	0.2003	89	0.1624	0.1619	137
0.2919	0.2887	42	0.2002	0.1992	90	0.1618	0.1613	138
0.2886	0.2854	43	0.1991	0.1981	91	0.1612	0.1607	139
0.2853	0.2823	44	0.1980	0.1970	92	0.1606	0.1602	140
0.2822	0.2792	45	0.1969	0.1960	93	0.1601	0.1596	141
0.2791	0.2763	46	0.1959	0.1949	94	0.1595	0.1591	142
0.2762	0.2734	47	0.1948	0.1939	95	0.1590	0.1585	143
0.2733	0.2706	48	0.1938	0.1929	96	0.1584	0.1580	144
0.2705	0.2680	49	0.1928	0.1920	97	0.1579	0.1574	145
0.2679	0.2653	50	0.1919	0.1910	98	0.1573	0.1569	146
0.2652	0.2628	51	0.1909	0.1900	99	0.1568	0.1564	147
0.2627	0.2604	52	0.1899	0.1891	100	0.1563	0.1558	148
0.2603	0.2580	53	0.1890	0.1882	101	0.1557	0.1553	149

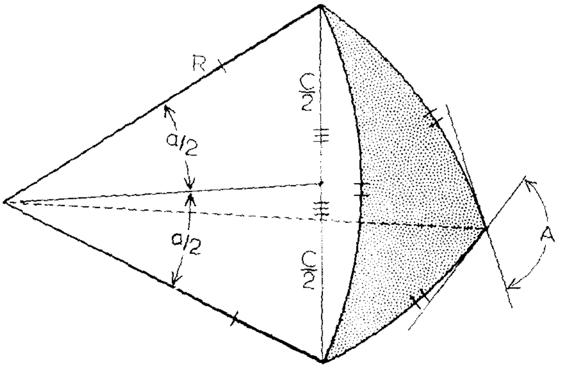

Fig.4. Elements of the equilateral spherical triangle.

Thus N is seen to be a function of a since only that parameter appears in the expressions for F and B′.

From Fig.4 it is readily seen that a is related to the C/D ratio by:

$$a = 2\sin^{-1}(\mathrm{C/D}) \tag{5}$$

Thus N is computed by first evaluating a from the C/D ratio via eq.5, then calculating F and B′ from eq.1 and eq.2 and, finally calculating N via eq.4.

With the aid of a CDC 1604 computor at the University of Minnesota, eq.5 was evaluated for C/D ratios ranging from 0.7071 ($N \approx 6$), to 0.1553 ($N = 149$), in increments of 0.001, and the resulting values of N rounded to the nearest integer and tabulated in Table II. From this table it is observed that a variation of 5% in the C/D ratio results in ca.10% variation in pore number, implying that accurate measurements are necessary to avoid large uncertainties in the assignment of pore numbers.

Discussion

The mathematical model of pore distribution on the surface of a pollen grain presented here is, strictly speaking, an impossible one. In general, a finite, arbitrary number of equidistant points cannot be placed on a spherical surface. In the actual case of N points distributed "uniformly" on a sphere, there is no unique C/D ratio but rather a distribution of values. The validity of this model rests on the plausible, but as yet unproven, assumption that the mean of this distribution (for the total number of chords) satisfies eq.4 and that as the pore population density increases, the dispersion becomes vanishingly small. Our rather simple model provides no clues as to the truth of these assumptions. Presently being explored is the possibility of verification with synthetically generated computor models where points are distributed on the sphere in an otherwise random manner while enforcing (for example) the constraint of maximum separation of adjacent points.

The principal justification for our model lies in the observational facts of (*1*) an essentially uniform distribution of pores rather than locally high pore-population densities and (*2*) the regular distribution of pore sites which appear to be at the verticies of equilateral triangles rather than being in random array.

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