STEREOSCAN OBSERVATIONS ON THE
POLLEN GENUS CLASSOPOLLIS PFLUG 1953

by Y. REYRE

ABSTRACT. The diagnosis of the pollen form genus Classopollis Pflug 1953 is here emended after both a review of the literature and observation of numerous specimens recovered from Upper Triassic to Middle Cretaceous rocks in the Sahara, Israel, and France. Following a discussion of a proper definition of the species, twelve new species are described. Botanic affinity, taxonomic value, and stratigraphic occurrence are also discussed.

Numerous species have been validly assigned to the genus Classopollis both before and after the emendation by Pocock and Jansonius (1961). However, among isolated grains of apparently homogeneous assemblages from African or European Mesozoic rocks, it has proved impossible by light microscope to identify these species with certainty. Scanning electron microscope observations indicate four possible reasons: (a) the number of potential Classopollis species is greater than that of described species, (b) inexactness of the majority of specific diagnosis in the description of the exinal structure and sculpture, (c) the hierarchy of characters used to define species is variable depending on the individual author (often it is not indicated), (d) it seems that certain species have been defined on the basis of plurispecific assemblages, often unsuspected by the authors themselves. Because of its paleobotanic and stratigraphic importance, a review of the genus has been undertaken using large assemblages extracted from the following formations: Upper Triassic (above Carnian) in the Tunisian and Algerian Sahara, Infra-riassic and Lower Liassic in the Sahara and France (Saintonge, Massif Central), Jurassic and Lower Cretaceous in the Sahara, Israel, and France.

PREVIOUS LITERATURE

The genus Classopollis was instituted by Pflug (1953), although some species were previously assigned to other genera. Pocock and Jansonius (1961) presented an extensive review of past works and Boltenhagen (1968) completed this review by a critical survey of the literature.

Couper (1958, pp. 156–7, pl. 28, figs. 2–7) emended the genus Classopollis Pflug 1953, considering that Pflug’s interpretation was inexact. After observations on pollen of Pagophyllum communis Kendall, he tried to show that the genus Classopollis is a morphographical taxonomic entity including all the species of the type met with in the above-mentioned fossil. Thus he suggested a very wide generic definition in which one must principally note an equatorial endexine thickness and a vague proximal trilet mark; he regarded P. tororsa Reissinger as the type-species. Klaus (1960, pp. 165–7, pl. 36, figs. 57–60) emended the genus Corollina Maljivakina 1949 and included in particular Pflug and Couper’s Classopollis species. In addition, Klaus suggested his species Circulina meyeriana as the type-species of the genus Circulina Maljivakina 1949. In his opinion this genus is recognizable by the following characters: a Y-form dehiscence, a distal polar area, a sub-equatorial ring which is not bordered with a thickening.


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occasionally parallel folds in the ring zone, and infrastructure without midrib, line, reticulum, or ring (striation?)

Pocock and Janssions (1961, pp. 443-4, pl. 1, figs 1-9) emended Pflug's genus, considering the attributions of Couper (1958) and Klaus (1960) as unfounded. They also emended C. classoides Pflug which they retained as type-species of the genus, and defined the genus with the following characters: (a) distally monoporate, (b) exoexine two-layered, (c) exoexine absent or much reduced over a circular area surrounding the distal pole and absent or reduced over a triangular area with its centre at the proximal pole, (d) intine frequently bearing a reduced trilete scar, which has no germininal function, (e) exine always ornamented by striations, (f) the band, usually but not always, marking a zone of exinal thickening. Pettitt and Chaloner (1964) studied by electron microscope pollen grains extracted from a cone of Cheiroplepis muensteri Schenk. They assigned these grains to the morphographical species C. torosus (without naming the author). They established that the exine of Classopolis is composite with a lamellate endonexine and a complicated ectonexine within which they distinguished an inner layer (ecn 2), a middle massive layer (ecn 1), and a tegillum. Burger (1966) suggested that the columellars (equivalent to ecn 2 of Pettitt and Chaloner) join in the equatorial belt and are reduced at the rimula. Reyre (1968d), using scanning electron microscope observations, established that at least in many cases trilete scars are functional, the outer layer of the exoexine is continuous with an invariable sculpture, the appearance of the grain is explained by variations of the infrastructure (similar to ecn 2 of Pettitt and Chaloner). In different parts of the grain it disappears, resulting in a subequatorial circular furrow, in a distal circular area and also in the proximal triangular area (when that exists); in these places, the outer part of exoexine (tegillum and possibly columellars of Pettitt and Chaloner) collapses and lines the lamellate endonexine which has the shape of a separate internal spheroidal envelope.

DEFINITION OF THE SPECIES

Numerous morphographic species have been described from various stratigraphic periods; they probably corresponded in most cases to different botanical species. However, the assignment of a dispersed Classopolis grain to a definite species is always difficult and often impossible.

Table 1 has been assembled from the diagnoses of five authors who have made detailed studies on Classopolis. It shows that, strictly, only the two extreme cases of size justify the recognition of two species on this one single character. If, however, one takes into account for each character, only the species in which it is clearly indicated, the number of possibilities for differentiation is one for all the characters except the sculpture where it is four. Table 1 underlines also the concomitant variations which affect the light visible characters. The statistical methods of symbolic dispersion diagrams (Pons 1964) can often record the different types or species an assemblage contains, but do not always permit the assignment of one or a few characters particular to each type.

For example, in the Jurassic and Lower Cretaceous rocks of the Tunisian Sahara, five Classopolis groups have been described: L1, L2, L3, scabrate-verrucose group, and gemmulate group (Medus and Reyre 1966). However, none can be assigned with any
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Number of species recognizable by each single character:

- 0 (1 above 12)
- 0 (massive)
- 0 (0-75)
- 0 (10)
- 0 (11-14)
- 0 (12)
- 4

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certainty to definite species, because each has common points with several species depending on the characters under consideration. In addition, except for the gemmulate group, none has a constant individual character which allows a possibility of erecting a new species. L₄ is something like C. classoides of Pocock and Jansoni, but the pore diameter is smaller; it also resembles C. torosus sensu Burger but it is smaller, psilate, and sometimes massive. In the same way, L₅ resembles C. multistriatus Burger, but it is often larger, scabrate, and finer; its pseudopore is larger and the belt can have less striations. Only the gemmulate and scabrae- verrucose types are theoretically separated on sculpture; the first is easily distinguished but for the second this delicate and variable observation of sculpture cannot be made reliably with a light microscope.

Hierarchical order of use of characters. Two authors have put forward a hierarchical order. Pocock and Jansoni indicate successively the characters (as numbered in Table 1): 6, 2, 7, 8 and 9, 5 or 10 and 1. Their interpretation is not very clear on whether the ornamentation mentioned refers to the sculpture or the infrastructure although it would seem to be the latter because the authors have not mentioned the sculpture of their species. For Burger the order of characters is as follows: 10 and 5 (which can be different on the distal and proximal hemispheres of the grain), 2, 7, 8, and 6. Neither authors have indicated the reasons for their choice. However, the choice of hierarchical order is important, (a) to obtain a natural classification of Classopolis species (which will be attempted below), and (b) because it will be determinative in defining the different species. This fundamental study can only be undertaken on a homogeneous assemblage containing only one species. In fact it is difficult to predict, and experience shows that formations containing only one species are rare. Examples are:

1. Sample from bore-hole Lamarque 1, Aquitaine (Esso France: X = 358, 7; Y = 314, 4), depth 1742 m., Rhaetian age (Dupin 1965), contains a Classopolis assemblage. Two extreme types are easily distinguishable by light microscope observation of the infrastructure. The first, type A (Pl. 55, figs. 1, 5) is light, almost translucent, with a massive infrastructure. The second, type C (Pl. 54, figs. 9, 11) is darker, with a pseudoreticate infrastructure which is poorly defined in the area of the equatorial thickening. Between these extreme types, the infrastructure can be finely or poorly pseudoreticate in the type B (Pl. 54, fig. 10 and Pl. 55, fig. 8).

2. Sample of argillaceous sandstone from bore-hole S.P., Massif Central (B.R.G.M.; X = 566.500; Y = 179.075; Z = 190.90), depth 47-40 m., Hettangian (B.R.G.M. dating), contains a Classopolis assemblage of type C only (Pl. 55, figs. 11, 12).

Light microscope observation. Table 2 has been made up by selecting ten grains of each of the three types. It shows for these types whose general appearance and sculpture are perfectly homogenous, the following points (each character is numbered in Table 2):

1. Size (diameter) is not fixed, but the variation is peculiar to the species

   \[ \frac{\text{diameter of the smallest}}{\text{diameter of the largest}} \]

2. When there is a circular furrow, it exists in all the grains.

3. Length of laesurae of trilet scar varies as much as 1:4.
TABLE 2. Character variations in the forms A, B, C (see p. 306). Measured characters: 1, size (diameter); 2, circular furrow width; 3, length of laesurae; 4, pseudopore diameter; 5, average exine thickness; 6, equatorial exine thickness; 7, type of stereoan-visible sculpture.

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<td>26</td>
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<td>1:5</td>
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4. Pseudopore diameter varies as much as 2:5.
6, 7. Exinal thickness remains constant at comparable points and especially when there is an equatorial thickening.

Scanning electron microscope observations. Technical conditions for observations of exinal sculpture by the scanning electron microscope has already been set out in detail (Reyre 1968d). Results of the observations are as follows:

(a) In the case of the sample 2 (optically very homogenous infrastructure) the sculpture of the tegillum is identical in all the grains, grumous-verrucose (Pl. 55, figs. 13, 14).
(b) In the sample 1 three types of sculpture are observed. The optical type A can be micro-echinulate (Pl. 55, figs. 3, 7) or echinulate; the optical type B can be micro-echinulate or echinulate (Pl. 55, fig. 10) and rarely verrucose; the optical type C can be rarely micro-echinulate, generally echinulate (Pl. 54, fig. 13) or grumous-verrucose (cf. Pl. 55, fig. 14).

(c) Interpretation: the only light microscope visible characters (1–7 in Table 2) cannot establish how many species there are in the sample 1 or how they are distinguishable. Scan observations confirm that there is one species in the sample 2 and establish that there are at least three species in the sample 1. In sample 1 one species is common with the sample 2 (optical type C, grumous-verrucose) and two (optical types A and B, micro-echinulate or echinulate) correspond probably to two closely related botanical species, but one fossil pollen species is made because of the occurrence in the same sample. It thus appears on one hand that light microscope observation alone is generally insufficient to define the ultimate morphographical species, and on the other hand that infrastructure of one species can have a certain variability, generally limited. It also appears that each precise type of sculpture has the properties of one botanical species or a group of closely related species; that suggestion comes from the results established on actual gymnospermous pollen (Reyre 1968d) and on higher plants such as the closely related species of the genus Aristida L. (Bourreil and Reyre 1968) between which slight variations of outer sculpture can be observed and are peculiar to each species. It comes also from the observation of several homogeneous assemblages of Classopolis the sculpture of which is identical for all the grains (as the assemblage C, sample 2).

Inference. In the genus Classopolis, the outer sculpture of the grains is at the same time the most consistent and the most distinguishable character of a species; it is the ultimate specific character necessary for diagnosing the species; the consequence is that a diagnosis would not be valid, either from a morphological point of view or from a botanical point of view if it does not show the exine outer sculpture observed by electron microscope.

LIMITS OF THE GENUS

In his generic diagnosis, Couper (1958) extended the genus to all the pollen with an equatorial thickening and a vague trilete scar. The definition of Pocock and Jansonius (1961) was different and narrower, requiring the presence of striations, of a distal pore, and of a proximal triangular area either with or without a trilete aperture. The form-genus Classopolis can thus be conventionally limited to the simultaneous presence of the above-mentioned characters. However, this convention could result in a separation of closely related palaeobotanic entities and so we must consider that the absence of each of these characters on one of these pollens excludes it from the genus Classopolis when this absence results in either the absence or a notable modification of the other characters.

Striations. Considering the pollen groups A, B, and C, in which no striations are observed on the first two and a vague line arrangement on the third, it can be seen that they all have a pseudopore, a subequatorial circular furrow, an equatorial thickening, and an outer sculpture very similar to that of Classopolis with clearly defined and
continuous striations (compare Pl. 55, figs. 8, 10 and Pl. 57, figs. 1, 5). Further, in the succession of types A, B, and C, it is easy to distinguish a progressive passage from a massive infracturation to pseudostriations. It would be unhelpful to limit the genus *Classopolis* by the actual presence of striations, as Pocock and Jansoniussenuse them. 

**Equatorial thickening.** The pollen shown on Plate 55, figs. 5-7, has no equatorial thickening. It is, however, in all other characters, similar to the grains of the group B, in which it has been included. Pocock and Jansoniussen (1961), Groot and Groot (1962), and Burger (1965), recorded no equatorial thickening in several of their species with striations.

On account of these two factors I consider that the formgenus *Circulina* (Maljavkina) Klaus 1960 is an exceptional case within the genus *Classopolis*, corresponding to the coincidence of the limiting cases of the two characters, equatorial thickening and ornamentation of the infracturation.

**Trilete scar.** Table 2 shows clearly that a homogeneous assemblage can have a variable trilete scar (in particular length of the laesurae). Many assemblages have only a trifid or sinuous fold (Pl. 55, fig. 4) so that it is sometimes impossible, especially with a light microscope, to see a vestigial mark. But all the other characters are similar.

**Pseudopore.** All *Classopolis* have a more or less distinct pseudopore which is visible in polar view or with a scanning electron microscope. In certain species, however, it is less distinct, especially when the exine is thin. I have so far found only one form with striations but without a pseudopore (Pl. 54, figs. 8, 9) but neither does it have a trilete scar or a circular furrow, and this justifies its inclusion in the genus *Aporina* Naumova 1937 (in Boltenhagen 1968). The European Jurassic species of the formgenus *Exestipollenites* Balme have a similar pseudopore, but no trilete scar and no circular furrow and they cannot be assigned to the genus *Classopolis*. Also, some species show an outer sculpture similar to that of recent Cupressales (Pl. 59, fig. 5).

**THE TYPE SPECIES**

I consider the generic name *Classopolis* is valid because the genera *Circulina* Maljavkina 1949 and *Circulina* Maljavkina 1949 were defined too vaguely. Like Pocock and Jansoniussen (1961) I consider that because of the impossibility of proving the exact similarity of *C. classoides* Pflug with another previously published species, the name of the type-species is *classoides*; but Pflug's diagnosis is inexact.

Of the grains selected for the diagnosis of the *classoides* species, it must be pointed out that the sample studied by Pflug could, in fact, include several species. Thus, even if Pflug's diagnosis is exact, it is impossible to recognize the species he wished to describe since there is no precise indication of the outer sculpture. From comparison of the relevant figures it appears that the species *C. classoides* (Pflug) Pocock and Jansoniussen 1961 does not correspond to the species represented by Pflug (1953). For reference these authors figure (Pocock and Jansoniussen 1961, pl. 1) a tetrad (figs. 1, 2) from Pflug's residue but different from the Pflug's *classoides* species by distinctive striations, circular furrow invisible and different infracturation. They assign to the same species a distinctly intrapunctate grain without distinct striations (fig. 4) and a massive form without
any striations (figs. 6, 7). It seems, therefore, that Pocock and Jansonius have also
described a plurispecific assemblage; there is also no precise indication of sculpture. In
fact the Classopolis type-species has never been fully described. Re-description of the
type species classoides from Pflug's original residue would be difficult; after chemical
or washing operations on this residue in glycerine, how could a grain be chosen? The
new species, C. kieseri (Pl. 54, figs. 9-14) which resembles Pflug's classoides is erected in
this paper from new material; but in practice, for illustrating the genus Classopolis it
would be preferable to refer to another species showing all the characters proper to
this form genus, striations in particular.

SYSTEMATIC SECTION

Diagnoses and descriptions of the species here described include in the same order
all the characters mentioned in Table 1. The high-power Scan micrographs are very
important because they show the general disposition of sculptural elements (simple,
mixed, double), the similarity or the plurality of shapes and sizes of elements, the shape
of these, their length, breadth, and abundance (number of elements on a surface unit).
All these characters are mentioned in the same order in the descriptions. The detailed
explanation of the method used for describing the exinal sculpture is indicated in a
previous paper (Reyes 1968d), but see also the text-fig. 2. Light and electron photo-
graphs are not always of the same grain; it is difficult to take an immersion photograph
of a grain which must be recovered from the liquid before being observed by the
scanning electron microscope. However, they always represent grains of the same
optical assemblage (which is electronically observed on numerous grains). Holotypes
or paratypes of the species here described are preserved at the Geological Laboratory
of the National Museum of Natural History, Paris.

Genus Aporina Naumova 1937

Remarks. This genus is separate morphographically, but the corresponding palaeo-
botanical taxa are closely related to the taxa which produced Classopolis and may be
species of the same genus.

Aporina sp.
Plate 54, figs. 1, 2

EXPLANATION OF PLATE 54

Light microscope figures approximately ×1000; Stereoscans figures approximately ×2000 and 10 000.

Figs. 1, 2. Aporina sp. 1, L.M. tetrad view showing striations. 2, S.E.M. view on which no pseudopore
is observed.

Figs. 3-5. Classopolis simplex sp. nov. 3, L.M. holotype, showing massive to micro-alveolate infra-
structure. 4, 5, S.E.M., showing the nipples of the outer sculpture.

Figs. 6-8. Classopolis querculi sp. nov. 6, L.M. tetrad holotype, showing striations. 7, 8, S.E.M.
holotype showing the outer double sculpture rough with bowls.

Figs. 9-14. Classopolis kieseri sp. nov. 11, L.M. paratype, showing pseudovernicleate to pseudo-
reticulate infrastructure, trilette scar, subequatorial circular furrow, pseudopore and exinal thickness.
9, 10, L.M. paratypes, figures very similar to that of Pflug. 12-14, S.E.M. holotype, showing outer
sculpture of exine, hairy with spines; S.E.M. paratype, showing the trilette scar.
Description. No subequatorial furrow; no trilete scar; no pseudopore; infratructure massive; average exinal thickness 0·5 μ; equatorial thickening 1 μ; 4·6 striations 6 μ; band width 4·5 μ. Sculpture simple, isomorphous, nearly isodiametric, slightly rough and nearly psilate.

Size range. 17–22 μ (28 specimens).

Stratigraphic position. Upper Triassic (post-Carnian) of the Sahara; bore-hole ON4 (X = 31° 46' 07", Y = 6° 25' 36", Z = 140 m.), depth 2660 m.

Text-fig. 1. Outer sculpture (designed on the distal hemisphere above); from left to right: rugose, verrucose, mixed, double, echinate or hairy with sticks, echinate or hairy with needles or spines. Infratructure (designed on the proximal hemisphere—below): from left to right: massive, alveolate, reticulate, vermiculate, pseudoreticulate, punctate.

Genus Classopolis Pflug 1953 emend.

Text-fig. 1

Emended diagnosis. More or less spherical prepollens with, both more or less marked, a distal circular pseudopore and a proximal trilete scar; this latter is clearly visible, but sometimes it is vestigial or a sinuous (or trifid) crease takes its place; often it is open and it appears to have had a germinal function (unlike the pseudopore). Exine is two-layered with distinct endoexine and exoexine. Endoexine is shaped into an internal spheroidal separate envelope. Exoexine composition is variable on different parts of the grain; it is composed of an inner complicated layer which constitutes the light microscope visible infrastructure and a tegillum. The tegillum is shaped into a separated outer envelope present all over the grain and covered with an outer sculpture uniformly distributed on the whole surface of the grain. Infrastructure is massive, alveolate, punctate, vermiculate or pseudovermiculate, reticulate or pseudoreticulate but can be absent, reduced, thickened, and differently organized on different parts of the grain;
it is absent or reduced at the distal pole (pseudopore) or only along the circular line surrounding it, absent along a subequatorial line (circular furrow) and sometimes at the proximal pole (triangular area), generally thickened in the equatorial zone of the grain under the circular furrow (equatorial band) where the infrastructural elements are organized into more or less continuous striations.

Remarks. Two reasons justify this emendation: (a) in respect of the generic diagnosis of Pocock and Janssenius the present emended diagnosis takes into account the actual knowledge on the structure of Classopollis grains; this is important for the understanding of the species and allows recognition and definition of the different species or records by consideration of precise characters. (b) the limits of the form genus Classopollis are different from those indicated in the diagnosis of Pocock and Janssenius.

**Classopollis simplex** sp. nov.

Plate 54, fgs. 3-5

**Diagnosis.** Subequatorial circular furrow present; trilete scar present, length of laesurae 3–6 µ; pseudopore diameter 2–4 µ; infrastructure massive to micro-alveolate; average exinal thickness 1 µ; no equatorial thickening; no striations. Sculpture simple-mixed, isomorphic, heterodiamic, with nipples; nipple height 0.1–0.2 µ, breadth 0.2–0.3 µ, abundance 12 per µ². Many elements overlap a little the bases of the nipples; they are also less rounded nipples, 4 µ high.

**Size range.** 18–24 µ (40 specimens).

**Holotype.** Plate 54, fgs. 3–5; size 20 µ.

**Stratigraphic position.** Upper Triassic (post-Carnian) of the Sahara; borehole ON, (X = 31° 46’ 07” , Y = 6° 25’ 36” , Z = 140 m.), depth 2660 m.

**Classopollis quezeli** sp. nov.

Plate 54, fgs. 12–14

**Diagnosis.** Subequatorial circular furrow present; trilete scar vestigial; pseudopore diameter 4 µ; infrastructure massive (to micro-alveolate); average exinal thickness less than 1 µ (bowl not included); equatorial thickening 1 µ; 4–5 striations; band width 5 µ. Sculpture double, heteromorphic, heterodiamic, rough with bowls; processes height 0.1–0.2 µ; breadth 0.1–0.2 µ; bowls 0.9–1 µ.

**Explanation of Plate 55**

Light microscope figures approximately ×1000; Stereoscop figure approximately ×2000 and 10 000.

Figs. 1–10. **Classopollis kieseri** sp. nov. 1, L.M. paratype, showing massive infrastructure and equatorial thickening. 2, 3, S.E.M. view of same grain showing small spines of outer sculpture. 4, S.E.M. view of same grain showing outer layer of exocline lacerated at the proximal pole. 5, L.M. view of a paratype without equatorial thickening. 6, 7, S.E.M. view of same grain, sculpture microechinulate. 8, L.M. holotype, showing micropseudoreticulate infrastructure and sinuous circular furrow. 9, 10, S.E.M. holotype, showing sculpture echinulate, hairy with needles.

Figs. 11–14. **Classopollis chattenovi** sp. nov. 11, L.M. paratype, showing vague pseudostriations. 12, L.M. holotype, showing pseudoreticulate infrastructure and pore. 13, 14, S.E.M. holotype, showing grumose-verrucose sculpture.
Size range. 18–24 μ (36 specimens).

Holotype. Plate 54, figs. 12–14; size 23 μ.

Stratigraphic position. Upper Triassic (post-Carnian) of the Sahara; bore-hole ON4 (X = 31° 46' 09", Y = 6° 23' 39", Z = 140 m), depth 2660 m.

Remarks. Processes are rounded so that the surface seems nearly mammilated.

Classopolis kieseri sp. nov.
Plate 54, figs. 9–13; Plate 55, figs. 1–10

Diagnosis. Subequatorial circular furrow present, narrow (1 μ) or wide (to 3 μ) by distortion and often sinuous; functional trilete scar present, length of laesurae 2.5–10 μ; pseudopore diameter 4–10 μ; infrastructure massive, pseudoreticulate or finely so; average thickness 1.5 μ; equatorial thickening 1.5–2.5 μ; no striations, to vaguely defined pseudostriations; band width 8–10 μ. Sculpture simple, isomorphous, isodiometric, micro-echinulate to echinulate (hairy with little needles); varying from grain to grain, needle height 0.1–0.5 μ, breadth 0.1–0.2 μ, abundance 9 per μ² (large needles) to 80 per μ² (small needles).

Size range. 21–(28)–34 μ (100 specimens).

Holotype. Plate 55, figs. 8–10; size 31 μ.

Stratigraphic position. Hettangian, bore-hole Lamarque I, Aquitaine, (X = 358, 7; Y = 314, 4), depth 1742 m.

Remarks. By scan observation of the sculpture it seems that there are three closely related species, in which the spines or needles are constant on any one grain but may be very small (micro-echinulate, Pl. 55, fig. 7), medium (Pl. 55, fig. 3) or larger (echinulate, Pl. 55, fig. 10); but these characters do not each correspond to one precise infrastructure type. For this reason and because of their simultaneous occurrence in the same sample one Classopolis species is made.

C. kieseri resembles C. classoides Pflug 1953 in many characters visible on the illustrations of this species. In Pflug 1953, plate 16, figs. 29, 30 show a pollen finely pseudoreticulate, with a sinuous circular furrow, a pseudopore, a trilete scar not visible but suspected, an exine thickness of 2 μ without striations.

Classopolis chateaucomi sp. nov.
Plate 55, figs. 11–14

Diagnosis. Subequatorial circular furrow present; trilete scar present, length of laesurae 5–12 μ; pseudopore diameter 5–10 μ; infrastructure pseudoreticulate; average exinal thickness 1.5 μ; equatorial thickening 2.5 μ; only vague pseudostriations; band width 8 μ. Sculpture simple, isomorphous, isodiometric, grumous-verrucose; breadth of grumes 0.2–0.3 μ.

Size range. 20–32 μ (100 specimens).

Holotype. Plate 55, figs. 12–14; size 31 μ.

Stratigraphic position. Hettangian, Massif Central, bore-hole B.R.G.M. S6, X = 566.500, Y = 179.075, Z = 190, 91), depth 47–40 m.
Diagnosis. Subequatorial circular furrow present; trilite scar present, length of laeustrae 3–10 μ; pseudopore diameter 4–10 μ; infrastructure finely punctate; average exinal thickness 0·5–1 μ; equatorial thickening 1 μ; 7–11 striations; band width 7 μ. Sculpture simple, isomorphic, isodiametric, rugose-verrucose; height of warts 0·2 μ, breadth 0·5–0·8 μ.

Size range. 23–32 μ (100 specimens).

Holotype. Plate 3, figs. 1–3; size 28 μ.

Stratigraphic range. Middle and Late Jurassic and Lower Cretaceous of the Sahara. Holotypes from bore-hole SB 1 (Tunisia, X = 8 g, 21° 87' E, Y = 34 g, 91° 16' W, Z = 282 m.), depth 1210 m., Callovian.

Remarks. This species is included in the type L4 (Medus and Reyre 1966), see Table 1.

Classopollis rarus sp. nov.

Plate 56, figs. 5–7

Diagnosis. Subequatorial circular furrow present, with a prominent swelling; trilite scar vestigial; pseudopore infrastructure reduced at the distal pole, but no well-shaped hollow is observed with electron microscope; infrastructure punctate to pseudoreticulate; average exinal thickness 1 μ; equatorial thickening 2 μ; 7–9 striations; band width 7 μ. Sculpture simple-targeted, isomorphic, lightly heterodiametric, hairy with short sticks processes with well-rounded tips; height of processes 0·3–1 μ, breadth 0·2–0·5 μ, abundance 15 per μ². The targeted appearance is explained by crowding of processes with the higher projecting above the shorter.

Size range. 23–34 μ (32 specimens).

Holotype. Plate 55, figs. 5–7; size 32 μ.

Stratigraphic position. Lower Portland of Charente, France; bore-hole Vignolles S2 (X = 390.6, Y = 29.3, Z = 15–50 m.), depth 14–80 m.

Classopollis aquitanus sp. nov.

Plate 57, figs. 1–5

Diagnosis. Subequatorial circular furrow present but difficult to distinguish; trilite scar present; pseudopore diameter 5–9 μ; infrastructure clearly reticulate (lumina 1–1·5 μ); average exinal thickness 1 μ; equatorial thickening 1·5–2 μ; 9–10 striations; band width 10 μ. Sculpture simple, isomorphic, heterodiametric, echinulate (hairy with

Explanation of Plate 56

Light microscope figures approximately ×1000; Stereoscan figures approximately ×2000 and 10 000.

Figs. 1–4. Classopollis hussoni sp. nov. 1, L.M. holotype, view of finely punctate infrastructure and striations. 2, 3, S.E.M. holotype, showing rugose-verrucose outer sculpture with warts. 4, S.E.M. paratype.

Figs. 5–7. Classopollis rarus sp. nov. 5, L.M. holotype, showing punctate to pseudoreticulate infra- structure and striations. 6, 7, S.E.M. holotype, showing rounded short sticks of the outer sculpture.

Figs. 8–10. Classopollis caratinii sp. nov. 8, L.M. holotype, showing loosely punctate infrastructure, pseudopore, and trilite scar. 9, 10, S.E.M. views showing strongly rough sculpture.
spines); height of spines 0.3–0.9 μ, breadth of base 0.1–0.4 μ, abundance 9 per μ². Some very short spines among the others.

Size range. 28–36 μ (100 specimens).

Holotype. Plate 57, figs. 1, 4, 5; size 31 μ.

Stratigraphic position. Lower Portland of Charente, France; bore-hole Vignolles S₂ (X = 390.6, Y = 89.3, Z = 15–50 m), depth 28.90 m.

Classopollis caratinii sp. nov.

Plate 56, figs. 8–10

Diagnosis. Subequatorial circular furrow distinct; trilete scar present, length of laesurae 2.5 μ; pseudopore diameter 4 μ; infrastructure loosely punctate; average exinal thickness 1 μ; equatorial thickening 1–5 μ; 3–4 weak pseudostratations. Sculpture simple, heteromorphous, heterodiometric, strongly rough; height of processes 0–1–0.7 μ, breadth 0.1–1 μ; the shapes of the heteromorphous processes appear to be wrinkles, nipples, warts, blisters, or spines, although no shape is clear.

Size range. 16–20 μ (28 specimens).

Holotype. Plate 57, figs. 8–10; size: 18 μ.

Stratigraphic position. Lower Portland of Charente, France; bore-hole Vignolles S₂ (X = 390.6, Y = 89.3), depth 21–65 m.

Classopollis martinottii sp. nov.

Plate 57, figs. 6–11

Diagnosis. Subequatorial circular furrow present but often difficult to distinguish; trilete scar present, or trace; the outline of the pseudopore is not clearly marked and the infrastructure is only reduced at the distal pole which is often folded in Stereoscan observation; infrastructure finely punctate; average exinal thickness 1 μ; equatorial thickening 1–5 μ; 4–7 striations more or less discontinuous (lining of intra points); band width 5 μ. Sculpture simple, isomorphous, isodiometric echinulate (hairy with spines of which the ends are not sharp but rounded); height of spines 0.4–0.5 μ, breadth of base 0.2–0.3 μ, abundance 14–16 per μ².

Size range. 28–33 μ (70 specimens).

Holotypes. Plate 57, figs. 9–11; size 30 μ.

Stratigraphic position. Berriasian-Valanginian of Israel; bore-hole Heletz 2 (E = 115963, N = 110807, K.B., +92 m); depth 1465–71 m.

Remarks. This pollen is not easy to observe optically because of the crowded sculptural elements.

Classopollis pujoli sp. nov.

Plate 58, figs. 1–4

Diagnosis. Subequatorial circular furrow present and large; trilete scar present, or trace; pseudopore diameter 3–4 μ; infrastructure pseudoreticulate; average exinal thickness 1–5 μ; equatorial thickening 2 μ; 5–6 striations; often anastomosing; band
width 6-7 μ. Sculpture simple, isomorphous, isodiametric echinate (hairy with needles); height of needles 0.6 μ, breadth 0.15 μ, abundance 24 per μ².

Size range. 20–6 μ (80 specimens).

Holotype. Plate 58, figs. 1–3; size 22 μ.

Stratigraphic position. Lower Portland of Charente, France; bore-hole Vignalles S₁ (X = 390.6; Y = 89.3); depth 6.80 m.

Remarks. C. pyjoli differs from C. ammonoides Burger in the three following characters: circular furrow is more distinct, equatorial thickening more distinct, the tracey of the intrapseudoreticulum is less distinct.

**Classopolis mirabilis** sp. nov.

Plate 58, figs. 5–11

Diagnosis. Subequatorial circular furrow distinctly present; trilet scar present, or trace; pseudopore diameter 4–12 μ; infructification punctate to pseudoreticulate; average exinal thickness 2 μ; equatorial thickening 2.5 μ; 5–6 striations; band width 5–6 μ. Sculpture simple, isomorphous, more or less isodiametric, echinate (hairy with spines); height of spines 1–1.5 μ, breadth of bases 0.3–0.4 μ, abundance 6 per μ².

Size range. 24–36 μ (100 specimens).

Holotype. Plate 58, figs. 8, 10–11; size 35 μ.

Stratigraphic position. Lower Portland of Charente, France; bore-hole Vignalles S₁ (X = 390.6, Y = 89.3); depth 6.80 m.

Remarks. By light microscope observation C. mirabilis resembles C. echinatus Burger 1966; because of the absence of a clear illustration of the sculpture, it was preferable

**EXPLANATION OF PLATE 57**

Light microscope figures approximately ×1000; Stereoscopic figures approximately ×2000 and 10 000.

Figs. 1–5. **Classopolis aquitanus** sp. nov. 1, L.M. holotype, showing reticulate infructification, striations, narrow subequatorial circular furrow. 2, S.E.M. tetrad, ×1000. 3, Detail of distal polar area of central grain of tetrad showing vertical appearance of spines. 4, 5, S.E.M. holotype, showing echinate sculpture, hairy with spines.

Figs. 6–11. **Classopolis martini** sp. nov. 6, L.M. paratype, showing finely punctate infructification, subequatorial circular furrow, equatorial thickening. 7, 8, S.E.M. views of same tetrad showing end-rounded spines of the echinate sculpture. 9, L.M. holotype. 10, 11, S.E.M. views of the holotype. (There is a prominent scratch on the negative of fig. 7.)

**EXPLANATION OF PLATE 58**

Light microscope figures approximately ×1000; Stereoscopic figures approximately ×2000 and 10 000.

Figs. 1–4. **Classopolis pyjoli** sp. nov. 1, L.M. holotype, showing infructification, striations, pseudopore, triangular proximal area, and exinal thickness. 2–4, S.E.M. holotype, showing echinate sculpture, hairy with needles.

Figs. 5–11. **Classopolis mirabilis** sp. nov. 5, L.M. paratype, showing punctate to pseudoreticulate infructification. 9, L.M. paratype, showing striations, equatorial thickening, and subequatorial circular furrow, ×2000. 8, L.M. holotype, showing pseudopore. 10, 11, S.E.M. views of same grain showing radially combed strong spines of echinate sculpture.
to make a new species. Only scan observation of the C. echinatus holotype can indicate whether these species are synonyms or not.

*Classopolis noeli* sp. nov.

*Plate 59, figs. 1–3*

**Diagnosis.** Subequisatorial circular furrow present; trilete scar present, length of laesurae 5–12 μ; pseudopore diameter 3–10 μ; infracture punctate; average exinal thickness 1 μ; equatorial thickening 2 μ; 7–12 striations, band width 7 μ. Sculpture simple isomorphous, isodiamic, verrucose-papillate; height of warts 0·2–0·4 μ, abundance 12–15 per μ².

*Size range. 22–40 μ (100 specimens).*

*Holotype.* Plate 59, figs. 1–3; size 30 μ.

**Stratigraphic position.** Upper Jurassic to Aptian of the Sahara. Holotype from bore-hole Tammera 1, Algeria, (X = 4 g. 04° 03′ E., Y = 37 g. 13° 72′ N.), depth 1479 m. (Aptian).

*Remarks.* This species is one of the components of the optical type population 'scabrate-verrucose' (Medus and Reyre 1966).

**BOTANICAL AFFINITY AND TAXONOMIC VALUE**

Barnard (1968), studying male cones containing *Classopolis*, established that the genus does not belong to the Araucariales; he underlined the similarity between *Cheirolepis muensteri* Schenk cones described by Hörhammer (1933), *Macrostrobus* Seward and those of *Taxus*; however, he put forward no formal conclusion. Perhaps the sculpture of the pollen exine is more significant. Three arrangements of sculptural elements can be recognized: simple (the most common), mixed or double. From observation of the sculpture of Recent gymnosperm pollen (Reyre 1968d) it appears that a very important fossil plant taxon is concerned, having at least the rank of an order. Indeed, Cupressales generally have a double sculpture, Taxodiaceae a mixed sculpture, and Taxales a simple sculpture. Among *Classopolis* simple sculpture is by far the most frequent. However, the elements of the sculpture are, in the main, quite different; the species of recent Taxales show nipples or marked warts, regular and perfectly shaped; on the contrary *Classopolis* show grana, warts, blisters, coarse spines or large distinct needles. In addition, the wide variety of sculpture suggests that there may have been a great number of species; so, if we consider Mesozoic pollen assignable to Taxales for their structural character, we observe a very limited variety of sculpture, as for living Taxales. All these differences seem to show that the paleobotanical taxon, which produced *Classopolis*, if it had a morphological relationship with *Taxus* (established by observation of the cones), was taxonomically distinct.

In spite of the highly evolved character of the exine, the presence of a proximal trilete scar (sometimes vestigial) is a primitive character. Other Conifers such as Araucariales, Taxodiaceae, and Taxales no longer show any trace of this ancestral character. Therefore plants which produced *Classopolis* may not be assigned to any Recent order of Coniferales; they corresponded probably to a special and very large fossil taxon having at least the rank of an order. In any case, it is established that *Classopolis* grains were produced by several botanical genera of Coniferales (Barnard 1968).
CLASSIFICATION

Is it possible to establish from pollen a classification likely to indicate the presumed phylums of the palaeobotanical taxon which produced Classopolis? Table 3 represents the geographical and stratigraphical distribution of the species described. For each a symbol indicates the nature of the infrastructure, the absence or presence of pseudo-striations or distinct continuous striations, the elementary type of sculpture and nature of the elements of this sculpture. If one considers this last character, it can be seen that the rugose-verrucose sculpture (under this name are grouped the psilate, grumose, rugose, and verrucose sculptures) existed in the Sahara from the Late Triassic, and continued to be the most frequent during the Jurassic and Early Cretaceous time. On the contrary, in Aquitaine (France), the echinate sculpture (hairy with points, spines, and needles) is widely represented since the Rhaetian, and undergoes an extreme development during the Early Cretaceous. It should be noted that after the species C. kieserl found in Rhaetian and Early Liassic of Aquitaine with echinate sculpture, there follow the Late Jurassic species C. aquitanaus, C. pugi, C. mirabilis which also have an echinate sculpture. In the same way, in the Sahara, the double sculpture of C. quezeli of the Late Triassic formations is also to be found in the Early and Middle Jurassic (pennulare type, Medus and Reyre 1966).

In Table 3 the botanical environment indicated results of a personal interpretation of the Stereoscopic appearance of pollens (see explanation of Pl. 59). It is remarkable that in the Sahara, where disaccate pollen is almost impossible to find after the Carnian, the succeeding species of Classopolis have a rugose-verrucose sculpture, and are principally associated with pollen of Taxales, Araucariales, or Ephedrales. On the other hand, in Aquitaine, numerous echinate species are associated, in the Rhaetian as in the Early Cretaceous times, with pollens that may be compared with that of recent Pinales of Cupressales. It would seem that different groups, linked with different ecological conditions, have each evolved separately. These different successions of species, during the Mesozoic era, geographically localized with similar sculptures, suggest that sculpture is not an accidental specific character but phyletic.

As for the infrastructure, it may be seen that in each group defined by the sculpture (for example echinate) the massive species are principally found in the Upper Triassic or the Infracarnian. In the same way the absence of striations or the presence of ill-defined striations (pseudo-striations) is the most common at these times, while during the Jurassic and Early Cretaceous one often observes very distinct striations, contrasting with

EXPLANATION OF PLATE 59

Light microscope figures approximately × 1000; Stereoscopic figures approximately × 2000 and 10,000.

Figs. 1–3. Classopolis novi sp. nov. 1, L.M. holotype, showing punctate infrastructure, striations, and axial thickness. 2, 3, S.E.M. holotype, showing general shape (× 5000) and verrucose-targeted sculpture (× 12,500).

Fig. 4. Mesozoic pollen with a simple sculpture assigned to a fossil species of Taxa (Reyre 1968d), × 5000.

Fig. 5. Pollen of a fossil (presumed Cupressales) showing outer sculpture with glomerules (Reyre 1968d).

Figs. 6, 7. Pollen assigned to a fossil Mesozoic species of Araucaria (Reyre 1968d). 6, S.E.M. general shape. 7, S.E.M. view showing sculpture.
### Table 3. Stratigraphic and geographic localization of *Classopolis* species and botanical environment.

<table>
<thead>
<tr>
<th>Species</th>
<th>Saharan Characters</th>
<th>Environment</th>
<th>Species</th>
<th>Israel Characters</th>
<th>Environment</th>
<th>France Characters</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aptian</td>
<td>nooli</td>
<td>p, s, sv</td>
<td><em>Cenolea</em>, <em>Ephedrales</em>, <em>Araucariales</em></td>
<td>maristril</td>
<td>mp, sp, 6o</td>
<td>Araucariales</td>
<td>Taxodiaceae</td>
</tr>
<tr>
<td>Barremian</td>
<td>nooli</td>
<td>p, s, sv</td>
<td><em>Ephedrales</em>, <em>Araucariales</em></td>
<td>maristril</td>
<td>mp, sp, 6o</td>
<td><em>+ others</em></td>
<td></td>
</tr>
<tr>
<td>Valanginian</td>
<td>nooli</td>
<td>p, s, sv</td>
<td><em>Araucariales</em>, <em>Bennettitales</em></td>
<td>maristril</td>
<td>mp, sp, 6o</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Berriasian</td>
<td>nooli</td>
<td>p, s, sv</td>
<td><em>Bennettitales</em></td>
<td>maristril</td>
<td>mp, sp, 6o</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower Portland</td>
<td>buzzoni</td>
<td>p, s, sv</td>
<td><em>Bennettitales</em></td>
<td>maristril</td>
<td>mp, sp, 6o</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle to Upper</td>
<td>buzzoni</td>
<td>p, s, sv</td>
<td><em>Bennettitales</em></td>
<td>maristril</td>
<td>mp, sp, 6o</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jurassic</td>
<td>gumnulate*</td>
<td>p, s, sd</td>
<td><em>Araucariales</em></td>
<td>Taxodiaceae</td>
<td>(+ others)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper Liassic</td>
<td>L.</td>
<td>mp, s, sv</td>
<td><em>Araucariales</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hettangian</td>
<td>buzzoni</td>
<td>p, s, sv</td>
<td><em>Cn. umb. complexes</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper Triassic</td>
<td>buzzoni</td>
<td>p, s, sv</td>
<td><em>Aporina</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carnian</td>
<td>No descriptive</td>
<td></td>
<td><em>Podocarpaceae</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Explanation.** *Infrastructure:* m, massive; v, vermiculate; mp, micropunctate; p, punctate; pr, pseudoreticulate; r, reticulate. *Striation:* So, no striations; Sp, pseudostriations; S, striations distinctive. *Sculpture:* srv, rugose-verrucose; se, colliculate; sm, mixed; sd, double.
the general infrastructure, and without a progressive organization of this infrastructure.
It would be necessary to observe all the known *Classopolis* species to affirm the results
concerning the distinction of the groups and the internal evolution of them. The remarks
above do permit, however, of our advancing the following inferences:

![Text-fig. 2. Shape and dimensions of the sculptural elements of the *Classopolis* species

1. *Classopolis* species should be classed according to the exine sculpture. This system
seems to be expressive of the botanical entities in the plant group which produced
*Classopolis*. From our present knowledge, four groups might be suggested with rugose-vertecos, echinulate, mixed or double structure.

2. The palynological evolution inside each group might be different, but it seems
that the massive infrastructure has preceded differentiated infrastructure (alveolate,
punctate, reticulate, etc.). This is organized into more and more clear and distinct
striations. Thus a species with distinct striations may be considered highly evolved.

Although certain exceptional cases may not confirm this hypothesis, on the whole
it seems valid. It explains why species with similar infrastructures can have, in fact,
different sculptures; inversely that species with similar sculptures can have dissimilar
infrastructures.
Y. REYRE: POLLEN GENUS CLASSOPOLIS PFLUG 1953

Barnard (1968, table 1) described pollen grains assignable to the form-genus Classopolis extracted from fossil cones of different palaeobotanical genera; to each genus corresponds a different infrastructure and the scanning observation of these grains should therefore be all the more interesting. But, to discern generic and specific characters, it would be necessary to observe also pollen grains extracted from cones of other species of the same genera.

Conclusion. Classopolis grains are the fossilized vestiges of a very important plant group which had, during the Mesozoic, variable radiations and discontinuous evolution according to the geographical province. No species seems to have had a world-wide distribution, but in some countries the abundance and diversity of these pollens in certain periods make them suitable for stratigraphic correlation.

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REYRE. Triassic and Jurassic Classopolis
REYRE, Jurassic and Cretaceous Classopolis
REYRE, Jurassic and Cretaceous Classpollis
REYRE, Clavulopollis and other pollen