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Fundamental reassessment of the taxonomy of five Normapolles pollen genera

France Polette[a], David J. Batten[b, c *]

[a]*UMR CNRS 6118 Géosciences Rennes, Université Rennes 1, Campus de Beaulieu, 263 avenue du Général Leclerc, 35042 Rennes, France*

[b]*Department of Geography and Earth Sciences, Aberystwyth University, Penglais, Aberystwyth SY23 3DB, UK*

[c]*School of Earth, Atmospheric and Environmental Sciences, The University of Manchester, Oxford Road, Manchester M13 9PL, UK*

ABSTRACT

Diagnoses of the Normapolles pollen genera *Hungaropollis*, *Krutzschipollis*, *Longanulipollis*, *Oculopollis* and *Trudopollis* and 55 of their species are emended and many specimens illustrated in order to provide a basis for more successful and consistent identification than has been possible hitherto. These taxa were recovered from palynological preparations of selected samples from Upper Cretaceous deposits in Europe and the eastern USA. As indicated on an accompanying range chart the majority are encountered in Santonian and/or Campanian deposits. Eleven of the species described have been transferred from other genera and are therefore in new combinations, namely: *Hungaropollis granulatus* (Kedves et Herngreen), *Longanulipollis coronatiformis* (Góczán et Siegl-Farkas), *L. orbicularis* (Góczán), *L.*

ornatus (Kedves et Diniz), *L. parvoculus* (Góczán), *L. skarbyae* (Kedves et Diniz), *Oculopollis artifex* (Weyland et Krieger), *O. rector* (Pflug), *O. triceps* (Skarby), *Trudopollis cuneolis* (Góczán et Siegl-Farkas), and *T. spinulosus* (Skarby). Six are new: *Hungaropollis pinguis*, *Krutzschipollis cucullus*, *K. immanis*, *Longanulipollis amabilis*, *L. lobus* and *Oculopollis viriosus*. Thirteen genera are regarded as synonyms of *Hungaropollis* (*Aveiropollenites* and *Romeinipollenites*), *Longanulipollis* (*Coronatipollis*, *Intercalaripollis*, *Portaepollenites* and *Verruoculopollis*), *Oculopollis* (*Druggipollenites*, *Pseudoculopollis* and *Semioculopollis*) and *Trudopollis* (*Cuneipollis*, *Felderipollenites*, *Hofkeripollenites* and *Kriegeripollenites*) respectively. As a result of some of these nomenclatural changes 14 other species are in new generic combinations but are not otherwise considered. Seven morphotypes are identified in open nomenclature and two placed in comparison. This taxonomic synthesis, which updates work published since the 1950s, is aimed primarily at rendering biostratigraphic analyses easier, but it is also a necessary first step towards the resolution of Normapolles taxonomy and the relationships between these pollen grains and biological species.

Keywords: Normapolles Province, Late Cretaceous, Paleogene, Europe, USA

*Corresponding author

E-mail addresses: david.batten@manchester.ac.uk; djb23@aber.ac.uk (D.J. Batten); fe.polette@gmail.com (F. Polette)

1. Introduction

More than 160 genera identified as members of the Normapolles group of angiosperm pollen grains have been described. According to Batten and Christopher (1981, p. 359), who referred to the criteria documented by Pflug (1953), Góczán et al. (1967) and Tschudy (1975), the Normapolles are "oblate, mostly triporate or brevitricolp(or)ate pollen having complex, commonly protruding apertures and typically a triangular amb, although some are more or less circular in polar view." Although there is considerable morphological variation within the group, and the apertures are not as complex as originally thought, these characteristics continue to differentiate Normapolles from the majority of other pollen types, at least within the Late Cretaceous to early Paleogene Normapolles Province.

Many Normapolles grains display characters that overlap to varying degrees and to such an extent that it can be difficult to decide which genus, let alone species, is most appropriate to accommodate a particular morphotype. The fact that the number of genera purported to belong to the Normapolles group has almost doubled since Batten and Christopher (1981) published a dichotomous key to their recognition serves to demonstrate that there has been no satisfactory basis for reliable identification of most representatives of the group. Many of the descriptions fail to indicate truly diagnostic characters and, therefore, can equally apply to other genera and species. It follows that the majority of the species that have been erected are not adequately compared with, or distinguished from, other similar forms.

In this paper, we deal with some of the issues that pertain to the identification of five Normapolles genera: *Hungaropollis*, *Krutzschipollis*, *Longanulipollis*, *Oculopollis* and *Trudopollis*. We clarify the basis for differentiation of morphotypes attributable to them in order to make it easier to place specimens in appropriate genera and species with greater confidence than has been possible hitherto. This necessitated a detailed examination of palynological preparations of rocks from different locations within the European and eastern North American parts of the Normapolles Province. Numerous species of Normapolles pollen have been described previously from several of these (e.g., from Scania, southern Sweden, the Aachen Formation in Germany, and boreholes in Hungary: see below). By photographing many hundreds of specimens, we found it easier to determine both the range of variation that might be expected within a species and the characters that seemed most reliable for distinguishing them. We then compared our observations with the original diagnoses and descriptions of almost all of the species that have been described previously, the exceptions being a few that have apparently been diagnosed in literature we have been unable to obtain so far (see Supplementary Files). This enabled us to determine to which previously described species it might be possible to refer our material, in each case once we had emended the original diagnosis in order to accommodate the characters that distinguish it.

In this paper, we briefly comment on the significance of the Normapolles Province with respect to our analysis and supply more background to the problem of identifying taxa and the approaches that have been adopted hitherto before providing revised diagnoses and synonyms of 55 species of the five genera noted above. Six new species are also erected. Numerous illustrations accompany our presentation. We

conclude with a discussion of the significance of our study, which, among other things, we think will render future biostratigraphic analyses using species of the genera described a little easier than has been possible previously. A range chart based on our records and those from the literature is included.

2. The Normapolles Province

During the Late Cretaceous Epoch, the core of the Normapolles Province extended from eastern and southern North America across Europe, including southern Scandinavia, to the West Siberian Plain, the longitudinal boundaries being around 95–100°W in the Western Interior of North America and 80°E in West Siberia. The northern and southern boundaries are less precisely delineated but in current geographical terms, they are approximately 56°N and 36°N respectively in Western Europe. In North America, both are further south, i.e., very approximately around 46°N and 25°N. Taking into account the configuration of the continents during the Late Cretaceous, the northern and southern boundaries were somewhere in the region of 20 and 40°KrN (Batten, 1984).

It is apparent that the boundaries became rather more diffuse during the early Paleogene, with representatives of some of the Normapolles being recorded from much further north (e.g., *Trudopollis* in Spitsbergen: Manum, 1962) and east (e.g., *Trudopollis* and other genera in China: Zhao et al., 1982; Wang et al., 1990; Song, 1996a–c) in particular, but a few papers on Late Cretaceous palynofloras have also

served to suggest that at least some Normapolles grains were dispersed well beyond the floral province as delineated above, in India for example (e.g., Nandi, 1983) and again in China (e.g., Song and Huang, 1997). On the other hand, several taxa in these and other publications (e.g., *Oculopollis tropicus*, recorded from Gabon by Boltenhagen, 1976) are not convincing representatives of the group. A few Normapolles-like pollen have even been reported from Australia (Jarzen and Dettmann, 1992), but these are considered to have been derived from plants having evolutionary origins that differ from those of the northern taxa. This latter observation may also apply to Normapolles-like grains in the Indian Subcontinent and the Far East. Some of the records from these regions are clearly suspect and call into question the basis for recognizing Normapolles pollen as opposed to other, similar grains that are not, or are only doubtful, representatives of the group, despite being identified as, for example, species of *Oculopollis*, *Trudopollis*, *Pseudotrudopollis* and *Subtrudopollis*.

3. Problems with identification

A common problem with much of the taxonomic literature on Normapolles pollen is that many of the species and genera erected are from single localities and are compared only with other morphotypes from the same locality. Even if there are comparisons with taxa described from elsewhere, these seldom refer to more than one or two forms when in fact many others could also have been considered. An equally common problem is that likely morphological variation is not taken into account.

Single specimens have all too often formed the basis for erecting species and even genera. Both practices effectively render the majority of these taxa very difficult to identify subsequently. It is apparent that when faced with identifying Normapolles grains, some palynologists have resorted to erecting many new genera and species for their material because they found it difficult to place specimens in previously described taxa. It is not surprising, therefore, and somewhat ironic that despite the very large number of genera and species available, many Normapolles forms reported in the literature are identified in open nomenclature (e.g., Christopher, 1979; Méon et al., 2004: see also Section 9.2).

Skarby (1968) was highly critical of the taxonomic approach of Pflug (1953), Thomson and Pflug (1953) and Weyland and Krieger (1953). She noted that several of the supposed diagnostic characters are based on misinterpretations or are otherwise insignificant. She also pointed out the tendency of others subsequently (e.g., Góczán, 1964) to erect more genera to accommodate what are commonly only minor differences in basic morphology. She found that with few exceptions, the species referred to *Extratriporopollenites* and other genera of Pflug (1953) and in Thomson and Pflug (1953) could not be satisfactorily identified on the basis of their descriptions. She was also unable to locate on their slides the specimens that they illustrated. Some of those described and figured by Weyland and Krieger (1953) and Weyland and Greifeld (1953) were identifiable, but their slides were generally poorly preserved. As a result, in her study of Normapolles grains from Scania, she referred all of her assemblage to a much more broadly defined *Extratriporopollenite*s. In so doing she erected 14 new species, transferred to this genus several other previously described

forms that had been referred to different genera, and placed others in synonymy with her new combinations.

Although use of more broadly defined genera would have alleviated the problem of identifying Normapolles at generic level, referring all of them to *Extratriporopollenites* was not the answer. Tschudy (1975) maintained that the paper by Góczán et al. (1967), in which 56 Normapolles genera were described and differentiated, removed most of her objections. He noted that he had little difficulty in distinguishing genera on the basis of their observations and did not believe that Skarby's decision to refer a large range of morphotypes to species of *Extratriporopollenites* served any useful purpose. Skarby did not mention the work of Góczán et al., perhaps because she was unaware of it or it was published while her own paper was in press. Regardless of the reason, the fact that she did not modify her taxonomy subsequently indicates that, unlike Tschudy, she did not agree that their synthesis was especially helpful. Neverthless, as she noted later (Skarby et al., 1990, p. 146), her attempt at evaluating the morphological characters that she regarded as diagnostic and reducing the number of taxa had "met with little positive response." We think that the solution to the genus and species identification problem lies somewhere in between her approach and that of Góczán et al., otherwise there would not have been the perceived need to erect so many more genera after 1967.

This problem was well demonstrated by Hultberg et al. (1984). These authors applied Fourier analysis to three species of dispersed Normapolles grains from southern Sweden, identified as *Extratriporopollenites triceps* Skarby, *E. artifex* (Weyland et Krieger) Skarby and *E. firmus* Skarby, and of pollen extracted from a

single anther identified as *E. artifex*. They found that some specimens initially identified as *E. triceps* are indistinguishable from *E. artifex* on the basis of their analysis, the overlap being a result of the fact that the apertures of the former are less pronounced than usual so that they are more similar to those of *E. artifex*. According to Pflug's (1953) classification, *E. artifex* and *E. triceps* would be referred to *Trudopolli*s and *Oculopollis* respectively. Both are placed in *Oculopollis* herein.

4. Material

The samples upon which our analysis is based range in age from Turonian to Campanian–Maastrichtian and are from the following locations (Fig. 1):

Sweden, Åsen, Scania, Iföverken clay pit: according to Skarby (1968, p. 5), collected in 1930, probably by Lundegren, and labelled "Prov III A vid 12,59 m"; sample courtesy of A. Skarby in 1980, earliest Campanian. Slide preparation MCP805-2, National Museum Wales catalogue number NMW 2017.1G1.

Germany, Aachen Formation, collected by DJB in 1980, sample DJB80/AA.7, mid–late Santonian. MCP1610-2, NMW 2017.1G2.

Portugal, Chousa do Fidalgo (Arada) Formation: collected by DJB in 1982, sample DJB82/54, Campanian–Maastrichtian. MCP2573-3, NMW 2017.1G3.

Netherlands, Maastricht, Borehole GB7348, 200.2–201.2 m, "Aachen Sandstone Formation", provided by H. van der Laar in 1984, mid–late Santonian. MCP3193-3, NMW 2017.1G4.

Belgium, Gulpen, Borehole sample 33, Hergenrath Clay, Aachen Formation, made available by M. Streel in 1984, mid–late Santonian. MCP3283-3, NMW 2017.1G5.

Hungary, Sümeg, Borehole Süt-16, Jákó Marl, courtesy of G. Lelkes in 1985, late early Campanian. MCP3482-3, NMW 2017.1G6.

Hungary, Gyepükaján Gy-9 borehole, Zone A, sample courtesy of A. Siegl-Farkas and F. Góczán in 1986, late Santonian. MCP3853-1, NMW 2017.1G7.

Hungary, near Zalagyömörő, Cr-1 borehole, Zone C, sample courtesy of A. Siegl-Farkas and F. Góczán in 1986, originally regarded as early Campanian, now considered to be late Santonian (Bodor and Baranyi, 2012), but because there is some doubt regarding correlation with other sections, we record it as late Santonian–early Campanian. MCP3856-1, NMW 2017.1G8.

Hungary, Zalaszentlászló Z1-3 borehole, Zone F (see Siegl-Farkas, 1987), sample courtesy of A. Siegl-Farkas and F. Góczán in 1986, late Campanian. MCP3860-1, NMW 2017.1G9.

Hungary, Zalagyömörő Zgy-1 borehole, Zone G, sample courtesy of A. Siegl-Farkas and F. Góczán in 1986, originally regarded as early Maastrichtian, now considered to be late Campanian (Siegl-Farkas and Wagreich, 1996). MCP3862-1, NMW 2017.1G10.

France, Aquitaine Basin, Dordogne, Sainte-Mondane Formation, sample provided by D. Néraudeau in 2014, late Turonian. QPR3675-2, 3, NMW 2017.1G11, 1G12.

USA, Monmouth County, New Jersey, Magothy Formation, miscellaneous sample in DJB's collection, early–mid Santonian. Misc-R-18, NMW 2017.1G13.

5. Methods

The terminology used in many published diagnoses and descriptions of Normapolles pollen grains is often unnecessarily complex. Commonly included are characters that are not diagnostic. A great many are poorly described and illustrated. As a result, it is difficult to determine their distinguishing features. In order to overcome these problems, we considered it necessary to emend the diagnoses of all of the taxa we consider in this paper, preparing them in a standard way using fewer terms (see below) and omitting undiagnostic characters. The diagnoses of some of these have been emended previously but the criteria for doing so have seldom made identification easier. Our approach to the characters that may be used to differentiate between the taxa we consider has effectively rendered these emendations redundant so we do not discuss them. It has also meant that owing to their similar characters, we have been able to reduce the number of both genera and species by placing many in synonymy. We discuss only a few of these where we think additional comments are helpful. The synonymies also include records from the literature that seem to fit well with our identifications. The occurrences of these forms are taken into account in our plot of stratigraphic ranges (see Section 9). For this part of our analysis we checked only a selection of papers from each of the geographic regions represented by the samples examined, and if we had any doubts about the identifications they were not included. We also omitted papers for which age determinations lack precision or do not contain

photographs that provide evidence of correct identification. Hence our synonymies are by no means complete.

We did not consider it necessary to take into account characters of some of the taxa that have been observed under scanning and transmission electron microscopes (SEM and TEM: see e.g., Batten, 1986, 1989; Skarby et al., 1990), the primary purpose of our work being to identify and categorise them under the light microscope. Both SEM and TEM studies have revealed that most have, to a greater or lesser extent, perforated walls, and that below the surface of their ekannuli the sexine commonly has a less homogeneous, more granular or intrabaculate structure (for explanations of terms, see below: Section 6). The fact that these features are not always clearly visible under the light microscope can be significant in distinguishing between some morphotypes.

Size ranges are provided for most of the species described. These are commonly lacking in the published literature. As a result, the previous records that we have noted often consist only of a single measurement, typically of the holotype. In the absence of evidence to the contrary, we have assumed that all of these measurements record the maximum diameter of the pollen grains concerned.

We compare all of the species we describe with the others that are discussed. Differences from some other members of the genus that we have not examined under the microscope may also be noted. Supplementary File, Table 1, lists all of the species previously described as belonging to the five genera considered and the 13 we have placed in synonymy along with their authors, year of publication, page references, and brief notes on each of them.

All slides containing figured specimens have been deposited in the collections of the National Museum Wales, Cardiff: catalogue numbers NMW 2017.1G1–1G13, as noted under Material (Section 4) above .

6. Terminology

Here we list, illustrate (Fig. 2), and provide definitions of the terms we have used in our diagnoses of the taxa considered. These are mainly selected and abbreviated or otherwise modified from the work of Batten and Christopher (1981), who documented most of the terms that have been applied to representatives of the Normapolles group. We do not make use of quite a few of these, including area of solution (or solution area), incidence, mesogerminal, and tumescence, because we regard them as unnecessary.

Annulus (-li): a thickening of the **outer wall/sexine** [Fig. 2f] (hence **ektannulus** [Fig. 2j, n]) or **inner wall/nexine** [Fig. 2e, o] (hence **endannulus** [Fig. 2g]) surrounding the **exogerminal/exoaperture** [Fig. 2a] or **endogerminal/endoaperture** [Fig. 2p, q] respectively.

Atrium (-ia): an area of the wall within the germinal that is delineated by the termination of the nexine [Fig. 2k, q].

Cuneus (-ei): a structure formed by the termination of the nexine at the endogerminal that gives rise to a V-shaped atrium which points towards the centre of the grain [Fig. 2h].

Germinal: includes both sexine and nexine components of the aperture that served as a potential point of emergence of the pollen tube, hence a **porate** [Fig. 2p] or **brevicolpate** aperture.

Inner contour: outline of the inner surface of the nexine.

Intrabaculate structure: applies to rod-like elements that may comprise the inner part of the sexine in the exogerminal [Fig. 2b].

Interloculum (-la): separation of the sexine and nexine around most or all of the pollen grain [Fig. 2c]. When separation is only partial then effectively it is a wide **vestibulum** [Fig. 2i].

Oculus (-li): a swelling or thickening of the sexine on one or both ("upper" or "lower") surfaces of the exogerminal of a grain [Fig. 2d].

Platea (-eae): lack of a nexine extending from each endogerminal to, or nearly to, the poles creating a triradiate feature [Fig. 2m].

Vestibulum (-la): a chamber formed by the separation of the sexine and nexine in the germinal region [Fig. 2i, l].

7. Systematic palaeontology: analysis

Hungaropollis Góczán, 1964 emend.

1981 *Romeinipollenites* Kedves et Herngreen, pp. 516, 517.

1983b *Aveiropollenites* Kedves et Diniz, p. 21.

Type species: *Hungaropollis krutzschii* Góczán, 1964, p. 264, pl. 8, fig. 5.

Emended diagnosis. Breviaxal pollen grain, triangular with straight, slightly concave or convex sides in polar view. Exine (sexine and nexine) very thick, surrounding a comparatively small circular, subcircular to rounded-triangular central cavity: nexine very thick, may be thicker than sexine in interradial regions. Exogerminals comprise mostly structureless ektannuli with rounded outlines. Exoapertures are vertical slits: endoapertures are of similar form but may widen slightly towards interior. Very shallow or no atria. No vestibula. Interloculum commonly present but very narrow. Oculi may be present. Surface usually smooth to maculate on one side and ornamented on the other, commonly with verrucae, sometimes forming a negative reticulum.

Size range. 31 (41.9) 53 µm (based on our material); no size range given by Góczán (1964).

Remarks. *Hungaropollis* is distinguished from all other Normapolles genera in having a very thick nexine that surrounds a circular to rounded-triangular central cavity and very shallow or no atria in the endogerminals.

Hungaropollis granulatus (Kedves et Herngreen, 1981) comb. nov. emend. (Plate II, 1, 4)

1981 *Romeinipollenites granulatus* Kedves et Herngreen, p. 517, pl. 8, figs. 18–20.

Emended diagnosis. A *Hungaropollis* with a subcircular outline. Inner contour triangular. Nexine thicker than sexine in interradial regions. Ektannuli fairly small and squat, beak-like, mostly unstructured but become less homogeneous near base. Surface smooth to scabrate on one side, maculate to granulate on the other, with flat-topped verrucae around and over pole.

Size. 37 µm (one specimen), 30–38 µm for *R. granulatus* (Kedves and Herngreen, 1981).

Remarks. We place this species within the genus *Hungaropollis* because of its very thick nexine and the very shallow, or lack of, atria and the absence of vestibula in the endogerminals. It differs from the other species of the genus in having a very rounded-triangular equatorial outline and relatively small ektannuli.

Occurrence. Belgium (our material), Netherlands (Kedves and Herngreen, 1981).

Stratigraphic range. Middle–upper Santonian (our material), Maastrichtian (Kedves and Herngreen, 1981).

Hungaropollis hollossyi Góczán et Siegl-Farkas, 1989 emend. (Plate I, 3–7)

1989 *Hungaropollis hollossyi* Góczán et Siegl-Farkas, p. 63, pl. 6, figs. 10–12.

Emended diagnosis. A *Hungaropollis* with straight to slightly convex sides interradially giving way to pronounced elongated, rounded, commonly slightly swollen germinals resulting from a considerable increase in thickness of sexine to form ektannuli around brevicolpate exoapertures. Inner contour subtriangular. Nexine in interradial regions as thick as, or considerably thicker than, sexine, surrounds pores that widen inwards. Surface smooth to maculate, but commonly also with grana and irregularly shaped verrucae on one side.

Size range. 42 (45.7) 49 µm (11 specimens); holotype 46 µm (Góczán and Siegl-Farkas, 1989).

Remarks. The morphology of this species is close to that of the genus *Krutzschipollis*: indeed, *K. elegans* Góczán et Siegl-Farkas, 1989 is very similar, but it is somewhat less robust and, in particular, its nexine becomes significantly thinner adjacent to the endoapertures. *Hungaropollis hollossyi* differs from *H.* sp. A in having a more convex

equatorial outline, and from the other species of *Hungaropollis* as emended herein by its protruding ektannuli, which affect the overall shape of the grain, and its proportionally thinner sexine.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Upper Santonian–lower Campanian (our material), upper Campanian (Góczán and Siegl-Farkas, 1989).

Hungaropollis krutzschii Góczán, 1964 emend. (Plate I, 8–17; cf. Plate I, 1, 2)

1964 *Hungaropollis krutzschi* Góczán, p. 254, pl. 8, figs. 4, 5.

1964 *Hungaropollis ajkanus* Góczán, pp. 254, 255, pl. 8, fig. 6a–c.

1983a *Hungaropollis medusi* Kedves et Diniz, pp. 333, 334, pl. 2, figs. 4–6.

2012 *Hungaropollis krutzschi* Góczán, 1964; Bodor and Baranyi, pl. 1, fig. e.

Emended diagnosis. A *Hungaropollis* with straight, slightly convex or slightly concave sides. Inner contour subtriangular to circular. Nexine thick, but not usually as thick as sexine in interradial regions. Ektannuli result from an increase in thickness of sexine from equatorial interradial to radial regions. Oculi absent. Surface varies from being essentially smooth but somewhat uneven to being covered by irregularly shaped verrucae on one or both sides of the grain, especially around the poles.

Size range. 31 (40.4) 46 µm (15 specimens); holotype 53 µm (Góczán, 1964); holotype 50 µm for *H. ajkanus* (Góczán, 1964), 38–52 µm for *H. medusii* (Kedves and Diniz, 1983a).

Remarks. *Hungaropollis krutzschii* differs from both *H. rectilineus* and *H. pinguis* by its more rounded equatorial outline and lack of oculi. The specimens referred to as *Hungaropollis* sp. cf. *H. krutzschii* (Plate I, 1, 2) have been separated from *H. krutzschii* on the basis of their thinner interradial sexine.

Occurrence. Hungary (our material; Góczán, 1964; Kedves and Diniz, 1983a; Bodor and Baranyi, 2012)

Stratigraphic range. Upper Santonian (our material; Bodor and Baranyi, 2012), lower Campanian (our material; Góczán, 1964), upper Campanian (our material); no range given by Kedves and Diniz (1983a).

Hungaropollis pinguis sp. nov. (Plate II, 7–14)

1988 *Hungaropollis oculus* Góczán; Siegl-Farkas, pl. 9, figs. 1, 2. [nomen nudum].

Derivation of name. L., *pinguis*, fat, with reference to the bulky aspect of specimens of this species.

Holotype. Specimen in palynological preparation/slide MCP3856-1, NMW 2017.1G8, Plate II, 11, 14.

Type locality. Hungary, near Zalagyömörő, Cr-1 borehole, Zone C.

Diagnosis. A *Hungaropollis* with straight to slightly concave sides. Inner contour subtriangular. Nexine interradially as thick as, or a little thicker than, sexine. Ektannuli wide and very robust. Germinals overall form oculi with uneven "wavy" surfaces developed on both sides of grain. Surface smooth.

Size range. 35 (40.2) 42 µm (12 specimens).

Remarks. *Hungaropollis pinguis* differs from *H. rectilineus* in being smaller and in having a smooth surface and more pronounced oculi. For differentiation from *H. krutzschii*, see remarks under this species.

Occurrence. Hungary (our material).

Stratigraphic range. Upper Santonian–lower Campanian and upper Campanian (our material).

Hungaropollis rectilineus Góczán et Siegl-Farkas, 1989 emend. (Plate II, 2, 3, 5, 6)

1989 *Hungaropollis rectilineus* Góczán et Siegl-Farkas, pp. 61, 62, pl. 6, figs. 1–5.

Emended diagnosis. A *Hungaropollis* with straight to concave sides. Inner contour subtriangular. Nexine generally thinner than sexine. Ektannuli robust, slightly protruding. Germinals overall form variably developed oculi. One of the surfaces bears a few large flat-topped verrucae, mainly in vicinity of, and over, pole.

Size range. 49 (51) 53 μm (three specimens); 40–45 μm (Góczán and Siegl-Farkas (1989).

Remarks. For differentiation of *H. rectilineus* from *H. krutzschii* and *H. pinguis*, see remarks under these species.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Lower Campanian (our material), upper Campanian (Góczán and Siegl-Farkas, 1989).

Hungaropollis sp. A (Plate II, 15, 16)

Description. A *Hungaropollis* with markedly concave sides. Inner contour triangular with truncated apices. Nexine interradially thicker than sexine, becomes thicker still adjacent to endoapertures. Ektannuli robust and elongate; no oculi. Surface essentially smooth, but uneven on one side and sculptured by a negative reticulum on the other in vicinity of, and over, pole.

Size. 39 µm (one specimen).

Remarks. For differentiation of *H*. sp. A from *H. hollossyi*, see remarks under this species. Its concave sides combined with its proportionally much thicker nexine in interradial regions distinguish it from the other species of the genus considered herein.

Occurrence. Hungary (our material).

Stratigraphic range. Upper Campanian (our material).

Krutzschipollis Góczán in Góczán et al., 1967 emend.

Type species. *Krutzschipollis spatiosus* Góczán in Góczán et al., 1967, pp. 470, 471, pl. 8, figs. 16–19.

Emended diagnosis. Breviaxal pollen grain, triangular with straight to convex sides in polar view. Exine (sexine and nexine) thick, surrounding a subcircular to rounded-triangular or trilobate central cavity. Nexine may be thinner than, as thick as, or thicker than sexine in interradial regions. Exogerminals comprise structureless ektannuli that have a beak-like shape in polar view. Exoapertures are vertical slits. No interloculum. Endogerminals are wide pores usually associated with wide atria of variable depth. Vestibula sometimes present. No oculi. Surface sculpture varies from a fine negative reticulum to coarsely verrucate.

Size range. 32 (44) 58 µm (based on our material); no size range given by Góczán et al. (1967).

Remarks. *Krutzschipollis* is distinguished from all other Normapolles genera in being a robust, thick-walled, commonly strongly sculptured pollen grain with a thick nexine that thins rapidly adjacent to a wide pore within each endogerminal.

Krutzschipollis crassis (Góczán, 1964) Góczán in Góczán et al., 1967 emend. (Plate III, 1–9)

1964 *Extratriporopollenites crassus* Góczán, pp. 252, 253, pl. 8, figs. 1, 2.

1967 *Krutzschipollis crassis* (Góczán, 1964) Góczán in Góczán et al., p. 471.

1986 *Krutzschipollis crassus* (Góczán, 1964) Góczán in Góczán et al., 1967 [sic]; Siegl-Farkas, pl. 6, figs. 7, 8.

1989 *Krutzschipollis rotundus* Góczán et Siegl-Farkas, p. 64, pl. 7, figs. 4–6.

Emended diagnosis. A *Krutzschipollis* with convex sides. Inner contour subcircular to trilobate. Nexine ranges from being thinner to thicker than sexine in interradial regions, but becomes abruptly thinner adjacent to endogerminals, which are wide pores associated with shallow to moderately deep atria. Ektannuli robust. Surface negatively reticulate to verrucate.

Size range. 40 (41.8) 46 µm (13 specimens); 30–50 µm for *E. crassus* (Góczán, 1964); diameter of figured specimen of *K. rotundus* 32 µm (Góczán and Siegl-Farkas, 1989).

Remarks. *Krutzschipollis crassis* differs from *K. elegans* by its coarser sculpture and its wider and deeper atria; *K. immanis* in being much smaller and in having less elongated ektannuli; *K. spatiosus* in its somewhat more rounded outline, finer sculpture and less protruding ektannuli, and in having shallower vestibula; and *K.* sp. A by its more rounded outline and again less elongated ektannuli.

Occurrence. Hungary (our material; Góczán, 1964; Góczán et al., 1967; Siegl-Farkas, 1986; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Upper Campanian (our material; Góczán, 1964; Góczán et al., 1967; Siegl-Farkas, 1986; Góczán and Siegl-Farkas, 1989).

Krutzschipollis cucullus sp. nov. (Plate III, 10–17)

Derivation of name. L., *cucullus*, cap, with reference to the presence of a polar thickening on many specimens of this species.

Holotype. Specimen in palynological preparation/slide MCP3482-3, NMW 2017.1G6, Plate III, 13.

Type locality. Hungary, Sümeg, Borehole Süt-16, Jákó Marl.

Diagnosis. A *Krutzschipollis* with slightly to strongly convex sides. Inner contour rounded-triangular to trilobate. Nexine usually thicker but may be of similar thickness or somewhat thinner than sexine in interradial regions, becomes rapidly thinner adjacent to endogerminals where it borders wide endopores associated with shallow atria. Vestibula narrow. Ektannuli robust, elongate, influencing overall shape of grain of some specimens. Surface verrucate. Commonly a large swelling is present on one face, usually over the pole but sometimes off-centre.

Size range. 40 (46.5) 52 µm (12 specimens).

Remarks. *Krutzschipollis cucullus* is similar to *K. immanis* but somewhat smaller, more unevenly verrucate and more often than not has a polar thickening, the last of these characters also distinguishing it from most other species of the genus. *Capipollis oculis* Góczán in Góczán et al., 1967 is similar but has a thinner wall, the inner contour is subcircular rather than trilobate, and the occuli are more pronounced.

Occurrence. Hungary (our material)

Stratigraphic range. Upper Santonian–lower Campanian (our material).

Krutzschipollis elegans Góczán et Siegl-Farkas, 1989 emend. (Plate IV, 1–4)

1989 *Krutzschipollis elegans* Góczán et Siegl-Farkas, pp 64, 65, pl. 7, figs. 7–9.

Emended diagnosis. A *Krutzschipollis* with convex sides. Inner contour rounded-triangular to weakly trilobate. Nexine thicker than sexine in interradial regions, borders pores associated with shallow atria. Ektannuli fairly robust. Surface sculptured with closely spaced grana and low verrucae, the latter commonly forming a negative reticulum.

Size range. 32 (35.3) 40 µm (five specimens); holotype 45 µm (Góczán and Siegl-Farkas, 1989).

Remarks. The morphology of *Krutzschipollis elegans* is similar to that of species of *Longanulipollis*, the main difference being that it is more robust, owing to its thick exine. For differentiation from *K. crassis*, see remarks under this species.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Upper Campanian (our material; Góczán and Siegl-Farkas, 1989).

Krutzschipollis immanis sp. nov. (Plate IV, 5–9; cf. Plate IV, 11)

Derivation of name. L., *immanis*, huge, with reference to the size of specimens of this species.

Holotype. Specimen in palynological preparation/slide MCP3482-3, NMW 2017.1G6, Plate IV, 8, 9.

Type locality. Hungary, Sümeg, Borehole Süt-16, Jákó Marl.

Diagnosis. A very large *Krutzschipollis* with straight to convex sides. Inner contour subcircular to weakly trilobate. Nexine thicker than, or about same thickness as, sexine in interradial regions. Endogerminals are pores, sometimes quite wide, associated with shallow atria. Vestibula very narrow. Ektannuli robust, elongate, influencing overall shape of grain of some specimens. Surface undulose to verrucate, the verrucae when flat-topped forming a negative reticulum on one side of grain.

Size range. 51 (54.8) 58 µm (10 specimens).

Remarks. For differentiation of *Krutzschipollis immanis* from *K. crassis* and *K. cucullus*, see remarks under these species. The specimen referred to *Krutzschipollis* sp. cf. *K. immanis* (Plate IV, 11) has been separated from *K. immanis* because it lacks vestibula and has a smooth surface.

Occurrence. Hungary (our material).

Stratigraphic range. Lower Campanian (our material).

Krutzschipollis magnoporus Góczán in Góczán et al., 1967 emend. (Plate V, 8–11)

1967 *Krutzschipollis magnoporus* Góczán in Góczán et al., p. 471, pl. 8, figs. 20–23.

Emended diagnosis. A *Krutzschipollis* with convex sides. Inner contour strongly trilobate. Nexine thinner than, or approximately as thick as, sexine in interradial regions but becomes abruptly thinner adjacent to endogerminals, which are wide endopores associated with very wide and deep atria. Vestibula absent or very narrow. Ektannuli elongate, influencing overall shape of grain. Sculpture consists of closely spaced, commonly flat-topped verrucae that may form a negative reticulum.

Size range. 32 (34.3) 37 μm (six specimens); holotype 47 μm (Góczán in Góczán et al., 1967).

Remarks. Góczán et al. (1967) placed *Extratriporopollenites crassus* Góczán, 1964 pro parte (pp. 252, 253, pl. 7, fig. 10a–c) in synonymy with *K. magnoporus*, a transfer that we do not think is wholly convincing. The atria of our specimens are more rounded than in those figured by Góczán et al., which are somewhat V-shaped. *Krutzschipollis magnoporus* can be distinguished from other species of the genus by the shape of its endogerminals. We think that the discrepency between the size of the holotype provided by Góczán (in Góczán et al., 1967) and our size range is of no consequence. This is because (1) the characters used to differentiate this species from others of the genus do not include size, and (2) Góczán illustrated only the holotype, which means that morphological variations within the species are not documented.

Occurrence. Hungary (our material; Góczán in Góczán et al., 1967).

Stratigraphic range. Upper Santonian–lower Campanian (our material), lower Maastrichtian (Góczán in Góczán et al., 1967).

Krutzschipollis spatiosus Góczán in Góczán et al., 1967 emend. (Plate V, 1–7)

1967 *Krutzschipollis spatiosus* Góczán in Góczán et al., pp. 470, 471, pl. 8, figs. 16–19.

1989 *Krutzschipollis* sp.; Médus and Alvarez Ramis, pl. 1, figs. 18, 19.

Emended diagnosis. A *Krutzschipollis* with convex sides. Inner contour rounded-triangular to trilobate. Nexine usually thinner, but sometimes as thick as, or slightly thicker than, sexine in interradial regions, becomes rapidly thinner adjacent to endogerminals where it borders wide endopores associated with relatively deep atria and vestibula that are wider and deeper than in other species of genus. Ektannuli robust, elongate, influencing overall shape of grain of some specimens. Surface coarsely verrucate.

Size range. 39 (41.5) 47 μm (11 specimens); holotype 49 μm (Góczán in Góczán et al., 1967).

Remarks. Góczán et al. (1967) transferred *Extratriporopollenites crassus* Góczán, 1964, pro parte (pp. 252, 253, pl. 7, fig. 11) to *K. spatiosus*, but we do not accept this transfer. For differentiation from *K. crassis*, see remarks under this species.

Occurrence. Hungary (our material; Góczán, 1964; Góczán et al., 1967), Spain (Médus and Alvarez Ramis, 1989).

Stratigraphic range. Lower Campanian (Góczán et al., 1967), upper Campanian (our material; Góczán, 1964), Campanian (Médus and Alvarez Ramis, 1989).

Krutzschipollis sp. A. (Plate IV, 10, 13)

Description. A *Krutzschipollis* with straight to slightly convex or concave sides. Inner contour subcircular. Nexine thinner than, or approximately same thickness as, sexine in interradial regions. No vestibula. Endogerminals are wide endopores associated with relatively deep atria. Ektannuli very elongate. Surface granulate.

Size. 45 µm (one specimen).

Remarks. For differentiation of *K.* sp. A from *K. crassis*, see remarks under this species.

Occurrence. Hungary (our material).

Stratigraphic range. Upper Campanian (our material).

aff. *Krutzschipollis* sp. A (Plate IV, 12, 14)

Description. A *Krutzschipollis*-like pollen grain with convex sides. Inner contour subcircular. Nexine thinner than sexine in interradial regions, separated by a thin interloculum, which is not typical of the genus. No vestibula. Endogerminals are wide pores associated with shallow atria. Ektannuli elongate, protruding. Surface uneven to weakly verrucate on one surface to more strongly verrucate on the other, especially towards and over the pole.

Size. 45 µm (one specimen).

Remarks. This morphotype differs from species of *Krutzschipollis* in the form of the nexine and the presence of an interloculum. There is a superficial resemblance to *Endopollis* Góczán et al., 1967, but its characters do not match the only species of this genus, *Endopollis latiporis* Góczán in Góczán et al., 1967 (p. 459, pl. 5, figs. 1–6).

Occurrence. Hungary (our material).

Stratigraphic range. Lower Campanian (our material).

Longanulipollis Góczán in Góczán et al., 1967 emend.

1989 *Coronatipollis* Góczán et Siegl-Farkas, p. 53.

1989 *Intercalaripollis* Góczán et Siegl-Farkas, pp. 57, 58.

1983a *Portaepollenites* Kedves et Diniz, p. 336.

1983a *Verruoculopollis* Kedves et Diniz, p. 334.

Type species. *Longanulipollis longianulus* Góczán in Góczán et al., 1967, p. 473, pl. 9, figs. 6–8.

Emended diagnosis. Breviaxal pollen grain, triangular with straight to convex or slightly concave sides in polar view. Inner contour varies from subcircular to strongly trilobate. Nexine usually as thick as, or thicker than, sexine in interradial regions. Exogerminals comprise structureless ektannuli that have a beak-like shape in polar view, the length of which is usually at least one-third of diameter of central cavity. Exoapertures are vertical slits. Usually no interloculum. Endogerminals are pores, commonly associated with small, shallow U-shaped atria. Vestibula when present, normally shallow. Surface varies from smooth to verrucate, but usually granulate. Oculi may be present.

Size range. 19 (30.8) 61 µm (based on our material); no size range given by Góczán et al. (1967).

Remarks. *Longanulipollis* is distinguished from *Hungaropollis* and *Krutzschipollis* in having a thinner exine and a nexine of different morphology adjacent to the endoapertures. It differs from *Oculopollis* and *Trudopollis* in possessing beak-like ektannuli.

Longanulipollis amabilis sp. nov. (Plate V, 12–22, 25, 26)

Derivation of name. L., *amabilis*, lovely, with reference to the attractive appearance of many specimens of this species.

Holotype. Specimen in palynological preparation/slide MCP3853-1, NMW 2017.1G7, Plate V, 13.

Type locality. Hungary, Gyepükaján Gy-9 borehole, Zone A.

Diagnosis. A *Longanulipollis* with straight to convex sides. Inner contour subcircular to rounded-triangular. Nexine usually as thick as, or thicker than, sexine in interradial regions, borders narrow endopores, which are sometimes associated with shallow atria in the endogerminals. Vestibula when present, shallow. Ektannuli elongate, their

length being approximately one-third to half of diameter of central cavity. Germinals overall commonly slightly modify the essentially triangular shape of the grains and are swollen forming oculi on one side. Surface granulate to verrucate: verrucae commonly largest close to, and around bases of, oculi giving them an irregular appearance.

Size range. 24 (28.6) 40 µm (22 specimens).

Remarks. *Longanulipollis amabilis* differs from *L. lobus* in having less protruding ektannuli and more strongly developed, commonly verrucate sculpture; *L. monstruosis* by its usually smaller size, more visible oculi, and thinner nexine; *L. ornatus* by its less protruding ektannuli and non-merging oculi (intermediate forms between *L. amabilis* and *L. ornatus* are illustrated on Plate V, 23, 27); *L. skarbyae* by its more triangular shape overall, shallower atria, and more pronounced oculi; and *L.* sp. B in being more triangular in shape and having shallower atria. It can be distinguished from all the other species of *Longanulipollis* described and emended herein on account of its verrucate sculpture coupled with clearly defined oculi.

Occurrence. Hungary (our material).

Stratigraphic range. Upper Santonian–lower Campanian (our material).

Longanulipollis bajtayi (Góczán, 1964) Góczán in Góczán et al., 1967 emend. (Plate VI, 1–5)

1964 *Extratriporopollenites bajtayi* Góczán, p. 252, pl. 7, figs. 8, 9.

1967 *Longanulipollis bajtayi* (Góczán, 1964) Góczán in Góczán et al., p. 473, pl. 9, fig. 11.

1983a *Semioculopollis medius* Kedves et Diniz, pp. 337, 338, pl. 2, figs. 16, 17, text-fig. 7.

1989 *Longanulipollis polanyensis* Góczán et Siegl-Farkas (pro parte), pp. 55, 56, pl. 2, figs. 4–6 only (holotype).

Emended diagnosis. A *Longanulipollis* with straight to slightly convex sides. Inner contour rounded-triangular to trilobate. Nexine thicker than sexine in interradial regions, may be slightly thicker forming weak endannuli adjacent to endopores, which are associated with shallow atria. Shallow vestibula usually present. Ektannuli large, elongate, their length commonly nearly half that of diameter of central cavity. Germinals overall may be slightly swollen on one side to form weak oculi. Surface smooth to granulate.

Size range. 31 (37.5) 42 µm (seven specimens); holotype of *E. bajtayi* 30 µm (Góczán, 1964); 28–35 µm for *S. medius* (Kedves and Diniz, 1983a); holotype of *L. polanyensis* 38 µm (Góczán and Siegl-Farkas, 1989).

Remarks. *Longanulipollis bajtayi* differs from *L. parvoculus* by its proportionally larger ektannuli and in having straight or less convex sides in interradial regions. It differs from *L. coronatiformis* by its more elongated ektannuli and its straighter sides, but these differences are minor: it is possible that *L. coronatiformis* is merely a morphological variant of this species. *Longanulipollis bajtayi* differs from *L. fornicatus* in being larger and in having more elongated ektannuli; *L. monstruosis* by its finer sculpture and its usually thinner nexine; and *L. polanyensis* by its less elongated ektannuli, its thinner nexine, and its "bulkier" aspect overall.

Occurrence. Hungary (our material; Góczán, 1964; Góczán et al., 1967; Kedves and Diniz, 1983a; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Lower Campanian (our material; Kedves and Diniz, 1983a), upper Campanian (our material; Góczán, 1964; Góczán et al., 1967; Góczán and Siegl-Farkas, 1989).

Longanulipollis coronatiformis (Góczán et Siegl-Farkas, 1989) comb. nov. emend. (Plate VI, 6)

1989 *Semioculopollis coronatiformis* Góczán et Siegl-Farkas, pp. 60, 61, pl. 5, figs. 1–6.

1989 *Coronatipollis* cf. *coronatus* Góczán et Siegl-Farkas, pl. 4, figs. 16–18.

Emended diagnosis. A *Longanulipollis* with slightly convex sides. Inner contour rounded-triangular to trilobate. Nexine usually thicker than sexine in interradial regions, surrounds endopores that are associated with small, shallow atria. Shallow vestibula usually present. Ektannuli large, their length commonly nearly half that of diameter of central cavity. Germinals overall may be slightly swollen on one side to form weak oculi. Surface smooth to maculate.

Size. 35 μm (one specimen); both holotype and paratype of *S. coronatiformis*, 31 μm; *C.* cf. *coronatus* 29 μm (Góczán and Siegl-Farkas, 1989).

Remarks. As noted above, it is possible that *L. coronatiformis* is a morphological variant of *L. bajtayi*.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Upper Campanian (our material), lower Maastrichtian (Góczán and Siegl-Farkas, 1989).

Longanulipollis coronatus (Góczán, 1964) Góczán in Góczán et al., 1967 emend.

(Plate VI, 7–16)

1964 *Extratriporopollenites coronatus* Góczán, p. 253, pl. 8, fig. 3a–b.

1967 *Longanulipollis*? *coronatus* (Góczán, 1964) Góczán in Góczán et al., p. 473.

1989 *Coronatipollis coronatus* (Góczán, 1964) Góczán et Siegl-Farkas, p. 55 [transfer invalid: lacks full reference to the basionym].

1989 *Coronatipollis corpulentus* Góczán et Siegl-Farkas, pp. 54, 55, pl. 4, figs. 13–15.

1989 *Intercalaripollis arcuatus* Góczán et Siegl-Farkas, pp. 58, 59, pl. 3, figs. 4–6.

Emended diagnosis. A *Longanulipollis* with markedly convex sides. Inner contour trilobate. Nexine sometimes thinner, but usually as thick as, or thicker than, sexine in interradial regions; endopores generally associated with shallow atria. Vestibula when present, very shallow. Ektannuli comparatively short, their length being about one-third of diameter of central cavity. Germinals overall may be slightly swollen to form weakly developed oculi on one side of grain. Surface granulate to verrucate, sometimes forming an irregular negative reticulum.

Size range. 25 (27.4) 31 μm (12 specimens); holotype of *E. coronatus* 25 μm (Góczán, 1964); c. 36 μm for *C. corpulentus*, 34 μm for *I. arcuatus* 34 μm (Góczán et Siegl-Farkas, 1989).

Remarks. *Longanulipollis coronatus* differs from most other species of the genus as emended herein by its more rounded, compact aspect.

Occurrence. Hungary (our material; Góczán, 1964; Góczán et al. 1967; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Upper Santonian–lower Campanian (our material), upper Campanian (Góczán, 1964; Góczán et al. 1967), upper Campanian–lower Maastrichtian (Góczán and Siegl-Farkas, 1989).

Longanulipollis fornicatus Góczán et Siegl-Farkas 1989 emend. (Plate VI, 17–29)

1989 *Longanulipollis fornicatus* Góczán et Siegl-Farkas, p. 57, pl. 3, figs. 1–3.

Emended diagnosis. A *Longanulipollis* with straight or very slightly concave or convex sides. Inner contour circular to weakly trilobate. Nexine usually as thick as, or thicker than, sexine in interradial regions, borders narrow endopores, which are associated with shallow atria in endogerminals. Vestibula when present, shallow. Ektannuli elongate, their length being approximately half of diameter of central cavity. Germinals overall do not significantly modify the essentially triangular shape of the grains but are often somewhat swollen forming oculi on one side. Surface usually maculate to granulate, rarely with weakly developed low verrucae.

Size range. 27 (29.3) 32 μm (10 specimens); holotype 35 μm (Góczán and Siegl-Farkas, 1989).

Remarks. *Longanulipollis fornicatus* differs from *L. orbicularis* in having a more triangular outline and more weakly developed oculi; *L. parvoculus* in having elongated ektannuli and an equatorial outline that is less convex between the germinals; and *L. polanyensis* by its smaller ektannuli and thinner nexine. For differentiation from *L. bajtayi*, see remarks under this species.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Upper Santonian–lower Campanian (our material), upper Campanian (our material), upper Campanian–lower Maastrichtian (Góczán and Siegl-Farkas, 1989).

Longanulipollis lobus sp. nov. (Plate VII, 1–20)

Derivation of name. L., *lobus*, an elongated projection or protuberance, with reference to the well-developed oculi of specimens referred to this species.

Holotype. Specimen in palynological preparation/slide MCP3853-1, NMW 2017.1G7, Plate VII, 7, 8.

Type locality. Hungary, Gyepükaján Gy-9 borehole, Zone A.

Diagnosis. A *Longanulipollis* with slightly to strongly convex sides interradially. Inner contour subcircular to rounded-triangular, sometimes weakly trilobate. Nexine usually thicker than sexine except within endogerminals surrounding endopores, which are associated with shallow atria. Vestibula when present, usually shallow but sometimes fairly deep. Ektannuli large, their length commonly being approximately one-third, but may be up to nearly half of diameter of central cavity, and within well-developed oculi that are usually more pronounced on one surface than on the other. Surface maculate to granulate and/or microrugulate.

Size range. 19 (25.5) 33 µm (18 specimens).

Remarks. *Longanulipollis lobus* is usually smaller than *L. orbicularis* and has more protruding ektannuli and smaller oculi. It differs from *L. amabilis* and *L.* sp. B by its more protruding ektannuli and more weakly developed sculpture; *L. ornatus* in being more weakly sculptured and in having oculi that do not connect over one of the poles; *L. parvoculus* by its more elongated and less robust ektannuli, and its usually thinner nexine; and from the other species of *Longanulipollis* as emended herein by its very well-developed oculi.

Occurrence. Hungary (our material).

Stratigraphic range. Upper Santonian (our material).

Longanulipollis longianulus (Góczán, 1964) Góczán in Góczán et al., 1967 emend. (Plate VII, 27–30)

1964 *Extratriporopollenites longianulus* Góczán, p. 249, pl. 7, figs. 1–3.

1967 *Longanulipollis longianulus* (Góczán, 1964) Góczán in Góczán et al., p. 473, pl. 9, figs. 6–8.

Emended diagnosis. A *Longanulipollis* with essentially concave to straight sides. Inner contour subcircular to trilobate. Nexine usually thicker than sexine in interradial regions, surrounds endopores, which are associated with shallow atria and usually wide but shallow vestibula. Ektannuli large, very elongate, their length being at least equal to diameter of central cavity. Germinals overall somewhat swollen forming weak oculi on one side of grain. Surface granulate to verrucate.

Size range. 44 (52) 61 µm (four specimens); 30–40 µm for *E. longianulus* (Góczán, 1964).

*Remark*s. *Longanulipollis longianulus* can be distinguished from the other species of *Longanulipollis* as emended herein by its very elongated ektannuli.

Occurrence. Hungary (our material; Góczán, 1964; Góczán et al., 1967).

Stratigraphic range. Lower Campanian (our material), upper Campanian (Góczán, 1964; Góczán et al., 1967)

Longanulipollis monstruosis Góczán et Siegl-Farkas 1989 emend. (Plate VII, 21–26)

1989 *Longanulipollis monstruosis* Góczán et Siegl-Farkas, p. 56, pl. 2, figs. 10–12.

Emended diagnosis. A *Longanulipollis* of stocky aspect with straight to slightly convex or concave sides. Inner contour subcircular to rounded-triangular or weakly trilobate. Nexine quite thick, usually thicker than sexine except within endogerminals surrounding endopores, which are associated with shallow atria. Vestibula wide and shallow. Ektannuli large, moderately elongate, their length being at least one-third of diameter of central cavity. Oculi often very distinct on one side of grain. Surface granulate and/or sculptured with closely spaced, irregularly shaped, flat-topped verrucae.

Size range. 33 (37) 42 μm (nine specimens); holotype 38 μm (Góczán and Siegl-Farkas, 1989).

Remarks. *Longanulipollis monstruosis* differs from *L. polanyensis* in overall shape, its sides being essentially convex interradially and ektannuli usually a little wider. For differentiation from *L. amabilis* and *L. bajtayi*, see remarks under these species.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas 1989).

Stratigraphic range. Upper Santonian–lower Campanian (our material), upper Campanian (Góczán and Siegl-Farkas, 1989).

Longanulipollis orbicularis (Góczán, 1964) comb. nov. emend. (Plate VIII, 1–14)

1964 *Oculopollis orbicularis* Góczán, p. 245, pl. 6, figs. 1, 2 only.

1980 *Oculopollis* sp. 1; Médus et al., pl. 14, figs. 9, 10.

1981 *Oculopollis* "rond-verruqueux"; Médus, pl. 1, fig. 9.

Emended diagnosis. A *Longanulipollis* with convex sides. Inner contour subcircular to rounded-triangular. Nexine thicker than sexine in interradial regions, surrounds narrow pores within endannuli that are associated with shallow atria. Vestibula when present, shallow. Ektannuli comparatively short and wide, their length being about one-third to half of diameter of central cavity. Germinals overall swollen to form well-developed oculi with undulating surfaces that extend almost to poles on both sides of grain. Surface maculate to granulate, sometimes micro-verrucate.

Size range. 26 (31.7) 38 µm (18 specimens); 23–28 µm for *O. orbicularis* (Góczán, 1964).

Remarks. The species *Oculopollis orbicularis* is better placed in *Longanulipollis* because of its beak-like ektannuli, hence our transfer to this genus. For differentiation from *L. fornicatus* and *L. lobus*, see remarks under these species. Specimen 3856-1, P34.1 (Pl. VIII, 13, 14) has a slightly more triangular outline and less pronounced oculi. It could be regarded as a form that is intermediate between *L. orbicularis* and *L. fornicatus*.

Occurrence. Hungary (our material; Góczán, 1964), France (Médus et al., 1980; Médus, 1981).

Stratigraphic distribution. Turonian (Médus et al., 1980), Coniacian (Médus, 1981), upper Santonian (our material; Góczán, 1964), lower Campanian (our material).

Longanulipollis ornatus (Kedves et Diniz, 1983) comb. nov. emend. (Plate V, 24, 28)

1983a *Portaepollenites ornatus* Kedves et Diniz, p. 337, pl. 2, figs. 11–13, text-fig. 6.

Emended diagnosis. A *Longanulipollis* with straight to convex sides. Inner contour subcircular. Nexine thinner than sexine in interradial regions, generally increases slightly in thickness about endopores, which are associated with shallow atria. Narrow, shallow vestibula. Ektannuli relatively large and elongate, their length being at least one-third of diameter of central cavity. Oculi especially distinct on one side of grain where they extend onto and merge at pole. Surface sculptured with closely spaced verrucae of irregular shape and size.

Size. 34 µm (one specimen); 40–50 µm for *P. ornatus* (Kedves and Diniz, 1983a).

Remarks. For differentiation of *Longanulipollis ornatus* from *L. amabilis* and *L. lobus*, see remarks under these species.

Occurrence. Hungary (our material; Kedves and Diniz, 1983a).

Stratigraphic range. Upper Santonian (our material), lower Campanian (Kedves and Diniz, 1983a).

Longanulipollis parvoculus (Góczán, 1964) comb. nov. emend. (Plate VIII, 15–37)

1964 *Oculopollis parvoculus* Góczán, p. 247, pl. 6, fig. 9a–c.

2007 *Oculopollis* sp.; Ferguson et al., pl. 1, fig. 7.

Emended diagnosis. A *Longanulipollis* with straight to convex sides. Inner contour rounded-triangular. Nexine quite thick, usually thicker than the sexine except within endogerminals surrounding endopores, which are associated with shallow atria. Vestibula when present, usually shallow. Ektannuli large, their length being at least one-third of diameter of central cavity. Germinals overall slightly swollen to form weakly developed oculi. Surface sometimes almost smooth but more commonly maculate to granulate and/or sculptured with closely spaced, irregularly shaped, flat-topped verrucae.

Size range. 22 (27.8) 32 µm (25 specimens); holotype of *O. parvoculus* 41 µm (Góczán, 1964).

Remarks. This species is transferred from *Oculopollis* to *Longanulipollis* on the basis of the beak-like ektannuli and weakly developed oculi that characterize it. For differentiation from *L. bajtayi*, *L. fornicatus* and *L. lobus*, see remarks under these species. In common with our observations above on the size of *Krutzschipollis magnoporus*, we consider the discrepancy between the size of the holotype illustrated by Góczán (1964) and the range size of our specimens to be of no consequence.

Occurrence. Hungary (our material; Góczán, 1964), Austria (Ferguson et al., 2007).

Stratigraphic range. Santonian (Ferguson et al., 2007), upper Santonian–lower Campanian (our material), lower Campanian (Góczán, 1964).

Longanulipollis polanyensis Góczán et Siegl-Farkas, 1989 emend. (Plate IX, 1–4)

1989 *Longanulipollis polanyensis* Góczán et Siegl-Farkas (pro parte), pp. 55, 56, pl. 2, figs. 7–9 only (paratype).

Emended diagnosis. A *Longanulipollis* with essentially concave sides. Inner contour subcircular to weakly trilobate. Nexine quite thick, usually thicker than sexine except within endogerminals surrounding endopores, which are associated with shallow atria. Vestibula wide and usually shallow but sometimes quite deep. Ektannuli large and elongate, their length being at least one-third of diameter of central cavity. Oculi often distinct on one side of grain. Surface granulate and/or sculptured with closely spaced, irregularly shaped, flat-topped verrucae.

Size range. 36 (37.7) 39 μm (six specimens); paratype 35 μm, for holotype see under *L. bajtayi* (Góczán and Siegl-Farkas, 1989).

Remarks. For differentiation of *Longanulipollis polanyensis* from *L. bajtayi*, *L. fornicatus* and *L. monstruosis*, see remarks under these species.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Upper Santonian–lower Campanian (our material), upper Campanian (Góczán and Siegl-Farkas, 1989)

Longanulipollis skarbyae (Kedves et Diniz, 1983) comb. nov. emend. (Plate IX, 5–8)

1983a *Verruoculopollis skarbyae* Kedves et Diniz, p. 336, pl. 2, figs. 14, 15, text-fig. 9.

Emended diagnosis. A *Longanulipollis* with markedly convex sides. Inner contour subcircular to weakly trilobate. Nexine about same thickness as, or thicker than, sexine in interradial regions; endopores usually associated with shallow atria, but sometimes deeper invaginations. Vestibula when present, very shallow. Ektannuli comparatively short, about one-third of diameter of central cavity. Germinals overall may be slightly swollen to form weakly developed oculi on one side of grain. Surface verrucate.

Size. Two specimens, both 39 µm in maximum diameter; 30–40 µm for *V. skarbyae* (Kedves and Diniz, 1983a).

Remarks. The erection of *Verruoculopollis* for pollen grains that are similar morphologically to *Oculopollis* and *Longanulipollis* merely on the basis of verrucate

sculpture, almost always a specific character within the Normapolles group, serves no useful purpose at generic level, hence our transfer of *V. skarbyae* to *Longanulipollis*. It differs from *L*. sp. B in being larger and in having less developed oculi and shallower atria. For differentiation from *L. amabilis*, see remarks under this species.

Occurrence. Hungary (our material; Kedves and Diniz, 1983a).

Stratigraphic range. Upper Santonian–lower Campanian (our material), lower Campanian (our material; Kedves and Diniz, 1983a).

Longanulipollis sp. A. (Plate IX, 9–12)

Description. A *Longanulipollis* with straight to slightly convex sides. Inner contour weakly trilobate. Nexine as thick as, or thicker than, sexine in interradial regions. Vestibula deeper and wider than in the other species of the genus. Endopores wide, associated with moderately deep atria. Ektannuli large and quite elongate, about one-third to half of diameter of central body. Oculi distinct on one side of the grain. Surface granulate to rugulate.

Size range. 34 (35.5) 38 µm (four specimens).

Remarks. This form can be separated from the other species of *Longanulipollis* as emended herein on the basis of its granulate to largely rugulate sculpture.

Occurrence. Hungary (our material).

Stratigraphic range. Upper Santonian–lower Campanian (our material).

Longanulipollis sp. B (Plate IX, 13–16)

1984 *Oculopollis vixclausus* Siegl-Farkas, pl. 1, figs. 10, 11 [nomen nudum].

Description. A *Longanulipollis* with markedly convex sides. Inner contour trilobate. Nexine thicker than sexine. Vestibula relatively large. Ektannuli fairly short and wide, their length being about one-third of diameter of central cavity. Oculi developed on both sides of grain. Surface irregularly verrucate to rugulate.

Size range. 29, 32 µm (two specimens).

Remarks. For differentiation of *Longanulipollis* sp. B from *L. amabilis* and *L. lobus*, see remarks under these species.

Occurrence. Hungary (our material).

Stratigraphic range. Upper Santonian (our material).

Oculopollis Pflug, 1953 emend.

1967 *Pseudoculopollis*, Góczán et al., p. 494.

1967 *Semioculopollis* Góczán, Krutzsch et Pacltová in Góczán et al., p. 503.

1981 *Druggipollenites* Kedves et Herngreen, p. 526.

Type species. *Oculopollis concentus* Pflug, 1953, p. 110, pl. 19, figs. 45–49.

Emended diagnosis. Breviaxal pollen grain, triangular in polar view with straight or convex sides interradially. Sexine and nexine usually quite well separated by an interloculum. Nexine about same thickness as sexine, but can be slightly thinner or thicker. Exogerminals prominent, influencing overall shape of grain, formed by often structured (intrabaculate) ektannuli having rounded or club-like outlines in polar view. Exoapertures are vertical slits. Endogerminals within nexine are commonly narrow pores (sometimes barely visible) associated with shallow atria. Oculi present, usually very protruding, often more strongly developed on one face than on the other, sometimes connected over pole by a ridge or sculpture. Surface generally smooth to granulate, but some species have a rugulate sculpture.

Size range. 22 (32.2) 49 µm (based on our material); no size range given by Pflug (1953).

Remarks. *Oculopollis* is characterized by having at least weakly developed oculi and a relatively thin nexine that is not, or is only very slightly, invaginated in the endogerminals. *Trudopollis* may also be weakly oculate but has an invaginated nexine within the germinals, and the ektannuli generally do not protrude to the extent that they modify the overall shape of the grain in polar view.

Despite the fact that we transferred some species of *Semioculopollis* to *Trudopollis* and *Longanulipollis* (see Section 8), the type species of this genus, *S. minutus* Krutzsch et Pacltová in Góczán et al., 1967, has the characters of *Oculopollis*, so we consider *Semioculopollis* to be a junior synonym of this genus.

Oculopollis aestheticus Weyland et Krieger, 1953 emend. (Plate IX, 17–23)

1953 *Oculopollis aestheticus* Weyland et Krieger, p. 20, pl. 2, fig. 8.

Emended diagnosis. An *Oculopollis* with straight to convex sides interradially. Inner contour circular to subtriangular. Nexine slightly thinner than sexine in interradial regions, commonly separated by a narrow interloculum. Ektannuli prominent and elongate, with a clearly visible intrabaculate structure. Oculi well developed, more pronounced on one side than on the other. Surface scabrate to maculate.

Size range. 32 (32.5) 33 µm (11 specimens); 25 µm (Weyland and Krieger, 1953).

Remarks. *Oculopollis aestheticus* differs from *O*. *concentus* in having more swollen oculi, rendering the interradial regions less convex, and the ektannuli have a more obvious radiating intrabaculate structure. It also differs from *O*. *cardinalis* in having larger oculi, and from *O*. *triceps* in its less robust aspect.

Occurrence. Germany (our material; Weyland and Krieger, 1953), Sweden (our material).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953), lowermost Campanian (our material).

Oculopollis artifex (Weyland et Krieger, 1953) comb. nov. emend. (Plate X, 1–10; cf: Plate X, 11–14)

1953 *Trudopollis artifex* Weyland et Krieger, p. 14, pl. 2, fig. 21.

1968 *Extratriporopollenites artifex* (Weyland et Krieger, 1953) Skarby, pp. 33, 34, pl. 7, figs. 1–10; pl. 8, figs. 1–8.

1981 *Druggipollenites cretaceus* Kedves et Herngreen, p. 526, pl. 11, figs. 1, 2.

Emended diagnosis. An *Oculopollis* with concave, straight or slightly convex sides interradially. Inner contour subcircular to subtriangular. Nexine thinner than sexine in interradial regions, the latter being very thick and penetrated by numerous, clearly visible, closely spaced perforations. Interloculum narrow. Ektannuli strongly intrabaculate, sometimes protruding depending on thickness of interradial sexine. Endogerminals are very wide pores associated with very shallow atria. Vestibula absent. Oculi usually absent, but can be faintly discernible on one side of some specimens. Surface uneven, maculate.

Size range. 26 (31.6) 35 µm (13 specimens); c. 25 µm for *T. artifex* (Weyland and Krieger, 1953); 26–43 µm for *E. artifex* (Skarby, 1968); 30–35 µm for *D. cretaceus* (Kedves and Herngreen, 1981).

Remarks. We transfer *Trudopollis artifex* to the genus *Oculopollis* on the basis of the absence of an invagination of the nexine in the endogerminal. In common with some other Normapolles grains, the abundant perforations through the wall of the specimens attributed to this species are considered to be essentially primary structures (see Discussion, Section 9.2) although probably enhanced to some extent by degradation during fossilization.

Oculopollis artifex differs from *O. bulbosus* in having a thicker sexine, less developed oculi, and less protruding ektannuli; *O. viriosus* in having a perforated sexine, thinner nexine, and less robust aspect; and the other species of *Oculopollis* discussed herein on the basis of its very thick, perforated sexine. The specimens

referred to *Oculopollis* sp. cf. *O. artifex* (Plate X, 11–14) have been separated from *O. artifex* because the perforations of the sexine are less evenly distributed and look more like corrosion.

Occurrence. Germany (Weyland and Krieger, 1953; Skarby, 1968), Sweden (our material; Skarby, 1968), Belgium (our material), Netherlands (Kedves and Herngreen, 1981).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953; Skarby, 1968), lowermost Campanian (our material; Skarby, 1968), Maastrichtian (Kedves and Herngreen, 1981).

Oculopollis bulbosus Weyland et Krieger, 1953 emend. (Plate X, 15–26)

1953 *Oculopollis bulbosus* Weyland et Krieger, p. 19, pl.2, fig. 16.

1953 *Extratriporopollentes iustus* Weyland et Krieger, p. 18, pl. 2, fig. 56.

1953 *Oculopollis antibulbosus* Weyland et Krieger, p. 19, pl. 5, figs. 8, 9.

1953 *Oculopollis* Formen Weyland et Krieger, pl. 2, figs. 12–14.

1953 *Oculopollis* cf. *pneumaticus* Pflug; Weyland and Krieger, pl. 2, figs. 17, 18.

1968 *Extratriporopollenites parmatus* Skarby (pro parte), pp. 34–36, pl. 10, fig. 8a–b; pl. 12, figs. 1, 2 only.

Emended diagnosis. An *Oculopollis* with straight to slightly convex or concave sides interradially. Inner contour circular to subtriangular. Nexine usually about as thick as sexine in interradial regions and clearly separated from it by an interloculum. Ektannuli prominent but not elongate, with a coarse intrabaculate structure. Oculi often well developed on one side of grain. Surface maculate but appearance strongly affected by numerous, clearly visible perforations through the sexine.

Size range. 25 (30.8) 39 µm (seven specimens); 20–30 µm (Weyland and Krieger, 1953); c. 20 µm for *E. iustus*, 25 µm for *O. antibulbosus* (Weyland and Krieger, 1953).

Remarks. As for *O. artifex*, the abundant, very obvious perforations through the wall of the specimens attributed to this species are considered to be essentially primary structures, although probably enhanced to some extent by degradation during fossilization. Small grains that are similar in appearance to *Oculopollis baculatus* Pacltová et Krutzsch, 1970 (Plate X, 27, 28 herein) may be aberrant forms of *O. bulbosus* that did not reach maturity in the anther before they were dispersed. For comparison between *O. bulbosus* and *O. artifex*, see remarks under these species. *Oculopollis bulbosus* is differentiated from the other species of *Oculopollis* discussed herein in having clearly visible perforations through the sexine.

Occurrence. Germany (Weyland and Krieger, 1953), Sweden (our material; Skarby, 1968)

Stratigraphic range. Middle–upper Santonian (Weyland and Krieger, 1953), lowermost Campanian (our material; Skarby, 1968).

Oculopollis cardinalis Weyland et Krieger, 1953 emend. (Plate XI, 1–8; cf: Plate XI, 9, 10)

1953 *Oculopollis cardinalis* Weyland et Krieger, p. 18, pl. 2, figs. 10, 11.

1953 *Oculopollis principalis* subsp. *obligatus* Weyland et Krieger, pp. 18, 19, pl. 5, figs. 11, 12.

1953 *Oculopollis suboculus* Weyland et Krieger, p. 20, pl. 2, figs. 7, 15.

?1963 *Trudopollis abnormis* Zaklinskaya, p. 215, pl. 29, figs. 1–3.

1967 *Oculopollis obligatus* (Weyland et Krieger, 1953) Krutzsch in Góczán et al., p. 484.

1968 *Oculopollis suboculus* Weyland et Krieger, 1953; Skarby, pl. 30, fig. 5.

Emended diagnosis. An *Oculopollis* with essentially straight sides interradially. Inner contour subtriangular. Nexine slightly thinner than, or as thick as, sexine in interradial regions. Interloculum often present. Ektannuli robust and prominent, quite elongate, usually unstructured but can be very finely intrabaculate or become slightly less homogeneous at their base. Germinals overall slightly swollen to form oculi that are more pronounced on one side of grain than on the other. Surface essentially smooth or maculate to weakly granulate.

Size range. 29 (36.6) 45 µm (14 specimens); c. 30 µm (Weyland and Krieger, 1953); c. 30 µm for *O. principalis*, c. 25 µm for *O. suboculus*, c. 30 µm for *O. obligatus* (Weyland and Krieger, 1953).

Remarks. *Oculopollis cardinalis* is similar to *O. principalis* but differs in usually being larger, more triangular and stockier, in having more pronounced ektannuli, and by the absence of a weakly defined connection between the oculi over one pole. Its triangular shape differentiates it from *O. concentus*, most specimens of which also have a subcircular to more rounded-triangular inner contour. It differs from *O. concentricoides* in having a thinner nexine, less robust annuli, and an interloculum. For differentiation from *O. aestheticus*, see remarks under this species. The specimens referred to *Oculopollis* sp. cf. *O. cardinalis* (Plate XI, 9, 10) have been separated from *O. cardinalis* on the basis of their slightly more convex sides interradially, less obvious oculi, and proportionally less pronounced ektannuli.

Occurrence. Belgium (our material), Netherlands (our material), Germany (Weyland and Krieger, 1953).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953).

Oculopollis concentricoides Weyland et Krieger, 1953 emend. (Plate XI, 11–14)

1953 *Oculopollis concentricoides* Weyland et Krieger, p. 20, pl. 2, fig. 5.

1967 *Pseudoculopollis concentricoides* (Weyland et Krieger, 1953) Krutzsch in Góczán et al., p. 495.

Emended diagnosis. An *Oculopollis* with straight to concave sides interradially. Inner contour circular to subcircular. Nexine thick, thicker than sexine in interradial regions. No interloculum. Ektannuli robust and prominent, unstructured or finely intrabaculate. Endogerminals are fairly wide pores associated with very shallow atria. Vestibula moderately wide and very narrow. Surface fairly smooth to maculate.

Size range. 32, 39 µm (two specimens); c. 25 µm (Weyland and Krieger, 1953).

Remarks. *Oculopollis concentricoides* differs from *O. rector* on account of its more pronounced ektannuli, somewhat more elongated shape, thicker nexine, and thinner sexine. For differentiation from *O. cardinalis*, see remarks under this species.

Occurrence. Sweden (our material), Belgium (our material), Germany (Weyland and Krieger, 1953).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953), lowermost Campanian (our material).

Oculopollis concentus Pflug, 1953 emend. (Plate XI, 15–22, 24–27; cf: Plate XI, 23)

1953 *Oculopollis concentus* Pflug, p.110, pl. 19, figs. 45–49.

1953 *Oculopollus extensus* Weyland et Krieger, p. 19, pl. 2, fig. 9.

Emended diagnosis. An *Oculopollis* with straight to convex sides interradially. Inner contour circular to subtriangular. Nexine usually about same thickness as sexine in interradial regions, but sometimes slightly thinner or thicker, separated by a more or less discernible interloculum. Ektannuli prominent, elongate, with a club-like outline in polar view, unstructured or faintly showing a less homogeneous, more granular, slightly radial structure; no clear separation between vestibulum and atrium associated with each endopore. Nexine commonly slightly thicker around endopores forming endannuli, below which a thin lamella of nexine may also be present. Germinals overall somewhat swollen forming oculi that sometimes almost connect over the pole. Surface smooth or maculate.

Size range. 22 (32.9) 41 µm (11 specimens); c. 25 µm Pflug (1953); 30 µm for *O. extensus* (Weyland and Krieger, 1953).

Remarks. *Oculopollis concentus* differs from *O. triceps* in having a less stocky aspect. For differentiation from *O. aestheticus* and *O. cardinalis*, see remarks under these

species. The specimen referred to as *Oculopollis* sp. cf. *O. concentus* (Plate XI, 23) has been separated from *O. concentus* on the basis of its more convex sides interradially and less pronounced ektannuli.

Occurrence. Belgium (our material), Germany (our material; Pflug, 1953; Weyland and Krieger, 1953), Netherlands (our material).

Stratigraphic range. Middle–upper Santonian (our material; Pflug, 1953; Weyland and Krieger, 1953).

Oculopollis praedicatus Weyland et Krieger, 1953 emend. (Plate XII, 2–7; cf: Plate XII, 9–11)

1953 *Oculopollis praedicatus* Weyland et Krieger, pro parte, p. 18, pl. 1, figs. 39–42 only.

1967 *Semioculopollis praedicatus* (Weyland et Krieger, 1953) Krutzsch in Góczán et al. 1967, pp. 503, 504.

Emended diagnosis. An *Oculopollis* with convex sides. Inner contour rounded-triangular to subcircular. Nexine as thick as, or thicker than, sexine. Endogerminals are either clearly delineated pores associated with small atria or poorly delineated small apertures. No vestibula or interloculum. Ektannuli unstructured, quite short and

commonly also fairly wide. Germinals overall slightly to quite strongly swollen forming oculi that are more pronounced on one side of grain than on the other. Surface sometimes more or less smooth but more commonly maculate or granulate to verrucate.

Size range. 24 (29.2) 38 µm (six specimens); 10–20 µm (Weyland and Krieger, 1953).

Remarks. Pollen grains placed in this species are commonly small and display a morphology that suggests incomplete development in the anther prior to being dispersed. Others, such as those similar to *Oculopollis triperforinus* Zaklinskaya, 1963 (Plate XII, 8, 12 herein), are also quite likely to be aberrant forms. The specimens referred to *Oculopollis* sp. cf. *O. praedicatus* (Plate XII, 9–11) differ from *O. praedicatus* because their oculi are connected at the pole by a raised structure.

Occurrence. Belgium (our material), Hungary (our material), Germany (Weyland and Krieger, 1953).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953), upper Santonian–lower Campanian (our material).

Oculopollis principalis Weyland et Krieger, 1953 emend. (Plate XII, 13–39; cf: Plate XII, 1)

1953 *Oculopollis principalis* subsp. *typicus* Weyland et Krieger, pp. 18, 19, pl. 5, figs. 13, 14.

1963 *Trudopollis ordinatus* Zaklinskaya, pp. 210, 211, pl. 27, figs. 4, 5, 8.

1967 *Pseudoculopollis principalis* (Weyland et Krieger, 1953) Krutzsch in Góczán et al., p. 495, pl. 14, figs. 7–13.

Emended diagnosis. An *Oculopollis* with straight or slightly convex sides. Inner contour subcircular to rounded-triangular. Nexine about as thick as sexine in interradial regions. No clear separation between vestibulum and atrium associated with each endopore. Interloculum usually visible. Ektannuli prominent but not especially elongate, their length being about one-quarter, and not more than one-third of diameter of central cavity, most showing a more or less finely or weakly intrabaculate structure. Germinals overall somewhat swollen forming oculi that are more pronounced on one side of grain where they are also connected over the pole by a slightly raised and/or a more strongly sculptured, more or less granular surface; elsewhere surface is usually maculate, sometimes granulate.

Size range. 22 (26.6) 30 µm (23 specimens); c. 30 µm (Weyland and Krieger, 1953); 27–35 µm for *T. ordinatus* (Zaklinskaya, 1963).

Remarks. *Oculopollis principalis* differs from *O. rector* in being smaller overall, and in having a thinner exine, less obvious intrabaculate structure within the ektannuli, and oculi that connect over one of the poles; and from *O*. sp. A in having less robust

ektannuli, an interloculum, and a less clear connection between the oculi. The specimen referred to *Oculopollis* sp. cf. *O. principalis* (Plate XII, 1) differs from *O. principalis* in being considerably larger (47 µm).

Occurrence. Sweden (our material), Germany (Weyland and Krieger, 1953), general boreal Central Europe (Góczán et al., 1967), West Siberian Plain (Zaklinskaya, 1963).

Stratigraphic range. Middle–upper Santonian (Weyland and Krieger, 1953), lowermost Campanian (our material), middle Santonian–lower Campanian (Góczán et al., 1967), Paleocene (Zaklinskaya, 1963).

Oculopollis rector (Pflug, 1953) comb. nov. emend. (Plate XIII, 1–7)

1953 *Oculopollis lapillus* Pflug, p. 110, pl. 19, figs. 53–56, 61–65.

1953 *Trudopollis rector* Pflug, p. 99, pl. 23, figs. 8, 18, 19.

1953 *Trudopollis arector* Pflug, p. 101, pl. 23, figs. 16, 17.

1953 *Trudopollis arector* Pflug, 1953; Weyland and Krieger, pl. 5, fig. 35.

1967 *Bohemiapollis arector* (Pflug, 1953) Krutzsch in Góczán et al., p. 452.

1967 *Semioculopollis lapillus* (Pflug, 1953) Krutzsch in Góczán et al., p. 504.

Emended diagnosis. An *Oculopollis* with straight to slightly convex sides. Inner contour subcircular to rounded-triangular. Nexine thinner than a fairly thick sexine in

interradial regions, separated by a narrow interloculum. No clear separation between vestibulum and atrium associated with each endopore. Ektannuli with intrabaculate structure, quite large but not usually protruding enough to affect shape of grain. Germinals overall slightly swollen, forming oculi that are more pronounced on one side of grain than on the other. Surface maculate.

Size range. 32 (33.5) 37 µm (eight specimens); c. 22 µm for *T. rector*, c. 25 µm for *T. arector*, 15–25 µm for *O. lapillus* (Pflug, 1953).

Remarks. We transfer *Trudopollis rector* to *Oculopollis* because the endogerminals within the nexine are pores associated with only shallow atria, and oculi are clearly present. It differs from *O. triceps* in having less robust and protruding ektannuli and less obvious oculi, and from *Oculopollis viriosus* in that oculi are always present and more strongly developed, the exine is thinner, and the intrabaculate structure within the ektannuli is more obvious. For differentiation from *O. concentricoides*, see remarks under this species.

Occurrence. Germany (our material; Pflug, 1953; Weyland and Krieger, 1953), Sweden (our material).

Stratigraphic range. Middle–upper Santonian (our material; Pflug, 1953; Weyland and Krieger, 1953), lowermost Campanian (our material).

Oculopollis triceps (Skarby, 1968) comb. nov. emend. (Plate XIII, 8–13)

1968 *Extratriporopollenites triceps* Skarby, 1968 (pro parte), pp. 30, 31, pl. 1, fig. 1 only (Holotype).

Emended diagnosis. An *Oculopollis* with slightly convex sides interradially. Inner contour subcircular to rounded-triangular. Nexine about as thick as sexine in interradial regions; no clear separation between vestibulum and atrium associated with each endopore. Interloculum usually visible. Ektannuli prominent, their length being between one-third and half of diameter of central cavity, most clearly showing intrabaculate structure. Germinals overall swollen, forming oculi that are more pronounced on one side of grain where they also nearly connect over pole. Surface smooth to maculate or more or less granulate.

Size range. 25 (31.2) 37 µm (10 specimens); 30–47 µm for *E. triceps* (Skarby, 1968).

Remarks. Skarby (1968) included a number of different morphotypes in *Extratriporopollenites triceps*, in our opinion too many for practical purposes. For ease of identification we transfer *E. triceps* to *Oculopollis* because it displays all the characters that are typical of this genus, but have included in the species only forms that are similar to the holotype. Hence, *O. triceps* sensu stricto is similar to *O. rector* but differs in having more robust and protruding ektannuli, and more pronounced oculi.

For differentiation from *O. aestheticus* and *O. concentus*, see remarks under these species.

Occurrence. Sweden (our material; Skarby, 1968).

Stratigraphic range. Lowermost Campanian (our material; Skarby, 1968).

Oculopollis sp. cf. *O. triceps* (Skarby, 1968) comb. nov. emend. (Plate XIII, 14, 15)

Remarks. Skarby (1968) included specimens similar to those figured here in *O. triceps*. These differ from our restricted interpretation of this species principally in having a thicker nexine and somewhat larger germinals in which the ektannuli lack a clearly defined intrabaculate structure.

Occurrence. Sweden (our material; Skarby, 1968).

Stratigraphic range. Lowermost Campanian (our material; Skarby, 1968).

Oculopollis viriosus sp. nov. (Plate XIII, 16–25; Plate XIV, 1–4)

1968 “Undetermined forms related to *E. triceps*, *E. artifex* and *E. parmatus*” Skarby (pro parte), pl. 9, figs. 1–6 only.

Derivation of name. L., *viriosus*, robust, strong, with reference to the general aspect of the specimens of this species.

Holotype. Specimen in palynological preparation/slide MCP3283-3, NWM 2107.1G5, Plate XIII, figs. 17, 20.

Type locality. Belgium, Gulpen, Borehole sample 33, Hergenrath Clay, Aachen Formation.

Diagnosis. A large *Oculopollis* with straight, slightly convex or slightly concave sides interradially. Inner contour subcircular to subtriangular. Nexine thick but thinner than sexine in interradial regions, the latter being very thick. No interloculum. Ektannuli robust, unstructured to very finely intrabaculate. Endogerminals are wide pores associated with shallow atria. Vestibula sometimes present, usually narrow and shallow. Oculi only weakly developed, may be absent in some specimens. Surface smooth to maculate.

Size range. 30 (39.5) 49 µm (21 specimens).

Remarks. For differentiation of *Oculopollis viriosus* from *O. artifex* and *O. rector*, see remarks under these species. It is distinguished from the other species of *Oculopollis* considered herein in being larger and in having a thick nexine and sexine, oculi that are only weakly developed and sometimes absent, and less protruding ektannuli.

Occurrence. Belgium (our material), Sweden (Skarby, 1968).

Stratigraphic range. Middle–upper Santonian (our material), lowermost Campanian (Skarby, 1968).

Oculopollis sp. A (Plate IX, 24–26)

Description. An *Oculopollis* with straight to convex sides interradially. Inner contour circular. Separation between nexine and sexine not clear, but nexine seems to be about same thickness as sexine in interradial regions. No interloculum. Ektannuli fairly elongate and robust, unstructured. Endogerminals are narrow pores associated with very shallow atria. Vestibula short and narrow. Germinals overall somewhat swollen forming oculi that are clearly connected over one of the poles.

Size. Two specimens, both 30 µm in maximum diameter.

Remarks. For differentiation of *Oculopollis* sp. A from *O. principalis*, see remarks under this species.

Occurrence. Sweden (our material).

Stratigraphic range. Lowermost Campanian (our material).

Trudopollis Pflug, 1953 emend.

1981 *Hofkeripollenites* Kedves et Herngreen, p. 512.

1981 *Kriegeripollenites* Kedves et Herngreen, p. 511.

1981 *Felderipollenites* Kedves et Herngreen, pp. 518, 520.

1989 *Cuneipollis* Góczán et Siegl-Farkas, p. 52.

Type species. *Trudopollis pertrudens* (Pflug in Thomson and Pflug, 1953) Pflug, 1953, p. 98, pl. 22, figs. 8–19.

Emended diagnosis. Breviaxal pollen grain, triangular to subcircular in shape with straight or convex sides in polar view. Sexine and nexine usually quite well separated by an interloculum. Nexine weakly to strongly trilobate, about same thickness as sexine but can be a little thinner or thicker. Exogerminals of varying size, consisting of often structured (intrabaculate) ektannuli having club-like outlines in polar view.

Exoapertures are vertical slits. Endogerminals can be wide or narrow pores associated with more or less deep atria, or cunei of varying size, sometimes reaching centre of grain (platea). Vestibula occasionally present. Oculi usually absent, but may be weakly developed on one or both sides of grain in a few species. Surface generally smooth to granulate, sometimes verrucate, rarely echinate.

Size range. 21 (30.7) 52 µm (based on our material); no size range given by Thomson and Pflug (1953) or Pflug (1953).

Remarks. Polar thinning and minor fissuring of the sexine may be apparent in some specimens of *Trudopollis* but, unlike *Papillopollis* Pflug, 1953, it is not reduced to islands of granules, papillae or other bodies at one or both poles (Batten and Morrison, 1987).

Trudopollis acinosus (Agranovskaya in Pokrovskaya and Stel'mak, 1960) Gray et Groot, 1966 emend. (Plate XIV, 8, 9)

1960 *Extratriporopollenites acinosus* Agranovskaya in Pokrovskaya and Stel'mak, p. 124, pl. 5, figs. 7–10.

1966 *Trudopollis acinosus* (Agranovskaya in Pokrovskaya and Stel'mak, 1960) Gray et Groot, p. 130, pl. 43, fig. 14.

Emended diagnosis. A *Trudopollis* with slightly convex sides. Inner contour subcircular to weakly trilobate. Nexine a little thinner than sexine in interradial regions. Interloculum, if discernible, very narrow. Ektannuli small, appear to be essentially unstructured. Endogerminals are fairly wide pores associated with shallow atria. Vestibula narrow and more or less deep. No oculi. Surface covered with very small verrucae.

Size. 24, 25 µm (two specimens); 20 (22) 24 µm (Gray and Groot, 1966); 27–33 µm for *E. acinosus* (Agranovskaya in Pokrovskaya and Stel'mak, 1960).

Remarks. *Trudopollis acinosus* is very similar to *T. fossulotrudens* but differs in being more finely sculptured and lacking oculi. It is distinguished from *T. lativerrucatus* on the basis of its finer sculpture, more convexly triangular outline, and thinner nexine, and from *T. nonperfectus* in being sculptured with small verrucae as opposed to having a maculate surface.

Occurrence. Urals (Agranovskaya in Pokrovskaya and Stel'mak, 1960), New Jersey (our material; Gray and Groot, 1966).

Stratigraphic range. Lower–middle Santonian (our material), Santonian (Agranovskaya in Pokrovskaya and Stel'mak, 1960), lower Campanian (Gray and Groot, 1966).

Trudopollis articulus Weyland et Krieger, 1953 emend. (Plate XIV, 5–7)

1953 *Trudopollis articulus* Weyland et Krieger, p. 15, pl. 2, fig. 32.
1963 *Trudopollis articulus* Weyland et Krieger, 1953; Zaklinskaya, pl. 27, fig. 10.

Emended diagnosis. A *Trudopollis* with straight to convex sides. Inner contour trilobate. Nexine thinner than, or about same thickness as, fairly thick sexine in interradial regions. Very narrow interloculum sometimes present. Ektannuli fairly small, not protruding, intrabaculate. Endogerminals are wide pores associated with fairly deep atria. Vestibula when present, narrow and shallow. No oculi. Surface maculate.

Size. 32, 35 µm (two specimens); c. 35 µm (Weyland and Krieger, 1953).

Remarks. *Trudopollis articulus* is similar to *T. pertrudens* but differs in having a maculate rather than an essentially smooth or scabrate surface, and a thicker sexine. It is distinguished from *T.* sp. cf. *T. rotundus* in having more pronounced ektannuli, a less rounded outline, and a thicker sexine, and from *T. conrectiformis* in being significantly smaller.

Occurrence. Germany (Weyland and Krieger, 1953), Belgium (our material), West Siberian Plain (Zaklinskaya, 1963).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953), Maastrichtian–Paleocene (Zaklinskaya, 1963).

Trudopollis capsula Pflug, 1953 emend. (Plate XIV, 10–15)

1953 *Trudopollis capsula* Pflug, p. 101, pl. 23, figs. 24, 25.
1967 *Longanulipollis* (?) *capsula* (Pflug, 1953) Krutzsch and Góczán in Góczán et al., p. 473.

Emended diagnosis. A *Trudopollis* with straight to slightly convex sides. Inner contour trilobate. Nexine slightly thinner than, or as thick as, sexine in interradial regions. Interloculum barely discernible. Ektannuli small and squat, but can be fairly robust in some specimens, finely intrabaculate or unstructured apart from close to base where they become more granular. Endogerminals are wide pores associated with very deep atria. Vestibula when present, usually narrow and fairly shallow. No oculi. Surface smooth.

Size range. 21 (26.5) 29 µm (seven specimens); c. 27 µm (Pflug, 1953).

Remarks. *Trudopollis capsula* differs from other species of *Trudopollis* in that the nexine is markedly trilobate with very wide and deep atria associated with the endopores.

Occurrence. Hungary (our material), Belgium (our material), New Jersey (our material), Germany (Pflug, 1953), "Boreal area" (Góczán et al., 1967).

Stratigraphic range. Lower–middle Santonian (our material), middle–upper Santonian (our material; Pflug, 1953), Maastrichtian (Góczán et al., 1967).

Trudopollis conrectiformis Zaklinskaya, 1963 emend. (Plate XIV, 22–25)

1963 *Trudopollis conrectiformis* Zaklinskaya, pp. 206, 207, pl. 25, figs. 4, 5.

Emended diagnosis. A large *Trudopollis* with convex sides interradially. Inner contour trilobate. Nexine thick, about same thickness as, or slightly thicker than, sexine in interradial regions. Very narrow interloculum. Ektannuli relatively small, intrabaculate. Endogerminals are wide pores associated with deep, U-shaped atria. Vestibula narrow and fairly deep. No oculi. Surface maculate.

Size range. 41 (48.3) 52 µm (five specimens), 45–60 µm (Zaklinskaya, 1963).

Remarks. *Trudopollis conrectiformis* differs from *T.* sp. B in lacking a clearly perforated sexine, and *T. oculoides* in having shallower atria, a thicker sexine, and smaller ektannuli. For differentiation from *T. articulus*, see remarks under this species.

Occurrence. Belgium (our material), West Siberian Plain (Zaklinskaya, 1963)

*Stratigraphic rang*e. Middle–upper Santonian (our material), Paleocene (Zaklinskaya, 1963).

Trudopollis conrector Pflug, 1953 emend. (Plate XIV, 16–21)

1953 *Trudopollis conrector* Pflug, p. 101, pl. 23, figs. 20–23.

1981 *Hofkeripollenites hemimechanicus* (Pflug, 1953) Kedves et Herngreen subsp. *magnus* Kedves et Herngreen, p. 516, pl. 8, figs. 12, 13.

2004 *Trudopollis* sp. forme 2; Méon et al., pl. 3, fig. 27.

Emended diagnosis. A *Trudopollis* with straight to slightly concave or convex sides. Nexine thick, as thick as, or thicker than, sexine in interradial regions. A narrow interloculum may be present. Ektannuli robust, more or less elongate, essentially unstructured except perhaps close to base where sexine becomes more granular, or with a faintly discernible intrabaculate structure. Endogerminals are fairly wide pores

associated with deep, U-shaped atria. Vestibula when present, fairly wide and deep. Surface usually smooth or maculate, but can be finely granulate.

Size range. 24 (29.8) 37 µm (10 specimens); c. 25 µm (Pflug, 1953); 28–35 µm for *H. hemimechanicus* (Kedves and Herngreen, 1981).

Remarks. *Trudopollis conrector* differs from *T. hemimechanicus* in that both nexine and sexine are thicker and the ektannuli larger, and from *T. retigressus* in that the nexine is usually thicker, the ektannuli proportionally larger, and no cunei are developed.

Occurrence. Netherlands (Kedves and Herngreen, 1981), Germany (Pflug, 1953), Belgium (our material), Czech Republic (Méon et al., 2004).

Stratigraphic range. Upper Turonian (Méon et al., 2004), middle–upper Santonian (our material; Pflug, 1953), Maastrichtian (Kedves and Herngreen, 1981).

Trudopollis cuneolis (Góczán et Siegl-Farkas, 1989) comb. nov. emend. (Plate XV, 5–7)

1989 *Cuneipollis cuneolis* Góczán et Siegl-Farkas (pro parte), pp. 52, 53, pl. 4, figs. 1–7 only.

Emended diagnosis. A *Trudopollis* with convex sides interradially. Inner contour trilobate. Nexine thicker than sexine in interradial regions. No interloculum. Ektannuli elongate, beak-like in shape, unstructured. Endogerminals are pores associated with fairly narrow and deep cunei extending from one-third to half-way to pole. Vestibula narrow and very shallow. No oculi. Surface granulate to microverrucate.

Size range. 32 (34.3) 36 µm (four specimens); 28–34 µm (Góczán and Siegl-Farkas, 1989).

Remarks. We transfer *Cuneipollis cuneolis*, the type species of the monospecific genus *Cuneipollis*, to *Trudopollis* not only because Góczán and Siegl-Farkas (1989) stated that it is closest morphologically to this genus (and *Hofkeripollenites*, which we also regard as a synonym of *Trudopollis* herein) but also because we think that a separate genus for this morphotype is unnecessary. The characters of the species are in fact transitional between *Trudopollis* and *Longanulipollis* as emended herein. It has the characteristic beak-like ektannuli of the latter, but its deep cunei are typical of some species of *Trudopollis*. It is similar to *T. oculoides* but differs in that the cunei are narrower and the ektannuli are beak-like. The latter feature also distinguishes it from the other *Trudopollis* species discussed in this paper.

Occurrence. Hungary (our material; Góczán and Siegl-Farkas, 1989).

Stratigraphic range. Lower Campanian (our material), upper lower Campanian–upper lower Maastrichtian (Góczán and Siegl-Farkas, 1989).

Trudopollis exemplum (Pflug in Thomson and Pflug, 1953) comb. nov. emend. (Plate XV, 3, 4)

1953 *Extratriporopollenites exemplum* Pflug in Thomson and Pflug, p. 75, pl. 6, figs. 102–105.

1953 *Trudopollis exemplum* (Pflug in Thomson and Pflug, 1953) Pflug, p. 100, pl. 25, fig. 50.

1953 *Extratriporopollenites pertinax* Pflug in Thomson and Pflug, p. 74, pl. 6, fig. 97.

1953 *Oculopollis pertinax* (Pflug in Thomson and Pflug, 1953) Pflug, p. 110, pl. 19, fig. 71.

1973 *Oculopollis pertrudoides* Krutzsch, pp. 86, 87, pl. 2, figs. 11–15.

1973 *Oculopollis minoris* Krutzsch, pp. 87, 88, pl. 2, figs. 16–20.

1981 *Semioculopollis verrucosus* Christopher, 1979 [sic]; Azema et al., pl. 6, fig. 12.

Emended diagnosis. A *Trudopollis* with convex sides interradially. Inner contour trilobate. Nexine moderately thick, about same thickness as sexine in interradial regions, may be separated from it by a very narrow interloculum. Ektannuli only slightly protruding, intrabaculate. Endogerminals are narrow pores associated with shallow, U-shaped atria. Narrow, shallow vestibula may be present. Oculi discernible

on both sides of grain, but not protruding. Surface very uneven, maculate to weakly verrucate.

Size. 31 µm (one specimen); 25–40 µm for *E. exemplum* and *E. pertinax* (Pflug in Thomson and Pflug, 1953); 28–35 µm for *O. pertrudoides*, c. 25 µm for *O. minoris* (Krutzsch, 1973).

Remarks. *Trudopollis exemplum* differs from *T. fossulotrudens* in having maculate to less obvious verrucate sculpture, an intrabaculate structure within the ektannuli, a thicker exine, and pronounced oculi; *T. maestrichtiensis* on account of its coarser sculpture and thicker exine; and the other species of *Trudopollis* considered herein by the presence of oculi.

Occurrence. Germany (Thomson and Pflug, 1953; Pflug, 1953; Krutzsch, 1973), Belgium (our material), France (Azema et al., 1981).

Stratigraphic range. Lower–middle Santonian (Azema et al., 1981), middle–upper Santonian (our material), upper Maastrichtian (Krutzsch, 1973), "oldest Tertiary" (Pflug in Thomson and Pflug, 1953), Danian (Pflug, 1953).

Trudopollis fossulotrudens (Pflug in Thomson and Pflug, 1953) Pflug, 1953 emend. (Plate XV, 8–10)

1953 *Extratriporopollenites fossulotrudens* Pflug in Thomson and Pflug, pp. 74, 75, pl. 6, figs. 91, 99–101.

1953 *Extratriporopollenites anoculus* Pflug in Thomson and Pflug, p. 74, pl. 6, fig. 98.

1953 *Trudopollis anoculus* (Pflug in Thomson and Pflug, 1953) Pflug, p. 102, pl. 22, fig. 54; pl. 23, figs. 1–4.

1953 *Trudopollis fossulotrudens* (Pflug in Thomson and Pflug, 1953) Pflug, p. 102, pl. 23, figs. 6, 7.

1963 *Oculopollis fossulotrudens* (Pflug, 1953) Zaklinskaya, pp. 174, 176, pl. 14, figs. 7, 8.

1965 *Trudopollis meekeri* Newman, pp. 14, 16, pl. 1, fig. 12, text-fig. 5a.

Emended diagnosis. A *Trudopollis* with slightly convex sides. Inner contour slightly trilobate. Separation between nexine and sexine not clear. No interloculum. Ektannuli rounded, only slightly prominent, essentially unstructured. Endogerminals are fairly narrow pores associated with moderately deep atria. Vestibula when discernible, narrow and very shallow. Oculi may be present but only weakly developed. Surface granulate to irregularly verrucate.

Size range. 22 (26.3) 32 µm (five specimens); 18–35 µm for *E. fossulotrudens*, 25–45 µm for *E. anoculus* (Pflug in Thomson and Pflug, 1953); 10–22 µm for *O. fossulotrudens* (Zaklinskaya, 1963); 19–28 µm for *T. meekeri* (Newman, 1965).

Remarks. Unlike Zaklinskaya (1963), we decided that this species is better referred to the genus *Trudopollis* rather than to *Oculopollis* because of its U-shaped atria, relatively short ektannuli and, when present, only weakly developed oculi. It differs from *T. lativerrucatus* in being sculptured with smaller verrucae and in having proportionally less robust ektannuli; *T. maestrichtiensis* in being more coarsely sculptured and again in having proportionally less robust ektannuli; and *T. rusticus* owing to its finer sculpture, thinner exine, the presence of faint oculi, and its less sturdy aspect overall. For differentiation from *T. acinosus* and *T. exemplum*, see under remarks for these species. It is distinguished from the other species of *Trudopollis* considered herein in being sculptured with verrucae.

Occurrence. Germany (Thomson and Pflug, 1953), West Siberian Plain, Kazakhstan, Urals (Zaklinskaya, 1963), Hungary (our material), New Jersey (our material), Colorado (Newman, 1965).

Stratigraphic range. Lower–middle Santonian (our material), lower Campanian (our material), Campanian (Newman, 1965), Maastrichtian–Paleocene (Zaklinskaya, 1963), Paleocene (Thomson and Pflug, 1953).

Trudopollis geometricus Weyland et Krieger, 1953 emend. (Plate XV, 11–19)

1953 *Trudopollis geometricus* Weyland et Krieger, p. 16, pl. 2, figs. 42, 43; pl. 5, fig. 31.

1953 *Trudopollis ametricus* Pflug, p. 102, pl. 20, figs. 37, 42, 43.

1968 *Extratriporopollenites geometricus* (Weyland et Krieger, 1953) Skarby, pp. 42–44, pl. 18, figs. 1–9, text-fig. 9: 1, 2.

Emended diagnosis. A triangular *Trudopollis* with straight or slightly concave sides. Inner contour triangular. Both nexine and sexine thin in interradial regions and usually separated by a narrow interloculum. Ektannuli elongate, intrabaculate. Endogerminals are wide pores associated with U- to slightly V-shaped, fairly deep atria. No vestibula or oculi. Surface may be essentially smooth but commonly maculate to granulate.

Size range. 30 (33.4) 39 µm (13 specimens); c. 20 µm (Weyland and Krieger, 1953); c. 20 µm for *T. ametricus* (Pflug, 1953); 27–39 µm for *E. geometricus* (Skarby, 1968).

Remarks. *Trudopollis primigenius* is fairly similar to *T. geometricus* but differs in having a subcircular inner contour and usually slightly to more strongly convex sides in equatorial aspect. The triangular to concave-triangular equatorial outline coupled with the elongated, intrabaculate ektannuli that characterize *T. geometricus* distinguish it from the other species of *Trudopollis* considered herein. It differs from species of *Vacuopollis* Pflug, 1953 in having an invaginated nexine in the germinals.

Occurrence. Belgium (our material), Germany (our material; Weyland and Krieger, 1953; Pflug, 1953; Skarby, 1968), Sweden (our material; Skarby, 1968).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953; Pflug, 1953; Skarby, 1968), lowermost Campanian (our material; Skarby, 1968).

Trudopollis hemimechanicus Pflug, 1953 emend. (Plate XV, 20–28)

1953 *Trudopollis hemimechanicus* Pflug, p. 100, pl. 24, figs. 21–23.

1953 *Trudopollis orthomechanicus* Pflug, p. 99, pl. 24, figs. 1–15.

1968 *Extratriporopollenites hemiperfectus* Pflug in Thomson and Pflug, 1953; Skarby (pro parte), pp. 39–42, pl. 17, figs. 1, 2, 4 only.

1981 *Hofkeripollenites capsula* (Pflug, 1953) Kedves et Herngreen, p. 512, pl. 8, figs. 8–11.

1981 *Hofkeripollenites hemimechanicus* (Pflug, 1953) Kedves et Herngreen, subsp. *hemimechanicus* Kedves et Herngreen, p. 516, pl. 8, figs. 6, 7.

1982 *Trudopollis pflugii* Kedves, subsp. *pflugii* Kedves in Kedves and Russell, p. 97, pl. 7, figs. 7, 8.

1982 *Trudopollis pflugii* Kedves, subsp. *minor* Kedves in Kedves and Russell, p. 97, pl. 7, figs. 9, 10.

Emended diagnosis. A usually small *Trudopollis* with straight to slightly convex sides interradially. Inner contour trilobate. Nexine as thick as, or thicker than, sexine in interradial regions. Interloculum clearly visible in some specimens but barely discernible in others. Ektannuli small but fairly robust, finely intrabaculate. Endogerminals are fairly wide pores associated with deep, U-shaped atria. Vestibula absent or narrow and shallow. No oculi. Surface smooth to maculate or finely granulate.

Size range. 23 (26.5) 29 µm (eight specimens); c. 20 µm (Pflug, 1953); c. 18 µm for *T. orthomechanicus*, c. 27 µm for *T. capsula* (Pflug, 1953); 20–21 µm for *H. capsula*, 28–35 µm for *H. hemimechanicus* (Kedves and Herngreen, 1981); 18–23 µm for *T. pflugii* subsp. *minor*, 23–28 µm for *T. pflugii* subsp. *pflugii* (Kedves in Kedves and Russell, 1982).

Remarks. *Trudopollis hemimechanicus* differs from *T. hemiperfectus* by its thicker exine, larger ektannuli, and the absence of true cunei; *T. oculoides* by its smaller size, less protruding ektannuli, and lack of cunei; *T. retifectus* by its more triangular outline, larger ektannuli, and thicker exine; and *T. retigressus* by its usually smaller size and the absence of cunei. For differentiation from *T. conrector*, see remarks under this species.

Occurrence. Germany (our material; Pflug, 1953; Skarby, 1968), Netherlands (Kedves and Herngreen, 1981) Belgium (our material), Sweden (Skarby, 1968), France (Kedves in Kedves and Russell, 1982).

Stratigraphic range. Middle–upper Santonian (our material; Pflug, 1953), lowermost Campanian (Skarby, 1968), Maastrichtian (Kedves and Herngreen, 1981), Paleocene (Kedves in Kedves and Russell, 1982).

Trudopollis hemiperfectus (Pflug in Thomson and Pflug, 1953) Pflug, 1953 emend. (Plate XVI, 1–9)

1953 *Extratriporopollenites hemiperfectus* Pflug in Thomson and Pflug, p. 75, pl. 6, figs. 112–115.

1953 *Trudopollis hemiperfectus* (Pflug in Thomson and Pflug, 1953) Pflug, p. 101, pl. 23, figs. 13–15.

1953 *Trudopollis succedanus* Pflug (pro parte), p. 103, pl. 23, figs. 48, 49, 52 only.

1968 *Extratriporopollenites hemiperfectus* Pflug in Thomson and Pflug, 1953; Skarby (pro parte), pp. 39–42, pl. 16, figs. 1, 2, 9, 12, 13a–b; pl. 17, figs. 5–7 only.

1981 *Kriegeripollenites hemiperfectus* (Pflug, 1953) Kedves et Herngreen, p. 511.

2002 *Trudopollis hemiperfectus* (Pflug in Thomson and Pflug, 1953) Pflug, 1953; Zetter et al., p. 220, pl. 6, figs. 10–12.

Emended diagnosis. A small *Trudopollis* with convex sides. Inner contour strongly trilobate. Nexine as thick as, or a little thicker than, sexine in interradial regions. Interloculum barely discernible. Ektannuli small, weakly developed and essentially unstructured except close to base where they become less homogeneous (more granular) or with fine intrabaculate structure. Endogerminals are fairly deep cunei extending from one-third to half-way to pole. Vestibula very short and narrow. No oculi. Surface granulate.

Size range. 23 (25.2) 26 µm (nine specimens); 18–35 µm (Pflug in Thomson and Pflug, 1953); 18–25 µm for *T. succedanus* (Pflug, 1953); 22–25 µm (Zetter et al. 2002).

Remarks. *Trudopollis hemiperfectus* differs from *T. oculoides* in being smaller and having non-protruding ektannuli; *T. retifectus* in that the endogerminals are cunei and not associated with U-shaped atria; *T. retigressus* in being slightly smaller and having non-protruding ektannuli; and *T. succedanus* in usually being smaller and having shallower cunei. For differentiation from *T. hemimechanicus*, see remarks under this species.

Occurrence. Germany (our material; Thomson and Pflug, 1953; Pflug, 1953; Skarby, 1968), Sweden (Skarby, 1968), Netherlands (our material; Kedves and Herngreen, 1981), Belgium (our material), Austria (Zetter et al., 2002).

Stratigraphic range. Middle–upper Santonian (our material; Thomson and Pflug, 1953; Pflug, 1953; Skarby, 1968), Santonian (Zetter et al., 2002), lowermost Campanian (Skarby, 1968), Maastrichtian (Kedves and Herngreen, 1981).

Trudopollis imperfectus (Pflug in Thomson and Pflug, 1953) Pflug 1953 emend. (Plate XVI, 10–15)

1953 *Extratriporopollenites imperfectus* Pflug in Thomson and Pflug, p. 75, pl. 6, fig. 111.

1953 *Trudopollis imperfectus* (Pflug in Thomson and Pflug, 1953) Pflug, p. 101.

Emended diagnosis. A *Trudopollis* with convex sides. Inner contour subcircular to weakly trilobate. Nexine quite thick, about same thickness as sexine in interradial regions, but can be a little thinner or thicker, the two layers commonly separated by a narrow interloculum. Ektannuli range from being small and weakly expanded to somewhat larger and more robust, usually with finely intrabaculate structure. Endogerminals are fairly wide pores associated with shallow atria. When interloculum is not discernible, vestibula are shallow and narrow. No oculi. Surface smooth to scabrate or maculate/weakly verrucate.

Size range. 25 (26.8) 29 µm (12 specimens); 20–40 µm for *E. imperfectus* (Pflug in Thomson and Pflug, 1953).

Remarks. *Trudopollis imperfectus* differs from *T. nonperfectus* mainly in having a thicker nexine, wider atria, and a more rounded equatorial outline; *T. pertrudens* in usually being smaller, and in having a thicker nexine, a less obvious interloculum, and less clearly delineated intrabaculate structure in the ektannuli; and *T. retifectus* in having a thicker exine and shallower atria, and in lacking the granulate sculpture that characterizes most specimens of this species.

Occurrence. Germany (Thomson and Pflug, 1953), Belgium (our material), France (our material).

Stratigraphic range. Upper Turonian (our material), middle–upper Santonian (our material), lower Paleocene (Thomson and Pflug, 1953).

Trudopollis lativerrucatus Kedves et Herngreen, 1981 emend. (Plate XVI, 16, 17)

1981 *Trudopollis lativerrucatus* Kedves et Herngreen, pp. 508, 510, pl. 7, figs. 11, 12.

Emended diagnosis. A small *Trudopollis* with straight to slightly convex sides. Inner contour trilobate. Nexine about same thickness as sexine in interradial regions. Interloculum when present, narrow. Ektannuli fairly robust, more or less unstructured or slightly less homogeneous internally. Endogerminals are fairly narrow pores

associated with moderately deep, U-shaped atria. Vestibula when present, can be wide and narrow or fairly deep. Oculi very weakly developed. Surface verrucate.

Size. 22, 24 µm (two specimens); 18–23 µm (Kedves and Herngreen, 1981).

Remarks. Trudopollis lativerrucatus differs from *T. nonperfectus* in having deeper atria and coarser sculpture, and *T. rusticus* in being smaller and sculptured with smaller verrucae. For differentiation from *T. acinosus* and *T. fossulotrudens*, see remarks under these species.

Occurrence. New Jersey (our material), Belgium (our material), Netherlands (Kedves and Herngreen, 1981).

Stratigraphic range. Lower–middle Santonian (our material), middle–upper Santonian (our material), Maastrichtian (Kedves and Herngreen, 1981).

Trudopollis maestrichtiensis Kedves et Herngreen, 1981 emend. (Plate XVI, 19, 20)

1963 *Oculopollis retigressus* (Weyland et Krieger, 1953) Zaklinskaya (pro parte), pp. 169, 171, pl. 13, figs. 1, 2 only.

1981 *Trudopollis maestrichtiensis* Kedves et Herngreen, pp. 506, 508, pl. 7, figs. 7, 8.

Emended diagnosis. A *Trudopollis* with markedly convex sides interradially. Inner contour weakly trilobate. Nexine thin, thinner than sexine in interradial regions. No interloculum. Ektannuli relatively small but protruding, and with a very fine intrabaculate structure. Endogerminals are wide pores associated with fairly shallow atria. Oculi weakly developed. Vestibula narrow and shallow. Surface maculate.

Size. Two specimens, both 30 µm; 30 µm for *O. retigressus* (Zaklinskaya, 1963); 20–25 µm (Kedves and Herngreen, 1981).

Remarks. For differentiation of *Trudopollis maestrichtiensis* from *T. exemplum* and *T. fossulotrudens*, see remarks under these species. It differs from the other species of *Trudopollis* considered herein in having weakly developed oculi.

Occurrence. Belgium (our material), Netherlands (our material; Kedves and Herngreen, 1981).

Stratigraphic range. Middle–upper Santonian (our material), Maastrichtian (Kedves and Herngreen, 1981).

Trudopollis nonperfectus (Pflug in Thomson and Pflug, 1953) Pflug, 1953 emend. (Plate XVI, 21–26)

1953 *Extratriporopollenites nonperfectus* Pflug in Thomson and Pflug, p. 75, pl. 6, figs. 109, 110.

1953 *Trudopollis nonperfectus* (Pflug in Thomson and Pflug, 1953) Pflug, p. 101, pl. 23, figs. 9–12.

1963 *Trudopollis nonperfectus* (Pflug in Thomson and Pflug, 1953) Pflug, 1953; Zaklinskaya, pl. 29, figs. 18, 19.

1968 *Extratriporopollenites nonperfectus* Pflug, 1953; Skarby (pro parte), pp. 37–39, pl. 15, figs. 2, 6–8 only.

1972 *Extratriporopollenites nonperfectus* Pflug in Thomson and Pflug, 1953; Srivastava, pl. 13, figs. 5–9.

1975 *Trudopollis variabilis* Tschudy, pp. 25, 26, pl. 16, figs. 13–22, text-fig. 26.

1979 *Trudopollis* sp. A; Christopher, pl. 5, figs. 6, 7.

1979 *Trudopollis* sp. B; Christopher, pl. 5, figs. 8, 9.

2010 *Trudopollis meekeri* Newman, 1965; Christopher and Prowell, fig. 14, G–K.

Emended diagnosis. A small *Trudopollis* with straight to slightly convex sides. Inner contour subcircular to weakly trilobate. Nexine quite thin, slightly thinner than, or about same thickness as, sexine in interradial regions. No interloculum. Ektannuli usually relatively small and rounded, unstructured to very finely intrabaculate. Endogerminals are fairly wide pores associated with shallow atria. Vestibula narrow and shallow. No oculi. Surface maculate.

Size range. 22 (23.7) 26 µm (six specimens); 15–25 µm for *E. nonperfectus* (Pflug in Thomson and Pflug, 1953); 22–29 µm for *T. variabili*s (Tschudy, 1975).

Remarks. *Trudopollis nonperfectus* differs from *T. obexemplum* in lacking an interloculum and in having shallower atria and a maculate surface, and from *T. pertrudens* in being smaller, also lacking an interloculum, and in having a thinner exine, a more triangular equatorial outline, and a maculate surface. For differentiation from *Trudopollis acinosus*, *T. imperfectus* and *T. lativerrucatus*, see remarks under these species.

Occurrence. Germany (Thomson and Pflug, 1953; Skarby, 1968), Sweden (Skarby, 1968), New Jersey (our material; Christopher, 1979), Tennessee (Tschudy, 1975), Alabama (Srivastava, 1972), South Carolina (Christopher and Prowell, 2010), Belgium (our material), north-west Siberian Plain (Zaklinskaya, 1963).

Stratigraphic range. Lower–middle Santonian (our material; Christopher, 1979), middle–upper Santonian (our material; Thomson and Pflug, 1953; Skarby, 1968; Christopher and Prowell, 2010), lowermost Campanian (Skarby, 1968), Campanian (Tschudy, 1975; Christopher and Prowell, 2010), Turonian and "Senonian" (Zaklinskaya, 1963), Paleocene (Srivastava, 1972).

Trudopollis obexemplum (Pflug in Thomson and Pflug, 1953) Pflug, 1953 emend.

(Plate XVI, 18)

1953 *Extratriporopollenites obexemplum* Pflug in Thomson and Pflug, p. 75, pl. 6, fig. 106.

1953 *Trudopollis obexemplum* (Pflug in Thomson and Pflug, 1953) Pflug, p. 101, pl. 25, fig. 49.

Emended diagnosis. A *Trudopollis* with straight to slightly convex sides. Inner contour subtriangular. Nexine thin, as thick as sexine in interradial regions, the two layers being clearly separated by an interloculum. Ektannuli slightly protruding, finely intrabaculate. Endogerminals are very wide pores associated with fairly deep atria. No vestibula or oculi. Surface smooth to finely granulate.

Size. 26 µm (one specimen); 25–40 µm for *E. obexemplum* (Pflug in Thomson and Pflug, 1953).

Remarks. *Trudopollis obexemplum* is similar to some of the smaller specimens attributed to *T. protrudens* but differs in having a less convex equatorial outline, a thinner sexine that is not obviously perforated, and deeper and wider atria. It is also morphologically close to some species of *Vacuopollis* and might be better placed in that genus. For differentiation from *T. nonperfectus*, see remarks under this species.

Occurrence. Germany (our material; Thomson and Pflug, 1953).

Stratigraphic range. Middle–upper Santonian (our material), Paleocene (Pflug, 1953).

Trudopollis oculoides Krutzsch, 1968 emend. (Plate XVI, 31–35)

1968 *Trudopollis oculoides* Krutzsch, pp. 792, 794, pl. 2, figs. 1–8.

1970 *Semioculopollis oculoides* (Krutzsch, 1968) Pacltová et Krutzsch, p. 589.

[transfer invalid: lacks full reference to the basionym].

Emended diagnosis. A large *Trudopollis* with convex sides interradially. Inner contour trilobate. Nexine thicker than sexine in interradial regions. No interloculum. Ektannuli robust and protruding, club-like, more or less unstructured to slightly less homogeneous internally, especially close to base, but more commonly finely intrabaculate. Endogerminals associated with fairly deep cunei extending from one-third to half-way to the pole. No vestibula or oculi. Surface scabrate to granulate.

Size range. 39 (43.3) 46 µm (seven specimens); 45–60 µm (Krutzsch, 1968).

Remarks. *Trudopollis oculoides* differs from both *T. retigressus* and *T. succedanus* in being larger and in having more pronounced ektannuli. In addition, it has shallower

cunei than *T. succedanus*. For differentiation from *T. cuneolis*, *T. conrectiformis*, *T. hemimechanicus* and *T. hemiperfectus*, see remarks under these species.

Occurrence. Germany (our material; Krutzsch, 1968), Belgium (our material).

Stratigraphic range. Middle–upper Santonian (our material), middle Paleocene–Eocene (Krutzsch, 1968).

Trudopollis peneperfectus (Pflug in Thomson and Pflug, 1953) Pflug, 1953 emend. (Plate XVI, 27, 28)

1953 *Extratriporopollenites peneperfectus* Pflug in Thomson and Pflug, p. 76, pl. 6, figs. 119–123.

1953 *Trudopollis peneperfectus* (Pflug in Thomson and Pflug, 1953) Pflug, p. 103, pl. 23, figs. 31–34.

1960 *Extratriporopollenites sectilis* Stel'mak in Pokrovskaya and Stel'mak, p. 233, pl. 11, fig. 16.

1967 *Pompeckjoidaepollenites peneperfectus* (Pflug in Thomson and Pflug, 1953) Krutzsch in Góczán et al., p. 492, pl. 13, figs. 28, 29.

Emended diagnosis. A *Trudopollis* with a rounded-triangular equatorial outline. Inner contour trilobate and effectively tripartite. Nexine a little thicker than sexine in

interradial regions. An interloculum may be present. Ektannuli fairly small, finely intrabaculate. Endogerminals are pores associated with deep atria and plateae. No vestibula or oculi. Surface granulate.

Size. 31, 33 µm (two specimens); 20–35 µm for *E. peneperfectus* (Pflug in Thomson and Pflug, 1953); holotype of *E. sectilis* 31.2 µm (Stel'mak in Pokrovskaya and Stel'mak, 1960).

Remarks. *Trudopollis peneperfectus* is similar to *T. pompeckjii* but differs in usually being larger and less rounded in equatorial outline, and in having more pronounced ektannuli; and from *T. succedanus* in that no specimens lack plateae and these do not converge over the pole.

Occurrence. Germany (Thomson and Pflug, 1953), Belgium (our material), Kazakhstan (Stel'mak in Pokrovskaya and Stel'mak, 1960).

Stratigraphic range. Turonian (Stel'mak in Pokrovskaya and Stel'mak, 1960), middle–upper Santonian (our material), Paleocene (Góczán et al., 1967).

Trudopollis pertrudens (Pflug in Thomson and Pflug, 1953) Pflug, 1953 emend. (Plate XVII, 1–7)

1953 *Extratriporopollenites pertrudens* Pflug in Thomson and Pflug, p. 74, pl. 6, figs. 74–90, 92–94.

1953 *Trudopollis pertrudens* (Pflug in Thomson and Pflug, 1953) Pflug, p. 98, pl. 22, figs. 8–19; pl. 25, fig. 59.

1981 *Trudopollis rector* Pflug, 1953; Azema et al., pl. 7, fig. 6.

Emended diagnosis. A *Trudopollis* with slightly to strongly convex sides. Inner contour trilobate. Nexine slightly thinner than sexine in interradial regions, these layers usually separated by an interloculum. Ektannuli can be slightly protruding, but usually quite small and not greatly expanded, and with an intrabaculate structure. Endogerminals are fairly wide pores associated with more or less deep, U-shaped atria. Vestibula narrow and shallow. No oculi. Surface smooth or scabrate.

Size range. 25 (33.3) 41 µm (10 specimens); 25–60 µm for *E. pertrudens* (Pflug in Thomson and Pflug, 1953).

Remarks. *Trudopollis pertrudens* is similar to *T. protrudens* but differs in lacking visible perforations of the sexine, and in having a smoother surface and a somewhat stockier aspect. It also differs from *T. retifectus* in having a thicker exine, shallower and narrower atria, and more pronounced ektannuli, and *T.* sp. cf. *T. rotundus* in that the ektannuli are more pronounced and it has a generally less rounded aspect in equatorial view. For differentiation from *T. articulus*, *T. imperfectus* and *T. nonperfectus*, see remarks under these species.

Occurrence. Germany (Thomson and Pflug, 1953), Belgium (our material), France (Azema et al., 1981).

Stratigraphic range. Middle–upper Santonian (our material), lower Turonian–lower Campanian (Azema et al., 1981), Senonian–lower Paleocene (Pflug, 1953), lower Paleocene (Thomson and Pflug, 1953).

Trudopollis pompeckjii (Potonié, 1931) Pflug, 1953 emend. (Plate XVI, 29, 30)

1931 *Pollenites pompeckji* Potonié, p. 332, pl. 1, fig. 9.

1953 *Extratriporopollenites pompeckji* (Potonié, 1931) Pflug in Thomson and Pflug, p. 76, pl. 6, figs. 124–144.

1953 *Trudopollis pompeckji* (Potonié, 1931) Pflug, p. 103, pl. 23, figs. 28, 29, 35–43, 50, 51.

1953 *Trudopollis platoides* Pflug, p. 103, pl. 23, figs. 44–47.

1954 *Trudopollis subhercynicus* n. nom. Krutzsch, p. 287, pl. 1, figs. 19–22.

1961 *Trudopollis subhercynicus* Krutzsch, pp. 94–96.

1963 *Trudopollis pompeckji* (Potonié, 1931) Pflug, 1953; Zaklinskaya, pl. 32, fig. 1.

1967 *Pompeckjoidaepollenites platoides* (Pflug, 1953) Krutzsch in Góczán et al., p. 492, pl. 13, figs. 19, 20.

1967 *Pompeckjoidaepollenites subhercynicus* (Krutzsch, 1954) Krutzsch in Góczán et al., p. 492, pl. 13, figs. 21–27.

1968 *Extratriporopollenites hemiperfectus* Pflug in Thomson and Pflug, 1953; Skarby (pro parte), pp. 39–42, pl. 16, figs. 10, 11 only.

1973 *Trudopollis nonplatoides* Manykin, pp. 143, 144, pl. 7, fig. 21.

1973 *Trudopollis dubius* Manykin, p. 144, pl. 7, fig. 20.

2015 *Pompeckjoidaepollenites subhercynicus* (Krutzsch, 1954) Krutzsch in Góczán et al., 1967; Daly and Jolley, pl. 2, fig. 5 (mislabelled as *Coratinipollenites paleocenicus* in the plate caption).

Emended diagnosis. A small *Trudopollis* with a subcircular equatorial outline. Inner contour trilobate and effectively tripartite. Nexine thin, about same thickness as sexine in interradial regions. An interloculum may be present. Ektannuli small and weakly expanded, usually finely intrabaculate. Endogerminals are pores associated with deep atria and plateae. No vestibula or oculi. Surface finely granulate.

Size. 24 µm (one specimen); 18–40 µm for *E. pompeckji* (Pflug in Thomson and Pflug, 1953); c. 18 µm for *T. platoides* Pflug (1953); no sizes or size range given for *T. subhercynicus* in Krutzsch (1954) or Krutzsch in Góczán et al. (1967); 30–32 µm for both *T. dubius* and *T. nonplatoides* (Manykin, 1973).

Remarks. *Trudopollis pompeckjii* is smaller than *T. succedanus*, has less pronounced ektannuli and better developed plateae. For differentiation from *T. peneperfectus*, see remarks under this species.

Occurrence. Germany (our material; Thomson and Pflug, 1953), Sweden (Skarby, 1968), Belarus (Manykin, 1973), eastern North America to Central Asia (Góczán et al., 1967), Urals, Western and Eastern Europe, West Siberia and Kazakhstan (Zaklinskaya, 1963), Ukraine (Daly and Jolley, 2015).

Stratigraphic range. Middle Turonian–upper Eocene with main occurrence between Maastrichtian and middle Eocene (Góczán et al., 1967), middle–upper Santonian (our material), lowermost Campanian (Skarby, 1968), Paleocene (Manykin, 1973), Campanian–Paleocene (Góczán et al., 1967), Paleocene–Middle Eocene (Manykin, 1973), lower Paleocene–Middle Eocene (Thomson and Pflug, 1953), lower "Senonian"–Oligocene (Zaklinskaya, 1963), Danian (Daly and Jolley, 2015).

Trudopollis primigenius Krutzsch, 1973 emend. (Plate XVII, 25, 31)

1973 *Extratriporopollenites* [aut *Trudopollis*] *primigenius* Krutzsch, p. 83, pl. 1, figs. 34–38.

1979 *Trudopollis hojrupensis* Kedves, p. 170, pl. 1, figs. 15, 16.

1981 *Felderipollenites triangulus* Kedves et Herngreen, pp. 520, 522, pl. 9, figs. 3, 4.

1981 *Felderipollenites granulatus* Kedves et Herngreen, p. 522, pl. 9, figs. 5, 6.

Emended diagnosis. A *Trudopollis* with straight to slightly convex sides interradially. Inner contour subcircular. Nexine about same thickness as sexine in interradial regions. No interloculum. Ektannuli fairly elongate and with a finely intrabaculate structure. Endogerminals are wide pores associated with shallow atria and fairly deep vestibula. No oculi. Surface smooth to finely granulate.

Size. 21, 31 µm (two specimens); 28–35 µm (Krutzsch, 1973); 18–25 µm for *T. hojrupensis* (Kedves, 1979); 24–28 µm for *F. granulatus*, 27–32 µm for *F. triangulus* (Kedves and Herngreen, 1981).

Remarks. For differentiation of *Trudopollis primigenius* from *T. geometricus*, see remarks under this species. It differs from all the other species of *Trudopollis* considered herein in that the bases of the ektannuli are separated from the nexine by deep vestibula.

Occurrence. France (our material), Belgium (our material), Netherlands (Kedves and Herngreen, 1981), Denmark (Kedves, 1979), Germany (Krutzsch, 1973).

Stratigraphic range. Upper Turonian (our material), middle–upper Santonian (our material), Maastrichtian (Krutzsch, 1973; Kedves and Herngreen, 1981), lower Danian (Kedves, 1979).

Trudopollis protrudens (Erdtman in Ross, 1949) Pflug, 1953 emend. (Plate XVII, 8–17)

1949 *Tricolporites protrudens* Erdtman in Ross, pp. 35, 37, pl. 2, fig. 25, pl. 3, fig. 42, fig. 3.

1953 *Extratriporopollenites baculotrudens* Pflug in Thomson and Pflug, p. 74, pl. 6, figs. 95, 96.

1953 *Trudopollis protrudens* (Erdtman in Ross) Pflug, p. 98, pl. 23, figs. 61–73.

1953 *Trudopollis mechanicus* Pflug, p. 99, pl. 24, figs. 16–20.

1953 *Trudopollis baculotrudens* (Pflug in Thomson and Pflug, 1953) Pflug, p. 100, pl. 22, fig. 34.

1953 *Trudopollis exotrudens* Weyland et Krieger, p. 14, pl. 2, figs. 48, 49.

1953 *Trudopollis incessus* Weyland et Krieger (pro parte), p. 16, pl. 5, fig. 44 only.

1953 *Trudopollis* cf. *incessus* Weyland et Krieger, pl. 5, fig. 52.

Emended diagnosis. A *Trudopollis* with slightly to strongly convex sides. Inner contour weakly trilobate. Nexine thin, thinner than, or about same thickness as, sexine in interradial regions, the two layers usually being clearly separated by an interloculum. Sexine penenetrated by numerous, closely spaced perforations that are usually clearly visible. Ektannuli slightly protruding and with an intrabaculate structure. Endogerminals are fairly wide pores associated with moderately deep atria.

Vestibula and interlocula grade into each another. No oculi. Surface scabrate to maculate and perforated.

Size range. 23 (31.9) 39 µm (seven specimens); c. 28 µm Pflug (1953); 25–60 µm for *E. baculotrudens* (Pflug in Thomson and Pflug, 1953); c. 15 µm for *T. mechanicus* (Pflug, 1953); c. 25 µm for *T. exotrudens* and *T. incessus* (Weyland and Krieger, 1953).

Remarks. We place *Trudopollis mechanicus* in synonymy with *T. protrudens* because of statements made by Pflug (1953, p. 99, in German, translated here) in his diagnoses of *T. mechanicus* and *T. orthomechanicus*. In connection with the former he wrote "Similar to *T. orthomechanicus* but contour convex", and for *T. orthomechanicus* he wrote "Similar to *T. protrudens*, but smaller. Contour rigidly triangular." Therefore, if some intraspecific variability is taken into account, and the specimen illustrated on Plate XVII, 10 herein is included in *T. protrudens*, this species and *T. mechanicus* become synonyms, and *T. orthomechanicus* is better placed in synonymy with *T. hemimechanicus* because of its more triangular equatorial outline.

We put *T. baculotrudens* in synonymy with *T. protrudens* because the diagnosis provided by Thomson and Pflug (1953, p. 74) merely states (in translation) "Corresponds to *Extratriporopollenites pertrudens*, but is significantly intrabaculate and baculate", which is equally true for *T. protrudens*. However, we did not put *Oculopollis baculotrudens* (Pflug, 1953) Zaklinskaya, 1963 in synonymy because the specimens figured by Zaklinskaya (pl. 14, figs. 1–5) do not match Thomson and

Pflug's diagnosis. *Trudopollis exotrudens* was described by Weyland and Krieger (1953, p. 14, in translation) as being similar to the "*Protrudens*-type". We think it is simply a morphological variant of *T. protrudens* and therefore include it in this species.

Trudopollis protrudens differs from *T. retifectus* mainly in having a sexine that is generally clearly perforated, and narrower and shallower atria, and from *T.* sp. cf. *T. rotundus* in not only usually having an obviously perforated sexine but also more protruding ektannuli. For differentiation from *T. obexemplum* and *T. pertrudens*, see remarks under these species.

Occurrence. Germany (our material; Pflug, 1953; Weyland and Krieger, 1953), Belgium (our material), Sweden (our material).

Stratigraphic range. Middle–upper Santonian (our material; Pflug, 1953), lowermost Campanian (our material).

Trudopollis retifectus Weyland et Krieger, 1953 emend. (Plate XVII, 18–24)

1953 *Trudopollis retifectus* Weyland et Krieger, p. 15, pl. 5, fig. 25.

1981 *Magnoporopollis prezaensis* Kedves et Diniz, 1980 [sic]; Kedves and Herngreen, pl. 11, figs. 5, 6 [nomen nudum].

Emended diagnosis. A *Trudopollis* with a subcircular to rounded-triangular equatorial outline. Inner contour trilobate. Nexine very thin, about same thickness as sexine in interradial regions. Very fine perforations in the sexine in some specimens may be suggested when viewed in optical section. Interloculum commonly apparent. Ektannuli small and rounded, more or less unstructured to slightly less homogeneous internally, especially close to base, but usually very finely intrabaculate. Endogerminals are wide pores associated with deep, U-shaped atria. Vestibula when present, shallow and narrow. No oculi. Surface smooth to granulate.

Size range. 27 (30.2) 32 µm (12 specimens); c. 25 µm (Weyland and Krieger, 1953).

Remarks. *Trudopollis retifectus* differs from *T.* sp. cf. *T. rotundus* in having a thinner exine and deeper atria. For differentiation from *Trudopollis hemimechanicus*, *T. hemiperfectus*, *T. imperfectus*, *T. pertrudens* and *T. protrudens*, see remarks under these species.

Occurrence. Germany (our material; Weyland and Krieger, 1953), Netherlands (our material; Kedves and Herngreen, 1981), Belgium (our material).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953), Maastrichtian (Kedves and Herngreen, 1981).

Trudopollis retigressus Weyland et Krieger, 1953 emend. (Plate XVIII, 1–7)

1953 *Trudopollis retigressus* Weyland et Krieger (pro parte), p. 15, pl. 2, figs. 26, 28; pl. 5, figs. 32, 33 only.

1963 *Oculopollis retigressus* (Weyland et Krieger, 1953) Zaklinskaya (pro parte), pp. 169–171, pl. 13, fig. 3 only.

1981 *Kriegeripollenites retigressus* (Weyland et Krieger, 1953) Kedves et Herngreen, p. 511, pl. 7, figs. 25, 26.

Emended diagnosis. A *Trudopollis* with straight to slightly convex sides interradially. Inner contour strongly trilobate. Nexine varies in thickness, about same thickness as sexine or a little thicker in interradial regions. An interloculum may be present. Ektannuli fairly large, protruding, more or less unstructured to slightly less homogeneous internally, especially close to base, but more commonly finely intrabaculate. Endogerminals associated with fairly deep cunei extending from one-third to half-way to the pole. Vestibula when present, narrow and fairly deep. No oculi. Surface smooth to maculate or finely granulate.

Size range. 30 (32.6) 35 μm (13 specimens); c. 30 μm (Weyland and Krieger, 1953); 33 μm for *K. retigressus* (Kedves and Herngreen, 1981).

Remarks. *Trudopollis retigressus* can be regarded as morphologically intermediate between *T. hemiperfectus* and *T. oculoides*. It differs from *T. succedanus* in having

shallower cunei and more pronounced ektannuli. For differentiation from *Trudopollis conrector, T. hemimechanicus, T. hemiperfectus* and *T. oculoides,* see remarks under these species.

Occurrence. Germany (Weyland and Krieger, 1953), Western Europe (Zaklinskaya, 1963), western Aral Sea region (Zaklinskaya, 1963), Siberia (Zaklinskaya, 1963), Netherlands (Kedves and Herngreen, 1981), Belgium (our material).

Stratigraphic range. Middle–upper Santonian (our material; Weyland and Krieger, 1953), Maastrichtian (Kedves and Hengreen, 1981), Campanian, Maastrichtian and Paleocene (Zaklinskaya, 1953).

Trudopollis sp. cf. *T. rotundus* Manum, 1962 (Plate XVIII, 8–10)

1962 *Trudopollis rotundus* Manum, pp. 51, 52, pl. 12, figs. 28–31, text-fig. 17.

Description. A *Trudopollis* with a subcircular equatorial outline. Inner contour weakly trilobate. Nexine thinner than sexine in interradial regions. Infratectum clearly granular. Ektannuli small, apparently unstructured or finely intrabaculate. Endogerminals are fairly wide pores associated with fairly shallow atria. Vestibula very narrow and shallow. No oculi. Surface maculate to finely granulate.

Size range. 28 (30.7) 32 µm (three specimens); holotype 31 µm, paratype 30 µm (Manum, 1962).

Remarks. This morphotype is very similar to Manum's (1962) species but he stated (p. 52) that "No connecting elements could be distinguished between the apparent interstice between the two main layers", and this is emphasized in his drawing (fig. 17). It is partly for this reason that we only compare our specimens with *T. rotundus*. The fact that his species was described from Paleocene deposits in Svalbard, which is well outside the Normapolles Province of the Late Cretaceous Epoch (see Section 2), is another reason for being cautious about our identification. For differentiation from *Trudopollis articulus*, *T. pertrudens*, *T. protrudens*, and *T. retifectus*, see remarks under these species.

Occurrence. Svalbard (Manum, 1962), New Jersey (our material), Belgium (our material).

Stratigraphic range. Lower–middle Santonian (our material), middle–upper Santonian (our material), Paleocene (Manum, 1962; recorded as Paleocene–Eocene but now known to be Palaeocene).

Trudopollis rusticus Pflug, 1953 emend. (Plate XVIII, 11–19)

1953 *Trudopollis rusticus* Pflug, p. 101, pl. 23, fig. 5.

Emended diagnosis. A *Trudopollis* with convex sides interradially. Inner contour circular to subcircular. Exine thick; nexine slightly thinner than, or more or less the same thickness as, sexine in interradial regions. Interloculum sometimes discernible. Ektannuli quite robust and squat, more or less unstructured to slightly less homogeneous internally. Endogerminals are fairly small pores associated with fairly shallow atria. Vestibula narrow and shallow. No oculi. Surface covered with closely spaced, irregularly shaped verrucae, sometimes forming a negative reticulum.

Size range. 29 (32) 34 µm (14 specimens); c. 28 µm (Pflug, 1953).

Remarks. For differentiation of *T. rusticus* from *T. fossulotrudens* and *T. lativerrucatus*, see remarks under these species. Its coarsely verrucate surface coupled with its robust aspect distinguish it from all the other species of *Trudopollis* considered herein.

Occurrence. France (our material), Germany (Pflug, 1953).

Stratigraphic range. Upper Turonian (our material), middle–upper Santonian (Pflug, 1953).

Trudopollis spinulosus (Skarby, 1968) comb. nov. emend. (Plate XVII, 26–29)

1968 *Extratriporopollenites spinulosus* Skarby, p. 57, pl. 25, fig. 7a–b, text-fig. 12: 5.

Emended diagnosis. A *Trudopollis* with a subcircular to convexly triangular equatorial outline. Inner contour trilobate. Nexine thin, as thick as, or a little thicker than, sexine in interradial regions, these two layers sometimes separated by a very narrow interloculum. Ektannuli very small and only weakly developed, finely intrabaculate. Endogerminals are narrow pores associated with more or less deep, U-shaped atria. Vestibula absent or very narrow. No oculi. Surface echinate.

Size range. 25 (28.5) 33 µm (four specimens); 22–24 µm, four specimens of *E. spinulosus* (Skarby, 1968).

Remarks. *Trudopollis spinulosus* differs from all other species of *Trudopollis* in having an echinate surface.

Occurrence. Portugal (our material), Germany (our material; Skarby, 1968), Belgium (our material), Sweden (Skarby, 1968).

Stratigraphic range. Middle–upper Santonian (our material; Skarby, 1968), lowermost Campanian (Skarby, 1968), Campanian–Maastrichtian (our material).

Trudopollis succedanus Pflug, 1953 emend. (Plate XVIII, 20–26)

1953 *Trudopollis succedanus* Pflug (pro parte), p. 103, pl. 23, figs. 53–60.

1953 *Trudopollis retigressus* Weyland et Krieger (pro parte), p. 15, pl. 2, fig. 29 only.

1981 *Kriegeripollenites laevigatus* Kedves et Herngreen, pp. 511, 512, pl. 8, figs. 1–3.

Emended diagnosis. A *Trudopollis* with straight to convex sides. Inner contour strongly trilobate to tripartite. Nexine as thick as, or a little thicker than, sexine in interradial regions, these layers separated by an interloculum in some specimens. Ektannuli fairly small, most with a delicate intrabaculate structure. Endogerminals are associated with very deep cunei that sometimes reach pole to form plateae. Vestibula very narrow and fairly shallow. No oculi. Surface granulate.

Size range. 29 (33.4) 37 µm (nine specimens); 18–25 µm (Pflug, 1953); 33–38 µm for *K. laevigatus* (Kedves and Herngreen, 1981).

Remarks. For differentiation from *T. hemiperfectus, T. oculoides, T. peneperfectus, T. pompeckjii* and *T. retigressus*, see remarks under these species.

Occurrence. Belgium (our material), Netherlands (Kedves and Herngreen, 1981) Germany (Pflug, 1953; Weyland and Krieger, 1953).

Stratigraphic range. Middle–upper Santonian (our material; Pflug, 1953; Weyland and Krieger, 1953), Maastrichtian (Kedves and Herngreen, 1981).

Trudopollis sp. A. (Plate XVII, 30)

Description. A small *Trudopollis*, rounded-triangular in equatorial outline. Inner contour trilobate. Nexine fairly thick, about same thickness as sexine in interradial regions. Interloculum barely discernible. Ektannuli small and robust, with a finely intrabaculate structure. Endogerminals are fairly wide pores associated with moderately shallow atria. Vestibula narrow and shallow. No oculi. Surface covered with coarse verrucae.

Size. 24 µm (one specimen).

Remarks. This form of *Trudopollis* differs from *T. fossulotrudens* in that it is more coarsely sculptured, has a thicker nexine, and is more rounded in equatorial outline; *T. exemplum* in being smaller and more coarsely sculptured, and in lacking oculi; and *T. rusticus* in being much smaller and more rounded in equatorial outline.

Occurrence. Sweden (our material).

Stratigraphic range. Lowermost Campanian (our material).

Trudopollis sp. B (Plate XV, 1, 2)

Emended diagnosis. A large *Trudopollis* with convex sides. Inner contour strongly trilobate. Nexine fairly thick, thinner than sexine in interradial regions, the latter being very thick and separated from it by an interloculum. Sexine penetrated by numerous closely spaced perforations except at extremities of germinals. Ektannuli relatively small, intrabaculate. Endogerminals are fairly wide pores associated with wide and deep, U-shaped atria. Vestibula narrow and deep. No oculi. Surface undulating and perforated.

Size. 51 µm (one specimen).

Remarks. *Trudopollis* sp. B differs from *T. conrectiformis* in having a clearly perforated sexine and deeper atria and vestibula. As for *Oculopollis artifex* and *O. bulbosus*, the abundant perforations through the sexine are considered to be essentially primary structures, although probably enhanced to some extent by degradation during fossilization.

Occurrence. Belgium (our material).

Stratigraphic range. Middle–upper Santonian (our material).

8. Systematic palaeontology: species transfers

Consequent upon some of the nomenclatural changes at generic level made in the preceding section it is necessary to transfer several species that we have not otherwise considered to four of the genera discussed, as follows:

Hungaropollis laevigatus (Kedves et Herngreen, 1981) comb. nov.

1981 *Romeinipollenites laevigatus* Kedves et Herngreen, pp. 517, 518, pl. 9, figs. 1, 2.

Hungaropollis triangulus (Kedves et Diniz, 1983) comb. nov.

1983b *Aveiropollenites triangulus* Kedves et Diniz, p. 21, pl. 1, figs. 9–14, fig. 2.

Longanulipollis pflugii (Kedves et Diniz, 1983) comb. nov.

1983a *Verruoculopollis pflugii* Kedves et Diniz, p. 335, pl. 2, figs. 7, 8, text-fig. 3.

Longanulipollis proprius (Góczán et Siegl-Farkas, 1989) comb. nov.

1989 *Coronatipollis proprius* Góczán et Siegl-Farkas, 1989, pp. 53, 54, pl. 4, figs. 10–12.

Longanulipollis tschudyi (Kedves et Diniz, 1983) comb. nov.

1983a *Verruoculopollis tschudyi* Kedves et Diniz, pp. 335, 336, pl. 2, figs. 9, 10, text-fig. 4

Oculopollis admirabilis (Tschudy, 1975) comb. nov.

1975 *Pseudoculopollis admirabilis* Tschudy, p. 20, pl. 11, figs. 9–18, text-fig. 17.

Oculopollis cardinaloides (Krutzsch, 1973) comb. nov.

1973 *Pseudoculopollis cardinaloides* Krutzsch, pp. 88, 89, pl. 2, figs. 25–30

Oculopollis granulosus (Kedves et Herngreen, 1981) comb. nov.

1981 *Semioculopollis granulosus* Kedves et Herngreen, pp. 504, 506, pl. 6, figs. 13–16.

Oculopollis minutus (Krutzsch et Pacltová in Góczán et al., 1967) comb. nov.

1967 *Semioculopollis minutus* Krutzsch et Pacltová in Góczán et al., p. 503, pl. 16, figs. 13–17.

Oculopollis verrucosa (Christopher, 1979) comb. nov.

1979 *Semioculopollis verrucosa* Christopher, pp. 117, 118, pl. 7, figs. 10, 11; pl. 9, figs. 18–30.

Trudopollis crassiexinus (Kedves et Herngreen, 1981) comb. et nom. nov.

1981 *Semioculopollis maestrichtiensis* Kedves et Herngreen, subsp. *maestrichtiensis* Kedves et Herngreen, pp. 500, 502, pl. 6, figs. 9, 10.

1981 *Semioculopollis maestrichtiensis* Kedves et Herngreen, subsp. *crassiexinus* Kedves et Herngreen, pp. 502, 504, pl. 6, figs. 11, 12.

Remarks. It is necessary to provide a new specific epithet for this species because Kedves and Herngreen (1981, pp. 506, 508) described another form as *Trudopollis maestrichtiensis*. Since we do not think that the two subspecies of *Semioculopollis* erected are adequately differentiated for practical purposes, we have selected the name of one of these to accommodate them.

Trudopollis croxtonae (Kedves, 1979) comb. nov.

1979 *Semioculopollis croxtonae* Kedves, p. 168, pl. 1, figs. 7, 8.

Trudopollis daniensis (Kedves, 1979) comb. nov.

1979 *Semioculopollis daniensis* Kedves, p. 169, pl. 1, figs. 9, 10.

Trudopollis hofkeri (Kedves et Herngreen, 1981) comb. et nom. nov.

1981 *Hofkeripollenites triangulus* Kedves et Herngreen, p. 516, pl. 8, figs. 4, 5.

Remarks. It is necessary to provide a new specific epithet for this species because Kedves and Herngreen (1981, pp. 510, 511) described another form as *Trudopollis triangulus*.

9. Discussion

9.1. Taxonomic observations

A major handicap to the identification of the majority of Normapolles pollen is that so many of the taxa described previously are virtually unusable for one or more of the reasons mentioned in the introductory sections of this paper. We aimed to place in

established species most of the morphotypes that we encountered in order to avoid erecting yet more taxa. However, for many this required interpretation of obscure descriptions often full of unnecessarily complicated terminology describing features that are commonly unrecognizable in the accompanying figures.

Skarby (1968) considered the structure of Normapolles grains to be less complex than had been thought by those who described the majority of genera and species during the 1950s and early 1960s (Pflug, 1953; Thomson and Pflug, 1953; Weyland and Krieger, 1953; Krutzsch, 1959; Góczán, 1964). Unfortunately, this observation did not deter others (especially Kedves and co-authors, and Song) from erecting many more taxa subsequently. Based on the results of scanning, and especially transmission electron microscopy of species representing several Normapolles genera, Batten (1986, 1989) noted that fewer basic differences occur between pollen within the group than many previous taxonomic studies had suggested, thus providing support for Skarby's (1968) contention. These revelations were taken into account when preparing our diagnoses, which, partly as a result, are mostly very different from what has been published previously.

During the course of our analysis we encountered many species in the literature that seemed to be very similar if not identical to our specimens. This led to the synonymies that accompany the majority of our identifications. Only those for which we felt there was sufficient morphological evidence are included. Many could not be listed because satisfactory data are wanting (diagnoses too obscure and/or incomplete and illustrations inadequate). Most of these have rarely, if ever, been identified subsequent to their original description, in many cases probably because there is no

adequate basis for doing so. The resulting reduction in the number of genera and species available for similar forms should make it easier than previously to identify species of the five genera considered herein.

Some of the assemblages that we examined contain many forms that are not easy to differentiate. This was not surprising. Skarby (1986) showed that a range of morphological types can be recovered from a single anther, including intermediate forms (her plate I, 3) that we would hesitate to assign to *Oculopollis* or *Trudopollis*. However, in the dispersed state, for practical purposes it is only possible to treat the pollen as morphological rather than biological species. In our diagnoses, we have allowed for a certain amount of variation, but not too much, otherwise we would have included too many morphotypes and ended up with species that cannot be readily identified. Most of those described by Skarby (1968) are difficult to recognize for this reason. Her approach would have been more effective had assemblages of Normapolles pollen grains been recovered in situ first. Only following precisely defined specific characteristics can the degree of morphological variation encountered be extrapolated to dispersed material.

9.2. Biostratigraphic implications

All of the preparations that we examined for this study derive from successions for which palynological data have been published mostly between 25 and more than 63 years ago. In the meantime, age determinations of some of the formations

concerned have been modified based on further geological and palaeontological research. For example, whereas the Aachen Formation was commonly considered to be mid Senonian (e.g., Pflug, 1953) or early Campanian (Góczán et al., 1967), the general consensus now is that the palynologically productive part of the succession was deposited during the mid–late Santonian (Batten et al., 1988). Similarly, Skarby (1968) considered that the assemblages she examined from Scania were "probably Campanian" whereas subsequent palaeomagnetic correlation suggested an earliest early Campanian age for the samples discussed by Hultberg et al. (1984). Also, following previous uncertainties, the Magothy Formation of New Jersey is now widely regarded as early–mid Santonian (USGS Mineral Resources On-line Spatial Data).

Hence, our plot of the ranges of the species considered in this paper (Fig. 3) take into account these and other changes that refer to taxa from sections we have not examined, such as the "Longyear-seam" in Manum (1962), which is now dated as Paleocene rather than Paleocene–Eocene, and the Merchantville Formation of Delaware and New Jersey, which is regarded as early Campanian rather than "probably Santonian", as reported by Gray and Groot (1966). They are also based on our appraisal of ages noted and ranges, if provided, for the species that we have placed in synonymy, and on occurrences reported by others. The seven morphotypes that we identified in open nomenclature and the two placed in comparison with previously described species are not included in the range chart.

The reduction in the number of genera and species, and the uncomplicated diagnoses accompanied by photographs illustrating the features we describe, simplifies identification of the different Normapolles types and increases their biostratigraphic

importance. Useful biostratigraphic studies based on Normapolles have been published previously for some successions. For example, the Santonian–Campanian/Maastrichtian Bakony Mountains section in western Hungary has been subdivided into zones and subzones (based on relative abundances rather than stratigraphic ranges) that encompass relatively short periods of geological time (e.g., Góczán and Siegl-Farkas, 1990). However, despite the number of potential species available, almost 40% of the Normapolles grains figured by Góczán and Siegl-Farkas (1990) in connection with their zonation are identified in open nomenclature. Batten et al. (1987, 1988) encountered similar difficulties when attempting to identify Normapolles pollen from the Aachen Formation in the Netherlands and Belgium, with approximately 50% of the forms illustrated being compared with published species or placed in open nomenclature (see also remarks in Section 3 concerning papers by Christopher, 1979 and Méon et al., 2004). The situation is no different now. When it was necessary recently to identify Turonian pollen grains including Normapolles recovered from the Sainte-Mondane Formation in the Aquitaine Basin, south-west France, the majority of forms had to be compared with one or more taxa (Batten and Polette in Néraudeau et al., 2016). We hope that our approach to the recognition of species of the Normapolles genera considered here will reduce the number of uncertain identifications in future.

10. Conclusions

Differentiation of Normapolles taxa has been a major problem for palynologists owing to the fact that far too many genera and species have been erected in the past based on inadequate criteria. In dispersed palynomorph assemblages, distinguishing species from what sometimes can seem like a morphological continuum can be a daunting task. Where does one draw the line between different morphotypes? Do forms that are morphologically intermediate between two species in fact belong to a single species and merely reflect intraspecific variation? Pollen grains with characters intermediate between *Longanulipollis amabilis* and *L. ornatus*, and between *Oculopollis concentus* and *O. triceps*, noted above, fall into this category. Each of these pairs of named species and those specimens having intermediate characters perhaps belong to the same polymorphic biological taxon. Unless identical forms are found in situ in the anthers of flowers, there is no way of knowing. On the other hand, the majority of specimens of the named species are sufficiently different for them to be recognized as distinct morphospecies.

The morphological boundaries between the taxa we have described are conventional. If too much variation is allowed, it is all too easy to end up with genera and species that contain such a wide range of morphological variation that they become biostratigraphically useless. It is not possible to be sure that given features of pollen morphology are taxonomically meaningful in representing a biological species (cf. Batten, 1989). As noted above, the morphology of some Normapolles grains that have been recovered from anthers may vary rather widely (Skarby, 1986). Previous identifications of pollen recovered from pollen sacs in “Normapolles flowers” have been described and illustrated but, with very few exceptions (e.g., in Friis, 1983, and

Sims et al., 1999), generally compared only with dispersed genera rather than species. Of the genera described here, comparisons with *Trudopollis* have been recorded most often, but other in situ pollen grains have been compared with *Oculopollis* and the two genera placed in synonymy with this genus herein, *Pseudoculopollis* and *Semioculopollis*, as well as with *Interporopollenites*, *Minorpollis*, *Plicapollis*, *Pseudopapillopollis* and *Pseudoplicapollis*, not discussed in this paper (e.g. Schönenberger et al., 2001; Friis et al. 2003, 2006, 2010; Heřmanová et al., 2011, 2016).

Our paper is aimed primarily at making better use of the Normapolles group in biostratigraphic analyses. In order to do this, it has been necessary to reduce the unnecessarily large number of both genera and species that are currently available in the literature so that they are easier to identify than previously. It proved essential to emend the diagnoses of all of the previously published taxa investigated. These are presented in a straightforward way using relatively few terms so that they can be easily compared with each other. Despite the fact that there is scope for further work on species referable to the genera that form the basis of this paper, the emended diagnoses coupled with illustrations that reveal the distinguishing features have helped to put the taxonomy of this group of Normapolles taxa into perspective.

Although one can question the biological reality behind the clarification of existing taxa and the establishment of those described as new, this problem is not confined to the Normapolles group. It is common to the majority of dispersed fossil spores and pollen grains.

In due course, it should be possible to determine in situ pollen in terms of dispersed taxa more accurately than has usually been attempted hitherto, thus revealing the correspondence between dispersed pollen genera and/or species and the variability within a particular pollen sac, flower, or entire plant species. This should help to determine which characters of Normapolles pollen are more stable and characterize their parent plants, and which are variable and merely reflect individual or interspecific differences. In the long run, the boundaries between some of the dispersed Normapolles taxa might well be rendered less artificial than they are at present.

In the meantime, in order to prepare the ground for future studies on Normapolles pollen grains in situ, and the establishment of morphological characteristics applicable to biological species, it is essential to synthesize, standardize and clarify the large amount of work on purely morphological taxa that has been published hitherto. In addition to facilitating biostratigraphic analyses by reducing the number of taxa to which newly encountered specimens can be referred, our paper should, therefore, also be considered as a necessary first step towards the resolution of the botanical relationships of Normapolles pollen.

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Figure captions

Fig. 1. Palaeogeographic representation of Europe and eastern USA during the Late Cretaceous (75 Ma) with the locations (numbered black dots) of the samples and hence palynological preparations on which this study is based (see Section 4). 1: Sainte-Mondane, France (QPR3675-2, 3, NMW 2017.1G11, 1G12); 2: Gulpen, Belgium (MCP3283-3, NMW 2017.1G5); 3: Åsen, Sweden (MCP805-2, NMW 2017.1G1); 4: Maastricht, Netherlands (MCP3193-3, NMW 2017.1G4); 5: Aachen, Germany (MCP1610-2, NMW 2017.1G2); 6: Monmouth County, USA (Misc-R-18, NMW 2017.1G13); 7: Arada, Portugal (MCP2573-3, NMW 2017.1G3); 8: Sümeg and Zalagyömörő, Hungary (MCP3482-3, 3853-1, 3856-1, 3860-1, 3862-1, NMW 2017.1G6, 1G7, 1G8, 1G9, 1G10). Scale bar represents 400 km. Map modified from cpgeosystems.com.

Fig. 2. Line drawings of Normapolles grains showing their main morphological features. a, exoaperture; b, intrabaculate structure; c, interloculum; d, oculus; e, nexine; f, sexine; g, endannulus; h, cuneus; i, vestibulum (i1, wide and deep; i2, wide and narrow; i3, shallow and narrow; i4, shallow and deep); j, ektannulus (beak-like shape); k, atrium (shallow); l, vestibulum (narrow and shallow); m, platea; n, ektannulus (unstructured); o, laminated nexine; p, endopore; q, atrium (wide and deep); r, diameter of pollen grain; p and q, endogerminal; a and j (or n), exogerminal.

Fig. 3. Stratigraphic range chart (based on our own work and ages provided in previous publications) of the species presented and illustrated herein. L, lower; M, middle; U, upper; light grey bars, the authors recorded a range at stage level (e.g., Maastrichtian); dark grey bars, the authors or we recorded a range at sub-stage level (e.g., upper Campanian–lower Maastrichtian); partly shaded dark grey bars, some authors recorded a range at stage level but others or we recorded the same range at sub-stage level [e.g., *Trudopollis acinosus*: Agranovskaya (1960) recorded Santonian, we recorded lower–middle Santonian].

Plate captions

Plate I. Species of *Hungaropollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1, 2. *Hungaropollis* sp. cf. *H. krutzschii*. 1: 3482-3, 1G6, L17.0; 2: 3482-3, 1G6, L42.1.

3–7. *Hungaropollis hollossyi*. 3, 4: 3856-1, 1G8, N29.4; 5, 6: 3482-3, 1G6, M33.0; 7: 3482-3, 1G6, U20.4.

8–17. *Hungaropollis krutzschii*. 8: 3856-1, 1G8, O29.1; 9: 3482-3, 1G6, P17.0; 10: 3860-1, 1G9, K43.1; 11, 14: 3856-1, 1G8, T28.1; 12: 3853-1, 1G7, P37.0; 13: 3862-1, 1G10, V29.1; 15: 3482-3, 1G6, X28.3; 16: 3860-1, 1G9, S38.0; 17: 3862-1, 1G10, L31.0.

Plate II. Species of *Hungaropollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1, 4. *Hungaropollis granulatus* comb. nov., 3283-3, 1G5, T17.1.

2, 3, 5, 6. *Hungaropollis rectilineus*. 2, 3: 3482-3, 1G6, X50.3; 5, 6: 3482-3, 1G6, L55.0.

7–14. *Hungaropollis pinguis* sp. nov. 7: 3482-3, 1G6, O49.4; 8: 3482-3, 1G6, F17.2; 9: 3856-1, 1G8, N34.4; 10, 13: 3856-1, 1G8, K29.0; 11, 14, holotype: 3856-1, 1G8, S34.0; 12: 3856-1, 1G8, S34.0.

15, 16. *Hungaropollis* sp. A. 3862-1, 1G10, Q42.1.

Plate III. Species of *Krutzschipollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–9. *Krutzschipollis crassis*. 1: 3862-1, 1G10, R29.1; 2: 3862-1, 1G10, H39.3; 3, 4: 3862-1, 1G10, N39.3; 5: 3862-1, 1G10, N35.2; 6, 7: 3860-1, 1G9, N34.1; 8, 9: 3862-1, 1G10, O30.0.

10–17. *Krutzschipollis cucullus* sp. nov. 10: 3856-1, 1G8, N29.0; 11, 14: 3856-1, 1G8, N34.3; 12: 3482-3, 1G6, Y32.1; 13, holotype: 3482-3, 1G6, M22.3; 15: 3856-1, 1G8, G41.0; 16, 17: 3482-3, 1G6, H30.2.

Plate IV. Species of *Krutzschipollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–4. *Krutzschipollis elegans*. 1, 2: 3862-1, 1G10, N30.4; 3: 3860-1, 1G9, T37.0; 4: 3860-1, 1G9, Q34.3.

5–9. *Krutzschipollis immanis* sp. nov. 5: 3482-3, 1G6, O20.0; 6: 3482-3, 1G6, S26.2; 7: 3482-3, 1G6, K27.0; 8, 9, holotype: 3482-3, 1G6, W51.4.

10, 13. *Krutzschipollis* sp. A. 10, 13: 3862-1, 1G10, K32.3.

11. *Krutzschipollis* sp. cf. *K. immanis*. 3860-1, 1G9, P36.1.

12, 14. aff. *Krutzschipollis* sp. A, 3482-3, 1G6, X28.0.

Plate V. Species of *Krutzschipollis* and *Longanulipollis*. Representatives of the two genera are separated by a grey line. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–7. *Krutzschipollis spatiosus*. 1: 3862-1, 1G10, H34.1; 2, 3: 3860-1, 1G9, M34.0; 4, 7: 3862-1, 1G10, R27.4; 5, 6: 3862-1, 1G10, L43.0.

8–11. *Krutzschipollis magnoporus*. 8, 9: 3856-1, 1G8, W37.0; 10, 11: 3856-1, 1G8, P36.1.

12–22, 25, 26. *Longanulipollis amabilis* sp. nov. 12: 3853-1, 1G7, G34.3; 13, holotype: 3853-1, M34.4; 14: 3853-1, 1G7, V38.0; 15: 3853-1, 1G7, M35.1; 16: 3856-1,

1G8, K39.1; 17: 3856-1, 1G8, T29.0; 18, 21: 3856-1, 1G8, M29.2; 19: 3856-1, 1G8, P29.0; 20, 25: 3856-1, 1G8, M34.3; 22: 3856-1, 1G8, O30.4; 26: 3856-1, 1G8, R37.4.

23, 27. Intermediate forms between *L. amabilis* sp. nov. and *L. ornatus* comb. nov. 23: 3853-1, 1G7, L36.1; 27: 3856-1, 1G8, Q30.2.

24, 28. *Longanulipollis ornatus* comb. nov., 3853-1, 1G7, M44.0.

Plate VI. Species of *Longanulipollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 μm.

1–5. *Longanulipollis bajtayi*. 1: 3862-1, 1G10, E29.1; 2, 3: 3862-1, 1G10, K31.0; 4: 3482-3, 1G6, U19.1; 5: 3862-1, 1G10, F28.1.

6. *Longanulipollis coronatiformis* comb. nov., 3862-1, 1G10, K34.4.

7–16. *Longanulipollis coronatus*. 7, 13: 3856-1, 1G8, M38.3; 8, 9: 3856-1, 1G8, J31.4; 10, 15: 3856-1, 1G8, L28.1; 11: 3856-1, 1G8, O32.4; 12, 16: 3856-1, 1G8, L29.2; 14: 3856-1, 1G8, N28.0.

17–29. *Longanulipollis fornicatus*. 17–19: 3856-1, 1G8, J31.3; 20: 3856-1, 1G8, Q32.0; 21: 3856-1, 1G8, T29.0; 22: 3856-1, 1G8, T33.3; 23: 3856-1, 1G8, R30.2; 24: 3860-1, 1G9, R32.4; 25, 26: 3856-1, 1G8, L38.0; 27, 28: 3856-1, 1G8, V34.1; 29: 3856-1, 1G8, R41.0.

Plate VII. Species of *Longanulipollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–20. *Longanulipollis lobus* sp. nov. 1, 2: 3853-1, 1G7, L30.3; 3, 4: 3853-1, 1G7, Q38.2; 5, 6: 3853-1, 1G7, Q30.0; 7, 8, holotype: 3853-1, 1G7, K37.4; 9: 3853-1, 1G7, M33.4; 10: 3853-1, 1G7, P36.0; 11, 16: 3853-1, 1G7, U35.3; 12, 18: 3853-1, 1G7, M34.0; 13: 3853-1, 1G7, N34.0; 14: 3853-1, 1G7, J41.1; 15, 19: 3853-1, 1G7, L36.3; 17: 3853-1, 1G7, T28.2; 20: 3853-1, 1G7, R26.2.

21–26. *Longanulipollis monstruosis*. 21, 23: 3856-1, 1G8, S40.1; 22: 3856-1, 1G8, X36.1; 24, 25: 3482-3, X33.4; 26: 3482-3, 1G6, T23.0.

27–30. *Longanulipollis longianulus*. 27, 30: 3482-3, 1G6, K19.4; 28: 3482-3, 1G6, F34.0; 29: 3482-3, C54.0.

Plate VIII. Species of *Longanulipollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–14. *Longanulipollis orbicularis* comb. nov. 1: 3856-1, 1G8, X29.2; 2: 3853-1, 1G7, M29.4; 3: 3853-1, 1G7, L35.3; 4, 5: 3856-1, 1G8, N30.4; 6: 3856-1, 1G8, P28.3; 7: 3853-1, 1G7, F34.3; 8, 9: 3856-1, 1G8, U38.4; 10, 11: 3856-1, 1G8, R29.2; 12: 3856-1, 1G8, V28.0; 13, 14: 3856-1, 1G8, P34.1.

15–37. *Longanulipollis parvoculus* comb. nov. 15: 3482-3, 1G6, G19.2; 16, 22: 3856-1, 1G8, H29.2; 17: 3856-1, 1G8, W27.4; 18, 19: 3856-1, 1G8, G32.4; 20, 21: 3856-1, 1G8, F29.0; 23, 24: 3856-1, 1G8, P44.1; 25, 26: 3856-1, 1G8, Q32.2; 27: 3856-1, 1G8, M34.2; 28: 3856-1, 1G8, M31.3; 29: 3856-1, 1G8, Q37.3; 30: 3856-1, 1G8, K28.3; 31, 34: 3856-1, 1G8, M34.2; 32: 3482-3, 1G6, S30.0; 33: 3482-3, 1G6, E21.3; 35, 36: 3856-1, 1G8, N42.3; 37: 3856-1, 1G8, Q27.4.

Plate IX. Species of *Longanulipollis* and *Oculopollis* (The two genera are separated by a grey line). Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–4. *Longanulipollis polanyensis*. 1: 3482-3, 1G6, N23.4; 2: 3482-3, 1G6, J18.2; 3, 4: 3856-1, 1G8, M45.0.

5–8. *Longanulipollis skarbyae* comb. nov. 5, 6: 3856-1, 1G8, N35.0; 7, 8: 3482-3, 1G6, D35.0.

9–12. *Longanulipollis* sp. A. 9: 3856-1, 1G8, L41.4; 10: 3856-1, 1G8, G44.0; 11, 12: 3853-1, 1G7, W40.1.

13–16. *Longanulipollis* sp. B. 13, 14: 3853-1, 1G7, F34.3; 15, 16: 3853-1, 1G7, W44.4.

17–23. *Oculopollis aestheticus*. 17: 1610-2, 1G2, M37.2; 18, 19: 1610-2, 1G2, C26.0; 20, 21, 22: 805-2, 1G1, Q14.0; 23: 1610-2, 1G2, U39.3.

24–26. *Oculopollis* sp. A. 24, 25: 805-2, 1G1, K29.0; 26: 805-2, 1G1, G51.0.

Plate X. Species of *Oculopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–10. *Oculopollis artifex* comb. nov. 1: 3283-3, 1G5, L18.4; 2, 3: 805-2, 1G1, F26.0; 4: 805-2, 1G1, D12.0; 5: 805-2, 1G1, Q23.2; 6, 7: 805-2, 1G1, B14.3; 8, 9: 805-2, 1G1, F22.1; 10: 805-2, 1G1, J13.4.

11–14. *Oculopollis* sp. cf. *O. artifex*. 11, 12: 805-2, 1G1, T17.3; 13, 14: 805-2, 1G1, S18.4.

15–26. *Oculopollis bulbosus*. 15, 16: 805-2, 1G1, W24.0; 17: 805-2, 1G1, E45.1; 18, 26: 805-2, 1G1, W15.2; 19, 24: 805-2, 1G1, W23.1; 20, 25: 805-2, 1G1, D29.2; 21: 805-2, 1G1, Y43.4; 22, 23: 805-2, 1G1, D36.1.

27, 28. *Oculopollis baculatus*. 27: 805-2, 1G1, Q16.3; 28: 805-2, 1G1, V18.0.

Plate XI. Species of *Oculopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–8. *Oculopollis cardinalis*. 1, 2: 3283-3, 1G5, W17.0; 3: 3193-3, 1G4, H51.1; 4, 8: 3283-3, 1G5, X20.0; 5: 3283-3, 1G5, U15.2; 6, 7: 3283-3, 1G5, O17.0.

9, 10. *Oculopollis* sp. cf. *O. cardinalis*. 9: 3283-3, 1G5, J19.1; 10: 3283-3, 1G5, W20.4.

11–14. *Oculopollis concentricoides*. 11, 12: 3283-3, 1G5, E21.4; 13, 14: 805-2, 1G1,B14.4.

15–22, 24–27. *Oculopollis concentus*. 15: 3283-3, 1G5, W22.3; 16: 3193-3, 1G4, J33.1; 17: 3283-3, 1G5, H17.1; 18: 3283-3, 1G5, K17.0; 19, 20: 1610-2, 1G2,

H54.3; 21: 1610-2, 1G2, G44.3; 22: 3283-3, 1G5, T16.0; 24: 3283-3, 1G5, V20.2; 25: 1610-2, 1G2, X31.0; 26: 3283-3, 1G5, X22.4; 27: 3283-3, 1G5, U17.0.

23. *Oculopollis* sp. cf. *O. concentus*, 3193-3, 1G4, F42.4.

Plate XII. Species of *Oculopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP except where indicated, and by NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1. *Oculopollis* sp. cf. *O. principalis*. 3283-3, 1G5, E21.1.

2–7. *Oculopollis praedicatus*. 2: 3856-1, 1G8, P35.4; 3: 3283-3, 1G5, K28.4; 4: 3482-3, 1G6, S32.0; 5: 3283-3, 1G5, S17.0; 6: 3853-1, 1G7, L36.4; 7: 3482-3, 1G6, C30.1.

8, 12. *Oculopollis* sp. cf. *O. triperforinus*. 8: 3862-1, 1G10, Q37.0; 12: 3860-1, 1G9, L35.4.

9–11. *Oculopollis* sp. cf. *O. praedicatus*. 9, 10: 3482-3, 1G6, T30.1; 11: Misc-R-18, 1G13, V13.3.

13–39. *Oculopollis principalis*. 13, 14: 805-2, 1G1, F16.3; 15, 16: 805-2, 1G1, F42.4; 17, 18, 24: 805-2, 1G1, S18.0; 19, 20: 805-2, 1G1, E20.1; 21, 26: 805-2, 1G1, R50.4; 22, 23: 805-2, 1G1, M20.4; 25, 31, 32: 805-2, 1G1, U15.0; 27: 805-2, 1G1, G15.2; 28: 805-2, 1G1, J24.0; 29: 805-2, 1G1, G16.3; 30: 805-2, 1G1, D15.1; 33: 805-2, 1G1, L16.4; 34, 39: 805-2, 1G1, D13.4; 35: 805-2, 1G1, V31.1; 36, 37: 805-2, 1G1, G18.2; 38: 805-2, 1G1, W33.3.

Plate XIII. Species of *Oculopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP and NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–7. *Oculopollis rector* comb. nov. 1, 2: 1610-2, 1G2, F27.4; 3: 805-2, 1G1, Q40.0; 4, 5: 805-2, 1G1, S27.4; 6, 7: 1610-2, 1G2, C27.3.

8–13. *Oculopollis triceps* comb. nov. 8: 805-2, 1G1, C13.1; 9: 805-2, 1G1, J17.1; 10, 11: 805-2, 1G1, H28.0; 12: 805-2, 1G1, H15.0; 13: 805-2, 1G1, R12.0.

14, 15. *Oculopollis* sp. cf. *O. triceps*, 805-2, 1G1, V17.0.

16–25. *Oculopollis viriosus* sp. nov. 16: 3283-3, 1G5, H16.1; 17, 20, holotype: 3283-3, 1G5, G16.4; 18, 19: 3283-3, 1G5, W17.4; 21: 3283-3, 1G5, V19.0; 22: 3283-3, 1G5, V19.1; 23: 3283-3, 1G5, S37.2; 24: 3283-3, 1G5, H22.1; 25: 3283-3, 1G5, O21.0.

Plate XIV. Species of *Oculopollis* and *Trudopollis* (The two genera are separated by a grey line). Accompanying data are palynological preparation and slide numbers (all prefixed by MCP except where indicated, and by NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–4. *Oculopollis viriosus* sp. nov. 1: 3283-3, 1G5, C26.1; 2: 3283-3, 1G5, G21.4; 3: 3283-3, 1G5, V24.4; 4: 3283-3, 1G5, S24.0.

5–7. *Trudopollis articulus*. 5, 6: 3283-3, 1G5, T17.3; 7: 3283-3, 1G5, D38.1.

8, 9. *Trudopollis acinosus*. 8: Misc-R-18, 1G13, O23.0; 9: Misc-R-18, 1G13, E12.0.

10–15. *Trudopollis capsula*. 10: 3283-3, 1G5, E28.1; 11: 3853-1, 1G7, P30.3; 12: 3283-3, 1G5, M22.0; 13: Misc-R-18, 1G13, K20.4; 14: 3283-3, 1G5, W22.0; 15: 3283-3, 1G5, T20.2.

16–21. *Trudopollis conrector*. 16: 3283-3, 1G5, W18.0; 17: 3283-3, 1G5,, P23.0; 18: 3283-3, 1G5, H15.0; 19: 3283-3, 1G5, W15.4; 20: 3283-3, 1G5, L40.0; 21: 3283-3, 1G5, T16.1.

22–25. *Trudopollis conrectiformis*. 22: 3283-3, 1G5, R28.3; 23: 3283-3, 1G5, O37.2; 24: 3283-3, 1G5, E20.2; 25: 3283-3, 1G5, E21.0.

Plate XV. Species of *Trudopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP except where indicated, and by NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1, 2. *Trudopollis* sp. B, 3283-3, 1G5, T26.4.

3, 4. *Trudopollis exemplum*, 3283-3, 1G5, Q21.3.

5–7. *Trudopollis cuneolis* comb. nov. 5: 3482-3, 1G6, H17.2; 6: 3482-3, 1G6, F20.4; 7: 3482-3, 1G6, U38.0.

8–10. *Trudopollis fossulotrudens*. 8: Misc-R-18, 1G13, W8.0; 9: Misc-R-18, 1G13, P18.4; 10: 3482-3, 1G6, W51.2.

11–19. *Trudopollis geometricus*. 11: 3283-3, 1G5, X24.3; 12, 16: 805-2, 1G1, T37.3; 13: 3283-3, 1G5, S15.2; 14: 3283-3, 1G5, E24.1; 15: 805-2, 1G1, O26.0; 17, 18: 1610-2, 1G2, C32.4; 19: 1610-2, 1G2, R47.0.

20–28. *Trudopollis hemimechanicus*. 20: 1610-2, N48.3; 21, 22: 3283-3, 1G5, T17.0; 23: 3283-3, 1G5, K21.3; 24: 3283-3, 1G5, M38.3; 25: 3283-3, 1G5, U21.2; 26: 3283-3, 1G5, G41.1; 27: 3283-3, 1G5, R40.0; 28: 3283-3, 1G5, J16.2.

Plate XVI. Species of *Trudopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP except where indicated, and by NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–9. *Trudopollis hemiperfectus*. 1, 2: 1610-2, 1G2, M18.0; 3, 4: 3193-3, 1G4, J23.0; 5, 6: 1610-2, 1G2, E32.0; 7, 8: 1610-2, 1G2, H21.1; 9: 3283-3, 1G5, D17.1.

10–15. *Trudopollis imperfectus*. 10: 3283-3, 1G5, H28.0; 11: 3283-3, 1G5, T19.3; 12: QPR3675-2, 1G11, H23.3; 13: 3283-3, 1G5, V38.3; 14: QPR3675-2, 1G11, V36.0; 15: 3283-3, 1G5, E32.0.

16, 17. *Trudopollis lativerrucatus*. 16: 3283-3, 1G5, Q38.1; 17: Misc-R-18, 1G13, R14.0.

18. *Trudopollis obexemplum*, 1610-2, 1G2, O42.0.

19, 20. *Trudopollis maestrichtiensis*. 19: 3283-3, 1G5, L18.3; 20: 3193-3, 1G4, G43.3.

21–26. *Trudopollis nonperfectus*. 21: Misc-R-18, 1G13, V19.2; 22: Misc-R-18, 1G13, P10.4; 23: 3283-3, 1G5, E21.3; 24: 3283-3, 1G5, T22.3; 25: Misc-R-18, 1G13, O7.3; 26: Misc-R-18, 1G13, Y17.0.

27, 28. *Trudopollis peneperfectus*. 27: 3283-3, 1G5, E16.1; 28: 3283-3, 1G5, E23.1.

29, 30. *Trudopollis pompeckjii*, 1610-2, 1G2, B25.3.

31–35. *Trudopollis oculoides*. 31: 3283-3, 1G5, H22.1; 32: 3283-3, 1G5, O39.0; 33, 35: 3283-3, 1G5, D27.0; 34: 1610-2, 1G2, B30.4.

Plate XVII. Species of *Trudopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP except where indicated, and by NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–7. *Trudopollis pertrudens*. 1: 3283-3, 1G5, C22.4; 2: 3283-3, 1G5, U40.3; 3: 3283-3, 1G5, N22.0; 4: 3283-3, 1G5, J31.2; 5, 6: 3283-3, 1G5, T16.0; 7: 3283-3, 1G5, U16.3.

8–17. *Trudopollis protrudens*. 8, 9: 1610-2, 1G2, X24.0; 10: 805-2, 1G1, X17.0; 11: 3283-3, 1G5, C17.3; 12: 1610-2, 1G2, D41.0; 13: 1610-2, 1G2, M46.0; 14, 15: 1610-2, 1G2, T29.3; 16, 17: 3283-3, 1G5, O18.1.

18–24. *Trudopollis retifectus*. 18: 3193-3, 1G4, J23.1; 19, 20: 1610-2, 1G2, S35.0; 21: 3283-3, 1G5, G40.1; 22: 3283-3, 1G5, F21.4; 23: 3283-3, 1G5, R16.0; 24: 3283-3, 1G5, N22.0.

25, 31. *Trudopollis primigenius*. 25: 3283-3, 1G5, V16.3; 31: QPR3675-2, 1G11, U21.0.

26–29. *Trudopollis spinulosus* comb. nov. 26: 3283-3, 1G5, J40.3; 27: 3283-3, 1G5, S17.0; 28: 2573-3, 1G3, D20.0; 29: 1610-2, 1G2, O19.2.

30. *Trudopollis* sp. A, 805-2, 1G1, F24.0.

Plate XVIII. Species of *Trudopollis*. Accompanying data are palynological preparation and slide numbers (all prefixed by MCP except where indicated, and by NMW 2017) followed by England Finder coordinates. For authors, see systematic section. Scale bar represents 10 µm.

1–7. *Trudopollis retigressus*. 1: 3283-3, 1G5, F15.0; 2: 3283-3, 1G5, E40.0; 3: 3283-3, 1G5, M20.1; 4: 3283-3, 1G5, W38.1; 5: 3283-3, 1G5, O38.2; 6: 3283-3, 1G5, U20.1; 7: 3283-3, 1G5, E38.4.

8–10. *Trudopollis* sp. cf. *T. rotundus*. 8: 3283-3, 1G5, Q29.0; 9: Misc-R-18, 1G13, W17.2; 10: 3283-3, 1G5, K39.0.

11–19. *Trudopollis rusticus*. 11: QPR3675-2, 1G11, E47.4; 12, 13: QPR3675-2, 1G11, W34.0; 14: QPR3675-2, 1G11, D30.1; 15, 16: QPR3675-3, 1G12, D22.4; 17, 18: QPR3675-2, 1G11, U31.3/0; 19: QPR3675-2, 1G11, O38.2.

20–26. *Trudopollis succedanus*. 20, 21: 3283-3, 1G5, T40.0; 22: 3283-3, 1G5, Q21.3; 23: 3283-3, 1G5, M18.0; 24: 3283-3, 1G5, Q21.0; 25, 26: 3283-3, 1G5, P17.4.

Supplementary files

Table 1. List of all of the species of the five genera emended herein, and the 13 genera that have been placed in synonymy with four of these. Each species is accompanied by the name(s) of the author(s), year of publication, page number(s) on which it is described and a brief comment. *, nomen nudum; •, typographical error; ^, species transferred to another genus in our paper but not re-described; °, transfer invalid; NZ, information received from N. Zavialova.

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Figure 1

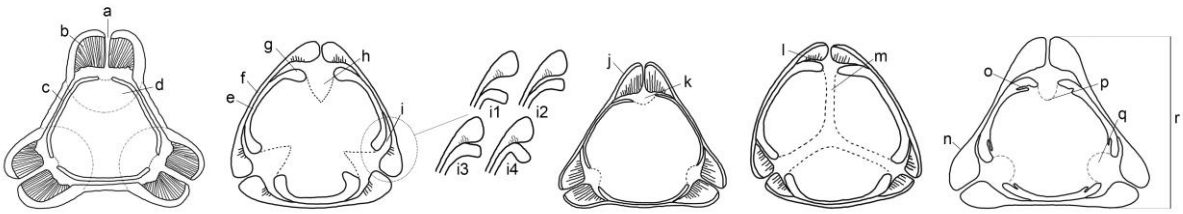


Figure 2

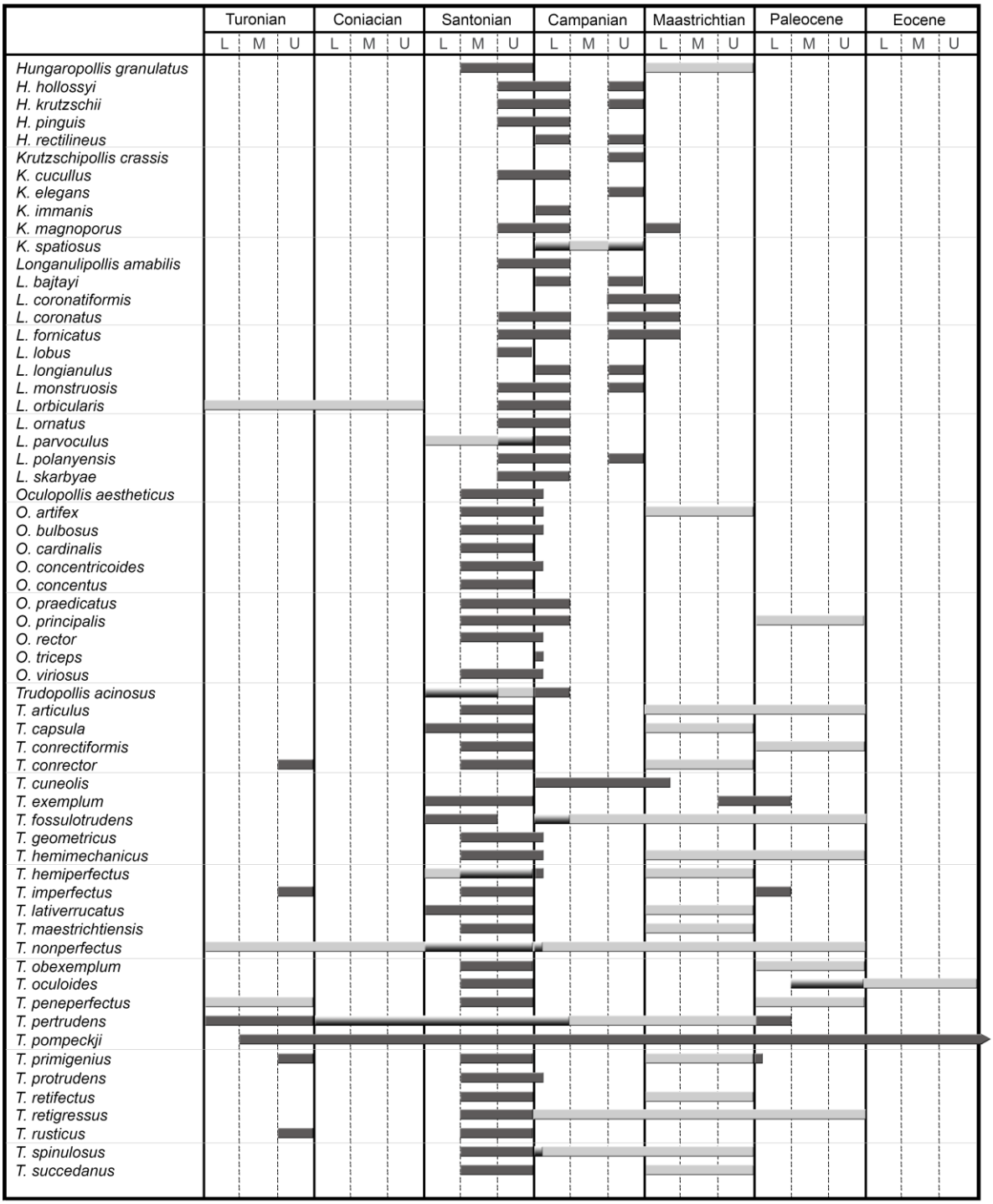
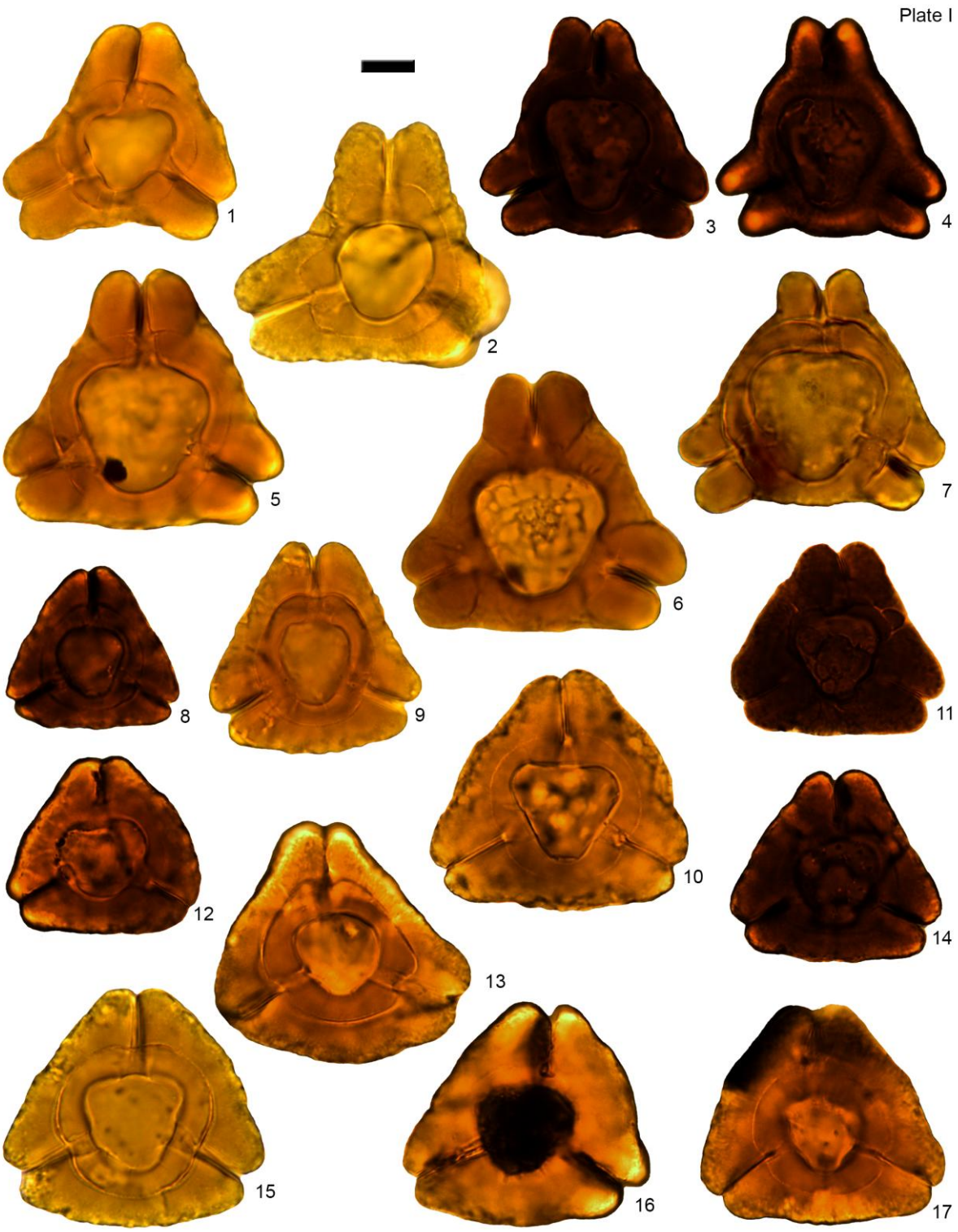
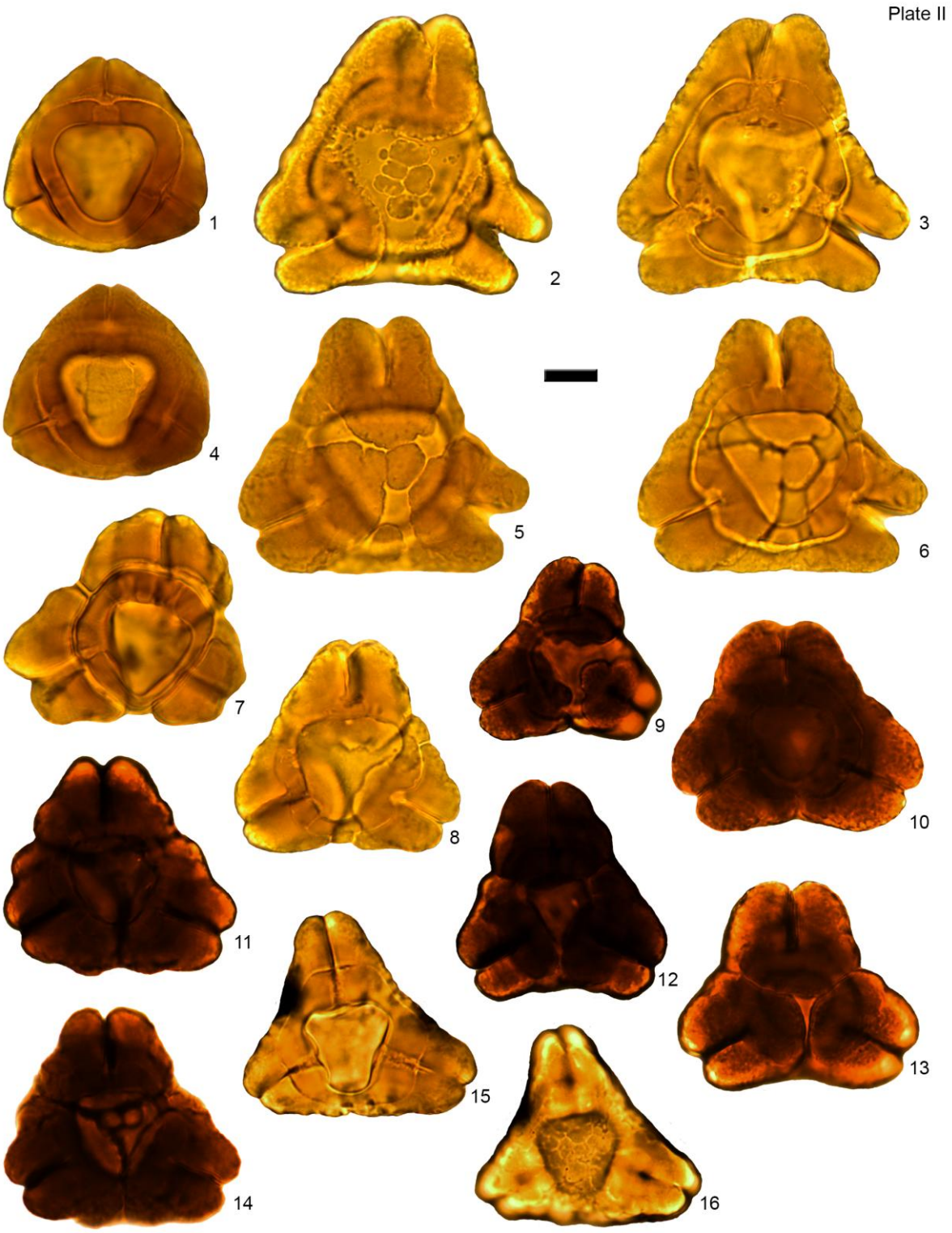


Figure 3





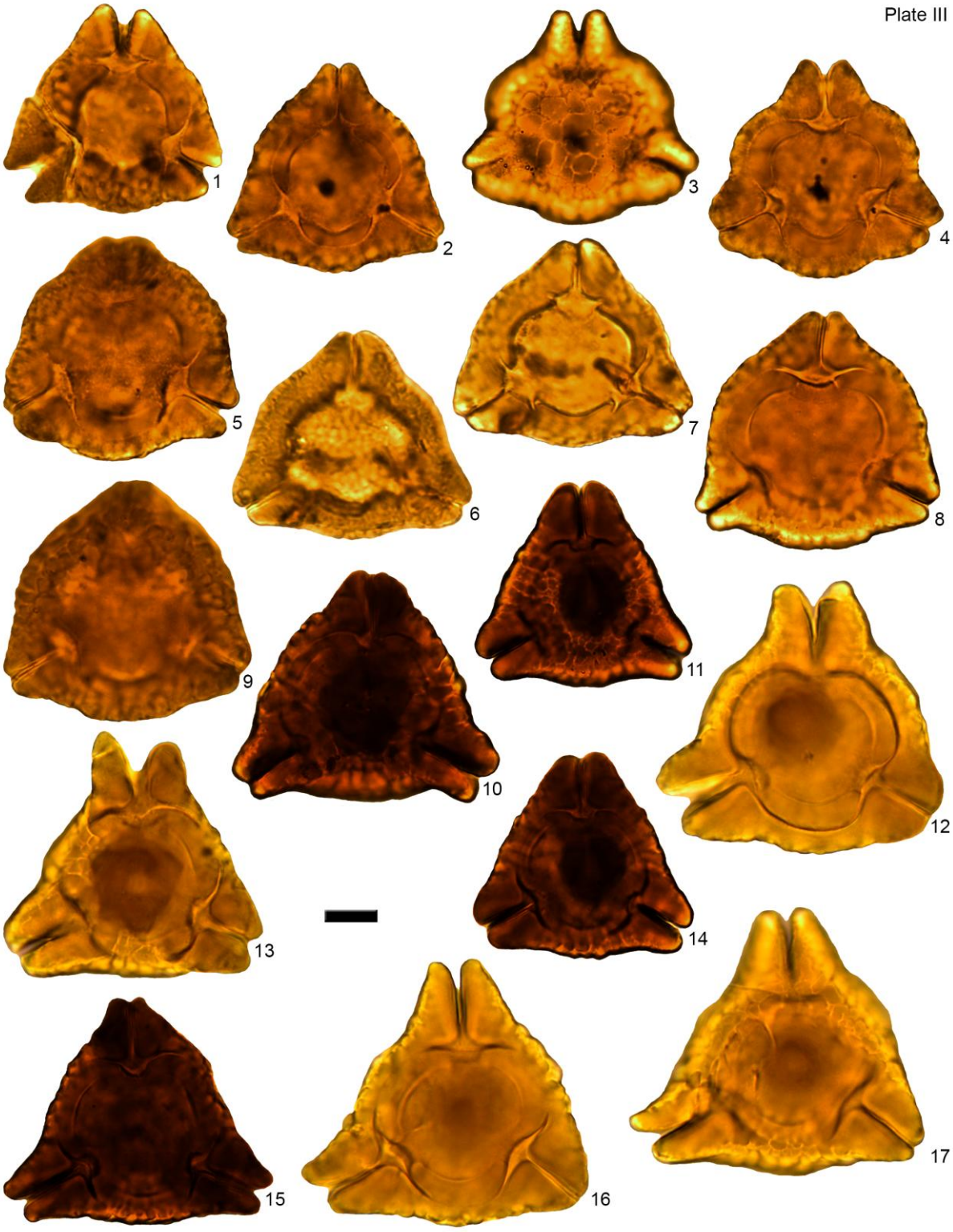
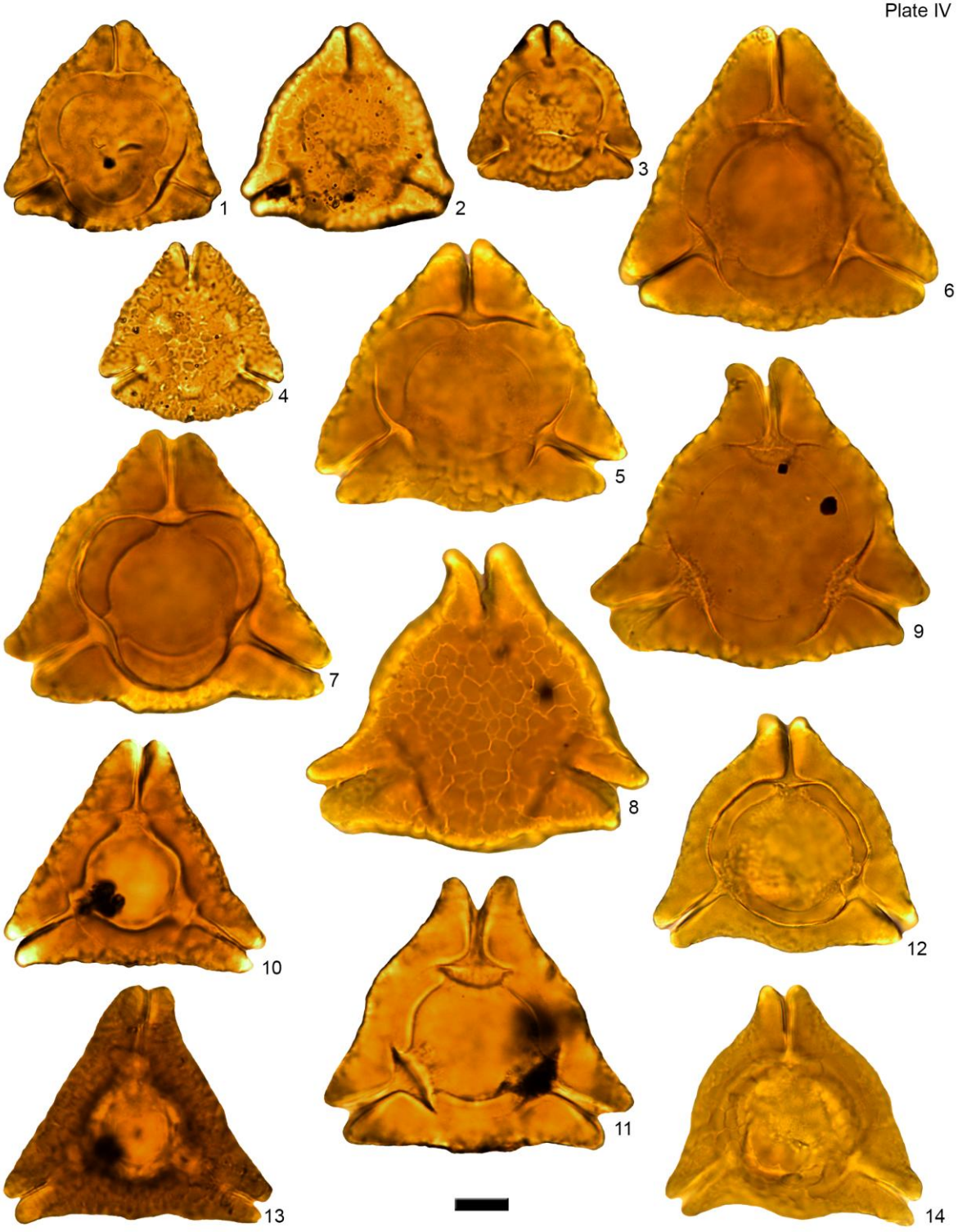
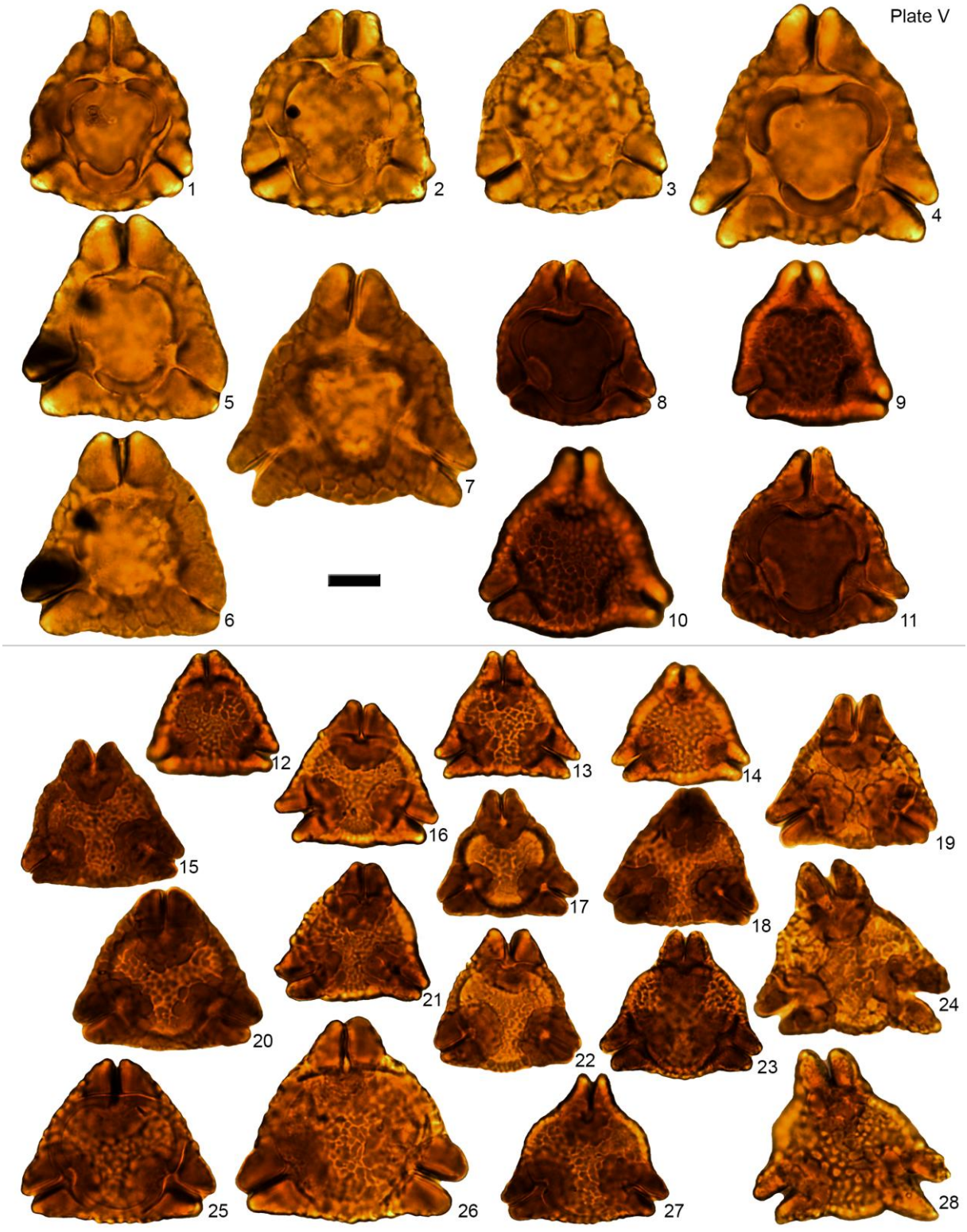
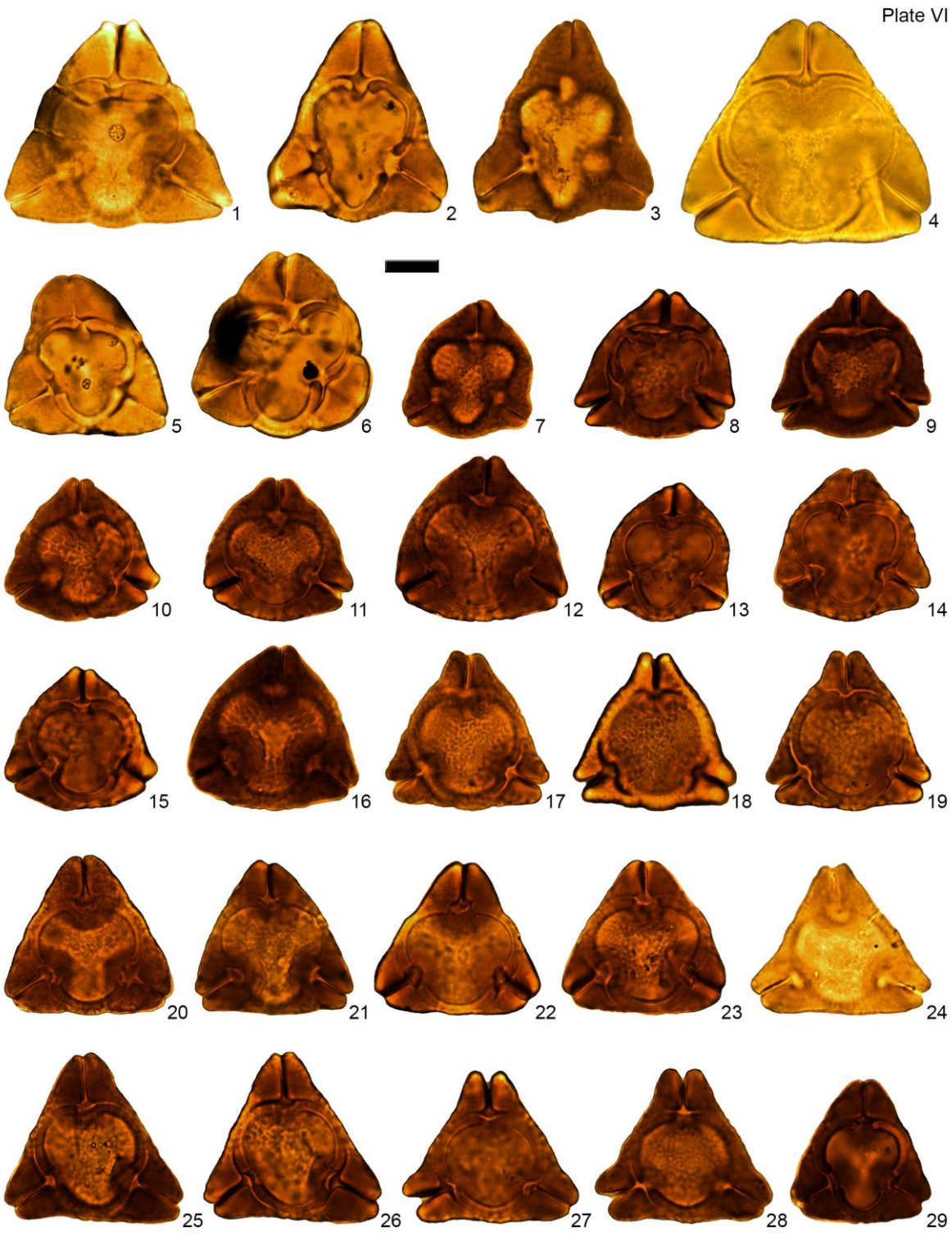
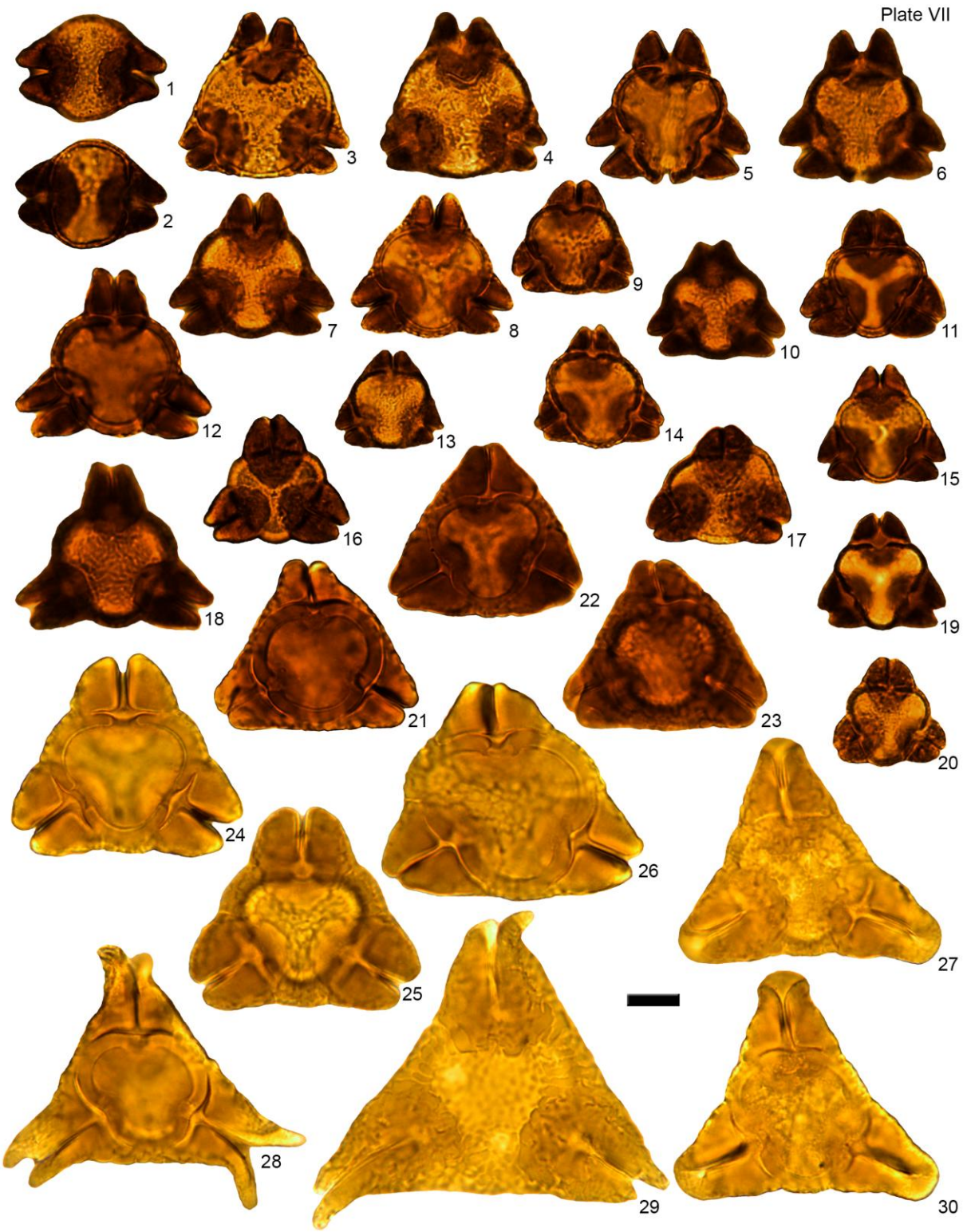


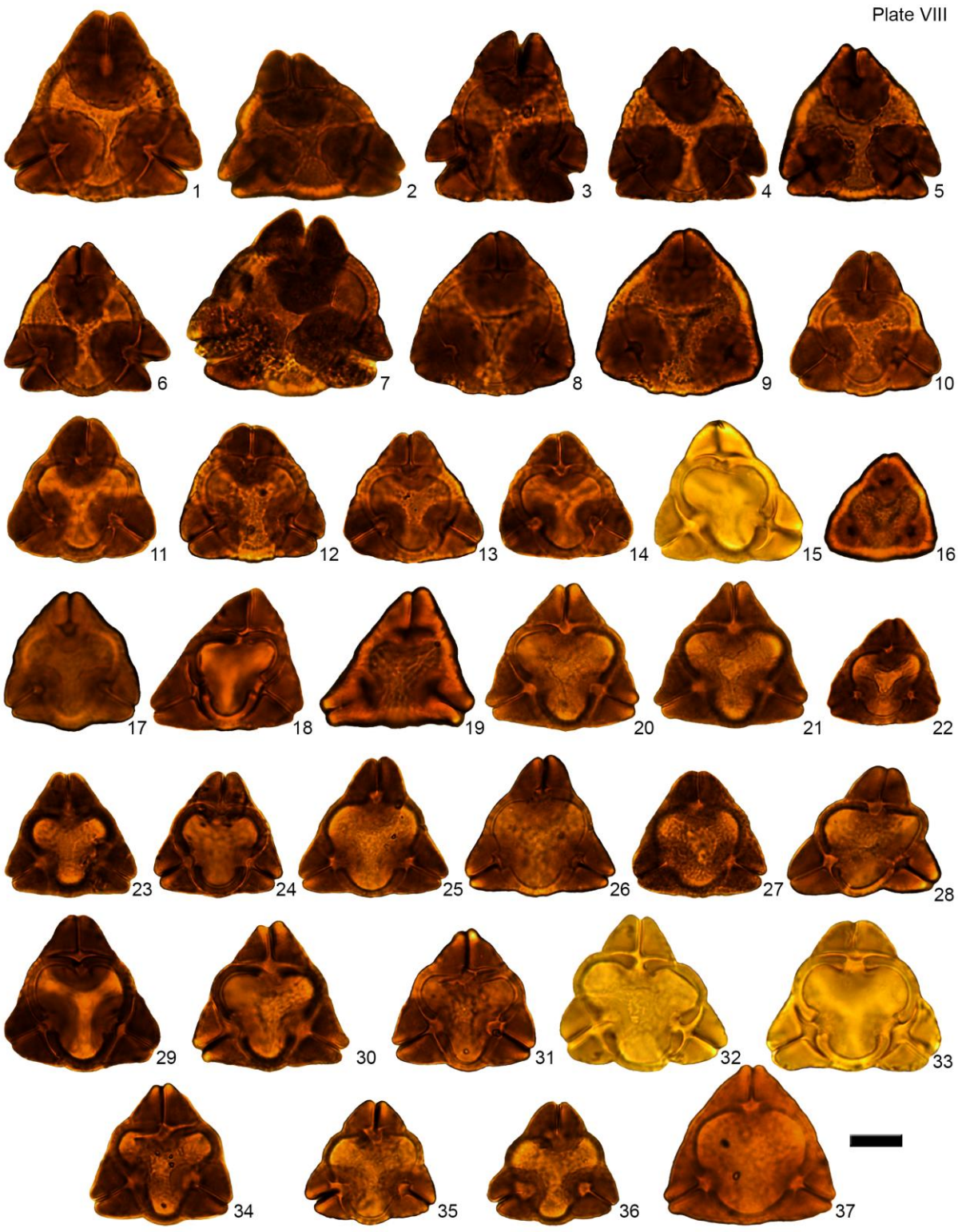
Plate IV











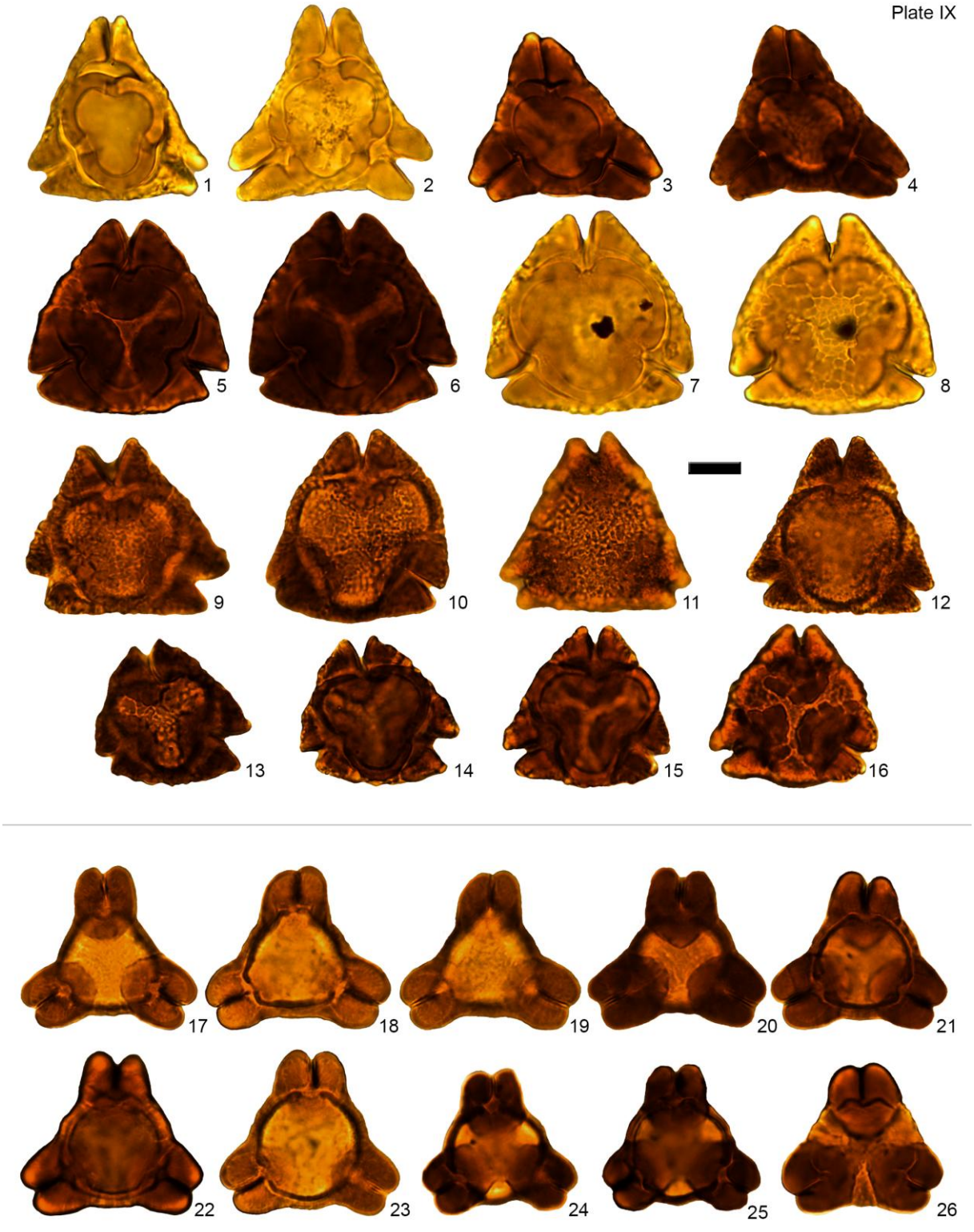
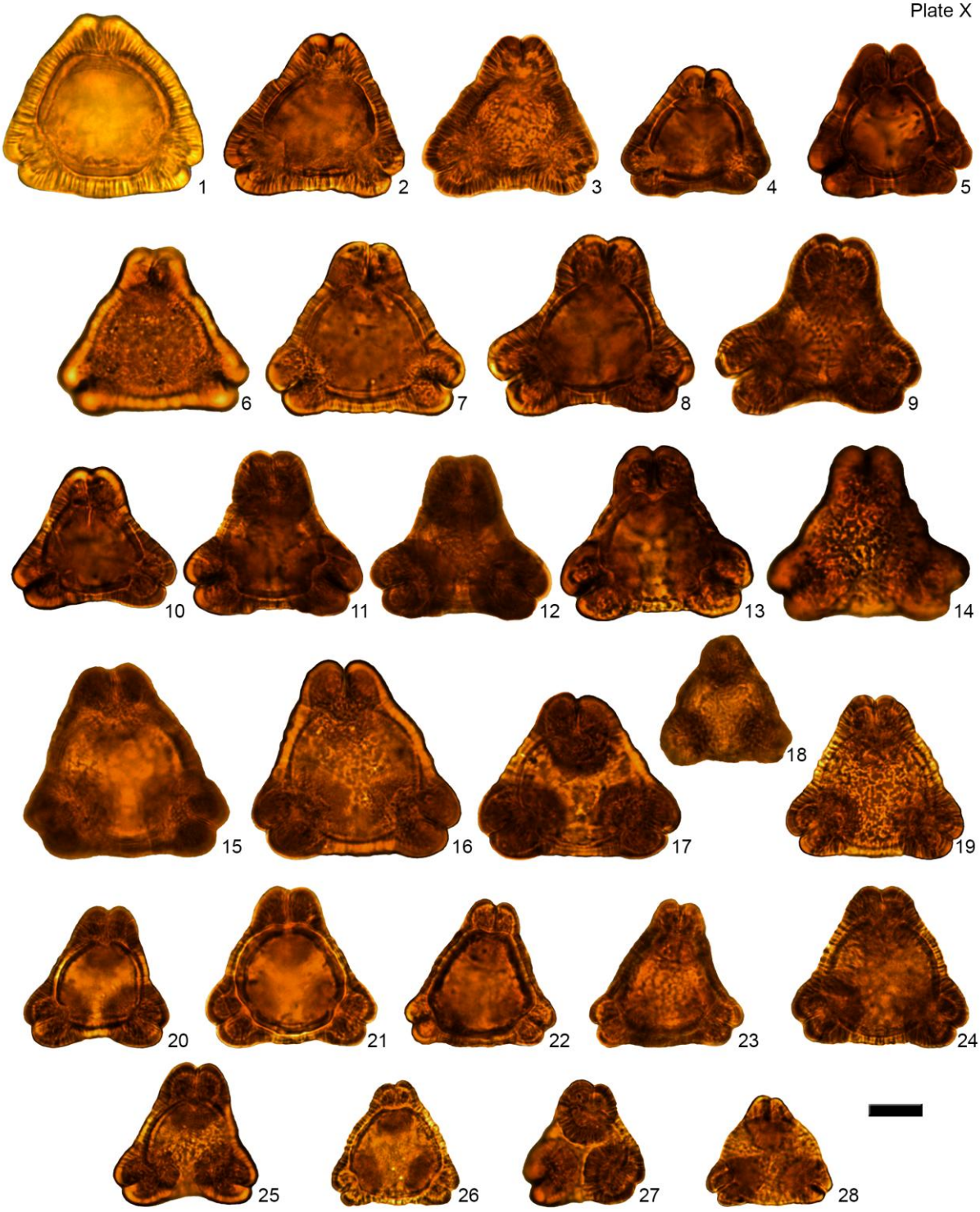
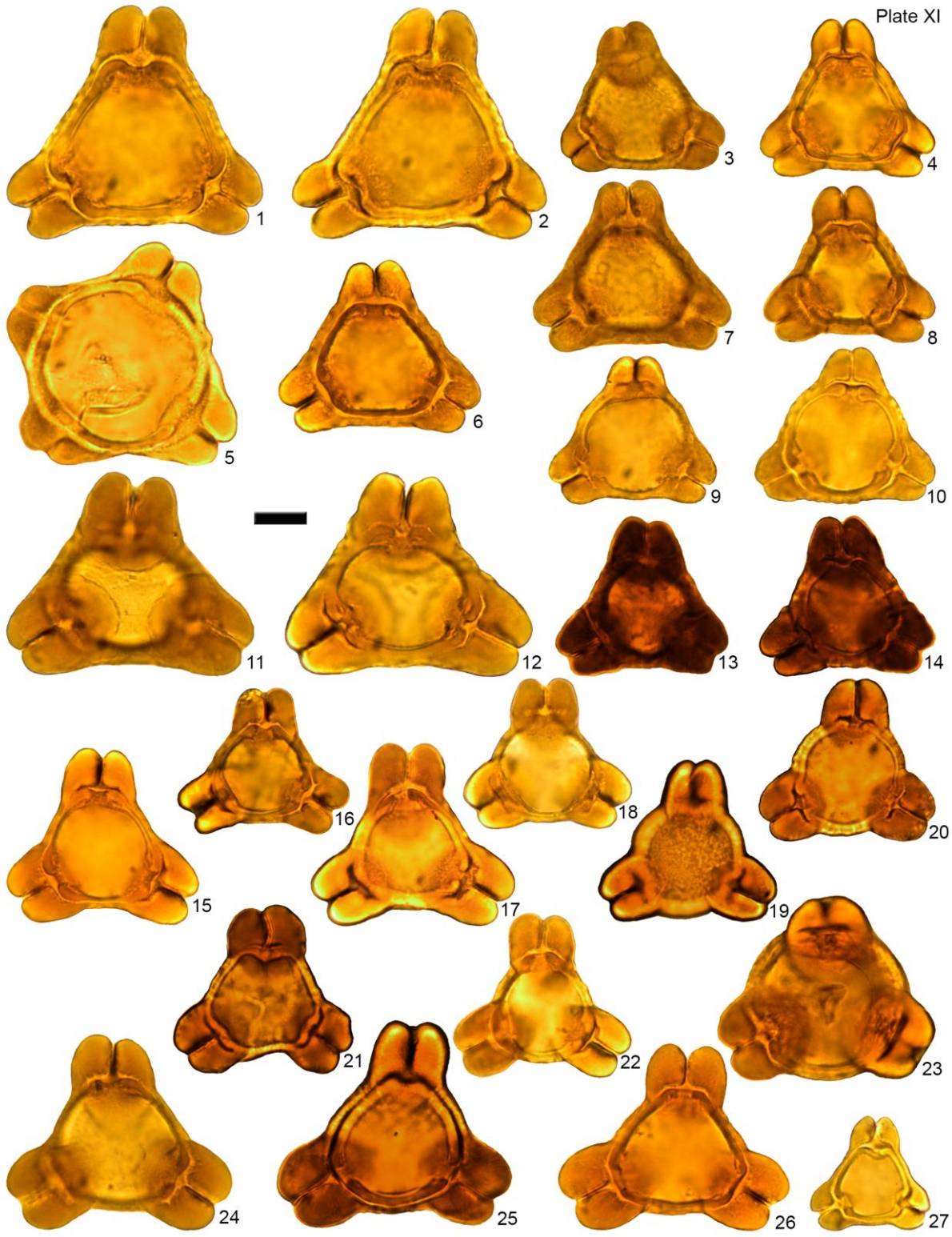
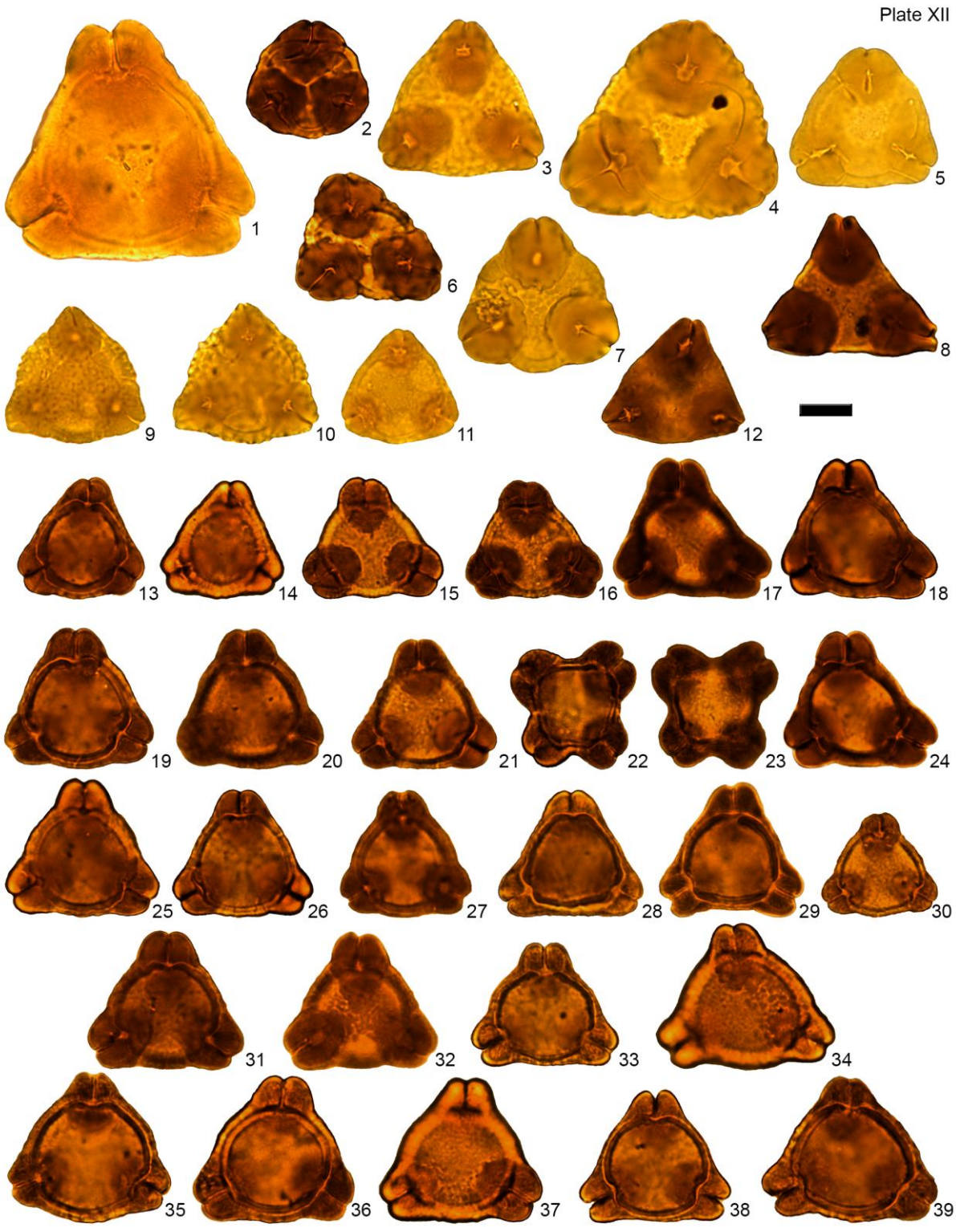
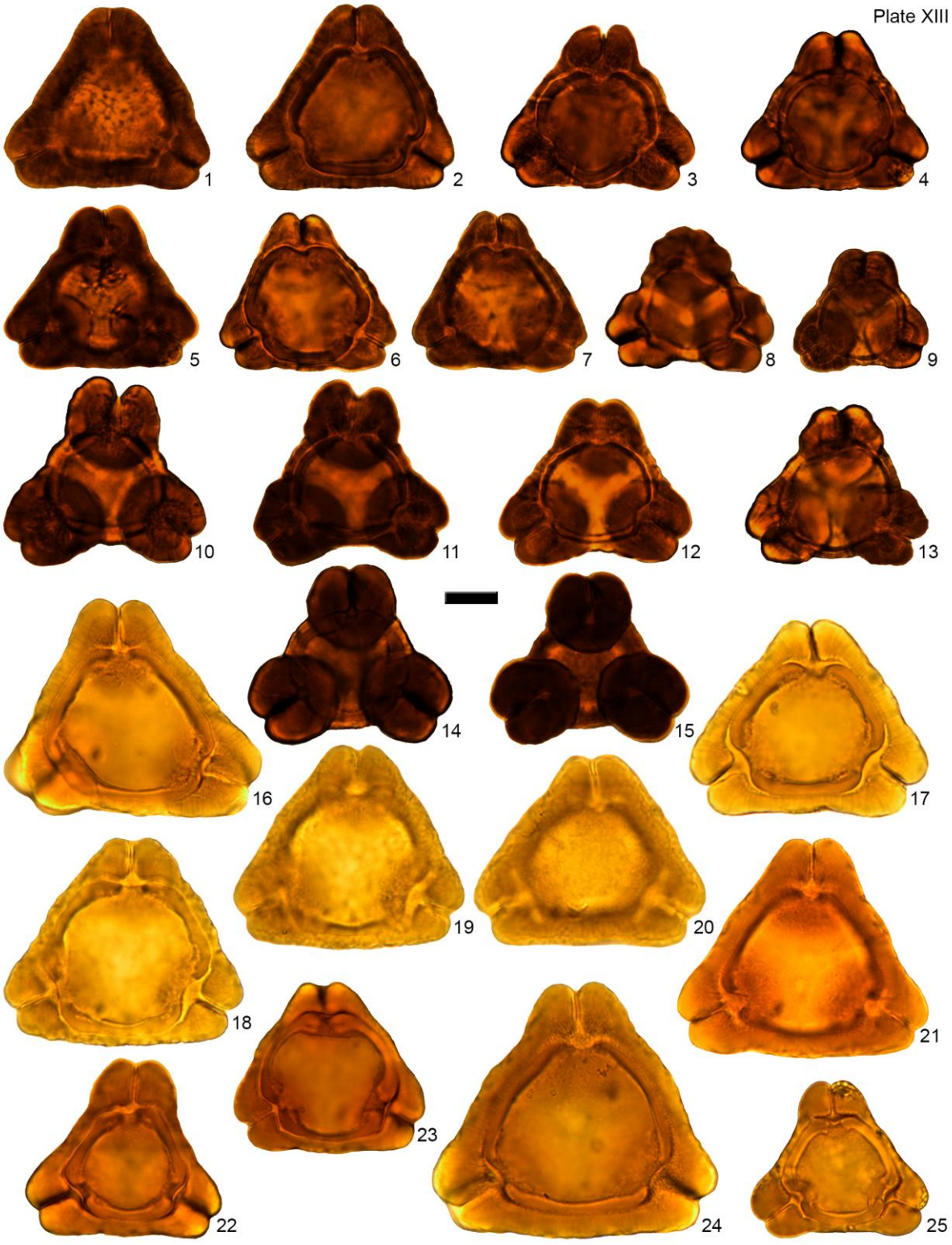


Plate X









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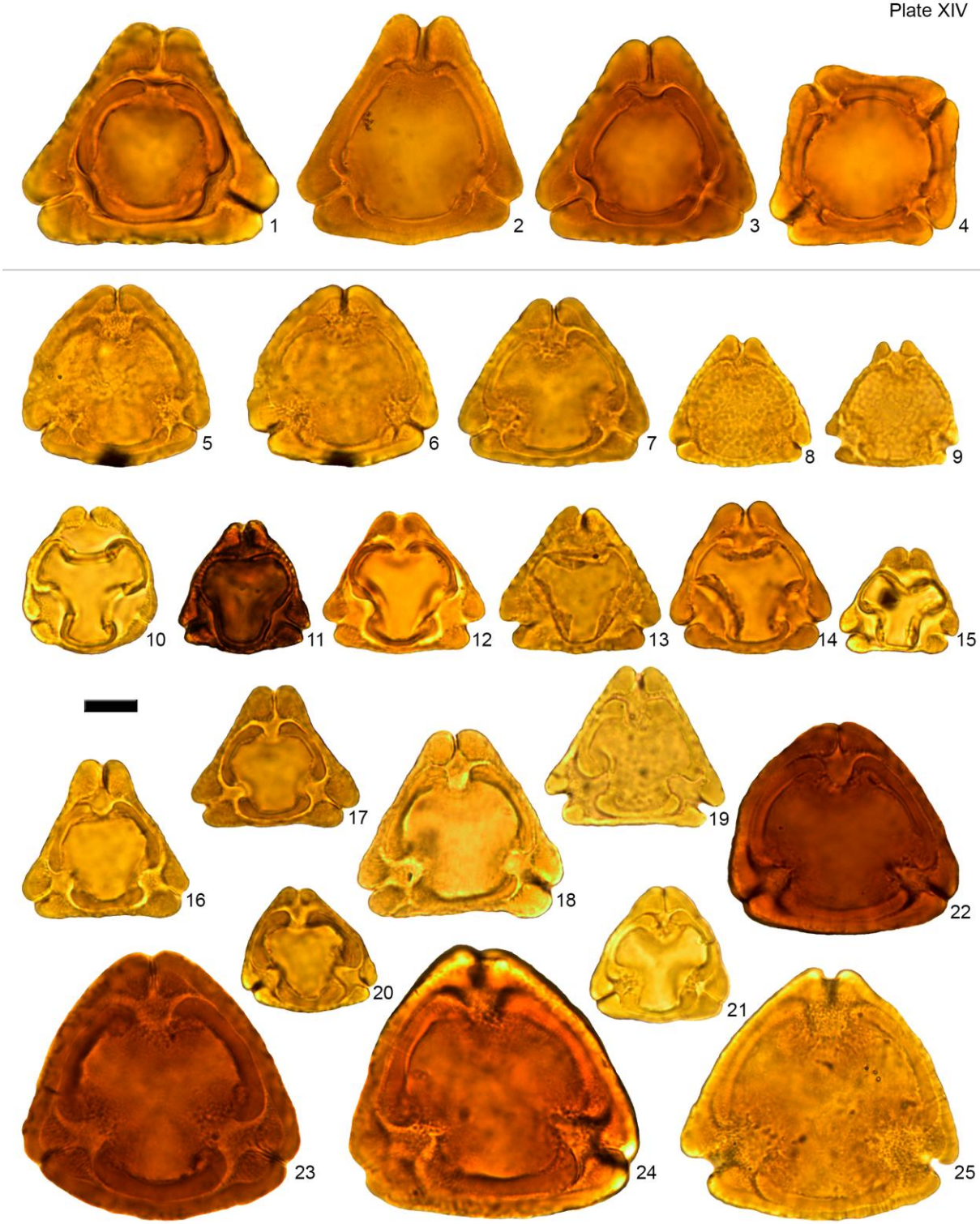

Plate XV

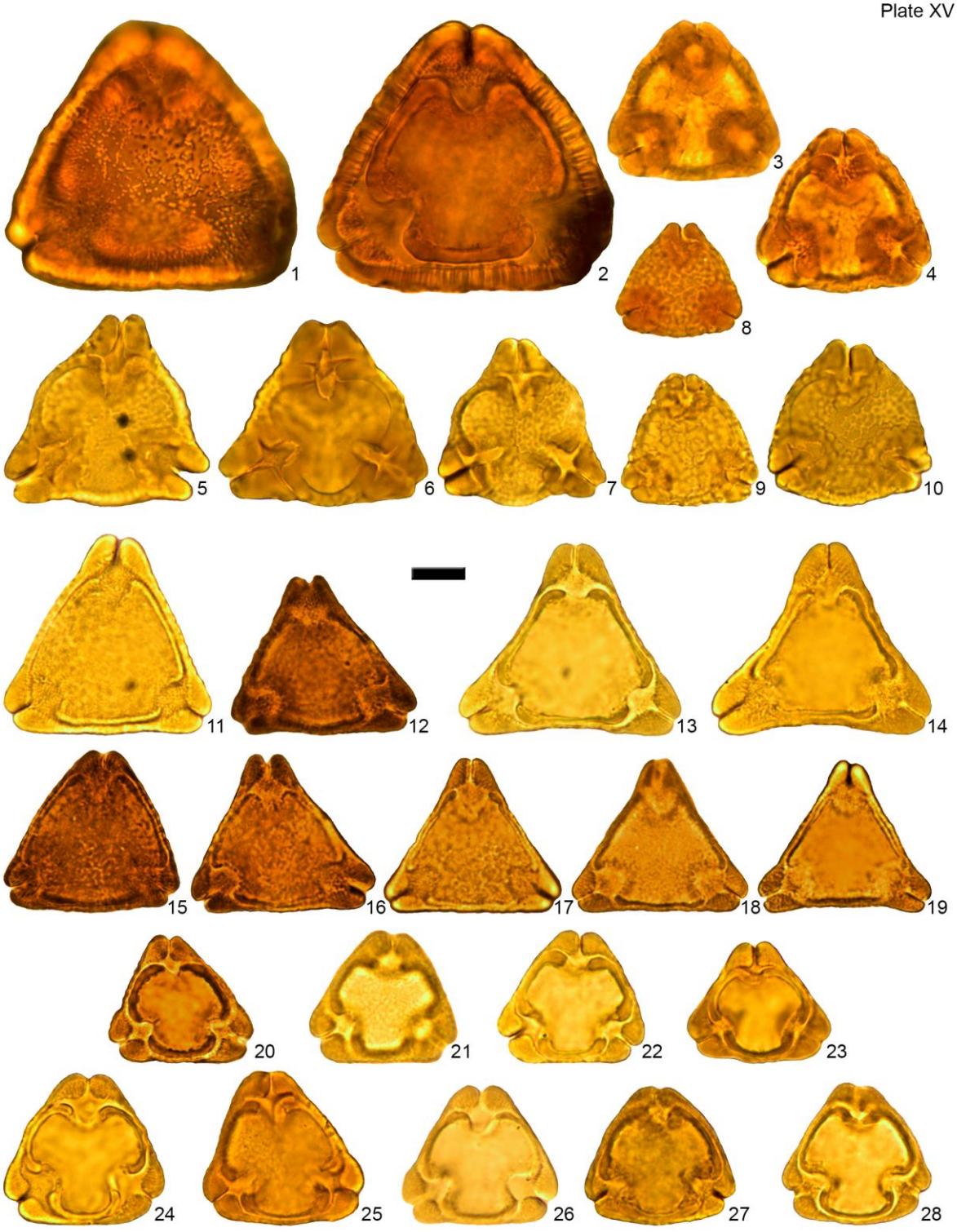

Plate XVI

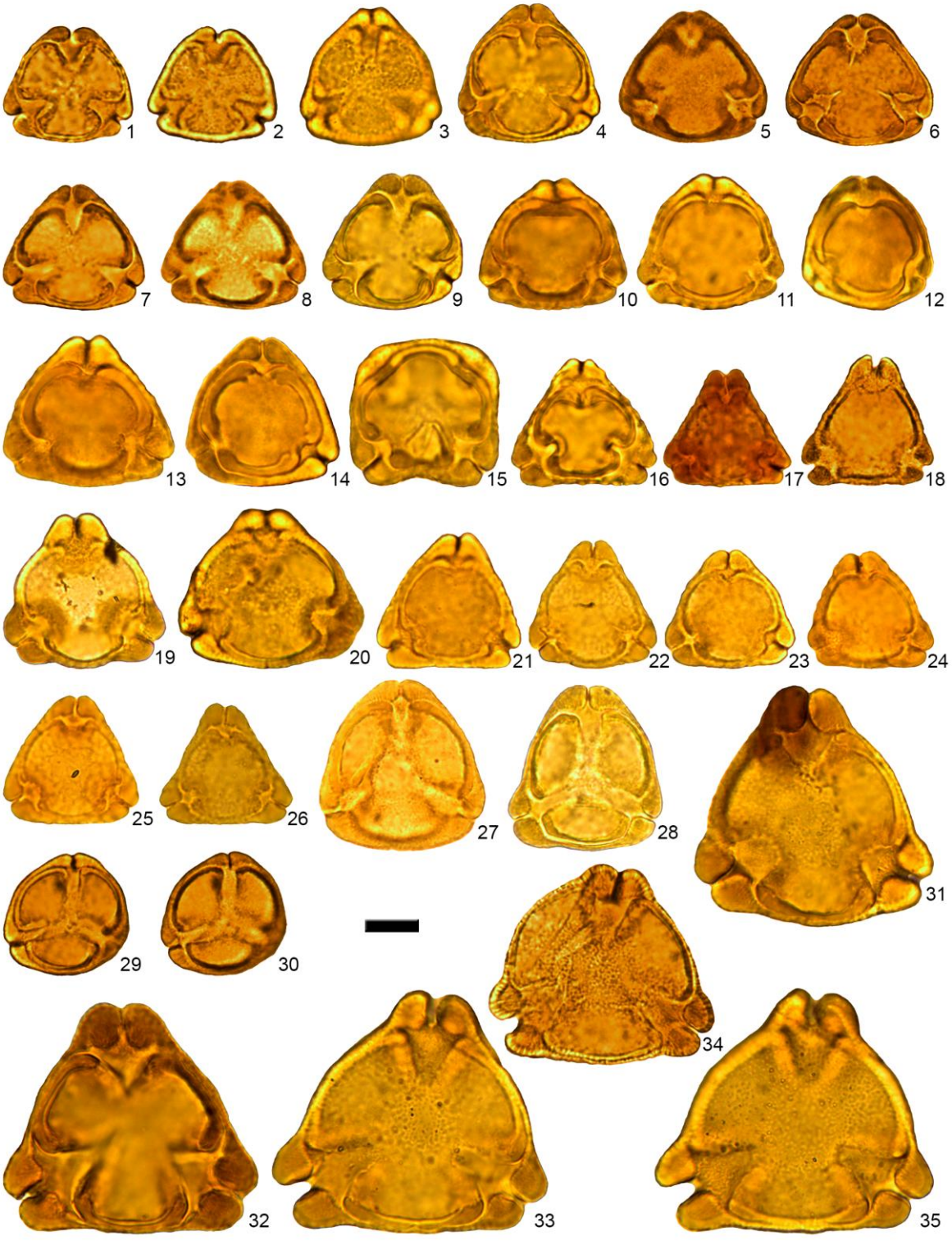

Plate XVII

Highlights

Revision of *Hungaropollis*, *Krutzschipollis*, *Longanulipollis*, *Oculopollis* and *Trudopollis*

Diagnoses of 55 species of these genera are revised, 11 of which are in new combinations

14 other species are in new generic combinations but are not otherwise considered

Many specimens are illustrated and six new species are described

13 genera are regarded as junior synonyms of four of the five genera discussed