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Re-evaluation of *Cerebropollenites thiergartii* Eberh.Schulz 1967 and related taxa: priority of *Sciadopityspollenites* and nomenclatural novelties

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Abstract
The important marker species for the base of the Jurassic, *Cerebropollenites thiergartii*, occurs contemporaneously with at least nine related taxa. However, their distinction is difficult and has been confused in the past. In addition, a long history of numerous recombinations with different genus names (e.g. *Tsugaepollenites* and *Sciadopityspollenites*), and inconsistent classifications or synonymisations, further complicate the taxonomic framework of *Cerebropollenites thiergartii*. A comprehensive study of these ten taxa, summarising their crucial distinctive characteristics and potential synonymy, is currently missing. This limits the stratigraphic value of *Cerebropollenites thiergartii* and associated taxa relevant to the Triassic–Jurassic transition. Here, we revisit relevant holotype material, related taxa and investigated new material for potential interspecific and intraspecific morphological variation. Based on an empirical analysis of name use and an extensive literature review, we identified previous sources of confusion, re-evaluated the distinctive characteristics and stratigraphic value of these taxa, and their relevance for the Triassic–Jurassic transition. Finally, we argue that the recombination as *Sciadopityspollenites thiergartii* is taxonomically and nomenclaturally imperative, not only due to priority, but also because it unifies previous disjunct use of *Cerebropollenites* for Mesozoic and *Sciadopityspollenites* for Cenozoic taxa, or Mesozoic species in many Russian studies. Thus, we propose a series of nomenclatural novelties: *Sciadopityspollenites* emend., *Sciadopityspollenites thiergartii* comb. nov. et emend., *S. thiergartii* ssp. nov. *thiergartii*, *S. thiergartii* ssp. *multiverrucosus* stat. nov., *S. megaorbicularius* sp. nov., *S. carlylensis* comb. nov. et emend., *S. serratus* emend., *S. macroverrucosus* emend., *S. mesozoicus* emend., *Cryptopalynites* gen. nov., *Cryptopalynites pseudomassulae* comb. nov. et emend.

Keywords: *taxonomy, revision, marker fossil, Triassic–Jurassic,* Tsugaepollenites, macroverrucosus, mesozoicus

In Mesozoic floras, *Cerebropollenites thiergartii* Eberh.Schulz 1967 and other related taxa like *Cerebropollenites macroverrucosus* (Thierg. 1949) Eberh.Schulz 1967, *Cerebropollenites mesozoicus* (Couper 1958) Tage Nilsson 1958, and *Sciadopityspollenites multiverrucosus* (Sachanova et Iljina 1968) Iljina 1985, are some of the few new elements to join the Jurassic palynofloral assemblages after the end-Triassic biotic crisis (Iljina 1985; Kürschner et al. 2007; Bonis et al. 2009; von Hillebrandt et al. 2013; Lindström et al. 2017b; Gravendyck et al. 2020b). After diversification, their abundance remains relatively low in the Jurassic but increases significantly in the Lower Cretaceous, where they even constitute the *Cerebropollenites* palynofloral province in the Northern Hemisphere (Zauer & Mchedlishvili 1966; Herngreen et al. 1996).

Unfortunately, vast taxonomical confusion exists for the more than ten pollen taxa related to

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Cerebropollenites thiergartii, especially *Tsugaepollenites pseudomassulae* (Mädler 1964b) Morbey 1975. This taxonomic confusion is much greater than for other taxa occurring in Triassic–Jurassic boundary assemblages. Especially the morphologically similar and potentially synonymous *Cerebropollenites mesozoicus* (Couper 1958) Tage Nilsson 1958 and *Cerebropollenites macroverrucosus* (Thierg. 1949) Eberh.Schulz 1967 (Nilsson 1958; Mädler 1963; Pocock 1964) have caused some authors to inconsistently use either name (Lund & Pedersen 1984), and others to use consistently only one (*Cerebropollenites mesozoicus*: Guy-Ohlson 1978, 1986; De Renéville & Raynaud 1981; Shang & Zavada 2003) or the other (*Cerebropollenites macroverrucosus*: Bóna 1969; Morbey and Neves 1974; Guy-Ohlson and Malmquist 1985; Srivastava 1987; Dybkjær 1991; Hofmann et al. 2021). This has subsequently led to a great deal of confusion, to the extent that even the authorities are used inconsistently (compare the wrong authority '*Cerebropollenites macroverrucosus* Nilsson 1958' in Boulter and Windle [1993]). Last but not least, the recombination of some *Cerebropollenites* species with the genus *Sciadopityspollenites* in mostly Eastern European and Russian publications, e.g. *Sciadopityspollenites macroverrucosus* (Thierg. 1949) Iljina 1985 (Waksmundzka 1981; Iljina 1985; Kuzmichev et al. 2018), complements the taxonomic and nomenclatural patchwork.

Inconsistent identification and naming of *Cerebropollenites thiergartii* and related taxa is particularly problematic because of its stratigraphic significance for the base of the Jurassic (e.g. Kürschner et al. 2007; Bonis et al. 2009; von Hillebrandt et al. 2013), and that of *Cerebropollenites macroverrucosus* for the Lower Jurassic (Dybkjær 1991). Distinguishing the taxa in question is further hampered by often poorly illustrated specimens and lack of access to the original descriptions and plates. Although some authors partially revised and commented on the subject (e.g. Mädler 1963; Schulz 1967; Pocock 1970; Morbey 1975; Waksmundzka 1981), a comprehensive study summarising the crucial distinctive characteristics and synonymy of the form-complex is still missing.

The present study thus aims to clarify the taxonomic and nomenclatural confusion (1) between the genera *Cerebropollenites* Tage Nilsson 1958, *Tsugaepollenites* (R.Potonié et Venitz 1934) R.Potonié 1958 and *Sciadopityspollenites* Raatz 1937 ex R.Potonié 1958, and (2) ten species of Mesozoic taxa relevant for the Triassic–Jurassic transition, especially in regard to *Cerebropollenites thiergartii*, *Cerebropollenites macroverrucosus/mesozoicus* and *Tsugaepollenites pseudomassulae*.

To achieve this, we re-evaluated the type material for *Cerebropollenites thiergartii* and type material for six other taxa associated over the years, such as the prominent *Pollenites macroverrucosus* Thierg. 1949, *Camerosporites pseudomassulae* Mädler 1964b, and *Tsugaepollenites mesozoicus* Couper 1958, and also *Sciadopityspollenites multiverrucosus* (Sachanova et Iljina 1968) Iljina 1985 and the dubious *Pollenites serratus fa. helmstedtensis* Thierg. 1949, *Pollenites macroserratus Keuperianus* Thierg. 1949, *Pollenites macroserratus doggerensis* Thierg. 1949, that have been associated with the taxa in question in the past. Additionally, we compared their holotypes/paratypes to original and new material, and reviewed interspecific and intraspecific morphological variation. Together with an empirical analysis of name use and an extensive literature review, we identified previous sources of confusion, re-evaluated their relation to other previously described taxa for whom type material is presumably lost (*Cerebropollenites carlylensis* S.A.J.Pocock 1970 and *Cerebropollenites findlaterensis* S.A.J.Pocock 1970). Subsequently, we clarified distinctive characteristics in a classification key and revised taxonomy including recommendations for the consistent differentiation and recognition of these taxa.

Materials and methods

To clarify genus and species distinction of *Cerebropollenites thiergartii* and related species, we tried to gather type material for genus names (Figure 1A) and holotype material for species names (Figure 1B) from the relevant publications (Potonié 1931; Potonié & Venitz 1934; Thiergart 1949; Couper 1958; Mädler 1964; Schulz 1967; Iljina 1968; Pocock 1970). Unfortunately, type specimens were often no longer stored at the originally indicated location or were lost completely. For example, except for some Upper Carboniferous and material from the Geiseltal, most of Potonié's material was probably destroyed in World War II and is assumed to be lost (Hartkopf-Fröder 2018; Gravendyck et al. 2020a). Accordingly, the type material for Potonié (1931), Potonié and Venitz (1934) has to be considered 'lost' (C. Hartkopf-Fröder, Geological Survey of Krefeld, pers. comm., 25 July 2019). Potential material for Pocock (1970) could be relocated at the Geological Survey of Canada, but slides complying with labelling of the holotype are missing (K. Boyce, pers. comm., 27 January 2021).

In the following, we explain the provenance and details of the material that could be retrieved for study by JG between 2018 and 2021. It is presented

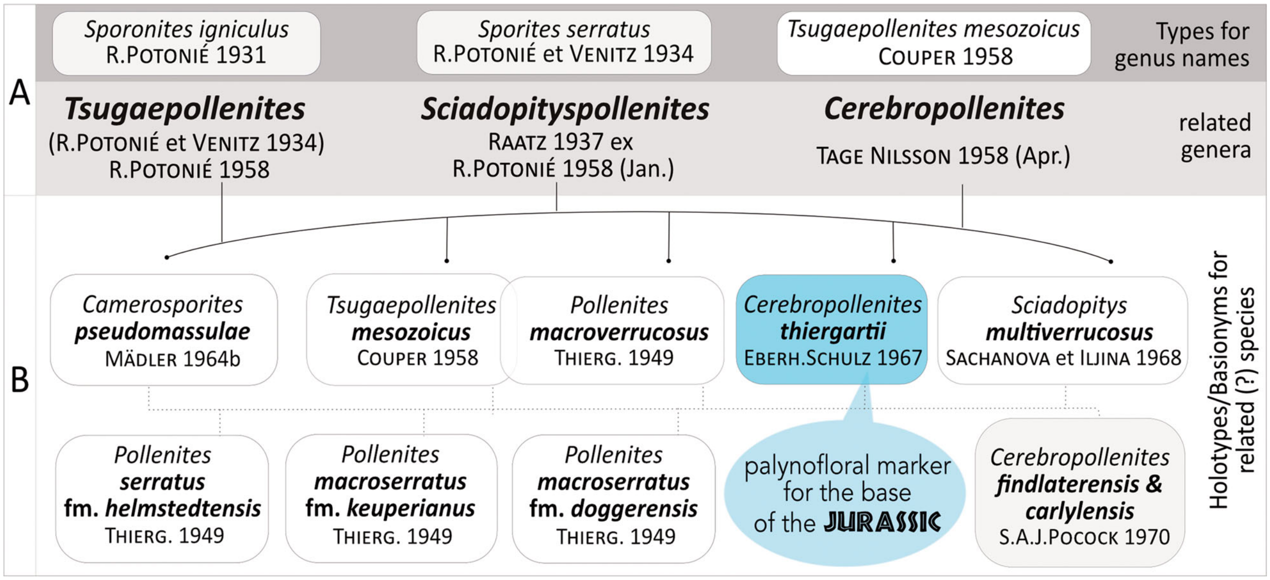


Figure 1. Problem and material overview. **A.** Relevant names and types for distinction on genus level. **B.** *Cerebropollenites thiergartii* and associated taxa relevant for distinction on species level. Holotypes unavailable for study are shown in grey rectangle. The distinction and relationship between several species is problematic (dotted line) as well as their genus assignation (black lines ending in points).

in chronological order of original description, first for types for genus names and then for holotypes/paratypes for species names. Herbarium codes according to the Index Herbariorum are given to refer to collections where the material is currently stored. Abbreviations for collections without standard international herbarium codes are indicated with an asterisk (*) (summary of abbreviations used in this manuscript can be found in Supplementary Material 1). Authorities for scientific names follow the author standard form according to Brummit and Powell (1992) as listed in the International Plant Names Index (IPNI).

Type material, provenance, and details

Type for the genus **Tsugaepollenites** *(R.Potonié et Venitz 1934) R.Potonié 1958.* — A specimen from the Beisselgrube (Miocene) that Potonié illustrated in 1931 as *Sporonites* (≡ *Tsugaepollenites*) *igniculus* (Potonié 1931), was designated as type for the genus in 1958 when Potonié provided the first genus diagnosis (Potonié 1958). Unfortunately, the original type material from the Beisselgrube (Miocene) is amongst Potonié's presumably lost material.

The closest we might get to the holotype are slides from Thiergart (1938) from the Grube Marga. The material is in excellent condition and can serve to designate a neotype and might even be interpreted as original material, to designate a lectotype, in the sense of the *International Code of Nomenclature for algae, fungi, and plants* (hereafter *Code*) Art. 9.4. Thiergart was Potonié's doctoral student (Stach 1975) and Potonié had suggested the project to Thiergart which resulted in the said publication (Thiergart 1938). Later, accompanying the new genus diagnosis for *Tsugaepollenites* (Potonié 1958), Potonié cites one other specimen (aside the lost specimen) for the species *Tsugaepollenites igniculus* (R.Potonié 1931) R.Potonié et Venitz 1934 from one of his own publications written together with Thiergart (Potonié et al. 1951). That specimen was figured first by Thiergart and appeared in several publications by both Thiergart and Potonié (Thiergart 1938, 1940; Potonié et al. 1950; Potonié 1951). This specimen is designated as a lectotype here to replace the lost type and is particularly valuable, since Potonié himself implicitly confirmed its classification as *Tsugaepollenites igniculus*.

The Thiergart collection could be rediscovered only after intensive search. After Thiergart's death in 1977 (Pegler 2017), the custodian for palaeobotany at the time from the Natural History Museum in Berlin (Dr Barbara Mohr) retrieved the remaining material and transferred it to the museum's collection, where it is currently stored in the Reuchlinstraße (Berlin, BHUPM). Going through the uninventoried and uncurated part of the collection, we could relocate the relevant Thiergart samples. The slide (inventory number MB.Pb.2019/0228) with a red-circled label saying '*igniculus*' has an ink ring marking the frequently reproduced specimen (Figure 2A) that dates back to Thiergart (1938) where it was first classified as *Tsuga-pollenites igniculus*.

Type for the genus **Sciadopityspollenites** *Raatz 1937 ex R.Potonié 1958 (Jan.).* — Potonié (1958) designated the specimen from the Beisselgrube (*Sporites serratus* ≡ *Sciadopityspollenites serratus*) that served as the model for the drawing in Potonié and Venitz (1934) as the type for the genus name. The specimen originates from the same location as *Sporonites igniculus* and is lost as well. Potonié (1958) alongside his genus validating diagnosis cites one additional specimen for *Sciadopityspollenites* (from Thiergart, from the Grube Marga, which was figured in several publications ([Thiergart 1938, 1940; Potonié et al. 1950; Potonié 1951]). The slide (inventory number MB.Pb.2019/0230) is stored at the BUHPM and has a red-circled label annotated with '*serratus*' (Figure 2D) and holds several specimens that were published as *Sciadopitys-pollenites serratus* (R.Potonié et Venitz 1934) Thierg. 1938.

Type for the genus **Cerebropollenites** *Tage Nilsson 1958 (Apr.).* — Nilsson (1958) designated the holotype of *Tsugaepollenites mesozoicus* of Couper (1958) as the type for his newly erected genus *Cerebropollenites* (Figure 1A). The slide with Couper's holotype (Figure 3F) is still stored at the Sedgwick Museum in Cambridge (CGE) as originally indicated (Couper 1958).

Holotypes or Paratypes for ***names designated in Thiergart*** *(1949).* — This material is located like the slides for Thiergart (1938) at BHUPM. However, in contrast to the 1938 publication, none of the slides from the 1949 publication were specially labelled in red. Thanks to the standard location, depth, and slide number, we could still identify the slides that should contain three syntypes for *Pollenites serratus fa. helmstedtensis* and two syntypes for *Pollenites macroserratus Keuperianus* (both inventory number 'MB.Pb.2021/0101', Figure 2H), the holotype for *Pollenites macroverrucosus* (inventory number 'MB.Pb.2019/0231', Figure 3A) and the last remaining syntype of *Pollenites macroserratus doggerensis* on the same slide (Figure 4I).

Holotype for **Camerosporites pseudomassulae** *Mädler 1964b.* — The holotype (Figure 3J–K) is still stored at its original institution, since its designation in 1964, and can be found at the Landesamt für Bergbau, Energie und Geologie in Hannover in Germany (LBEG*) under the inventory number of the 'Typenkatalog' 'TK-Nr.3141'.

Holotype for **Cerebropollenites thiergartii** *Eberh.Schulz 1967.* — The holotype is stored at the Bundesanstalt für Geowissenschaften und Rohstoffe at the side-branch in Berlin-Spandau (BGR-S*) in the 'Mikroflora Originale' collection. The slide Marnitz 5/30–59/2 holds the holotype specimen and is indicated with the inventory number X11369. Unfortunately, the storage conditions in the facility are suboptimal. The type material is stored in metal cupboards in an old, brick building with very cold temperatures in winter, and very hot conditions in summer. The slide in question and other original material from Schulz stored in this facility was altogether in very poor condition. The desiccated glycerine jelly is apparent with the naked eye. The slide with the holotype (Figure 4D) was photographed annually for three years to monitor the ongoing decay of some remaining glycerine jelly pockets (Figure 4A–C).

Holotype for **Sciadopitys multiverrucosus** *Sachanova et Iljina 1968.* — The holotype is stored at the Trofimuk Institute of Petroleum Geology and Geophysics – Siberian Branch of the Russian Academy of Sciences (IPGG SB RAS*, Herbarium Code KUZ). Since the holotype was not available for loan, Ekaterina Peshchevitskaya from the KUZ kindly documented the holotype on our behalf (Figure 4L).

Intraspecific and interspecific variation in original and new material

An author's perception of a new species is likely primed by the taxon's intraspecific and interspecific variation observed prior to or during the process of description. Slides holding holotypes were mostly strew mounts (except for Mädler's slide with *Camerosporites pseudomassulae*) and were also studied for their microfloral assemblage (e.g. stratigraphically important taxa, preservation) and especially for the morphological variation of the newly described and associated taxa.

Additionally, new material from the Bonenburg section (Schobben et al. 2019; Gravendyck et al. 2020b), Kuhjoch (Global Boundary Stratotype Section and Point [GSSP] for the base of the Jurassic) (Bonis et al. 2009; von Hillebrandt et al. 2013) and two samples from the Swedish Höllviken-2 core (HV1308.95 m and HV1316.5 m, Toarcian–Aalenian) (sedimentary log in Lindström et al. 2017a) were studied for interspecific and infraspecific variation. The Höllviken-2 material was chosen, because abundant *Cerebropollenites thiergartii* and

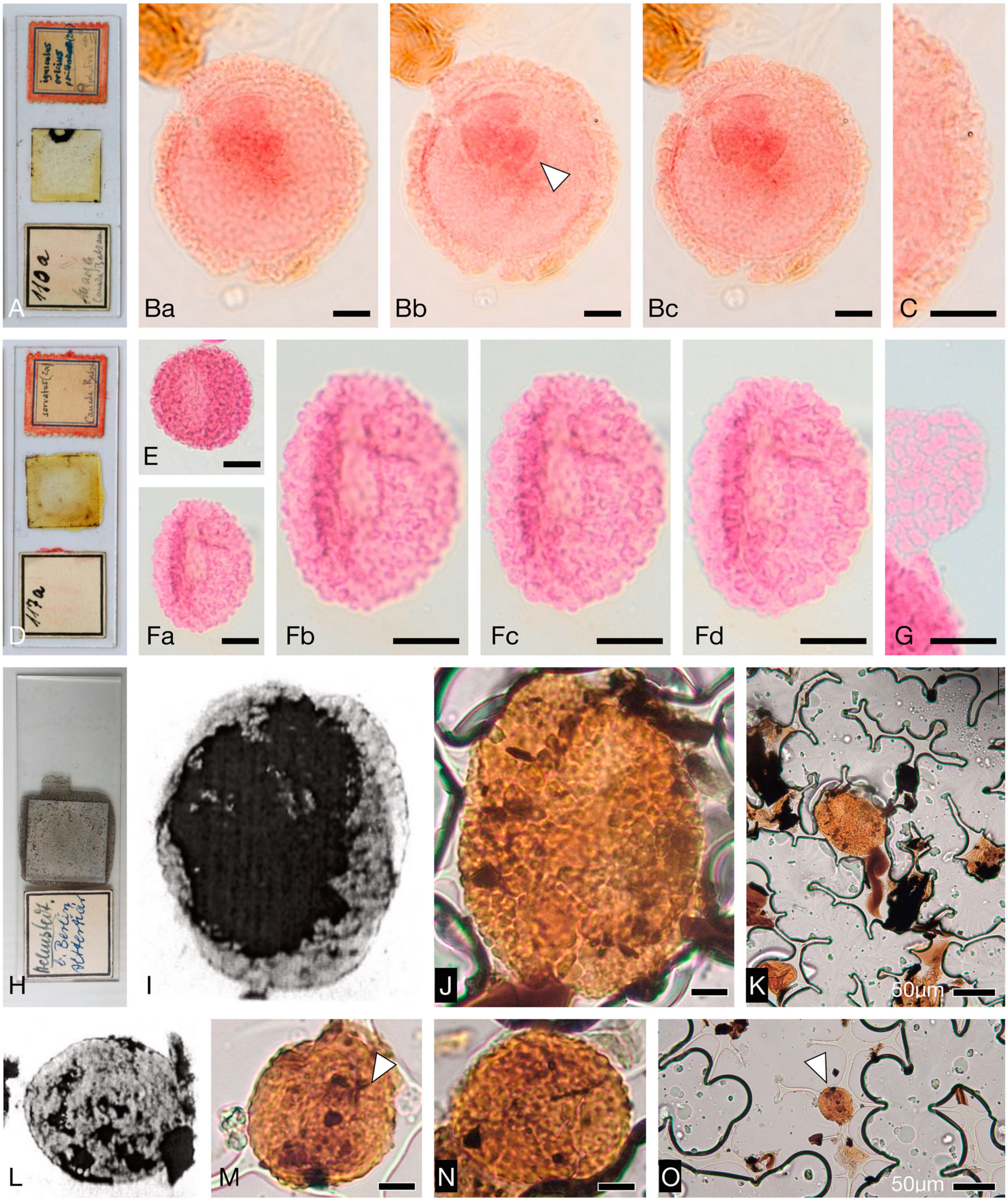


Figure 2. (Original) Material for Thiergart (1938) and Thiergart (1949). **A–C.** Lectotype for *Tsuga-pollenites igniculus* from Thiergart (1938); **A.** Strew mount slide, specimen indicated with ink ring; **B.** *Tsuga-pollenites igniculus* in three focal planes; **C.** Detail of the fringe, i.e. the monosaccus. **D–G.** Lectotype for *Sciadopitys-pollenites serratus* from Thiergart (1938) cited in the protologue of Potonié (1958); **D.** Strew mount slide; **E, F.** *Sciadopitys-pollenites serratus*; **F.** *Sciadopitys-pollenites serratus* in different focal planes; **G.** Detail of ornamentation on a fragment of a *Sciadopitys-pollenites serratus* specimen. **H–K.** *Pollenites serratus fa. helmstedtensis* from Thiergart (1949); **H.** Strew mount slide, cover slip not sealed; **I.** Original photograph of Thiergart (1949) for *Pollenites serratus fa. helmstedtensis*, original photograph from Thiergart (1949, plate II, figure 19) reprinted with permission from Schweizerbart Science Publishers www.schweizerbart.de/journals/palb; **J.** The exact specimen could not be relocated, but a conspecific specimen is shown; **K.** Preservation of the slide, glycerine jelly desiccated. **L–O.** *Pollenites macroserratus Keuperianus*; the specimen from the original photograph (**L,** reprinted with permission from Schweizerbart Science Publishers www.schweizerbart.de/journals/palb) could not be relocated, but conspecific specimen (**M** and **N**) are shown, in **M.** The trilete mark is visible (arrowhead); **O.** Preservation of the slide, original glycerine jelly could be partially re-embedded, hence the double desiccation lines. Scale – 10 µm (unless indicated otherwise).

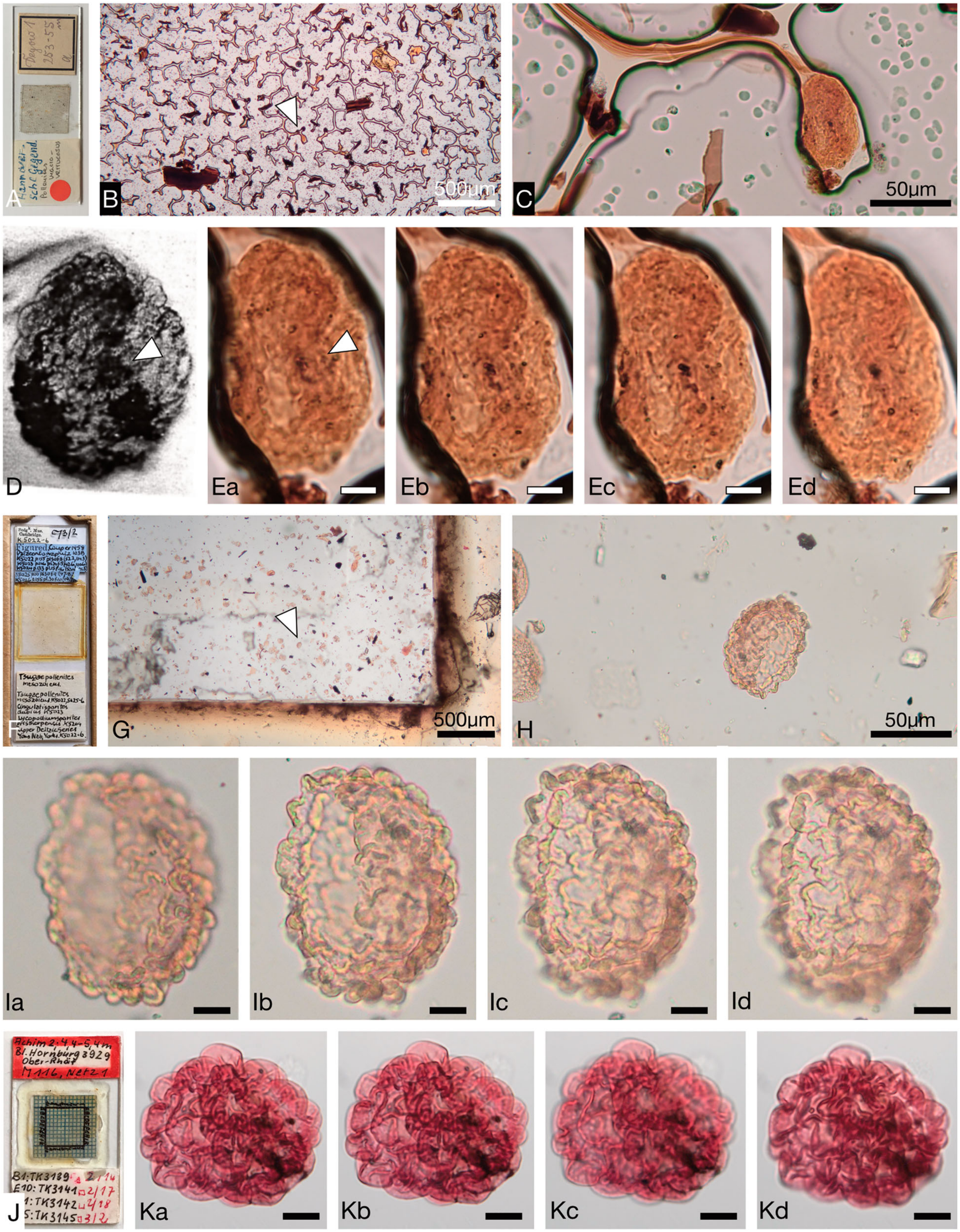
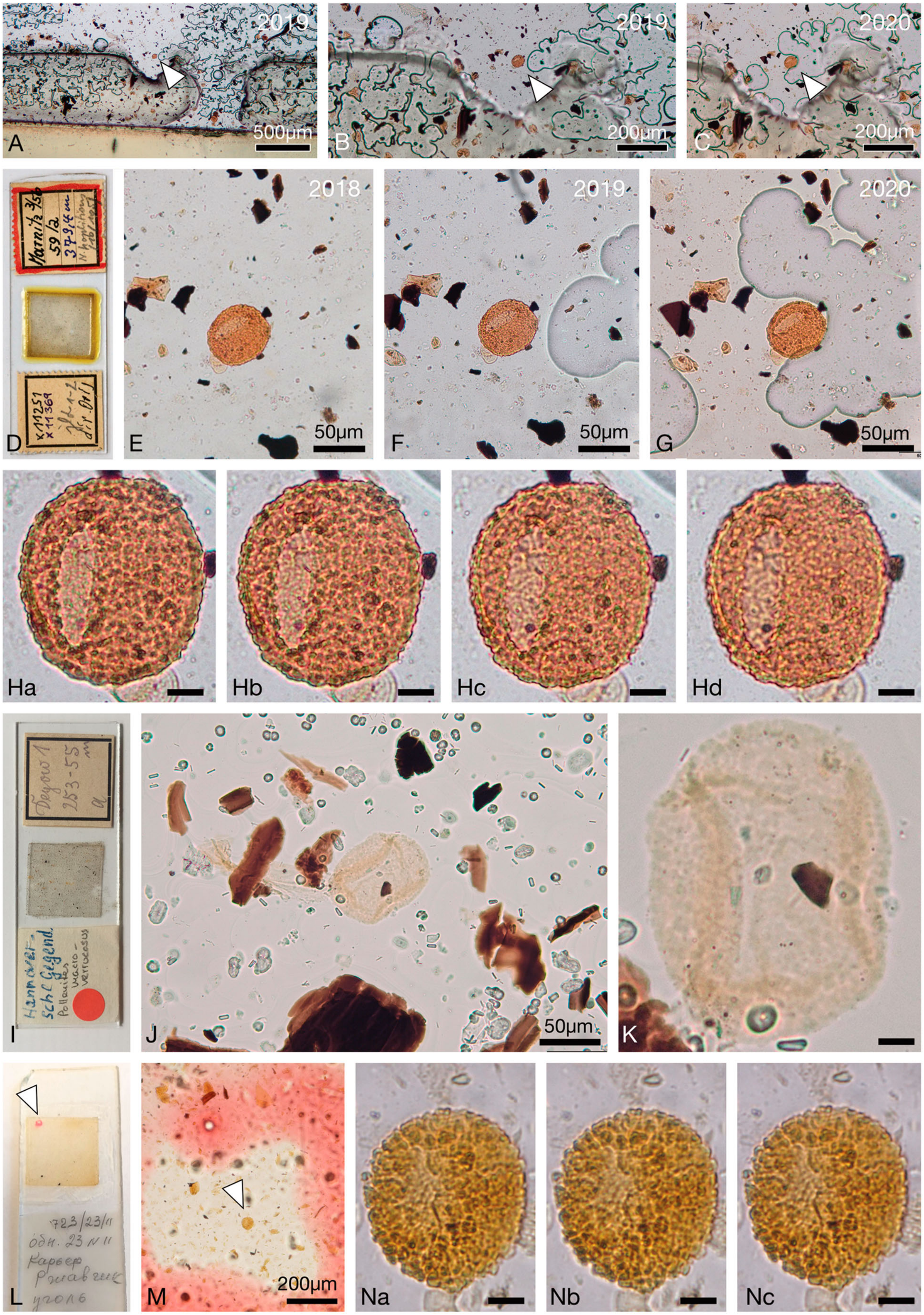


Figure 3. Holotypes of *Pollenites macroverrucosus*, *Tsugaepollenites mesozoicus* and *Camerosporites pseudomassulae*. **A–E**. Holotype for *Pollenites macroverrucosus*; **A.** Strew mount slide without cover-slip seal. The red dot and indication of the type was added; **B**. Overview of the preservation of the slide. Glycerine jelly has desiccated to dendritic remains; **C**. Partial mounting of the holotype causing prismatic effect at the edge; **D**. Original photograph from Thiergart (1949, plate II, figure 19) reprinted with permission from Schweizerbart Science Publishers www.schweizerbart.de/journals/palb; **E.** *Pollenites macroverrucosus* in different focal planes. **F–I**. Holotype for *Tsugaepollenites mesozoicus*; **F.** Strew mount slide; **G**. Location of the holotype at the very corner of the cover slip; **H.** Embedding of the holotype is still intact; **I.** Holotype for *Tsugaepollenites mesozoicus* in different focal planes. **J, K**. Holotype for *Camerosporites pseudomassulae;* **J**. Smaller slide with an embedded net with coordinates with several single-grain mounts; **K.** Holotype for *Camerosporites pseudomassulae.* Scale – 10 µm (unless indicated otherwise).


A
2019
500μm
B
2019
200μm
C
2020
200μm
D
Marnitz 3/56
59/a
37-37,4 m
N. hopliticus
1961/1957
x11251
x11369
D
E
2018
50μm
F
2019
50μm
G
2020
50μm
Ha
Hb
Hc
Hd
Bezow 1
253-55 m
a
Hannover-
sche Gegend
Pollenites
macro-
verrucosus
I
J
50μm
K
L
723/23/11
обн. 23 N 11
Карьер
Ржавчик
уголь
M
200μm
Na
Nb
Nc

Cerebropollenites macroverrucosus were documented from those samples (S. Lindström, pers. comm., unpublished results). Courtesy of Sofie Lindström and the Geological Survey of Sweden (SGU). Some of the Bonenburg material was mounted as double-coverslip mounts (i.e. two coverslips together without microscope slide) to be able to flip the mount and investigate palynomorphs equally-well from both sides in a permanent mount (for description of the technique inspired by holotype material of Klaus [1960] see Gravendyck et al. 2021).

Microscopy

Light microscopy was conducted using an Olympus CX31 mounted with an Olympus SC50 camera. Most specimens were studied with an ×100 oil immersion objective. Only the material from Schulz (1967) and Couper (1958) were mostly documented with a ×40 objective because the sealing of the slide and the location of the holotypes at the very edge of the cover slip did not permit oil immersion without risking further damage. Scanning electron microscopy (SEM) images are reproduced from previous studies with permissions.

Empirical analysis of name use

To study the stratigraphic range and geographical association of taxon names, information on their use was retrieved from Palynodata, the John Williams Index of Palaeopalynology and Google Scholar (see principles in Gravendyck et al. 2022a). Retrieved data was grouped and colour-coded in nine regions (see Figures 11–13). Rather than strict geographical regions, this grouping roughly reflects the different schools of palynologists, operating in particular regions and languages of the world. Citation rates (CRs) were calculated for all studied taxa (Figure 12) and the Establishment Index (EI) was calculated for competing names (Figure 13, and see Gravendyck et al. [2022b] for further information on these metrics).

Results

Taxonomy: revisiting the type material

Palynomorphs are studied in chronological order, first those types for genus names and secondly the holotypes for species names (compare Figure 1 for an overview of studied material). The state of preservation is described as condition. Many of the original descriptions are published in relatively old and often difficult to obtain publications. Therefore, the original descriptions/diagnoses are here restated and translated into English for the first time (see Supplementary Material 1 for original German texts for comparison accompanied by a list of full names with authorities used in this manuscript). This is complemented with re-descriptions of holotypes or descriptions of the newly chosen lectotypes. Restudying the material also allowed us to assign England Finder (EF) references for the first time; instead of variable microscope coordinates.

Type for the genus **Tsugaepollenites** *(R.Potonié et Venitz 1934) R.Potonié 1958. —* Figure 2B.

Type. — Sporonites igniculus R.Potonié 1931, p. 556, figure 2 (drawing of specimen from sample V80a).

Condition. — The holotype is presumably 'lost'. Lectotype: *Tsuga-pollenites igniculus* in Thiergart (1938), Marga 110a, specimen indicated with an ink ring, EF: M43/2; plate 23, figure 16; here refigured (Figure 2B).

Lectotype condition. — The specimen from Potonié et al. (1951) cited by Potonié (1958) is easily recognisable because of a smaller pollen lying behind the specimen in question (Figure 2Bb, arrowhead), which also permits reidentification of the very same specimen from Thiergart through a series of publications (Thiergart 1938, 1940; Potonié et al. 1950; Potonié 1951). Thiergart stated that the strew mount is embedded in Kayser's glycerine jelly and stained with fuchsin (Thiergart 1938). The slide itself, however, says 'Canada balsam'. The palynomorphs found in this medium were the best-preserved specimens of the entire study, despite being

Figure 4. Holotypes of *Cerebropollenites thiergartii*, *Pollenites macroserratus doggerensis*. **A–H.** Holotype for *Cerebropollenites thiergartii*; **A–C.** Location and preservation of the holotype in a remaining (but narrowing) pocket of glycerine jelly indicated with an arrowhead; **D.** Strew mount slide with cover-slip seal (which is severely cracked); **E–G.** Decay of the holotype over three years, the continuous desiccation of the last pocket of jelly is evident; **Ha–Hd.** Holotype for *Cerebropollenites thiergartii* in different focal planes. **I.** strew mount slide without cover-slip seal. The red dot and indication of the type was added. **J, K.** Holotype for *Pollenites macroserratus doggerensis.* **L, M.** Location and preservation of the holotype (indicated with an arrowhead) at the edge of the cover slip indicated in red. **Na–Nc.** Holotype for *Sciadopitys multiverrucosus.* Scale – 10 µm (unless indicated otherwise).

the oldest preparations. Some minor yellowing of the mounting medium and some bleaching of the palynomorphs was compensated by the staining and is thus not problematic for use as a lectotype.

Original description. — Polygonal to circular. Outline irregularly wavy to notched. Thickness of exoexine 4–6 µm. Surface like a network [reticulate]; 'lines of the net' lighter in colour than protruding interspaces. (Translated from Potonié & Venitz 1934, p. 17.)

Description. — Thiergart's specimen (Figure 2B) is almost circular. The specimen is *c.* 61 µm long and 59 µm wide. The corpus of the pollen is *c.* 49 µm in diameter and has a distinct equatorial fringe of *c.* 6 µm thickness (i.e. 10% of the overall pollen diameter). The fringe has a very different structure than the corpus (Figure 2C). The corpus possesses rounded to elongate sculptural elements that are 2–4 µm long, varied in shape and up to 1 µm high. (Note, that the darker element [Figure 2B] in the top left corner is not a feature of the described pollen, but another palynomorph that is lying behind the pollen in question.)

Type for the genus **Sciadopityspollenites** *Raatz 1937 ex R.Potonié 1958 (Jan.).* — Figure 2D–G.

Type. — *Sporites serratus* R.Potonié et Venitz 1934, p. 15, plate 1, figure 7, specimen in sample VII 17.

Condition. — The holotype is presumably 'lost'. **Lectotype**: *Sciadopitys-pollenites serratus*, Marga 117a (material from Thiergart [1938]), EF: U38/3, refigured and designated here (Figure 2F).

Lectotype condition. — The specimens depicted by Thiergart cannot be relocated with certainty (probably specimen depicted in Figure 2E, which does not allow a very clear view on the ornamentation). The slide provides many and more representative specimens from which the lectotype was chosen.

Original description. — Shape mostly spindle-shaped to oval, but sometimes also rounded. Outline irregularly wavy/sinuate; the protruding sculptural elements ('humps') sometimes 1–1.5 µm in size. Sculpture wrinkled-'streaky'. Dehiscence not visible. (Translated from Potonié & Venitz 1934, p. 15.)

Description. — Shape oval to rounded, 25–45 µm long and 27–32 µm wide (see Figure 2E, F). Outline finely serrated/corrugated because of the rounded sculptural elements which are between 1–2.5 µm wide and long. The elements are not homogeneous in size or shape, some are more rounded, others more elongate (see Figure 2F). Sulcus usually visible, oval and *c.* 15–35 µm long, but sometimes indistinct (Figure 2E, F). Exine between 0.7 and 1 µm thick.

Type for the genus **Cerebropollenites** *Tage Nilsson 1958 (Apr.)* — Figure 3F–I. Note that the type for the genus *Cerebropollenites* is also the holotype for the species name *Tsugaepollenites mesozoicus* Couper 1958. It will therefore be described only once.

Type/holotype. — *Tsugaepollenites mesozoicus* Couper 1958, p. 155, plate 30, figure 8; refigured here (Figure 3Ia–Id).

Condition. — The glycerine jelly mount is in excellent condition. Unfortunately, the holotype is located right at the edge and in the corner of the mount and is partially covered by the sealing of the cover slip. (Figure 3F).

Original description. — Grains saccate; equatorial contour circular to broadly elliptical; exine of distal surface very thin and almost smooth over a circular area (corresponding to the distal sulcus of disaccate grains); surrounding this circular area is a well-developed equatorial fringe of twisted saccate protrusions, about 5–6 µ high; exine at the proximal pole is also saccate, but individual sacs are not so well developed as around the equatorial area, sculpture pattern of the polar area gradually merges into the pattern of the equatorial fringe. (Couper 1958, p. 155).

Re-description. — The holotype is 67 µm long and 49.5 µm wide, i.e. overall oval in shape. The pollen lies partially on the side with the sulcus on the left. The sulcus area appears smooth, but this is hard to describe with certainty, because the underlying ornamentation obscures a clear view. The most characteristic feature is the very big protrusions, that are far bigger than in the previously described material. They are 3–6 µm high and winding creating a maze-like pattern, similar to what was described for *Pollenites macroverrucosus*, but in the present specimen, the spaces in between these winding elements are bigger with enough space to fit a protrusion in between two others, and the elements themselves are bigger as well, i.e. overall less compact and generally bigger than in *Pollenites macroverrucosus.* It is important to note that due to the size of the protrusions, they can create the impression of an equatorial fringe. However, this is merely an optical effect of the ornamentation protruding at the equator, which is perceived differently for the ornamentation on the corpus. Except for the sulcus area the ornamentation is uniform on either side of the grain, consisting of heterogeneously long and short protrusions. While the protrusions vary a bit in height and length (due to their meandering), their width is relatively uniform of about 1.5–2 µm (Figure 3Ia–Id).

Holotype for **Pollenites serratus *fa.* helmstedtensis** *Thierg. 1949.* — Figure 2H–K.

Syntypes (no holotype designated). — Pollenites serratus fa. *helmstedtensis* Thierg. 1949, p.13, plate 2, figures 2, 6, 8.

Condition. — All syntypes are lost: Thiergart shows three specimens for this new taxon. Two of them (plate 2 figures 6, 8, Thiergart [1949]) are spores, probably *Polypodiisporites,* and thus neglected here. The pollen tetrad shown by Thiergart (1949, plate 2, figure 2) depicts a pollen with serrated outline and could not be relocated either; a taxonomically identical specimen is studied here (Figure 2J).

Original description. — Size 42 µm. The pollen is evenly oval, the outline is wavy, as a result of the wavy/sinuate surface sculpture, without any indication of a germination area. As plate II, figure 8 shows, the pollen seems to burst open, similar as described for the Taxodiae (*Pollenites hiatus* R.Potonié). It differs from *Sciadopitys* pollen, with which it can be compared, by its regular oval shape and the coarser ornamentation. In the slide it occurs several times as four pieces glued together (plate II, figure 2). It probably belongs to a conifer. (Translated from Thiergart 1949, p. 13.)

Re-description. — The tetrahedral pollen tetrad consists of monosulcate grains. The sulcus is only visible as a thinner area when focusing through the different focal planes of the tetrad. The sulcus is directed outward. The pollen have a tuberculate ornamentation with big and irregularly shaped and sized verrucae of 3–7 µm in diameter. The tetrad measures 83 µm × 63 µm. All in all, the pollen as described is conspecific with *Ricciisporites tuberculatus*. See the section on systematic palynotaxonomy for nomenclatural implications of this classification.

Holotype for **Pollenites macroverrucosus** *Thierg. 1949* — Figure 3C, E.

Holotype. — Pollenites macroverrucosus Thierg. 1949, p. 17, plate 2, figure 19.

Condition. — The slide Degow 253–255 m a (Figure 3A) is in very poor condition (Figure 3B), the glycerine jelly has desiccated, leaving only dendritic remains of the medium partially embedding the organic material (Figure 3B). Despite the poor condition of the mounting medium, a pollen identified as the holotype was relocated. However, this relocation is a bit ambiguous, due to the very different impression compared to the original photograph, which is partially caused by different illumination and the halo covering the left-hand side of the outline (Figure 3Ea–Ed). Nevertheless, the tracheid remains at the top of the pollen (Figure 3C, D) and the characteristics shadow in the lower left corner of the pollen and forming a C-shaped shadow (Figure 3D, E, arrowhead) on the right-hand side permit identification of the specimen as the holotype with reasonable certainty. No other remotely similar pollen grain could be found on the slide that was due to the labelling clearly identified as the slide containing the holotype.

Original diagnosis. — Size: 65 µm. The shape forms a fairly regular ovaloid and is reminiscent of the previously described form *Pollenites macroserratus Keuperianus*. It differs from this, however, in the size of the sculptural elements of the ornamentation, which is 2 µm in the Keuper form, but exceeds 5 µm in the Dogger form. (Translated from Thiergart 1949, p. 17.)

Re-description. — The pollen grain is *c.* 64.2 µm long and 41 µm wide. The distal side is directed at the viewer, the proximal side with the sulcus is shining through. It is much clearer visible than in the original photograph and is roughly 30 µm long. Although the sculptural elements appear rather big on the original microphotograph, differentiated focusing back and forth through the specimen reveals that these are densely arranged winding and rounded muri with a length up to 8 µm and a width of 3–6 µm, it is important to note, that these elements are not very high, *c.* 1.5 µm. Depending on the angle, and especially at the outline these elements appear bigger, because one is looking at section through the width or part of the longitudinal view of the sculptural element. The arrangement of these muri is probably best described as rugulate, creating a maze-like pattern, but with very little space in between the winding muri. An equatorial fringe is not visible. The muri protruding at the equator give the impression of a sinuate or corrugated outline, but there is no real fringe in the sense of a saccus present. (Figure 2Ea–Ed).

Holotype for **Pollenites macroserratus Keuperianus** *Thierg. 1949.* — Figure 2L–O.

Syntypes (no holotype designated). — Pollenites macroserratus Keuperianus Thierg. 1949, p. 7, plate 1 figures 5, 6, 8, 9.

Condition. — All syntypes lost: the slide with the specimens described from Hohenwestedt (plate 1, figures 5 and 6 in Thiergart [1949]) is assumed to be lost. The available slide from Magdala (a) (plate 1, figures 8 and 9 in Thiergart [1949]) was searched for palynomorphs resembling the original photographs. Except for some spores complying with the circumscription of *Polypodiisporites polymicroforatus* (Orł.-Zwol. 1966) Lund 1977, we could not find any specimen that remotely resembles the depicted specimens. We could however relocate a specimen from slide 'Helmstedt' which Thiergart does not mention in the protologue but depicts in plate 2, figure 1 (here Figure 2L). The glycerin jelly of the original slide was strongly desiccated. In an attempt to re-embed the material, the cover slip was partially lifted to inject new glycerin jelly, which was only partially successful. Now two different prismatic lines are visible, the darker where the younger mounting medium ends, the less strong prismatic edge where the old mounting medium ends. Despite re-mounting the specimen, this does not entirely prevent prismatic effects of the primary layer of glycerin jelly at the outline of the specimen (Figure 2M, N). Nevertheless, re-mounting slightly improved visibility and the specimen is in reasonable condition for study.

Original description. — Potonié's name for the fringeless *Tsuga* pollen was deliberately chosen here because this Mesozoic form is best characterised by comparison with that one, even if the fineness of the ornamentation does not completely match. The Rhaetian forms from Helmstedt and those from the lower Keuper from Magdala have coarse warts; the shape is oval, in contrast to the Dogger forms that will be described later, and which do not retain their original spherical shape, but are folded. The ornamentation also differs from the Keuper form. The forms from the middle Keuper of the Hohenwestedt borehole are also folded. (Translated from Thiergart 1949, p. 7.)

Description. — The only available specimen figured by Thiergart (none of the syntypes), is about 46 μm long and 42 μm wide and thus oval to subcircular. The exine is *c.* 1.5–2 μm thick and the surface is covered by many small verrucae that give a sinuate impression when looking at the outline. The laesura permits identification as a spore. The laesura consists of one long slit with one shorter perpendicular slit at the middle (Figure 2M, arrowhead). The type of the laesura, ornamentation, and overall shape, are very compliant with the description of *Polypodiisporites polymicroforatus*.

Holotype for **Pollenites macroserratus doggerensis** Thiergart 1949 — Figure 4J, K.

Syntypes (no holotype designated). — *Pollenites macroserratus doggerensis* Thiergart 1949, p. 18, plate 2, figures 26, 29, 30 (remaining syntype refigured in Figure 4K).

Condition. — The preservation of the only remaining syntype is similar to that of *Cerebropollenites macroverrucosus* which is contained on the same slide (Figures 3A, 4I). The specimen is rather bleached and the characteristics are therefore hard to identify (Figure 4J, K). Digital contrast enhancement helped to improve this (compare Figure 6N).

Original diagnosis. — Size: 55–80 μm. The form roughly corresponds to our present-day *Tsuga canadensis* (Carrière 1855). The ornamentation of the dogger form is slightly finer than that of the pollen of the extant *Tsuga* species. Most of the specimens have secondary folds as a result of the mounting, which is contrasting to the similar Rhaetian forms, which have retained their original oval shape. The mentioned similarity with extant forms, of course, does not mean that today's genus existed back then already. (Translated from Thiergart 1949, p. 18.)

Re-description. — The specimen is *c.* 88 μm long and 66 μm wide and oval. However, the original shape is probably subcircular if secondary folds are taken into consideration. A distinct germination area is not visible but the area enclosed by the secondary folds depicts less distinct ornamentation and is interpreted as a sulcus. The sculptural elements are more or less spherical and up to 1.5 μm in size (Figure 4K).

Holotype for **Camerosporites pseudomassulae** *Mädler 1964b* — Figure 3K.

Holotype. — *Camerosporites pseudomassulae* Mädler 1964b, p. 183, plate 2, figure 17.

Condition. — The holotype is mounted in cell E10 of a mesh used for several single grain mounts. The glycerin jelly is preserved perfectly, permitting a clear view on the holotype.

Original description. — The almost spherical spores with a diameter of 40–50 μm are densely covered with thick, hemispherical protrusions (Papillen). The protrusions (Papillen) are 12–14 μm wide and 8–10 μm high, and appear to be hollow inside, as they are partially collapsed. A darker coloured triangle indicates the germination area. Although no laesurae are visible, the spores are provisionally considered as trilete forms. (Translated from Mädler 1964, p. 183.)

Note that the translation avoids the term 'papillen' which is not used in the sense of either definition of 'papillae' found in Punt et al. (2007), but rather in the sense of spherical, hollow protrusions. Hence the use of 'protrusion', which is a necessary interpretation to find an adequate translation for the term used by Mädler.

Re-description. — The specimen measures *c.* 52 µm × 46 µm. It is stained red with fuchsin (Mädler 1964), which does not allow an impression of the original colour of the specimen, except for the generally hyaline character of the exine. There is no clear corpus visible, the specimen instead gives the impression of an aggregation of rounded protrusions of *c.* 7–12 µm in diameter that form an overall unit that appears circular. The protrusions appear wrinkled, thin (exine thickness *c.* 0.5–0.7 µm), and hollow which allows the other protrusion in layers behind the one in question to shine through. Some protrusions in the centre appear folded in such a way that they give a misleading impression of a triangle, which does not represent a trilete mark. The specimen does not show any differentiation on either side.

Holotype for **Cerebropollenites thiergartii** *Eberh.Schulz 1967.* — Figure 4A–Hd.

Holotype. — Cerebropollenites thiergartii Eberh.Schulz 1967, p. 603, plate 11, figures 7, 8.

Condition. — When we re-examined the holotype for the first time in 2018, the slide was in very poor condition, which became increasingly worse over the next two years. Most of the glycerine jelly had desiccated already. By chance a tiny pocket of mounting medium was left at the very edge of the cover slip, and in exactly that pocket the holotype was preserved (Figure 4A). Nevertheless, the progressing desiccation was already evident in the near vicinity, coming closer to the holotype every year (Figure 4A–C, E–G), which left the specimen partially exposed in 2020 (Figure 4G).

Original description. — Size 40–80 µm (holotype 56 µm). Outline subcircular, exine about 1 µm thick, densely covered on all sides with warts fused together at the base. The size of the warts measures 1–3 µm on average. Sulcus not always visible (or present?), up to 36 µm long, exine often with secondary folds. (Translated from Schulz 1967, p. 603.)

Re-description. — The holotype is *c.* 60 µm long and 53 µm wide and overall subcircular. The sulcus is clearly visible, directed at the observer and *c.* 34 µm long and 11 µm wide. The exine is 1–2 µm thick and covered with many densely arranged verrucae, in contrast to Schulz description we cannot confirm, that the individual verrucae are merged at the base, they appear rather distinct. Where very densely arranged, certain focal planes can give the impression that they are merged when they are simply very close together. The verrucae are about 1–2 µm wide and high (Figure 4Ha–Hd).

Holotype for **Sciadopitys multiverrucosus** *Sachanova et Iljina 1968* — Figure 4L–N.

Holotype. — Sciadopitys multiverrucosus Iljina 1968, p. 42, plate 5, figures 1, 2.

Condition. — The location of the holotype was clearly indicated by a red square (Figure 4L, M). Although the holotype is located at the edge of the coverslip, it is still in excellent condition and fully embedded.

Re-description. — The holotype is *c.* 53 µm long and 45 µm wide and subcircular. The sulcus is a bit indistinct, but visible as a more hyaline oval area and approximately 27 µm long. The exine is *c.* 1 µm thick and covered with many densely arranged rounded verrucae similar to those in the holotype of *Cerebropollenites thiergartii*, but on average, have a slightly bigger size of 1–4 µm (in diameter).

Taxonomy: interspecific and infraspecific variation

At first, the diversity and variation of species associated with *Cerebropollenites thiergartii* can be overwhelming. Even more so as they can often be linked by intermediate forms forming a continuum between the taxa, especially when poor preservation makes characteristics ambiguous. However, sorting of the observed forms shows several typical distinctive characteristics, and consistent features. The most distinctive variation is observable in the ornamentation. Forms can be arranged along a continuum of sculptural elements increasing in size, from those with very small sculptural elements to those with very large and protruding elements. Because genus assignations are highly ambiguous for the taxa we discuss, we here refer to the different forms only by their specific epithets whenever possible and appropriate.

Forms with small ornamentation. — The holotype of *Cerebropollenites thiergartii* (Figure 5K) looks rather iconic, but the three other specimens contained on the same slide that comply with the description look rather variable (Figure 5E, L, M). Nevertheless, they are generally characterised by the typical ornamentation of small verrucae. The specimen that is most like the holotype is seen from the side, obscuring the view on the sulcus (Figure 5M). The two others are either much bigger and more folded (Figure 5L), or smaller with a more circular sulcus (Figure 5E).

Some specimens with very fine infrareticulate to (diffusely) granulate or rugulate ornamentation (Figure 5A–D, F–J) might be confused with *thiergartii*. One of these false friends is *Chasmatosporites apertus* (Rogalska 1954) Tage Nilsson 1958 with a rather thick exine (2–3 µm) (Figure 5A–D). Due to their thicker exine, individuals of this taxon are less likely secondarily folded and a thickening clearly delimits the sulcus. Although *Chasmatosporites apertus* can appear similar, especially in poor preservation (Figure 5D), it is not verrucate like *thiergartii*.

Other false friends are poor or semi-preserved spores. For instance, the ornamentation of *Polypodiisporites polymicroforatus* may appear very similar to that of the holotype *Cerebropollenites thiergartii* (Figure 5K), especially at the amb (Figure 5F) and with the many small autonymous perforations in between the rugulae which give a verrucate impression, depending on the focal plane and preservation (Figure 5F–H). Specimens with a very rigid outline (Figure 5F, H) modelling an opening (because of poor preservation or folding) also make distinction difficult. Nevertheless, the generally smaller size and rugulate ornamentation (best observable in high focal plane [Figure 5H] or semi-preserved specimens [Figure 5G]) distinguish *Polypodiisporites polymicroforatus*. Remains of verrucate or baculate spores (Figure 5I, J), especially those with a visible thinning or opening (Figure 5I), are also challenging unless a trilete mark is visible (Figure 5J). As a result, some specimens are hard to impossible to identify with certainty (e.g. Figure 5N, R), even more so in samples of overall poor preservation.

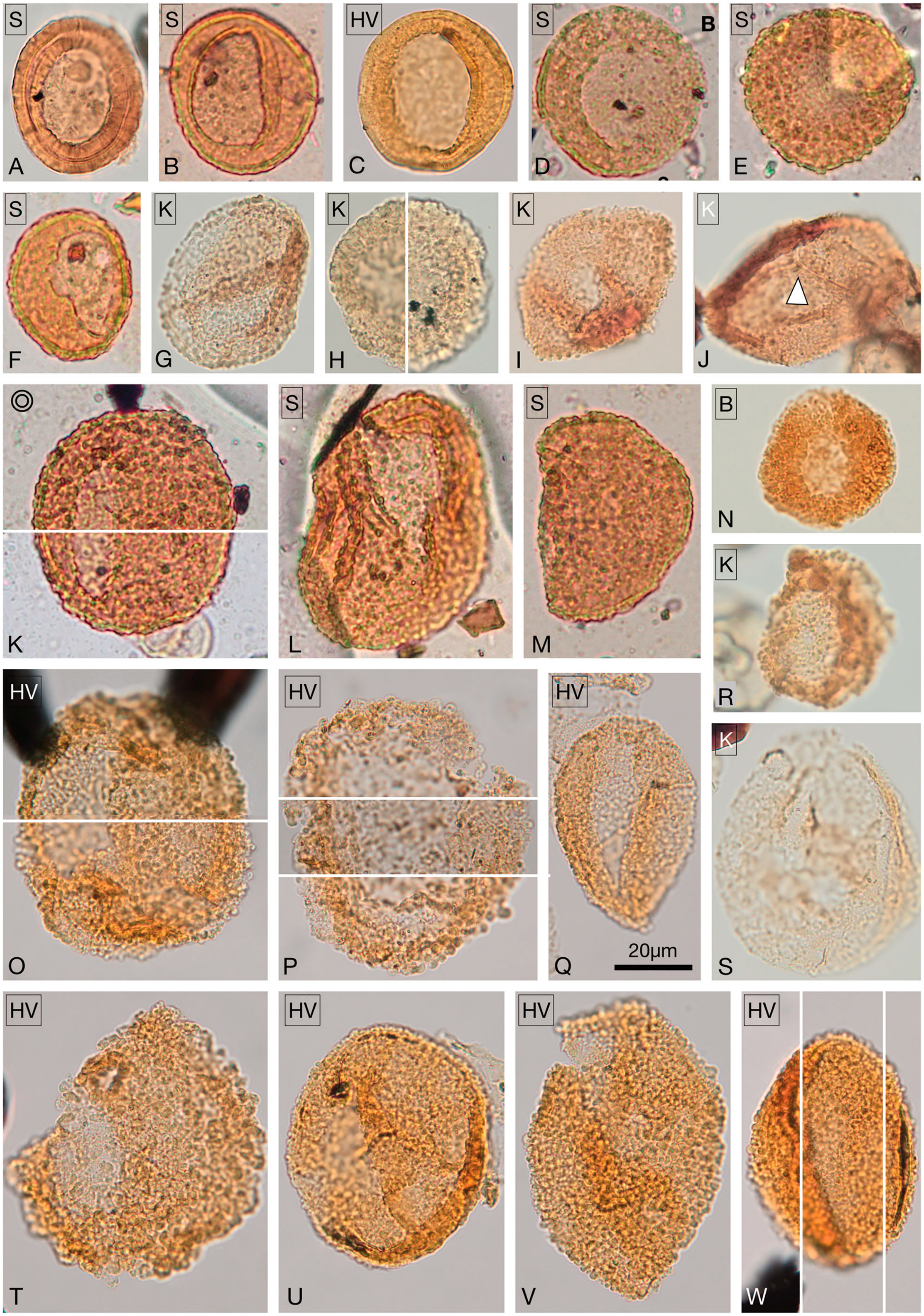
This is a known problem for the much-cited Kuhjoch material (compare Figure 5R, S). A definitive classification of this material is today further complicated by partially desiccated glycerine jelly (Supplementary Material 3). As a result, many specimens documented previously in Bonis et al. (2009) and von Hillebrandt et al. (2013) were impossible to restudy. Studying the remaining non-desiccated areas of the slides, we observed specimens comparable to *Camerosporites pseudomassulae*, together with *Polypodiisporites polymicroforatus* and poor remains thereof from the Schattwald Beds. In addition, we confirmed the presence of *Ischyosporites variegatus* in all samples following the Schattwald Beds (K 050926.4 onwards), as well as specimens of varying degrees of preservation and similarity with Schulz' holotype (Supplementary Material 3). The first cf. *thiergartii* occurs in sample K 051025.4.

The Swedish material (Höllviken) is, in contrast, much better preserved but still contains only few specimens that are directly comparable to the holotype of *thiergartii* (Figures 5U, W, 6B). In most cases the exine appears partially dissolved, with mainly the ornamentation remaining to varying degrees (Figure 5O, P). The ornamentation and thinner sulcus area usually allow identification, even when the overall shape varies from the typical oval-subcircular (Figures 5O, U, 6B) to more spindle-shaped specimens probably because of compression and folding (Figures 5Q, V, 6A). Size varies between 40 µm (Figure 5Q) up to 70 µm (Figure 5T). Common in all these specimens is a very fine ornamentation consisting of sculptural elements that are less than 1.5 µm in diameter.

In addition, we found pollen more like the holotype of *Sciadopitys multiverrucosus* (Figure 6S) with slightly bigger sculptural elements ranging from 1.5 µm up to 2 µm (Figure 6C, D), and even up to 3 µm (Figure 6E–O). One can see a progradation of increasing size (Figure 6A–F). The lower half of the spectrum includes the holotype of Schulz and the intraspecific variation observed in his material. The upper half of the spectrum is most like the holotypes for *Pollenites macroserratus* f. *doggerensis*. (Figure 6N) and *Sciadopitys multiverrucosus* (Figure 6S). With increasing size of the verrucae (Figure 7Q–S), some specimens can appear a bit evocative of *Sciadopityspollenites serratus* (Figure 7A–P). However, the pollen *Sciadopityspollenites serratus* is usually smaller, the sculptural elements more distant from each other, and generally more elongate (i.e. rugulae rather than verrucae) (Figure 7A–P).

In addition, we also observed other intermediate forms with very big and round verrucae (Figure 7U–X), in a size range much beyond that of previously described forms. In comparison to forms assignable to *mesozoicus* or *macroverrucosus*, the sculptural elements are more massive, solid, and perfectly rounded. SEM images from existing literature have also illustrated such forms before (Figure 7W), and while previous authors assigned them to *mesozoicus*, they are unlike any of the other holotypes documented in this study.

Notably, all figured forms (Figures 5, 6) are from material of Jurassic age or the Triassic–Jurassic boundary interval. Only one specimen (Figure 6I) originates from the Middle Rhaetian, i.e. from the Contorta Beds and could be classified as *Ricciisporites tuberculatus* Lundbl. 1954 emend. Lundbl. 1959. It was unusual to find this specimen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so perfectly preserved as a single grain. Normally, *Ricciisporites tuberculatus* pollen occur in tetrads and when found as singular grains, partial tetrad remains are still attached. Its resemblance with other depicted specimens is uncanny (Figure 6, especially comparing Figure 6I, J). The only perceivable difference is that the verrucae shining through from the back in the sulcus area are merged, and look like the remains of the tetrad attachment (Figure 6I).

Forms with intermediate-sized ornamentation. — Comparison of the holotypes of *Pollenites macroverrucosus* (Figure 8A) and *Tsugaepollenites mesozoicus* (Figure 9Aa, Ab) shows that they are overall similar but differ in size and density of their sculptural elements. The observed variation in the studied material can then be categorised to belong mostly to one of the two respective holotypes.

The sculptural elements in specimens similar to the holotype *macroverrucosus* (specimens in Figure 8) all show a very dense arrangement of rugulae (compare especially Figure 8B, E). The rugulae are very variable in length and shape. However, they are rather uniform in thickness (*c.* 1.2–1.5 µm), and are appressed against each other with little space in between, reminiscent of the arrangement of the gyri in the brain. This ornamentation is best illustrated by an existing SEM image (Figure 8H). As a result of the ornamentation, the outline of these individuals is only slightly sinuate. Note that two specimens similar to the holotype *macroverrucosus* are reported here for the first time from the Schattwald Beds in Kuhjoch (Figure 8K) and the Triletes Beds in Bonenburg (Figure 8L).

Specimens which are best compared with the holotype of *mesozoicus* are identifiable by their fewer, bigger, and more loosely arranged rugulae, best illustrated by an SEM image (Figure 9L), which corresponds perfectly with a specimen from Couper's material (Figure 9Ka, Kb). Due the stronger contrast of protruding rugulae and grooves in between them, the outline is much more sinuate (e.g. Figure 9D, I, J). This becomes especially obvious when comparing SEM images of specimens with ornamentation arranged as loosely as in *mesozoicus* (Figure 9L) to those with denser ornamentation as in *macroverrucosus* (Figure 9M). Depending on the locality, the material was either dominated by *macroverrucosus* (Höllviken) or *mesozoicus* (Couper) forms, and always with some specimens of the other (e.g. Figure 8E–G), even in Thiergart's holotype slide (Figure 9H).

Notably, many *mesozoicus* specimens appear much more hyaline than *macroverrucosus* specimens depicted in Figure 8. This is partially an observation artefact due to the different objectives used. While the Höllviken material could be studied with a ×100 oil objective, the holotypes and material from Couper was observed using a standard ×40. The ×40 objective used generally gives a more hyaline and less saturated image (compare Figure 9Ca taken with ×100 and Figure 9Cb taken with a ×40 objective). However, this does not compensate for the fact that the specimens here assigned to *mesozoicus* from the Couper material are generally more hyaline, although this effect is augmented by the objectives used for study. The more hyaline character appears to be the result of the less dense packing of the sculptural elements, with bigger empty spaces in between them and the bigger elements which are themselves very hyaline as well.

When focusing on the equator of the observed *mesozoicus* specimens, the rather big protrusions give the illusion of a 'fringe' visible in the holotype and other specimens (e.g. Figure 9K). However, this is not comparable with the fringe, i.e. the saccus, characteristic of the genus *Tsugaepollenites* and visible for example, by its foldings perpendicular to the corpus and the ornamentation consisting of small verrucae and rugulae in *Tsugaepollenites igniculus* (Figure 10K–M). In contrast, the impression of a fringe in *mesozoicus* specimens is merely an optical effect of the overlying protrusions at the equator and reinforced by the more transparent sulcus area. SEM images from literature further confirm its absence in species comparable to the holotype of *Tsugaepollenites mesozoicus* and confirm the bigger spaces in between the sculptural elements (Figure 9L) in comparison to species that are better comparable to *Pollenites macroverrucosus* (Figures 8H, 9M).

◄

Figure 5. Intraspecific variation of forms with small ornamentation I. **A–D.** Forms similar to *Chasmatosporites apertus*. **E.** specimen with intermediate characteristic from Holotype slide of *Cerebropollenites thiergartii*. **F–H.** Forms similar to *Polypodiisporites polymicroforatus*. **I, J.** Forms similar to baculate spores, trilete mark indicated with arrowhead. **K–W.** Forms similar to the holotype of *Cerebropollenites thiergartii*. **R, S.** Kuhjoch specimens complimenting reports from Bonis et al. (2009) and von Hillebrandt et al. (2013), Kuhjoch 051025.5(1) EF:V42/0 and Kuhjoch 051026.4(1) EF:M40/2, respectively. Framed letter in the top-left corner indicates the locality of the material: **B** = Bonenburg; **C** = Couper; **HV** = Höllviken; **K** = Kuhjoch **S** = Schulz; ◎ = holotype.

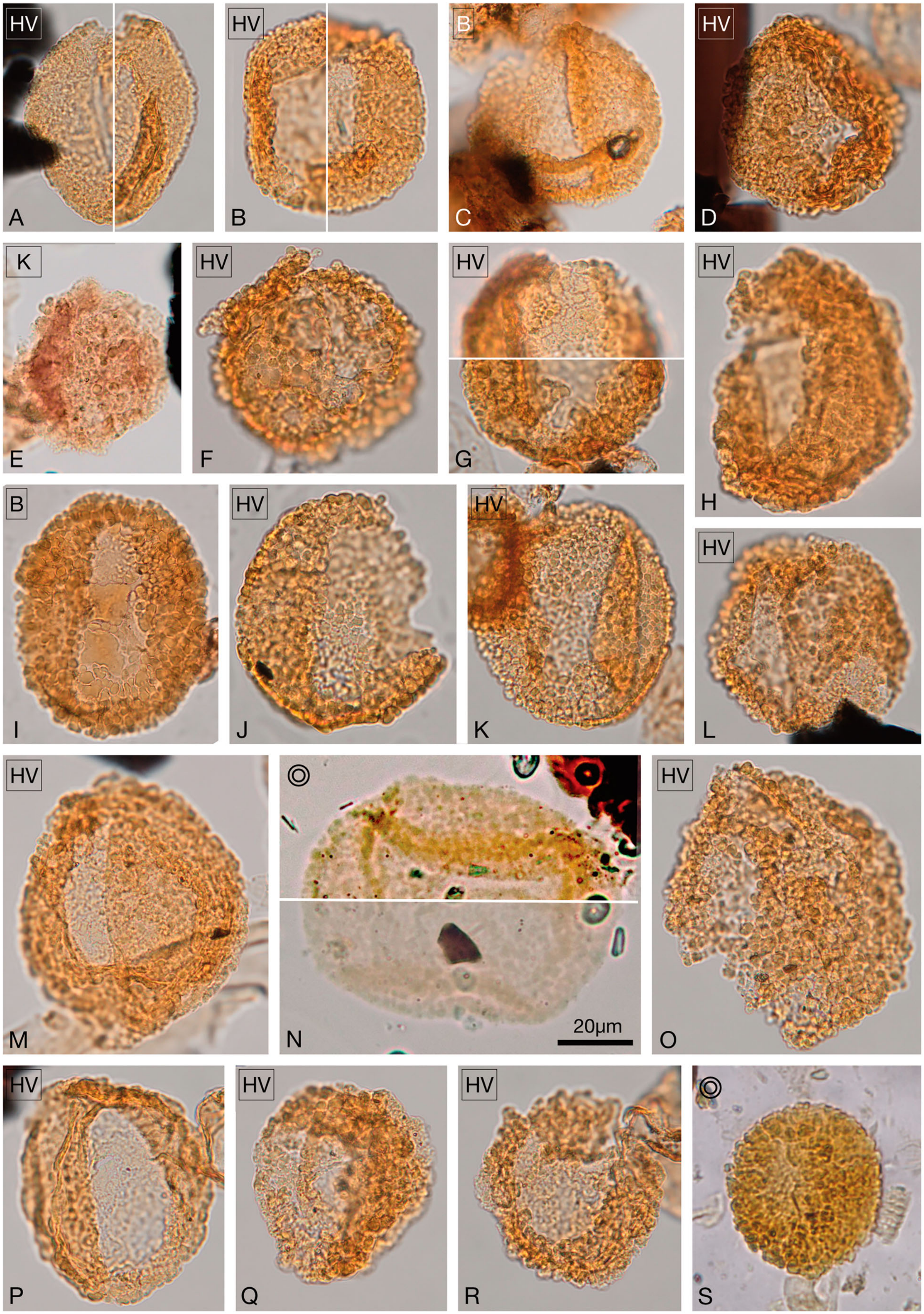


Figure 6. Intraspecific variation of forms with small ornamentation II. **A–M.** Variation in forms similar to *Cerebropollenites thiergartii*. **N.** Holotype for *Pollenites macroserratus doggerensis*, upper half contrast enhanced. **O–R.** Variation in specimens with poorer preservation tentatively assigned to the epithet *thiergartii* but showing transitionary ornamentation to *macroverrucosus*. **S.** Holotype for *Sciadopitys multiverrucosus*. Framed letter in the top-left corner indicates the locality of the material: **B** = Bonenburg; **HV** = Höllviken; **K** = Kuhjoch (051025.4(2), EF: J46/4); ◎ = holotype.

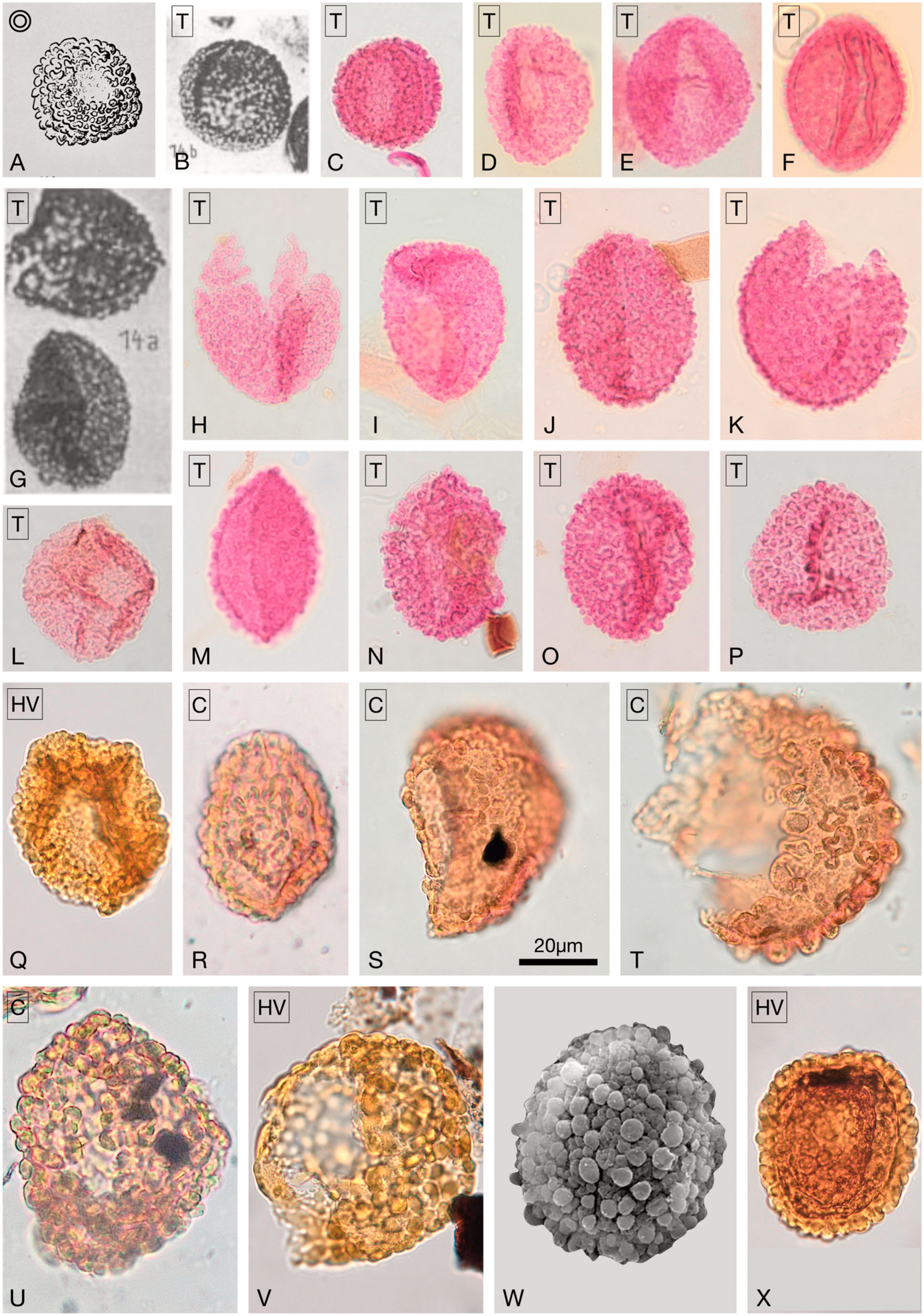


Figure 7. Intraspecific variation in *Sciadopityspollenites serratus* (**A–P**) and variation in *Cerebropollenites* sp. (**Q–X**). **A.** Drawing of the holotype for *Sciadopityspollenites serratus* reprinted with permission of the LBEG/BGR from Potonié (1958); **B, G.** Original photographs reprinted from Thiergart (1938) with permission of LBEG/BGR. **W.** SEM image reprinted from Shang and Zavada (2003, figure 5) with permission of Taylor and Francis, there assigned as '*Cerebropollenites mesozoicus*'. Framed letter in the top-left corner indicates the locality of the material: **C** = Couper; **HV** = Höllviken; **T** = Thiergart.

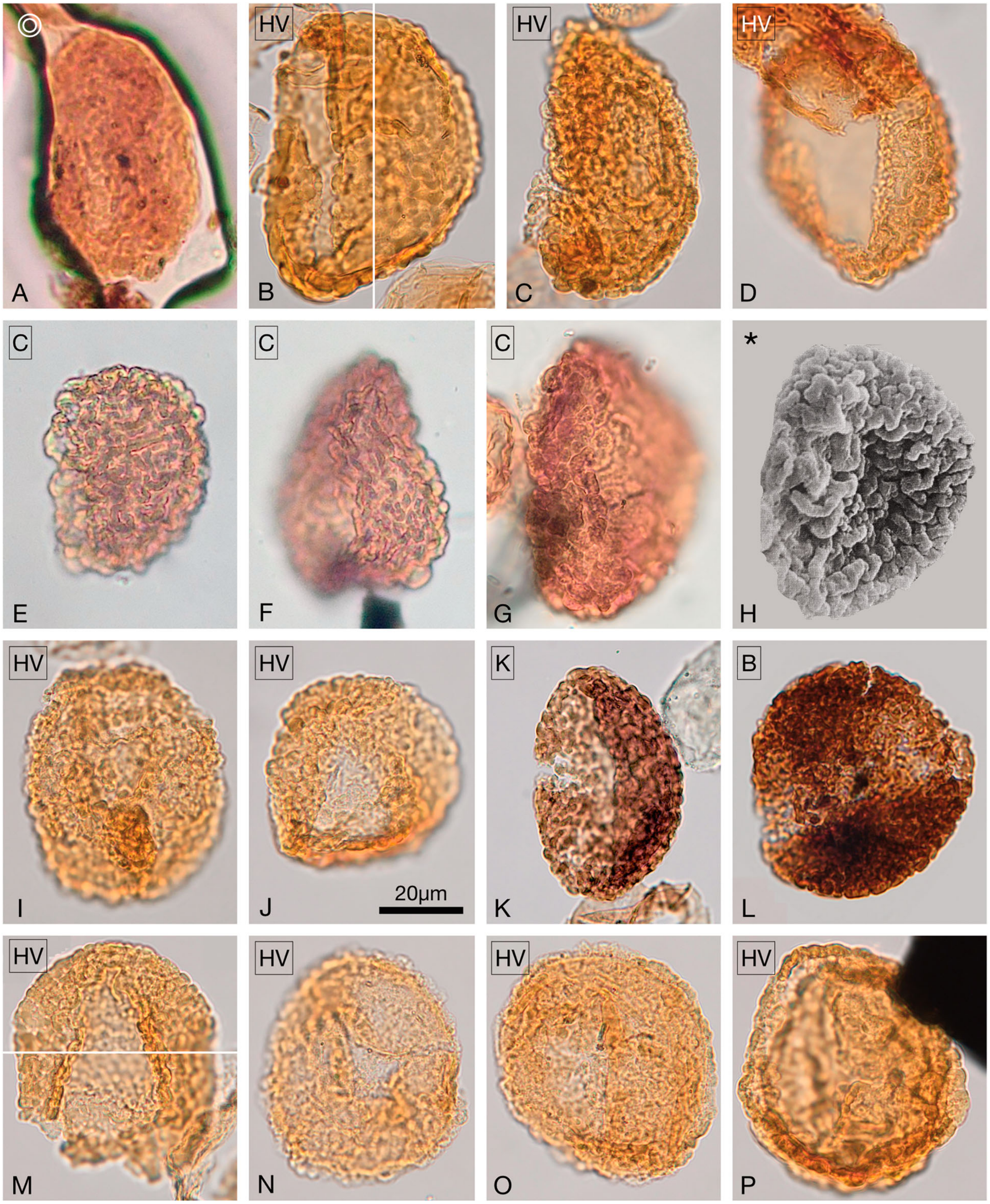
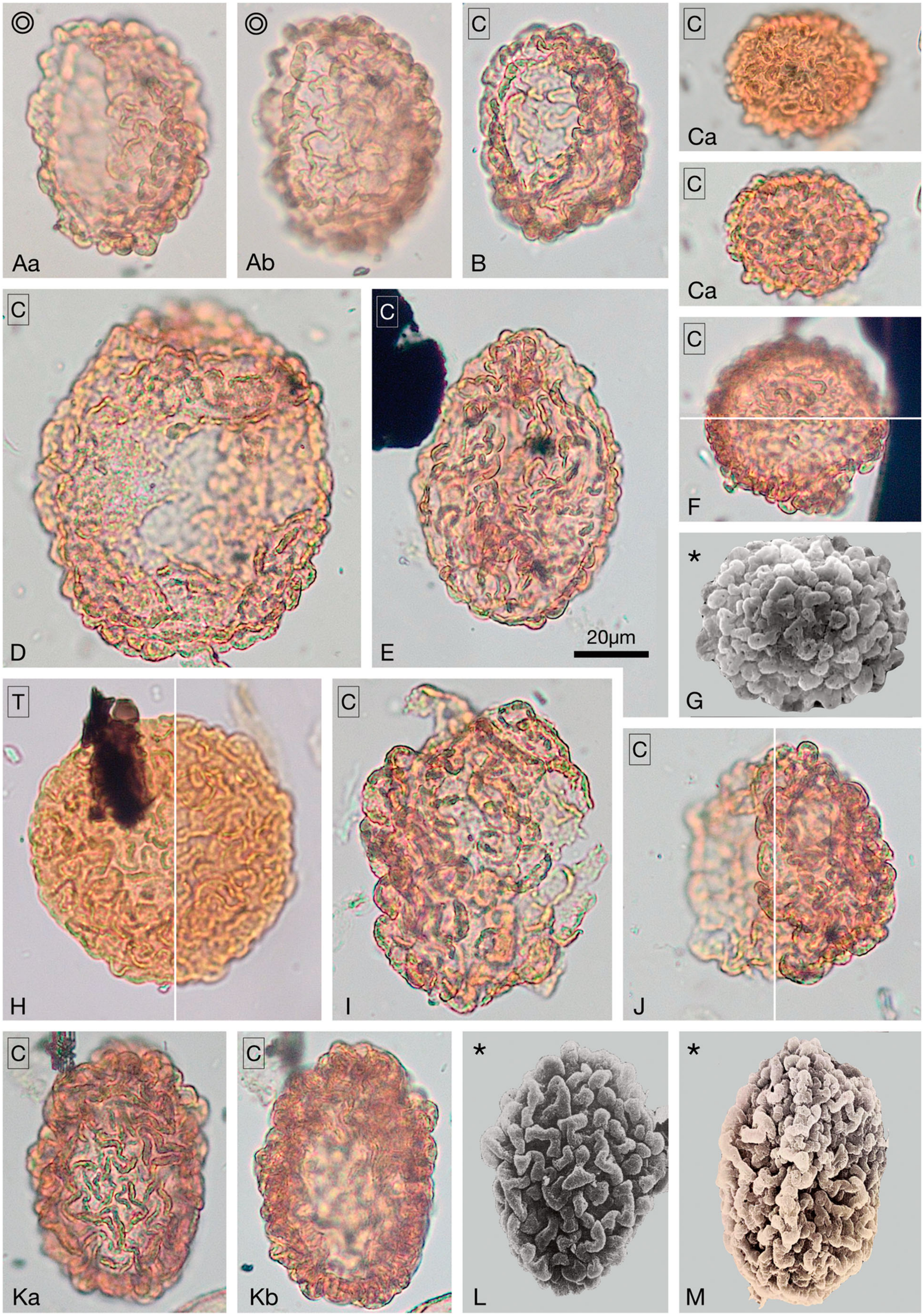


Figure 8. Intraspecific and interspecific variation in rugulate forms I that are most similar to the holotype of *Pollenites macroverrucosus*. **A.** Holotype for *Pollenites macroverrucosus*. **B–G.** Variation in densely rugulate forms. **H**. SEM image of '*Cerebropollenites* sp.' from Guy-Ohlson and Malmquist (1985, plate 3, figure F), reprinted with permission of the SGU (case nr.2021:0325). **I–P.** Variation in densely rugulate forms. Framed letter in the top-left corner indicates the locality of the material: **B** = Bonenburg; **C** = Couper; **HV** = Höllviken. **K** = Kuhjoch Schattwald Beds (051026.5(1), EF: M32/2). Specimens indicated with an asterisk (*) are not to scale.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Interestingly, in less well-preserved specimens (Figure 9I), there is no indication of a fringe whereas in poorly preserved specimen of *Tsugaepollenites igniculus* (Figure 10L), the view on the fringe is even better.

The Swedish material from Höllviken contained many specimens in varying degrees of preservation which can make classification more difficult (Figure 8B–D, I–P). The preservation can influence how the sculptural elements are perceived (compare Figure 8M–P). Nevertheless, the density of their arrangement and less wavy outlines characteristics of *macroverrucosus* is still perceivable and characteristically different even from poorly preserved specimens of either *thiergartii* (Figures 5P, 6N) or *mesozoicus* (Figure 9I). We also documented a third kind of specimens that are smaller, usually more circular and have muri that are similarly high as in other specimens of *mesozoicus*, but much shorter, at most making a loop (Figure 9C, F), rather than meandering as in *mesozoicus* (Figure 9K). Again, SEM images from existing literature document specimens with this morphology (Figure 9G).

Forms with large and hyaline protrusions. — While the previous described forms show a relatively large infraspecific variation in their sculptural elements, those with the largest and very hyaline protrusions (5–20 µm), assigned to *pseudomassulae*, do not. Although these pollen can vary greatly in size (45–63 µm in diameter), their overall appearance is rather uniform and mostly influenced by preservation, i.e. pyrite impressions (e.g. Figure 10D, G), or thermal maturation, especially towards the Rhaetian 'dark zone' (Van De Schootbrugge et al. 2009) (compare Figure 10C, from the Contorta Beds, to Figure 10D from the Triletes Beds). Increased thermal maturation can mask the otherwise strongly hyaline yellow-brown impression of the palynomorph wall, and when looking at the more hyaline representatives (e.g. Figure 10D–G), these specimens appear not to have a fringe but a collection of rather large and simple convolutions (compare fringe in Figure 10K–M). These convolutions are usually rounded, and their edge can appear a bit sharper at times but is never angular (Figure 10E, J). In specimens mounted between two cover-slips that could be turned to investigate both proximal and distal side equally well, a germinal area could not be identified, instead protrusions are equally well developed on either side (Figure 10E, F).

Nomenclature – name use statistics

The name *Cerebropollenites* with 16 described species is used exclusively for taxa occurring in the Mesozoic, whereas *Sciadopityspollenites* with at least 26 species is used from the Mesozoic to the Cenozoic (Figure 11). However, there is a notable gap between Mesozoic *Sciadopityspollenites* species reaching until the Albian and species described from the Paleogene onwards. Only a few Cenozoic species, amongst them *Sciadopityspollenites serratus,* might already occur in the Mesozoic (Figure 11, dotted line). Several of the Mesozoic *Sciadopityspollenites* names are recombinations of epithets otherwise combined with *Cerebropollenites* and are mostly used in studies from Russia (*macroverrucosus*, *mesozoicus*, *carlylensis,* Figure 11). Calculating citations for all species per genus together amounts to roughly 500 citations for *Sciadopityspollenites* and about double the amount (1074) for *Cerebropollenites*, partially because *Cerebropollenites mesozoicus* alone has almost as many citations (430) as all *Sciadopityspollenites* species together.

Despite the large number of species, only few names are used more than twice per decade, i.e. have a CR of 0.2 or more (Figure 11). Some names have never been recombined with either *Cerebropollenites* or *Sciadopityspollenites* (e.g. *Cerebropollenites thiergartii*, *Cerebropollenites findlaterensis*, *Sciadopityspollenites multiverrucosus*, *Sciadopityspollenites osmundaeformis* [Zhang 1965] Li 1984) or have not been

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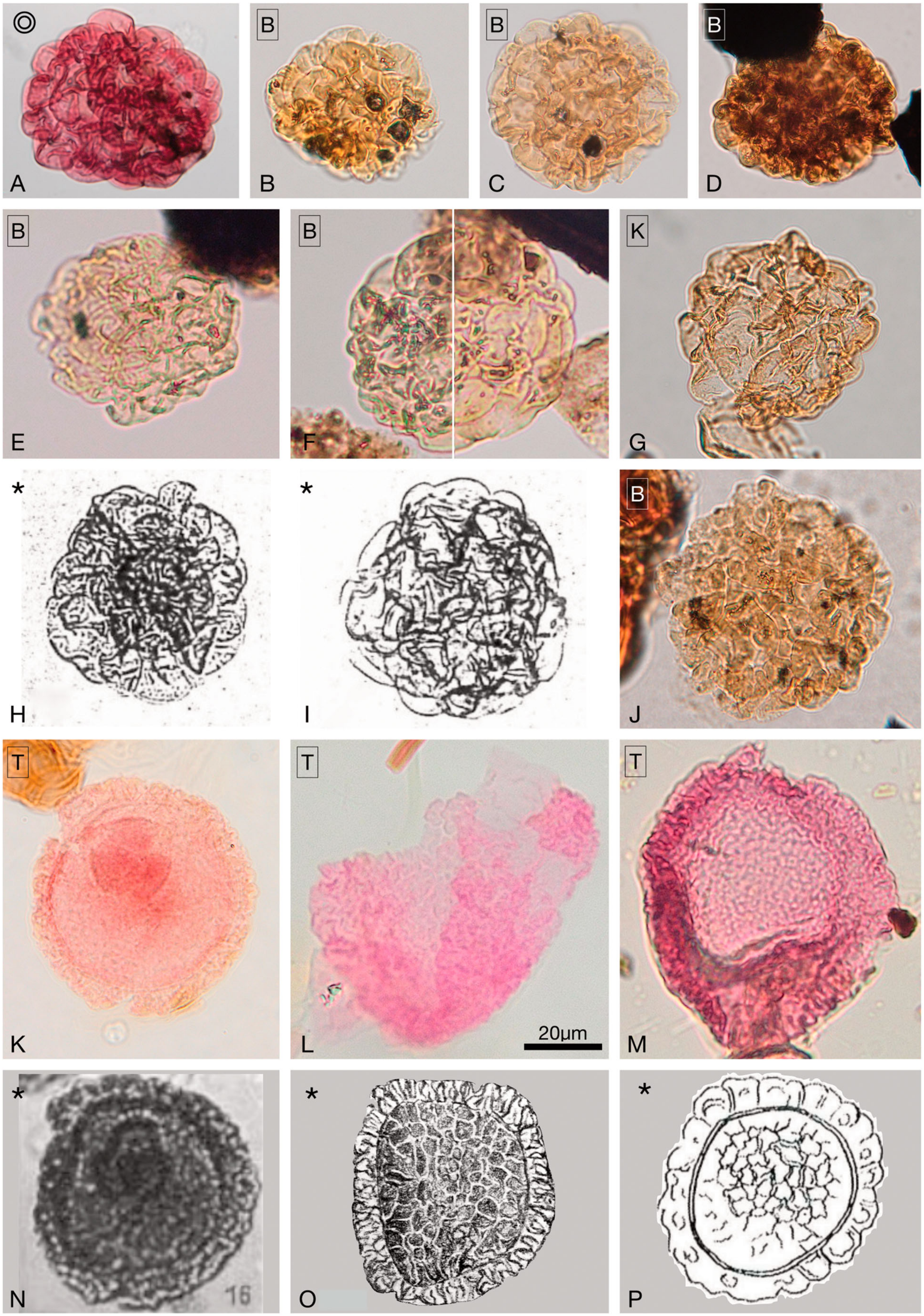
Figure 9. Intraspecific and interspecific variation in rugulate forms II. **A.** The holotype for *Tsugaepollenites mesozoicus* in two focal planes (**Aa** and **Ab**). **B.** Form conspecific with the holotype. **Ca.** Specimen considered conspecific with *Cerebropollenites carlylensis*, photograph taken with ×100 oil immersion objective. **Cb.** The same specimen photographed with a ×40 objective. **D, E.** Specimens with intermediate ornamentation in size of the protrusions, but density more similar to *mesozoicus*. **F.** Specimen as intermediate form between epithets of macroverrucosus and *carlylensis*, type of the ornamentation considered conspecific with *carlylensis*. **G.** SEM image reprinted from Shang and Zavada (2003, figure 3) with permission of Taylor and Francis. **H–K.** Intraspecific variation of forms conspecific with *Tsugaepollenites mesozoicus*. **L.** SEM image altered after Guy-Ohlson (1989, figure 34) with permission of the Micropaleontological Society. There assigned as '*Cerebropollenites mesozoicus'*, which complies very well with specimen shown on its left. **M.** SEM image reprinted from Guy-Ohlson (1986, plate 14, figure 1) with permission of the Natural History Museum Sweden. There assigned as '*Cerebropollenites mesozoicus'*, which complies best with specimen presented in Figure 8 especially in direct comparison with SEM image on its left. Framed letter in the top-left corner indicates the locality of the material: **C** = Couper; **T** = Thiergart. Specimens indicated with an asterisk (*) are not to scale.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adopted afterwards even though recombined (*Sciadopityspollenites carlylensis*). However, some recombinations of epithets (*mesozoicus, macroverrucosus,* and *pseudomassulae*) are used so frequently (here we apply a threshold of once every two years, i.e. CR around 0.5; Figure 11) that their inconsistent recombinations can cause nomenclatural and taxonomic confusion.

Comparing the use of these frequently combined epithets with that of *Cerebropollenites thiergartii* also shows that the epithets have variable popularity over the decades (Figure 12). The epithet *mesozoicus* is the most popular in general, with increasing use up to the 1980s, after which it declines in favour of *macroverrucosus* which is less often, but relatively consistently used over the decades from the 1980s onwards (Figure 12A). The epithets *pseudomassulae* and *thiergartii* are used similarly often until the 2000s, when *thiergartii* is increasingly used (Figure 12A). In the 2010s citations of *thiergartii* are six times higher than *pseudomassulae* and circa a third more than *mesozoicus* (Figure 12A). This increase is mainly constituted by number of citations that cannot be assigned regionally, i.e. reviews or meta-analytical studies that reference the name, but do not document it for a particular region (Figure 13). It is striking, that the name is absent in studies on Russian material.

Apart from the interspecific change of name use, the intraspecific change of the recombinations of both *mesozoicus* and *macroverrucosus* is significant. The epithet *mesozoicus* was first combined in the basionym as *Tsugaepollenites mesozoicus* (Figure 12B). While the combination with *Tsugaepollenites* was still more favoured in the 1960s, the recombination with *Cerebropollenites* took over in the 1970s, peaking in the 1980s before declining use thereafter. It is noteworthy, that the trend of *Sciadopityspollenites mesozoicus* (Couper 1958) Waksm. 1981 use increases until most recently although the overall number of citations is very low (CR = 0.46; Figures 11, 12B). Amongst the three competing recombinations, the name *Cerebropollenites mesozoicus* is clearly the most common (CR = 6.95) and established name (EI value = 1.2). The use of names in the different regions of the world was mixed until the 1980s, after which the recombination with *Sciadopityspollenites* appears to be preferred only in studies with material from Russia.

The very same pattern is visible for the recombination of *macroverrucosus* with *Sciadopityspollenites*, yet with higher amplitude, i.e. higher CR (CR = 1.5) and much higher EI value (EI = 0.47) of *Sciadopityspollenites macroverrucosus* (Figure 12C). In addition to studies for Russian material, several studies from Eastern Europe use this recombination too (especially in the 1990s and 2000s [Figure 12C]). Irrespective of its recombination, it is noteworthy, that the epithet *macroverrucosus* is increasingly used over *mesozoicus* after the 1980s, but the most favoured recombination is *Cerebropollenites* (CR = 5.67; EI = 1.56).

The epithet *pseudomassulae* is used much less frequent than the previous two and it has never been recombined with *Sciadopityspollenites* (Figures 11, 12D). Since its original description with the basionym *Camerosporites pseudomassulae* in 1964 there is a significant time gap until its recombination as *Tsugaepollenites pseudomassulae* in 1975. Consequently, the number of citations is still low in the 1970s before having more than 15 citations per decade in the 1970s–2000s (Figure 12A). The recombination with *Cerebropollenites* occurs concurrently from the 1980s onwards, but with decreasing values from decade to decade till today (CR = 0.27). *Tsugaepollenites pseudomassulae* is in comparison the most favoured recombination (CR = 1.73, EI = 1.76), but it is striking that the names occur almost exclusively in European and North American studies (Figure 12D).

Discussion: commented literature review

The distinction of *Cerebropollenites thiergartii* and associated taxa and their respective genus assignations is a long-standing problem with convoluted discussions. The following literature review provides an

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Figure 10. Intraspecific and interspecific variation of *Camerosporites pseudomassulae* and *Tsugaepollenites igniculus*. **A.** Holotype for *Camerosporites pseudomassulae* Mädler 1964b. **B–J.** Intraspecific variation for specimen comparable to the holotype of *Camerosporites pseudomassulae*; **H–I.** Specimens from Orbell (1973) there assigned as '*Cerebropollenites mesozoicus*', reprinted with permission of the British Geological Survey (permit nr. CP21/005). **K.** Rephotographed *Tsuga-pollenites igniculus* from Thiergart (1938). **L, M.** *Tsugaepollenites igniculus*. **N.** Original photograph for *Tsuga-pollenites igniculus* from Thiergart (1938) reprinted with permission from LBEG/BGR. **O.** Drawing for *Tsuga-pollenites igniculus* from Potonié and Venitz (1934) reprinted with permission from LBEG/BGR. **P.** Drawing for *Tsuga-pollenites igniculus* reprinted from (Potonié 1931). Framed letter in the top-left corner indicates the locality of the material: **B** = Bonenburg; **K** = Kuhjoch; **T** = Thiergart. Specimens indicated with an asterisk (*) are not to scale.

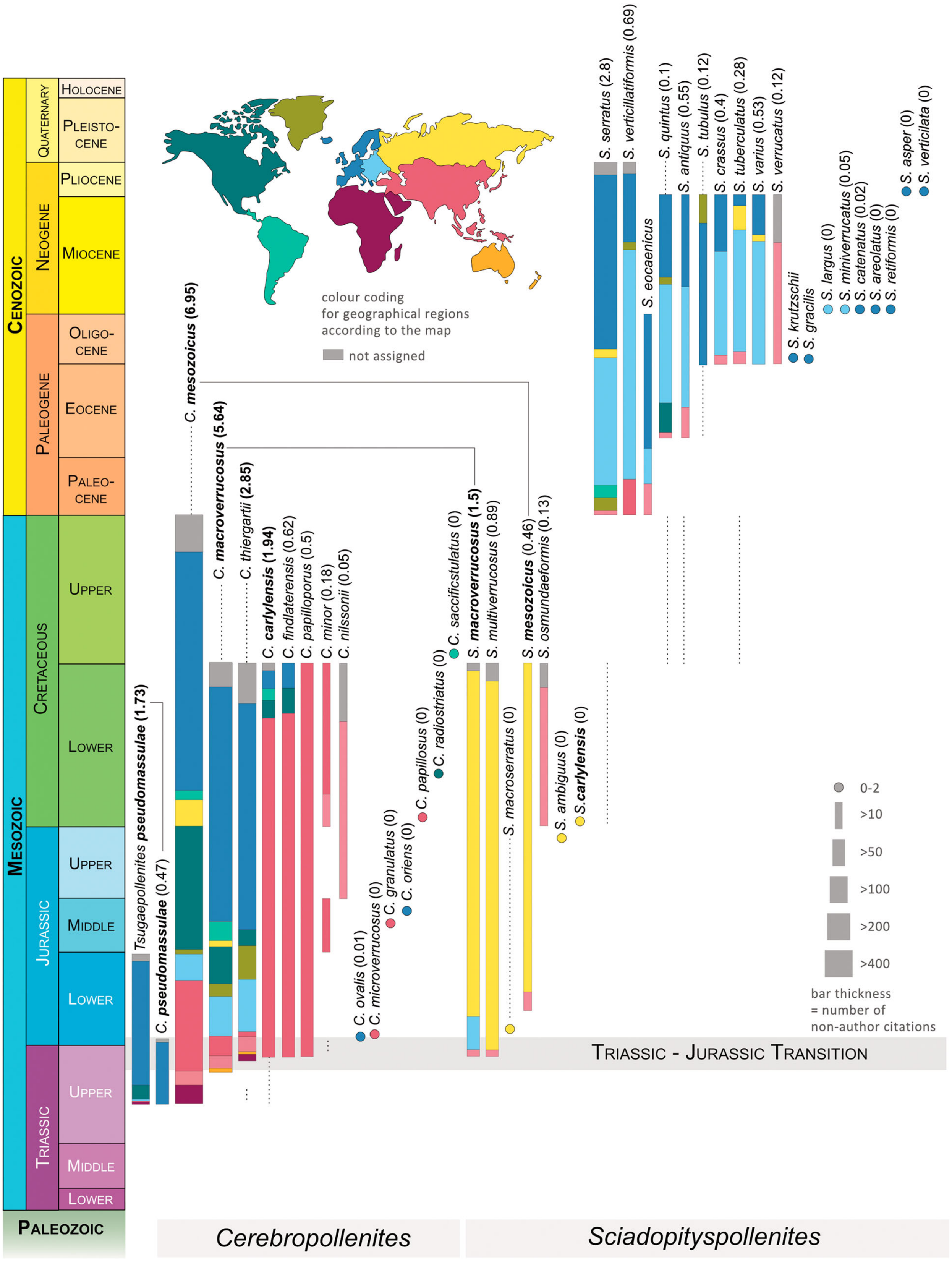


Figure 11. Stratigraphic ranges of *Cerebropollenites* and *Sciadopityspollenites* and all described taxa, colour-coded according to country of origin. Thickness of the bars indicates the number of citations. Length of the bars indicate stratigraphic range. Additionally, the full length represents 100% of the citations of each taxon, colour coded subdivisions, represent percentage share of citations from the geographical region represented by that colour. Note that occurrences of taxa with the epithet *mesozoicus* in the Triassic most likely reflect potential misidentifications and confusion with *pseudomassulae*.

overview of previous perspectives on relationships of the relevant taxa and aims to identify sources of confusion. Although discussed often together, the question of genus assignation is separated from species distinction. For clarity, we therefore discuss them separate whenever possible, but with cross-references where needed. In a first step we discuss genus distinctions, genus by genus, in chronological order of their description. As a starting point, we provide a translation of the original descriptions/diagnosis for each genus. In a second step we discuss species distinction in the order of increasing size of ornamentation (*thiergartii*, *macroverrucosus* versus *mesozoicus*, *pseudomassulae*) comparing existing understandings with our new results.

Genus **Tsugaepollenites** *(R.Potonié et Venitz 1934) R.Potonié 1958*

Type. — *Sporonites igniculus* R.Potonié 1931, p. 556, figure 2 (drawing after V80a), LOST.

Genus description. — Genotype 35 µm, equator more or less circular, with an equatorial velum, which can be very narrow, this fringe is radially folded, outline irregularly convoluted to sinuate. Exine of the central body rugulate, i.e. covered with irregular short more or less winding muri to warts. (Translated after Potonié 1958, p. 48.)

Discussion. — Without making a formal emendation, Manum (1962) adds or clarifies two important diagnostic features for the genus:

> 1. The corrugated protrusions forming the conspicuous sculpturing are hollow. This may easily be observed both in surface view and in optical section of the exine. […] 2. The grains are heteropolar […]. The ventral side has a central area which has a less ‘puffy’ and corrugated sculpturing than the dorsal side, and it is usually depressed. Protrusions of a more puffed-out nature than those of the dorsal side surround the area and are present in the equatorial region where they produce a more or less prominent equatorial fringe, noticeable in polar aspect of the grains. German examples of Tsugaepollenites which I have seen possess these characters. (Manum 1962, p. 45)

Manum’s additions are very important and appear adequate in view of our study of the type for the genus. Additionally, as will be pointed out later, these additions are crucial to distinguish *Cerebropollenites* and *Sciadopityspollenites* or other associated taxa. Manum’s clarified diagnostic features are supported by an SEM study on pollen assigned to *Tsuga* from the Middle Miocene (Grímsson & Zetter 2011). The SEM study highlights the very same distinguishing characteristics pointed out by Manum (1962), and illustrates that a monosaccus, heteropolarity through the difference in sculpture on the proximal and distal face, and the large subcircular germinal area which almost encompasses the entire proximal face, are crucial to separate *Tsugaepollenites* from other superficially similar looking taxa.

Genus **Sciadopityspollenites** *Raatz 1937 ex R.Potonié 1958 (Jan.)*

Type. — *Sporites serratus* R.Potonié et Venitz 1934, p. 15, plate 1, figures 6, 7.

Genus description. — Shape round to oval to spindle-shaped. As a result of the verrucate (‘warty’) ornamentation, the outline appears irregularly undulated (‘wavy’). Dehiscence never perceivable. (Translated after Raatz 1937, p. 13.)

Discussion. — Interestingly, Potonié and Venitz (1934) were very ambiguous in describing the new species whose holotype was later chosen to serve as type for the genus. In their systematic section (p. 15) they refer to it as a spore (*Sporites*), but call it *Pollenites* in the legend of the plate (plate 1), ironically illustrating the conflicting affinities (*Ophioglossum* and *Tsuga)* they speculate about. Raatz (1937) also calls attention to this, and references Thiergart in Gothan (1936), who introduces the idea that pollen compliant with *Pollenites serratus* is produced by extant *Sciadopitys*. Raatz subsequently uses the new genus name *Sciadopitys-pollenites*. He does not provide a clearly labelled genus diagnosis/description, but does provide the earlier given description. According to Art. 38.5 *Code* this is sufficient for valid publication of the genus, because the genus was monotypic at the time.

Potonié (1958) later provides a more elaborate and clearly indicated genus description. Our English translation thereof reads:

> Equator more or less circular; germinal area not always recognizable, sometimes partly covered by secondary folds, not like a colpus (as stated by Thomson & Pflug 1953) but roughly circular to slightly oval; when it [germinal area] has opened, it appears as a more or less triangular gap. The exine is ornamented with small warts, which in the type of the genus protrude over the equator with mostly over 30 more or less irregular protrusions. The warts are rather homogeneous in size and have a slightly uneven but rounded surface; their diameter is about half their height; their outline is irregularly

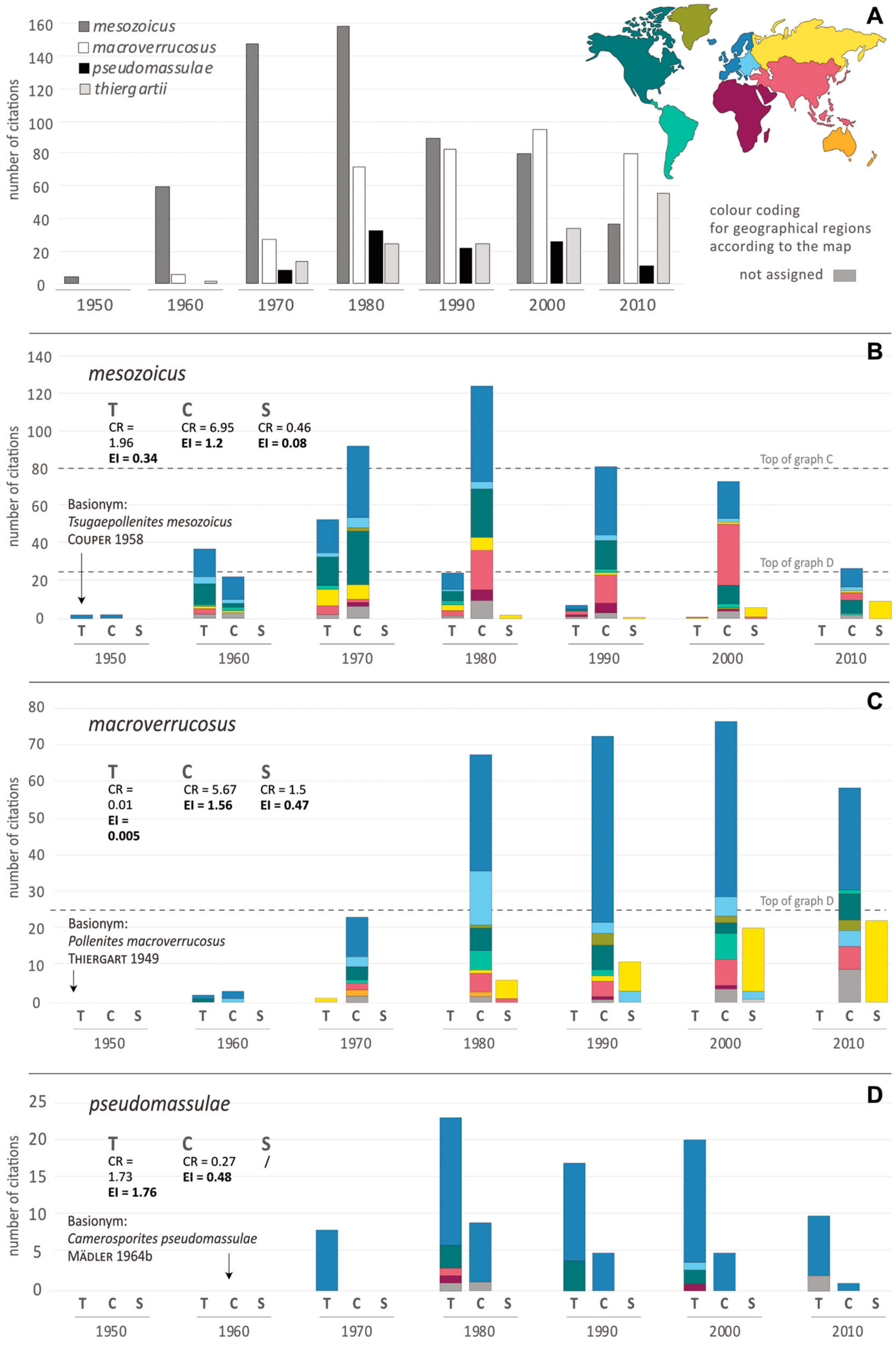


Figure 12. Name use statistics for the epithets *mesozoicus*, *macroverrucosus*, *pseudomassulae*. Historically each epithet is most commonly assignable to either T (*Tsugaepollenites*), C (*Cerebropollenites*) or S (*Sciadopityspollenites*). **A.** Overview of number of citations per epithet (irrespective of its genus assignation). The data for *Cerebropollenites thiergartii* is given for comparison. **B.** Number of citations for the epithet *mesozoicus* per genus per decade. **C.** Number of citations for the epithet *macroverrucosus* per genus per decade. Note the different scale in comparison to the other graphs (see **A** for comparison of taxa). **D.** Number of citations for the epithet *pseudomassulae* per genus per decade. Note the different scale in comparison to the other graphs (see **A** for comparison of taxa).

> circular to polygonal, also rugulate elongated or irregularly triangular. The verrucae cover the whole exine except for the area of germination.
>
> (translated after Potonié [1958], but also compare translation in Jansonius and Hills [1976, card 2547])

Based on the lack of a genus diagnosis in 1937, Jansonius and Hills (1976) argue that the genus was not validly published until this criterion was fulfilled in January 1958 by Potonié. Therefore, they cite the genus as '*Sciadopityspollenites* Raatz ex R.Potonié 1958' (see Fensome et al. 2019; Gravendyck et al. 2021 on the nomenclatural implications of 'ex'). Potonié appears to think differently, as indicated by his later citations as '*Sciadopityspollenites* (Raatz 1937) R. Pot 1958' (Potonié 1966). Even if one disagrees with this later interpretation, the name would have been effectively and validly published as late as January 1958 by Potonié (1958).

Genus **Cerebropollenites** *Tage Nilsson 1958 (Apr.)*

Type.— *Tsugaepollenites mesozoicus* Couper (1958), p.155, plate 3 figures 8–10 designated by Nilsson (1958).

Genus description. — Inaperturate, azonate pollen grains with more or less angular, oval or circular outline. Exine not very thick; especially thin and almost without ornamentation in a circular area on the distal face. Surface of the other areas big and irregular folds; the folds more or less deeply sinuous seen from longitudinal view. (Translation from Nilsson 1958, p. 155; altered after Jansonius & Hills 1976, card 443.)

Discussion. — Potonié (1960) considers the new genus superfluous based on his implied interpretation that Couper's holotype is saccate and should be incorporated in the genus *Tsugaepollenites*. Similarly, yet more formally, Dettmann (1963) reinterprets the equatorially protruding ornamentation of Couper's holotype as having several 'intercommunicating vesiculate protrusions' leading her to synonymise the younger *Cerebropollenites* with the senior synonym *Tsugaepollenites*. Omitting any reference to this interpretation and recombination, Schulz (1967) retains the assignation to *Cerebropollenites* and indicates without formal emendation that the genus *Cerebropollenites* is, in fact, monosulcate and not inaperturate as described by Nilsson. A year later, Singh and Kumar (1968) emend to counter the merging of *Cerebropollenites* with *Tsugaepollenites* (Jansonius & Hills 1976, card 443) as follows:

> Pollen grains oval to circular in flattened condition, numerous vesiculae of variable size present on both the faces, distal exine marked by a thinner polar region small, circular or of variable shape having smooth to granulose ornamentation, the remaining surface being rough and covered by vesiculae, individual vesiculae variable in size and shape, *extrema lineamenta* usually deeply corrugated. (Singh & Kumar 1968)

Pocock (1970) provides another genus diagnosis which alters the used terminology, but also adopts the interpretation of *Cerebropollenites* as saccate. However, Pocock's new diagnosis is not indicated as a formal emendation and is subsequently not referenced in Jansonius and Hills (1976) or later by other authors citing the genus. Nevertheless, Pocock (1970) is a very relevant publication that does not only conduct the first broader study on interspecific intraspecific variation, but also describes two new species based on size distribution patterns. He also states that the conventional practice of assigning all Jurassic grains of the genus to *Cerebropollenites mesozoicus* would be an oversimplification.

A very important observation on Couper's holotype made by Mädler (1963), however, is not mentioned in the previously cited publications. Mädler (1963) distinguishes Couper's type from *Tsugaepollenites* based on the lack of an 'equatorial velum' and interprets the protrusion as simple ornamental elements that are 'even if they were hollow, not comparable to a saccus' (translated from Mädler [1963, p. 364]). He argues that, based on morphology, the holotype of Couper should be assigned to the Tertiary *Sciadopityspollenites*. Although regarding them morphologically identical, Mädler assigns his specimens to *Cerebropollenites* as the equivalent Mesozoic predecessor of *Sciadopityspollenites*, following convention rather than morphologic reasoning to consider them congeneric (Mädler 1963).

In summary, two basic questions underlie all these arguments. (1) Is the type of the genus *Cerebropollenites* compliant with the description of *Tsugaepollenites* and if not, is (2) *Cerebropollenites* or *Sciadopityspollenites* the correct genus name to adopt?

When Couper (1958) described his new species *mesozoicus* from the Middle Jurassic, he compared it with extant *Tsuga* pollen which he also studied for his publication. Reissinger (1950) had already depicted pollen like Couper's holotype and speculated about an affinity with *Tsuga* or *Sciadopitys*. Reissinger notes that the pollen he documented (plate 17, figures 33, 34) are size-wise in between the size ranges of extant representatives of the two genera. Based on a not depicted specimen that he describes as slightly different than the two illustrated pollen, i.e. with a bigger and rounder sulcus area, he

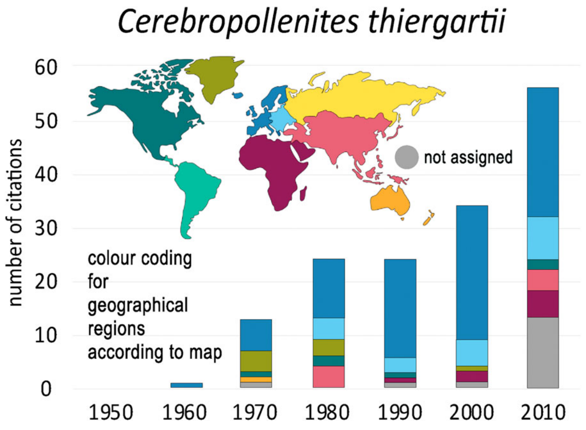


Figure 13. Name use statistics for *Cerebropollenites thiergartii.* Number of citations of the name *Cerebropollenites thiergartii* per decade per geographical region of the world (for colour coding of the regions see Figure 12).

interprets all three pollen to be most likely representatives of *Tsuga* (Reissinger 1950).

Reissinger's strongly expressed view of a relation with *Tsuga* might have influenced later workers like Couper, who also studied pollen grains of extant *Tsuga* taxa and explicitly cites him to support his newly described species. Indeed, Couper's interpretation of the new taxon appears strongly influenced by the assumed *Tsuga* affinity, which is reflected in his phrasing of the diagnosis stressing particularly the existence of a fringe, i.e. a monosaccus in this context, using very interpretative rather than descriptive terminology. After considering Couper's and other representations of *Tsuga* and *Sciadopitys* pollen using light microscopy and SEM (Couper 1958, plate 30, figures 6, 7; Grímsson & Zetter 2011, figures 23, 24, 26, 27), we must stress the difference between Couper's new holotype and younger *Tsuga* pollen, as well as the type specimen for the genus *Tsugaepollenites* (see Figure 10K–P). Typical for *Tsuga* and *Tsugaepollenites* pollen is the existence of a monosaccus, which morphologically appears like a fringe at the equator of the pollen grain (see also Grímsson & Zetter 2011, figures 23, 24). During re-examination of Couper's holotype, we observed an equatorially protruding ornamentation that, especially when elements from different focal planes are overlain, can give the impression of a fringe. However, change of focal plane does not perpetuate that impression (compare Figure 9Aa and Ab or Figure 9Ka and Kb). On top of that, the effect of hollowness that emphasises the impression of a fringe can be augmented by the objective used for observation (compare Figure 9Ca and Cb).

It should be noted that some *Tsuga* pollen species with a very narrow monosaccus (*Tsuga* sp. 2 or '*Tsuga canadensis* type', see Grímsson & Zetter 2011), can appear similar to Couper's type with light microscopy. Yet, in contrast to Couper's holotype, the very round sulcus area possesses a very distinct ornamentation in *Tsuga* pollen and *Tsugaepollenites*. Assignation to *Tsugaepollenites* might in the end have been an effect of priming, since Couper only studied extant material from *Tsuga* but not of *Sciadopitys*. However, pollen of the latter are much more similar to the holotype of Couper in shape, size, sulcus, and absence of a saccus (Grímsson & Zetter 2011; Uehara & Saiki 2011; Bykowska & Klimko 2016).

Ultrastructural studies on various *Cerebropollenites* grains from the Upper Jurassic and Cretaceous (Kurmann 1990; Batten & Dutta 1997; Shang & Zavada 2003) further corroborate the distinct absence of a saccus in *Cerebropollenites* compared to fossil *Tsugaepollenites* and pollen of extant monosaccate *Tsuga* (Kurmann 1990). All of these studies emphasise that the convoluted protrusions give the impression of a fringe or saccus, but that *Cerebropollenites* is missing the tectum and alveolate structure typical of saccate pollen and instead, possesses (still) at least a partially fused sexine and nexine. In addition, the degree of the fusion of sexine in nexine is varying from species to species and might be an ancestral stage in the development of a monosaccus, like in extant *Tsuga*. So far the ultrastructural studies on late Mesozoic *Cerebropollenites* pollen show that they do not have a vesiculate saccus but consist of more massive and solid structures, i.e. not saccate (Batten & Dutta 1997; Shang & Zavada 2003). While our observations of early Mesozoic taxa discussed in this article suggest the lack of a vesiculate saccus, additional ultrastructural studies could help to verify the nature of their pollen wall.

The fact that historically many authors lean towards a one-sided comparison with extant *Tsuga*, is possibly owed to the priming effect of the genus assignation of the basionym '*Tsugaepollenites*'. To allow a more balanced comparison with extant analogues it is worth noting, that SEM and ultrastructural studies on fossil and extant asaccate *Sciadopitys* pollen suggest much greater similarity of *Cerebropollenites* with *Sciadopitys* rather than with *Tsuga* (Surova & Kvavadze 1988; Grímsson & Zetter 2011; Uehara & Saiki 2011; Hofmann et al. 2021). Waksmundzka (1981) pointed out in her SEM study of fossil *Sciadopityspollenites mesozoicus* (Couper 1958) Waksm. 1981, that the verrucae are ornamented with 'small clavate elements' (compare plate 24, figure 5 in Waksmundzka [1981]). The same feature was documented by Shang and Zavada (2003), and is particularly pronounced in the species *Cerebropollenites papilloporus*, which possesses distinct 'pappilae' on the verrucae (compare figures 12–14 in Shang and Zavada [2003]). Most recently Hofmann et al. (2021) examined Lower Cretaceous specimens they assigned to *Cerebropollenites thiergartii*, *Cerebropollenites macroverrucosus* and Upper Cretaceous specimens assigned *Sciadopityspollenites serratus* and documented a 'supratectal microechinate' ornamentation that is characteristic for Sciadopityaceae. The very same characteristic is visible in fossil *Sciadopitys* pollen from the Miocene (compare figure 28 in Grímsson and Zetter [2011]), and in pollen grains of extant *Sciadopitys verticillata* (plate 3, figure 14 in Ho and Sziklai [1973], figure 4 in Bykowska and Klimko [2016] and figure 1 in Hofmann et al. [2021]). The reference to the microornamentation as microechinate in the more recent studies is only a semantic difference, as all studies demonstratively show the same typical morphological feature.

So, the answer to the first question, i.e. whether the type for *Cerebropollenites* is compliant with the genus diagnosis of *Tsugaepollenites* is 'no'. We dismiss this assignation because of the lack of different ornamentation on the proximal and distal face, as would be typical for *Tsugaepollenites*, and on the absence of a saccus supported by ultrastructural studies of fossil *Cerebropollenites* species (Batten & Dutta 1997; Shang & Zavada 2003) and extant *Sciadopitys* pollen (Uehara & Saiki 2011). It should also be noted, that the lack of differentiation between proximal and distal faces typical for *Tsugaepollenites* was already pointed out by Nilsson (1958), and was the main reason for the erection of the new genus *Cerebropollenites*. Despite the initial increase of the name *Tsugaepollenites mesozoicus* use that was still observed in the 1970s (Figure 12), the recombination with *Cerebropollenites* took over, and suggests that most of the scientific community is acknowledging the earlier laid out differences and is further corroborated by recent studies.

The subsequent question then is whether *Cerebropollenites* or *Sciadopityspollenites* is the correct genus assignation for the various species assigned to either or both genera. In other words, are they congeneric and if yes, which one has priority? Nilsson (1958) in his genus diagnosis for *Cerebropollenites* does not describe any morphology that would not be already circumscribed by the earlier diagnosis of *Sciadopityspollenites*. Mesozoic (*Cerebropollenites*) as opposed to Cenozoic (*Sciadopityspollenites*) occurrences as pointed out by Mädler (1963) is an artificial, rather than a morphological difference, which was introduced by conventional use as such over the decades. The negative consequence of this practice is that it masks the continuity and evolution of the pollen and its mother plant (see Figure 11). Since extinction and origination rates are often calculated at the genus level, artificial separation based on different stratigraphic ranges potentially increases interpretations of extinction and origination. To prevent this, synonymisation is not only advisable but a necessity. Since *Sciadopityspollenites* was described first (either 1937 or the latest by January 1958), *Cerebropollenites* (published April 1958) must be considered the junior synonym. Although this practice is numerically underrepresented in name use, it should be adopted to adhere to the principle of priority, like many Russian workers have for many years (see yellow in Figure 12).

The epithet ***thiergartii***

Already prior to and after Schulz (1967) described the new *Cerebropollenites thiergartii*, authors documented pollen that occurred together with *macroverrucosus* forms, but with a much finer ornamentation. Thiergart (1949) himself already erected *Pollenites macroserratus doggerensis* for such forms. Unfortunately, the description below species level of this and similar forms (*Pollenites serratus* f. *helmstedtensis* and *Pollenites serratus macroserratus* f. *keuperianus*) and poor images might have reduced the impact of these three taxa. Following or re-evaluation of type material, we consider the latter two forms to be conspecific with *Ricciisporites tuberculatus* and *Polypodiisporites polymicroforatus*. The similarity with *Pollenites macroverrucosus* has however caused other authors to use these names for forms conspecific with *thiergartii*. Rogalska (1954) reports specimens differing from *Pollenites macroverrucosus*, by much smaller verrucae assigning them to 'cf. *Pollenites serratus* f. *helmstedtensis*' (compare plate 6, figures 13 and 14 in Rogalska [1954]). She also remarks on the intraspecific variation in the size of the verrucae of the two depicted specimens. Bóna (1969) also depicts such a specimen (plate 8, figure 7 in Bóna [1969]), but assigns it to the newly recombined *Tsugaepollenites macroserratus* f. *doggerensis* (Thierg. 1949) Bóna 1969.

These uses show the ambiguity and inconsistent application of the names for the different 'formae' of *Pollenites serratus* or *macroserratus* erected by Thiergart (1949) and might explain why they were hardly used, especially not after Schulz' revision which, interestingly, does not comment on *macroserratus* f. *doggerensis*. In contrast, the use of *Cerebropollenites thiergartii* quickly increased after its description (Figure 13). The lesser overall number of citations in comparison to *Cerebropollenites mesozoicus*/

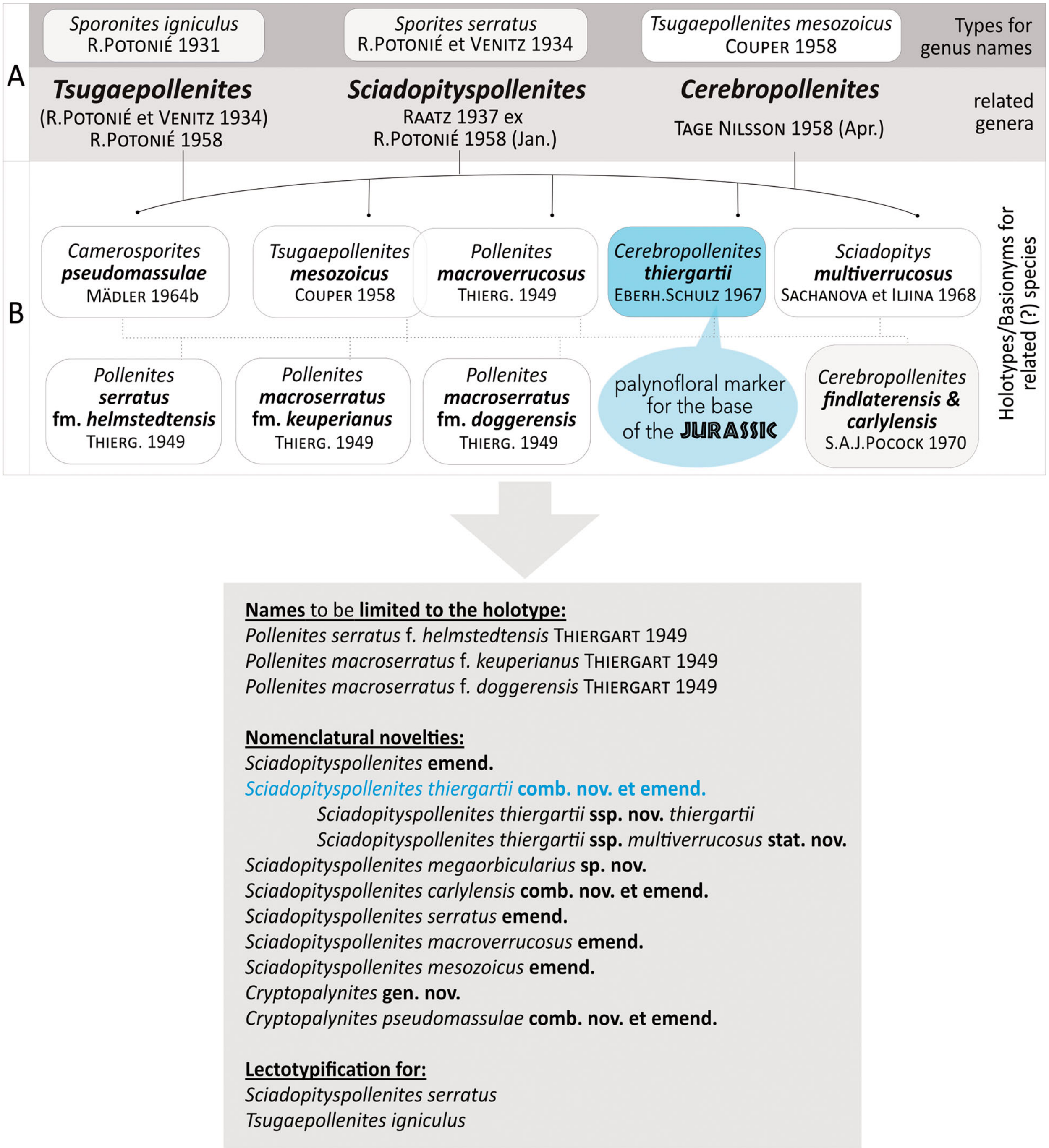
macroverrucosus probably reflects on the abundance patterns of these taxa. The rise of citations for *Cerebropollenites thiergartii* after the turn of the century is then driven by the evaluation of its stratigraphic value in the discussion of the new GSSP for the base of the Jurassic and its role as the palynofloral marker for it (Morton 2012; von Hillebrandt et al. 2013) (see increase of not geographically assigned citations [grey] in Figure 13).

The entire absence of citations for *Cerebropollenites thiergartii* in Russia is striking, even more so as there is no recombination with *Sciadopityspollenites* like for the other *Cerebropollenites* taxa (no yellow in Figure 13). This might be explained by the use of the name *Sciadopityspollenites multiverrucosus*, the second most used taxon of the genus in the Mesozoic after *Sciadopityspollenites macroverrucosus* (compare yellow in Figure 11). Since *Sciadopityspollenites multiverrucosus* is reversely not recombined with *Cerebropollenites* and has the same stratigraphic range (Figure 11), it appears to be the vicarious name for *Cerebropollenites thiergartii* in mostly Russian studies. It was erected as *Sciadopitys multiverrucosus* (Iljina 1968) and later recombined with *Sciadopityspollenites* (Iljina 1985). With her recombination, Iljina (1968) shows a bright-field image together with an SEM image of a pollen that looks very similar to the holotype of *Cerebropollenites thiergartii*, only with verrucae that are more in the bigger size range of variation we showed in this article (Figure 6). Although Iljina (1985) speculates on a potential synonymy with *Cerebropollenites carlylensis*, probably because of the relatively small size of the specimen, our observations on intraspecific and interspecific variation and comparison of holotypes confirm that *Cerebropollenites thiergartii* and *Sciadopityspollenites multiverrucosus* are conspecific. The current geographic isolation of the two taxa and apparent endemism of *multiverrucosus* to the area that is nowadays Russia, is unlikely the result of biological speciation but rather a result of literary isolation fostered by different languages, alphabets and schools of the scientists that use these names. Considering the holotypes to be conspecific makes *Sciadopityspollenites multiverrucosus* the one-year younger name, i.e. the junior synonym of *Cerebropollenites thiergartii*.

Most publications document *Cerebropollenites thiergartii* from the Jurassic onwards. It occurs within the turn to more negative δ^{13}C values in the lower part of the main carbon-isotope excursion, well above the extinction level of Triassic biota, but significantly below the lowest occurrence of the first Jurassic ammonite (Kürschner et al. 2007; Bonis et al. 2009; von Hillebrandt et al. 2013). Bonis et al. (2010) reported *Cerebropollenites thiergartii* and *Ischyosporites variegatus* about 4 m above the base of the Blue Lias Formation (Fisher & Dunay 1981) in St Audrie's Bay. Moreover, *Cerebropollenites thiergartii* has been reported from lowermost Liassic sediments in the Germanic Triassic basin in the Mariental core 1 (Van De Schootbrugge et al. 2009; Heunisch et al. 2010), the Bonenburg outcrop (Schobben et al. 2019; Gravendyck et al. 2020b), in the Kamien Pomorski core in Poland (Pieńkowski et al. 2012), as well as in Greenland (Pedersen & Lund 1980; Mander et al. 2010), the Sverdrup Basin (Suneby & Hills 1988), from Kong Karls Land (Svalbard archipelago) (Smelror et al. 2019) and in the Eastern Tethys realm and the Alborz Mountains in Iran (Achilles et al. 1984).

Based on detailed palynological studies in the Northern Calcareous Alps, previous studies (Kürschner et al. 2007; Bonis et al. 2009) proposed *Cerebropollenites thiergartii* and *Ischyosporites variegatus,* found 3.2 m below the entry level of *Psiloceras spelae,* as accessory palynological markers close to the base of the Jurassic (see also discussion in Cirilli [2010]). Re-evaluating previously reported occurrences can be difficult (Kürschner et al. 2007; Bonis et al. 2009; von Hillebrandt et al. 2013), as not all documented specimens are visually represented and because images and limited focal planes can be misleading. Based on the remaining preserved material and specimens which could be relocated, the earliest occurrences of cf. *thiergartii* (from sample K_051025.4) is reported from *c.* 1.3 m below the entry level of *Psiloceras spelae* (additional specimens are depicted in Supplementary Material 3 and are subject to taxonomic opinion because of their very poor preservation). *Ischyosporites variegatus* however can be confirmed to occur from 3.2 m below the entry level of *Psiloceras spelae* (see also Supplementary Material 3).

Cerebropollenites thiergartii is a particular relevant taxon because of the paucity of other palynofloral markers. Yet, the documentation of this taxon as early as the Middle Rhaetian (Lund 1977) challenges the application as a marker fossil as suggested by Lindström et al. (2017b). Lund (1977) reported a singular occurrence of *Cerebropollenites thiergartii* in his stratigraphic table already from the Middle and Upper Rhaetian in cores (Rødby 1 and Maasbüll 1) from the Danish basin. However, Lund's findings are questionable as the illustrations of his pollen do not show the typical morphological features of *Cerebropollenites thiergartii*. Lund's report of a potentially much earlier appearance of *Cerebropollenites thiergartii* has thus casted doubt on the stratigraphic significance of this taxon despite its continued use as such. Intriguingly, only three years after the publication of his monography, Lund inferred together with K.R. Pedersen the base of the Hettangian in



Names to be limited to the holotype:
Pollenites serratus f. *helmstedtensis* THIERGART 1949
Pollenites macroserratus f. *keuperianus* THIERGART 1949
Pollenites macroserratus f. *doggerensis* THIERGART 1949

Nomenclatural novelties:
Sciadopityspollenites **emend.**
Sciadopityspollenites thiergartii **comb. nov. et emend.**
    Sciadopityspollenites thiergartii **ssp. nov.** *thiergartii*
    Sciadopityspollenites thiergartii **ssp.** *multiverrucosus* **stat. nov.**
Sciadopityspollenites megaorbicularius **sp. nov.**
Sciadopityspollenites carlylensis **comb. nov. et emend.**
Sciadopityspollenites serratus **emend.**
Sciadopityspollenites macroverrucosus **emend.**
Sciadopityspollenites mesozoicus **emend.**
Cryptopalynites **gen. nov.**
Cryptopalynites pseudomassulae **comb. nov. et emend.**

Lectotypification for:
Sciadopityspollenites serratus
Tsugaepollenites igniculus

Figure 14. Problem overview of related taxa relevant for the distinction of *Sciadopityspollenites thiergartii* comb. nov. et emend. and other proposed nomenclatural novelties.

the Triassic–Jurassic boundary deposits on Greenland by the first occurrence of *Cerebropollenites thiergartii* (Pedersen & Lund 1980). It should be noted that none of the earlier mentioned palynological studies (e.g. Van der Schootbrugge et al. 2009; Heunisch et al. 2010; Gravendyck et al. 2020) have ever reported the presence of *Cerebropollenites thiergartii* in Lower to Middle Rhaetian deposits in the Germanic or Danish Triassic basins.

The less clearly defined species boundaries and the often poor quality of images, or representation of a single focal plane and extremely poor preservation in many samples can make it difficult to identify or distinguish *Cerebropollenites thiergartii* from forms assigned to the epithet *macroverrucosus*, with relatively small and densely packed sculptural elements (compare Figure 6O, P). Although *macroverrucosus* possesses rugulae rather than verrucae, this is not always easily discernible from a photograph, and has surely complicated identification of *Cerebropollenites thiergartii*, especially of those specimens with larger verrucae (compare Figure 6). This might explain Lund's documentation of *Cerebropollenites thiergartii* as low as the Middle Rhaetian (Lund 1977). The specimen he depicts in plate 7, figure 15 as *Cerebropollenites thiergartii* is better assigned to the epithet *macroverrucosus*. We attempted to consult the original slides at GEUS to confirm this interpretation based on the photograph. Although most of Lund's material is available there, the slides in question were not (S. Lindström, pers. comm. 2018). Indeed, forms assigned to the epithets *macroverrucosus* were also reported in the Rhaetian in Bonenburg and probably Kuhjoch (compare Figure 8K, L).

The misapplication of *Cerebropollenites mesozoicus* to *Tsugaepollenites pseudomassulae* of Orbell (1973), i.e. a taxon that occurs most commonly and is probably limited to the Rhaetian, has further complicated the stratigraphic range of all involved taxa. Further studies using the herein presented classification will be needed to confirm the exact ranges of the respective taxa, and although we cannot entirely resolve the documentation of *Cerebropollenites thiergartii* in the Rhaetian, it seems most likely to be a result of taxonomic confusion, neglectable in correlations, unless other studies can confirm such early occurrence.

The epithets ***macroverrucosus*** *and* ***mesozoicus***

Nilsson (1958) points out that Thiergart's *macroverrucosus* might be related to *mesozoicus*, but refrains from a final judgment as the description and photograph would be insufficient. Nevertheless, he argues that a pollen shown by Rogalska (1956, plate 19, figure 4) classified as *Pollenites macroverrucosus* would be identical with his specimens. After examination of Rogalska's photograph, we noted that the density of their sculptural elements is higher and the elements generally smaller, with the outline much less undulated than in Nilsson's photographs and comparable to Thiergart's holotype. Similarly, Mädler (1963) opposes synonymisation of *macroverrucosus* and *mesozoicus* based on the differences in ornamentation, and considers *macroverrucosus* to possess more 'wart-like' structures.

Schulz (1967), however, expressed the opinion that Thiergart's type (which he had re-examined) and the type of Couper (which he did not re-examine) would be conspecific. Consequently, he synonymised them in favour of *macroverrucosus*, i.e. the older name having priority. The strong increase in use of the name *macroverrucosus* from the 1960s to the 1970s, might have been fostered by Schulz' recombination (Figure 12C) bringing it back into the spotlight and the majority of authors adopt this view (e.g. Bóna 1969; Lund 1977; Pedersen & Lund 1980; Iljina 1985; Dybkjær 1991; Batten & Dutta 1997). Few express their doubt, whether synonymisation of *mesozoicus* and *macroverrucosus* is justified (e.g. Mädler 1963; Tralau 1968; Morbey 1975). The fact that the use of the epithet *mesozoicus* still increases until the 1980s (Figure 12B) might be owed to Pocock's judgment of such a synonymised treatment as an 'oversimplification' (Pocock 1970), leading to a more differentiated use by authors thereafter (compare Tralau 1968; Fisher & Dunay 1981; Waksmundzka 1981; Guy-Ohlson & Malmquist 1985; Guy-Ohlson 1986; Zhichen et al. 2000; Shang & Zavada 2003; and trends in Figure 12B, C).

One very problematic use of the name *Cerebropollenites mesozoicus* is found in Orbell (1973). Under this name he figures two specimens with very hyaline protrusions which are clearly conspecific with the holotype for *Camerosporites pseudomassulae* (Figure 10H, I). Dybkjær (1991) explicitly clarifies this as an erroneous assignation prior to her establishment of the *Cerebropollenites macroverrucosus* zone. Despite this clarification, Orbell and less critical readers of his paper, might have added to the taxonomic and nomenclatural confusion around the epithets *macroverrucosus* and *mesozoicus*, and even *pseudomassulae* thereafter.

In the most extensive revision of *Cerebropollenites* to date, Pocock (1970) analysed the size distribution of different *Cerebropollenites* species and observed four distinct peaks leading him to keep *mesozoicus* and *macroverrucosus* apart, and describing two additional species, i.e. *carlylensis* and *findlaterensis*. He considers *findlaterensis* to be the largest and most convoluted species, while *macroverrucosus* is the second largest and more ovoid in shape than the others, with a very longitudinal sulcus. He also considers *carlylensis* to be the smallest species and *mesozoicus* to be the second smallest and more spherical, although noting a considerable size overlap with *macroverrucosus*.

We agree that the general lumping of *mesozoicus* and *macroverrucosus* is oversimplistic considering the variation we observed and described earlier. Nevertheless, shape, sulcus shape and especially size as the main sorting criteria as practiced by Pocock is difficult as well. Firstly, these criteria are very variable (see for example the variation in the holotype slide for *Cerebropollenites thiergartii* from Schulz, Figure 5J–M) and might be influences by the fossilisation process (depth, temperature, pressure) (Hofmann et al. 2021). Secondly, size and shape are highly ambiguous criteria, because different preparation techniques (e.g. reagents in preparation) and mounting (medium and thickness) and even the age of the slide and time of observation can secondarily alter these characteristics (Andersen 1960, 1978; Reitsma 1969; Sluyter 1997; Harley and Baker 2001; Meltsov et al. 2008; Cushing 2011; Riding 2021). Therefore, they are here, contrary to the practice of Pocock (1970), not considered the most useful criteria to categorise the observed diversity. Even more so, as the sulcus is not always clearly discernible to measure. Sorting the observed variation on a gradient of sculptural elements of increasing size and according to the density of their arrangement permits distinction of *macroverrucosus* and *mesozoicus*.

Although not using size as the sorting criterion, it should be noted that we also observed a series of grains with slightly elongate more hook-shaped rugulae which are generally more circular with a rounder sulcus and might represent specimen best addressed as *carlylensis* (Figure 9C, F). As they are generally smaller it is unclear whether they represent an immature form, or whether it is a taxon that is consistent in size and shape, remains unclear. Either way, addressing these smaller, rounder forms with a separate name enables precise data collection producing datasets that can still serve once biological knowledge as to their production has increased. Lumping these forms is then still possible at the interpretative stage, depending on the palaeobiological interpretation and study question of the author.

The epithet ***pseudomassulae***

More than 10 years after description of the basionym *Camerosporites pseudomassulae* Mädler 1964, Morbey (1975) recombined it, tentatively, with *Tsugaepollenites*. In his synonymy he lists *Cerebropollenites mesozoicus* (Couper 1958) Tage Nilsson 1958 in (Orbell 1973). Later in the text Morbey's distinguishes forms assignable to this epithet from *Tsugaepollenites mesozoicus/macroverrucosus*. Nevertheless, his listing of Orbell's misidentification (which is strictly speaking not a synonym, see Gravendyck et al. [2021] for semantic differences) in the synonymy might have inspired confusion amongst other workers who considered the *mesozoicus/pseudomassulae* to be synonymous (e.g. Achilles 1981; Brenner 1986; Holstein 2004).

When Mädler (1964) described the new species as *Camerosporites pseudomassulae*, he assigned it to the genus mainly because of an alleged trilete mark, which would distinguish the genus from *Rubinella* (Malyavk. 1949) R.Potonié 1960. In our re-investigation we found no trilete mark, but only something that appears to be an artefact in the preparation of Mädler's holotype. Our re-interpretation is supported by the absence of such a trilete mark in all other investigated specimens, including those that were investigated from both sides facilitated by a double-coverslip mount. An assignation to *Rubinella*, a fern spore with much smaller verrucate structure (Potonié 1960; Jansonius & Hills 1976, card 2450), can thus be excluded.

The fact that the discussion of this taxon is entwined with the discussion of the epithet *mesozoicus* (see previous section) is probably owed to its recombination with *Tsugaepollenites*, which is problematic, however. Despite the apparent consensus amongst workers to assign it to *Tsugaepollenites* (Figure 12D), this might be the result of it being the lesser evil in lieu of other options. The alleged 'fringe' of *pseudomassulae* is usually the characteristic on which the assignation to *Tsugaepollenites* is based on. Although the protrusions give the impression of a fringe, they lack the internal alveolate structure and an interpretation as a saccus must be rejected on the same terms as for the holotype for *Tsugaepollenites mesozoicus*. Further, the lack of heteropolarity and variation of ornamentation on either side of the palynomorph prevents justifiable assignation to the genus *Tsugaepollenites*. Lacking an aperture as in *Cerebropollenites* and *Sciadopityspollenites* also prevents assignation to either of these genera or any other taxon known to us. Further ultrastructural studies will be needed, to better understand the structure, morphology, and potential botanical affinity of the holotype for *Camerosporites pseudomassulae* and conspecific specimens.

It is noteworthy that the hyaline character of this taxon is somewhat reminiscent of the outer layer of *Perinopollenites*, but whether it is a pollen at all is not self-evident. Heunisch et al. (2010) pointed out that due to their similar hyaline colour and surface, together with the convolutions, taxa identified with the epithet *pseudomassulae* can resemble *Cymatiosphaera* (compare plate 9, figure 11 in Heunisch et al. [2010]). Since the compressed septa of *Cymatiosphaera* result in more angular appearance of the convolutions, it can be still differentiated however. Heunisch et al. (2010) also argue that the newly described *Tsugaepollenites schlimmii* (Achilles 1981) is in fact a specimen of

Cymatiosphaera. We concur with this view and note that this is a good example how the hyaline impression of specimens assigned to *pseudomassulae* appear relatively similar to the exine of various aquatic palynomorphs which are usually isopolar as well. Without any visible aperture, an unambiguous assignation to existing gymnosperm pollen taxa cannot be made, nor can a potential relationship with an algae group be excluded.

It is remarkable that the taxon is mostly documented from Central Europe (Figure 12D). Since some reports, however few, are from beyond Europe (e.g. Olsen & Sues 1986; Lachkar et al. 2000), this is probably not necessarily attesting for a limited geographical occurrence. Yet, not all references can be checked for their adequacy and since there has been some confusion concerning the distinction with *mesozoicus*, it will be interesting to see whether future workers, upon clarified distinction of the taxon can confirm the occurrence beyond Europe. Given that the taxon is most common in (and probably limited to) the Rhaetian, disappearing latest in the Early Jurassic (Herngreen et al. 2003; Cirilli 2010; Heunisch et al. 2010; Gravendyck et al. 2020b), an unambiguous naming is desirable for stratigraphic and palaeoecological purposes. Because the species cannot be clearly assigned to any existing genus that stands to reason, we propose erection of the new genus *Cryptopalynites* to accommodate this taxon later.

Revision: systematic palynotaxonomy

The earlier given literature review showed that problems distinguishing the different taxa associated with *Cerebropollenites thiergartii* did not only arise by the lack of distinguishing characteristics. Poor photographic documentation, and isolated focal planes likely fostered confusion. Conflicting and inconsistent recombinations in addition to vicarious use of names has further complicated the situation. Following our re-evaluation of holotype material and intraspecific and interspecific variation we now clarify typical features and distinguishing characteristics for the variation of forms in and around *Cerebropollenites thiergartii* in a series of nomenclatural novelties (see overview in Figure 14) that will be described in the following. Most importantly, we consider *Sciadopityspollenites* to be the senior synonym of *Cerebropollenites*. Following nomenclatural rules, *Sciadopityspollenites* has priority and must be adopted. Additionally, this is reconciling artificially separated use of names (in Russian and non-Russian works) as well as temporally separated occurrences (of pre- and post-Mid-Cretaceous records) of the genus.

Names to be limited to the holotypes

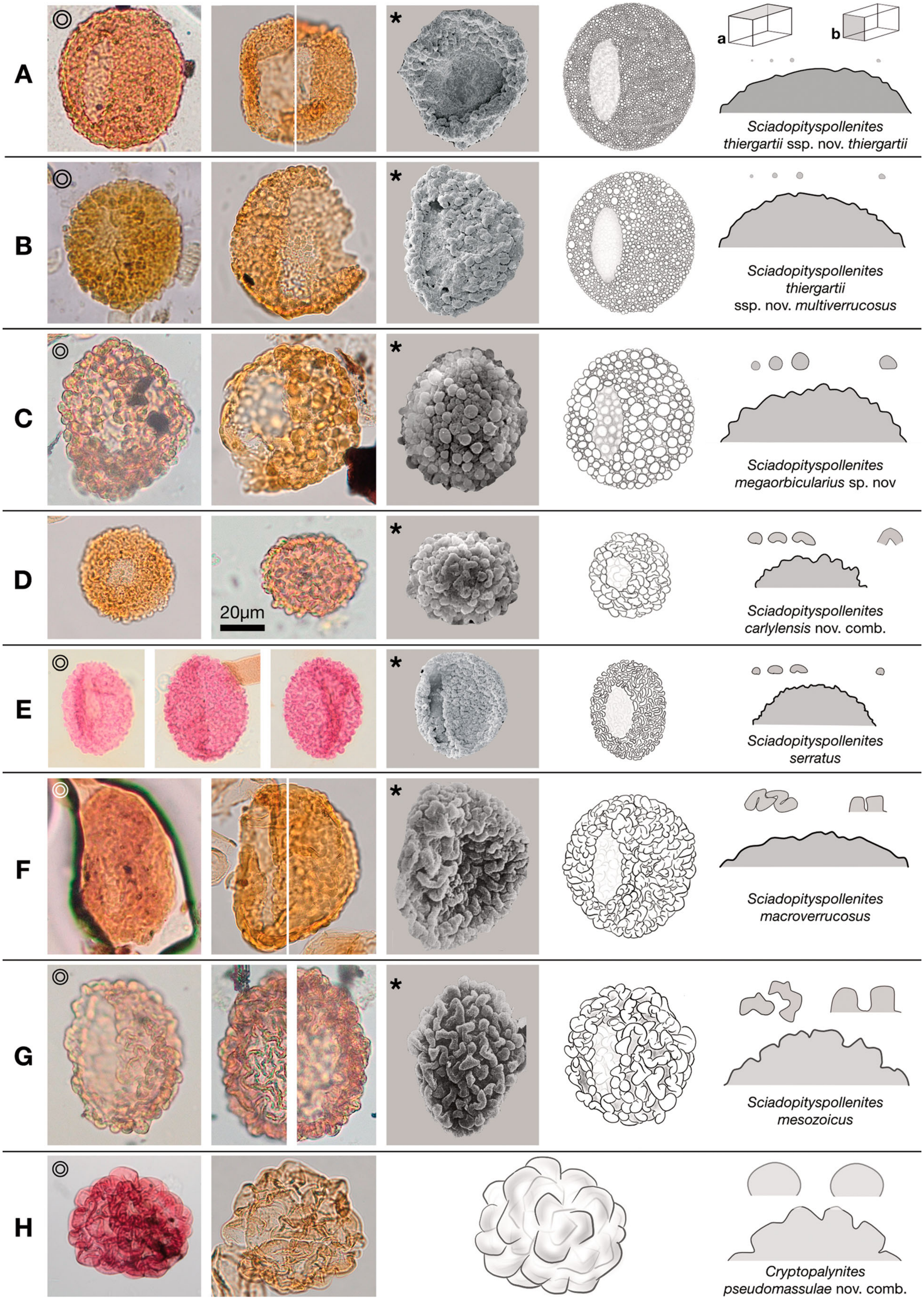
After re-evaluation of Thiergart's (1949) type material, we consider the taxa *Pollenites serratus* f. *helmstedtensis*, *Pollenites macroserratus* f. *keuperianus* and *Pollenites macroserratus* f. *doggerensis* to be conspecific with *Ricciisporites lundbladii* and *Polypodiisporites* cf. *polymicroforatus* and *Cerebropollenites thiergartii,* respectively. All of them are typical for the time interval from which they are described (e.g. Lindström 2016; Lindström et al. 2017b; Gravendyck et al. 2020b), but Thiergart's material has not been considered in the erection of the later names.

Although Thiergart's names are older, they were only established as subspecies and do not threaten the species names commonly used because names compete for priority only against names at the same rank (Art. 11.2 *Code*). Nevertheless, we discourage the use of these three Thiergart names, i.e. to limit the names to the respective holotypes (Figure 14). Note that this practice is commonly applied in the Lentin and Williams Index of Fossil Dinoflagellates (Fensome et al. 2019), and is applied here accordingly.

Categorising the intraspecific and interspecific variation

We propose to categorise the variation observed in *Cerebropollenites thiergartii* and associated taxa in six main categories (Figure 15A–F). Although not always clearly visible, specimens sorted in these six categories typically depict an aperture and some (at least minor) differentiation in ornamentation on either side of the specimens. Forms that have been previously assigned to the epithet *pseudomassulae* (Figure 15G), do not show these characteristics, and are thus assigned to a new genus *Cryptopalynites* gen. nov. described later.

We found the ornamentation to be the most distinctive feature to separate the different forms we observed. The relatively poor images (especially in older literature), and poor preservation of many specimens partially hampers clear characterisation of the ornamentation. This might have tempted earlier workers to rely on less subjective criteria such as size and shape. This has been especially complicated as printed photographs often depict only one focal plane. The precise nature of the ornamentation makes it necessary to study various focal planes to determine the size, shape, and density of the arrangement of sculptural elements. This has complicated


A
a
b
Sciadopityspollenites thiergartii ssp. nov. *thiergartii*
B
Sciadopityspollenites thiergartii ssp. nov. *multiverrucosus*
C
Sciadopityspollenites megaorbicularius sp. nov
D
20µm
Sciadopityspollenites carlylensis nov. comb.
E
Sciadopityspollenites serratus
F
Sciadopityspollenites macroverrucosus
G
Sciadopityspollenites mesozoicus
H
Cryptopalynites pseudomassulae nov. comb.

comparison of photographs and specimens in the past, which is probably one source of the rather inconsistent use of names (compare the (mis-)application list of names in Supplementary Material 2 and classification presented here).

Throughout the years several authors have provided SEM images of *Cerebropollenites* species (Guy-Ohlson 1978; Waksmundzka 1981; Guy-Ohlson & Malmquist 1985; Ilyina 1986; Batten & Dutta 1997; Shang & Zavada 2003; Hofmann et al. 2021), and although classified rather inconsistently as well, these forms correlate very well with the categorisation presented here (Figure 15). The SEM images provide the best view on the ornamentation, which is, with these images in mind, also easily discernible in brightfield view. Following our observations on the holotype specimens and the observed interspecific and intraspecific variation, we sort forms in categories A–F, according to increasing size of the sculptural elements, ornamentation type (from verrucate [Figure 15A–C] to rugulate [Figure 15D–F]) and according to the density of their arrangement. It should be considered that transitionary forms and unfavourable preservational states can, like for all classifications, make assignations to individual categories more difficult. Nevertheless, these groups presented here are considered the endmembers of morphological variation to aid more consistent use of the names.

Categories A and B (Figure 15A, B). — They encompass what we assign to the epithet *thiergartii*, which will be recombined as *Sciadopityspollenites thiergartii* comb. nov according to the discussion earlier. Schulz in his original description noted that verrucae can be up to 3 µm in size. Reviewing the variation of forms assignable to *thiergartii* (compare transition from smaller to bigger verrucae in Figure 6A–D), we found forms with smaller sculptural elements (more on the 1 µm size range, Figure 5K–W) and forms with bigger elements (more towards the 3 µm size range, Figure 6E–O). Lund (1977) and Heunisch et al. (2010) already noted, that *Chasmatosporites apertus* can be hard to distinguish from *Sciadopityspollenites thiergartii* comb. nov., which is especially true for the forms with smaller ornamentation. Iljina (1985) described the new *Sciadopityspollenites multiverrucosus* and although we believe them to be conspecific, her photograph depicts a specimen with relatively big verrucae. Many taxa have been distinguished for less, and if there is stratigraphic or palaeoecological desire to distinguish these forms, we propose to treat them as different subspecies especially as the chosen threshold for distinction is rather artificial and might not provide any stratigraphic merit as these forms usually occur together (which remains to be tested however). Those with smaller verrucae (Figure 15A), more similar to Schulz' specimen, are here described as *Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *thiergartii*, and those with bigger verrucae (Figure 15B), using Iljina's junior synonym, are described as *Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *multiverrucosus*.

Category C (Figure 15C). — This category contains specimens with exceptionally large verrucae. Different focal planes, as well as the SEM image illustrate, that these elements are no rugulate (and rather hollow looking) muri as occurring in the holotype for *Tsugaepollenites mesozoicus*, but solid and very rounded verrucae. Forms of this kind were relatively rare but were found in Couper's material (Figure 7U) and in the Höllviken material (Figure 7V) alike. It is not trivial to distinguish these from forms probably better assigned to *Sciadopityspollenites mesozoicus* (Figure 7T) or forms more similar to *Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *multiverrucosus* (Figure 7Q), especially when encountering rather smaller and compact specimen (Figure 7X). Nevertheless, these forms with particularly large and solid verrucae stand out and are here assigned to the new species *Sciadopityspollenites megaorbicularius* sp. nov.

Category D (Figure 15D). — This category contains forms that are considerably smaller, rounder and possess an ornamentation that represents a transition between verrucate (Figure 15A–C) to rugulate (Figure 15D–F). The verrucae are more elongate and more looped, through which they can appear as rounded verrucate elements in superficial bright field view, yet the SEM image, and more detailed focusing through different focal planes in bright field view give a more adequate impression of the looped or hook-shaped elements for specimens depicted in Figures 7R, 9F and 15D. These forms can be best addressed as

Figure 15. Overview of the newly defined categories (**A–H**) for observed intraspecific and interspecific variation. Each row (**A–H**) depicts images and idealised drawings and newly applied names for that category. The last column shows the outline of specimens from the respective category, and shows sculptural elements as seen from above (a) or as seen in a section view (b) as an analogue to similar overview for Cenozoic taxa found in Krutzsch (1962). Holotypes are indicated with a double circle (◎). SEM images reprinted from previous literature indicated with an asterisk (*) are not to scale. SEM images reprinted with permission from: **A, B, E** – Hofmann et al. (2021); **C** and **D** – Shang and Zavada (2003); **F** – Guy-Ohlson and Malmquist (1985); **G** – altered after Guy-Ohlson (1989).

Sciadopityspollenites carlylensis comb. nov., although we find Pocock's descriptions, which is mainly based on size-differences, insufficient and will be emended later.

Categories E and F (Figure 15E, F). — These categories contain forms with rugulate ornamentation and are assigned to *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus* respectively based on their different size and density of muri. The forms assigned to *Sciadopityspollenites macroverrucosus* possess smaller rugulae, which are more densely packed (Figure 15E), creating a less corrugated outline. Forms assigned to *Sciadopityspollenites mesozoicus* (Figure 15F) possess the biggest rugulae of all forms studied here, and variation in Couper's slide and SEM images show, that the spaces in between the sculptural elements are relatively large. Although we acknowledge, that there are intermediate forms (especially when preserved poorly), it is noteworthy that the samples from Couper were dominated by *Sciadopityspollenites mesozoicus,* while samples from Höllviken were dominated by *Sciadopityspollenites macroverrucosus* with a considerable number of *Sciadopityspollenites thiergartii.* This might suggest stratigraphic and/or palaeoecological differences. Potential differences are particularly relevant, because Dybkjær (1991) described the *Cerebropollenites macroverrucosus* Zone (now better *Sciadopityspollenites macroverrucosus* Zone) for the Sinemurian to the Pliensbachian (Lower Jurassic). Because of inconsistent use of the two names this cannot be evaluated with existing datasets yet and it will be interesting to further investigate whether *Sciadopityspollenites macroverrucosus* is indeed the name giving constituent. Similarly, for the *Cerebropollenites* palynofloral province (i.e. now better called the *Sciadopityspollenites* province) described for the boreal region of the Early Cretaceous (Herngreen et al. 1996) it will be interesting to further investigate what the actual taxa are in this province and how their diversity patterns relate to the *Sciadopityspollenites macroverrucosus* Zone. It will depend on future studies to disentangle potential stratigraphic or regional differences between these two forms, or lack thereof, to better evaluate their respective temporal and geographic distribution and stratigraphic value. Consistent taxonomic classification will be key to that.

Classification key

The earlier given distinctions can be summarised in the following classification key. Note that this key is not conclusive, but only intends to help distinguish the taxa discussed in this article.

1a. Isopolar palynomorph with very large (> 6 µm high and wide), hyaline protrusions covering the entire grain on either side. Without visible germinal area. .... *Cryptopalynites* gen. nov.

1b. Heteropolar palynomorphs with small verrucae or rugulae (max. 6 µm high) that can protrude equatorially, possibly creating the impression of a fringe. 2

2a. Monosaccate Pollen. Saccus appears as a wide to very narrow fringe of hollow, vesiculate equatorial protrusions that can or may not be radially folded. Pollen heteropolar, with larger sculptural elements (verrucae and or rugulae) on one side and smaller sculptural elements on the other side, which is usually more depressed in a dehydrated state and takes up more than half of one side of the pollen grain. .... *Tsugaepollenites* (consult relevant literature)

2b. Asaccate pollen. The sculptural elements can however give the impression of an equatorial fringe, especially when sculptural elements are large (< 2–3 µm). Ornamentation can vary from verrucae to more or less rugulate muri. Sulcus round to oval, non-ornamented, taking up less than half of the area on one side of the grain, often only partially shining through as a more hyaline area when changing the focal plane. *Sciadopityspollenites* 3

3a. Pollen ornamented with verrucae....................4

3b. Pollen ornamented with rugulae or elongate muri (focus on the corpus) that can appear as large (< 2–3 µm) verrucae at the equator. 8

4a. Verrucae very small and not elongate. Verrucae less than 2 µm in in size. .... *Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *thiergartii*

4b. Verrucae bigger than 2 µm in in size, that can but may not be elongate. 5

5a. Verrucae evenly rounded..............................6

5b. Verrucae not evenly rounded, with slightly uneven surface and shape that can be partially elongate..7

6a. Spherical verrucae up to 4 µm in diameter. .. .... *Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *multiverrucosus*

6b. Spherical verrucae bigger than 4 µm in diameter. .... *Sciadopityspollenites megaorbicularius* sp. nov.

7a. Verrucae more or less rounded, sometimes a bit elongate, rugulate or appearing dumbbell shaped. Surface of these verrucae rounded to angular; never looped. Pollen subcircular to spindle-shaped. ....*Sciadopityspollenites serratus*

7b. Verrucae a bit elongated into rugulae but not stretched out lengthwise, rather looped and thereby appearing rounded. Pollen circular to sub-circular. ....*Sciadopityspollenites carlylensis* emend.

8a. Pollen outline weakly corrugated (Figure 14E). Dense arrangement of the sculptural elements (most similar to the densely packed gyri of a brain); little empty space in between the sculptural elements maximum ¼ of the width of the rugulate muri. ....*Sciadopityspollenites macroverrucosus* emend.

8b. Pollen outline strongly corrugated (Figure 14F). Looser arrangement of the sculptural elements (more similar to the windings of a walnut embryo); larger spaces in between the sculptural elements *c.* $^1/_2$–$^1/_3$ of the width of the rugulate muri. .... *Sciadopityspollenites mesozoicus* emend.

Revised descriptions

Genus **Sciadopityspollenites** *(Raatz 1937) R.Potonié 1958 emend. Gravendyck*

Type. — *Sporites serratus* R.Potonié et Venitz 1934, Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine, vol. 5, pp. 1–54, p. 15, plate 1, figure 6, specimen in sample VII 17 (lost).

Lectotype. — *Sciadopitys-pollenites serratus*, Marga 117a, material from Thiergart (1938), EF: U38/3, refigured and designated here (Figures 2F, 7D).

Synonyms. —
= *Cerebropollenites* Tage Nilsson 1958 in Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund, 53: 72.

Emended description. — Asaccate pollen with a (sub)-circular, oval to spindle-shaped outline. Circular to oval sulcus not always recognisable, when (partly) covered by secondary folds or due to the position of the grain. The exine is ornamented with small verrucae or rugulae, which protrude over the equator which can give it the impression of a fringe. The sculptural elements are varying in shape, size and density depending on the species. The sculptural elements are relatively homogeneous around the pollen grain and cover the whole exine except for the area of germination.

Emended diagnosis. — The genus *Tsugaepollenites* is distinguished by a monosaccus, which appears as an equatorial velum. Although the ornamentation in the present genus can give a misleading impression of a vesiculate saccus, this should be identified as the protruding ornamentation through changing of the focal plane. Apart from that *Tsugaepollenites* is distinguished by differences in size of ornamentation on the proximal and distal face. The genus *Cryptopalynites* gen. nov. is distinguished by much larger, more hyaline protrusions and lack of clearly identifiable germinal area. The genus *Ricciisporites* can appear similar based on ornamentation, but the verrucae in *Ricciisporites* are mostly very large, often best described as tubercles. On top of that this genus is commonly occurring as tetrads whereas *Sciadopityspollenites* is shed as monads.

Stratigraphic range. — Mesozoic (maybe Upper Triassic, surely Jurassic) to Cenozoic (Pliocene).

Botanical affinity. — There are to date no known *in situ* finds in microsporangia. Bose (1955) documented some possible male cone scales with *Sciadopitys*-like pollen complying with the genus diagnosis of *Sciadopityspollenites*, but he noted that the shales in which they were found were very full of this type of pollen, the grains could have thus attached themselves to the scales in the process of maceration. However, one can also argue that concentration of this pollen was so high, exactly because they could come from the male cone scales with which they were found together.

Later, Manum (1987) described *Sciadopitys*-like leaves from the Upper Jurassic. Similar finds associated with a palynoflora containing, amongst others, abundant '*Cerebropollenites macroverrucosus*' and '*Cerebropollenites thiergartii*', were also recorded from the Middle and Upper Jurassic from the Svalbard archipelago (Bose & Manum 1990; Manum et al. 1991). However, these fossils were recombined as *Oswaldheeria* and assigned to a different and new family (Miroviaceae) by the authors themselves (Bose & Manum 1990; Manum et al. 1991). Distinction of this genus from the Sciadopityaceae by erecting a new family was further supported and emphasised by later anatomical studies which drew comparisons to other groups (e.g. ginkgophytes and podocarps) based on the difference in vasculature and absence of brachyblasts in *Oswaldheeria* (Gordenko 2007; Taylor et al. 2009). To date the relationship of the Miroviaceae to the Sciadopityaceae is unresolved.

Macrofossils, including reproductive structures, assignable to Sciadopityaceae (e.g. *Sciadopityophyllum*, *Sciadopityostriobus*, *Sciadopityoides*) are generally known from the Upper Cretaceous onwards (Christophel 1973; Sveshnikova 1981; Ohsawa et al. 1991; Saiki 1992; Taylor et al. 2009). Due to the unique wood anatomy of Sciadopityaceae (Ohsawa 1994), wood of the *Protosciadopityoxylon*-type from the Middle Jurassic can be linked to the family and suggests much older occurrences (Jiang et al. 2012, 2019). Given the hypothetical relative age of the family of *c.* 225–200 My based on molecular clock data (Crisp & Cook 2011), findings of this type of wood and pollen of Sciadopityaceaen affinity in the Jurassic appear plausible.

Despite the lack of certain *in situ* finds that link *Sciadopityspollenites*, the circumstantial evidence, together with the overall compliant morphology, typical supratectal micro-echinate ornamentation and ultrastructure of fossil *Sciadopityspollenites* with extant *Sciadopitys* pollen, further supports affiliation with the Sciadopityaceae. Although many authors have favoured a potential affinity with extant *Tsuga* (Couper 1958; Nilsson 1958), this is not supported when comparing surface and ultrastructural characteristics (Ho & Sziklai 1973; Grímsson & Zetter 2011; Hofmann et al. 2021).

Through the basionym *Tsugaepollenites mesozoicus* Couper 1958, the genera *Cerebropollenites* (= *Sciadopityspollenites*) have been historically linked to *Tsuga*, but these studies only considered the suggested similarities with *Tsuga* and completely omitted potential association with *Sciadopitys* (compare Couper 1958; Nilsson 1958; Batten & Dutta 1997; Shang & Zavada 2003). However, other studies based on SEM and transmission electron microscopy (TEM) for both taxa corroborate early assumptions based on morphology visible in light microscopic studies and that the name *Sciadopityspollenites* rightly suggest an affiliation with Sciadopityaceae (Raatz 1937; Kirchheimer 1938; Thiergart 1938; Zauer & Mchedlishvili 1966; Iljina 1968, 1985).

Remarks. — Forms formerly assigned to *Cerebropollenites* are considered congeneric and therefore, as a junior synonym, do not demand distinction. The original nomenclatural type is lost. A new type, i.e. a lectotype, could be chosen from Thiergart's material which was cited by Potonié (1958) and is interpreted as original material (see Material and methods section).

Sciadopityspollenites thiergartii *Eberh.Schulz 1967 comb. nov. et emend. Gravendyck*

Holotype/Basionym. — *Cerebropollenites thiergartii* Eberh.Schulz (1967). Marnitz-3–59/2 (EF:V39.1); Paläontologische Abhandlungen Abteilung B 2: 541–633; p. 603, plate 11, figures 7, 8 (here Figure 4Ha–Hd).

Synonyms. —
= *Pollenites macroserratus* f. *doggerensis* Thierg. 1949 in Palaeontographica Abteilung B, 89: 18, plate 2, figure 30.
= *Tsugaepollenites macroserratus* f. *doggerensis* (Thierg. 1949) Bóna 1969 in Annales Instituti Geologici Publici Hungarici 51: 695.
= *Sciadopitys multiverrucosus* Iljina 1968 in Comparative analysis of spore-pollen complexes of Jurassic deposits of the Southern Part of Western Siberia [in Russian]: 42, plate 5, figures 1, 2.
= *Sciadopityspollenites multiverrucosus* (Sachanova et Iljina 1968) Iljina 1985 in Jurassic Palynology of Siberia [in Russian]: 97, plate 9, figures 1, 2.

Emended description. — Asaccate pollen with a subcircular to oval outline. Size range variable from smaller (usually more circular) grains of 40 µm to grains larger usually less rounded grains of up to 80 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to two-thirds the length of the pollen and is visible as a thinning of the pollen grain. The exine is 1–(2) µm thick and covered with many densely arranged verrucae. The size of the verrucae measures 1–4 µm on average in width and height. Due to the protrusion of the verrucae at the equator the specimens show a finely serrated outline. (Figure 15A, B).

Emended diagnosis. — From all *Sciadopityspollenites* species the one with the smallest sculptural elements (compare overview for Cenozoic taxa in Krutzsch [1971]). *Sciadopityspollenites megaorbicularius* sp. nov. has also verrucae but much larger in size (> 3 µm). *Sciadopityspollenites carlylensis* comb. nov. has more elongate sculptural elements. *Sciadopityspollenites mesozoicus* and *Sciadopityspollenites macroverrucosus* are distinguished by muri instead of verrucae.

Stratigraphic range. — Base of the Jurassic to upper Lower Cretaceous.

Remarks. — We have observed two kinds of specimens that can be differentiated by the size of their verrucae. Since both are included in the size range originally given by Schulz and because there is (currently) no stratigraphic need to divide them on species level, the two forms are divided only at infraspecific rank. Using the two subspecies separately might show by application in the future, whether there is stratigraphic and/or ecological difference or not. Since the type for *Sciadopitys multiverrucosus* is rather ambiguous we also designate an epitype to clarify application of the name.

Sciadopityspollenites thiergartii *Eberh.Schulz 1967 ssp. nov.* **thiergartii** *Gravendyck*

Holotype. — *Cerebropollenites thiergartii* Eberh.Schulz (1967) in Paläontologische Abhandlungen Abteilung B 2: 541–633; p. 603, plate 11, figures 7, 8 (here Figure 4Ha–Hd); Marnitz-3–59/2 (EF:V39/1) stored at BGR-S.

Paratypes. — (1) Marnitz-3, slide 59/2, specimen at EF:N46/1 stored at BGR-S (Figure 5M); (2) Marnitz-3, slide 59/2, specimen at EF:E44/4 stored at BGR-S (Figure 5L) designated here.

Description. — Forms with verrucae in the lower size range; verrucae around 1.5 µm, maximum up to 2 µm in height and width (Figure 15A).

Derivatio nominis. — Automatically created autonym according to Art. 26.3 (*Code*).

Sciadopityspollenites thiergartii *Eberh.Schulz 1967 ssp. nov.* **multiverrucosus** *stat. nov. Gravendyck*

Holotype. — *Sciadopitys multiverrucosus* Iljina 1968 in Comparative analysis of spore-pollen complexes of Jurassic deposits of the Southern Part of Western Siberia [in Russian]: 42, plate 5, figures 1, 2 (here Figure 4Na–Nc); slide 723/23/II stored at KUZ.

Epitype. — Höllviken-2 1316.5 specimen at EF:M47/2 stored at SGU (Figure 6J).

Description. — Forms with verrucae in the bigger size range; verrucae around < 2 µm, maximum up to 4 µm in height and width (Figure 15B).

Sciadopityspollenites megaorbicularius *sp. nov. Gravendyck*

Holotype. — slide C73.2 from Couper (1958) specimen at EF:C48/3 stored at CGE, Figure 7U.

Paratype. — Höllviken-2 1316.5 specimen at EF: L35/2 stored at SGU, Figure 7V.

Description. — Asaccate pollen with a subcircular to oval outline. Size range variable from smaller (usually more circular) grains of 40 µm to grains larger usually less rounded grains of up to 70 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to two-thirds the length of the pollen and is visible as a thinning of the pollen grain. The exine is 1–2 µm thick and covered with many large and densely arranged verrucae. The size of the verrucae measures > 4 µm in width and height. Due to the protrusion of the verrucae at the equator the specimens show a corrugated outline. The verrucae are solid, not hollow or hyaline (Figure 15C).

Comparison. — Differs from *Sciadopityspollenites thiergartii* by having much larger verrucae. *Sciadopityspollenites carlylensis*, *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus* have elongate sculptural elements or rugulate ornamentation instead of verrucae. On top of that the sculptural elements of the new species are more solid and less hyaline than protrusions in *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus*.

Stratigraphic range. — Lower Jurassic, potential range beyond will demand further investigation.

Derivatio nominis. — The name is derived from the size and shape of the verrucae that are reminiscent of very large orbicules.

Sciadopityspollenites carlylensis *(S.A.J.Pocock 1970) comb. nov. et emend. Gravendyck*

Holotype/Basionym. — *Cerebropollenites carlylensis* S.A.J.Pocock 1970 in Palaeontographica Abteilung B, 130: 98, plate 21, figure 10.

Lectotype/neotype. — The holotype is assumed to be lost, therefore lectotypification or neotypification is necessary (Art. 9.3, 9.8 *Code*). The original material was not available for this study. Therefore, designation of a lectotype or neotype has to be postponed.

Synonyms. —
? = *Sciadopityspollenites osmundaeformis* (Zhang 1965) Wang et Li 1981 Acta Palaeontologica Sinica, 20: 533.

Emended description. — Asaccate pollen with a subcircular to oval outline. Grains usually rather sub-circular than oval, 25–50 µm in diameter. Subcircular to oval sulcus that measures approximately half the length of the pollen and is visible as a thinning of the pollen grain. The exine is 1–(2) µm thick and covered with slightly elongate sculptural elements that are no verrucae but rather muri that can be a bit looped (2–3 µm high). Due to the protrusion of the sculptural elements at the equator the specimens show a finely corrugated outline. (Figure 15D).

Emended Diagnosis. — Differs from *Sciadopityspollenites thiergartii* and *Sciadopityspollenites megaorbicularius* by not having verrucae, but rather more elongate sculptural elements. Differs from *Sciadopityspollenites* *macroverrucosus* and *Sciadopityspollenites mesozoicus* by not having equally windy and rugulate ornamentation (Figure 15).

Stratigraphic range. — Lower Jurassic – upper Lower Cretaceous. Probable occurrences in the Rhaetian (Upper Triassic) should be confirmed upon these new, clearer defined categories.

Remarks. — Tentative synonymisation of *Sciadopityspollenites osmundaeformis* is based upon expressed opinion in Zhichen et al. (2000) that we concur with upon re-investigation of the available photographs in Li (1984).

Sciadopityspollenites serratus *(R.Potonié et Venitz 1934) Raatz 1937 emend. Gravendyck*

Lost holotype. — *Sporites serratus* R.Potonié et Venitz 1934, p. 15, plate 1, figure 7, specimen in sample VII 17.

Neotype. — *Sciadopitys-pollenites serratus*, Marga 117a (material from Thiergart [1938]), EF: U38/3, refigured and designated here (Figure 2F).

Emended description. — Monad pollen. Spheroidal to oblate in shape, appearing elliptical to circular (polar view) or spindle-shaped or oval (equatorial view) depending on its orientation. Equatorial diameter between 28 and 53 µm (in light microscopy) | 26.450 µm (in SEM). Outline irregularly serrated/ corrugated, the protruding sculptural elements sometimes 1–1.5 µm in size. The elements are not homogeneous in size or shape, some are more rounded (verrucae), others more elongate (rugulate), between 1 and 2.5 µm wide and long. Exine between 1.5 and 2.8 µm thick. Nexine thinner than sexine. In SEM it becomes visible that the sculptural elements are faintly perforate and 'covered densely with evenly spaced supratectal echini, leptoma sulcus shaped and much less ornamented' (Figure 15E).

Emended diagnosis. — Most importantly, presence of verrucate to rugulate sculpture distinguishes it from *Sciadopityspollenites thiergartii* and *Sciadopityspollenites megaorbicularius* (which have no rugulae) and from *Sciadopityspollenites macroverrucosus* (which has no verrucae and more elongate rugulate). *Sciadopityspollenites mesozoicus* is distinguished by more loosely spaced ornamentation, even in forms that have more elongate sculpture. *Sciadopityspollenites carlylensis* looks fairly similar but is usually smaller and might represent an underdeveloped state of this or other *Sciadopityspollenites* taxa (Figure 15).

Stratigraphic range. — Common in the Paleogene and Neogene. Potential confusion with *mesozoicus* might have prevented reports from the Cretaceous (see Figure 11). Further study based on the new classification is needed to evaluate this.

Sciadopityspollenites macroverrucosus *(Thierg. 1949) Iljina 1985 emend. Gravendyck*

Holotype/Basionym. — *Pollenites macroverrucosus* Thierg. 1949 in Palaeontographica Abteilung B, 89: 17, plate 2, figure 19; Degow 1, 253–255 m, slide a, specimen at EF:P44/0, stored at BHUPM under inventory number MB.Pb.2019/0231 (Figure 3E).

Epitype, designated here. — Epitypes serve to disambiguate holotype material and while all other kind of types have to be specimens for names of fossils (Art. 8.5 *Code*), illustrations are eligible as epitypes (Art. 9.9 *Code*). Unfortunately, the ornamentation in the holotype is rather ambiguous, which is further complicated by the extremely poor preservation of the holotype. SEM images can best illustrate surface ornamentation and therefore, to disambiguate the precise nature of ornamentation that is harder to discern in the holotype, we designate an illustration from Guy-Ohlson and Malmquist (1985, plate 3, figure F) (reillustrated here in Figure 8H) as epitype, to illustrate the density of ornamental elements described in the revised circumscription.

Synonyms. —
≡ *Cerebropollenites macroverrucosus* (Thierg. 1949) Eberh.Schulz 1967 in Paläontologische Abhandlungen Abteilung B, 2: 603.
= *Tsugaepollenites macroverrucosus* (Thierg. 1949) Bóna 1969 in Annales Instituti Geologici Publici Hungarici, 51: 694–965.

Emended description. — Asaccate pollen with a subcircular to oval outline. Size range variable from 40 µm to larger grains of up to 80 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to two-thirds the length of the pollen and is visible as a thinning of the pollen grain. The exine is up to 1.5 µm thick, ornamentation rugulate. Dense arrangement of the sculptural elements (most similar to the densely packed gyri of a brain); little empty space in between the sculptural elements maximum ¼ of the width of the rugulate muri. The large sculptural elements (up to 4 µm high) protruding at the equator can give an impression of a fringe; the outline is corrugated (Figure 15F).

Emended diagnosis. — *Sciadopityspollenites thiergartii* and *Sciadopityspollenites megaorbicularius* are distinguished by verrucate ornamentation. *Sciadopityspollenites mesozoicus* has larger and more loosely arranged muri. *Sciadopityspollenites carlylensis* as less elongate and less winding sculptural elements (Figure 15).

Stratigraphic range. — Lower Jurassic–upper Lower Cretaceous. Probable occurrences in the Rhaetian (Upper Triassic) need further confirmation.

Remarks. — The distinction with *Sciadopityspollenites mesozoicus* is maintained and the two taxa regarded as morphological endmembers of intermediate forms. After preliminary observation of variation in the Contorta Beds in Bonenburg (Schobben et al. 2019; Gravendyck et al. 2020b; Figure 8L) and a specimen that could comply with the taxon from the Schattwald Beds in Kuhjoch (Figure 8K), *Sciadopityspollenites macroverrucosus* might already occur in the Rhaetian while *Sciadopityspollenites mesozoicus* joins the assemblages in the Jurassic. Whether or not there is such a stratigraphic and/or ecological difference needs further evaluation upon use of the newly defined categories.

Sciadopityspollenites mesozoicus *(Couper 1958) Waksm. 1981 emend. Gravendyck*

Holotype/Basionym. — *Tsugaepollenites mesozoicus* Couper 1958 in Palaeontographica Abteilung B 103: 155, plate 30, figure 8, Gristhorpe Bay (UK), slide C73.2, specimen at EF:Z53/2, stored at CGE under inventory number K5022 (Figure 3I).

Synonyms. —
≡ *Cerebropollenites mesozoicus* (Couper 1958) Tage Nilsson 1958 in Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 72, plate 6, figures 10–12.

Emended description. — Asaccate pollen with a subcircular to oval outline. Size range variable from smaller (usually more circular) grains of 40 µm to grains larger usually less rounded grains of up to 90 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to two-thirds the length of the pollen and is visible as a thinning of the pollen grain. The exine is up to 1 µm thick, ornamentation rugulate. Looser arrangement of the winding muri with larger spaces in between the sculptural elements *c.* $^1/_2$–$^1/_3$ of the width of the muri. The large sculptural elements (up to 6 µm high) protruding at the equator give an impression of a fringe; the outline is strongly corrugated (Figure 15G).

Emended diagnosis. — *Sciadopityspollenites thiergartii* and *Sciadopityspollenites megaorbicularius* are distinguished by verrucate ornamentation. *Sciadopityspollenites macroverrucosus* has less high and more densely arranged muri. *Sciadopityspollenites carlylensis* as less elongate and less winding sculptural elements (Figure 15).

Stratigraphic range. — Lower Jurassic–Upper Cretaceous, probably occurrences in the Rhaetian (Upper Triassic) should be confirmed upon these new, clearer defined categories.

Remarks. — See remark for *Sciadopityspollenites macroverrucosus*.

Cryptopalynites *gen. nov. Gravendyck*

Type. — *Camerosporites pseudomassulae* Mädler 1964 in Fortschritte in der Geologie von Rheinland und Westfalen 12: 169–200, p. 183, plate 2, figure 17, Achim-2, Blatt Hornburg 3929 (Germany), slide M116 mesh 1, cell E10 (Figure 3K).

Description. — Palynomorphs consisting entirely of an aggregation of large hyaline protrusions. A distinct corpus is not visible except for the space deliminated by the protrusions. No differentiation on either side of the palynomorph, protrusions equal in size all around, no germinal area or other features visible. Protrusions rounded, compression can make them appear more angular, but never with clear straight septa.

Comparison. — *Tsugaepollenites* is distinguished by a saccus and heteropolarity of the grain with different types of ornamentation on one grain. *Sciadopityspollenites* is distinguished by a sulcus and by different and more solid ornamentation.

Botanical affinity. — Unknown, given the earlier expressed doubts concerning the isopolar appearance, it is not even clear whether this is in fact a pollen at all.

Remarks. — The new genus is erected as a monotypic genus, to prevent assignation of the only species to other genera (with features that the present species does not show, e.g. saccus, heteropolarity) simply because of lack of other options (rather than compliance with other genus circumscriptions).

Derivatio nominis. — The genus name is alluding to the cryptic botanical affinity of this taxon and history of accommodating the so far monotypic species in various different, but unfitting genera.

Cryptopalynites pseudomassulae *(Mädler 1964) comb. nov. et emend. Gravendyck*

Holotype/basionym. — *Camerosporites pseudomassulae* Mädler 1964 in Fortschritte in der Geologie von Rheinland und Westfalen 12: 169–200, p. 183, plate 2, figure 17, Achim-2, Blatt Hornburg 3929 (Germany), slide M116 mesh 1, cell E10 (Figure 3K).

Synonyms. —
≡ *Tsugaepollenites? pseudomassulae* Morbey 1975 in Palaeontographica Abteilung B, 152: 30–31, plate 10, figures 9–12.

≡ 'Cerebropollenites pseudomassulae' Taugourdeau-Lantz et al. 1984 in Documents du Bureau des Recherches Géologiques et Minieres 81: 70, plate 3, figure 2; the name was not properly recombined, because it is missing the necessary full and direct reference to the basionym (Art. 41.5 *Code*).

Emended description. — (Sub)circular palynomorph with large, hyaline and hollow protrusions. Specimen diameter ranges (35)–55–(65) µm. No differentiation in ornamentation on either side of the grain. Protrusions semicircular, circa twice as broad as high (5–10 µm high and 10–18 µm wide), usually rounded or slightly folded, other protrusions are shining through the other due to the very hyaline and otherwise laevigate exine (Figure 15H).

Emended diagnosis. — *Sciadopityspollenites mesozoicus* (and even more so *Sciadopityspollenites macroverrucosus*) can be distinguished by the smaller, more winding and less hyaline sculptural elements. *Sciadopityspollenites megaorbicularius* sp. nov. is likewise distinguished by a sulcus and more solid, i.e. not so hyaline, and much smaller verrucae (Figure 15). The taxon can resemble *Cymatiosphaera* (compare plate 9 figure 11 in Heunisch et al. [2010]). The compressed septa of *Cymatiosphaera* result in more angular appearance of the convolutions, that differentiate it from *Cryptopalynites pseudomassulae*.

Stratigraphic range. — While the previously taxa are typical Jurassic elements, *Cryptopalynites pseudomassulae* is a typical Rhaetian (Upper Triassic) element. It is especially abundant prior to and after the transition from the Contorta to the Triletes Beds (i.e. the transition to the extinction interval) in Bonenburg (Gravendyck et al. 2020b) and in the Contorta Beds of Mariental (Heunisch et al. 2010). An acme of this taxon is reported for SAB2 zone in St Audrey's Bay (Bonis et al. 2010). It is a typical element in the Kössen Formation and Schattwald Beds (palynomorph zones H1–H2 zones of the Hochalplgraben and Tiefengraben sections, K1–K2 Kuhjoch section) in the Eiberg basin (Bonis et al. 2009). In St Audrey's Bay it is possibly ranging until the Hettangian (Lower Jurassic), but in much reduced numbers. Herngreen et al. (2003) already used this taxon as a stratigraphic marker for the Rhaetian, reporting the last occurrences at the top of the Triassic. It is not clear at this point whether sporadic Jurassic occurrences reported across basins (Bonis et al. 2009, 2010; Gravendyck et al. 2020b) might simply be reworked (van de Schootbrugge et al. 2020; Gravendyck et al. 2020b).

A note on nomenclature

The taxonomic and nomenclatural analysis of the competing names has shown that despite the very widespread and more frequent use of *Cerebropollenites* the name *Sciadopityspollenites* has priority and must be adopted. Unfortunately, the name *Sciadopityspollenites* is so far only commonly used in studies of Russian material but hardly beyond. To resolve this situation two scenarios are possible: (1) to conserve the more widely used name *Cerebropollenites* against the name that has priority, i.e. *Sciadopityspollenites* or (2) the community can simply stop using *Cerebropollenites*. Either scenario would require change of habits of naming taxa. The first scenario would additionally require a time-consuming formal proposal of conservation. The question is whether a part of the Mesozoic community (scenario 2) or whether all Cenozoic workers would have to change (scenario 1).

With the nomenclatural novelties made earlier, we propose to follow scenario 2, i.e. abandoning the use of *Cerebropollenites* in favour of the universal use of *Sciadopityspollenites*. This practice will put the burden of change on workers that are usually familiar with the disjunct use of the two taxa and will leave those studying the Cenozoic (and unaware of the discussion) unconcerned. Although names do not necessarily reflect their true botanical affinity, our proposed practice reflects in this case not only the assumed botanical affinity of the taxon, but also emphasises the evolutionary continuity and diversification of the taxa in question.

Conclusion

In the past, the numerous recombinations of names with *Tsugaepollenites*, *Cerebropollenites* and *Sciadopityspollenites* caused inconsistent use and confusion around the marker fossil *Cerebropollenites thiergartii*. Even more so as a part of the community consistently uses recombinations with *Sciadopityspollenites* (except for that marker fossil), whereas the majority uses recombinations with *Cerebropollenites*. The tentative and sometimes doubted assignation of the epithet *pseudomassulae* to the genus *Tsugaepollenites* and the unclear boundaries between the epithets *mesozoicus* and *macroverrucosus* also made classification difficult.

The main objective of the present study was thus to clarify taxonomic and nomenclatural confusion (1) on a generic level between *Cerebropollenites* Tage Nilsson 1958, *Tsugaepollenites* (R.Potonié et Venitz 1934) R.Potonié 1958 and *Sciadopityspollenites* Raatz 1937 ex R.Potonié 1958 and (2) on the species level for taxa relevant for the Triassic–Jurassic transition especially in regard to *Cerebropollenites thiergartii*, *Cerebropollenites macroverrucosus/mesozoicus* and *Tsugaepollenites pseudomassulae.* We restudied the relevant holotype material to distinguish the genus and species defining characteristics and evaluated the interspecific and intraspecific variation in original and new material. Together with an analysis of name use over time and an extensive literature review, we identified sources of previous confusion and redefined species classification.

The lack of differentiation between *Cerebropollenites* and *Sciadopityspollenites* support previous synonymisation. The use of *Sciadopityspollenites* is not only taxonomically and nomenclaturally imperative because of priority, but also because it will unify previous disjunct use of *Cerebropollenites* for Mesozoic and *Sciadopityspollenites* for Cenozoic taxa or Mesozoic species in between Russian and non-Russian studies.

The clarification of distinctive characteristics led to the revision of existing taxa and the following nomenclatural novelties: *Sciadopityspollenites thiergartii* comb. nov. et emend.; *Sciadopityspollenites thiergartii* ssp. nov. *thiergartii*; *Sciadopityspollenites thiergartii* ssp. *multiverrucosus* stat nov.; *Sciadopityspollenites megaorbicularius* sp. nov.; *Sciadopityspollenites carlylensis* emend.; *Sciadopityspollenites serratus* emend.; *Sciadopityspollenites macroverrucosus* emend.; *Sciadopityspollenites mesozoicus* emend.; *Cryptopalynites* gen. nov. and *Cryptopalynites pseudomassulae* comb. nov. et emend. Additionally, lectotypes were designated for *Sciadopityspollenites serratus* and *Tsugaepollenites igniculus*.

The taxonomical and nomenclatural clarifications presented here are the most extensive review of *Cerebropollenites/Sciadopityspollenites* to date. It also provides a new basis to better evaluate the stratigraphic value of *Cryptopalynites pseudomassulae* as a Rhaetian marker and to disentangle potential stratigraphic or regional differences between *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus*.

Most importantly the study provides clear differentiation of *Sciadopityspollenites thiergartii* comb. nov. et emend. from other species. Given the paucity of biostratigraphic markers for the base of the Jurassic, the presented clarification will be an important tool to resolve past confusion that potentially diminishes its stratigraphic value and to avoid future confusion. These clarifications are distinctive and should allow future workers to make full use of the stratigraphic potential of this important marker species.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Supplementary Material

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Specimens investigated

Earlier we provided multiple names and different recombinations of epithets that were erected (or erroneously used) in the literature. Supplementary Material 1 summarises all names referred to in this article and their authorities for easier reference.

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