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THE PALYNOLOGY OF SOME PALAEOGENE DEPOSITS BETWEEN THE RIO ESERA AND THE RIO SEGRE, SOUTHERN PYRENEES, SPAIN

BY

P. HASELDONCKX*

ABSTRACT

In this article the results of a palynological investigation of Palaeogene sediments in the Spanish Pyrenees are discussed. A statistical analysis is used to interpret the counts in the absence of extensive biological and stratigraphical information about the species studied. A broad picture of the climatic changes could be reconstructed together with the different vegetational zones in the coastal swamp area. The presence of *Nypa* and *Nothofagus*, probably allochthonous, is at least striking. The biozonation is fitted into a stratigraphic framework based on Foraminifera. A new genus and some new species are described and discussed under Systematics together with all species mentioned in this investigation. A Fortran IV computer programme for the statistical analysis of the data has been added to stimulate other comparative studies.

CONTENTS

INTRODUCTION

The Pyrenees in northeastern Spain consist of an elevated Palaeozoic core bordered in the south by Mesozoic and Cainozoic deposits. The present palynological study covers a Palaeogene sequence of marine, deltaic and fluvial conglomerates, sandstones, siltstones, clays and limestones. These deposits, which reach a total maximum thickness of 2000 m, range in age from Lower Palaeocene to Upper Eocene.

The aim of the study is to reconstruct a general picture of the vegetation and the depositional environment. A systematic study of the palynomorphs was necessary in the absence of earlier palynological investigations in the area. A number of biostratigraphical units is established insofar as the character of the sediments permitted

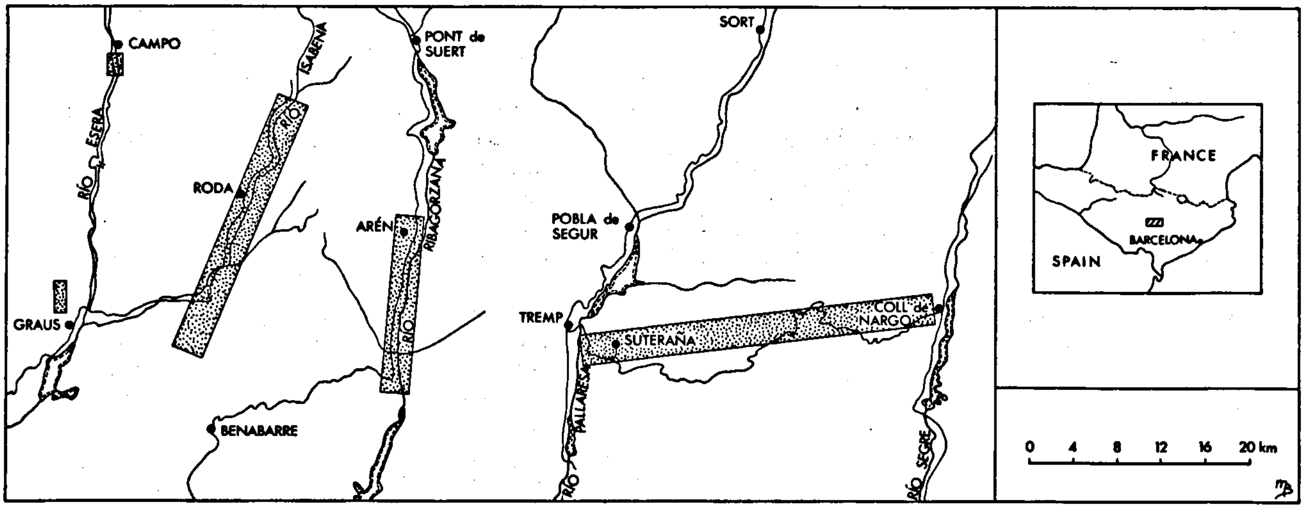

Fig. 1. Index map of Spain. Dotted rectangular is the area of study.

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* Dept. of Stratigraphy and Palaeontology, University of Leiden, The Netherlands.

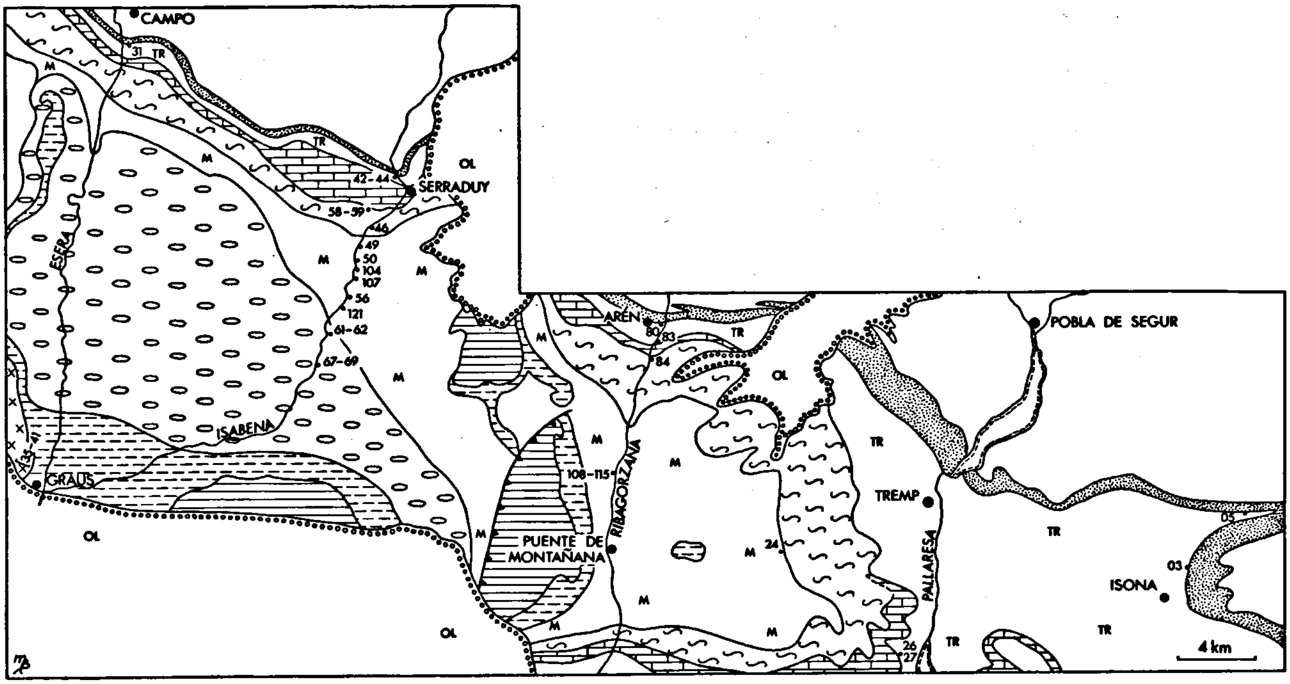

Fig. 2. Generalized geological map of the southern Pyrenees between the Rio Esera and the Rio Sègre with the numbers of the analysed samples.

adequate sampling. These biozones are correlated with the zones recognized on the basis of Foraminifera and Mammalia.

All pollen samples were treated with HCl in order to remove the calcareous cement and subsequently prepared according to Erdtman's procedure (boiling with KOH, followed by acetolysis according to the Faegri & Iversen method, 1950). Finally gravity separation was carried out by means of a bromoform alcohol solution (d = 2.3). All residues of the samples counted are kept in small glass tubes at the Hugo de Vries Laboratory of the University of Amsterdam, Netherlands.

Acknowledgments

I am greatly indebted to Dr. J. H. Germeraad for guiding my first steps in the field of computer and for the offered opportunity to use some basic elements from his palaeontological computer programme. The English text is corrected by Mrs. G. P. Bieger-Smith and Mrs. F. G. M. Madjlessi-Leenen typed the manuscript. The photographs are prepared by Mr. W. C. Laurijssen and the figures by Mr. M. L. Brittijn.

GEOLOGICAL SETTING

Figs. 2 and 3 show the general geological setting of the Lower Palaeogene deposits together with the names of the formations and the numbers of the samples statistically studied. The sequence is located in an anticlinal structure (Pyrenean phase of the Tertiary orogeny, Misch, 1934).

The lower boundary of the interval was taken as the base of the Tremp Formation, which consists of estuarine sediments with basal clay deposits. These clays are rich in vegetable material and some lignite lenses occur in the eastern part of the area. The basal estuarine deposits change into red mudstones with root horizons and lacustrine limestones with caliches, a clear indication of arid deposits. Lagoonal clays at the top of the Tremp Formation are characteristic of a slowly advancing transgression.

The Cadi Formation, following the Tremp Formation, consists mainly of organic limestones partly made up of Alveolinidae, indicating a shallow, tropical sea.

The Roda Formation is characterized by a marly facies, barrier islands and a great amount of plant debris indicating an open marine but coastal sea. The maximum transgressive extension during the Palaeocene and the Lower Eocene can be observed in this formation.

The natural levees, overbank flood plain silts, lagoonal clays and swamp deposits mark the Montañana Formation. These sediments are deltaic in character: the delta moved slowly diachronously during the Eocene from the east-southeast to the north-northwest. The result was a migration of the shore line and the deposition of turbiditic sediments in a deep marine environment.

Thick conglomerates, accumulated from a northern secondary source, overlie the deltaic deposits in the western part of the area and characterize the Santa Liestra Formation.

The overlying Capella and Escanilla Formations show coarse-grained fluvial deposits alternating with marls affected by pedogenesis. A minor transgressive period in

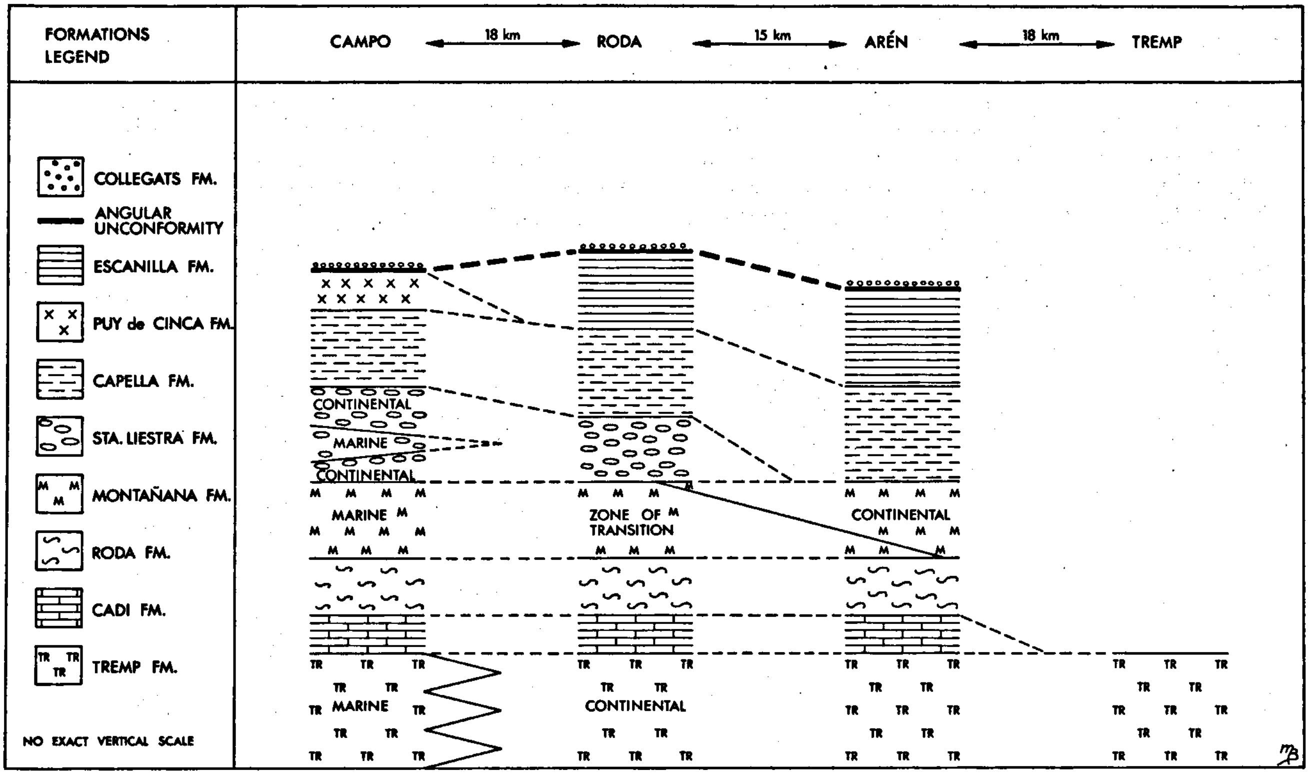

Fig. 3. Schematical E–W section through the studied area.

the southeast resulted in fine-grained sands and lagoonal clays, forming the Puy de Cinca Formation.

These sediments, with a total thickness of more than 2000 m, are unconformably overlain by unimpeded flood plain conglomerates of the Collegats Formation at the boundary of Eocene and Oligocene.

STATISTICAL ANALYSIS

The statistical analysis plays an important part in this investigation in the absence of extensive botanical and more especially stratigraphical information concerning the different species. The analysis includes the following elements: conversion of the counts into percentages, calculation of the probability of re-observation, mean and standard deviation for the different species, entropy determination for each sample and calculation of the correlation coefficient between different species and between successive stratigraphic samples. Finally, the averages of the percentages, the probability of re-observation, the entropy and the coefficient of correlation are calculated for the total of the data input. The statistical analysis is checked by means of the Chi-square test and the Student's T-test.

The counts form multivariate data, which can be analysed in a number of combinations. Thus the statistical analysis is applied to the samples of each section (sample run 1), the various species (species run 2) and all samples of each formation in all sections (formation run 3) and all samples in all sections (total run 4). The biostratigraphical zonation and the vegetational zones are based on conclusions resulting from the statistical analysis and from botanical and stratigraphical information from other and earlier investigations.

The occurrences are expressed in terms of the probability of re-observation (P), i. e. if a specified number of additional specimens from a new sample of the same rock or stratum were to be investigated. This re-observation of the species may be in any number of specimens, including one only (Germeraad et al., 1968, p. 192). In order to avoid the impression of high accuracy and to facilitate visual evaluation of the charts, the probability values on the distribution charts were grouped into classes, each class being indicated as follows:

P 0.01–0.75 = •
0.75–0.90 = /
0.90–0.95 = ○
0.95–0.99 = ◉
0.99–1. = ●

A vertical line on the biostratigraphical zonation charts indicates a P-value greater than 0.95, a dashed vertical line indicates a P-value between 0.75 and 0.95.

The mean and the standard deviation provide some fundamental indications of the depositional environment after pollen transport. If pollen grains are found in a terrestrial environment, the transport has to be minimal. This terrestrial environment can cause sharp fluctuations in the pollen spectra, dependent upon external factors such as changes in temperature, humidity, ground water level and so on. These fluctuations are reflected in relatively high values of standard deviation in contrast to the means. In the event of considerable transport of pollen grains in a fluvio-marine environment, the fluctuations in the pollen spectra will be less: this results in a certain degree of mixing of different species which will be reflected in the diagrams as a relatively low standard deviation in contrast to the mean (Fig. 4).

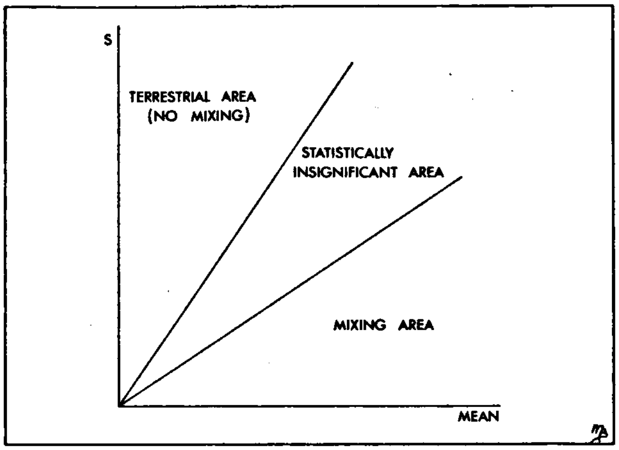

Fig. 4. The s/mean diagram, showing the different degrees of mixing.

A further study of the relationship between the mean and the standard deviation can give a broad indication of the depositional environment. These data are also important for biostratigraphical zonation, since they indicate the value of a species as a time indicator. The chance of finding a time indicator is greater when the facies influence is statistically lower.

The entropy for each sample studied is the degree of dominance of a species or an association of species in the pollen spectrum. Dominance has a value of 0 and the absence of dominance or chaos, a value of −100. The degree of mixing in one sample is indicated by the entropy and can be compared with the standard deviation in one species distribution.

The correlation coefficient is used in this statistical analysis for comparison between different species and between stratigraphically successive samples. The value of the correlation coefficient (R) fluctuates between +1 (full correlation) and −1 (full dissociation), which gives an indication of the change in flora between two samples.

A separation of species according to the area of origin is possible by the computation of the correlation coefficient for the different species. The value of R indicates the degree of association or dissociation and it has been found that values greater than 0.5 and less than −0.5 are useful for distinguishing between different species. A striking example of the possibilities of such a statistical analysis is the correlation coefficient for *Laevigatosporites gracilis* and *Laevigatosporites haardti*. The results demonstrate a dissociation of the two species in nearly all formations and add an extra dimension to our botanical information, which is restricted for both species to an affinity with the Familia Schizaeaceae. These species consequently must have different areas of origin.

SYSTEMATICS

Anteturma SPORITES H. Potonié 1893

Turma TRILETES Reinsch 1881

Leiotriletes microadriennis Krutzsch 1959
Leiotriletes adriennis (R. Potonié & Gelletich 1933) Krutzsch 1959 subsp. *pseudomaximus* (Thomson & Pflug 1953) Krutzsch 1959
Leiotriletes asp. *microsinuosoides* Krutzsch 1962
Concavisporites acutus Pflug 1953
Undulatisporites concavus Kedves 1961
Stereisporites stereoides stereoides (R. Potonié & Venitz 1934) Thomson & Pflug 1953 subsp. *stereoides* Krutzsch 1967
Cyclosporites hughesi Cookson & Dettmann 1959
Comments: a reworked spore from Mesozoic strata.
Cicatricosisporites dorogensis R. Potonié & Gelletich 1933
Cicatricosisporites chattenis Krutzsch 1961 subsp. *chattenis* Krutzsch 1967

Cicatricosisporites hispanicus n. sp.

Description: trilete microspore; contour convex. The laesurae are thin. Sculpture type: striate; the striae are highly developed, 3–4 μ thick and lie as bands around the spore. Exine M: 0.5 μ. Size: 37 x 41 μ.
Frequency: single specimen.
Stratigraphical range: Puy de Cinca Formation (Bartonian).
Botanical affinity: Schizaeaceae.
Holotype: Slide P 41. Loc.: 20.9 x 97.5 (micr. PO-1).
Locality: San Martin (Graus), Esera Valley, Pyrenees, Spain.

Trilites verrucatus Couper 1953
Foveotriletes crassifovearis crassifovearis Krutzsch 1962
Foveotriletes crassifovearis Krutzsch 1962 subsp. *microfovearis* Krutzsch 1967
Filtrotriletes nigeriensis Van Hoeken-Klinkenberg 1966
Planisporites sp. Knox 1950
Echinatisporis echinoides Krutzsch 1963 subsp. *treplinensis* Krutzsch 1963
Echinatisporis longechinus Krutzsch 1959
Comments: our specimens are smaller than those described by Krutzsch 1963, p. 102.

Microfoveolatosporis garumniensis n. sp.

Description: azonomonolete microspore; contour spherical. Very pronounced wall. Laesurae ca. 2 μ thick. Sculpture type: microfoveolate, not clear. Exine M: 1 μ. Size: 25 x 25 μ.
Frequency: single specimen.
Stratigraphical range: top Tremp Formation (Thanétian).
Botanical affinity: Schizaeaceae.
Holotype: Slide P 83. Loc.: 19.5 x 107.8 (micr. PO–1).
Locality: Arén, Ribagorzana Valley, Pyrenees, Spain.

Tabulasporites n. gen.

Diagnosis: free, anisopolar, bilateral, monolete spore; laesurae long. Spore plano-convex in lateral view, exine thin. The sculpture looks like 'corniches' (tabulae in latin), clearly visible at the margin of the spore as baculae.
Botanical affinity: Pteridophyta.

Tabulasporites kokki n. sp.

Description: bilateral, monolete microspore; contour planoconvex. Laesurae 28 μ long, 1.2 μ thick. Sculpture type: baculate, baculae 2 μ high and 1 μ wide at the base. 'Corniches' are 1.5 μ wide and form an irregular pattern on the spore wall. Exine M: 1 μ. Size: 25 x 35 μ. Size range: 20–35 μ.
Frequency: rare.
Stratigraphical range: Puy de Cinca Formation (Bartonian).
Botanical affinity: probably Lycopodiaceae.
Generotype: Slide P 41. Loc.: 23.5 x 104.7 (micr. PO–1).
Locality: San Martin (Graus), Esera Valley, Pyrenees, Spain.

Baculatisporites gemmatus Krutzsch 1959
Toroisporis longitorus Krutzsch 1959
Polypodiaceoisporites speciosus (R. Potonié 1934) R. Potonié 1954

Polypodiaceoisporites tumidus n. sp.

Description: trilete microspore; contour convex. Laesurae 4–5 μ thick, with a swelling (tumidus in latin) almost at the end. Sculpture type: psilate. Cingulum max. 6 μ wide, without sculpture and thinner at the coins of the spore. Exine M: 1.5 μ. Size: 26 x 24 μ.
Frequency: single specimen.
Stratigraphical range: Montañana Formation (Cuisian).
Botanical affinity: Schizaeaceae.
Holotype: Slide P 104. Loc.: 19.2 x 94. (micr. PO–1).
Locality: Isabena Valley, Pyrenees, Spain.

Polypodiaceoisporites sp. a

Description: a single specimen; poor conservation prohibits accurate description. The laesurae show a bifurcation at the end. Sculpture type: reticulate (indistinct). Exine M: 0.5 μ. Size: 26 x 24 μ.
Frequency: single specimen.
Stratigraphical range: Montañana Formation (Cuisian).
Botanical affinity: probably Schizaeaceae.
Example: Slide P 104. Loc.: 10.6 x 93.8 (micr. PO–1).
Locality: Isabena Valley, Pyrenees, Spain.

Verrucingulatisporites paxuderma n. sp.

Description: trilete microspore; contour convex. Sculpture type: verrucate; pseudocingulum, ca. 7 μ thick, is built up by great, basically melted verrucae. The laesurae, 3 μ thick, reach the pseudocingulum. Exine M: 0.2 μ. Size: 33 x 34 μ without pseudocingulum. Size range: 28–40 μ.
Frequency: rare.
Stratigraphical range: Tremp Formation (Thanétian), Sta. Liestra Formation (Lutetian) and Puy de Cinca Formation (Bartonian).
Botanical affinity: Pteridophyta, incertae sedis.
Holotype: Slide P 43. Loc.: 19.1 x 109.4 (micr. PO–1).
Locality: Serraduy, Isabena Valley, Pyrenees, Spain.

Laevigatosporites gracilis Wilson & Webster 1946
Laevigatosporites haardti (R. Potonié & Venitz 1934) Thomson & Pflug 1953
Echinosporis echinatus Krutzsch 1967
Cicatricosisporites pseudodorogensis Krutzsch 1959

Reticulosporis minimus n. sp.

Description: monolete spore; contour spherical; laesurae thin. Sculpture type: reticulate, dense pattern, lumina ca. 0.8–1 μ. Exine M: 0.5 μ. Size: 25 x 28 μ. Size range: 20–30μ.
Frequency: rare.
Stratigraphical range: Montañana Formation (Cuisian) and Sta. Liestra Formation (Lutetian).
Botanical affinity: Schizaeaceae.
Holotype: Slide P 68. Loc.: 20.8 x 105 (micr. PO–1).
Locality: Isabena Valley, Pyrenees, Spain.
Verrucatosporites alienus (R. Potonié 1931) Thomson & Pflug 1953

Anteturma POLLENITES R. Potonié 1931

Turma BILATERES Pflug 1953

Echigraminiditis arensis n. sp.

Description: monoporate, tectate pollen grain; contour spherical. Sculpture type: micro-echinate, echinae 1.5–2 μ long and 0.2 μ thick, pore not always clearly visible. Pore D: 1.5–2 μ. Exine M: 1 μ. Index pollinis:

subspheroidal. Size: 14 x 13 μ. Size range: 10–18 μ.
Frequency: rare.
Stratigraphical range: up to the Tremp Formation (Thanétian) and including the Roda Formation (Sparnacian).
Botanical affinity: Monocotyledonopsida, incertae sedis.
Holotype: Slide P 80. Loc.: 21.7 x 100.2 (micr. PO–1).
Locality: Arén, Ribagorzana Valley, Pyrenees, Spain.

Graminiditis laevigatus Krutzsch 1970
Spinizonocolpites baculatus Muller 1968
Spinizonocolpites echinatus Muller 1968
Monocolpopollenites tranquillus tranquillus (R. Potonié 1934) Thomson & Pflug 1953
Arecipites pseudoconvexus Krutzsch 1970
Arecipites longicolpatus Krutzsch 1970
Arecipites butomoides Krutzsch 1970
Arecipites convexus (Thiergart 1937) Krutzsch 1970

Turma INAPERTURES Thomson & Pflug 1953

Inaperturopollenites hiatus (R. Potonié 1931) Thomson & Pflug 1953
Inaperturopollenites dubius (R. Potonié & Venitz 1931) Thomson & Pflug 1953
Sequoiapollenites polymorfosus Thiergart 1937
Cupressacites cuspidataeformis (Zaklinskaja 1957) Krutzsch 1971

Turma SACCITES Erdtman 1947

Pityosporites insignis (Naumova, ex Bolchovitina 1953) Krutzsch 1971
Pityosporites macro-insignis Krutzsch 1971
Pityosporites scopulipites Wodehouse 1933
Pityosporites minutus (Zaklinskaja 1957) Krutzsch 1971
Pityosporites micro-alatus (R. Potonié 1931) Thomson & Pflug 1953
Zonalapollenites igniculus (R. Potonié 1931) Thomson & Pflug 1953
Sciadopityspollenites verticillatiformis (Zauer 1960) Krutzsch 1971

Turma ASSYMETRES Pflug 1953

Multiporopollenites maculosus (R. Potonié 1931) Thomson & Pflug 1953

Turma BREVAXONES Thomson & Pflug 1953 and LONGAXONES Pflug 1953

Both turma can no longer be used in modern systematic palynology, although today there is no better classification for European Tertiary pollen available. The species, belonging to these groups are classified alphabetically.

Compositoipollenites rizophorus (R. Potonié 1931) R. Potonié 1951
Ephedripites sp. Bolchovitina 1953
Ephedra voluta Stanley 1965

Nothofagidites duskritos n. sp.

Description: poly-orate pollen grain; ora (fissures) vestigial, 1.5–5 μ deep, six in number; grain subspheroidal, equator polygonal, straight to convex contour between the ora. Exine very thin, ca 0.5 μ, no further structure distinguishable. Sculpture type: finely papillate-granular, dense. Papillae projecting less than 0.4 μ in optical section. Size: 39 x 39 μ.
Frequency: a single specimen.
Stratigraphical range: Montañana Formation (Cuisian).
Botanical affinity: probably *Nothofagus* (Fagacae).
Holotype: Slide P 58. Loc: 15.8 x 107 (micr. PO–1).
Locality: Isabena Valley, Pyrenees, Spain.
Comments: The presence of *Nothofagus* pollen in the northern hemisphere during the Eocene is still speculative. However *Nothofagus* pollen were described by Ma Khin Sein (1961) in The London Clay and by Kedves (1964) in Hungary. Ma Khin Sein proposed the autochthony of *Nothofagus* in the London Clay on the basis of a leaf remnant, found and described by Bandulska in 1924 as *Nothofagus stopesae.* The determination of *Nothofagus stopesae* must be brought up for discussion: the morphology and the anatomy of the leaf may indicate a possible affinity with *Nothofagus* but nowhere does Bandulska describe the presence of resinuous papillae underneath the *Nothofagus stopesae* leaf, although these papillae are an important distinguishing feature of *Nothofagus.* We do not believe in the autochthony of *Nothofagus* in the northern hemisphere during the Eocene. Hardly any macrofossils are attributed to *Nothofagus* and there are only a few pollen grains with a possible affinity to *Nothofagus.* Therefore, long-distance transport seems to be more probable in view of our present-day knowledge of the distribution of *Nothofagus.*

Oculopollis sp. Pflug 1953
Periporopollenites perplexus Nakoman 1957
Plicapollis pseudo-excelsus (Krutzsch 1958) Krutzsch 1962
subsp. *luteticus* Kedves 1969
    semiturgidus Pflug 1953
    pseudo-excelsus Krutzsch 1962
Polycolpites clavatus Couper 1953

Stephanocolpites aletos n. sp.

Description: stephanocolpate pollen grain; grain subspheroidal, circular in polar view and convex between the colpi. Colpi 7–16 μ deep, four in number. Sculpture type: scabrate, scabrae ca. 0.8 μ high. Exine M: 1 μ. Size: 40 x 47 μ.
Frequency: a single specimen.
Stratigraphical range: top Tremp Formation (Thanétian).
Botanical affinity: incertae sedis.
Holotype: Slide P 26. Loc.: 21.7 x 96.5 (micr. PO–1).

Locality: Guardia de Tremp, Pallaresa Valley, Pyrenees, Spain.

Stephanocolpites exargilla n. sp.

Description: stephanocolpate pollen grain; grain subspheroidal, circular in polar view and convex between the colpi. Colpi 2 μ deep, four in number. Sculpture type: striate. Exine M: 0.4 μ. Size: 26 x 28 μ.
Frequency: single specimen.
Stratigraphical range: Sta. Liestra Formation (Lutetian).
Botanical affinity: incertae sedis.
Holotype: Slide P 67. Loc.: 22.8 x 108.3 (micr. PO–1).
Locality: Isabena Valley, Pyrenees, Spain.

Symplocoipollenites vestibulum R. Potonié 1951
Stephanoporopollenites hexaradiatus (Thiergart 1940) Thomson & Pflug 1953

Tetracolporites convexus n. sp.

Description: tetracolporate, tectate pollen grain: grain oblate, contour convex between the colpi. Colpi ca. 3 μ deep. Pore D: 0.4 μ. Sculpture type: reticulate; lumina D: 0.5 μ. Exine M: 1.5–2 μ. Size: 31 x 39 μ.
Frequency: frequent in the Montañana Formation.
Stratigraphical range: Montañana Formation (Cuisian).
Botanical affinity: incertae sedis.
Holotype: Slide P 110. Loc.: 24.1 x 113.5 (micr. PO–1).
Locality: Ribagorzana Valley, Pyrenees, Spain.

Tetracolporopollenites manifestus (R. Potonié 1931) Thomson & Pflug 1953 subsp. *contractus* Pflug 1953
Thomsonipollis magnificus (Thomson & Pflug 1953) Krutzsch 1960
Triatriopollenites rurensis Pflug & Thomson 1953
Triatriopollenites quietus (R. Potonié 1931) Thomson & Pflug 1953
Triporopollenites megagranifer (R. Potonié 1931) Thomson & Pflug 1953
Tricolpopollenites hians (Stanley 1965) Elsik 1968
Tricolpopollenites micro-henrici (R. Potonié 1931) Thomson & Pflug 1953

Tricolpopollenites montañanensis n. sp.

Description: tricolpate, tectate pollen grain. Contour triangular in polar view, convex between the colpi. Sculpture type: reticulate; lumina D: 0.2–0.4 μ; columellae indistinct. Exine M: 0.8 μ. Size: 40 x 39 μ. Size range: 38 x 45 μ.
Frequency: rare.
Stratigraphical range: Montañana Formation (Cuisian).
Botanical affinity: incertae sedis.
Holotype: Slide P 110. Loc.: 19.3 x 106.5 (micr. PO–1).
Locality: Ribagorzana Valley, Pyrenees, Spain.

Tricolporopollenites cingulum (R. Potonié 1931) Thomson & Pflug 1953
subsp. *pusillus* (R. Potonié 1934) Thomson & Pflug 1953
oviformis (R. Potonié 1934) Thomson & Pflug 1953
Tricolporopollenites kruschi (R. Potonié 1934) Thomson & Pflug 1953
Triporopollenites robustus Pflug 1953
Vacuopollis sp. Pflug 1953

Turma MASSULOIDES Thomson & Pflug 1953

Tetradopollenites ericius (R. Potonié 1931) Thomson & Pflug 1953

Fungal spores

Polyadosporites hammenii n. sp.

Description: inaperturate, psilate fungal spore, composed of several grains in a spherical pattern. The shape of the grains is variable. Wall thickness: 0.5 μ. Size: 24 x 24 μ.
Stratigraphical range: continuous.
Lecto-generotype: Slide P 80. Loc.: 22.7 x 102.2 (micr. PO–1).
Locality: Arén, Ribagorzana Valley, Pyrenees, Spain.
Comments: the generotype, described by van Der Hammen (1954), is not valid, according to R. Potonié, 1960 (Synopsis der Gattungen der Sporae Dispersae, Teil II).

Basidiosporites fournierri Elsik 1968

Lacrimasporites magnus n. sp.

Description: monoporate, psilate fungal spore; apical pore: 0.8 μ. Wall with two layers ca. 1.2 μ thick; inner layer 0.7 μ; no basal attachment area. Size: 15 x 26 μ.
Stratigraphical range: Sta. Liestra and Puy de Cinca Formations (Lutetian-Bartonian).
Holotype: Slide P 37. Loc.: 26.1 x 103.4 (micr. PO–1).
Locality: San Martin (Graus), Esera Valley, Pyrenees, Spain.

Multicellaesporites elongatus Sheffy & Dilcher 1971
Diporisporites hammenii Elsik 1968
Staphlosporonites allomorfosus Sheffy & Dilcher 1971
Pluricellaesporites serratus Sheffy & Dilcher 1971
Pluricellaesporites subcapsilaris Sheffy & Dilcher 1971
Comments: the holotype described by Sheffy & Dilcher 1971 is tricellate, our species are tetracellate. In our opinion, this is not sufficient to establish a new species or subspecies.
Dicellaesporites levis Sheffy & Dilcher 1971

Algal Spores

Monogemmites pseudosetarius (Weyland & Pflug 1957) Krutzsch 1970

Microplankton

Hystrichosphaera Wezel 1933
Tytthodiscus Norem 1955

Other Remains

Ovoidites parvus Cookson & Dettmann 1959
Affinity: statocysts of Bryozoa.
Ovoidites pococki Nakoman 1966
Affinity: statocysts of Bryozoa (Thomson & Pflug 1953), Magnoliaceae (Nakoman 1966).

THE BIOSTRATIGRAPHICAL ZONATION

The zones recognized in this investigation are biostratigraphical units in the sense of the 'International Subcommission on Stratigraphic Terminology', Copenhagen (1961). They should not therefore a priori be considered time stratigraphical units and in fact some of the boundaries of the zones are diachronous throughout the area studied. The statistical analysis can indicate the probable value of a species as a time indicator. The species characterizing a range-zone or belonging to an assemblage-zone are shaded if they are believed to have a probable value as time indicators. A limited number of key fossils, compiled by Krutzsch (1966a & b) and Kedves (1967, 1968), are also used. These key fossils are dotted in Fig. 5. A substantial handicap in establishing the stratigraphy is the large number of barren samples, due to marked oxydation and pedogenesis of most samples.

Zone 39: The *Arecipites butomoides* assemblage-zone is characterized by the presence of *Arecipites butomoides, Ephedra voluta, Arecipites convexus, Echigraminiditis arensis, Graminiditis laevigatus* and *Tricolpopollenites hians.* This zone is restricted to the base of the Tremp Formation. A more pronounced differentiation of species is found in the Ribagorzana section, where *Trilites verrucatus* and *Verrucingulatisporites paxuderma* also belong to this zone. The lignitic samples between Coll de Nargo and Tremp were almost all barren, due to a high content of coal. Medus (1970) investigated a sample from the base of the Tremp Formation near Suteraña and regarded this sample as Maastrichtian because of the strong dominance of Palmae pollen. The key fossils characterizing the Maastrichtian are missing from the samples of the *Arecipites butomoides* assemblage-zone. Since the dominance of Palmae extends to the Eocene in the area studied and since *Normapolles* are missing and stratigraphically younger tricolporate pollen types are found, this dating cannot be accepted. A correlation of this *Arecipites butomoides* assemblage-zone with an association of pollen grains from the Paris Basin does not seem meaningful, because the associations from Palaeogene deposits in the Spanish Pyrenees and in the Paris Basin differ too much. The same is almost true for the biozonation in Central Europe compiled by Krutzsch (1966b), although some zones can be correlated. The *Arecipites butomoides* assemblage-zone at the base of

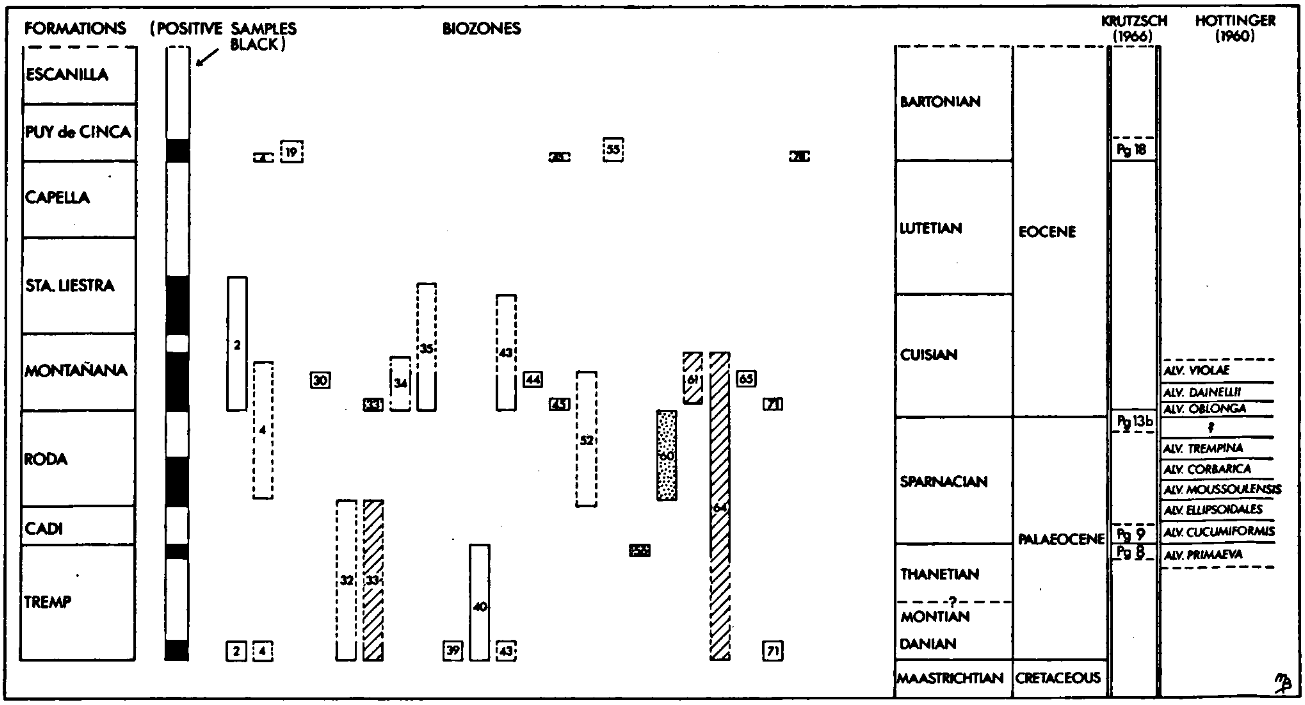

Fig. 5. Suggested correlations between the biozonation and the pollen zones in Central Europe (Krutzsch 1966b) and the *Alveolina* zones in the s. Pyrenees (Hottinger 1960).

the Palaeocene (Danian-Montian) can be regarded as *Plicapollis pseudo-excelsus* and the *Myricoid* pollen types do not occur in the Upper Cretaceous.

Zone 40: The *Arecipites convexus* assemblage-zone coincides with the Tremp Formation. The elements of the *Arecipites butomoides* zone and especially *Graminiditis laevigatus* are characteristic for this new zone. The top of the *Arecipites convexus* assemblage-zone coincides with the *Alveolina primaeva* zone and is placed in the Thanétian on the basis of micropalaeontological evidence. *Stephanoporopollenites hexaradiatus* is a key fossil for the Thanétian zones II and III in the Paris Basin and Foraminifera as well as palynomorphs here indicate the same age. The boundary between zones Pg. 8 and Pg. 9 of Krutzsch (1966b) lies in the uppermost part of the *Arecipites convexus* zone. Zone Pg. 8 is characterized by the presence of *Stephanoporopollenites hexaradiatus, Symplocoipollenites vestibulum* (Symplocaceae) and high percentages of *Triatriopollenites quietus.* Zone Pg. 9 starts with the first occurrence of the *Microfoveolatosporis pseudodentatus* group. A further limitation of zones Pg. 8 and Pg. 9 cannot be given for the area studied.

Zone 64: The *Tricolpopollenites hians* assemblage-zone, indicated in the statistical analysis as a probable time indicator, runs from the Tremp Formation through the Montañana Formation and includes a series of species with limited stratigraphical range. These species are discussed in detail in the *Arecipites convexus* zone, the *Triporopollenites megagranifer* zone and the *Compositoipollenites rizophorus* zone. These three zones may be considered subzones of the *Tricolpopollenites hians* assemblage-zone.

Zone 60: The *Triporopollenites megagranifer* range-zone starts at the base of the Tremp Formation and ends in the lower Montañana Formation. It is highly limited in occurrence. Krutzsch (1966b) places *Triporopollenites megagranifer* in zones Pg. 13b to Pg. 17 with the highest frequency in zone Pg. 15. The correlation with these Central European zones is problematical, because *Triporopollenites megagranifer* has a lower stratigraphical range in the area studied and already disappears in correlated zone Pg. 13b. The *Triporopollenites megagranifer* range-zone includes the *Alveolina moussoulensis* zone and the *Alveolina dainellii* zone. These *Alveolina* zones are dated by Hottinger (1960) from the Middle Ilerdian (Palaeocene) to the Middle Cuisian (L. Eocene). The *Triporopollenites megagranifer* range-zone is characteristic of the Isabena section and is absent in the other sections.

Zone 45: The *Ephedra voluta* assemblage-zone is determined by the co-occurrence of *Ephedra voluta* and *Pityosporites insignis.* This *Ephedra voluta* zone covers the base of the Montañana Formation and coincides with the *Alveolina dainellii* zone (M. Cuisian). Krutzsch (1966b) places the *Ephedroid* pollen types in the Eocene, so that the boundary of the Sparnacian and the Cuisian can be expected in the nodular limestone horizon of Roda de Isabena.

Zone 61: The *Compositoipollenites rizophorus* range-zone comprises the middle of the Montañana Formation and coincides with a part of the *Alveolina dainellii* and the *Alveolina violae* zones, dated by Hottinger (1960) as the top of the Cuisian. *Compositoipollenites rizophorus* runs from zone Pg. 11 to Pg. 18 (Eocene) in the stratigraphical column of Krutzsch (1966b) and this supports the conclusions from the *Ephedra voluta* assemblage-zone. The statistical analysis gives some indication of a probable value of *Compositoipollenites rizophorus* as a time indicator.

Zone 30: The *Reticulosporis minimus* assemblage-zone is determined by the occurrence of *Reticulosporis minimus. Cupressacites cuspidataeformis, Spinizonocolpites baculatus* and *Spinizonocolpites echinatus, Tricolpopollenites montañanensis* and *Tetracolporites convexus.* The *Reticulosporis minimus* assemblage-zone only occurs in the Ribagorzana section and lies in the middle of the *Compositoipollenites rizophorus* zone.

Zone 35: The *Spinizonocolpites echinatus* range-zone runs from the base of the Montañana Formation to the middle of the Sta. Liestra Formation. Kedves (1968) dates *Nypa* in the Paris Basin from Upper Cuisian to Lutetian.

Zone 19: The *Tabulasporites kokki* range-zone is characteristic of the base of the Puy de Cinca Formation, although this species shows a relatively low probability of re-observation. *Thomsonipollis magnificus* and *Tetradopollenites ericius* also appear in this zone. The *Tabulasporites kokki* range-zone can be correlated with zone Pg. 18 from Krutzsch (1966b) and must be placed at the base of the Bartonian. This zone is characterized by the presence of *Tabulasporites kokki,* related to the *Polypodiites* group which appears at first in the Bartonian, the disappearance of *Compositoipollenites rizophorus,* the low frequency of *Plicapollis pseudoexcelsus* and the high frequency of *Monocolpopollenites tranquillus.* The location of the Puy de Cinca Formation at the boundary of the Lutetian and Bartonian is also based on a Mollusca fauna.

To summarize this chapter, we can ascertain that it is possible to build up a biozonation and to place it in a stratigraphic framework despite the small number of positive samples and the occurrence of only a few key fossils in the area studied. This stratigraphic framework can be used for Foraminifera as well as palynomorphs. Correlation, based on palynomorphs, does not seem possible with the Paris Basin in view of our present knowledge. Correlation with the zonation, determined for Central Europe partly succeeded. This correlation is imperfect because of a difference in geographical position, and the resulting facies differentiation.

THE PALAEO-ECOLOGY

The vegetation zones, sketched in Fig. 7, show the most distinguishable zones in the Palaeogene.

a. The *Nypa* zone:

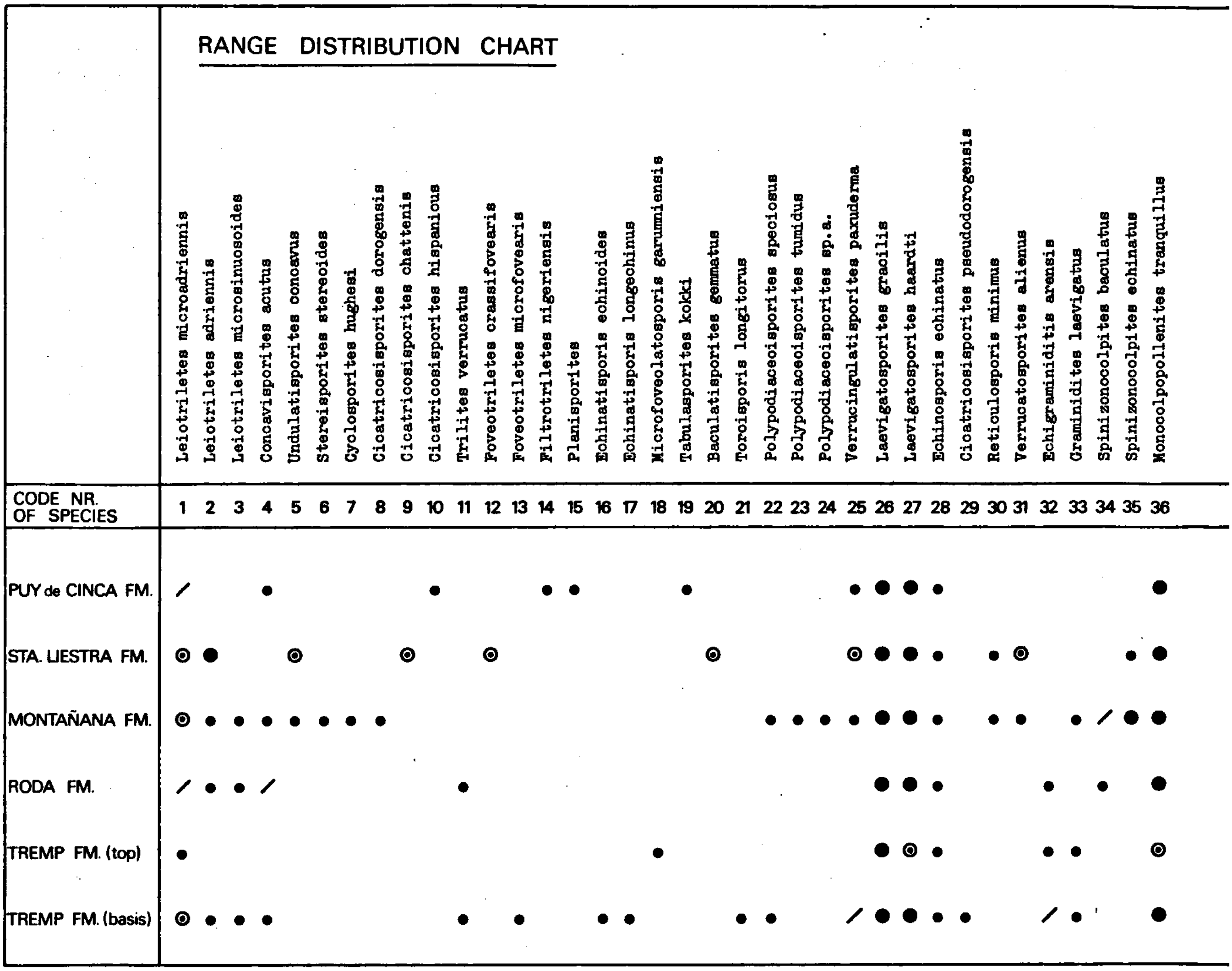

Fig. 6.

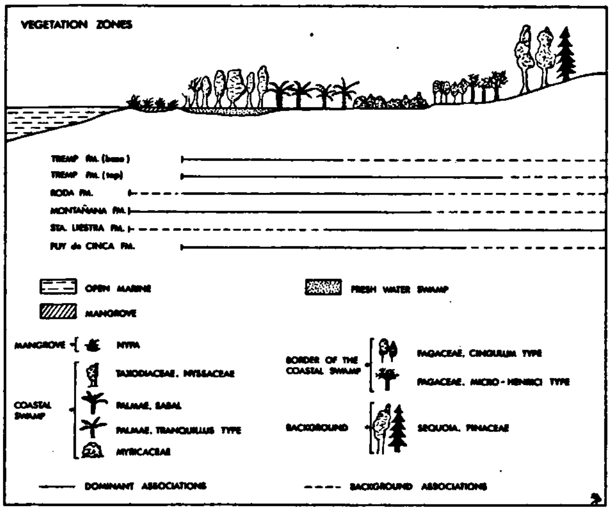

Fig. 7. Sketch illustrating the shore vegetation in the Palaeocene and Eocene.

Nypa fructicans is at present restricted to the mangrove environment of the humid Indo-Malesian tropics, from the Ganges delta to northern Australia. Tralau (1964, p. 17) noted the geographic distribution along the shores of the former Tethys and adjoining seas during the Eocene. The disappearance of *Nypa* during the Lutetian in S. America and Nigeria is explained by Germeraad et al. (1968, p. 204) by an increasing aridity coupled with the development of a pronounced seasonal climate. The autochthony of *Nypa* palms in southwestern Europe is discussed in Haseldonckx (1972). *Nypa* is dominant in the tidal environment and forms there a formation in itself.

b. The Taxodiaceae-Nyssaceae zone:

The Taxodiaceae and the Nyssaceae have no salt tolerance and grow in the most humid places in the coastal swamp (Gleason & Cronquist, 1964). The ground is generally below water. An association of Taxodiaceae-Nyssaceae and not Taxodiaceae-Cupressaceae is striking. Nyssaceae grow in cooler climatological conditions than

Arecipites pseudoconvexus 37	Arecipites longicolpatus 38	Arecipites butomoides 39	Arecipites convexus 40	Inaperturopollenites hiatus 41	Inaperturopollenites dubius 42	Sequoiapollenites polymorfosus 43	Cupressacites cuspidataeformis 44	Pityosporites insignis 45	Pityosporites macro-insignis 46	Pityosporites scopulipites 47	Pityosporites minutus 48	Pityosporites micro-alatus 49	Zonalapollenites igniculus 50	Sciadopityspollenites verticillatiformis 51	Vacuopollis 52	Oculopollis 53	Plicapollis pseudo-excelsus 54	Thomsonipollis magnificus 55	Stephanoporopollenites hexaradiatus 56	Triatriopollenites quietus 57	Triatriopollenites rurensis 58	Triporopollenites robustus 59	Triporopollenites megagranifer 60	Compositoipollenites rizophorus 61	Multiporopollenites maculosus 62	Tricolpopollenites micro-henrici 63	Tricolpopollenites hians 64	Tricolpopollenites montañanensis 65	Tricolporopollenites cingulum 66	Tricolporopollenites kruschi 67	Symplocoipollenites vestibulum 68	Periporopollenites perplexus 69	Ephedripites 70	Ephedra voluta 71	Tetracolporopollenites manifestus 72	Stephanocolpites exargilla 73	Stephanocolpites aletos 74	Tetracolporites convexus 75	Polycolpites clavatus 76	Nothofagidites duskritos 77	Tetradopollenites ericius 78
◎				•	○			•	•							•	/	•		○	◎	•				/			◎	●			•								•
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◎				•	◎	•		•							•	•	/			◎	◎	•	○			○	•		/	◎										•	
●					•						•	•	•		•		/		•	◎	●	/			•	◎	/		●	●	•			•							
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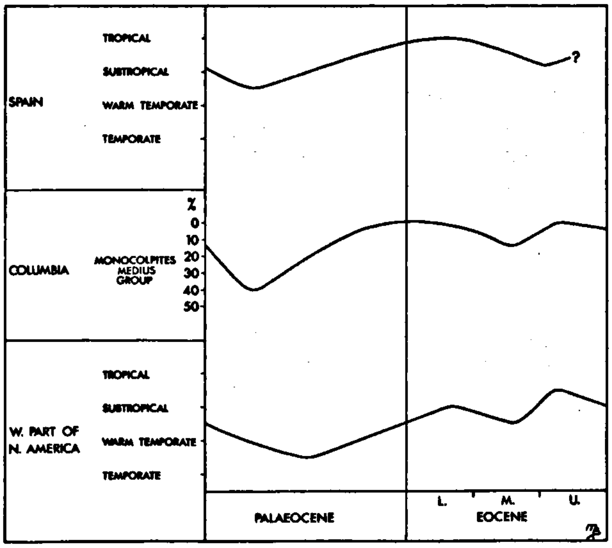

Fig. 8. Temperature curve for the Pyrenees, compared with a curve for the west of the United States, based on plant remains and a curve for Colombia, based on the *Monocolpopollenites medius* group.

the Cupressaceae. The highest Nyssaceae percentages are found together with the absence of *Nypa* and *Nypa* represents a maximum of humid, tropical warmth. The Nyssaceae percentages are very low when *Nypa* is present.

From these data a significant change in climatological conditions can be concluded: a slow increase in temperature from the Tremp Formation to the Roda Formation with a maximum of warmth in the Montañana Formation and a greater decrease in warmth, accompanied by seasonal influences (monsoonal climate), to the Puy de Cinca Formation, where the Pinaceae play an important role. Fig. 8 shows the changes in climatic conditions during the Palaeogene, correlated with Colombia (van der Hammen, 1964) and the western part of the United States (Dorf, 1955). The Taxodiaceae and Nyssaceae are the dominant elements in the most humid part of the coastal swamp; in addition we find Sapotaceae, Osmundaceae, Gleicheniaceae, Schizaeaceae and Polypodiaceae.

c. The Palmae zone:

The Palmae are a dominant group in the whole section. We can distinguish *Sabal,* a swampish palm, and the Palmae of the *tranquillus* pollen type growing under drier conditions, but unfortunately the botanical relationship of the *tranquillus* pollen type is not known accurately (Kedves, 1969, p. 61). Because of this uncertain relationship, it is difficult to reconstruct this type of vegetation. Pflug (1952) attributed this *tranquillus* pollen type to an eutrophic palm swamp forest.

d. The Myricaceae zone:

The Myricaceae show a constant s/mean relationship. This relationship indicates that the Myricaceae despite all the changes can maintain a constant value throughout. The Myricaceae occur in the driest and highest part of the coastal swamp; they frequently grow on islands in the more humid parts of the swamp and hence their constant value. Sapotaceae, Schizaeaceae, Polypodiaceae, Juglandaceae and Betulaceae occur in addition to the Myricaceae (Teichmüller, 1958). The Myricaceae zone (scrub vegetation) is not as conspicuous in the whole picture as the Palmae zone, although the Myricaceae grow regularly scattered throughout the coastal swamp.

e. The *cingulum* and *micro-henrici* zone:

These two pollen types, belonging to the Fagaceae, occur along the border of the coastal swamp. The *cingulum* pollen type grows in marshier conditions than the *micro-henrici,* which are related to the evergreen *Quercus.* The discussions concerning the intra- or extrapalustrine character of the *cingulum* pollen type are still in progress (Kedves, 1969, p. 63).

f. The *Sequoia* zone:

Sequoia and the different species of the Pinaceae do not belong to the typical coastal swamp elements and have to be seen as background pollen in the spectra.

THE S/MEAN DIAGRAMS

The transport of palynomorphs is an important element in palynology. Since recent investigations, the transport mechanism of tropical species is well understood so that it is now possible to use statistical data to study the dispersal of palynomorphs. The relationship between the standard deviation and the mean of a species in a formation can give some indication of the transport.

Fig. 4 can be divided into three parts: the upper part to the left in the diagram indicates a terrestrial environment (here terrestrial means no or relatively little transport and consequently no mixing of the association of species); the middle part is a statistically insignificant interval, and the lower part to the right in the diagram indicates transportation by wind and water and a lesser or greater degree of mixing of the species.

Three different types are found in the s/mean diagrams in Fig. 9:

a. the top of the Tremp Formation.

b. the Roda Formation.

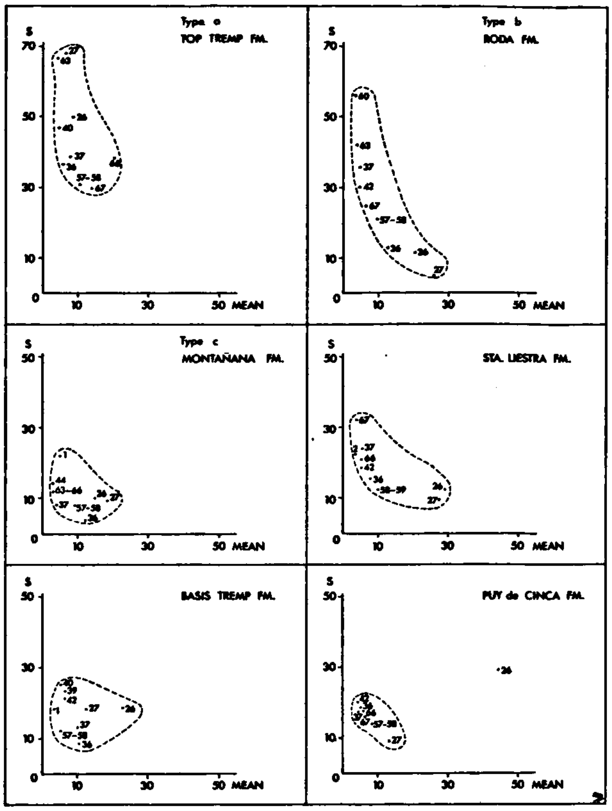

Fig. 9. The s/mean diagrams, showing the degree of mixing of the associations of species in the different formations. The code numbers and the corresponding species are described in the range distribution chart.

c. the Montañana Formation.

a. A high standard deviation together with a relatively low mean characterizes the top of the Tremp Formation. Strong fluctuations in the pollen spectra are possible in this case and the transport must have been absent or at least minimal. The absence of Hystrichosphaera and the low percentages of Fungi (Fig. 11) do not indicate a direct contact with a river mouth, delta or coast. The Cadi Formation, showing a clearly marine character by the presence of reefs, is difficult unless we accept a rapid transgressive period for the last few meters of the Tremp Formation.

b. The relationship between the standard deviation and the mean varies greatly in the Roda Formation. A low mean together with a high standard deviation and a high mean coupled with a low standard deviation give this formation a dualistic character. Untransported species as well as associations of species showing clear influences of mixing are present. The Palmae of the *tranquillus* pollen type and some Polypodiaceae were transported and show only slight fluctuations. The *tranquillus* pollen type, prefering drier conditions, was probably supplied from a lagoon or open bay as indicated by the presence of Hystrichosphaera and the high percentages of Fungi. The typical elements from swamp vegetation (Taxodiaceae, Nyssaceae, *Sabal* and Myricacae) must have grown in the immediate proximity of the lagoon, because clear indications of transport are missing.

c. The species from the Montañana Formation show a moderate mean coupled with relatively low standard deviations. These low standard deviations indicate a mixing of the present species, so that probable fluctuations are weakened. The presence of Hystrichosphaera and the high percentages of fungal spores offer some evidence of a coastal environment, where different currents affected the palynomorphs. Sedimentological evidence suggests a deltaic environment. This is supported by Hystrichosphaera, fungal spores, the relationship between the mean and the standard deviation and last but not least the presence of *Nypa*.

The relationships of s/mean for the base of the Tremp Formation, the Santa Liestra Formation and the Puy de Cinca Formation show practically the same picture as the Montañana Formation. Some degree of mixing can be found in all these formations and a coastal environment is very probable.

COMPUTER PROGRAMME

The different elements for this computer programme written in Fortran IV were taken from a palaeontological programme by Dr. J. H. Germeraad (National Museum of Geology and Mineralogy, Leiden, Netherlands). The basic elements were adapted to the special problems of this investigation.

Fig. 10 shows the flow diagram for this programme. The programme occupies a block of working storage of 136K in the I.B.M. 360/65 computer.

The composition and the sequence of the different data cards are described below. A detailed description of the columns can be found in the introduction to the computer programme.

Card (1): see the input of variables.

Card (2) to (k): see the input of data cards.

Card (k+1): 2 in column 1 for the calculation of averages.

Card (k+2): 3 in column 1 (=i1) for the end of the programme.

4 in column 1 for the processing of a new run or section (see flow diagram). Card (k+2) has to be followed by a completely new series of data cards in this last case.

The maximum value of a count is 99, otherwise Format label 60 has to be changed according the requirements. If N is greater than 35, several cards can be read for one sample (see label 70 to 76).

The maximum number of samples to be processed in one section or run may be changed by adjusting the dimension of all variables, now 400.

```
C     PALYNOLOGICAL PROGRAM  TERTIARY DEPOSITS  SPANISH PYRENEES.
C     ************* *******  ******** ********  ******* ********
C     CALCULATION OF THE MEAN, STANDARD DEVIATION, PERCENTAGES,
C                   ENTROPY, LINEAR CORRELATION COEFFICIENT,
C                   PROBABILITY OF REOBSERVATION.
C     ************************************************************
C     ************************************************************
C     MAX.NR. OF SPECIES -N- IN FIRST READ, FORMAT LABEL 5
C     PROBABILITY OF REOBSERVATION: AA=0, IF NOT AA=1
C     T-TEST: BB=0, IF NOT BB=1
C     CHI-SQUARE TEST:CC=0, IF NOT CC=1
C     LINEAR CORRELATION COEFFICIENT: DD=0, IF NOT DD=1
C     MEAN,ENTROPY AND VARIANCE: EE=0, IF NOT EE=1
C     ************************************************************
C     ************************************************************
C     THE INPUT OF VARIABLES:
C     *** ***** ** *********
C       FIRST READ, FORMAT LABEL 5
C         FIRST TO FOURTH COLUMN: 0000 FOR -N- (NUMBER OF SPECIES COUNTED)
C         FIFTH + SIXTH COLUMN: 00 FOR -AA-
C         SEVENTH + EIGTH COLUMN: 00 FOR -BB-
C         NINTH + TENTH COLUMN:00 FOR -CC-
C         ELEVENTH + TWELFTH COLUMN: 00 FOR -DD-
C         THIRTEENTH + FOURTEENTH COLUMN: 00 FOR -EE-
C     THE INPUT OF DATA CARDS :
C     *** ***** ** **** *****
C        FIRST COLUMN: 1 FOR EACH DATA ARRAY
C                      2 FOR THE END OF THE LAST DATA ARRAY
C                      3 FOR THE END OF THE DATA ARRAYS (END OF THE PROGRAM)
C                      4 FOR THE PROCESSING OF A NEW SERIES OF DATA ARRAYS.
C        SECOND+THIRTH COLUMN :  00 FOR RUN NUMBER (-IRUN-)
C        FOURTH TO SIXTH COLUMN: 000 FOR SECTIONNR. (-ISEC-)
C        SEVENTH TO TENTH COLUMN: 0000 FOR SAMPLENR. (-ISAM-)
C        ELEVENTH TO EIGTIETH COLUMN: 00,00,00, FOR THE COUNTS.
C                (MAX. VALUE OF A COUNT IS 99, SEE FORMAT LABEL  60)
C     MAXIMUM OF 400 INPUT CARDS PER RUN WITH THIS PROGRAM.
C                ********************************
C                ********************************
      DIMENSION X(400),BMEAN(90),BVAR(90),NB(90),Y(400),IAMT(400),
     -Z(400),Z1(400),Y1(400)
    1 CONTINUE
      N=0
      AA=0
      BB=0
      CC=0
      DD=0
      EE=0
      IRUN=0
      ISEC=0
      ISAM=0
      READ(5,5)N,AA,BB,CC,DD,EE
    5 FORMAT(I4,5I2)
      WRITE(6,6)N
    6 FORMAT(1H0,3X,' N=',I4/)
      WRITE(6,7)AA,BB,CC
    7 FORMAT(1H0,3X,' AA=',I2,5X,'BB=',I2,5X,' CC=',I2)
      WRITE(6,8)DD,EE
    8 FORMAT(1H0,3X,' DD=',I2,5X,'EE=',I2//)
      NMAX=N
C     -FF- IS COEFFICIENT OF 95% PROBABILITY IN T-TEST
      FF=1.96
   10 CONTINUE
      ITOT=0
      ISAM2=1
C     ALL STATISTICAL DATA TU ZERO
      DO 15  I=1,N
      Z(I) =0.0
   15 Z1(I) =0.0
      AH =0.0
      AN =0.0
   20 CONTINUE
      DO  30  I=1,N
C     TRANSFER X-VALUES TO Y-ARRAY
      Y(I) = X(I)
   30 X(I) =0.0
      XSUM = 0.0
   40 IF (N-35)                     50,50,45
   45 N=35
   50 READ(5,60)I1,IRUN,ISEC,ISAM,(IAMT(I),I=1,N)
   60 FORMAT(I1,I2,I3,I4,35I2)
      N=NMAX
      IF(I1.EQ.1) GO TO 70
      IF(I1.EQ.2) GO TO 450
      IF(I1.EQ.3) GO TO 490
      IF(I1.EQ.4) GO TO 1
   70 IF (N-35)                    80,80,75
   75 READ(5,76)(IAMT(I),I=36,75)
      READ(5,76)(IAMT(I),I=76,N)
   76 FORMAT(40I2)
   80 DO 90 I=1,N
      X(I)=IAMT(I)
      XSUM=XSUM+X(I)
   90 CONTINUE
C     PRINT DATA IN ORIGINAL SEQUENCE
      I1=1
      ISAM1=ISAM2
      ISAM2=ISAM
      WRITE(6,99)IRUN,ISEC
   99 FORMAT(1H0,///,3X,'DATA USED FOR THE FOLLOWING STATISTICS IN RUN',
     -I3,' SECTION',I4//)
      WRITE(6,260)N,(X(I),I=1,N)
  100 CONTINUE
      ITOT=ITOT+1
      NB(ITOT)=N
C     CALCULATION OF THE PERCENTAGES.
  110 JF=0
      DO 125  I=1,N
      IF (X(I))                    125,125,120
  120 JF=JF+1
      X(I)=X(I)/XSUM
  125 Z(I)=Z(I)+X(I)*100.0
      IF (AA-1)                    130,170,170
C     CALCULATION OF THE PROBABILITY OF REOBSERVATION
  130 DO 140 I=1,N
      Y1(I)=1.0-(1.0-X(I))**BB
      IF (Y1(I)-0.0005)            131,135,135
  131 Y1(I)=0.0000
  135 CONTINUE
      IF (Y1(I)-0.99995)           140,140,139
  139 Y1(I)=1.0000
  140 Z1(I)=Z1(I)+Y1(I)
      WRITE (6,150)
  150 FORMAT(3X,/' PROBABILITY OF REOBSERVATION IS: ')
      WRITE(6,160)(Y1(I),I=1,N)
  160 FORMAT(1H,//(3X,10F10.4/))
  170 BN=N
C     CALCULATION OF THE MEAN
      AMEAN=XSUM/BN
C     CALCULATION OF THE ENTROPY IN ONE SAMPLE POPULATION
      IF (EE-1)                    180,210,210
```

```
100 BMEAN(ITOT)=AMEAN
    HVEL=0.0
    HVAL=0.0
    IF (XSUM)                 206,206,190
190 DO 201  J=1,N
    IF (X(J))                 201,201,200
200 HVAL=HVAL+X(J)*ALOG(X(J))
    X(J)=X(J)*100.0
201 HVEL=HVEL+1.0-Y1(J)
    XMEAN=ALOG(FLOAT(N)-HVEL)
    IF (FLOAT(N)-HVEL-1.0) 202,203,202
202 IF (XMEAN)                204,203,204
203 HVAL=100.0
    GO TO                     207
204 HVAL=100.0*HVAL/XMEAN
    IF (HVAL-0.005)           205,205,207
205 IF (HVAL+0.005)           207,206,206
206 HVAL=0.0
207 WRITE (6,208)ISAM,HVAL
208 FORMAT(3X,///,' DEGREE OF ENTROPY IN SAMPLE',I4,' IS',F7.2)
    AH=AH+HVAL
210 CONTINUE
C     CALCULATION OF VARIANCE AND STANDARD DEVIATION
    SS=0.0
    DO 220 I=1,N
220 SS=SS+(X(I)-AMEAN)**2
    VAR=SS/(BN-1.0)
    IF (EE-1)                 230,230,240
230 BVAR(ITOT)=VAR
240 SD=SQRT(VAR)
    WRITE (6,250)
250 FORMAT(1H0,///3X,'THE SAME IN PERCENTAGES')
    WRITE (6,260)N,(X(I),I=1,N)
260 FORMAT(1H0,5X,' NUMBER OF DATA IS:',I5//(1H0,10F10.2/))
    WRITE(6,270)AMEAN
270 FORMAT(1H ,///,9X,'MEAN=',F11.5)
    WRITE(6,280)SD
280 FORMAT(1H0,9X,'ST.DEV.=',F8.5///)
C     STUDENT'S T-TEST
290 IF (BB-1)                 300,350,350
300 IF (ITOT-1)               20,20,310
310 AMEAN=ABS(BMEAN(ITOT-1)-BMEAN(ITOT))
    VAR=FF*SQRT((FLOAT(NB(ITOT-1)-1)*BVAR(ITOT-1)+FLOAT(NB(ITOT)-1)*BV
   -AR(ITOT))/FLOAT(NB(ITOT-1)+NB(ITOT)-2))*SQRT(FLOAT(NB(ITOT-1)+NB(
   -ITOT))/FLOAT(NB(ITOT-1)*NB(ITOT)))
    WRITE(6,320)
320 FORMAT(1H )
    WRITE(6,330)ISAM1,ISAM2,ISEC
330 FORMAT(3X,'COMPARISON OF SAMPLES',I4,' AND',I4,' IN SECTION',I4)
    WRITE(6,340)AMEAN,VAR
340 FORMAT(4X,'STUDENTS T-TEST: IF FIRST VALUE IS LARGER THAN SECOND
   -VALUE, THEN THE TWO SERIES OF CATA ARE SIGNIFICANTLY DIFFERENT (P
   -=0.95)'/10X,'FIRST VALUE=',F10.4,8X,'SECOND VALUE=',F10.4//)
C     CHI-SQUARE TEST
350 IF (CC-1)                 360,20,20
360 XSQ=0.0
    DO 370 I=1,N
    X1=0.0
370 XSQ=XSQ+((ABS(X(I)+X1-BMEAN(ITOT-1))-0.5)**2)
    XSQ=XSQ/BMEAN(ITOT-1)
    WRITE (6,380)XSQ
380 FORMAT(4X,'CHI-SQUARE IS:',F10.4/)
390 IF (DD-1)                 400,450,450
400 CONTINUE
C     CALCULATION OF LINEAR CORRELATION COEFFICIENT
    N=NMAX
    SX=0.0
    SY=0.0
    SXY=0.0
    SXQ=0.0
    SYQ=0.0
    SYYQ=0.0
C     CALCULATE SUM X AND SUM Y
    DO 420 I=1,N
410 SX=SX+X(I)
    SY=SY+Y(I)
C     CALCULATE SUM X  *  SUM Y
    SXY=SXY+X(I)*Y(I)
C     CALCULATE SUM X-SQUARE AND SUM Y-SQUARE
    SXQ=SXQ+X(I)*X(I)
420 SYQ=SYQ+Y(I)*Y(I)
C     CALCULATION OF COEFFICIENT OF LINEAR CORRELATION
430 R=(FLOAT(N)*SXY-SX*SY)/SQRT((FLOAT(N)*SXQ-SX*SX)*(FLOAT(N)*SYQ-SY*
   -SY))
    WRITE(6,440)R
440 FORMAT(1H0,//4X,'R-COEFFICIENT OF LINEAR CORRELATION IS',F10.4//4X
   -,'R=1 MEANS FULL CORRELATION, R=0 MEANS NO CORRELATION'//'   THIS
   -IS THE DEGREE OF CHANGE IN SAMPLE POPULATION'///)
    AM=AM+R
    GO TO                     20
C     CALCULATION OF THE MEAN ENTROPY,THE AVERAGE R  AND AV.COMPOSITION
450 CONTINUE
    AH=AH/ITOT
    AM=AM/(ITOT-1)
    DO 460   I=1,N
    Z(I)=Z(I)/ITOT
460 Z1(I)=Z1(I)/ITOT
    WRITE (6,470)AH,AM,ITOT,(Z(I),I=1,N)
470 FORMAT(3X,'AVERAGE ENTROPY IS',F7.2/3X,'AVERAGE CHANGE IN SAMPLE
   -POPULATION IS',F5.2/3X,'AVERAGE COMPOSITION OF THE',I4,'SAMPLES IS
   -: '/(1H ,10F10.2/)//)
    WRITE (6,480)(Z1(I),I=1,N)
480 FORMAT(3X,'AVERAGE PROB. OF REOBSERVATION IS:'/(1H ,10F10.2/)//)
    WRITE(6,485)
485 FORMAT(30X,////,' ***********************',//)
    GO TO                     40
490 CONTINUE
    STOP
    END
```

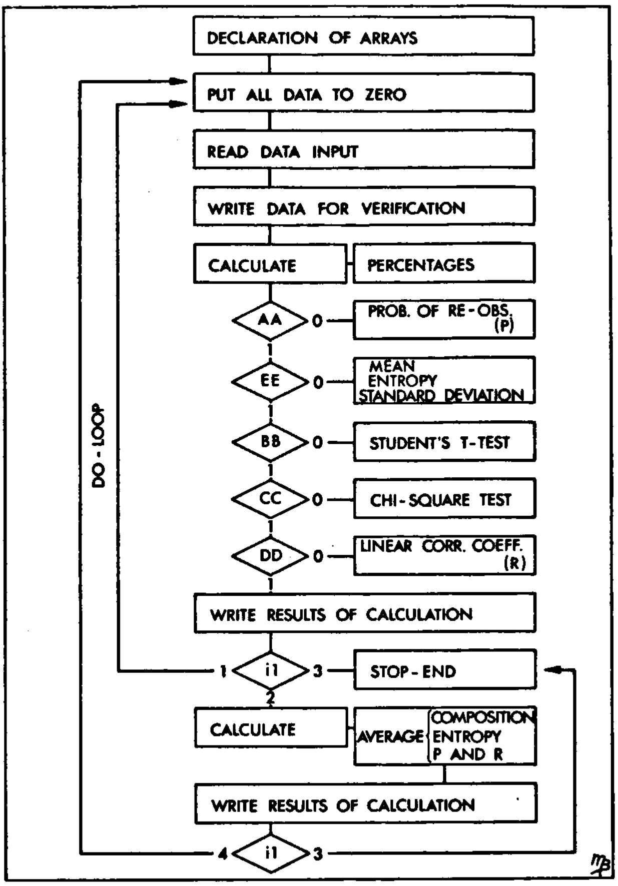

Fig. 10. Simplified flow chart illustrating the major steps in the computer programme.

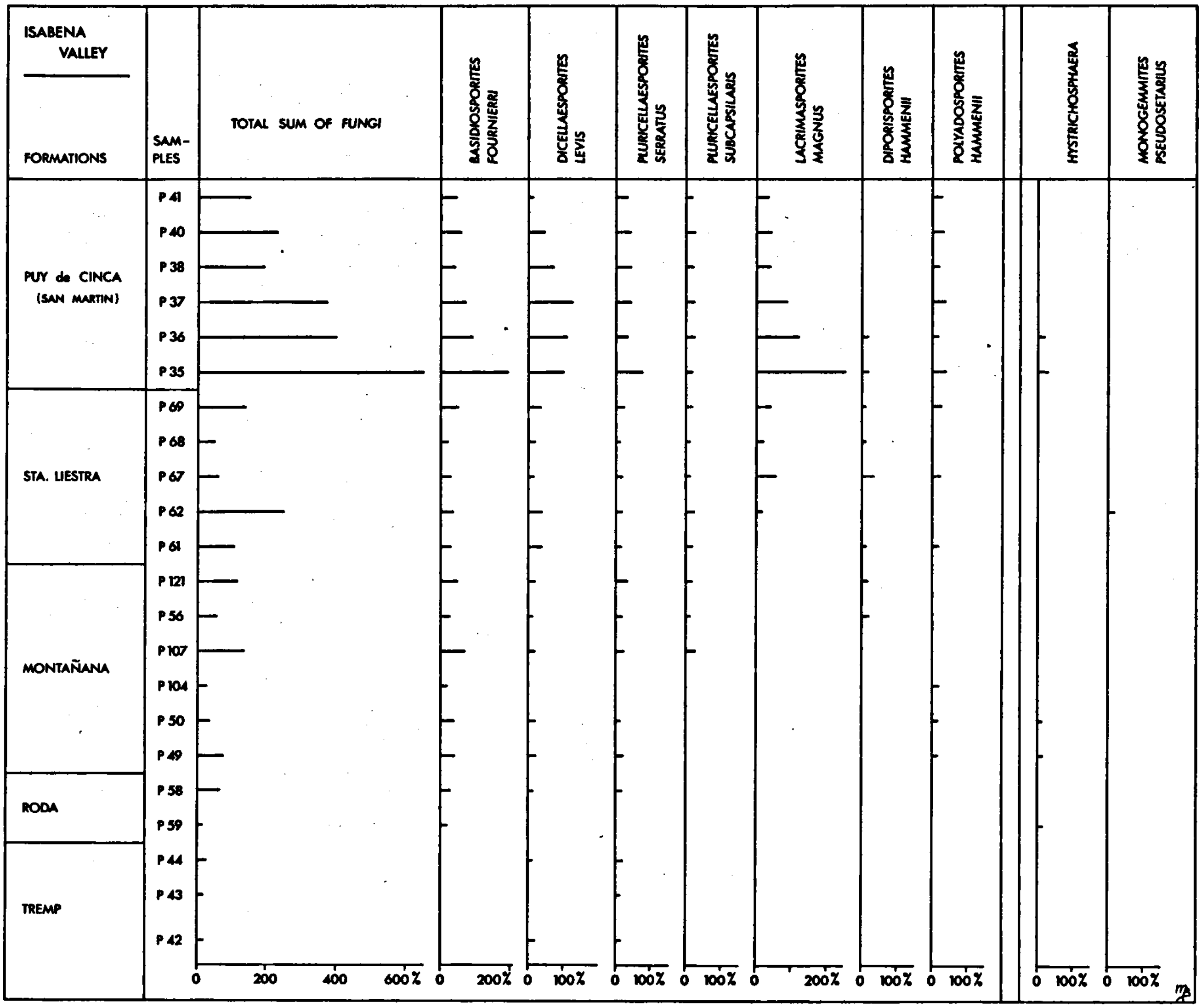

Fig. 11. Fungal spores diagram of the Isabena and the San Martin section.

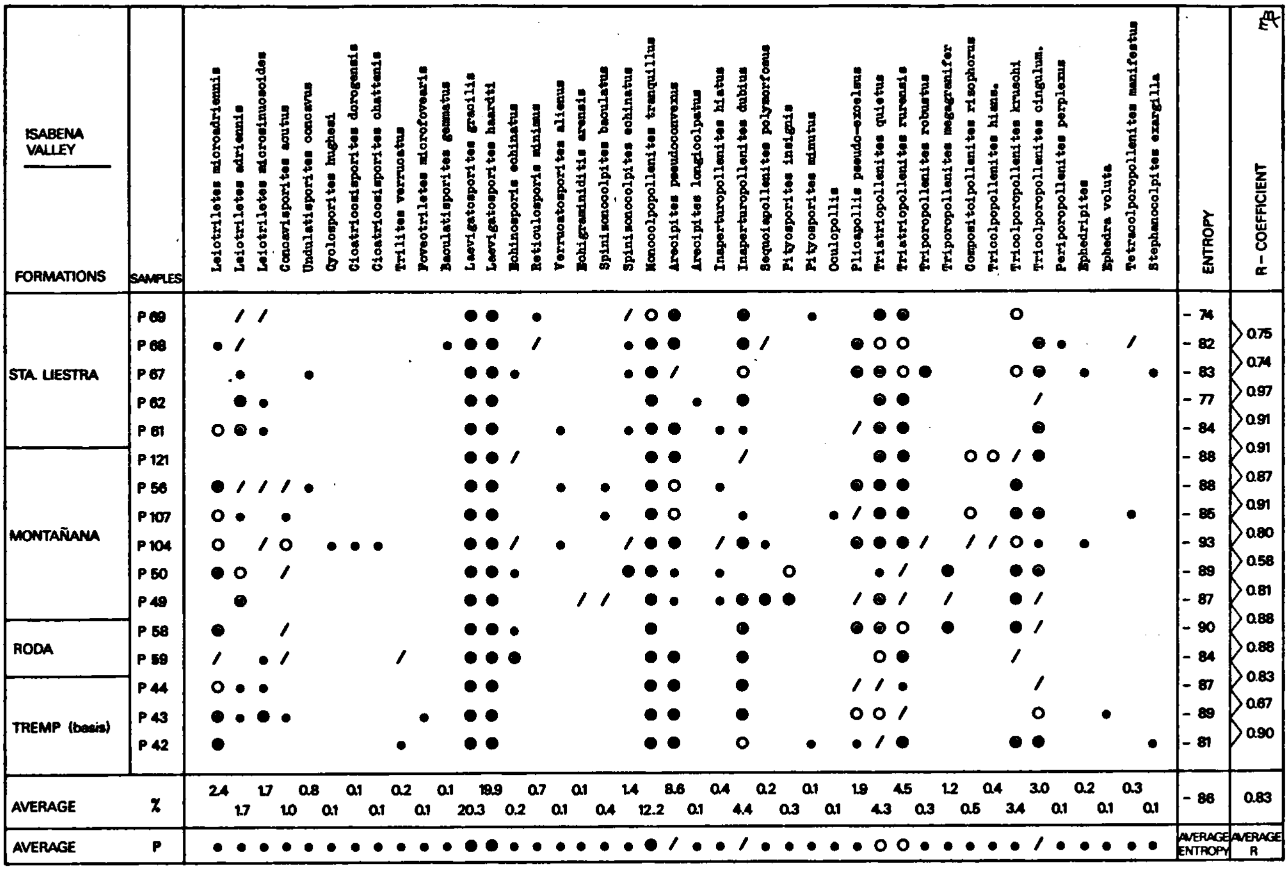

Fig. 12. Pollen diagram of the Isabena section (sample run 1) showing the probability of re-observation, the entropy and the correlation coefficient.

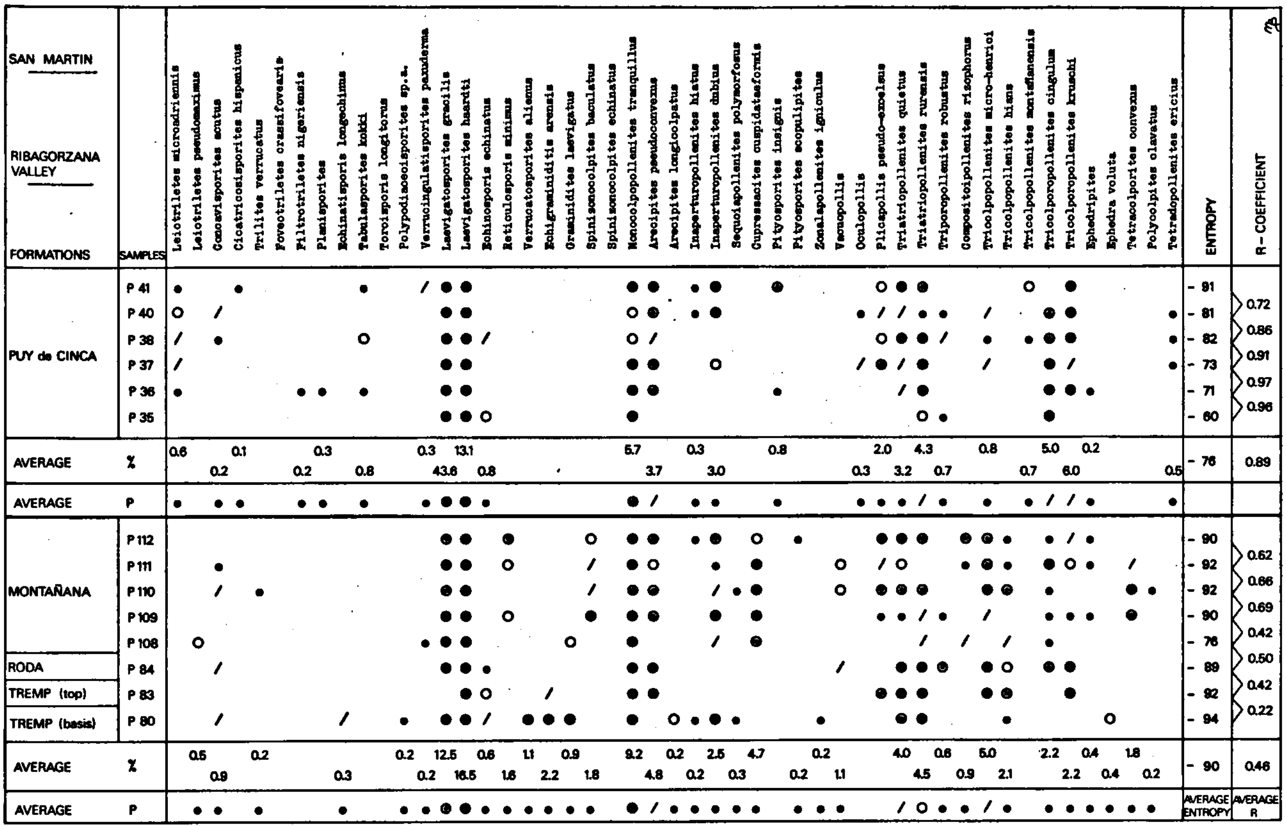

Fig. 13. Pollen diagram of the Ribagorzana and the San Martin section (sample run 1) showing the probability of re-observation, the entropy and the correlation coefficient.

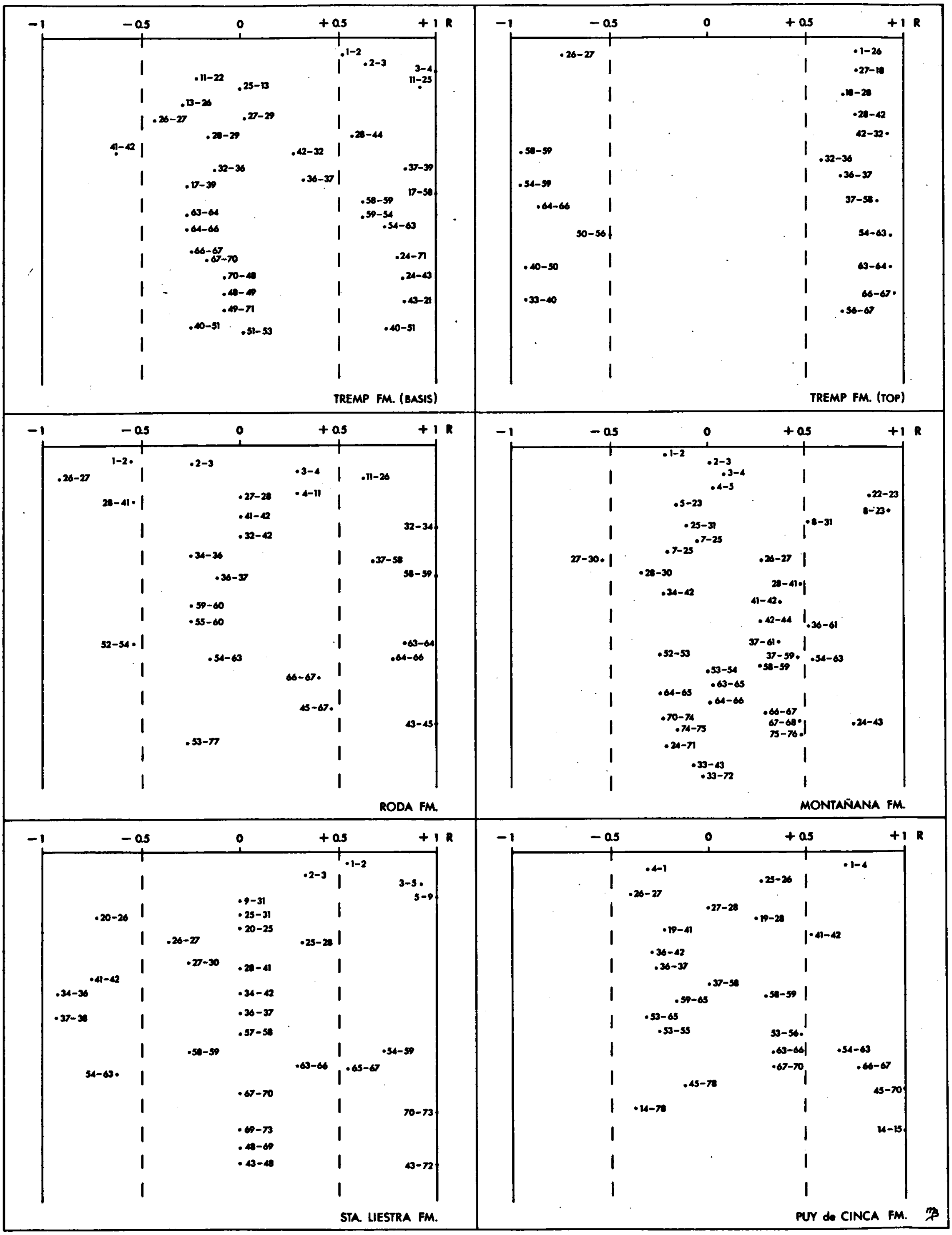

Fig. 14. Diagrams illustrating the degree of association or dissociation of the species (species run 2) in all formations. The code numbers and the corresponding species are described in the range distribution chart.

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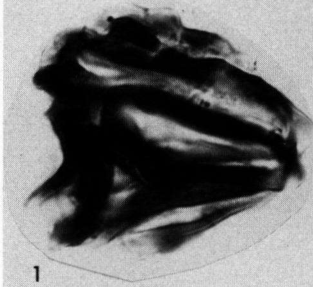
PLATE

1. *Cicatricosisporites hispanicus* n. sp.
2. *Cicatricosisporites hispanicus* n. sp.
3. *Tabulasporites kokki* n. sp.
4. *Microfoveolatosporis garumniensis* n. sp.
5. *Polypodiaceoisporites tumidus* n. sp.
6. *Polypodiaceoisporites tumidus* n. sp.
7. *Polypodiaceoisporites* sp. a.
8. *Verrucingulatisporites paxuderma* n. sp.
9. *Reticulosporis minimus* n. sp.
10. *Reticulosporis minimus* n. sp.
11. *Echigraminiditis arensis* n. sp.
12. *Echigraminiditis arensis* n. sp.
13. *Tricolpopollenites montañanensis* n. sp.
14. *Stephanocolpites exargilla* n. sp.
15. *Stephanocolpites aletos* n. sp.
16. *Tetracolporites convexus* n. sp.
17. *Tetracolporites convexus* n. sp.
18. *Nothofagidites duskritos* n. sp.
19. *Polyadosporites hammenii* n. sp.
20. *Lacrimasporites magnus* n. sp.

all magnifications: 1000X.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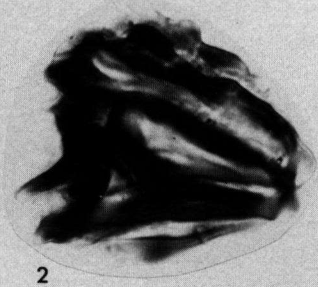
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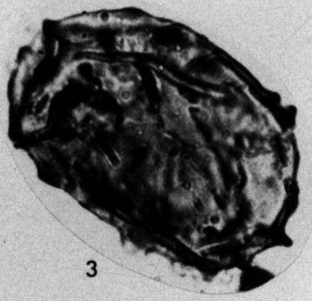
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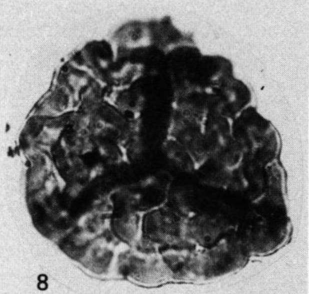
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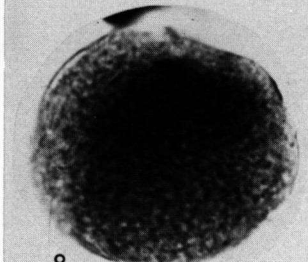
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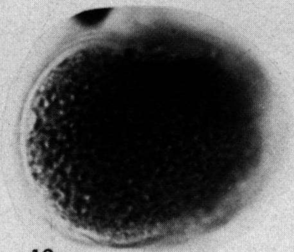
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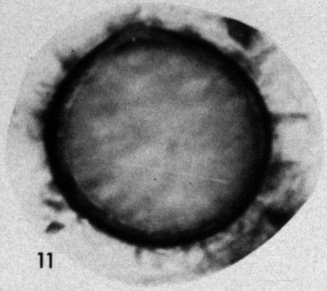
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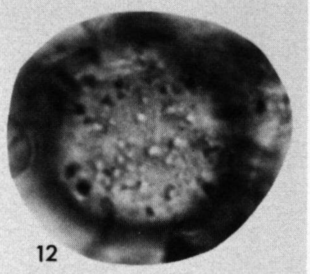
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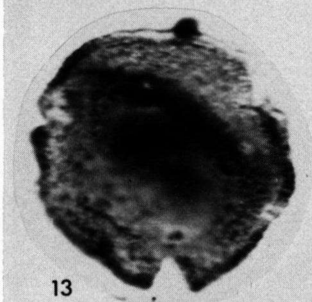
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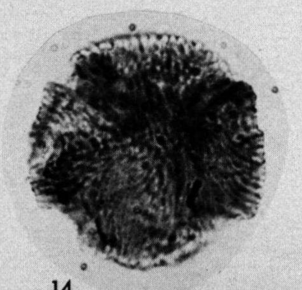
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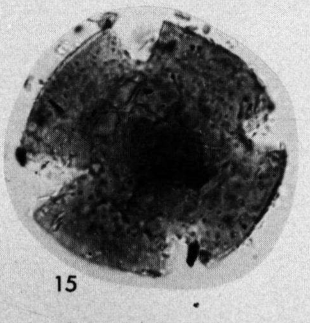
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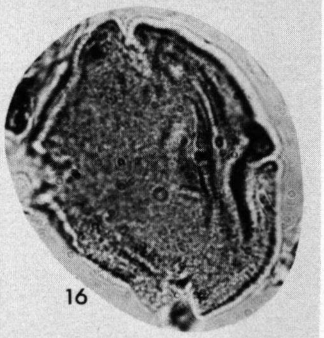
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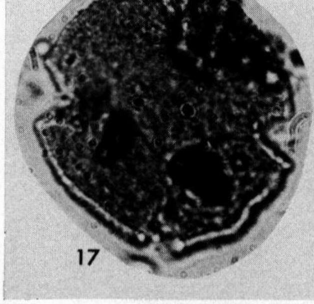
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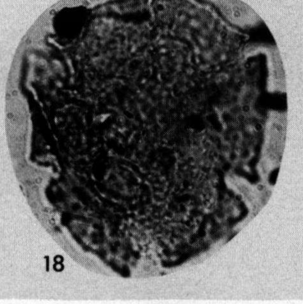
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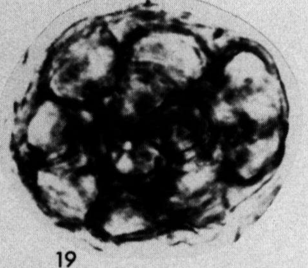
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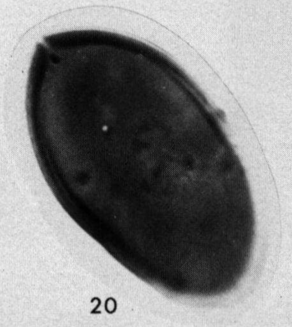
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