ABSTRACT

Following a review of previous literature on Classopollis *Pflug, 1953 and a discussion of its nomenclature, type species, and diagnosis, this pollen genus is here emended on the basis of numerous specimens recovered from Permian to Upper Cretaceous rocks in Canada. The type species,* Classopollis classoides *Pflug, is also emended, and three new species are described. The stratigraphic occurrence, possible depositional environment, and possible affinities of the genus are discussed.*

The pollen genus Classopollis Pflug, 1953

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INTRODUCTION

Pollen grains referable to the genus *Classopollis* Pflug are found in strata ranging in age from Permian to Eocene. Some Jurassic and Lower Cretaceous horizons in many parts of the world have yielded many thousands of well-preserved grains referable to this genus. Despite this abundance of well-preserved material, most published descriptions of species assignable to the genus, including the original generic description and subsequent emendations, are both inadequate and inaccurate. The position regarding nomenclature is no better, a combination of misinterpretation and of failure by some authors to check the synonymy sufficiently closely having resulted in a nomenclatural situation that is little short of chaotic. In the following paragraphs, the authors give some account of previous literature referring to this genus and an interpretation of it based on specimens isolated from Canadian strata, together with descriptions of a few Canadian species.

ACKNOWLEDGMENTS

The authors wish to thank Dr. H. D. Pflug, of Giessen, for correspondence regarding the genus *Classopollis* and for the loan of comparative material, and Dr. R. Potonié, of Krefeld, for the discussion of some problems relating to the genus. They also express thanks to the editors of *Palaeontographica*, and in particular Professor H. Weyland, for permission to reproduce the original figure of the holotype of *Pollenites torosus* Reissinger (pl. 1, fig. 13, of the present paper) and two figures of specimens assigned by Thiergart to his species *Bennettiteae-Pollenites reclusus*, and to Imperial Oil Limited for permission to publish this paper.

PREVIOUS LITERATURE

1933 – Pollen of *Cheirolepsis muensteri* Schenk. – HOERHAMMER, 1933, p. 134, pl. 4, fig. 27Aaa and Aab.

Hoerhammer discussed and illustrated pollen grains as those of *Cheirolepis muensteri* Schenk which appear identical to some of the dispersed grains assigned to *Classopollis*.

1949 – *Bennettiteae-Pollenites reclusus* Thiergart. – THIERGART, 1949, p. 11, pl. 2, figs. 14–16; pl. 3 fig. 6.

Pollen grains referred to this species of Thiergart have been cited as identical with *Classopollis classoides* Pflug by some authors. The specific description is, however, inadequate, and the plates are very poor, making positive comparison impossible. Pflug, who has examined Thiergart's type material, is of the opinion that the two species are quite distinct (personal communication).

1949 – Pollen grains of *(?) Brachyphyllum scottii* Kendall. – KENDALL, 1949, p. 307, text-fig. 1, J and K.

These pollen grains were described as 30–40μ in diameter, each bearing two wide bands of thickening sharply demarcated from the thinner polar and equatoral regions. The illustrations show a single grain and a tetrad which clearly belong to Pflug's genus *Classopollis*. The diagrams show a circular distal pore very clearly, a feature not recognized by many subsequent authors. These grains were found in association with megafloral remains of *Brachyphyllum scottii* Kendall, some being still attached to a male cone axis which probably belonged to that species.

1950 – *Pollenites torosus* Reissinger. – REISSINGER, 1950, p. 115, pl. 14, fig. 20.
Pollen of *Cheirolepis muensteri* Schenk. – REISSINGER, 1950, p. 114, pl. 14, figs. 10–14.
Conifer pollen. – REISSINGER, 1950, pl. 14, figs. 15–16; pl. 18, fig. 32a–b.
Conifer pollen. – REISSINGER, 1950, pl. 14, figs. 21–28.

In this paper, Reissinger described a series of grains which can be referred to Pflug's genus *Classopollis*, but only one specific name was proposed, *Pollenites torosus*. He compared these pollen grains with grains from male cones assigned to *Cheirolepis muensteri* Schenk and concluded that there is a definite natural relationship between the two types.

1952 – Pollen of *Pagiophyllum connivens* Kendall. – KENDALL, 1952, pp. 583–594.

Kendall described pollen grains from an araucarian male cone attributed to *P. connivens*. The grains were circular to oval, scabrate, with a thickened equatorial region. These grains have been compared with *Classopollis classoides* Pflug by some authors.

1953 – *Aporina striatella* Bolkhovitina. – BOLKHOVITINA, 1953, p. 101, pl. 16, fig. 36.

This species, although larger than any described by Pflug, appears to be referable to the genus *Classopollis*.

1953 – *Classopollis classoides* Pflug. – PFLUG, 1953, p. 91, pl. 16, figs. 20–25, 29–37.
Classopollis declassis Pflug. – PFLUG, 1953, p. 92, pl. 16, figs. 16–19.
Tetrads of *Classopollis* Pflug. – PFLUG, 1953, pl. 16, figs. 29–30.
Circumpollis pharisaeus Pflug. – PFLUG, 1953, p. 92, pl. 17, figs. 28–30.
Circumpollis philosophus Pflug. – PFLUG, 1953, p. 92, pl. 17, figs. 31–36.
Canalopollis maturus Pflug. – PFLUG, 1953, p. 93, pl. 17, figs. 48–60.

In this paper Pflug erected the genus *Classopollis*. Although the authors cannot accept his interpretation of the structure of this genus, the illustrations of the holotype (pl. 16. figs. 29–31) appear to them to be perfectly clear; these figures, together with the supplementary ones (figs. 20–25 and 32–37), leave no doubt as to the forms of pollen which should be assigned to the genus.

In addition to *Classopollis*, Pflug erected two other genera, *Circumpollis* and *Canalopollis*, which comprise very similar grains. Many workers dispute the validity of these two genera, and there appears to the authors to be little merit in separating these genera from the genus *Classopollis*. The action of Couper (1955 and 1958) in assigning all the forms that Pflug had described under the three genera to the one species *Classopollis torosus* appears, however, to be the other extreme.

1954 – *Tetradopollenites reclusus* (Thierg.). – SITTLER, 1954, pp. 338–341.

The generic name *Tetradopollenites* was applied by Sittler to species similar to Thiergart's *Bennettiteae-Pollenites reclusus* and habitually occurring in tetrads; it was presumably intended to include species falling in the genus *Classopollis*. As far as the authors can determine, this generic name was not validly published.

1954 – *Brachyphyllum* Brongn. – ZAUER AND MCHEDLISHVILI, 1954, pp. 7–9.

The stratigraphic value of pollen grains resembling those obtained by Kendall in 1949 is discussed. The grains pictured here appear identical to species assigned by Pflug to *Classopollis*.

1954 – Cheirolepidaceae Groups I–IV. – ROGALSKA, 1954, pl. 11. figs. 1–10.

Many of the specimens illustrated and described by Rogalska can be placed in the genus *Classopollis*. The validity of her four groups appears to be doubtful.

1955 – Tetrads of operculate grains. – KUYL, MULLER AND WATERBOLK, 1955, pl. 6, figs. 9–11.

Tetrads of grains which are certainly referable to the genus *Classopollis*, probably the species *C. classoides* Pflug, were illustrated.

1955 – *Trachytriletes* Type 3(?). – SAH, 1955, p. 63, pl. 1, fig. 6.
Liratoaletes Type 1. – SAH, 1955, p. 65, pl. 1, fig. 11–11a.
Liratoaletes Type 2. – SAH, 1955, p. 65, pl. 1, fig. 16.
Striatoaletes Type 1. – SAH, 1955, p. 64, pl. 1, fig. 18.
Trachyaletes Type 1. – SAH, 1955, p. 64, pl. 1, fig. 25.

The forms assigned to these groups appear to be referable to the genus *Classopollis*. Poor descriptions and illustrations make specific comparison impossible. It appears from the illustrations that Sah misinterpreted different orientations of the same species as different forms. His names *Liratoaletes*, *Striatoaletes*, and *Trachyaletes* are not valid since they are not properly described as new genera, and no type species are proposed.

1955 – *Classopollis*, *Circumpollis*, and *Canalopollis* types of pollen, – COUPER, 1955, pp. 471–474, pl. 20, fig. 8; pl. 21. figs. 1–10.
Pollen from an araucarian male cone attributed to *Pagiophyllum connivens* Kendall. – COUPER, 1955, pp. 472–474, pl. 21, figs. 11–12.

Couper's opinions regarding these forms will be discussed more fully in a later paragraph.

1955 – *Classopollis* Pflug. – KRUTZSCH, 1955, pl. 4, fig. 42.
cf. *Classopollis* Pflug – KRUTZSCH, 1955, pl. 4, figs. 51–52.
Circumpollis Pflug. – KRUTZSCH, 1955, pl. 4, figs. 45–47.
Altmark W-20 form. – KRUTZSCH, 1955, pl. 4, fig. 43.
Altmark W-21 form. – KRUTZSCH, 1955, pl. 4, figs. 48–49.
Altmark W-22 form. – KRUTZSCH, 1955, pl. 4, figs. 55–56.
Altmark W-23 form. – KRUTZSCH, 1955, pl. 4, fig. 57.
Altmark W-24 form. – KRUTZSCH, 1955, pl. 4, figs. 58–60.
Altmark W-25 form. – KRUTZSCH, 1955, pl. 4, fig, 61.
Altmark W-26 form. – KRUTZSCH, 1955, pl. 4, figs. 62–63.
Altmark W-27 form. – KRUTZSCH, 1955, pl. 4, fig. 64.
cf. Form Reissinger (1950 pl. 14, figs. 21, 27–28). – KRUTZSCH, 1955, pl. 4, fig. 44.
cf. Form Reissinger (1950, pl. 14, figs. 15–16). – KRUTZSCH, 1955, pl. 4, fig. 50.
cf. Form Reissinger (1950, pl. 14, fig. 20). – KRUTZSCH, 1955, pl. 4, figs. 53–54.

1957 – *Classopollis* cf. *C. torosus* (Reissinger). – BALME, 1957, pl. 11, figs. 114–119.
Classopollis sp. – BALME, 1957, pl. 11, figs. 120–122.

In this paper, Balme assigned Reissinger's species *Pollenites torosus* to Pflug's genus *Classopollis*. Although the authors agree with such an assignment, it appears to them that Balme's figured specimens appear closer to Pflug's species *C. classoides* than to Reissinger's *P. torosus*.

1958 – *Classopollis torosus* (Reissinger). – COUPER, 1958, pp. 156–157, pl. 28, figs. 2–7.

In this work, Couper amended Pflug's diagnosis of *Classopollis* and proposed Reissinger's type of the species *torosus* as the genotype on grounds of synonymy. He also repeated the arguments brought forward in 1955 for assigning all of Pflug's species of *Classopollis*, *Circumpollis*, and *Canalopollis* to the one species *Classopollis torosus* and for regarding them as identical with the pollen of *Pagiophyllum connivens* Kendall.

1958 – *Tetradopollenites reclusus* (Thierg.) Sittler. – LANTZ, 1958, p. 928, pl. 7, figs. 71–72.

Lantz refered spherical, operculate, striate grains with a vestigial trilete mark to this species, which she regarded as synonymous with *Classopollis torosus* (Reissinger) Couper (1958). The dimensions and structure of the figured grains appear, however, to be identical with Pflug's species *Classopollis classoides*.

1959 – *Pterocarya poropollenites* Rouse. – ROUSE, 1959, pl. 1, figs. 21–22.

The grains thus described by Rouse are, in the authors' opinion, rather corroded *Classopollis* grains. The authors have frequently observed such grains in samples from the Western Canadian foothills and mountains, which have suffered some alteration (metamorphism). Both of Rouse's figured specimens appear to be equatorially striate, and the specimen in figure 21 shows what appears to be a vestigial trilete. The dimensions of Rouse's specimens fall well within the range of *Classopollis classoides* Pflug.

1959 – KLAUS, 1959, p. 161.

A diagram illustrates a pollen tetrad which appears to belong to the genus *Classopollis*, from the Karnian (Upper Triassic) of the European Alps.

VALIDITY OF THE GENERIC NAME CLASSOPOLLIS PFLUG, 1953

Despite a host of names applied to the type of pollen under discussion, only two are possibly applicable:

CLASSOPOLLIS PFLUG, 1953

Pflug's description and photographs of the type species for this genus are quite clear; the generic name is thus perfectly valid under the rules of nomenclature, and has priority over the following name.

TETRADOPOLLENITES SITTLER, 1954

The assignment of the generic name *Tetradopollenites* to Thiergart's species *reclusus* might be argued as valid on the grounds that Thiergart's binomial generic name *Bennettiteae-Pollenites* is invalid. The assignment of Reissinger's *Pollenites torosus* and Pflug's *Classopollis classoides* to this species by Lantz and by Couper on grounds of synonymy is unwarranted, however, since such synonymy cannot be proven. It is doubtful if the generic name *Tetradopollenites* was validly published. The only reference that the authors can find to the original assignment of the name is a report of a lecture by Sittler in 1954, in which the name was mentioned. This would invalidate the name under Article 33, Provisions 2 and 3, of the International Code of Botanical Nomenclature.

All subsequently published generic names for the forms of pollen under discussion are invalid on grounds of priority of publication. Botanical organ-genera are not included in this discussion, since the authors consider that the mixing of natural and morphological terminology can only lead to confusion.

THE TYPE SPECIES OF CLASSOPOLLIS

Pflug (1953) proposed the species *Classopollis classoides* as the type for his genus *Classopollis*. The genotype is illustrated in plate 16, figures 29–31, of his 1953 paper, and it is from these figures only, together with the generic diagnosis and specific description, that the validity of the type species must be judged. If a previously validly named species can be shown to be identical with Pflug's genotype, it will automatically replace Pflug's species as the genotype of *Classopollis*, provided its holotype is in existance. Thus, if Thiergart's species *Bennettiteae-Pollenites reclusus* (1949) and Reissinger's *Pollenites torosus* (1950) are identical with *Classopollis classoides* Pflug (1953), Thiergart's *reclusus* will take precedence and become the genotype of Pflug's genus *Classopollis*.

Couper's rejection of Thiergart's species *reclusus* in favor of Reissinger's *torosus* on the grounds of invalidity of the binomial generic name for Thiergart's species is inadmissible under Article 70(3) of the International Code. In actual fact, however, it cannot be shown beyond reasonable doubt that either Thiergart's or Reissinger's species is identical with the genotype *Classopollis classoides* Pflug. In spite of the poor preservation of Thiergart's type, the authors are of the opinion that the two species are different. Pflug, who has examined Thiergart's type material, holds the same opinion.

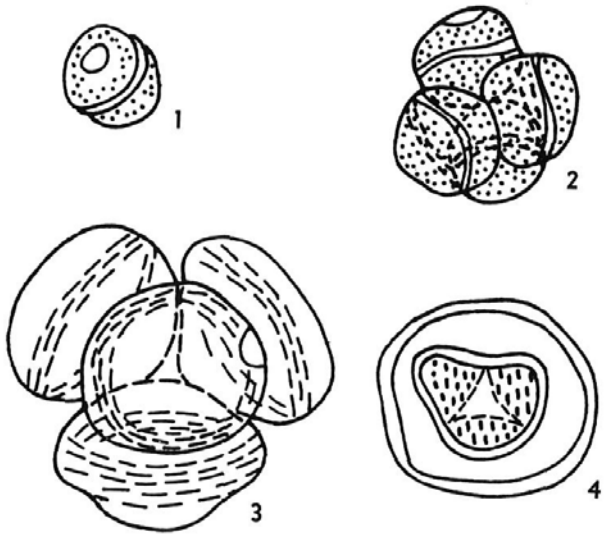
The type specimen of Reissinger's *Pollenites torosus* is shown in plate 14, figure 20, of his 1950 paper. The holotype itself is no longer in existence. Figures 15 and 16 on the same plate (particular figure 16) appear to be close to, if not identical with, the holotype of *Classopollis classoides* Pflug, and Pflug himself is in agreement with such a comparison. Reissinger, in the description of this plate and in the text (top of page 115), made it

perfectly clear that he regarded *Pollenites torosus* as a quite distinct and different species from the grains illustrated in figures 15 and 16, and comparison of the figures and descriptions of the two forms leads the authors to agree with this conclusion. Thus, it would appear that *Pollenites torosus* Reissinger and *Classopollis classoides* Pflug are not identical. *Classopollis classoides* Pflug holds priority over all subsequently described forms assignable to the genus and therefore remains the valid genotype.

GENERIC DIAGNOSIS

Pflug's (1953) generic diagnosis of *Classopollis* was: "tricolporate, rarely tetracolporate. Rimula well developed, germinales gaping. Poles never quite identical in appearance." In the text (pp. 73–74) he illustrated the position of what he termed the "rimula", or main colpus. The exine structure of many specimens also appears to support the theory that *Classopollis* possesses characters in common with both gymnosperms and angiosperms. Our figure 5 on plate 1 illustrates a grain from the Neocomian of Alberta which belongs to the genus *Classopollis* and has the appearance of a tricolpate grain with a two-layered tectate exine. Oblique squashing caused this misleading appearance.

Couper (1955 and again in 1958) criticized Pflug's interpretation, and compared *Classopollis* pollen with that from *Pagiophyllum connivens* Kendall, concluding that *Classopollis* pollen was derived from that or a related plant. In his 1958 paper he emended Pflug's diagnosis to: "Pollen grains circular to oval in polar view; equatorial region with distinct intexinal thickening; exine of polar regions comparatively thin, scabrate; proximal pole usually showing a vague tetrad marking, taking the form of a weak area in the exine." He designated Reissinger's *Pollenites torosus* as genotype, and noted that the genus is intended for the reception of dispersed pollen grains of the type met with in *Pagiophyllum connivens*. The authors, although agreeing that Pflug's original diagnosis is inaccurate, feel that Couper's emendation is unsatisfactory. In demonstrating the affinity between *Classopollis* and *Pagiophyllum connivens*, he stated: "Unfortunately, the pollen [i.e., of a *Pagiophyllum* male cone] preparation is rather deeply stained, undermacerated . . . and not clearly displayed." He therefore referred to his own "detailed description of *Classopollis torosus* (Reiss.) Couper,. . . based on hundreds. . . of dispersed grains." Then, in turn, in this description he stated that the wide "range of variation of the grains of *Pagiophyllum connivens*" warrants lumping all of Pflug's species and genera into this one species. The implied relations between these grains and the pollen of *Pagiophyllum connivens* is not proven, and thus the suggestion that the genus *Classopollis* should receive grains of the type met with in *Pagiophyllum connivens* is unwarranted. In any case, even in the most excellent preparations of associated microspores, we may expect the range of variation to be wider than in dispersed grains because of the immaturity of some of the grains.



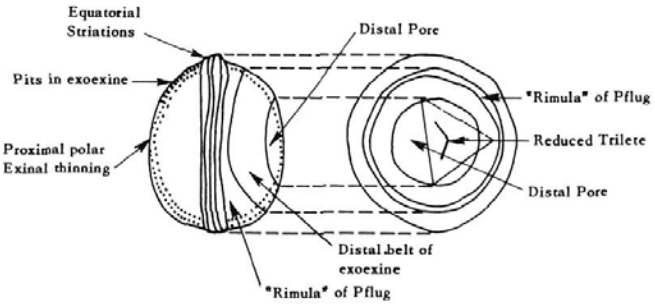
TEXT-FIGURES 1–4

1–2 (after Kendall, 1949), single grain and tetrad from male cone axis attributed to *Brachyphyllum scottii* Kendall; 3–4 (after Zauer and Mchedlishvili, 1954), pollen grains of "*Brachyphyllum*": 3, tetrad; 4, distal polar view of single grain showing "laceration" and vestigial trilete.

Balme (1957), although not proposing any formal emendation of Pflug's generic diagnosis, noted Pflug's misinterpretation of the structure of the grain and described two species of *Classopollis* as having the following characters in common: "Amb round or oval, flattened acorn-shaped in lateral view. Vestigial trilete markings often present in the form of a triangular or triradiate scar on the proximal face. Germination apparently by means of distal operculum. Exine thickened in a narrow equatorial zone which appears as an equatorial rim in polar view." Particularly significant in this description is the mention of a distal operculum. No such operculum was mentioned in Couper's diagnosis.

Two other contributions, although not specifically referring to the genus *Classopollis*, describe grains that belong to that genus and are important for purposes of interpretation. Kendall (1949) illustrated a grain and a tetrad of pollen grains recovered from a male cone axis, probably referable to the species *Brachyphyllum scottii*. She described the grains as "round, 30–40μ in diameter, and thickly cutinised. Each bears two wide bands of thickening, sharply demarcated from the thinner polar and equatorial regions. . . .The exine is not granular." The illustrations (text-fig. 1J and K) show grains that unquestionably belong to the genus *Classopollis*, each possessing a distal pore, a character not noted by many subsequent authors.

Zauer and Mchedlishvili (1954), following Kendall's (1949) interpretation of the affiliation, described pollen of the *Classopollis* type under the generic name *Brachyphyllum*, as follows: "The grains of this pollen usually



TEXT-FIGURE 5

occur in tetrads, seldom only in single grains. The grain is round-ellipsoidal. No pores or furrows. The capsule is multilaminated, thicker at the proximal side of the grain and thinner at the distal side. The grain shows an equatorial swelling with parallel striae, which are interrupted at one point only. Some grains have traces of a tetrad scar preserved. The distal side of the grain is sometimes lacerated. The color of the grain varies between light and dark brown." Although distal "laceration" of some grains was noticed, there was no mention of a distal pore, although this feature was shown in Kendall's illustrations. The figures accompanying their description also fail to show such a feature.

In the course of studying the microflora of Western Canada, many hundreds of well-preserved pollen grains assignable to the genus *Classopollis* were recovered from samples ranging in age from Permian to Upper Cretaceous, a majority of the specimens being obtained from samples of Middle and Upper Jurassic age. Many of the specimens resemble *Classopollis classoides* Pflug 1953. This identification was confirmed by Pflug, who examined some of the Canadian material and loaned the authors a slide containing some of his own specimens. With the aid of this well-preserved material, the authors propose to emend the generic diagnosis of *Classopollis* and to describe some of the Canadian species assignable to that genus.

SYSTEMATICS

Genus Classopollis Pflug, 1953, emended, Pocock and Jansonius

Diagnosis: Pollen grains; distally monoporate; ovoid, spherical, or flatly acorn-shaped; exine two-layered; exoexine absent or much reduced over a circular area surrounding the distal pole, and absent or reduced over a triangular area with its center at the proximal pole; intexine frequently bearing a reduced trilete scar, which has no germinal function, at the proximal pole; exine always ornamented by striations in a band or girdle surrounding the equator and interrupted (if at all) at only one point; the band usually, but not always, marking a zone of exinal thickening.

Type species: Classopollis classoides Pflug, 1953.

Classopollis classoides Pflug, emended, Pocock and Jansonius
Plate 1, figures 1–9

"Conifer pollen," REISSINGER, 1950, p. 114, pl. 14, figs. 15–16.
Classopollis classoides PFLUG, 1953, p. 91, pl. 16, figs. 29–31.

Description: Spherical, ovoid, or flatly acorn-shaped; circular in equatorial section; monoporate, with a circular distal pore 12–15μ in diameter; exine two-layered; intexine thin (about 1μ thick), laevigate, continuous over whole area of spore, occasionally showing a small trilete mark at the proximal pole, which does not function as a germinal aperture; rays of trilete, where present, not more than 3μ long; exoexine 1–2μ in thickness, divisible into two distinct zones; a wider zone enveloping the proximal hemisphere and a smaller zone forming a belt of exoexine, averaging 5μ in width, surrounding the exposed intexine of the distal pole; the distal belt is separated from the exoexine of the proximal hemisphere by a narrow band of exinal thinning slightly distal to the equator, over which the exoexine is absent or reduced (this band forms the "rimula" of Pflug); the exoexine of the proximal hemisphere is absent over a triangular area surrounding the proximal pole and thickens toward and over the equator; four or more annular bands of exoexinal thickening, which may or may not be quite pronounced, form a belt averaging 9μ in width surrounding the equator; exoexinal ornament appears to consist of small pits, distributed radially to the surface of the grain and frequently fusing at the surface to form continuous bands of ornamentation around the equator, and of a granulose or in some instances microreticulate pattern over the rest of the exoexine. (It is extremely easy to confuse this type of ornamentation with a tectate exine, which is, in fact, exactly the reverse structure, being made up of rods and not pits.)

Color of spore: Light yellow to deep yellowish brown.

Size range: Polar diameter 18 (23) 24μ; equatorial diameter 21 (29) 33μ.

Remarks: This species is very distinctive and easy to recognize. Plate 1, figure 1, shows a photograph of one of Pflug's specimens from the Lias of Siegelsum well no. 2, and figure 2 shows an enlargement of one grain of the tetrad. Figure 3 shows a tetrad from the Middle Jurassic of Saskatchewan, and figure 4 an enlarged grain assigned to the same species, showing quite clearly the distal pore and distal exoexinal belt, which occasionally pulls away from the equatorial belt in two diametrically opposite places. Both Pflug and the authors of this paper would assign all four specimens to the species just described. Figure 8 and 9 show a tetrad and a single grain from that tetrad, also assignable to *C. classoides* Pflug. These specimens are exceedingly well preserved and show the details of the ornament, the two-layered exine, and the nature of the distal pore very well. Figures 6 and 7 are a diagram and a photograph of the structure of a corroded grain

of *Classopollis* cf. *classoides*, showing the relationship between the proximal pole with reduced trilete mark and the distal pore.

Classopollis belloyensis Pocock and Jansonius, new species
Plate 1, figures 10–12

Description: Pollen grains; more or less circular in polar section; exine two-layered; intexine thin, scabrate, brownish yellow in color, constituting a globular central body; exoexine much thicker, averaging 2μ but increasing to 6μ in the equatorial region; pale yellow to colorless, hyaline, slightly roughened, enveloping the central body except at the distal and possibly at the proximal pole; at the distal pole the exoexine is absent over a circular area 12μ in diameter, forming a distal pore. Exoexine thickened in the equatorial area, forming a broad girdle, 12μ wide, which carries ornamentation consisting of eight to ten parallel equatorial ridges and grooves, possibly interrupted at one point; this ornamentation does not show up very clearly in outline, suggesting the possibility that it may be internal and caniculate in character. The symmetry is probably radial, but possibly bilateral, if the equatorial girdle has its greatest expansion in two opposite areas on the equator (cf. *Vittatina*). Pyrite crystals within the grain prevent observation of any proximal polar structures.

Size: Equatorial diameter about 38μ; polar diameter about 30μ.

Holotype: Imperial Belloy 12–14 (12–14–78–1W6M), at 4227 feet; locality approximately 180 miles northwest of Edmonton, Alberta, Canada. Slide No. Imp. H–385–2 (116.0′–27.2).

Stratigraphic position: Lower (carbonate) member, type section, Belloy formation. This falls about in the middle of the Upper Permian (Guadeloupean?).

Discussion: In appearance and stratigraphic position, this species agrees with what one would expect of the forerunner of the several Mesozoic *Classopollis* species. The holotype is well preserved, and several other specimens were observed in the same sample, which otherwise carries a dominantly marine assemblage. Jansonius recorded the same species from samples of shale and siltstone from the Hilton Plant Beds of Westmorland, England, which are of about the same age. Plate 1, figure 10, shows a photograph of the holotype. Figure 11 is an enlarged view of the same specimen, showing the exoexinal ornament, and figure 12 is a similar photograph, showing details of the scabrate endexine of the distal pore.

Classopollis minor Pocock and Jansonius, new species
Plate 1, figures 21–25

"Conifer pollen," REISSINGER, 1950, p. 114, pl. 14, figs. 21–28; pl. 18, fig. 33a–e.

cf. "Siegelsum N. Typus," PFLUG, 1953, pl. 17, figs. 38–40.

"Cheirolepidaceae Group II," ROGALSKA, 1954, p. 23, pl. 11, figs. 4–6.

Description: Pollen grains; oval to circular in polar section, circular in equatorial section; exine two-layered; intexine thin, laevigate; exoexine thicker (1–3μ), divisible into two zones; one zone envelops the proximal hemisphere but for a triangular aperture at the proximal pole, 5–7μ in diameter, through which the intexine is exposed; the other exoexinal zone envelops the distal hemisphere and carries a circular aperture about 4μ in diameter at the distal pole, where the intexine is exposed, forming a distal pore; this zone meets the exoexine of the proximal hemisphere approximately at the equator and is separated from it by a very narrow band where the exoexine is absent or very much thinned; this band of thinning is relatively less well developed than in *Classopollis classoides* Pflug; ornament of exoexine internally caniculate; exoexine of proximal hemisphere thickened in the equatorial area, forming a girdle about 6μ wide, ornamented by about ten parallel canals within the exine, which show a break at one point; a second series of similar canals is developed parallel to each side of the triangular proximal exoexinal aperture; these canals are truncated by the equatorial girdle; distal exoexine ornamented by a series of radially disposed pits, which are frequently united at the surface, giving the appearance of microreticulate ornamentation; grains usually deep yellow brown in color.

Size range: Equatorial diameter 21 (25) 27μ (holotype 25μ); polar diameter 21 (22) 24μ (holotype 22μ).

Holotype: Tidewater Southey 4–29–22–18W2M, at 2276–77 feet (south-eastern Saskatchewan); Gravelbourg formation (Bajocian). Slide No. 2119–1 (35.6–119.3).

Stratigraphic range: Lower Jurassic to Eocene; most abundant in Canada in the Middle and Upper Jurassic, where it appears in great abundance at some horizons. There appears to be little relationship between the abundance of this species and that of other species of the same genus at any one horizon, which suggests that these grains were derived from a natural species of plant distinct from those producing other species of *Classopollis* pollen.

Remarks: These grains are smaller than those of other described species of *Classopollis*, and the striation around the proximal aperture makes them very distinctive. The grains are usually seen in polar view, and tetrads are rare. Plate 1, figures 23–24, the holotype, shows the grain in equatorial view; figures 21 and 22 show distal and proximal polar views, respectively; figure 25 is an oil-immersion photograph of the proximal view of a grain, showing the striation parallel to the sides of the aperture and the band of thinning parallel to the equator marking the line of division between the proximal and distal exoexine (the "rimula" of Pflug).

Classopollis pflugii Pocock and Jansonius, new species
Plate 1, figures 16–20

"Possibly Taxodeacean pollen" REISSINGER, 1950, pl. 14, figs. 18–19

Description: Pollen grains; oval in polar section, circular in equatorial section; exine two-layered; intexine thin, laevigate, translucent; exoexine about 1.5μ thick, transparent, loosely enveloping the intexine, which forms a more or less spherical central body; exoexine divisible into two zones, one enveloping the proximal hemisphere and carrying a faint trilete mark at the proximal pole, the other enveloping the distal hemisphere and thinning over a circular area around the distal pole, although no distinct distal pore appears to be developed; this thinned area is frequently torn or distorted, indicating that it is a definite area of exinal weakness; it probably functioned as a germinal area. The two exoexinal zones are separated by a narrow unornamented band of exinal thinning; ornament of exoexine internally caniculate; exoexine of proximal hemisphere thickened in the equatorial region, forming a girdle about 6μ wide ornamented by about seven canals within the exoexine, which show a break at one point; the remainder of the exoexine, with the exception of the laevigate "rimula," is ornamented by a series of small pits distributed radially to the surface of the grain; it is characteristic of this species that the exoexine is only very loosely attached to the intexine, and this frequently results in the intexinal central body becoming detached from the exoexine; grains usually light yellow to yellowish brown in color.

Size range: Central body 21.0 (21.9) 22.8μ × 15.0 (16.5) 18.0μ (holotype 22.8μ × 18.0μ); whole grain 26.4 (28.3) 33.0μ × 21.0 (23.2) 27.0μ (holotype 26.4μ × 21.6μ).

Holotype: Blackfoot Devonian Test Syndicate No. 1, 12–15–50–2W4M, at 2014–26 feet. Slide No. 3510 (2014–26)–1(41.4–126.9).

Stratigraphic range: This species has been recognized only from the Lower Cretaceous of Western Canada, where its geographic distribution is somewhat restricted. Similar forms have, however, been seen in Upper Jurassic sediments of Western Canada, although these are not specifically identical. Two grains illustrated by Reissinger (see the synonymy) from the Upper Jurassic of Europe appear to be similar, if not identical, to this species. Some grains assignable to this species have been squashed in a direction parallel to the polar axis, resulting in the exoexine becoming folded around the equator to form a thick girdle. Such grains resemble fairly closely Reissinger's figure of his species *Pollenites torosus* (1950, pl. 14, fig. 20) (see pl. 1, fig. 13, of the present paper), although the poor quality of Reissinger's figure and the lack of an adequate specific description prevent any positive comparison of the Canadian specimens with Reissinger's species. If *C. pflugii* is, in fact, identical with any of Reissinger's specimens, its range is immediately extended, becoming Upper Jurassic to Cretaceous.

Remarks: Figure 20 is a photograph of the holotype, and figure 19 an oil-immersion photograph of the same specimen. Figure 17 shows an isolated torn exoexine of a grain of the same species, the central body having been lost. Figure 16 shows a folded tetrad which should be compared with figure 13, the holotype of *Pollenites torosus* Reissinger. Figure 18 shows a distal polar view of a grain assigned to this species.

MORPHOLOGICAL CHARACTER OF CLASSOPOLLIS

The descriptions of the preceding four species are not intended as a comprehensive account of species assignable to the genus, but merely to illustrate typical morphological characters. The principal features of the genus which appear to vary significantly from species to species and permit reliable specific differentiation to be carried out, appear to the authors to be:

1) The thickness of the exoexine and the tightness or looseness of its attachment to the central intexine.
2) The degree of differentiation of the exoexine into proximal and distal zones.
3) The degree of thickening of the equatorial girdle and the nature and distribution of its striate ornamentations.
4) The nature of the ornamentation of the distal and proximal exoexine. The extent of development of such ornamentation is, as pointed out by several previous authors, somewhat variable, dependent upon the extent of corrosion of the grain, but the basic pattern of ornamentation remains constant for any species so long as the exoexinal layer is not eroded so deeply that the ornamental layer is completely removed.
5) Ornament or lack of ornament of the intexine.
6) The size range of grains falling within any one species, which, although variable, is useful in specific determination provided enough specimens are available to determine size-variation ranges accurately.

OCCURRENCE AND POSSIBLE DEPOSITIONAL ENVIRONMENT

Grains assignable to the genus *Classopollis* have been recorded from almost every microfloral assemblage of Jurassic or Lower Cretaceous age, in varying abundance. At some horizons, particularly in the Jurassic, it occurs in considerable abundance and is frequently dominant. It may, in rare cases, constitute up to 98% of the entire assemblage. These assemblages, rich in *Classopollis*, frequently carry a very characteristic microflora containing, in addition to *Classopollis*, a moderate abundance of inaperturate pollen, fairly abundant Monosulcites, and a varying, but usually small, percentage of trilete spores. Conifer pollen is always scarce and frequently very rare or absent. Marine microflora is never abundant, but a small percentage of Dinophyceae and Hystrichospheridea are present in a

majority of the assemblages. Lithologically, samples rich in *Classopollis* are usually soft, light gray, gray-green, or brown shales or mudstones of the type deposited in shallow water. Strata carrying assemblages of this type frequently grade laterally in one direction into strata carrying predominantly marine assemblages and in the other into strata with assemblages rich in Monosulcites-type pollen. Since *Classopollis*-type pollen is obviously not of a nature that would be carried over great distances, it is reasonable to assume that almost pure thickets of the plant must have occurred in areas where *Classopollis* pollen makes up the bulk of the spore and pollen spectrum. Both the occurrence of marine microflora and the predominant lithology of the deposits containing the species in abundance suggest that the plants producing *Classopollis* pollen favored a coastal environment. The rarity of conifer pollen and trilete spores in such assemblages, together with the abundance of Monosulcites, probably derived from the Cycadaceae in laterally adjacent areas, suggests dry climatic conditions. Thus, it appears probable that an abundance of *Classopollis* pollen in a sample indicates that it was deposited in a coastal region under dry climatic conditions, a conslusion which is in accord with available geologic evidence.

POSSIBLE AFFINITIES OF CLASSOPOLLIS

No Recent pollen of a type similar to *Classopollis* has been recorded, and therefore the only certain manner by which it can be related to its parent plant is by the discovery of sporangia containing grains assignable to the genus, attached to identifiable megafloral parts. Such a discovery has not yet been made, and until such time, only very general conclusions regarding its affinities can be made.

The general structure of the pollen grains, in particular the inverse tectate and internal caniculate structure of the exoexine, indicates gymnospermous affinity. This conclusion has been accepted by most authors. The opinion of Pflug and some other workers that the grains show angiospermous characters is generally not accepted, as it is based upon misinterpretation of the structure of these grains.

Hoerhammer (1933) obtained well-preserved grains assignable to the genus *Classopollis* from male cones with similar cuticular structure to and associated with *Cheirolepis muensteri* Schenk. Since these cones were not actually attached to identifiable fragments of *Cheirolepis*, the association of *Classopollis* pollen with the species *C. muensteri* cannot be regarded as proven, but despite this element of uncertainty, Hoerhammer's data provide the most significant evidence regarding the affinity of *Classopollis* currently available. Couper (1958, p. 130) recorded grains of *Classopollis* type, "very similar to those of *Pagiophyllum connivens*," associated with *Cheirolepis muensteri* in the Lower Jurassic of Wales. In that case, however, the grains were dispersed in the rock carrying the megafloral remains and were not obtained from sporangia. (These grains showed a tendency to lose their ornamented outer coat.)

Reissinger (1950) and Rogalska (1954) also assigned *Classopollis*-type pollen grains to the Cheirolepidae but provided no additional evidence for such an assignment. The record of *Classopollis* grains attached to a male cone axis associated with but not attached to remains of *Brachyphyllum scottii* Kendall (Kendall, 1949) is not as reliable as that of Hoerhammer, since only one isolated cone axis was recorded, and the cuticular structure, although similar, was not identical with that

PLATE 1

1–9 *Classopollis classoides* Pflug. 1, tetrad of grains, and 2, an enlarged view of an isolated grain, from one of Pflug's slides; 3, tetrad, and 4, enlarged view of an isolated grain, from a Canadian Jurassic sample; 5, distorted grain showing spurious tricolpate structure; 6–7, *Classopollis* cf. *classoides*, diagram (fig. 6) and photograph (fig. 7) of a specimen illustrating the proximal and distal structures; 8, tetrad, and 9, enlarged view of an isolated grain, extremely well preserved, showing details of structure.

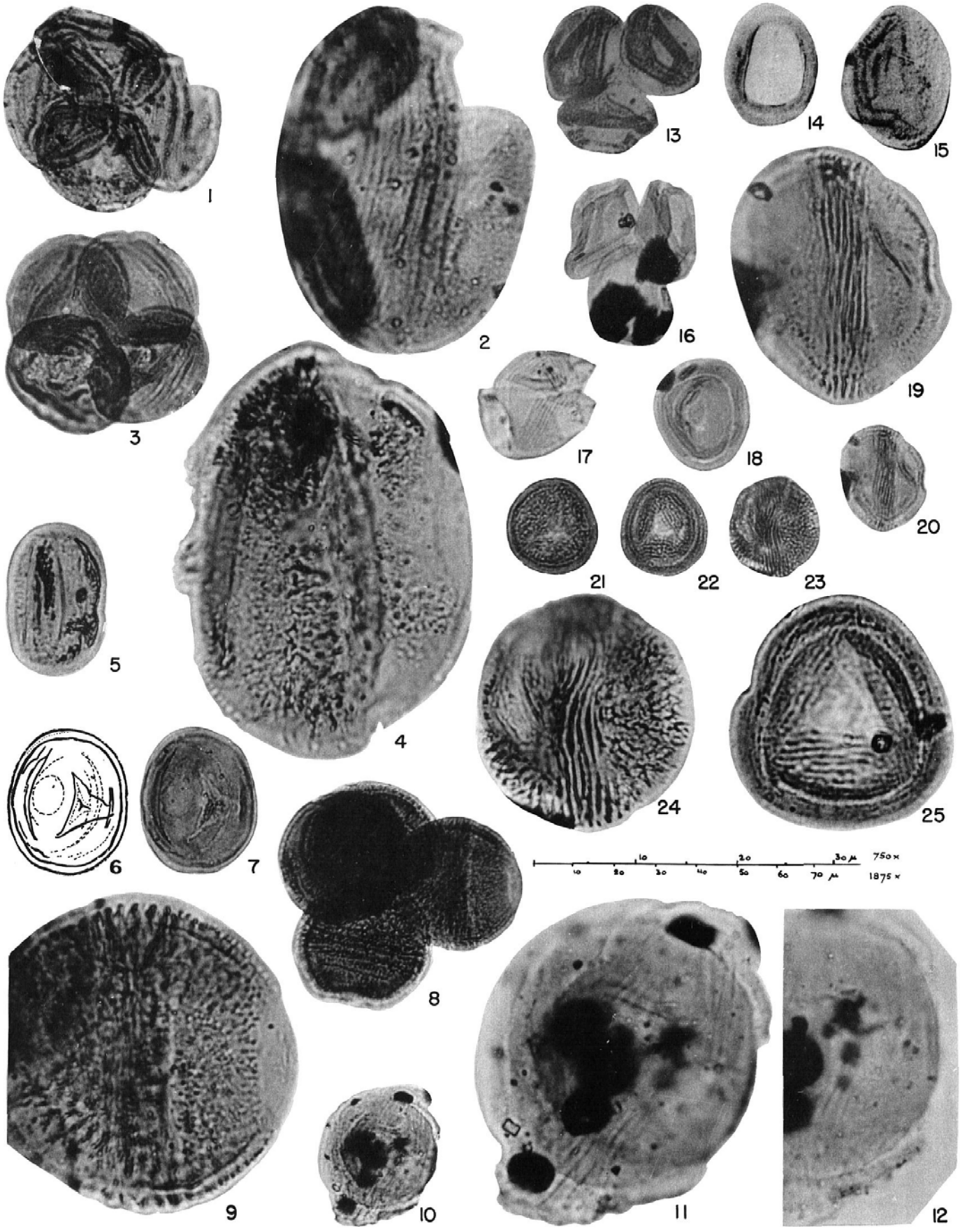
10–12 *Classopollis belloyensis* Pocock and Jansonius, n. sp. 10, equatorial view of holotype; 11–12, enlargements showing structural detail.

13 *Pollenites torosus* Reissinger. Original figure, after Reissinger (1950, pl. 14, fig. 20).

14–15 *Bennettiteae-Pollenites reclusus* Thiergart. Original figures, after Thiergart (1949): 14, Thiergart's pl. 3, fig. 6; 15, Thiergart's pl. 2, fig. 15.

16–20 *Classopollis pflugii* Pocock and Jansonius, n. sp. 16, tetrad of folded grains; 17, loose exoexinal coat (central intexinal body missing); 18, distal polar view of grain; 19–20, holotype: 19, enlarged view; 20, equatorial view.

21–25 *Classopollis minor* Pocock and Jansonius, n. sp. 21, distal polar view; 22, proximal polar view; 23, equatorial view of holotype; 24, enlarged equatorial view of holotype; 25, enlarged proximal view.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60
70 μ
1875×

of fragments belonging to *B. scottii*. Zauer and Mchedlishvili (1954) cited Kendall's evidence in assigning *Classopollis* grains to the genus *Brachyphyllum* but provided no further evidence.

Couper (1955, 1958) re-examined grains from a cone attributed to *Pagiophyllum connivens* Kendall (1952) and expressed the opinion that they are "comparable in all respects" with *Classopollis torosus* (Reissinger), which he regards as synonymous with *C. classoides* Pflug. However, since he admitted that these grains were not clearly displayed, and as he based most of his description on dispersed *Classopollis* grains from the same stratum from which the cone was obtained, his evidence is unconvincing.

Thus, it would appear that:

a) *Classopollis*-type pollen was produced by a plant of gymnospermous affinity which is now extinct.

b) *Classopollis*-type pollen may have been produced by plants belonging to the genera *Cheirolepis*, *Brachyphyllum*, or *Pagiophyllum*, the first-mentioned genus appearing to be the most probable.

c) Since the genera *Cheirolepis* and *Brachyphyllum* are probably related, and some species of *Pagiophyllum* are difficult to distinguish from *Brachyphyllum* (Seward, 1919), it is possible that some species of all three genera produced *Classopollis*-type pollen.

ADDENDA

Since completion of the manuscript the following points have come to the authors' attention:

1) The generic name *Tetradopollenites* Sittler 1954 is a homonym of *Tetradopollenites* Pflug and Thomson 1953; its genotype *T. ericius* (Pot.) Pfl. & Th. is an angiospermous pollen. This invalidates Sittler's use of the name, and makes its use by Klaus (1960, p. 164) as a new infraturma for *Classopollis* type grains inappropriate.

2) The genus *Classopollis* Pflug 1953 is cited by Klaus (1960, p. 167) as a junior synonym of the genus *Corollina* Maljavkina 1949, emend. Klaus 1960. Maljavkina's diagnosis (1949, p. 124), which also stands as the description of the genotype *C. compacta*, describes spherical pollen grains 25–50μ in diameter with a central body and a, presumably, rather loosely fitting thick walled exoexine which may be either "spotted" or "finely veined" and is slightly thickened around the equator. The figures (pl. 46, figs. 10,11, here reproduced) do not clarify or add to the diagnostic description.

Although *Corollina* is published in accordance with the International Code of Botanical Nomenclature, it lacks the detail necessary to allow assignment of further specimens to it with any degree of certainty. In his emendation of the genus Klaus (1960, p. 167) elects Maljavkina's fig. 10 as holotype, but actually bases his

TEXT-FIGURE 6

his precise and very clearly formulated diagnosis on the figured specimens of *Classopollis* cf. *C. torosus* (Reiss.) Balme (1957, pl. 11, figs. 119–121) which are called co-types ("Hilfstypen").

The validity of this emendation is doubtful, because:

a) it is not in accord with article 36 of the International Code, in that the cited figure of the genotype does not show the essential characters of the emended genus;

b) the emended diagnosis is based upon detailed description of co-types which are not admissable for purposes of establishing taxonomic validity;

c) it cannot be demonstrated with reasonable certainty that the genotype cited corresponds with the emended diagnosis; from examination of the original diagnosisand figures there is justification in believing that it does not.

The authors feel that Klaus' emendation of *Corollina* does not invalidate the genus *Classopollis* Pflug 1953. In this connection they want to draw attention to recommendation PB6F in the International Code: "Palaeobotanists should exercise great caution in applying to well preserved specimens names which have been originally attached to poorly preserved specimens or to specimens which have been inadequately described and figured."

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