

# PRACTICAL DIFFICULTIES IN THE APPLICATION OF THE SPECIES CONCEPT IN ALBIAN ANGIOSPERM POLLEN

by J. L. CHAPMAN

**ABSTRACT.** The definition of palynological species on continuously variable characters can cause difficulties in classifying borderline specimens and lead to blurring of morphological boundaries of the species. One group of grains from the Albian of Portugal with several discrete characters illustrates the difficulty of classifying grains into species where discrete characters are found associated in different combinations over a wide range of morphology of continuously variable characters.

THIS paper describes the problems of classifying pollen using scanning electron microscope (SEM) data. The pollen handled are from the Albian of Portugal, but the difficulties described are not limited to a particular geological time or locality, or even to fossil pollen.

The SEM shows levels of detail which are unclear or not visible under the light microscope (Hay 1971). The kinds of characters which can be appreciated with the SEM and not with the light microscope for Cretaceous angiosperm pollen include: the shape of the muri, distribution and shape of the supramural sculpturing, small variations in the dimensions of the muri and lumina, structure of the columellae, and the exact form of the aperture margins and membrane. Classification problems increase when these characters form continua or appear to be randomly distributed through the group of grains rather than in association with other characters.

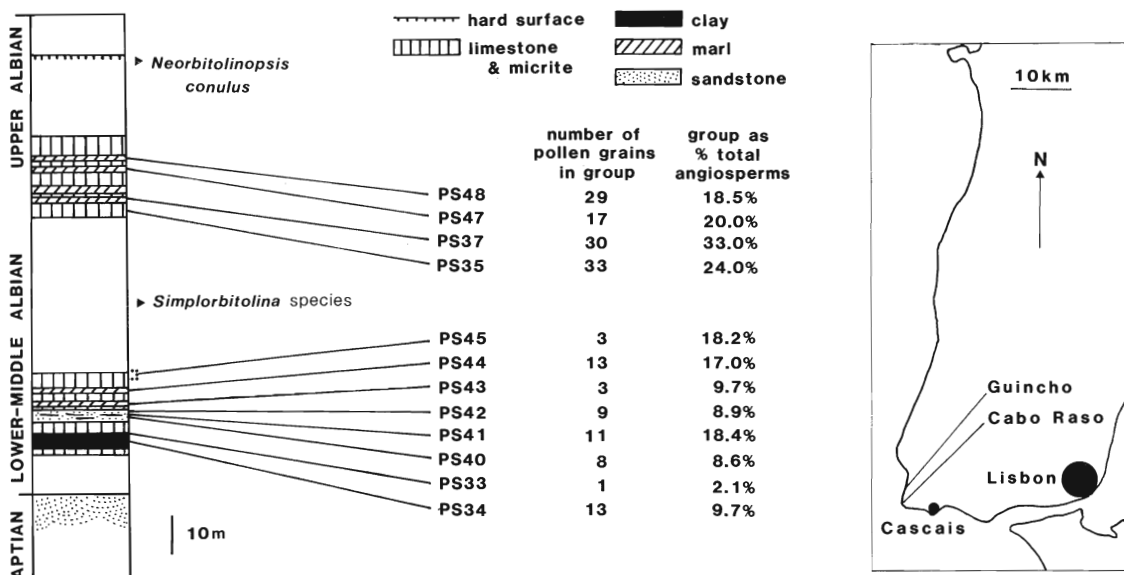
When classifying pre-Cenomanian angiosperm pollen grains it is easy to assign them to large groups on the strength of certain important unifying characters, but often very difficult to divide these groups into lower order taxa at the level of genera or species. This phenomenon is illustrated here by the use of one group of pollen grains which is found in the Aptian and Albian of Portugal. The pollen considered are from twelve Albian samples from one locality.

Strew mounts of prepared residues on stubs were searched for angiosperm pollen and the grains photographed at standard magnifications for direct comparison. A representative selection of the pollen referable to the group are figured in this paper; all have surface details shown at a standard high power magnification to illustrate directly the variation in structure of the reticulum. Stubs of all the figured grains are stored in the Sedgwick Museum, Cambridge. The pollen can be relocated because they are on Cambridge Mark II Geology Grids (Laing 1974; Hughes *et al.* 1979) for which grid references are given.

## COLLECTION SITE

Samples of fine-grained mudstones and siltstones were collected from cliffs on the west coast of Portugal between Cabo Raso, west of Cascais, and Guincho (text-fig. 1). These cliffs of gently dipping strata comprise the greatest thickness of mid-Cretaceous strata exposed in Portugal. Almost the whole of the Aptian and Albian is represented, but the Aptian is mostly barren of palynomorphs.

The marine sediments are dated at Guincho by the presence of Foraminifera in certain horizons. The early-middle Albian is marked by *Simplorbitolina conulus* Schroeder 1965 and *S. manasi* Ciry and Rat 1953 (Berthou and Schroeder 1979). The late Albian is determined by the presence of *Neorbitolinopsis conulus* Douville, whose range Berthou and Schroeder (1978) consider does not extend to the Albian-Cenomanian boundary.



TEXT-FIG. 1. Stratigraphic setting and geographical position of the samples from the cliffs between Cabo Raso and Guincho, on the Portuguese coast west of Lisbon. Only the strata adjacent to horizons sampled are shown; the remaining strata are mostly limestones with rudist bivalves and marls.

#### THE POLLEN GROUP

The pollen considered here fall within a group defined on the following important unifying characters: 1, a single slit-shaped aperture edged with a continuous murus no wider than the muri of the reticulum (Pl. 10, figs. 1, 6, 9); 2, an aperture membrane of smooth nexine which is sometimes rolled inwards, but usually has pulled apart along a line of weakness of unconsolidated nexine with a granular texture (Pl. 11, fig. 3; Pl. 12, fig. 2); 3, smooth muri; 4, sparse columellae which often taper towards their bases and may become detached from the nexine (Pl. 10, fig. 2; Pl. 11, fig. 2).

The group was chosen for this study because, although it is defined on characters found fairly regularly in fossil angiosperm pollen, it contains grains with one or more unusual characters. These are: 1, murus shape in cross section: i, round (Pl. 10, figs. 7 and 9); ii, triangular (Pl. 11, fig. 2); iii, tall and narrow (Pl. 11, figs. 4 and 8); 2, aperture length: i, short, about  $\frac{1}{3}$ – $\frac{1}{2}$  grain diameter; ii, long, almost encircling grain (Pl. 12, fig. 1); iii, completely encircling grain which then often separates into two halves—circumsulcate (Pl. 10, figs. 3 and 6; Pl. 11, fig. 1); 3, reticulum pattern: i, regular (Pl. 10, fig. 7; Pl. 11, fig. 2; Pl. 12, fig. 6); ii, bimodal, with very much smaller lumina at the corners

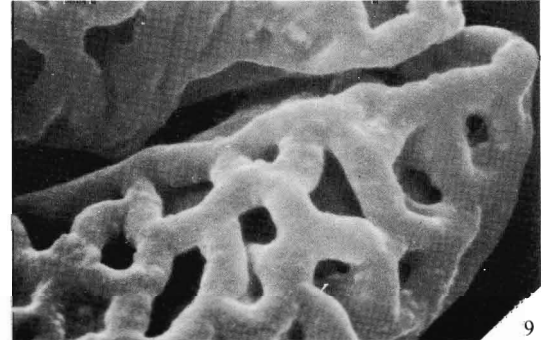
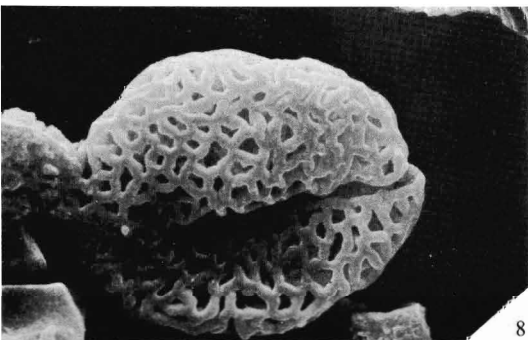
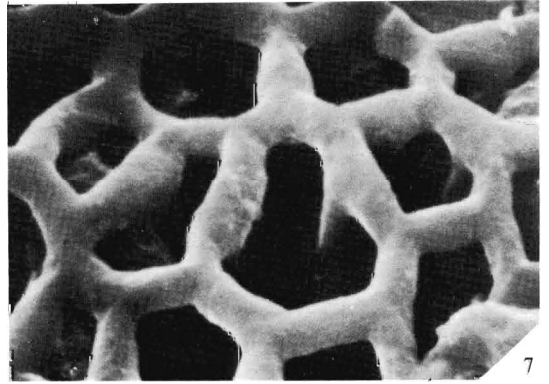
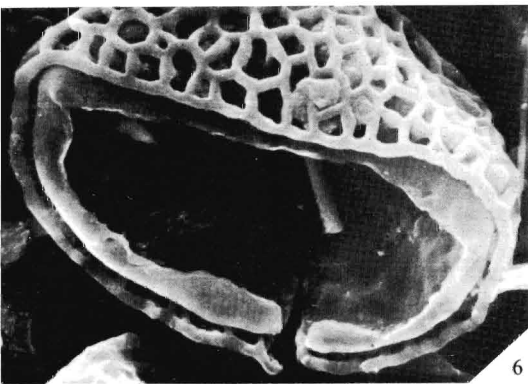
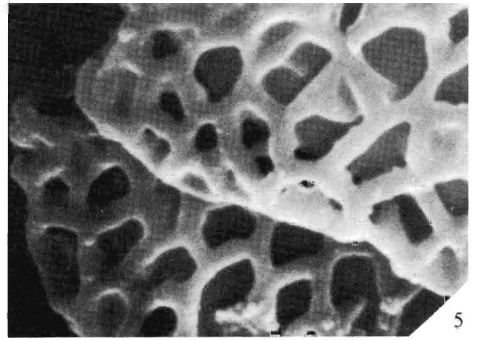
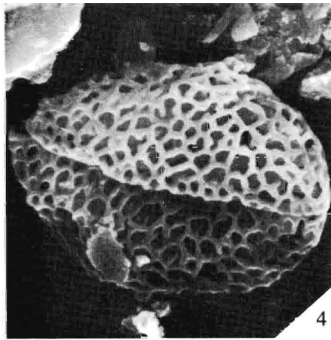
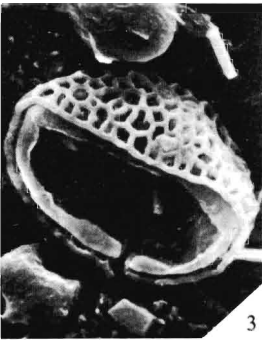
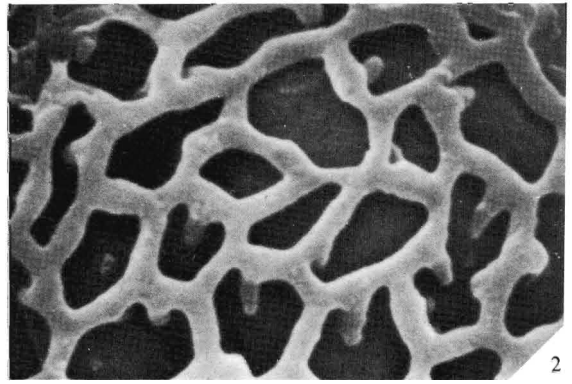
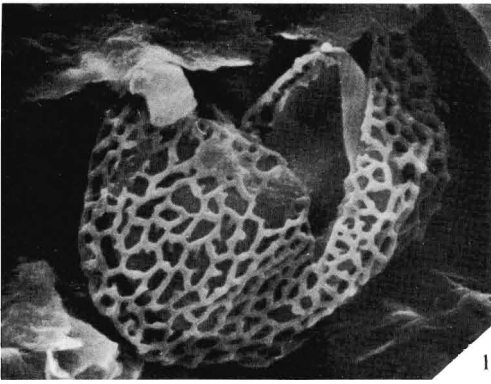
#### EXPLANATION OF PLATE 10

Figs. 1 and 2. Stub JLC57, Grid ref. 226806, C294/37, 41. Cluster grain from PS42 with round muri. 1, whole grain, gaping aperture,  $\times 3100$ ; 2, reticulum M2L4,  $\times 12\ 500$ .

Figs. 3, 6–7. Stub JLC130, Grid ref. 275825, C260/33–35. Circumsulcate grain from PS37 with round muri. 3, half grain,  $\times 1550$ ; 6, unbroken aperture margin showing grain is completely circumsulcate,  $\times 3100$ ; 7, reticulum M6L11,  $\times 12\ 500$ .

Figs. 4 and 5. Stub JLC122, Grid ref. 255785, C244/11–12. Cluster grain from PS44 with round muri. 4, whole grain,  $\times 3100$ ; 5, reticulum M2L2,  $\times 12\ 500$ .

Figs. 8 and 9. Stub JLC56, Grid ref. 300838, C135/2. Cluster grain from PS34 with round muri. 8, whole grain,  $\times 3100$ ; 9, reticulum M5L3 and aperture margin,  $\times 12\ 500$ .



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of the larger lumina (Pl. 11, figs. 7 and 10); iii, mazed, the muri not enclosing lumina (Pl. 11, figs. 5 and 6; Pl. 12, figs. 3, 4, 7, 10). Other characters are recognizable which are very variable within the group; namely 1, grain size 11 to 51  $\mu\text{m}$  in maximum diameter; 2, main lumina size (where present) 0.5 to 9.0  $\mu\text{m}$  in diameter, small lumina on bimodal grains 0.15 to 2.0  $\mu\text{m}$  in diameter; 3, muri < 0.1 to 1.0  $\mu\text{m}$  wide.

Some of the pollen in this group appear to be allied to the 'light microscope genus' *Retimonocolpites* and may be closely related to the type species *R. dividiuus* Pierce (1961). This species is described as 'monocolpate, aperture almost encircles grain dividing it into two hemispheres' and as 'finely reticulate, muri of distinct columellae fused apically, reticulum occasionally separated from endexine' (p. 47): all of these characters can be seen in the group described here. They are, however, totally unrelated to the *R. reticulatus/peroreticulatus* complex (Doyle *et al.* 1975) which consists of acolumellate grains with a shorter colpus and sharp supramural spines. This makes these quite distinct and not congruent with the original concept of the genus *Retimonocolpites* (Chapman 1982).

The range of reticulum and grain dimensions in the group discussed in this paper is far greater than described previously for *Retimonocolpites*, excluding *R. reticulatus/peroreticulatus* and the mazed reticulum pattern has not been reported before. Also the shape of the muri in cross-section in the original 'light microscope species' *R. dividiuus* is not known.

Insufficient information is available to correlate even a part of this Portuguese group with species described on the basis of observations under the light microscope and the records of additional characters in this SEM study simply highlight the problems faced by SEM workers in correlating their forms with existing light microscope-based taxa (e.g. Reyre 1971). The group is presented here, therefore, without further reference to previous classification.

#### CLASSIFICATION AT SPECIES LEVEL

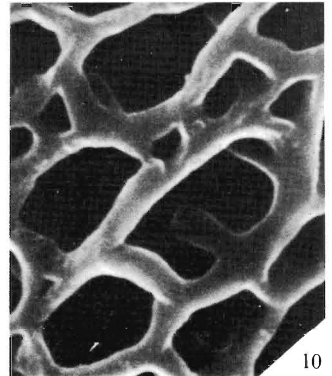
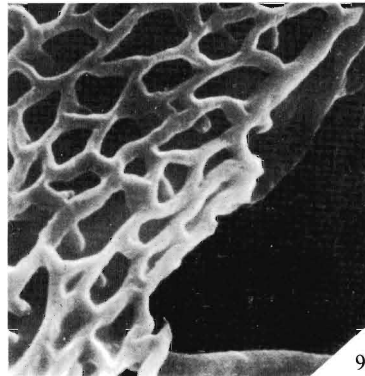
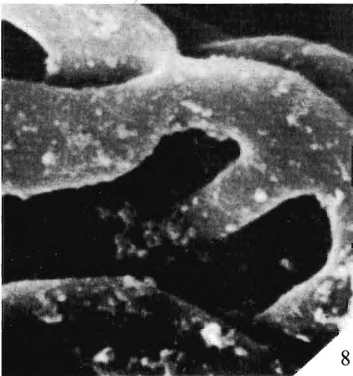
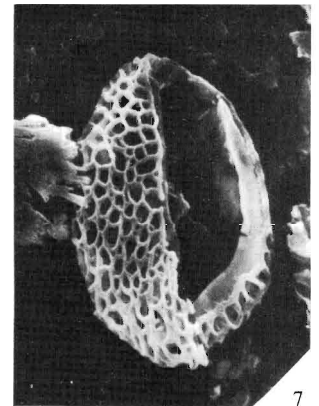
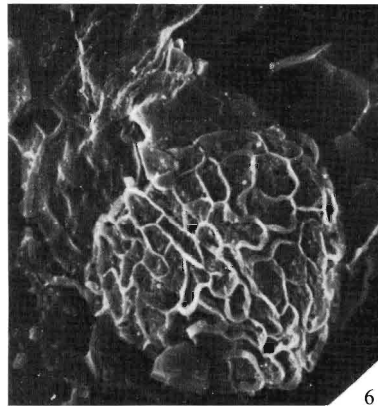
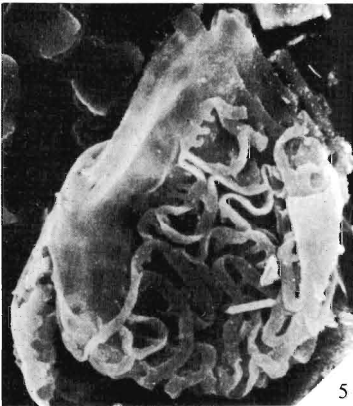
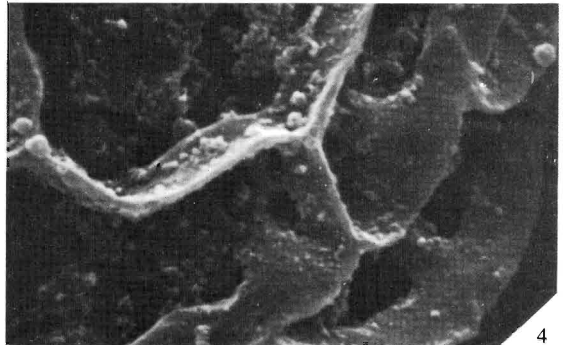
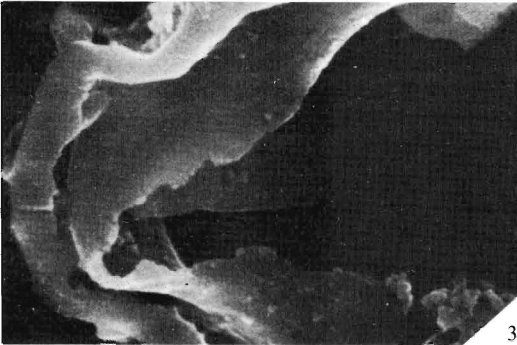
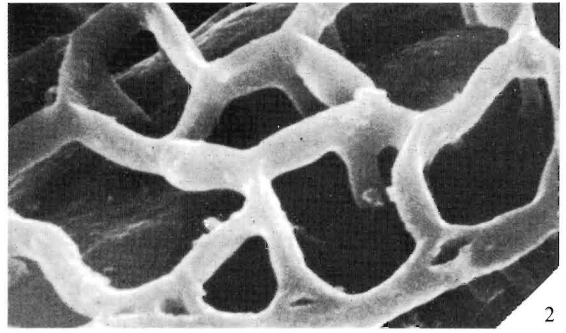
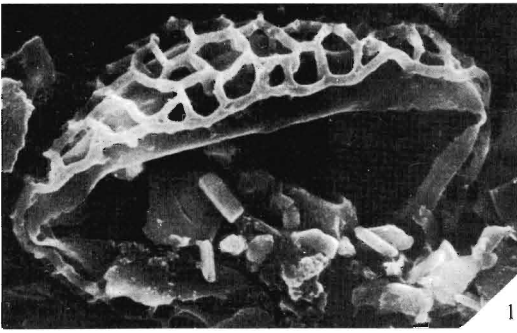
Two of the major applications of fossil species are to increase the accuracy and extent of biostratigraphic correlation and to indicate the biological importance and evolutionary relationships of the organisms. Fossil plant species can never be equivalent to those of living plants. Despite the fact that fossils are remains of living plant species, with breeding systems that were presumably similar to those found in plants today (Briggs and Walters 1984), they are based only on morphological characters. Because of this, the fossil species are defined in terms of the variation in particular characters, but these are arbitrary boundaries which may vary depending on the fossils and on who is classifying them.

The following points would define an ideal fossil species for the Cretaceous pollen: 1, one or more discrete characters defining the species—especially useful if the character is readily visible on all or most specimens and even better if it is visible under a light microscope; 2, one or more characters associated with the discrete defining character(s); 3, a fairly narrow morphological range within the continuously variable characters—for example width of muri, diameter of lumina, and grain size: there is a limited amount of variation in these characters (excluding aborted or malformed grains) within recent pollen species (Chapman 1982); 4, for stratigraphical purposes a fairly narrow

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#### EXPLANATION OF PLATE 11

- Figs. 1–3. Stub JLC122, Grid ref. 284758. Half grain from PS44 with triangular muri. 1, Half grain,  $\times 3100$ ; 2, reticulum M4L6,  $\times 12\ 500$ ; 3, aperture edge showing thin torn nexine,  $\times 12\ 500$ .  
 Figs. 4 and 6. Stub JLC133, Grid ref. 360870, C281/41, 43. Grain from PS48 with partially mazed reticulum and tall, narrow muri. 4, reticulum M1L11,  $\times 12\ 500$ ; 6, whole grain with gaping aperture,  $\times 1550$ .  
 Figs. 5 and 8. Stub JLC128, Grid ref. 316771, C251/43, 45. Half grain from PS35 with mazed reticulum and tall, narrow muri. 5, half grain,  $\times 1550$ ; 8, reticulum M4L12,  $\times 12\ 500$ .  
 Figs. 7, 9–10. Stub JLC126, Grid ref. 303854, C245/39, 45–46. Half grain from PS45 with bimodal lumina and triangular muri. 7, half grain,  $\times 1550$ ; 9, torn 'hinge' of long aperture,  $\times 3100$ ; 10, reticulum M4L5,  $\times 12\ 500$ .



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temporal range: this would not be determined until the species had been erected and would be incidental to the definition of the taxon.

#### CLASSIFICATION OF THE POLLEN GROUP

The 170 grains in the group recovered from the Guincho samples were graded for two continuous parameters: 1–14 for size of lumina (L1 = 0.5  $\mu\text{m}$  approx., L14 = 8.8  $\mu\text{m}$  approx.) and 1–9 for width of muri (M1 = < 0.1–0.2  $\mu\text{m}$  approx., M9 = 0.8  $\mu\text{m}$  approx.). Text-figs. 2, 3, and 4A show the scatter of grains for the 9 samples with more than three grains in this group. The shape of the cross-section of the muri—round, triangular, or narrow—and the mazed-reticulum type are also shown.

The scatter diagrams show the wide range of width of the muri and diameter of lumina which occur in the group as a whole and the extent of variation in each sample. Only sample PS41 has a distribution of grains which are clustered closely together with one type of murus (rounded) and a narrow range in diameter of lumina and width of muri. Similar groupings are seen within a range of greater variation in PS34, PS40, PS41, and PS44 and there is one grain in PS45 in the early–middle Albian, but not in late Albian samples PS35, PS37, PS47, and PS48. Of the grains with similar mural and luminal parameters in the late Albian: in PS37 the grain at M6L5 has rounded lumina, and M6L6 is circumsulcate with a different shape; in PS48, M4L4 is a grain with a thin, detached nexine of different appearance from that in the early–middle Albian grains.

The clusters of grains with rounded muri based on the distribution of those in PS41, and including those from the other early–middle Albian samples, are plotted on text-fig. 4B. The limits of the cluster were set wherever only one grain represented a category of diameter of lumina or width of muri. Hence the subgroup is bounded by outlying grains M3L1, M1L3, M6L4, and M5L6.

Thirty-eight grains fall in the cluster of which 21 have a visible aperture. Of these 4 seem short, 6 are gaping (Pl. 10, fig. 1) and 11 are long, extending more than half the circumference of the grain (Pl. 10, figs. 4 and 8). There is no evidence of any of this subgroup being completely circumsulcate: there are no half grains and some specimens are orientated to show a ‘hinge’ of normal reticulum (Pl. 12, fig. 1).

The value of this cluster as a potential fossil species can be established by consideration of the four points mentioned previously for defining an ideal fossil species: 1, Discrete defining characters—the cluster has no discrete character which is not possessed by other grains in the group. It is defined on an association of characters (round muri, whole grains, uniform size, slightly angular lumina) which occur throughout the range of morphology of the main group. Also the most important of these characters (round muri) is not detectable in the light microscope; 2, The cluster has the associated character of a long aperture which does not completely encircle the grain; 3, The continuously variable characters have a much narrower range in the cluster than in the group as a whole: grain diameter 11–23  $\mu\text{m}$  (only 2 grains are greater than 19  $\mu\text{m}$ ), lumina diameter 0.5–2.0  $\mu\text{m}$ ,

#### EXPLANATION OF PLATE 12

Figs. 1 and 2. Stub JLC62, Grid ref. 259788, C153/36, 40. Cluster grain from PS40 with round muri. 1, whole grain showing complete ‘hinge’,  $\times 3100$ ; 2, aperture margin showing continuous murus and thin granular texture of nexine along aperture, reticulum M5L6,  $\times 12\ 500$ .

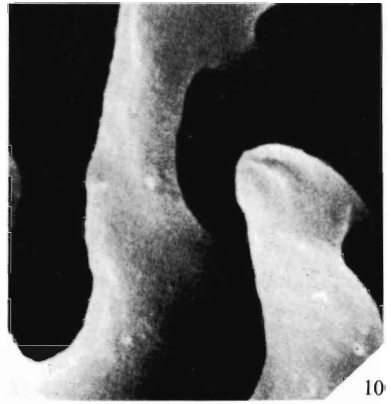
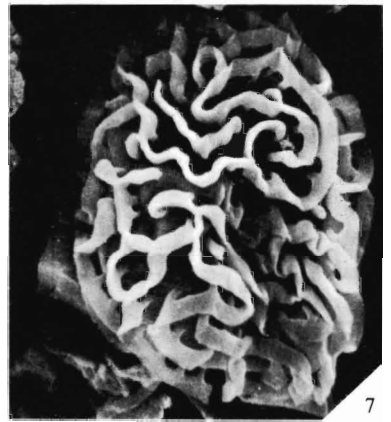
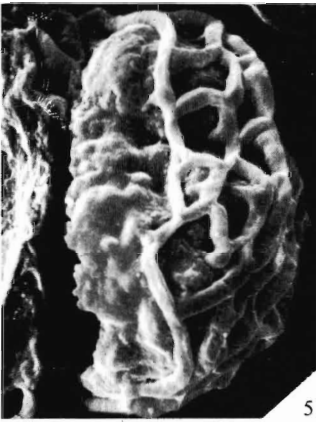
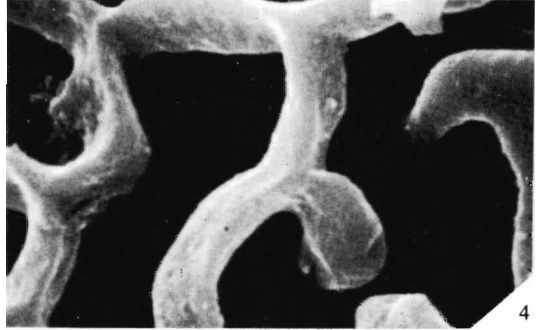
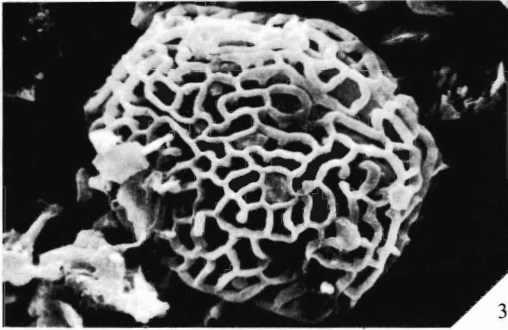
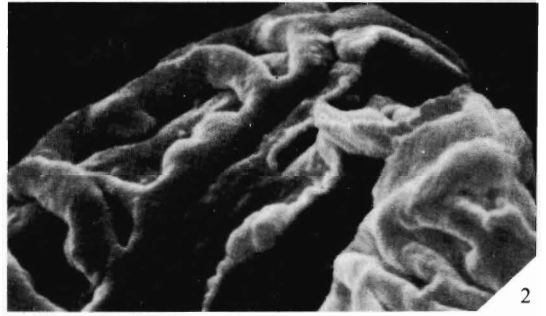
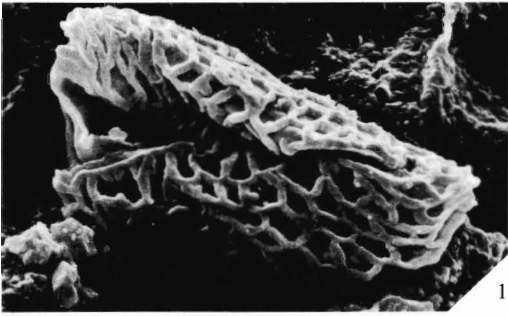
Figs. 3 and 4. Stub JLC128, Grid ref. 289761, C250/8, 12. Grain from PS35 with mazed reticulum and triangular muri. 3, possible half grain,  $\times 1550$ . 4, reticulum M8L11,  $\times 12\ 500$ .

Figs. 5 and 8. Stub JLC62, Grid ref. 304805, C157/10–11. Half grain from PS40 with triangular muri. 5, half grain showing torn nexine along aperture,  $\times 3100$ ; 8, reticulum M9L11,  $\times 12\ 500$ .

Figs. 6 and 9. Stub JLC120, Grid ref. 315761, C235/22–23. Grain from PS43 with tall narrow muri. 6, grain,  $\times 1550$ ; 9, reticulum M9L13,  $\times 12\ 500$ .

Figs. 7 and 10. Stub JLC128, Grid ref. 294852, C250/48, 50. Grain from PS35 with mazed reticulum and tall, narrow muri. 7, grain,  $\times 1500$ ; 10, reticulum M6L10,  $\times 12\ 500$ .





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and muri width 0.2–0.5  $\mu\text{m}$ ; 4, Stratigraphically the cluster has an apparent upper limit at the top of the middle Albian. The lower limit is not determinable from this locality as similar grains occur in the Aptian at other sites in Portugal.

The major weakness of describing this cluster as a species is the lack of any discrete defining character. The boundaries of the cluster were initially set using the continuously variable characters. This highlights one problem of poorly defined species in fossil classification where 'plastic' characters are important. The boundaries of the cluster were set where grain density for any category of muri of lumina was one. This defined the limits of the species on the dimensions of the muri and lumina. However, there is a strong possibility that further specimens from the group plotted on the scatter diagrams would make these boundaries less distinct or destroy them altogether.

The use of continuum characters leads to a paradox in species definition, namely that the smaller the number of specimens the more clearly defined the limits of the species are likely to be, whereas it is highly desirable to have as many specimens as possible representing a species. Species defined on variable characters can only lead to problems for later workers, especially those trying to classify specimens with overlapping morphology. The species is likely, if other grains are included later, to lose the clarity of its morphological limits and ultimately become a 'balloon' taxon (Hughes 1970).

The grains remaining after removal of the cluster are shown on two scatter diagrams (text-fig. 4C, D). Although several discrete characters are shown (triangular, round and tall, narrow muri; normal, bimodal, and mazed reticulum; circumsulcate half grains) there is no consistent association. Some characters do not occur together such as round muri with either bimodal or mazed reticulum. Others which might be expected to be species delimiting, such as the unusual maze-like pattern of muri, occur on grains with quite different mural shapes—triangular and very tall and narrow—and over a considerable range of luminal diameter and the complete range of mural width.

Of the continuously variable characters there is a distinct relationship between mural width and diameter of lumina. This is most obvious in grains with triangular-shaped muri (text-fig. 4C). The grains with narrow muri have small lumina and those with wide muri have large lumina. The alternative associations: narrow muri with large lumina and wide muri with small lumina are very uncommon. The grains with rounded muri seem to have slightly wider muri at any given lumina size than those with triangular muri, and, not surprisingly, the grains with tall, narrow muri have considerably narrower muri than grains with triangular muri and lumina of similar dimensions.

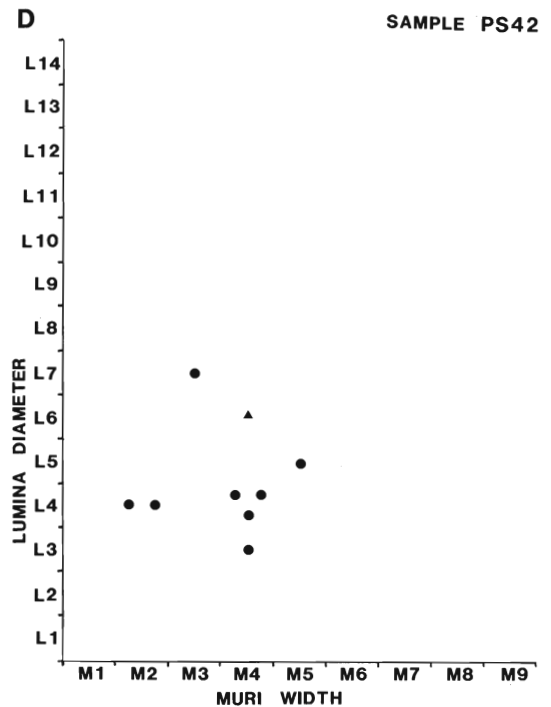
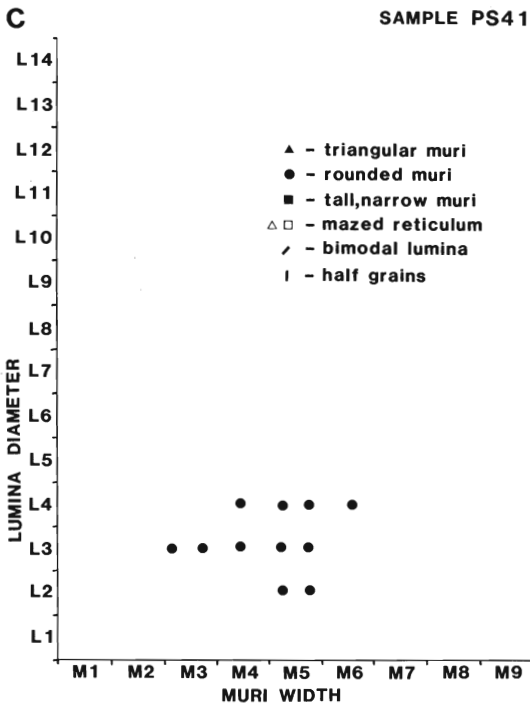
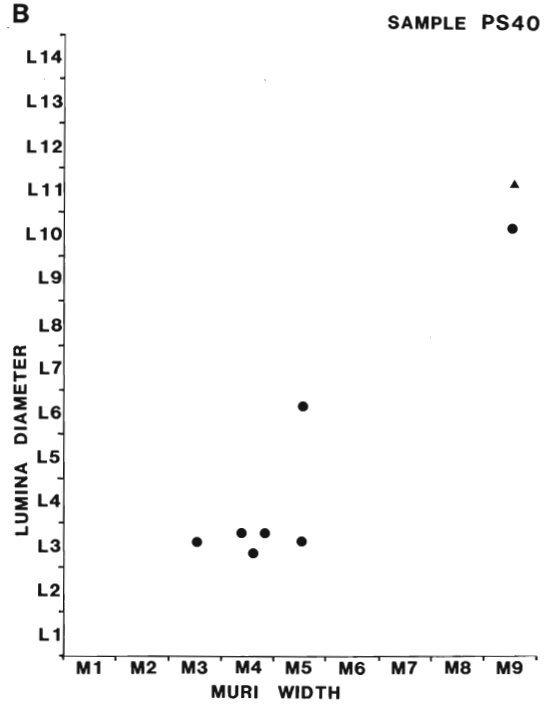
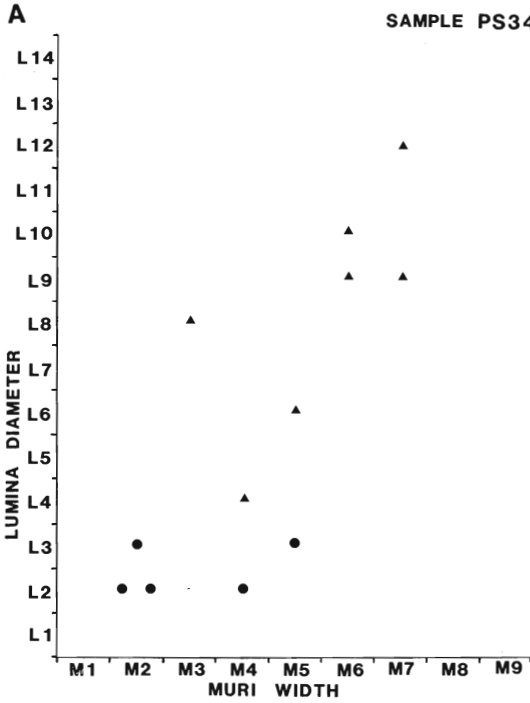
No obvious clusters of grains occur in text-fig. 4C and D which could be extracted and described as fossil species. The discrete characters all occur over too wide a range of continuously variable characters and no consistent combination occurs. This problem is not restricted to this group of pollen. Several other angiosperm pollen groups from Portugal and England show considerable ranges of variation in continuously variable characters. Continua of characters also occur in other fossil groups such as leaves, spores, seeds, and fruits.

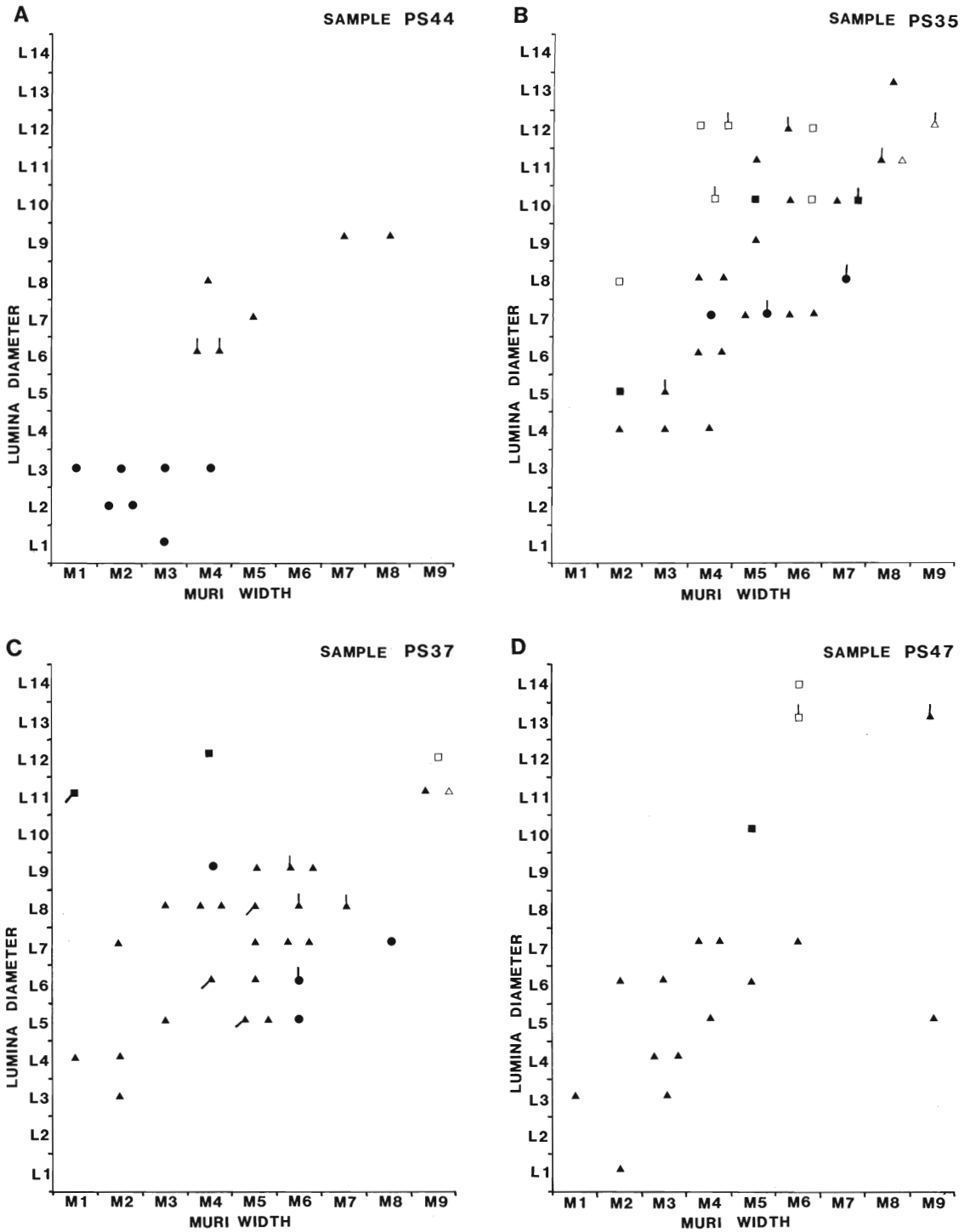
Such continuous variation in fossil groups, which makes it difficult or impossible to classify them into species, is likely to be the result of several different causes: 1, developmental variation due to internal effects, e.g. position of flower in inflorescence or pollen mother cell in anther; 2, environmental variation due to either short or long-term changes in external environment, e.g. climate, soil development, soil salinity affected by sea-level changes; 3, genetic variation within a population at one site and one time (Chapman 1982); 4, migration; 5, the presence of more than one closely

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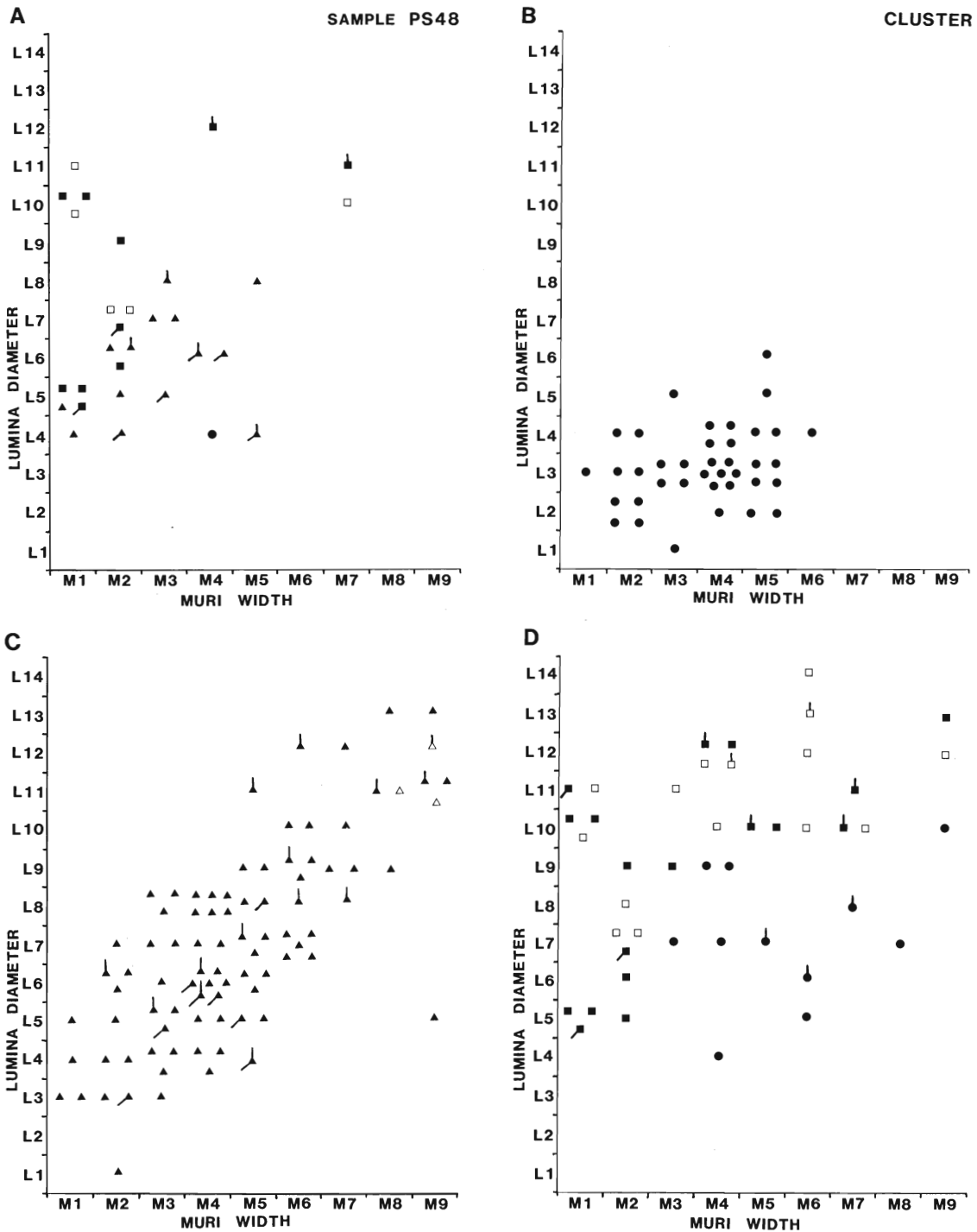
TEXT-FIG. 2A–D. Scatter diagrams of pollen from successive samples from the Albian of Portugal. Each symbol represents a single angiosperm pollen grain which is plotted on the axes of width of muri (M1 = narrowest muri, M9 = widest muri) and diameter of lumina (L1 = smallest lumina, L14 = largest lumina). Solid symbols represent angiosperm pollen grains with a normal regular reticulum, white centred symbols represent grains with the mazed-reticulum pattern and symbols with a slanting line attached are grains with two distinct lumina sizes in the reticulum. Symbols with a vertical line attached represent half grains with long apertures along which the grain has split and the two halves have become separated. The shape of each symbol represents the cross-sectional shape of the muri.







TEXT-FIG. 3A-D. Scatter diagrams of pollen from successive samples from the Albian of Portugal; for symbols see text-fig. 2c.



TEXT-FIG. 4. A, scatter diagram of pollen from sample PS48. B, cluster of grains with muri which are round in cross-section from early-middle Albian samples. C, all grains with muri which are triangular in cross-section. D, all remaining grains not figured in 4B or 4C. For symbols see text-fig. 2c.

related species with similar pollen (Chapman 1982); 6, evolution. The collection of palynomorphs from marine sediments with large catchment areas and of samples which due to settling phenomena, bioturbation, and compression represent several years (possibly several hundreds) will increase variation further.

### CONCLUSIONS

Any group of pollen grains with continuously variable characters (e.g. text-fig 4C, D) is not readily divisible into species. Three possible methods exist for handling data like this: 1, the whole continuum can be designated a single species or other taxon; 2, the continuum can be divided into two or more species or other taxa using one or two of the discrete characters such as shape of muri or reticulum pattern; this would result in other discrete characters occurring in more than one species or, in cases where no other discrete characters occur, in arbitrary boundaries; 3, each fossil can be considered individually and the fossil species concept abandoned.

Of these methods, considering 1 alone seems unsatisfactory as it is no more than a 'balloon' taxon to begin with, and therefore is in time likely to deteriorate in usefulness. Method 2 requires the choice of characters to define the species. In the group described here, suitable characters could be types of reticulum but the normal reticulum category is a continuum in itself. This group was chosen for study because of the large number of discrete characters; at least one much larger group in Portugal has only one or two rarely occurring discrete characters and a continuum of mural and luminal dimensions much greater than that described here. If species have to be erected based on continuous characters, one possible solution would be to define the limits of the species very precisely, and also to define 'halos' of relatedness around the original species for subsequent data which do not fit precisely (e.g. cf. A, cf. B as in the Hughesian biorecord system; e.g. Hughes 1976, p. 27).

Method 3 has validity as most fossils in a sample are probably from different individual plants and/or from different flowering seasons. It would require a very efficient storage and retrieval system as enormous numbers of records would quickly be generated, but has the added attraction of being ideographic (Martinsson 1969), composed of basic data without the 'averaging effect' of human classification. The existence of high-capacity computers makes method 3 possible, but expensive in man hours for fossils as abundant as pollen or spores.

As more SEM data accumulate it may become apparent that different databases from different localities or geological periods require other methods of handling and the same data may be classified in more than one way for different purposes. If fossils are classified by method 2, the problems involved in splitting taxa and erecting fossil species should be discussed fully in the literature.

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