THE CRETACEOUS NORMAPOLLES POLLEN GENUS *VANCAMPOPOLLENITES*: OCCURRENCE, FORM, AND FUNCTION

by D. J. BATTEN

ABSTRACT. The Late Cretaceous Normapolles genus *Vancampopollenites* Kedves and Pittau 1979 was erected to accommodate angiosperm pollen grains that have polar 'papillae' and 'secondary apertures'. Both of these features are, in fact, areas of exinal thinning. They have been considered to distinguish the genus from *Heidelbergipollis* Krutzsch in Góczán *et al.* 1967 although they are not always present. New descriptions and illustrations, and use of revised terminology, herein clarify the criteria for distinguishing the six published species of *Vancampopollenites*. Transmission electron microscopy of ultra-thin sections of three of these suggests that wall structure is not taxonomically significant within the genus and is comparable with that in other Normapolles. The pollen grains were probably dispersed by wind. The thinner, structurally modified parts of the wall may have had a harmomegathic function. Restriction of the genus to the Upper Cretaceous of Western Europe and differences in composition between pollen assemblages of similar age from northern and central Europe, Iberia, and eastern North America imply a range of vegetation-types and contrasting climates within the Normapolles Province.

THE taxonomy of Normapolles pollen grains is in a confused state. Many of the genera that have been erected are not clearly distinguishable from one another; some are little more than species. The criteria for their separation have become increasingly trivial in recent years with the result that yet more are being instituted and species are being used less for biostratigraphic purposes. Taxonomic descriptions of these angiosperm products are often based on very few specimens which are inadequately illustrated. Some rationalization of Normapolles systematics is essential if significant advances are to be made in using this group of very varied pollen grains both for age determinations of sedimentary sequences and for palaeoenvironmental interpretation. More complete recording of stratigraphic and geographic distributions is also necessary. With few exceptions, background data on the localities and sections from which many Normapolles have been described are sparse to non-existent.

Hughes would no doubt advocate use of his biorecord/genusbox method for handling Normapolles taxa (Hughes 1970 and elsewhere) as discussed in the biography and bibliography introducing this volume. I have recently argued, however, in favour of a traditional approach to palynomorph taxonomy in general, provided that the work is done with care (Batten, in press *a*). This does not, by any means, amount to a total rejection of Hughesian philosophy. Many of the criticisms raised in his papers are entirely valid and some of the suggestions for dealing with palynological data are very reasonable, but I am unable to accept his main proposals. This is because the 'old-fashioned' approach provides a measure of taxonomic and nomenclatural stability together with a common language which palynologists can speak no matter how imperfectly, and his methods do not. These latter now also include greater reliance on the scanning electron microscope (SEM) than is usual (see for example Hughes *et al.* 1979). I believe that the light microscope is likely to remain the basic tool of the palynologist for the foreseeable future. It is much cheaper and more convenient to use than the SEM, and often more helpful for analysing the morphology of palynomorphs (Batten, in press *a*).

It is true that some sculptural and structural details are not readily discernible optically, particularly in angiosperm pollen, but the appearance of palynomorphs in transmitted light should not be disregarded because vital characters may thus be omitted from consideration. This is clearly

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demonstrated herein. It is impossible to reliably identify *Vancampopollenites aradaensis*, *V. subporatus*, and *V. triangulus* using only scanning electron micrographs (cf. Pl. 8, figs. 1–3; Pl. 9, figs. 2–6). The bulk of the morphological information required to distinguish these species has been derived from optical examination. The SEM, and also thin sections examined under the transmission electron microscope (TEM), aid interpretation. It is not only more logical to begin any morphological study using a light microscope but also easier. Individual specimens can be picked from a residue and mounted on a stub for SEM examination subsequently without much difficulty. If palynomorphs are studied first under the SEM it is usually hard, and often impossible, to correlate precisely the micrographs obtained with specimens on a microscope slide.

In this paper the results of a study of all six species of the pollen genus *Vancampopollenites* Kedves and Pittau 1979 are presented. The grains were recovered from at least one and possibly two of the sections of Senonian (Upper Cretaceous) strata in Portugal from which the taxa were originally described (text-fig. 1), and from others besides. New descriptions with accompanying illustrations are provided and emphasis is placed on the criteria that can be used to distinguish the species. Observations on wall structure as seen in ultra-thin section under a TEM are included. Interpretation of morphology in terms of function is briefly considered, and both the stratigraphic and palaeoenvironmental significance of the distribution of the taxa are discussed.

MATERIAL

Unfortunately, much of the Portuguese Upper Cretaceous that is younger than Turonian is not only poorly exposed but also comprises sandy sequences and subordinate weathered, argillaceous units which do not contain palynomorphs. The samples that yielded *Vancampopollenites* are from seven outcrop sections and one borehole in the northern part of the Western Portuguese Basin (text-fig. 1); all are considered to be middle–late Senonian in age.

The largest number of samples from a single locality was collected from a quarry at Presa (near Ilhavo, text-fig. 1) which is currently being worked for the manufacture of bricks and tiles. The general age of the strata in the pit is Campanian–Maastrichtian (Berthou 1979), but the most productive interval is near the top of the section and may be Maastrichtian (see also Moron 1981). The outcrop at Vale is extremely limited; a possible Campanian age for the beds has been advocated by Moron (1981). The samples from the other localities, including the borehole, all yielded similar assemblages which again suggest Campanian–Maastrichtian deposition, although the possibility that some are slightly older (Santonian) cannot be ruled out entirely.

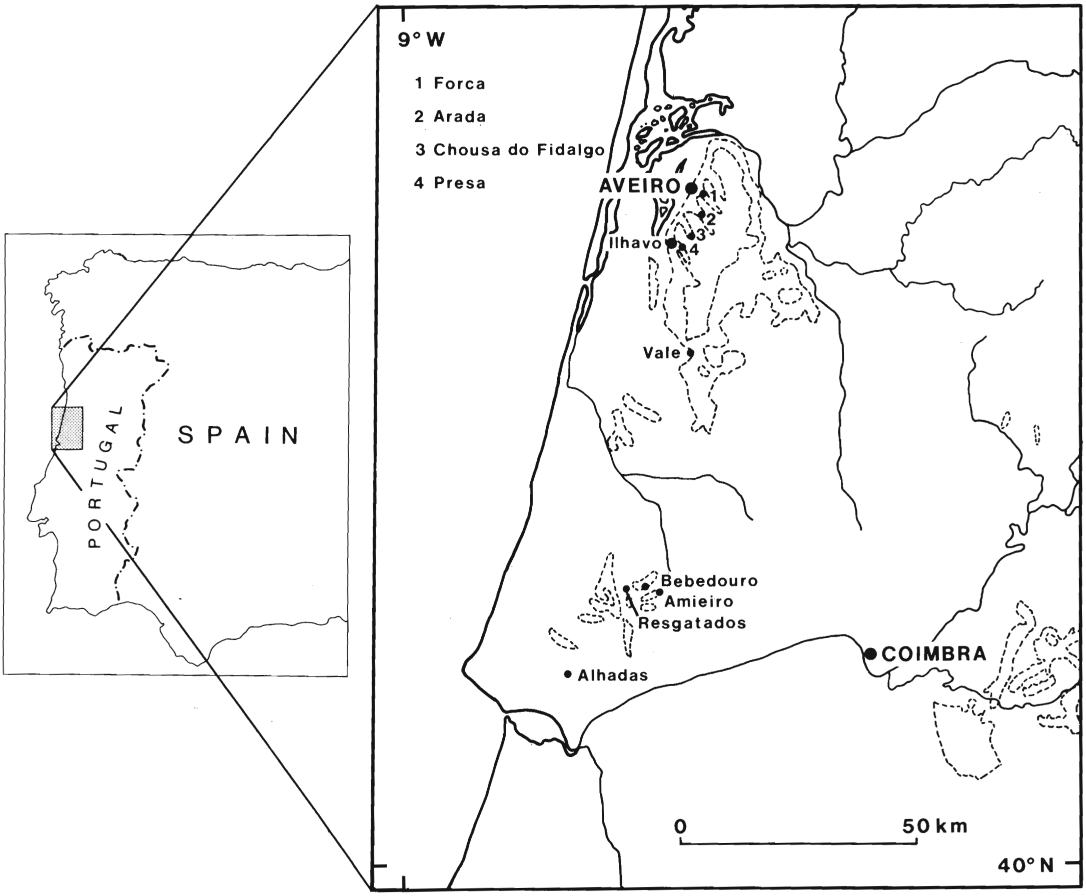
All rock samples and slides containing palynomorphs are stored in the palynological collection of the Geology Department, Aberdeen University.

METHODS

Concentrated HCl and 58–62% HF were used to digest the rock samples and extract the organic matter. The latter was subjected, where necessary, to brief ultrasonic vibration or oxidation, or to both, in order to remove unwanted detritus (for details of method, see Batten and Morrison 1983). Selected individual grains were mounted on developed, unexposed photographic film fixed to stubs with Araldite and coated with gold-palladium prior to being examined by scanning electron microscopy. Others were prepared for ultra-thin sectioning by initially immersing them in a saturated solution of Uranyl acetate for 30 min. followed by washing three or four times in distilled water, dehydration in Analar Acetone for 30 min., and soaking in a 1:1 mixture of EMix epoxy resin and Analar Acetone. They were then embedded in resin formulated to set to a medium hardness. The resin blocks were trimmed and thin sections cut using a Reichert Om U3 ultramicrotome. Selected sections were placed on Formvar-coated slot grids, examined under a Philips 400 electron microscope, and photographed.

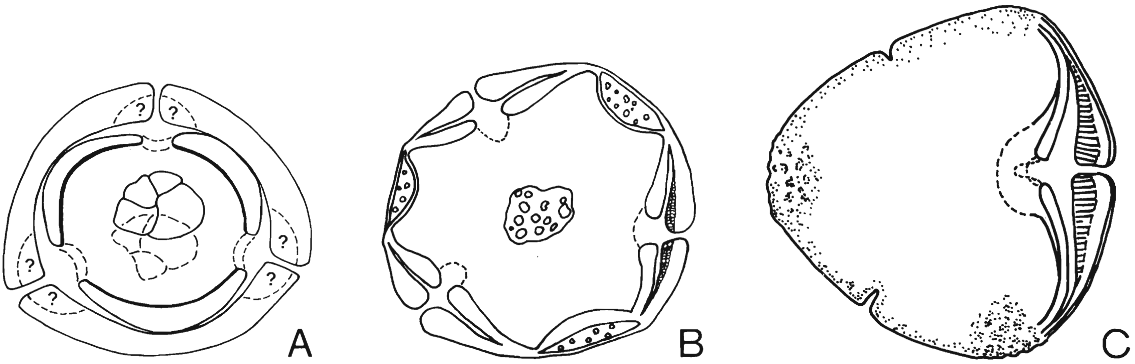
THE GENUS *VANCAMPOPOLLENITES*

Vancampopollenites was erected by Kedves and Pittau (1979) on the basis of pollen grains recovered from strata stated to be Santonian and/or Campanian in age exposed in the vicinity of Arada and



TEXT-FIG. 1. Location and map of the north of the Western Portuguese Basin. The area of Senonian rocks, delineated by dashed lines, is based on, and slightly modified from part of the 1:1000000 Carta Geológica de Portugal, published by Serviços Geológicos de Portugal in 1968. Place names mentioned in the text are included. Core material has come from a hole drilled in the Alhadas area. Localities 1–4, Vale, and the three places plotted to the north-east of Alhadas refer to surface exposures. Kedves and Pittau (1979) recovered species of *Vancampopollenites* from Arada, Aveiro, and Preza (Presa; no details given). The section I sampled at Forca in the vicinity of Aveiro failed to yield any specimens. The locality of Chousa do Fidalgo could be the same as that referred to as Arada (a near-by long, straggling village) by Kedves and Pittau.

Preza (Presa; text-fig. 1), Portugal. Although it is one of the more distinctive genera of the Normapolles, specimens referable to some of the species attributed to it display characters that are also found in *Heidelbergipollis* Krutzsch in Góczán *et al.* 1967 and, less commonly, in *Papillopollis* Pflug 1953. The latter, as currently defined, differs in that its apertures are radially disposed, and in *Heidelbergipollis* the sexine (outer wall layer) is not modified at the poles (text-fig. 2). *Papillopollis* also lacks equatorial or subequatorial inter-apertural thinnings and is well enough differentiated to be maintained as a separate genus but *Vancampopollenites* is sufficiently close to *Heidelbergipollis* for it to be tempting to consider the two synonymous. It is quite possible that the latter is merely a morphological variant of the more common *Vancampopollenites* type. Separation of the genera is maintained for the time being however, pending further investigation into their occurrence in northern Europe.



TEXT-FIG. 2. Diagrams of type species of the genera *Papillopollis*, *Vancampopollenites*, and *Heidelbergipollis*. A, *Papillopollis*, from *P. regulus* as originally described by Pflug (1953); the drawing is after fig. 45 in Góczán *et al.* (1967). B, *Vancampopollenites*, based on specimens of *V. lusitanus* Kedves and Pittau examined during the course of this study. C, *Heidelbergipollis*, from *H. tilioides* Krutzsch as interpreted by him in Góczán *et al.* (1967, fig. 29). All magnifications *c.* × 1250.

A, B, and the right-hand side of C show the grains as they appear in median focus: outer wall layer (sexine) with ectannulus around external opening and differentiated outer and inner laminae; inner wall layer (nexine) separated from it within germinal to form vestibulum; dashed line(s) adjacent to endopores indicate optical effects around them (delimiting atria). In A, sexine of polar areas is fissured, in B it comprises scattered granules. The equatorial inter-apertural regions are similarly structured in B and are shown invaginated. Those in C are reported to be sculptured with granules and verrucae.

Kedves and Pittau's (1979) descriptions of five of the six species they attributed to *Vancampopollenites* were based solely on observations made under a light microscope. Only the type species, *V. lusitanus*, was also examined using an SEM. This is the most common and readily identifiable form of the genus in the Portuguese Senonian, but distinction from *V. endotriangulus* is not always clear and *V. minor* appears to encompass merely immature or aberrant forms of this and perhaps other species. Difficulties experienced in trying to identify specimens to species level led to the formulation of the

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EXPLANATION OF PLATE 4

All magnifications × 1000.

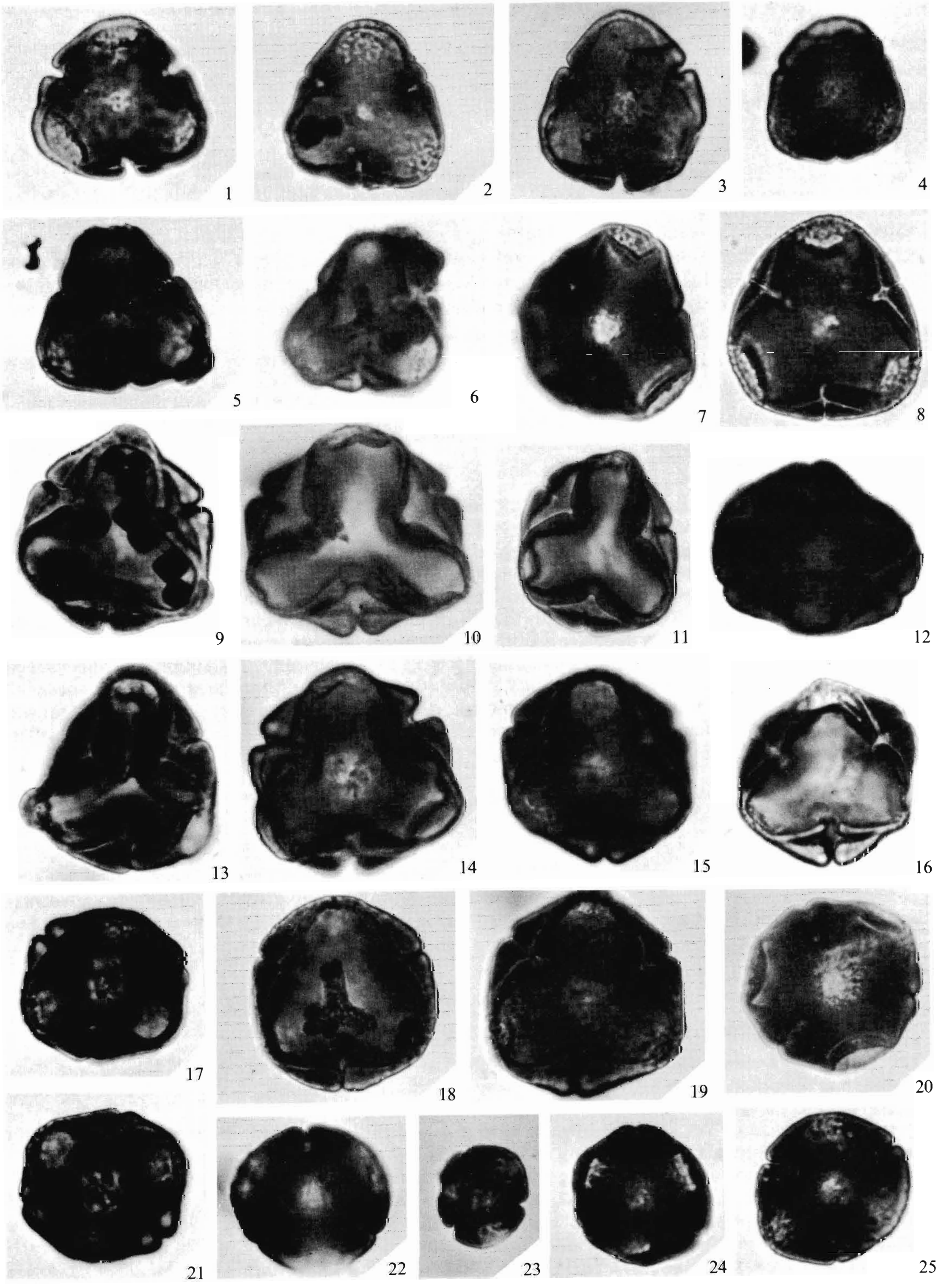
Figs. 1–8. *Vancampopollenites aradaensis*. 1 and 2, typical forms showing small patches of exinal thinning at poles and prominent subequatorial inter-apertural (radial) regions of sexinal reduction to granules, sample DJB79/113, slide preparation MCP437.2; 1, England Finder reference L25/3; 2, Q26/0. 3, similar to some specimens of *V. triangulus*, 79/113, 437.3, R50/0. 4, diminutive specimen only questionably referred to *V. aradaensis*; it is morphologically close to both *V. minor* and *V. subporatus*, 79/114, 438.2, O18/3. 5 and 6, showing Y-shaped (triradiate) finely granular structure over poles; 5, 79/113, 437.3, T33/3; 6, 79/113, 437.4, N45/0. 7 and 8, atypical forms; 7, 79/113, 437.3, J40/3; 8, 79/118, 425.4, O42/0.

Figs. 9–16. *V. endotriangulus*. 9–12, 14, typical forms showing prominent vestibula within germinals; 9, 82/63, 2376.4, R22/3; 10, 79/113, 437.2, F15/2; 11, 79/113, 437.3, R23/1; 12, 79/113, 437.2, S27/3; 14, 79/113, 437.3, S32/1. 13, more robust than usual, 82/63, 2376.4, X31/2. 15, vestibulum relatively narrow, granulate sculpture (cf. *V.* sp., figs. 17–19, 21), 82/63, 2376.4, L24/1. 16, damaged specimen, morphologically close to *V. lusitanus*, 79/117, 439.4, F33/1.

Figs. 17–19, 21. *V.* sp. Specimens whose characters differ from those of the six published species. 17, 79/113, 437.3, O35/2; 2; 18, with a granular triradiate structure over one pole, 79/118, 425.4, V36/0; 19, 82/62, 2375.3, F55/0; 21, 79/113, 437.3, O35/2.

Figs. 20, 22–25. *V. minor*. 20, has the appearance of an immature *V. lusitanus*, 79/113, 437.2, X23/0. 22–25, typical forms with two wall-layers barely distinguishable in germinals or not observed. 22, 82/64, 2377.2, X43/0; 23, 79/114, 438.2, R24/0; 24, 82/64, 2377.2, M49/0; 25, 82/63, 2376.4, T35/4.

PLATE 4



BATTEN, *Vancampopollenites*

new descriptions below, the preparation of more illustrations, and a re-examination of the criteria used for their separation.

SYSTEMATIC PALAEONTOLOGY

Genus VANCAMPOPOLLENITES Kedves and Pittau 1979

Revised diagnosis. Breviaxial pollen grain with three short, annulate, apertural furrows in sexine (outer wall) situated interradially at equator and orientated parallel to polar axis. Each germinal (germination structure) usually with an endopore within nexine (inner wall) which may also be bordered by an annulus. Sexine and nexine commonly separated within germinal forming a vestibulum. Polar and equatorial or subequatorial inter-apertural regions generally with sexine reduced to granules and sometimes absent altogether.

In common with the genus, the following six species were also originally described by Kedves and Pittau (1979).

Vancampopollenites aradaensis

Plate 4, figs. 1–8; Plate 8, figs. 1–3

Description. Breviaxial pollen grain, triangular with straight to convex sides and rounded angles in polar view. Maximum diameter 24 (28) 35μm (30 specimens). Outer surface more or less smooth to scabrate or undulating to finely granulate. Exoapertures comprise 3 short, equatorially-situated furrows orientated parallel to polar axis of grain. Sexine bordering these openings is 1·5–4·0 μm thick, forming an ectannulus, becoming thinner (to 1 μm or less) towards angles of grain where it merges with nexine; thickness of this single layer, 1·5–3·5 μm. Poles may lack structural modification of exine but usually there is a thinner patch of circular, triangular, or irregular shape between 2·0–5·5 μm in maximum diameter within which sexine is reduced to granules. Usually prominent are subequatorial inter-apertural thin areas of varying extent (3·5–13·0 μm long, 3–8 μm broad) where sexine is similarly reduced or absent altogether. Rarely a Y-shaped (triradiate), finely granular structure may occur close to or over one of the poles. Nexine is 0·5–1·0 μm thick, may be slightly more than this (up to 2·5 μm) within germinals forming an endannulus around endopore of 1–2 μm diameter. Little or no apertural separation of nexine from sexine; maximum width of vestibulum, 0·5 μm.

Vancampopollenites endotriangulus

Plate 4, figs. 9–16; Plate 8, figs. 4 and 5

Description. Breviaxial pollen grain, subcircular to hexagonal with rounded angles in polar view. Maximum diameter 26 (32) 36 μm (30 specimens). Outer surface scabrate to finely granular, rarely weakly verrucate. Exoapertures comprise 3 short, equatorially-situated furrows orientated parallel to polar axis of grain. Sexine

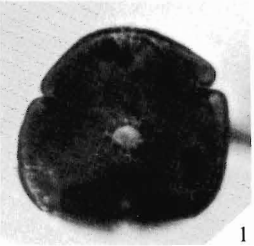
EXPLANATION OF PLATE 5

All magnifications × 1000.

Figs. 1 and 2. *Vancampopollenites minor*. 1, possibly an imperfect *V. aradaensis* or *V. lusitanus*, sample DJB82/63, slide preparation MCP2376.3, England Finder reference K18/4. 2, morphologically close to *V. lusitanus*, 79/113, 437.4, N32/3.

Figs. 3–19. *V. lusitanus*. 3–8, showing range of form in specimens lacking triradiate structure over one of the poles. 3, typical specimen, polar thinning with sexinal granules and equatorial invaginations, 79/113, 437.3, S28/3. 4, inter-apertural thin areas with granules clearly delineated, diminutive immature specimen attached, 79/113, 437.2, S37/2; 5, 79/113, 437.3, P25/0; 6, 79/113, 437.2, S27/0; 7, 79/122, 465.2, N41/0; 8, 79/122, 465.2, N41/0. 9–19, showing variable development of triradiate structure over one pole; 9, incomplete only, both polar thin areas clearly outlined; 13, incomplete; 18 and 19, the whole of one surface is affected; 9, 79/113, 437.3, L30/4; 10, 82/64, 2377.3, U27/2; 11, 79/113, 437.4, Q42/3; 12, 79/113, 437.4, Q31/1; 13, 79/113, 437.2, O20/0; 14, 79/113, 437.2, L35/0; 15, 79/113, 437.2, J41/4; 16, 82/83, 2376.4, N39/1; 17, 79/113, 437.4, H17/3; 18 and 19, 79/113, 437.3, W32/0.

PLATE 5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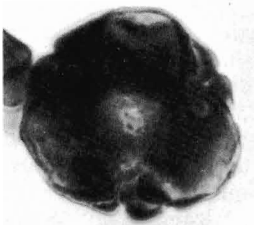
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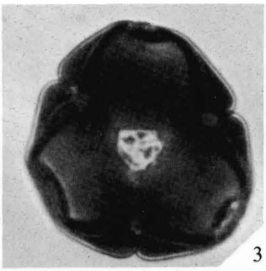
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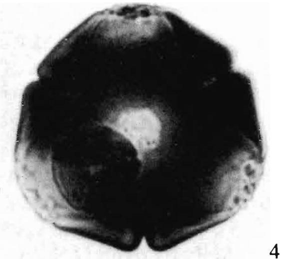
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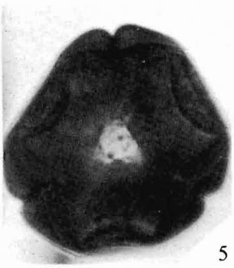
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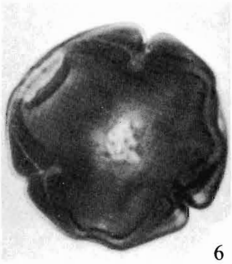
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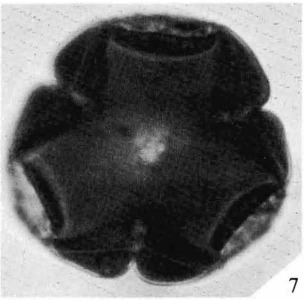
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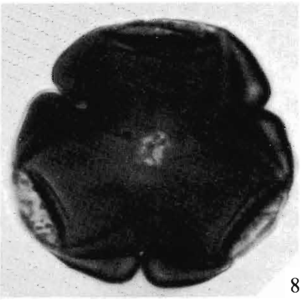
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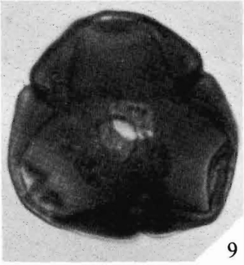
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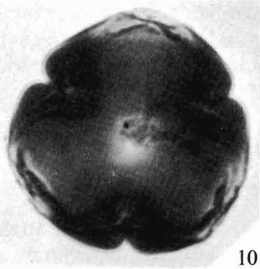
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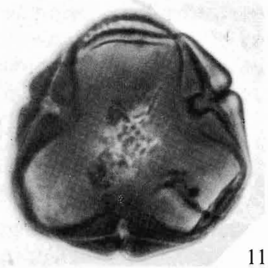
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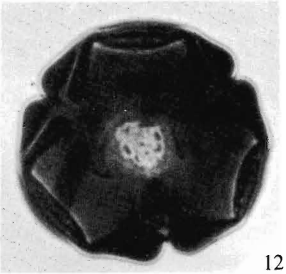
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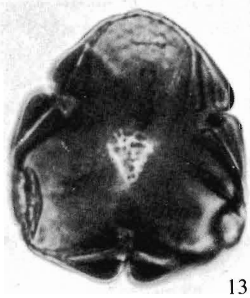
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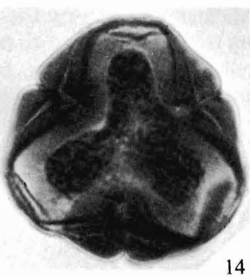
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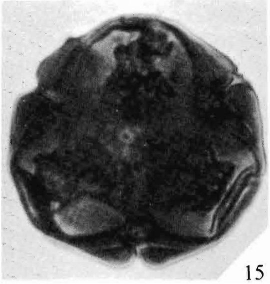
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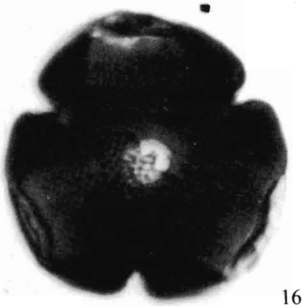
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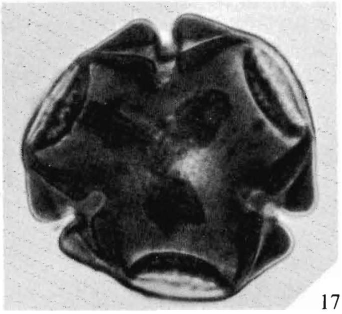
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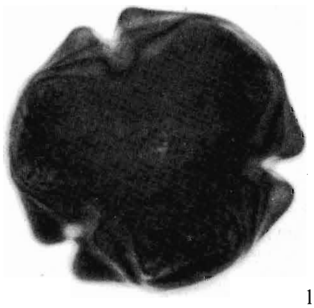
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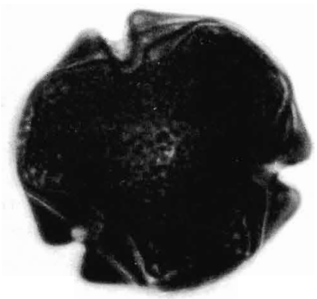
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BATTEN, *Vancampopollenites*

bordering these openings is 3–4 μm thick, forming an ectannulus, becoming thinner (to 0·5–1·0 μm) towards the equatorial, radial regions of grain where it merges with nexine; thickness of this single layer, *c.* 2 μm. Poles may be slightly depressed but otherwise lack any structural modification, or a weakly defined patch of thinner exine 4–7 μm in maximum diameter may be present. There may or may not be equatorial thin areas of exine between apertures. When observed, they vary from 5–12 μm in length and 3–5 μm in breadth and can be invaginated to a depth of up to 3 μm; sexine in these areas is < 0·5 μm thick or absent. Nexine is mainly 0·5–1·0 μm thick but becomes slightly thicker (maximum 3 μm) within germinals forming an endannulus around endopore of 1·5–3·0 μm diameter. Apertural separation of nexine from sexine usually considerable and this is reflected externally by exinal folding; maximum width of vestibulum, 2–5 μm.

Vancampopollenites lusitanus

Plate 5, figs. 3–19; Plate 7, figs. 2, 4, 5, 8; Plate 8, figs. 6 and 7

Description. Breviaxial pollen grains, subcircular to hexagonal with rounded angles in polar view. Maximum diameter 23 (34) 43 μm (75 specimens). Outer surface smooth to scabrate or undulating to finely granulate. Exoapertures comprise 3 short, equatorially-situated furrows orientated parallel to polar axis of grain. Sexine bordering these openings is 2–4 μm thick, forming an ectannulus, becoming thinner (to 0·5–1·0 μm) away from them. Poles often slightly depressed and usually there is a thinner patch of circular, subcircular, or triangular shape between 4–8 μm in maximum diameter within which sexine is reduced to scattered granules. Areas of thinning where sexine is similarly reduced or absent altogether occur at equator between apertures; these vary from 7–13 μm in length and 3–5 μm in breadth and are commonly invaginated to a depth of 1·0–3·5 μm. A Y-shaped (triradiate) granulose structure of varying dimensions, sometimes fragmentary or barely discernible, may occur close to or over one of the poles. Nexine is mainly 0·5–1·0 μm thick but becomes slightly thicker (maximum 2·5 μm) within germinals forming an endannulus around endopore of 1·5–4·0 μm diameter. Vestibulum 0·5–2·0 μm wide, resulting from separation of nexine from sexine.

Vancampopollenites minor

Plate 4, figs. 20, 22–25; Plate 5, figs. 1 and 2; Plate 6, fig. 19; Plate 7, figs. 6 and 7; Plate 9, fig. 1

Description. Breviaxial pollen grain, subcircular to hexagonal with rounded angles in polar view. Maximum diameter 16 (26) 29 μm (30 specimens). Outer surface smooth to scabrate or finely granulate, sometimes weakly verrucate. Exoapertures comprise 3 short, equatorially-situated furrows orientated parallel to polar axis of grain. Wall layering not always discernible. When present, sexine bordering these openings is 2–4 μm thick, becoming thinner towards equatorial, radial regions of grain where it merges with nexine; thickness of this single layer, 1·0–2·5 μm. At poles there is usually a thinner patch of circular to irregular shape between 3–7 μm in maximum diameter within which sexine is reduced to granules or absent altogether. Equatorial–subequatorial

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EXPLANATION OF PLATE 6

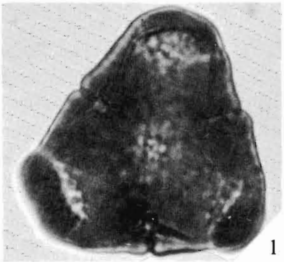
All magnifications except for fig. 19, × 1000.

Figs. 1–7. *Vancampopollenites subporatus.* 1, 4, 5, typical forms showing prominent subequatorial inter-apertural (radial) regions of sexinal reduction to granules and little or no separation of nexine from sexine in germinals; 1, sample DJB79/113, slide preparation MCP437.2, England Finder reference E35/0; 4, 79/113, 437.4, K26/2; 5, 82/63, 2376.3, Q50/1. 2 and 6, morphologically close to *V. triangulus*; 2, 79/113, 437.2, O16/0; 6, 82/63, 2376.4, L39/2. 3 and 7, no endannuli, endopores poorly defined; 3, 82/65, 2378.2, S48/0; 7, 82/63, 2376.3, G27/3.

Figs. 8–18, 20. *V. triangulus.* 8, 10–13, 15, 16, 18, 20, typical specimens, nexine clearly differentiated from sexine in germinals and usually also distinguishable at angles of grain. 8 and 12, same specimen, different focal-planes, 79/117, 439.2, Z30/3; 10, 79/113, 437.2, K20/0; 11, 82/62, 2375.3, M49/0; 13, RES10/228, 2985.3, F32/2; 15, RES10/228, 2985.3, T25/0. 16, with trace of triradiate structure over pole, 79/113, 437.3, P28/2; 18, 82/62, 2375.3, M49/0; 20, 79/117, 439.7, K38/0. 9 and 14, atypical, rather robust specimens; 9, 79/113, 437.2, K30/3; 14, 79/113, 437.8, U24/1. 17, not clearly separable from *V. subporatus*, 82/63, 2376.2, N19/1.

Fig. 19. Ultra-thin section of part of aperture of *V.* ?*minor* (probably a small *V. lusitanus*) showing perforated outer, and granular inner sexine, × 15,600.

PLATE 6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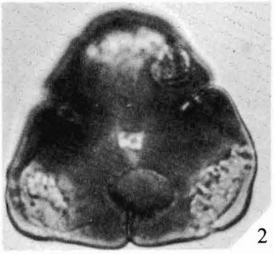
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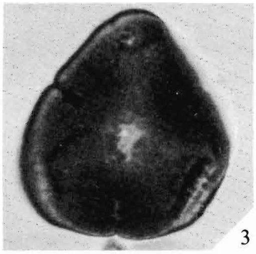
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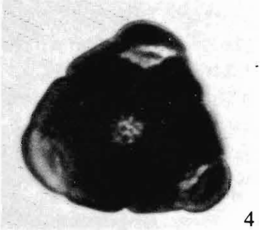
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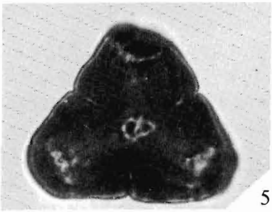
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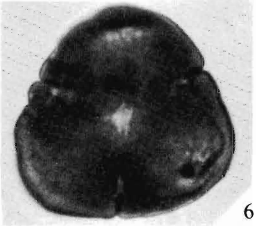
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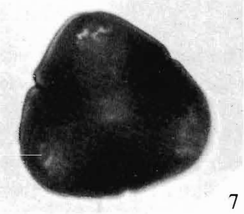
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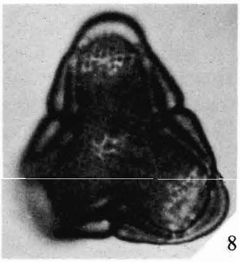
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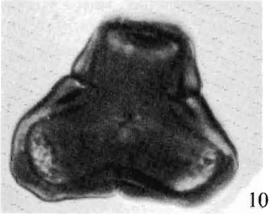
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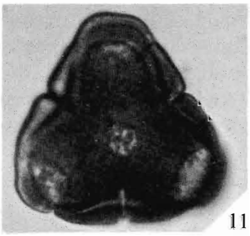
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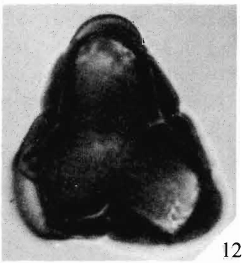
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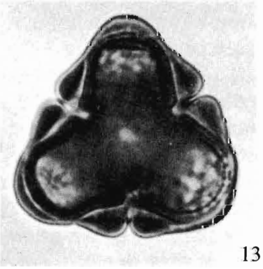
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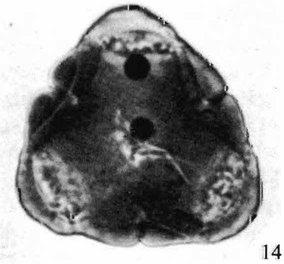
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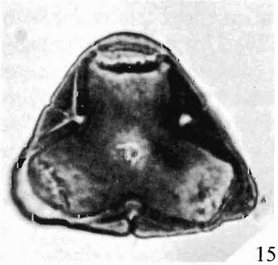
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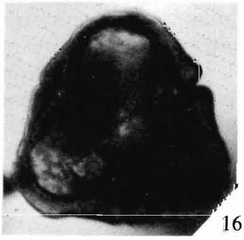
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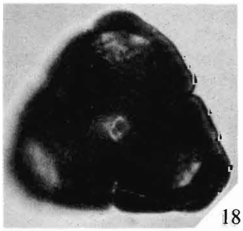
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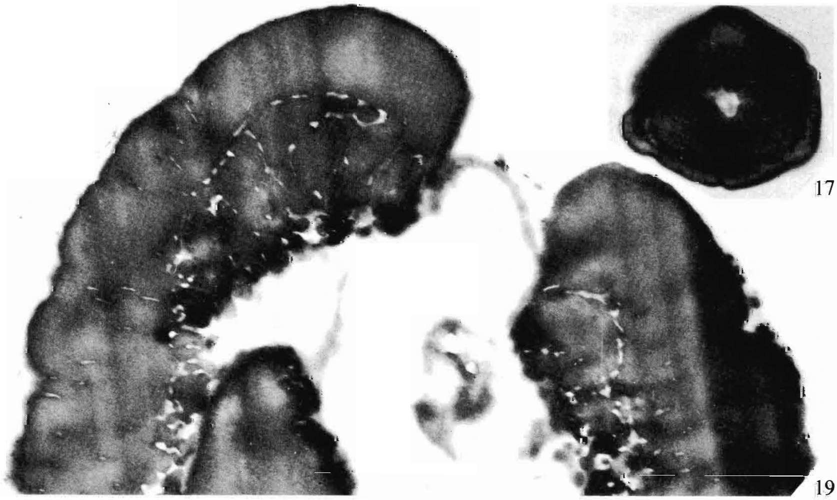
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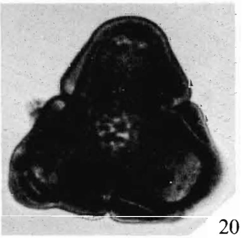
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BATTEN, *Vancampopollenites*

areas of thin exine where sexine is similarly reduced or absent may also occur; when present, they are of varying extent (4–10 μm long, 2–7 μm broad) and can be slightly invaginated by 1 or 2 μm. If distinguishable from sexine, nexine is 0·5–1·0 μm thick (rarely a little more than this; 1·5–2·0 μm) within germinals forming an endannulus around endopore of 1–2 μm diameter. Endannulus usually not properly formed or clearly defined, however, and an endoaperture may not be developed. Vestibulum absent or only weakly developed; maximum width of separation of nexine from sexine, < 0·5–1·5 μm.

Vancampopollenites subporatus

Plate 6, figs. 1–7; Plate 9, figs. 2 and 3

Description. Breviaxial pollen grain, triangular with straight sides and rounded angles in polar view. Maximum diameter 20 (27) 33 μm (30 specimens). Outer surface smooth to undulating-scabrate to weakly verrucate, often finely granulate. Exoapertures comprise 3 short, equatorially-situated, sometimes incompletely developed, furrows orientated parallel to polar axis of grain. Sexine bordering these openings is 2–3 μm thick, forming an ectannulus, becoming thinner towards angles of grain where it merges with nexine; thickness of this single layer, 1·5–3·5 μm. Poles may be slightly depressed but otherwise lack any structural modification, or there can be a thinner patch of triangular to irregular shape between 2–4 μm in maximum diameter within which sexine is reduced to scattered granules. Usually prominent are subequatorial inter-apertural thin areas of varying extent (dimensions vary between 3·5 and 10·0 μm in both length and breadth) where sexine is similarly reduced. Nexine is 0·5–1·0 μm thick, may be slightly more than this (1–2 μm) within germinals forming an endannulus around endopore of 0·5–2·0 μm diameter. However, not only may endannulus be absent but also endopore may not be clearly defined. Little or no separation of nexine from sexine in germinal; maximum width of vestibulum, 0·5 μm.

Vancampopollenites triangulus

Plate 6, figs. 8–18, 20; Plate 7, figs. 1 and 3; Plate 9, figs. 4–6

Description. Breviaxial pollen grain, triangular with straight or concave sides and rounded angles in polar view. Maximum diameter 22 (28) 33 μm (30 specimens). Outer surface smooth to scabrate or undulating to finely granulate. Exoapertures comprise 3 short, equatorially situated furrows orientated parallel to polar axis of grain. Sexine bordering these openings is 2·0–3·5 μm thick, forming an ectannulus, becoming thinner (to 1–2 μm) towards angles of grain but usually remaining distinct from nexine where total thickness of the two layers is 1·5–3·5 μm. Poles normally slightly depressed, and usually there is a thinner patch (sometimes barely discernible) of circular, subcircular, or irregular shape between 3–5 μm in maximum diameter within which sexine is reduced to granules or absent altogether. Subequatorial inter-apertural thin areas of varying extent (4–9 μm long, 3–8 μm broad) where sexine is similarly reduced or absent, are often present but may be poorly defined and occasionally lacking. Rarely a Y-shaped (triradiate) granular structure may be faintly distinguishable over one of the poles. Nexine 0·5–1·5 μm thick, increasing slightly to 1·0–2·5 μm within germinals forming an endannulus around endopore of 1·0–2·5 μm diameter. Vestibulum 0·5–1·0 μm wide, resulting from separation of nexine from sexine.

Remarks. This species was referred to as both *V. triangulus* and *V. triangulatus* by Kedves and Pittau (1979); I assume that the former spelling was intended (contrary to Batten 1981, pl. 1, fig. 17).

EXPLANATION OF PLATE 7

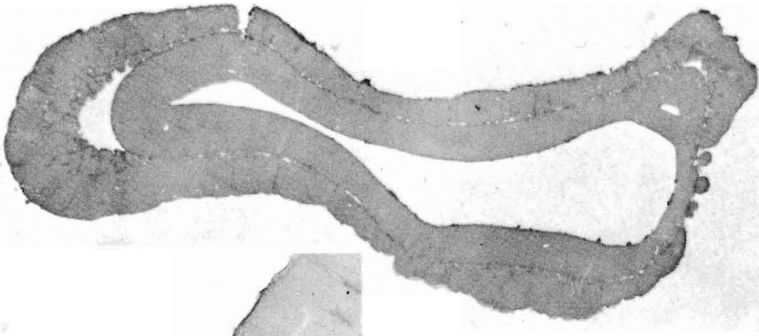
Ultra-thin sections of *Vancampopollenites* pollen grains.

Figs. 1 and 3. *Vancampopollenites triangulus*, same specimen. 1, oblique section showing clear separation of wall-layers, some radial elongation of granular inner sexine within germinals—left-hand and upper right-hand sides, and sexine reduced to granules on right, × 4320. 3, detail of granular structure of inner sexine and scattered perforations through outer, more homogeneous part, × 15,600.

Figs. 2, 4, 5, 8. *V. lusitanus*. 2 and 5, same specimen; 2, showing well-developed granular inner sexine and equatorial inter-apertural invagination of nexine with sexine reduced to granules, × 4320; 5, detail of sexine and part of nexine in germinal area; outer sexine finely perforated, × 6000. 4 and 8, same specimen; 4, oblique section displaying two apertures and inter-apertural reductions in exine thickness, × 3300; 8, detail of aperture, × 7800.

Figs. 6 and 7. *V. minor*, parts of same specimen; sexine strongly perforated and granular layer well-developed, × 4320.

PLATE 7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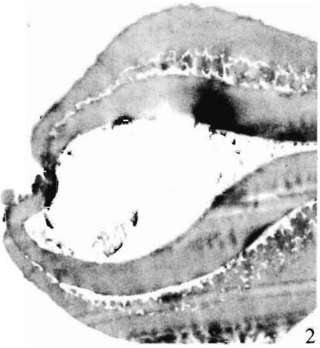
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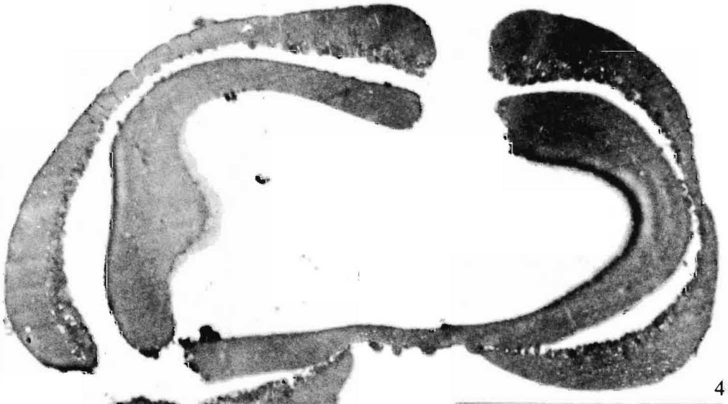
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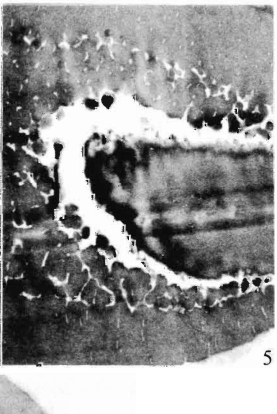
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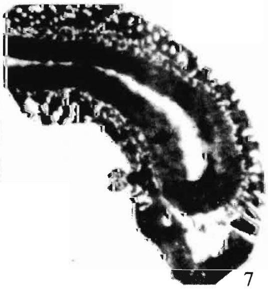
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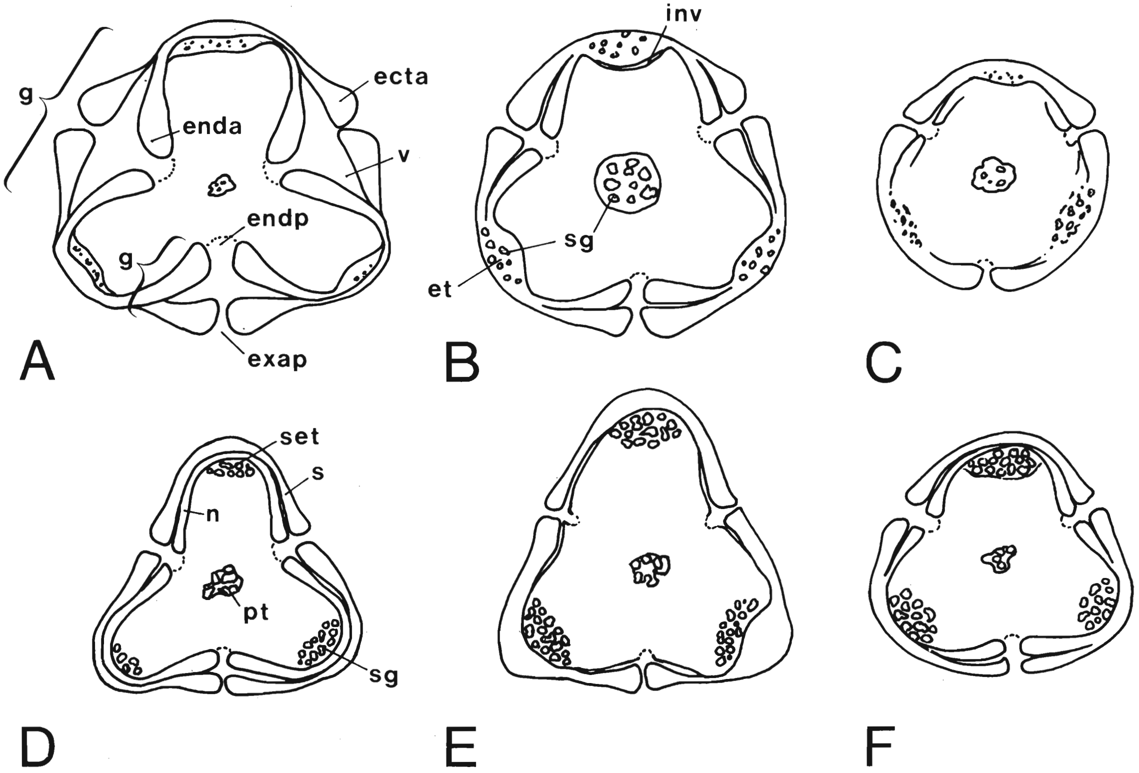
BATTEN, *Vancampopollenites*



TEXT-FIG. 3. Diagrammatic comparison between typical specimens of the six species of *Vancampopollenites* described: A, *V. endotriangulus*; B, *V. lusitanus*; C, *V. minor*; D, *V. triangulus*; E, *V. subporatus*; F, *V. aradaensis*. Abbreviations: g, germinal; s, sexine; n, nexine; exap, exoaperture; ecta, ectannulus; endp, endopore; enda, endannulus; v, vestibulum; et, equatorial thinning; set, subequatorial thinning; pt, polar thinning; inv, invagination; sg, sexinal granules. All magnifications *c.* × 1250.

DISTINCTION AND COMPARISON OF SPECIES

The foregoing descriptions are broadly comparable with those in Kedves and Pittau (1979) but they differ both in detail and in the terms employed. It also has to be said that, although I have sought to maintain use of the species, my concept of those other than *V. lusitanus* and *V. triangulus* differs somewhat from that of Kedves and Pittau. The terminology applied to the form of the germinal areas is less complex, and use of polpapillus, polar papillus, secondary and false apertures, and atrium has been avoided (text-fig. 3).

Papilla is Latin for nipple and is thus inappropriate for a polar exinal thinning (see also Jansonius and Hills 1980). The secondary or false apertures are merely thin areas of exine which may also be invaginated. Atrium is a term commonly used in Normapolles descriptions to denote an 'area of solution of the endexine' in the vicinity of the aperture. In other words, it delimits the termination of the endexine/nexine at the germinal (Batten and Christopher 1981). Although applicable to the morphology of some Normapolles, it serves no useful purpose when it is an optical effect of little consequence, as in *Vancampopollenites*.

Kedves and Pittau (1979) noted that the presence of a 'polpapillus' and 'secondary apertures' clearly distinguish *V. aradaensis* from *V. endotriangulus*. In practice, however, *V. aradaensis* is much more likely to be confused with *V. triangulus* (text-fig. 3). In addition to having generally more convex sides and less well-developed polar areas of sexinal reduction it usually differs from the latter in that the exine is thinner equatorially at the angles.

V. endotriangulus is similar to *V. lusitanus*. It differs, however, not only in having poorly defined equatorial inter-apertural areas of thinner exine (Kedves and Pittau 1979) and conspicuous vestibula which may coincide with the development of exinal folds (Pl. 8, figs. 4 and 5), but also in that there is commonly little or no reduction of the sexine at the poles (text-fig. 3).

The wall structure of *V. subporatus*, particularly adjacent to the apertures, suggests that this species encompasses immature or aberrant forms of *V. triangulus*. The exine of most specimens that are referable to the latter consists of two readily discernible layers. The similarity of these two species is very clear when only surface form is taken into account; scanning electron micrographs do not reveal any consistent differences (Pl. 9, figs. 2–6).

V. minor is separable from *V. subporatus* and *V. triangulus* on the basis of its well-rounded rather than distinctly triangular outline, but it is closely comparable with the other species which are similar in shape. The only criteria available to separate it are size and degree of architectural development. Some specimens of appropriate dimensions, however, are no more than diminutive *V. lusitanus*. Others are incompletely formed, particularly around the apertures, and may also lack a differentiated sexine and nexine (text-fig. 3). An extreme version of an under-developed, immature grain is illustrated on Plate 5, fig. 4; it is attached to a specimen of *V. lusitanus*.

Beyond the confines of *Vancampopollenites*, *Heidelbergipollis tilioides* Krutzsch in Góczán *et al.* 1967 is very similar to *V. lusitanus* (despite the apparent differences in text-fig. 2B, C), the only character that separates it being the lack of a thin area at the poles within which the sexine is reduced to granules. Since this feature is not consistently present within other species attributable to *Vancampopollenites*, logically it should not be used to distinguish between two genera. As mentioned earlier, the possibility that *H. tilioides* is merely a variant of the *V. lusitanus*-type cannot be dismissed.

For all species of *Vancampopollenites* there are some specimens in which two sexinal laminae are discernible in transmitted light, mainly about the ectannulus. The inner layer is generally 0·5 μm thick in *V. subporatus*, 0·5–1·0 μm in *V. aradaensis* and *V. triangulus* and normally within this range, but occasionally as much as 1·5 μm, in the other three species. This does not appear, however, to have any taxonomic significance (see below), nor does the fact that the inner layer occasionally shows weakly radial to infrabaculate structuring.

A morphological feature not noted by Kedves and Pittau (1979) is a granular zone that is roughly triradiate in most instances and centred over one of the poles. This slightly raised structure has been seen mainly on *V. lusitanus* (Pl. 5, figs. 9–19) but has also been noted in *V. aradaensis* (Pl. 4, figs. 3, 5, 6), *V. triangulus* (barely discernible and incomplete in Pl. 6, fig. 16), and in an, as yet, undescribed species (Pl. 4, fig. 18). It may be well delineated (e.g. Pl. 5, fig. 16) or present as only ragged traces (e.g. Pl. 5, fig. 10). Fragments of tissue close to the pole on a couple of specimens of *V. endotriangulus* (e.g. Pl. 4, fig. 13) are not definitely remains of such a feature. Although the arms on most entire examples extend to no more than two-thirds of the radius of the pollen, they may be longer (e.g. Pl. 5, fig. 15) and very occasionally cover most of one surface of a grain (Pl. 5, figs. 18 and 19).

ULTRASTRUCTURE

In common with most angiosperm pollen the exine of the majority of Normapolles grains consists of two main layers usually referred to as sexine and nexine, as herein, or ectexine and endexine; these terms are not synonymous. Well-developed columellae are not encountered, however, and there is no foot layer (Médus 1983; Batten, in press *b*).

A number of specimens of *Vancampopollenites* species have been thin-sectioned and all the transmission electron micrographs obtained show similar structural features. The nexine is the more homogeneous of the two wall layers (Pl. 6, fig. 19; Pl. 7, figs. 1, 4, 8). The outer part of the sexine also often appears rather dense and relatively unstructured but it becomes more granular and fissured internally (Pl. 7, figs. 2–5), and perforations which extend through to the granular layer reduce its homogeneity. The diameter of the perforations and their density vary considerably from being scattered and barely distinguishable (Pl. 7, fig. 3) to closely spaced and so pronounced that the sexine is by no means homogeneous (Pl. 7, figs. 6 and 7; Pl. 8, figs. 5 and 7).

The inward change to granular structure may take place more or less gradually (e.g. Pl. 7, fig. 3) or abruptly (e.g. Pl. 7, fig. 2), particularly in the vicinity of the apertures (Pl. 6, fig. 19; Pl. 7, figs. 5 and 6). Within the latter, the granules are often more elongated and radially orientated (Pl. 7, figs. 4 and 6). Polar and equatorial reduction of the sexine to granules is clearly evident in thin section (Pl. 7, figs. 1, 2, 4, 8) and in most scanning electron micrographs (Pls. 8 and 9).

FUNCTION

Interpretation of the morphology of fossil pollen grains in terms of function is not easy when there are no comparable modern grains on which to base conclusions. A few of the characters displayed by the species of *Vancampopollenites* do, however, have analogues in the pollen of some extant plants. Both their sculpture and wall structure strongly suggest that the grains were dispersed by wind. Modern anemophilous pollen mostly bear little surface ornament (Whitehead 1969). Also in common is the fact that the outer and inner wall-layers are not separated by columellae but by a granular zone.

The presence of polar, equatorial, and other thin areas of exine suggest a harmomegathic function. Most pollen grains have to be able to withstand changes in volume caused by fluctuations in the relative humidity of the atmosphere (Wodehouse 1935). The equatorial, radial thin areas in *V. lusitanus* in particular serve to emphasize a potential for accommodating increased hydration by expansion as well as dessication by contraction and invagination. It follows that other patches of exinal thinning were also capable of expanding and contracting, and that *Vancampopollenites* grains were both strong and flexible enough to prevent uncontrolled collapse.

The triradiate granulate structures seen on specimens of three of the six species and on one unnamed form of the genus (Pl. 4, fig. 18) are extra-sexinal. Unlike the other features considered, they do not suggest an adaptation to dissemination but rather, probably reflect a tetrahedral configuration of the pollen grains in the tetrad prior to break-up within the anther and subsequent dispersal.

STRATIGRAPHIC DISTRIBUTION

The limited exposures in the scattered outcrops of Upper Cretaceous deposits in the northern part of the Western Portuguese Basin, and uncertainties over their precise position within the sedimentary sequence as a whole, means that occurrences of *Vancampopollenites* species in the region are currently less useful for correlation than might be expected. Indeed, in the absence of other indicators of age, their presence merely suggests that the strata are unlikely to be older than Coniacian and younger than Maastrichtian (Kedves and Pittau 1979; Moron 1981; Batten, unpublished data). It is quite possible, however, that they have potential for dating and it is anticipated that as stratigraphic studies in the region progress, their ranges will become clearer.

EXPLANATION OF PLATE 8

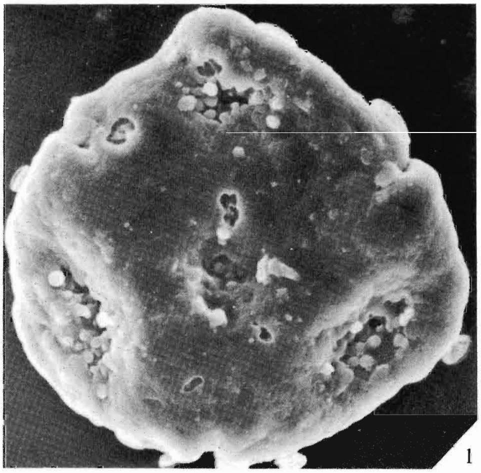
All scanning electron micrographs.

Figs. 1–3. *Vancampopollenites aradaensis.* 1 and 2, same specimen; 1, showing smooth to scabrate exine and both polar and subequatorial inter-apertural (radial) areas of sexinal breakdown to granules, × 2200; 2, details of one of the latter, × 5000. 3, undulating, hummocky, finely granulate surface; scattered perforations, × 7000.

Figs. 4 and 5. *V. endotriangulus.* 4, specimen sculptured with small granules; exinal folds coincide with wide vestibula internally; polar and equatorial inter-apertural areas of sexinal breakdown, × 2200. 5, as for 4 apart from strongly perforated wall and lack of granules, × 2000.

Figs. 6 and 7. *V. lusitanus.* 6, typical form with finely granulate surface and clearly delineated polar area of sexinal breakdown; one equatorial inter-apertural invagination visible, × 2200. 7, specimen particularly deflated between germinals; exine smooth, perforated, × 2500.

PLATE 8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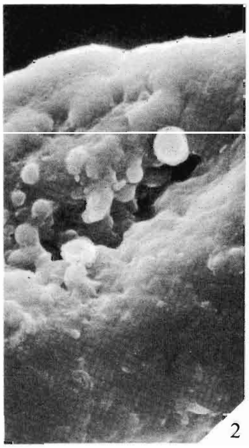
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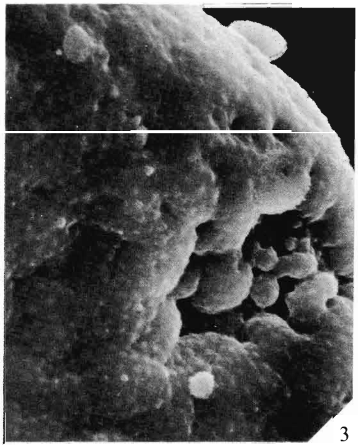
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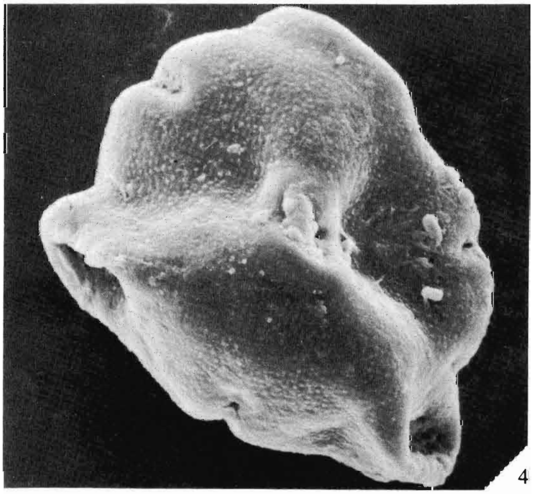
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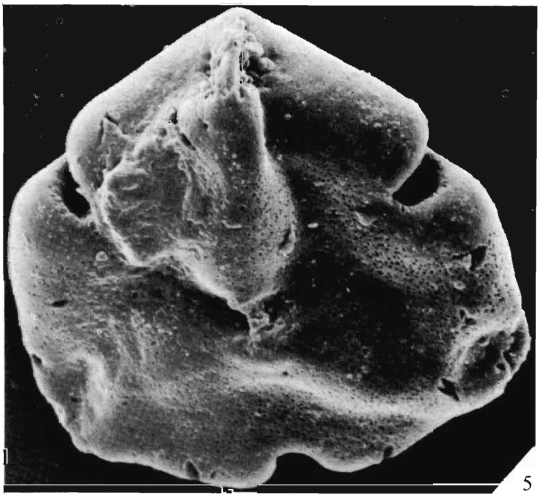
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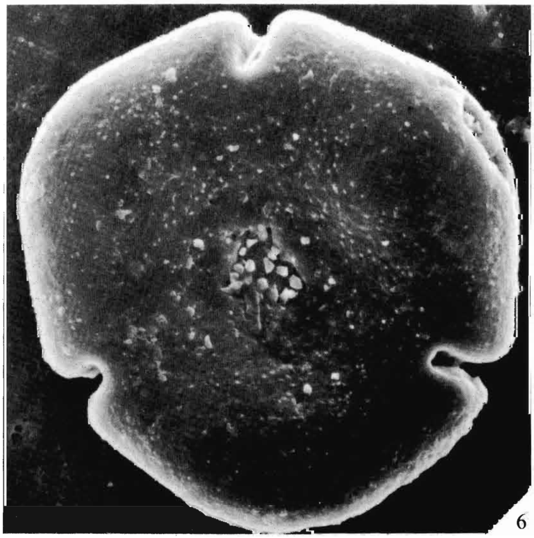
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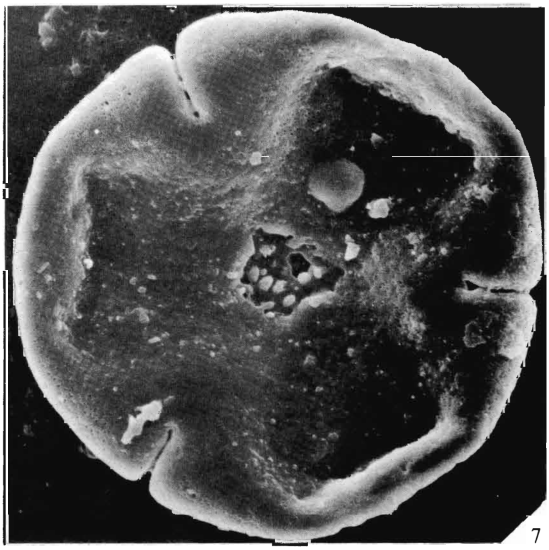
7

BATTEN, *Vancampopollenites*

Published records from outside Portugal are restricted to those in Azéma *et al.* (1981) and Viaud *et al.* (1983) for the Vendée region of France and to a mention by Vazquez Reyero (1983) of the occurrence of the genus in the Upper Cretaceous of Spain. Azéma *et al.* found *V. lusitanus* in an apparently late Turonian sample and in one of possible Campanian age from a Vendée borehole, although their figure (Azéma *et al.* 1981; pl. 7, fig. 9) appears to illustrate a *V. endotriangulus*. They also recovered *V. subporatus* (ibid.; pl. 7, fig. 10) and *V. triangulus* (ibid.; pl. 7, fig. 11; *V. triangulatus*) from the younger horizon. *Heidelbergipollis* sp. was identified at another ?Campanian level, and specimens considered to be *H.* cf. *H. tilioides* were noted in a palynological preparation of a sample from a clay bed at outcrop in the same area which Azéma and Viaud (1979) had previously suggested might be of early Santonian age.

H. tilioides was originally described from the 'Heidelbergschichten' of the German middle Santonian (Góczán *et al.* 1967) and has since been reported by Médus (1972, 1979, 1981) along with others identified merely as *Heidelbergipollis* sp. (Médus 1970, 1979, 1981) from strata ranging in age from Santonian to Maastrichtian in both France and Spain as well as from Ilhavo, Portugal. Specimens attributable to the genus have hardly ever been found in Hungary (Góczán, pers. comm. 1985). Although there are no North American records of *Vancampopollenites*, rare (and doubtful) *Heidelbergipollis* sp. have been reported from Coniacian–Santonian outcrops in the Atlantic Coastal Plain by Wolfe and Pakiser (1971) and Christopher (1979).

The broadly comparable age-ranges for the two genera lends further support to the argument that they may be related in the sense of having been produced by the same group of plants. There is, however, no palaeobotanical evidence to indicate where their familial affinities lie.

Kedves (1983) stated that *Papillopollis* may have been derived from the long-ranging Normapolles genus *Trudopollis*, which first appears during the Turonian. He also asserted that this led in turn to a *Heidelbergipollis*–*Vancampopollenites* line. All lineages based solely on pollen grains or spores must, however, be treated with caution and this one is no exception, particularly in view of the dating uncertainties that exist at present.

PHYTOGEOGRAPHIC AND CLIMATIC SIGNIFICANCE

Although Normapolles assemblages of Cenomanian and Turonian age on both sides of the Atlantic are broadly similar in composition, those recovered from younger Cretaceous strata differ in many ways, indicating that from the Coniacian onwards the opening ocean was an effective barrier to the dispersal of most groups of plants. Not least of the differences is the fact that both *Papillopollis* and *Vancampopollenites* have only been recorded from Europe. In addition, *Interporopollenites* Weyland and Krieger 1953, which often occurs abundantly in association, has not been found in the Cretaceous of North America although it has been reported from Tertiary strata (Tschudy, 1975, 1981; Batten, 1981, 1984). The occurrence of these genera, along with *Triangulipollis* Krutzsch in Góczán *et al.* 1967 and *Vacuopollis* Pflug 1953 in particular, and the virtual absence of *Trudopollis* Pflug 1953 and *Oculopollis* Pflug 1953 in Portugal, distinguishes Senonian Normapolles assemblages

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EXPLANATION OF PLATE 9

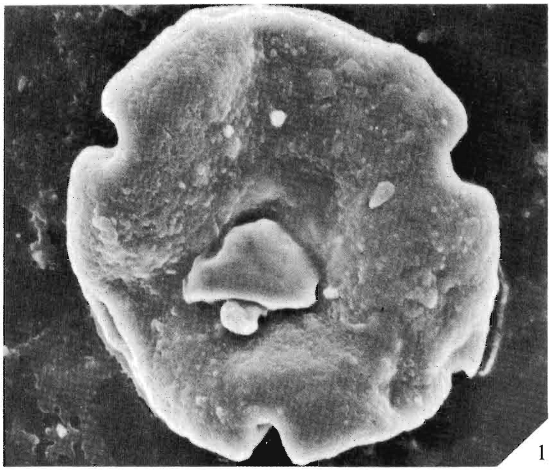
All scanning electron micrographs.

Fig. 1. *Vancampopollenites minor* with a roughened surface and structural characters closely similar to those of *V. lusitanus*; polar thinning mostly obscured by detritus, × 3000.

Figs. 2 and 3. *V. subporatus*. 2, two specimens of similar morphology with polar sexinal reduction clearly delineated but radial subequatorial thinnings poorly developed, × 1700. 3, surface of exine very finely granulate; subequatorial, radial areas of granular sexine strongly differentiated, × 2500.

Figs. 4–6. *V. triangulus*. When viewed under the SEM, pollen grains of this species usually cannot be distinguished from *V. subporatus*. The subequatorial areas of granular sexine on 4 and 5 are very similar to those on 3 and 2 respectively. Those on 6 are invaginated. 4 and 5, × 2200; 6, × 2500.

PLATE 9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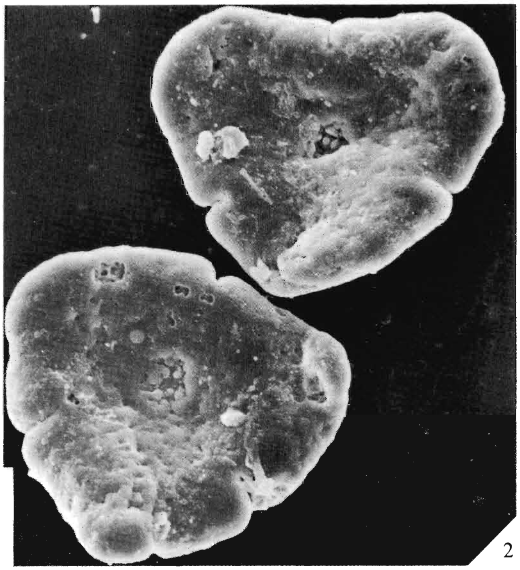
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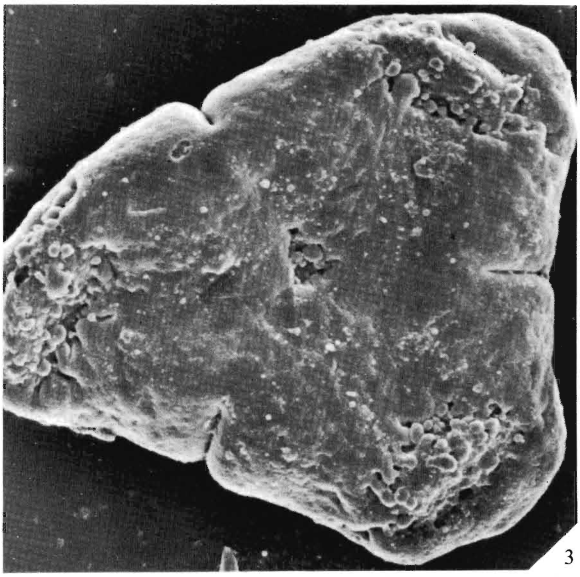
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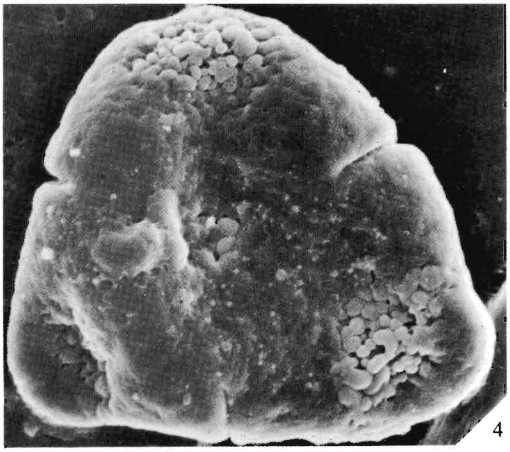
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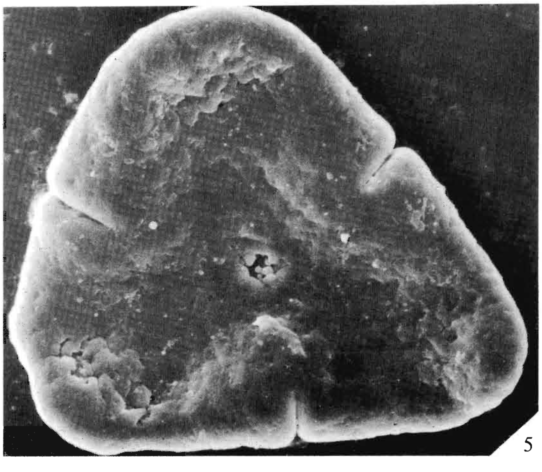
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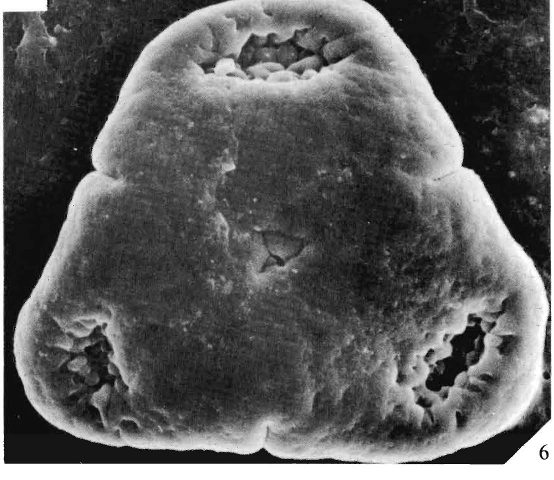
6

BATTEN, *Vancampopollenites*

of this region, and probably of Iberia in general, from those of similar age in northern Europe. Genera with swollen germinals, including numerous forms of *Trudopollis* and *Oculopollis*, are important components of the latter.

These variations in palynological assemblages, and others which require further investigation, must signify differences in composition of the vegetation that covered Europe and eastern North America. It is, however, impossible to speculate satisfactorily at present on what these were, owing to a scarcity of reliable plant megafossil data and because of the difficulty in determining palaeobotanical relationships from dispersed pollen grains.

A common non-angiospermous associate of the Normapolles at some horizons in Portugal is *Classopollis* Pflug 1953 *sensu lato* (i.e. including *Classoidites* Van Amerom 1965), a gymnosperm pollen which has frequently been considered to indicate at least seasonally dry, if not semi-arid conditions. Whatever the degree of seasonality and level of annual rainfall (cf. Batten and MacLennan 1984), the geographic distribution of the Normapolles and other pollen grains as well as spores (Batten, unpublished) suggests that the climate of Europe during the Senonian was by no means uniform and also differed from that in eastern North America.

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